

CHAPTER VII

CLASSIFICATION

"A ces trois espèces [des cigales], il y en aura apparemment encore d'autres à ajouter, lorsqu'on observera les cigales de différents pays avec une nouvelle attention. Le nombre des espèces de ces mouches est presque déjà trop grand, pour qu'on puisse les distinguer les unes des autres simplement par la grandeur ; mais on pourra les caractériser par d'autres particularités qu'elles nous offrent ; . . ."

RÉAUMUR, *Mem. Hist. Ins.*, 1740, V, p. 152.

WE already seen that cicadas are members of the great order *Hemiptera* or bugs. It remains in this chapter to indicate briefly their position in that order and their relationships among themselves. Réaumur knew three different kinds, while we have more than 1500 species to classify (1538).

The sub-order, *Homoptera*, comprises the vast assemblage of plant-feeding insects known, for instance, as leafhoppers, frog-hoppers, cicadas, plant-hoppers, scale-insects, and aphides. The first four of these and their relatives form the series, *Auchenorrhyncha*, of which the cicadas are the largest and most easily recognized members. They have been regarded by Tillyard and others as the most primitive existing Homoptera—an opinion influenced largely by venational considerations, for few other characters of the cicada body support such a view.

Cicadas are in general so large and exhibit such great individuality in appearance, habitat, behaviour, and song, that the rudest observer in every age and country where they occur, has been inspired to the invention of distinguishing names. Of popular epithets of this kind Japan (Hearn, 1900 ; Matsumura, 1898) can surely show the greatest list. The modern exponent of Western civilization is largely content with a general term save for species like *Magiccicada septendecim* which exhibit some striking peculiarity ; but that he has not entirely lost the graceful art of naming is shown by the wonderful variety of cicada names current among Australian colonial children, stimulated by a remarkably rich and varied fauna. These names are frequently obscure and sometimes not beautiful, but they are all spontaneous expressions of a characteristic Australian genius which has not yet reached full fruition in higher fields of art.

The first attempt at a scientific classification of Cicadas was that of Aristotle. The relevant passages have been rendered as follows :

"Plura earum sunt genera, quae magnitudinis modo differunt : atque etiam quod aliis corpus sub transverso septo praecinctum distinguitur, membranamque liquido refert : ut iis quas ab argutiolo sono, achetas appellarunt : alii non ita est, ut cicadastris (*De hist. anim.*, Gaze trans., lib. IV, cap. 7). Cicadarum duo sunt genera : aliae enim minores, quae primae prodeunt, et novissimae pereunt : aliae maiores, quae canunt, eademque novissimae prodeunt, et primae intereunt. Sunt quae canunt praecinctu dividuae, sive minores, sive maiores sunt ; quae autem non canunt, individuae constant. Vocant nonnulli grandiores illas et canentes argutas : minores mutas. Sed canere vel in secundo hoc genere possunt paululum, quae praecinctae prodierunt" (*op. cit.*, lib. V, cap. 30). *Cicadastra* is usually translated *tettigonia*, or rather is thus transcribed directly from the Greek.

From these passages it is clear that Aristotle distinguished two kinds, differing chiefly in size. The larger ones or Achetae are supplied with a ventral incision and are noted for their loud or shrill song. They appear later than the *tettigoniae* and die earlier. But Aristotle goes on to state that among both *achetae* and *tettigoniae* there are some without the incision and thus unable to sing. In the light of this last statement there are some grounds for the belief of Schultze and others that Aristotle applied the term *achetae* only to the males. In fact, it might well be suggested that *achetae* included the males of the larger cicadas only, e.g. *Tibicen plebeia* and *Cicada orni*, while *tettigonia* was restricted to the smaller true cicadas, such as *Cicadatra* and *Melampsalta*, rather than extended to other Auchenorrhyncha. We have seen, however, that Aristotle distinguished the sexes so clearly that it seems more probable that *Achetae* signified the larger cicadas, and *tettigoniae*—some of which sang and some not—the small cicadas plus some of the leafhoppers.

Pliny in accordance with his usual practice, copied Aristotle's scheme, but he adds a little of his own, apparently favouring the interpretation we have supported above. Thus : *Quae canunt vocantur achetae ; et quae minores ex eis sunt tettigoniae : sed illae magis canorae. Mares canunt in utroque genere : foemine silent.* But Pliny adds also a little taxonomic concept apparently of his own, based on ethological considerations : *Quidam duo alia genera faciunt earum : surculariam, quae sit grandior : frumentariam, quam alii avenariam vocant. Apparet enim simul cum frumentis arcescentibus.* Such a division, into tree-dwelling and herbage-frequenting forms is very good, whether applied to cicadas alone or to cicadas plus leafhoppers.

After the Renaissance the first renewed interest in cicadas as organisms rather than objects of classical reference, took shape in morphological studies culminating in the unrivalled memoir of Réaumur. It remained for the Linnean school to lay the foundations of Cicadid taxonomy. Thereafter the systematic study of the family

followed a course which may be instructively contrasted with that of myrmecology. The cicadas were large, conspicuous insects, almost entirely exotic and otherwise intriguing. Descriptions were based almost entirely on cabinet specimens, and couched largely in terms of colour, while names were published often with obscure localities, sometimes with none. Lepidopterists and arachnologists dallied with the Cicadidae and described an exotic species or so, to the confusion of their successors. That happy walking hand-in-hand of ethology and taxonomy which has made myrmecology a model for systematic entomology was never achieved in any degree in tettigology till Wm. T. Davis brought to bear his very wide field experience. In America also the external genitalia were easily used as taxonomic characters. It is the conviction of the writer, however, that the fullest use cannot be made of the differentiae supplied by these organs unless the aedeagus at least is dissected out and mounted for microscopic examination.

After Linnaeus and Fabricius one of the chief workers was Germar, who monographed the species of the world (1830-1834). Latreille concerned himself with the classification of species already known, more than with the description of new ones. For very long all cicadas were placed in the genus, *Cicada* L. (*Tettigonia* Fab.) and although Latreille founded the genus, *Tibicen*, in 1825, this was not generally adopted. In 1835 Burmeister erected the genus *Hemidictya*, and Westwood followed in 1839 with the even more remarkable *Cystosoma*; in 1840 with *Polyneura*. But the first whole-hearted attempt to classify the family was that of Amyot and Serville (1843), who proposed many new genera which stand to-day, and a subfamily differentiation which is now obsolete. The first set of characters chosen for the latter purpose were unsuitable, for if modern views are correct, the reticulate condition of the veins, on the presence or absence of which Amyot and Serville founded the two subfamilies, *Reticelli* and *Octicelli*, has arisen in at least three distinct branches of the family—the Polyneurini of the Platyleurinae, the Talaingini (Schmidt, 1919) of the Cicadinae, and the Hemidictyini of the "Tibicininae."

That most prolific of all species-makers, Francis Walker, began his work on cicadas about 1850, adding tremendously to the total of known forms, but contributing nothing to a knowledge of their relationships.

Ashmead (1888b) proposed an entirely new classification with remarkably little to recommend it, and with every sign of superficiality.

Distant's classification, based on that of Stål, was proposed in 1889, and with certain modifications remains to the present day. Two subfamilies, Cicadinae and Tibicininae, were established by Distant, for the forms on the one hand, in which the tymbals were completely covered by a forward projection of the second abdominal

segment, and on the other they were exposed. But there were intermediate conditions, the species exhibiting which were split off by Distant in 1905 as a third subfamily, Gaeanae.

Distant has been the chief worker to concern himself with tribal classification of the family as a whole, and to him more than to all other Homopterists, we owe the present system with its advantages and its defects. The Cicadidae were his favourite family and remained so to the end of his long and extremely productive life. His first paper dealing in part at least with Cicadidae was published in 1878, and his long list of contributions to the study of the family, including several sumptuous, more or less separate works, reached the grand total of 131 in 1920. When we consider the extent of his writings on other Hemiptera of every family, and his work in the Lepidoptera, we cannot but be amazed at his tremendous output. It would seem impossible that the whole of such a stupendous contribution should attain the critical standard of such work as that of his tireless critic, the great Heteropterist, Bergroth; and there have been no lack of other critics to point out his mistakes. Breddin and Kirkaldy, among others, lost no opportunity to inveigh against his shortcomings as a taxonomist, whilst Bergroth's own criticisms are among the most scathing in the annals of entomological controversy. It must be admitted that Distant worked essentially like an old-fashioned Lepidopterist, using morphological characters too little. If any of his divisions or tribes prove to be real morphological entities, it will be largely a happy chance, since most of them appear to be cabinet associations of superficially similar genera, for the elucidation of which a study of his collection is the first desideratum. Distant had unexampled opportunities at the British Museum, and he unquestionably made the most of them according to his lights, describing species with tireless industry and in many of his works publishing excellent and numerous figures. His *Synonymic Catalogue of Homoptera; Part I, Cicadidae* (1906), is an indispensable compilation.

Of other workers on Cicadid taxonomy, Karsch (1890-1894) described numerous African species, but did not modify the classification of the family; neither did the American Homopterists—Uhlar, Van Duzee, Davis, who had only a few dominant genera to deal with in this family but at the same time a continental fauna of other Homoptera to describe.

Goding and Froggatt in 1904 monographed the Australian forms. Breddin did considerable work on the exotic members of the family.

Schmidt (1919c), besides pointing out that the tribal names should terminate in *-ini* rather than *-aria* (Distant), a change already made by Van Duzee in his Catalogue (1917) also makes two changes in the tribes themselves. The Polyneurini are restricted to the two genera *Polyneura* Westwood, and *Angamiana* Distant, and the other members of Distant's Polyneurini, placed in a new tribe,

Platypleurini. In the Gaecaninae, the genus **Talainga** Distant, on account of its reticulate tegminal venation is made the type of a separate tribe, Talaingini.

While both the Cicadinae and the Gaecaninae formed more or less homogeneous groups, with a few genera like *Terpnosia*, *Calcagninus*, and *Hamza*, which strained the system, the subfamily, Tibicininae, with many more species than either of the others, was nothing but a dumping-ground for a miscellany of unrelated forms characterized by a single negative quality. Progress in classification must therefore take the form largely of splitting segregates from this third heterogeneous subfamily. Jacobi (1907c) made the first attempt by erecting the new subfamily, Tettigadinae, for the genera *Tettigades*, *Chonosia*, and *Babras*, characterized chiefly by the presence of a stridular surface on the mesonotum, but distinguished also by venational characters:

A retrograde step was taken in 1919 when Delétang proposed a new scheme incorporating the defects of the Amyot and Serville classification, with the additional absurdity of a new subfamily, Parocelli (*Parocellos*) for cicadas with fewer than eight apical cells in the tegmen. It is our impression that this Argentine worker had access to but little European literature published since 1843. Admittedly the Distant classification is imperfect, but assuredly the solution lies not here.

Handlirsch (1925) recently made an attempt to evolve a phylogenetic classification, at the same time complaining that Distant had entirely neglected this viewpoint, and had taken no account of convergence between unrelated groups.

This is perhaps the nearest to a "natural" system which has yet been achieved for the family as a whole.

Recent workers on the Cicadidae include Davis, Beamer, and Metcalf in North America, China in England, Haupt, Jacobi, Schmidt, and Schumacher in Germany, Moulton in Malaya, and Ashton in Australia.

It has not been hitherto widely realized that the genus **Tettigarcta** (White), forming the sole content of Distant's tribe Tettigarctini (*-aria*) differs far more from all other cicadas than they do *inter se*. Ashton (1924) has recently published an interesting partial account of the life-history of this extremely rare form, and through his generosity I have been enabled to study nymphal and adult female material. More recently Mr. F. Muir has kindly lent me a male. Ashton would question its being a cicada at all, but I cannot follow him so far. It is, however, so divergent in the characters of the head, pronotum, venation, and male genitalia, not to mention the complete absence of sound-organs and apparently of auditory organs, that however much we may deplore a dichotomy which leaves only one genus in the first subfamily, it unquestionably merits subfamily rank.

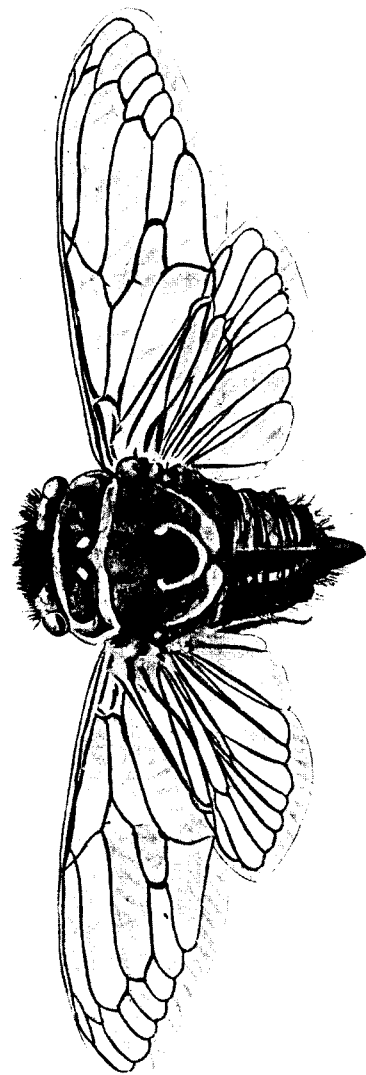


PLATE III

Tettigades ulmaria Dist. From Chile. Male
Enlarged

R. Stenton, photo

In conclusion, we believe that a more thoroughgoing morphological study than has yet been made of all the genera, will supply characters for a better classification than one depending on male characters alone, but we are not in a position to suggest many more changes at present.

"What we need for the present is not a new arrangement, the erection of a lot of new genera on superficially aberrant species and the raising of every subgenus to generic rank, but a painstaking study of all the species in the existing groups. Until such studies have made appreciable headway, the existing avowedly imperfect classification should not be discarded without at least as much thought as has been devoted to its construction" (Wheeler, *Ants*, 1910, p. 133).

We give below the grouping provisionally adopted.

Family *Cicadidae* Westwood

- Subfamily 1. *Tettigarctinae* Tillyard.
- Subfamily 2. *Tettigadinae* Jacobi.
- Subfamily 3. *Tibicininae* Dist.
 - Tribe 1. *Chlorocystini* (Dist.).
 - Tribe 2. *Hemidictyini* (Dist.).
 - Tribe 3. *Tibicinini* Handl.
- Subfamily 4. *Cicadinae* Van Duzee.
 - Tribe 1. *Moganniini* (Dist.).
 - Tribe 2. *Cicadini* m. = *Gaeaninae* Dist.
minus *Moganniaria*.
- Subfamily 5. *Platypleurinae* Handl.

Remarks: The tribe, *Tibicinini*, is a miscellaneous collection of all those forms which will not go into any of the other gymnotympanate divisions. The subfamily *Cicadinae* is retained as a temporary convenience for those cicadas with tymbals partially covered. As indicated previously these forms, except *Moganniini*, which is a natural group, are being gradually absorbed into other divisions. The *Platypleurinae* are fairly homogeneous, and difficult to split into tribes. In fact, the homogeneity of all the cicadas, other than *Tettigarcta*, is a most striking phenomenon, explicable possibly as Mr. Muir suggests by the safe, secluded, and extremely uniform existence of the nymph during its long subterranean life, compared with which the imaginal apotheosis is a mere flash in the pan.

CHAPTER VIII

THE EVOLUTION OF CICADAS

SOCRATES: A lover of music like yourself ought surely to have heard the story of the grasshoppers [*τέττιγες*] who are said to have been human beings in an age before the Muses. And when the Muses came and song appeared they were ravished with delight; and singing always, never thought of eating and drinking, until at last in their forgetfulness they died. And now they live again in the grasshoppers; . . .

PLATO, *Phaedrus*, Jowett's transl. (Plato, 3rd ed., 1892, col. 1, p. 434).

ON the phylogeny of Hemiptera in general there have been numerous recent discussions and suggestions, especially from Tillyard (1916, 1920, 1921a, 1921b, 1922, 1923), Muir (1921, 1923a, 1923b), and Crampton (1919, 1922a, 1922b). Less recently the question has been discussed by Kirkaldy (1910a, 1910b) and by Handlirsch (1906-1908), with later notes by the latter in 1921 (Bd. III, p. 359).

As suggested ancestral forms we have had the *Protohemiptera* represented by *Eugereon*, and the Palaeohemiptera, containing *Prosbole* and *Scytinoptera*. Handlirsch, who was responsible for these two orders, believed the lower Permian *Eugereon* to be a Palaeodictyopteroid type with sucking mouth-parts resembling those of Hemiptera in all save the fusion of the second maxillae. Tillyard was at first inclined (1916) to see in *Mesogereon* a link between *Eugereon* and the Palaeohemiptera, largely owing to his interpretation of the cross-ridging which the *Mesogereon* tegmen shares with that of Cicadidae, as the remnant of an archedictyon, or series of cross-veins in process of reduction. More recently, however (*in litt.*, 17th April, 1922), the same authority concludes that the Protohemiptera were merely Palaeodictyoptera with a sucking beak, and no more related to Hemiptera than are such insects as the fleas and Protura. Kirkaldy expressed the same view in 1910.

The Palaeohemiptera have fared no better as possible connecting links. The Russian upper Permian *Scytinoptera* was made by Tillyard (1921b) the type of the family Scytinopteridae of the Auchenorrhynchos Homoptera, while *Prosbole* (also of Russian Permian) and *Mitchelloneura* Till. a new genus from the upper Permian of N.S.W., originally placed in Palaeohemiptera, were ranked on the advice of Muir (Tillyard, 1922) as Tropicuchidae,

connected venationally with recent forms by the Neotropical genus *Alcestis*.

Since no other possible annectent forms have been discovered, the order Hemiptera stand to-day, a very orphan, the most isolated of the paurometabolous orders.

There is apparently unanimous agreement that the two sub-orders, Heteroptera and Homoptera, are homophyletic (Handlirsch, Muir, Tillyard); but as to which arose first, there is considerable question.

Handlirsch (1921, p. 359) considers the Homoptera in many ways more primitive, notably in wing structure, but yet obviously more highly specialized in other directions, e.g. head. He believed that *Prosbole* and *Scytinoptera*, which Muir and Tillyard place in Tropicuchidae, might easily belong to either sub-order; so therefore he made for them a separate order. He thought also that both sub-orders were present in the Mesozoic and arose from a common stem in the Palaeozoic.

Such was the state of knowledge before the rich fossil insect fauna of the Queensland and New South Wales Permian Triassic had been fully studied by Tillyard. This authority (1921b) finds the oldest known type of true Heteroptera to be the upper Triassic *Dunstaniiidae*, which he would derive from the Palaeohemiptera, i.e. from forms similar to or identical with recent Tropicuchids and at least almost certainly Homopterous. This view was modified (*in litt.*, 31 July, 1922) by the recognition that Tropicuchids are much more specialized in many respects than recent Heteroptera; and by a suggestion that the sub-ordinal dichotomy must have occurred very early. How early, may be imagined from the presence in the upper Permian of at least three true Homopterous families, of which one, the Tropicuchidae, is, as we have seen, a recent one. The upper Carboniferous *Dictyocicada antiqua* Brong. unclassified by Handlirsch, is considered by both Lameere and Tillyard (1921b) truly Hemipterous. We are thus, says Tillyard, led to envisage the Hemiptera as a highly specialized but exceedingly ancient offshoot of some more generalized upper Carboniferous order which was already stegopterous. This order, in his opinion, was surely the Protorthoptera of Handlirsch, which exhibits such variety that it may well have been the base of several orders.

Muir (1923b) considers that no true Homopteron could have been ancestral to the present Heteroptera; in fact, he would go further and see in the common stock predominantly heteropteroid characters especially so far as the head structure is concerned. From the standpoint of comparative anatomy Muir (*in litt.*, 2 February, 1926) regards the Tropicuchidae as much more specialized than the Cixiidae and still more so than the Tettigometridae.

Crampton (1919) has called attention more than once to the neuropteroid condition of the cicada thorax, and has studied

evidence of relationship between Hemiptera and other orders also in genitalic and venational characters. In 1922 (b) he wrote that the line of descent of Homoptera, instead of originating in *Eugereon*, arose at the base of a common Protorthopteron-Protoblattid stem, i.e. therefore in the Palaeodictyoptera. These ancestral forms were anatomically intermediate between the ancestors of the Psocids and those of the neuropteroid insects.

To summarize, it would appear that the Hemiptera arose in the upper Carboniferous either directly from Palaeodictyoptera or through the Protorthoptera. So far as our present knowledge of the fossil forms is concerned, the Homoptera are very much older, but most of the morphological evidence indicates the Heteroptera as more primitive.

Before discussing the cicadas, we must consider the phylogeny of the nodal line on the fore-wing; or, in other words, the development of the hemielytral condition. This is absent in typical Homoptera; present in normal Heteroptera, and to some degree in all Cicadidae (see Section on venation).

Is it a primitive or a secondary character? This question is of supreme importance in the phylogeny of the Cicadidae and its answer obviously depends on our conception as to the predominantly homopteroid or predominantly heteropteroid character of the common Hemipteran progenitor. And this conception is guided very surely as our view is influenced more largely by the palaeontological or by the morphological evidence. Tillyard considers there is an orthogenetic tendency in both sub-orders towards a hemielytral condition (*in litt.*, 23rd January, 1925)—a tendency in which the Heteroptera have outrun the Homoptera. He points out one very important difference between the hemielytral condition in Heteroptera and in those Homoptera which may exhibit it; namely, that in the former the thickened portion is the portion which lies free when at rest; the membranous portions overlap each other; whereas in Homoptera, on the other hand, the resting position is usually stegopterous and therefore more primitive and the above condition does not occur. Thus in the two sub-orders, hemielytral conditions do not arise from the same necessity. On this hypothesis the presence of the hemielytral condition is evidence, at least so far as that character is concerned, of greater specialization.

Let us examine the alternative explanation. If the morphological evidence is correct the Heteroptera are predominantly the more primitive and the common ancestor of the two sub-orders may well have exhibited the nodal line. In support of the latter supposition we may instance the occurrence of the maximum development of the hemielytral condition in the most primitive families of Heteroptera and its distinct presence in *Prosbote*, one of the oldest Homoptera known. With regard to the necessity of this condition it is important to remember that in Cicadidae at least the nodal line

forms a break or a joint at every vein it crosses, and these joints have been elsewhere (e.g. Imhof) interpreted as extremely valuable in the mechanics of flight. The structure is so complicated as surely to suggest some functional significance, and such significance may be valid in both sub-orders. On this second hypothesis, then, the nodal line is considered a primitive character with functional significance in both sub-orders. In the Cicadidae we believe it primitive because it is most highly developed in forms otherwise primitive and in nymphs.

The Cicadidae are palaeontologically extremely isolated, morphologically rather less so. "Structurally the *Cicadidae* are undoubtedly archaic in many of their characters. But they are not found fossil before the Cretaceous and the origin of the family is at present a mystery" (Tillyard, 1920, p. 892). Not a single form, fossil or recent, is yet known which can truly be considered annectant between Cicadidae and any other family of the Auchenorrhyncha. In fact, the position of the Cicadidae phylogenetically is an epitome of that of the whole order.

The cicadas have been regarded by Tillyard and many others as the most primitive existing Homoptera—an opinion influenced largely by venational considerations. The nymphal alar tracheation, as Comstock and Needham were the first to demonstrate, shows remarkably little deviation from the hypothetical primitive insect type. But few other characters of the cicada body support this view. Moreover the presence of a transverse basal trachea between the costo-radial and cubito-anal groups in the wing-base (Comstock, 1918, p. 275) shows the Cicadidae more primitive than Membracidae, Cercopidae, and some Cicadellidae, if the absence of this structure in the three latter groups be confirmed and its significance admitted. Admittedly the most primitive Homoptera must be sought in the Auchenorrhyncha, since as Muir has repeatedly stressed, the relative simplicity of the Sternorrhyncha is undoubtedly a secondary specialization. In completeness and complexity of the integumental sense-organs, notably on the antennae, the Cicadidae are certainly inferior to the Fulgoroidea, which are specialized also in many other directions; yet in these latter insects the filter-chamber is lacking—perhaps not primitively—while the presence of superabundant sensory pits does not perhaps overbalance the possession of a complex chordotonal organ in the Cicadidae. But this auditory organ and the complicated sound-producing apparatus are, according to present knowledge, confined to Cicadidae, where they are general save in one genus—*Tettigarcta*. The lowest of the Auchenorrhyncha are perhaps to be found in the Cicadellidae, which Osborn considered the highest, but they are greatly specialized in leg structure—and in the composite mesopleura (a character shared only with Cicadas*) and are moreover a dominant

* According to Taylor the mesothoracic episternum is 3-partite in these two groups only.

group. The Membracidae are lowest in most respects but show amazing modifications in the pronotum. In this connection it is interesting to note that *Tettigarcta*, which is the most primitive cicada in almost every other respect, is the most specialized in pronotal structure. There is a dim possibility that the hypertriphied prothorax in *Tettigarcta* is associated atavistically with the enlarged prothorax of the nymph—a general character in the family, but probably correlated with the powerful development of the fore-legs for digging.

Muir (*lit.*, 26 September, 1921) believes that the nearest approach to the ancestral Homoptera is seen in the Cercopidae. In this family, however, the peak of specialization in the digestive system is reached. The Cixiidae, as the same authority has noticed, are primitive in venation and in the possession of three ocelli, but like other Fulgoroids, they show great specialization in other directions, especially in head structure and in sensilla-equipment.

On all counts, as Muir believes, the nearest relatives of the Cicadidae are the Cercopids. If these two families arose from a common branch of the Auchenorrhyncha stem, as Handlirsch (1906–1908, p. 1246) thinks, then the Cicadidae must have split off before the filter-chamber attained a very high degree of complexity, although there is the possibility that the relative simplicity of the cicadid arrangement is due to reduction.

Practically no gradation exists between the complete absence of the sound-producing organs in *Tettigarcta* and their high development in the most primitive of other cicadas. Such variation as exists in respect to this apparatus affects rather the covers than the essential agents of sound. Moulton (1923) has shown that, on the whole, the forms without tymbal covers (projection of 2nd abdominal segment) and the shortest of opercula, usually show the greatest development of the nodal line, a feature which he regards as highly primitive, as also apparently does Horváth (1913). Moulton sees the most highly evolved section of Cicadidae in that exemplified by the genus, *Cosmopsaltria*, with extremely long opercula sometimes reaching nearly to the end of the body; a very complete tymbal cover; and wings perfectly hyaline and the nodal line, at least in its intervenal portions, reduced almost to invisibility.

Palaeontology has so far helped but little in cicada phylogeny. On the one hand it has contributed numerous descriptions of fossil "cicadas," and on the other it has set up two families apparently related to the Cicadidae but throwing no light on their origin. Many of the earlier descriptions, such as those of Brodie, Weyenbergh, were based on fossils not only non-cicadan but not even Homopterous (Handlirsch). Species that are undoubtedly cicadid usually show little venational divergence from recent forms. An exception to the last is *Hylaeoneura lignei* Lamcère and Severin (1897) (Handlirsch, 1906–1908, p. 668; 1921, p. 213), believed by the

authors to be a Sialid. It is from the lower Cretaceous of Belgium. Handlirsch considers this a true cicadid, and thus the earliest known. It occurred in the lower Cretaceous of Belgium. The fossil consists of an apical fragment of a wing estimated at 40 mm. in total length. The characteristic marginal vein—ambient of Tillyard—is well developed. Handlirsch considers,

“Der Verzweigung der Längsadern und ihrer Verbindung durch einzelne Queradern eine weitgehende Übereinstimmung mit Flügeln rezenter Cikaden.” (Handl., 1906–1908, p. 668).

It differs from recent forms chiefly in its five-branched radius.

Fifteen Tertiary species are listed by Handlirsch (1921, p. 281) under the following three genera—the first with practically family connotation:

Cicada, **Lithocicada** Ckll. and **Platypedia** Uhl. The species include:

- 2 from amber (Oligocene), (Burmeister, 1831; Berendt, 1830);
- 2 from lower Oligocene of Aix (Serres, 1829);
- 1 from lower Oligocene of Caylux (Flach, 1890);
- 3 from lower Miocene of Radoboj (Heer, 1853);
- 1 from upper Miocene of Oeningen (Heer, 1853);
- 3 from Miocene of Florissant (Scudder, 1892; Cockerell, 1915, 1908);
- 3 from Copal (Pleistocene), (Bloch, 1776).

The venation of *Cicada grandiosa* Scudder, (Cockerell, 1911) is almost identical with that of *Tibicen marginalis* (Walk.), found in neighbouring states to-day. Considering how relatively unimportant the venation is in the taxonomy of this family, it is little one can do with fossil species.

Among the most beautifully preserved of the fossil insect wings discovered in the upper Triassic of Ipswich, Queensland, were those of five species of large insects comprising the family Mesogereonidae of Tillyard (1916, 1921a). All belong to the type-genus *Mesogereon*, of which the type-species, *M. neuropunctatum*, was named by Tillyard in allusion to the remarkable formation of cross-ridges running between the main veins, and interrupted midway by an unridged area carrying strongly marked tubercles or macrotrichial sockets. We have already seen that this cross-ridge system was interpreted as an archidictyon. This condition is present to a greater or less extent in the tegmina of all recent Cicadidae, and, as Forbes (1922) has shown, it is much more distinct just at ecdysis. The presence of this feeble network is taken to indicate descent from one of the netveined forms of the Carboniferous. The venation of *Mesogereon* resembles that of recent cicadas very closely in the general disposition of the main veins and in the presence of an ambient vein

demarking a coriaceous border. These characters prove it definitely Homopterous, and Muir (1923, p. 217) would even place it in the modern family Cicadidae, a course in which I cannot follow him. The most striking differences lie in the absence of any sign of the nodal line on the tegmen, a character to which I assign more importance than do other workers, and the absence of the cross-veins which mark off the apical cells of a cicada tegmen. If, as I believe, the nodal line is a primitive character, then in both of these respects, *Mesogereon* is actually more specialized than modern cicadas, while the massing of the radius and medius on the anterior margin of the wing in *Mesogereon* as in most cicadas, renders the former more specialized in yet a third character than the most primitive of recent Cicadidae, *Tettigarcta*.

Tillyard restores *Mesogereon* as a cicada-like insect with roughly haired tegmina held roofwise over a moderately stout and hairy body; with high wings smooth and transparent, probably with their anal area folded; with no sound apparatus comparable with that of recent cicadas (1921a).

Although no one claims the Mesogereonidae as direct ancestors of the modern cicadas, Tillyard considers them probably very similar. But nearer relatives of these interesting Triassic insects are believed by Tillyard to be the much-disputed Jurassic Palaeontinidae, considered by Butler, the founder, as Lepidoptera, by Scudder, Oppenheim and Haase as cicadas, and finally by Handlirsch as Lepidoptera allied to the Limacodids. The material is unfortunately in such poor condition that there is ample room for guessing. Handlirsch definitely ascribed scales to the wings of *Eocicada lameeri* Handl., but Tillyard examined the type, found no trace of scales but saw instead traces of comparatively large tubercles and of a coriaceous border which made him refer the insect at once to the Homoptera, near the Mesogereonidae of which the venation is very similar, and rather more distinct from the modern Cicadidae. The Palaeontinidae show no signs of the archediectyl cross-ridging common to Cicadidae and to *Mesogereon*. Examination of other types and of a drawerful of unnamed Solenhofen Palaeontinidae at the Museum of Comparative Zoology, confirmed the above results.

Through the courtesy of Mr. Nathan Banks we have been enabled to examine the drawer of Solenhofen material mentioned above. We were particularly interested to see whether the nodal line was present. These fossils show a remarkable resemblance, possibly superficial, to cicadas. The tiny head, regarded by Tillyard as only a part of the crown, is not smaller proportionately than that of *Tettigarcta*. Just behind this, in one of the examples, are what appear to be pronotal expansions similar to those in *Platyleura*. Evidence of the tubercles on the tegmen is present as seen by Tillyard in *Eocicada*, but we saw no signs of a coriaceous border. The venation is extremely indistinct, but one specimen shows a distinct

break in the curvature of the fore border of the tegmen and from this node a transverse line convex towards the base, dividing off an evidently more coriaceous basal portion. No other specimens were in a condition to show whether this was present or absent. What little could be seen of the rest of the venation seemed more cicada-like than that of *Mesogereon*.

An examination of Handlirsch's figures (1906-1908, Taf. 49, figs. 8, 9, 10, 11, etc.) shows that several of the named Palaeontinidae possess a similar break in the costal curve, a condition attributed by Handlirsch to chance. *Phragmatocites damesi* Oppenheim shows this well. *Palaeocossus pirassicus* Oppenheim has Cu_2 and 1A well-separated as in the recent cicada, *Tettigades*.

Altogether it seems very probable that the Palaeontinidae form a family of Homoptera even more closely related to the cicadas than is *Mesogereon*, though Haase (1890) certainly goes too far in placing *Eocicada* in the family Cicadidae (Stridulantien). This author draws attention to the fact that *Tettigarcta*, which he conceives as the nearest living relative of *Palaeontina*, has

“nur schwach entwickelte Submarginalverbindungsadern wie *Palaeontina* und wie letztere verhältnissmässig stärker als bei den meisten recenten Singcicaden ausgebildetes Analfeld mit mehrerer selbständigen Dorsaladern.”

In this connection be it noted that more than one recent cicada has practically no coriaceous border, the ambient vein being practically coincident with the wing-margin (fig. 60). Haase would see in *Eocicada* a sign of that mesonotal structure commonly called the “cruciform elevation,” but this seems rather doubtful.

Before leaving the subject of cicada origins we are impelled to mention one of the wildest flights of imagination which ever masqueraded as a scientific hypothesis. Delétang (1919, p. 25) concludes that the Cicadidae:

“son originarios del Viejo Mundo y los Fulgóricos (Fulgoridae) cuyo desarrollo actual hace aparecer como americanos, pueden considerarse como los antecesores de aquéllos” (p. 53).

And this is how the American cicada-fauna arose:

“Quizá bajo la influencia de factores no conocidos, pero comparables a los que actualmente impulsan a la devastadora langosta a recorrer grandes distancias, ciertas especies ‘australianas’ o ‘malásicas’ de cicádidos hayan emprendido migraciones hacia la América del Norte.”

We wonder whether these enterprising Australian cicadas broke their long journey with the ancient Lemurians of whom the occultists tell us. With this as a sample we look forward with eager

curiosity to the same author's much-quoted "Ensayo de una monographía de los Cicádidos argentinos," which is, "próxima a aparecer."*

To sum up, the Cicadidae form a very isolated family with no ancestors among fossil forms yet described, and no very close relatives among recent Auchenorrhyncha. Two families—one Triassic and the other Jurassic—of Homoptera apparently belonging to this section, were large insects of Cicada-like form.

The earliest form referable with any degree of certainty to the family Cicadidae is *Hylaconeura* of the lower Cretaceous, and then there is a wide gap until distinctly modern types appear in the Oligocene amber. Thus the series Mesogereonidae-Palaentiniidae—*Hylaconeura*—modern Cicadidae, forms a chronological series but not a phylogenetic one. "The origin of the family is at present a mystery" (Tillyard, 1920, p. 892).

* A part of this has now appeared.

CHAPTER IX

EARLY LIFE-HISTORY

"Pariunt in arvis cessantius, excavantes asperitate praeacuta, quam parte habent posteriore, quomodo bruci etiam solo eiusmodi pariunt. . . . Quinetiam in harundinibus, quo adminiculo vites eriguntur, nidum foeturae excavant, et in caulibus squillae herbae interdum pariunt: sed hic foetus facile in terram dilabitur. Proveniunt large copia imbrum. Crescit primo in terra vermiculus; deinde fit ex eo quae tettigometra vocatur, parentis nomine; quo tempore gustu suavissimae sunt antequam cortex rumpatur: postmodum circa solstitia noctu exeunt, statimque, rupto cortice, prodeunt cicadae ex matrice illa cicada, quam modo tettigometram dixi, nigrae protinus, et duriusculae, et maiusculae, atque incipiunt canere."

ARISTOTLE, *De historia animalium*. Th. Gaza interprete, Lugduni, 1552, lib. V. cap. 30.

Few insects present to the student of life-history more difficulties than do the cicadas. The subterranean habits of the nymphs and the difficulty of keeping them in captivity, coupled with the usually long and sometimes phenomenally extended life-cycle render the rearing of isolated individuals from egg to adult almost an impossibility. Curiously enough the only two relatively complete breeding records established in the family concern the species with the longest known cycle—*Magicicada septendecim* (Marlatt, 1907, p. 112; Surface, 1906a). We consider cicada life-history below, under nine headings, endeavouring with our own observations and those collated from the literature, to trace development from conception to death.

It is on the whole surprising how very little more we have ascertained concerning the main facts of the life-history than was known to Aristotle and expressed in the quotation introducing this chapter.

MATING

The psychological aspects of mating behaviour will be treated in a later chapter. Copulation was early observed by Aristotle and considered at some length. *Coeunt tam maiores, quam minores supinae complexu mutuo: masque inserit in foeminam, sicut et caetera insecta agunt. Genitale foemina habet rescissum, quo recipit id quod mare iniicitur* (*Hist. anim.*, lib. V, cap. 30, Gaza interpr.).

And we have seen further that the Greeks, according to Mufet, probably kept cicadas not only for the sake of their song but also to watch their mating behaviour.

Few observations are on record concerning the numerical proportions of the sexes. Marshall (1896) would appear to indicate incidentally that they are more or less equal in an unknown species in Mashonaland. In New Zealand, when numbers are together in a small area it is usually found that the sexes are in equal proportions. Thus six *Melampsalta cingulata* caught in one net sweep as they flew alarmed from a tree-trunk (January, 1923) showed three males and three females. In the more solitary species it is a common occurrence to find a female very near a singing male, so that a kind of pre-

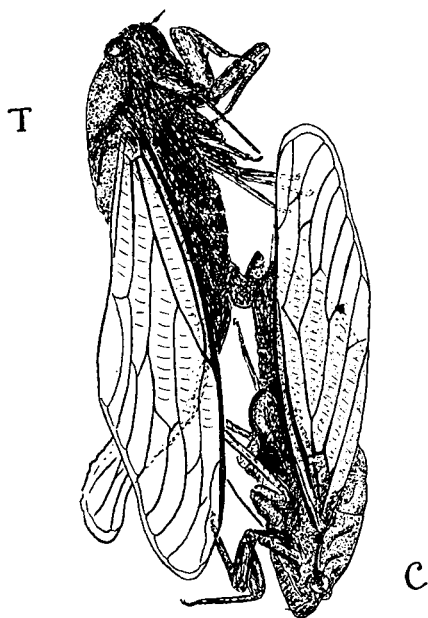


Fig. 80. Copulation between male *Cyclochila* (C) and female *Thopha*, redrawn from Rainbow.

nuptial pairing is a fact. This has been observed in *Melampsalta cauta*, *muta*, *subalpina*, *scutellaris*, *leptomera*, and *sericea*.

Copulation is not often observed. Apgar has described it in *Magiccada septendecim* (1887). In this cicada the phallosoma or body of the aedeagus contains an invaginated distal endosomatic appendage, complicated and spinous. The phallosoma or "case" of Apgar, is entirely within the vagina during coition, and remains there stationary, the endosome or "enclosed tube" of Apgar and its parts alone being active. This activity consists in thrusting the endosome violently forward and then retracting it—the resultant eversion rendering some of its spines retrorse. The pulsating move-

ments average about one per second and continue during the entire time of copulation. The discharge of seminal fluid occurs from the orifice at the tip of the everted endosome, at each protrusion.

Gadd (1908b, p. 143) found *Cicadatra querula* (Pall.) in copulation in June, in Crimea. He has observed the process to endure one hour without movement.

Swynnerton (1922) states that the Tanganyikan *Monomatapa insignis* Dist. was "very easily captured by hand when in coitu, attempting to escape in most cases merely by falling or gliding to the ground together." The cases seen by Swynnerton occurred between seven and eight in the morning.

In our New Zealand field experience we have seen copulation only once, the species concerned being *Melampsalta ochrina*. *M. leptomera* has mated in captivity. In a pair confined with suitable grasses for oviposition (December–January, 1923–1924) there were indications that almost throughout the day, intervals of oviposition and mating occupied the female alternately, and periods of singing and mating, the male. During copulation both members of the pair clung to the support, in a position alongside each other, with the heads pointing in the same direction—surely very unusual in Hemipterous copulation. The male pygophor was completely exerted and bent over laterally to the fullest extent of its narrow "neck" formed by intersegmental membrane. There are insufficient observations, either in this or in other species, to suggest whether the position taken by this *leptomera* pair is normal to Cicadidae. It is certainly very different from the attitude described by Rainbow in the only recorded case of miscegenation in the family (1904). We copy (fig. 80) Rainbow's figure of a cicada pair consisting of two large Australian cicadas of very different genera, though both of the same subfamily—the male *Cyclochila australasiae*, the female *Thopha saccata*. It would be interesting to compare the male genitalia of *Cyclochila* with those of *Thopha*. "When captured the female was suspended to a branch, which she had firmly grasped with her legs, whilst the male was hanging head downwards, but grasping his partner round the abdomen" (Rainbow, l.c.). The photograph was obviously taken after death, when the position had changed slightly.

Gadeau de Kerville (1902) observes that cicadas in copulation take up a position "en angle aigu," the heads thus pointing nearly in the same direction.

MATURATION OF THE GERM-CELLS: SPERMATOGENESIS

The earliest work on the chromosomes of Cicadidae, as on that of the Homoptera as a whole, was that of Wilcox (1895), who worked on *Tibicen linnei* S. and G. [= *tibicen* auctt.], and was apparently handicapped by scarcity of suitable material. He had only three

male cicadas which were killed immediately after ecdysis and had been preserved for a number of years. His work has been greatly extended, and his conclusions modified by Shaffer (1920) working on *Magicicada septendecim*. In the meantime members of most of the other Auchenorrhynchos families had been studied cytologically. We can give but a scant summary of Shaffer's very detailed paper, which should be referred to in the original.

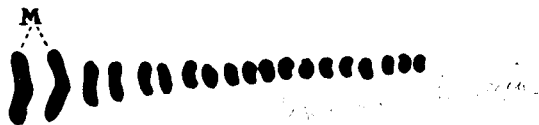


Fig. 81:

Wilcox found that the spermatogonia lie at the blind end of the testicular follicle, occupying only the single end compartment. Their size is less than that of the spermatocytes, which usually lie in two compartments next to that of the spermatogonia. Shaffer, using as his youngest material, ultimate instar nymphs about three weeks before emergence found in the testes most of the cells in the maturation stages, besides numerous spermatids, spermatozoa, and a few spermatogonia. In the adult he found the testes almost completely filled with sperm except for a small number of spermatogonia. After copulation the testes are reduced to about one-tenth their former size and contain only a small residue of spermatozoa, some degenerated cells, and a few spermatogonia which also show signs of degeneration.

Shaffer states that the diploid chromosome groups, as exemplified in the spermatogonia, the follicle cells and the somatic cells show no variation in form, number, or arrangement. The number is 19 in the male and 20 in the female. The diploid groups show one large pair of chromosomes—unfortunately named *macrochromosomes* by Kornhauser, though *megachromosomes* would have been preferable—and two pairs of somewhat smaller chromosomes, the remaining thirteen exhibiting no size differences. The odd number, of course, indicates an unpaired sex element, which, however, cannot be identified in the groups by size, shape, or differential staining, though it probably persists in the resting spermatogonia in the form of a single chromatin nucleolus.

In the material collected by Shaffer the earlier stages of the spermatocytes were lacking and a detailed study of synapsis was therefore not made. In the early prophase one pair of the homologous threads is distinguished by its size as derived from the spermatogonial macrochromosomes. In this pair the threads are very long and twisted about each other, but retain their connection at the ends, so that if untangled they would form a large ring, the space enclosed by which is the interchromosomal space marking the point of

synaptic union of the threads. In the later prophase the large ring condenses, the threads becoming much thicker and the interchromosomal space decreased until, in the definitive maturation tetrad it is reduced to a small oval slit between the two halves. The pair of threads derived from the second largest pair of spermatogonial chromosomes develops into a similar ring-tetrad of half the size. Tetrad development occurring in this manner is known as the *Stenobothrus* type and has been described in several Orthoptera. The other tetrads show no ring formation, but eventually exhibit the more typical dumb-bell shape.

“An odd chromosome is present which persists as a nucleolus in the growth stages of the spermatocyte. It passes undivided to one pole in the first maturation division and divides in the second division” (Shaffer).

Continuing Shaffer's account we find that in the metaphase plates of the first maturation division the chromosomes are always grouped in a characteristic manner. Eight are disposed in a circle surrounding the macrochromosome tetrad, while the sex chromosome lies completely outside the periphery, often in another plane. This position of the sex chromosome is apparently characteristic of numerous other forms in the Homoptera.

Shaffer gives very detailed studies of the mitochondria and reviews the theories propounded to explain their function. He found an apparently inordinate measure of cell-degeneration taking place in the testes, especially among the spermatogonia prior to the development of the spermatocytes, and to a greater extent in imagines than in nymphs. Mitochondria are apparently closely concerned in this process of degeneration, during which they increase in size and decrease in numbers by very evident agglutination, resulting finally in large, spherical intensely staining bodies which Shaffer identifies as lipoid globules. The process is viewed as one of fatty degeneration, with some possible function in the nutrition of the spermatozoa.

In the spermatogonia the mitochondria are granular; in the spermatocytes filar. In the latter “they surround the spindle peripherally at the time of the maturation divisions and become divided by the cell constriction . . .” (p. 426). The mitochondria of the spermatid form the round, compact *Nebenkern* which later becomes drawn out as a sheath surrounding the axial filament of the spermatozoon.

We shall return to the mitochondria when oogenesis has been discussed.

Giant sperm elements: Wilcox noticed that there are frequently seen spermatozoa and various stages in the metamorphosis of spermatozoa which are four or five times as large as the normal forms. They may be called *giant* spermatozoa. Wilcox believed they are

not functional—that they are excluded from the developmental series and come to nothing. He found that they arise in *Tibicen* directly from spermatogonia without cell-division, by a metamorphosis of the nucleus. This development may or may not be accompanied by amitotic division of the nucleus. He admits that it seems *a priori* improbable that the giant spermatozoa should arise directly from spermatogonia, yet his preparations leave no room for doubt. Shaffer studied these further in *Magiccada* and found giant spermatocytes originating from spermatogonia in which there had been a failure of division of the cell-body resulting in cells with double the diploid number of chromosomes. These double-chromosomed spermatocytes develop normally and give rise to giant spermatids or spermatozoa. Shaffer leaves it an open question whether the giant spermatozoa play any part in the fertilization of the egg.

OÖGENESIS

Shaffer found the ovarian tubules to contain a very great number of oocytes. The oldest oocyte of a last stage nymph is about one-seventieth the linear size of the oldest oocyte of the adult, which indicates the tremendous growth taking place in a few weeks.

In dissecting the females to remove the ovaries he found "a number of round, brown-pigmented bodies resembling eggs" in the abdomen. On sectioning these it was found that they were of a glandular nature and "are perhaps concerned in the secretion of adhesive materials for the eggs."

Shaffer was unable to ascertain the origin of the cell-elements—germ-, nurse-, epithelial-, and follicle-cells—of the ovary from a study of the nymphal and adult ovaries, but he was led to suppose that differentiation occurs at a comparatively early period in the life-cycle.

The ovarian tubules are typically Hemipterous. At the extremity of the tubule is the narrow end filament, of a ligamentous nature. The tubule is divisible into three zones according to the type of cells present.—At the extremity is the nurse-chamber containing all the nurse-cells. The chromatin of their nuclei consists of diffuse granules; and there is usually present a chromatin nucleolus and a true plasmosome. At the base of the nurse-chamber are various young oocytes in various stages of synapsis. Next are the older oocytes of the post-synaptic stages and in this region also are the follicle-cells which begin to form definite follicles round the oocytes. As the young oocytes begin to migrate from the base of the nurse-chamber they still retain protoplasmic connections with the cytoplasm of the nurse-cells, resulting in the formation of pseudopod-like projections from the oocytes—the egg-strings—by means of which nutriment is passed from the nurse-chamber to the oocytes. Even old oocytes, in which yolk is beginning to form, still retain

connection with the nurse-chamber by means of the egg-string. In the ovaries of the adult the nurse-cells are ingested at the upper end of the egg-string and their ingested products pass down into the oocyte.

Synapsis was studied in the oocyte, and the chromosomes were found to pair side by side. In the pre-synaptic stages *two* chromatic nucleoli were present in the oocyte, as compared with one in the spermatocyte. During the process of synapsis these disappear, but come once more in evidence during the post-synaptic changes. Not very conclusively Shaffer interprets these chromatic nucleoli as representing the two sex chromosomes of the female, which go through a synaptic phase like the autosomes. He suggests that the solitary sex chromosome of the spermatocyte remains aloof from the synaptic happenings because it has no mate with which to pair.

In all of the Cercopidae, Cicadellidae, Fulgoroidae, and in most of the Membracidae studied up to 1920, the sex chromosome is found to consist of one element as in *Magiccada*, which persists as a chromatin nucleolus through the growth stages of the spermatocyte. In the diploid chromosome complexes the presence of a pair of large, rod-shaped macrochromosomes is very usual in most Auchenorrhyncha studied, while one or two pairs of somewhat smaller chromosomes are also characteristic.

The mitochondria of the oocytes are always granular, never filar as in the spermatocytes. In the later stages they form a zone round the nucleus and increase greatly in numbers. At the time when the cytoplasmic volume of the oocyte is at its maximum the perinuclear zone of mitochondria occupies approximately a third of this volume. Subsequently the zone disintegrates and its constituent granules disperse towards the periphery of the cell, until in the older oocytes they are all concentrated in a cortical layer. There Shaffer believes the mitochondria are converted into yolk, a change which cannot be chemically very great, since, as he states, these bodies in composition are already phospholipoid.

With regard to the much disputed question of the origin of mitochondria Shaffer adduces evidence from *Magiccada* that they probably "arise as differentiated parts of the cytoplasm through specific chemical (enzyme) reactions of the nucleus upon the products of assimilation of the cell."

EGGS AND OVIPOSITION

The eggs of Cicadidae so far as known are remarkably similar in structure. Those of *Magiccada septendecim* are described by Marlatt (1907, p. 111, fig. 45), Heymons (1899, p. 426, fig. VI), and many others; of *Tibicen lyricen* (de Geer) by H. S. Barber (1912); of *Tibicen plebeia* (Scop.) by Fabre (1921, p. 274), Silvestri (1921, figs.), and others; of *Graptosaltria colorata* (Stål) by Nawa

(Matsumura, 1898); of *Tibicen erratica* (Osborne) by Wilmon Newell (1906); of *Hymenogaster planiceps* (Horv.) by Innes (1915, p. 143); of *Melampsalta montana* (Scop.) by Lyle (1913, fig.); of *Tibicen auletes* (Germ.) by Beamer (1925, p. 481); of *Tibicen viridifascia* (Walk.) by Osborn and Metcalf (1920, p. 249, Pl. III, fig. 2), of *Huechys sanguinea* by Maki. Beamer (l.c.) notes that there is very little variation in eggs of Cicadidae of different species.

The eggs of *Melampsalta muta* (figs. 82, 83) resemble most those described by Lyle in the European *M. montana*. The only other New



Fig. 82.



Fig. 83.

Zealand forms so far known are those of *M. cingulata* and *M. leptomera*.

Throughout the Cicadidae the long narrow shape, slightly more attenuated anteriorly than posteriorly, seems to be a general character; while the white colour is doubtless associated with the internal deposition.

With regard to the number of eggs laid by a single female, various estimates have been made. Pontedera (1718) dealing probably with *Tibicen plebeia*, was apparently the first, not only to describe eggs, but also to estimate their number (500-600, sometimes 700). Putius followed in 1721 (Zanotti, 1731, pp. 81-82), and Réaumur in 1740, the latter finding 300 in one about to lay. Gossard (1919) estimates 400-600 for the periodical cicada.

An error perhaps unmatched in the history of entomology was made when Costa (A., 1877), in his work on fruit-tree pests in Italy, described the eggs of *Cicada orni* as the pupae of a new genus and species, *Macroprotopus oleae*, of injurious insect, of which the imago was the newly hatched cicada nymph.

The process of oviposition abounds in interesting details, and has been described by numerous observers, beginning with Aristotle, as

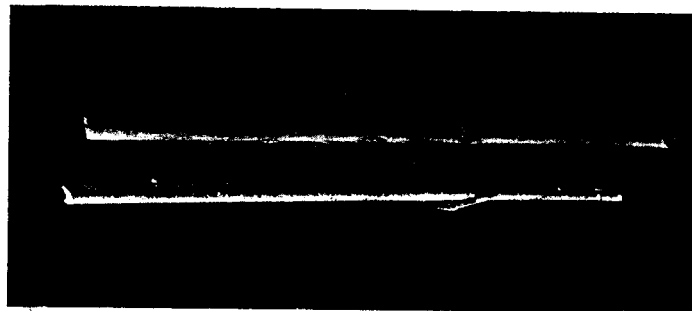


Fig. 1



Fig. 1. Egg nests of *Melampsalta leptomera* Myers
 Fig. 2. " " " " *muta* (Fabr.)
 In stems of grasses (marram and cocksfoot respectively)
 Reduced

E. Bruce Levy, photo

quoted above. Such a description is perhaps the best contribution in Pontedera's account (1718), though the treatment of the ovipositor is very little less superficial than that of Aristotle himself, and not to be compared with that of Pontedera's great critic, Réaumur. The latter's description of the mechanics of oviposition (1740, p. 178) is clear and simple :

“ Ainsi, chacune des limes peut alternativement être poussée vers le derriere et être retirée en avant par le mouvement alternatif de la solide queue cartilagineuse à laquelle elle tient. C'est au moyen de ce jeu alternatif des deux limes, que la cigale vient à bout de percer dans le bois, les trous dans lesquels elle veut loger ses œufs.”

This description has served as the basis for all later explanations, save those inspired by the work of Doyère (1837). This writer maintained that Réaumur's notion of the alternative saw-like action of the lateral pieces was mechanically inadequate. According to Doyère the middle piece is the only instrument essentially concerned in piercing, the side pieces being at first just slightly inserted and acting as grappling-hooks, retaining the advantage gained by each thrust of the median borer. Even the author, however, seems hardly to have been convinced, since he remarks :

“ S'il s'agissait de rendre compte de la perforation d'un bois offrant quelque résistance, je serais le premier à déclarer ce mode d'action tout-à-fait inadmissible ; mais Réaumur a pris soin de nous apprendre que les Cigales ne s'attagent jamais qu' à de petites branches de bois mort remplis de moelle, ce qui ne semble lever toute difficulté. . . .”

Burmeister subscribed to this hypothesis and it remained for the stout common sense of Westwood to reject it (1840). Later observers have fully substantiated Réaumur's original theory—and we say *theory* advisedly, for the account of cicada biology which was to constitute the chief authority for nearly a century and a half, and is indeed, still commonly quoted, was based solely on a study of the dead insect.

The charming sketch by Fabre (ed. 1921, pp. 270-271) concerns Réaumur's chief species, *Tibicen plebeia* ; but most of the other subsequent descriptions deal with *Magicicada septendecim* and have been admirably summarized by Marlatt (1907, p. 109). Silvestri (1921) has described the disposal of the eggs in *Cicada orni* and in *Tibicen plebeia*, while more recently Beamer (1925) has detailed the mechanics of oviposition in seven North American species of *Tibicen* and found them essentially the same. Wilmon Newell (1906) made an intensive study of oviposition in maize and cotton by *Tibicen erraticus*.

All cicada eggs known are inserted in the tissues of plants. There appear to be two main methods of egg-disposal within these tissues.

The type is largely constant for the species, save when irruptions of tremendous numbers give scope for variation and influence of competition; but it is not correlated with any higher taxonomic category. Two very closely allied species—as for instance in the genera *Tibicen* and *Melampsalta*—may employ methods of egg-disposal as divergent as the family habits will allow.

The extreme in one direction is furnished by those species which oviposit in woody plants, often in hard and relatively thick branches which require considerable excavating. Of the seven species of *Tibicen* studied by Beamer (1925) all use woody plants save *T. aurifera*, which illustrates the other extreme. Of the New Zealand cicadas, *Melampsalta cingulata* is probably the most closely confined to woody plants as oviposition hosts. Twigs of the undergrowth shrubs, especially in clearings or on the edge of the forest, are chosen most frequently by *M. cingulata*. Usually the cicada takes its stand with the head pointing up the branch or outward from the tree. Beamer says, "always," but on horizontal or slightly up-growing branches we have seen *M. cingulata* working with its head towards the trunk and Snodgrass (1921, p. 398) notes the same in *Magiccicada septendecim*. On such horizontal branches the egg-nests are nearly always on the under-side—perhaps invariably. A *cingulata* working head downward was watched on 3rd February, 1924. We saw her withdraw the ovipositor and move forward, i.e. downward, and seek a fresh point of application. The following are field-notes of the rest of the process: For a long time with abdomen arched and evidently great strain applied she drove the weapon diagonally into the branch. Meanwhile the portion of the abdomen ventral and caudad of the ovipositor was pulsating rhythmically—now swelling to the branch so that but little space was left between it and the sloping ovipositor—now retreating, until the ovipositor was buried to the base. Then it was withdrawn with much apparent effort—all but the extreme point—and thrust in again with slightly less difficulty and time than on the first occasion. This was done 10 times, not including the initial puncture, and the time for complete thrusting in up to the hilt was less every time—and the point of application was never changed—in fact, the tip of the ovipositor did not leave the hole. At the end of the last thrust, the caudal portion of the abdomen was closely applied, for a few moments, to the ovipositor after it was almost entirely withdrawn. The anal segment was deliberately curved over towards me and a strong curving jet of liquid hurled into the air. Next instant she was gone. From the first thrust at the new position till the time of departure 20 minutes had elapsed. In this case, as might be expected from the position of the female, the frayed wood fibres pointed towards the fixed end of the branch. This account agrees remarkably closely with Snodgrass's notes (1921b, p. 398) on *M. septendecim*, the time in his case, however, being 25 minutes.

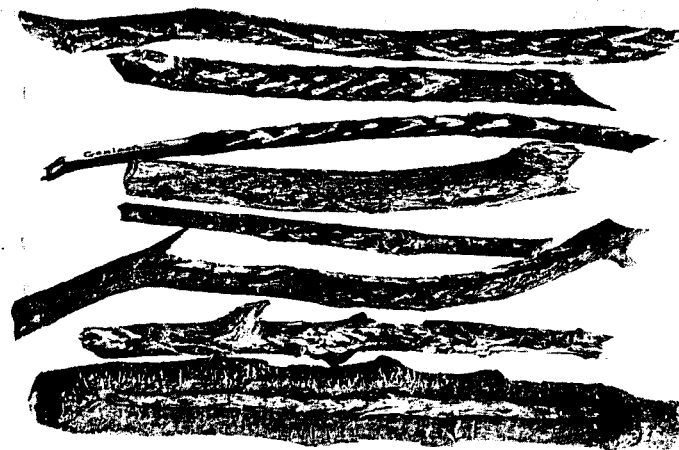


Fig. 1

Figs. 1 and 2. Egg nests of *Melampsalta* spp. in New Zealand
Reduced

H. Drake, photo

In *Melampsalta cingulata* as in *Magiccada septendecim*, there is invariably a row of such nests, marked by frayed wood fibres which cover the egg-pockets, the latter arranged in two rows down the twig, each pair communicating by the same external aperture, but the two rows separated by a remaining ridge of sound wood. With *M. cingulata* the bark is often broken for long intervals sometimes on one, sometimes on both sides of the line of egg-nests. This is conspicuous immediately after oviposition, but whether assisted or not by the female I do not know. Later, of course, the points of oviposition form very conspicuous scars, often increasing in visibility with age. But to quote Peter Collinson (1765):

“The darted twiggs, that lie before you, will better shew the manner, than I can describe it” (see Pls. IV-VI).

These figures will serve to show the great variety of plant species used. The twigs shown in Plate V, figure 1, almost certainly exhibit the work of *Melampsalta cingulata*; while those in Plate V, figure 2, are probably due to *M. cauta*.

Save in the very thinnest twigs, where the pith may be reached, the cell is always excavated in solid wood. The wounds, however, of adjacent cells, are so deep that, in the case of *cingulata*, the bark invariably breaks and dies between the members of a series as well as actually over them, thus leaving a characteristic continuous “herring bone” scar.

Another pattern of oviposition scar, indicating much less injury to the tissues, has been found commonly in New Zealand on koromiko, the common *Veronica salicifolia* Forst. f. As this plant is a prime favourite of *Melampsalta ochrina* we attribute these oviposition marks provisionally to this species, but direct proof is lacking. Examples of these are shown in Plate VI, figure 2. One oviposition area is some 25 mm. long, with a series of half a dozen disconnected, roughly circular openings, superficially quite unlike the usual *Melampsalta* wounds. But splitting brings to view the typical fish bone pattern on the wood beneath, hidden by the bark, which, though apparently dead over the area of oviposition, was still in position and unbroken save at each actual puncture. In some of the other *Veronica* twigs figured it would appear that the bark between punctures has not all died since each opening makes an individual scar.

Similar marks on an unknown woody plant sent in from Napier, and attributed by Mr. H. Hill to *Scolypopa australis* (Walk), an introduced Ricaniid, are certainly Cicadid in origin, as witnessed the empty egg-shells, and are probably also due to *ochrina*.

Plate V, figure 2, shows oviposition marks in twigs of *Coprosma lucida* Forst. f. and of *Aristotelia racemosa* (A. Cunn.) Hook. f. These seem to differ somewhat from the work of *Melampsalta*

cingulata. They were all found on bushes and in places much frequented by *M. cauta*, and were possibly made by this species. They resemble the marks of *Magiccada septendecim* as figured by Snodgrass (1921b, Pl. 4).

Cicada hieroglyphica Say in North America is recorded as ovipositing in "cedar" (*Juniperus*?) (Smith, J. B., 1910); while the common *C. orni* L. of Europe seems usually to choose woody plants, sometimes becoming quite a pest of olive and other fruit trees on this account (Costa, De Guercio, Silvestri). The later author, however (1912), records oviposition by *C. orni* also in herbs like endive, *Centaurea* and certain Umbelliferae, but such cases are unusual.

Beamer found that *Tibicen resh* and *T. auletes* are both especially fond of the "hardest, driest, dead twigs." So far as I know all the New Zealand species prefer live twigs, as does also the seventeen-year cicada. In one case, *Melampsalta cingulata* oviposited in a large apple, leaving a scar extending about a quarter the way round the equator, so to speak. Well over a hundred eggs had been inserted. R. L. Webster (1909) has recorded a similar instance in Membracidae (*Ceresa*).

Tibicen plebeia confines its attentions very largely to dead stems, but those not only of woody plants, but, more often of herbs, as noted by Aristotle and almost every observer since. This was explained as a provision against imprisonment or destruction of the eggs by the continued growth of the plant, and even Réaumur supposed that the pith formed the first nutriment of the newly-hatched young. Collinson (1765) and Gadd (1908a) were of the same opinion. On the other hand the almost invariable habit of *Magiccada septendecim* to use live twigs was ascribed also to Providence, since it was claimed that the eggs were dependent on the moisture of the plant-tissue, and failed to hatch if the stem containing them happened to die (Rathvon, 1869). The drying up of the eggs in twigs which have broken off or otherwise died and shrivelled is confirmed by Marlatt (1907, p. 107).

Silvestri (1921) found that eggs of *T. plebeia* in the favourite south Italian oviposition host, *Arundo pliniana*, failed to hatch if the stems were kept in a dry place. He concludes that in nature hatching must occur after rain or heavy dews.

Before considering more fully those species which, like *Tibicen plebeia*, prefer herbaceous oviposition hosts, we mention a habit which has led to considerable discussion. In 1718 Pontedera, describing oviposition, added the following words: *Linitur postremo gummitio quodam succo loculus, atque sic contra Coeli inclementiam munitur*. Réaumur regarded this waterproof covering as wholly fictitious, and in spite of the fact that de Geer, some thirty years later, reported, at second-hand it is true, a similar condition in *Tibicen lyricen* of North America, Pontedera's story has been

almost universally discredited, to the no small detriment of a true evaluation of his other work. In 1912, however, H. S. Barber re-described an adhesive secretion over the egg-nests of *lyricen*, while Beamer (1925) states definitely that both *Tibicen lyricen* and *T. aurifera* "secrete a glue-like substance in the opening of the cavity and pat down in place the ragged edges of the torn tissue with the two heavy sheaths of the ovipositor, leaving little evidence of their work."

Among the species which habitually seek their oviposition-hosts in lowlier and softer vegetation are *Tibicen aurifera* (Say), *T. erratica* (Osborne), *T. viridifascia* (Walk.), in North America; *T. plebeia* (Scop.), *Melampsalta montana* (Scop.), in Europe, and *M. muta* and *M. leptomera* in New Zealand, where, moreover, the mountain species dwelling above the bush line must almost necessarily follow a similar custom. In addition, though *Tibicen pruinosa* (Say) is said by Beamer to confine itself to woody plants, Packard (1873) describes a case of oviposition in a *Solidago* stem.

T. aurifera lays usually in *Panicum virgatum*, placing the punctures with meticulous care in a perpendicular line, every one about an ovipositor length above the last. The eggs are in two rows, separated by a little torn tissue (Beamer, 1925).

T. erratica, during its irruption of 1905 (Newell, W., 1906) oviposited in almost every local plant species, but corn and cotton were favoured sufficiently to constitute the insect a serious pest. In corn the attack was confined entirely to the stem supporting the tassel. Stems carrying three tassels contained 297, 181, and 215 egg-punctures respectively, with four to five eggs in each puncture. The average time to make one puncture and place eggs in it was 2.5 to 3 minutes. The number of eggs in each puncture seemed governed largely by the resistance offered by the tissue through which the ovipositor was forced. Punctures in cotton stems contained from 3-5 eggs; in corn, 4-8; while in a weed with a hollow stem 75 eggs were found, all of which had been inserted through a single puncture.

T. viridifascia, the salt-marsh cicada, is limited by its habitat to herbaceous hosts. It commonly oviposits in "sea-oats" (*Uniola paniculata*), in about the third or fourth internode of the stem, at a height of two or three feet and thus above high tide level.

In the Egyptian desert, near Cairo, *Hymenogaster planiceps* Horv. deposits its eggs in the stems of *Panicum turgidum*.

"Les œufs sont placés sur deux rangées en nombre de huit environ dans chaque . . . Ils sont placés presque transversalement à l'axe de la tige" (Andres, in Innes, 1915, p. 143).

M. montana in England has been known to oviposit in bracken. For a very detailed account of the process in *plebeia* we must refer to Fabre. His work is easily accessible (1921, Chap. 17).

M. muta very commonly chooses grasses in New Zealand, especially introduced species. In one case (31st December, 1920) a female was observed to make one puncture in a stem of rye grass (*Lolium perenne*), withdraw her ovipositor in a very leisurely fashion, climb slowly up the stem and finally fly away without depositing an egg. Is there a process of trial and error?

The same species oviposited readily in young wheat grown for the purpose in a breeding cage. Wayside grasses are commonly chosen. Each puncture is directed obliquely through the wall, and the series forms a regular row about 4 mm. apart, the cut fibres invariably projecting upward, showing that the female works with head upwards. Both in this species and the next the eggs are jumbled irregularly in the hollow grass stems and the necessity for separate punctures would seem not obvious (Pl. IV, fig. 2).

M. leptomera, both in the field and in captivity, oviposits in marram grass, *Psamma arenaria*, and probably also in other grasses,—it has laid for us in cocksfoot,—the punctures are rather farther apart than those of *muta*. It seems immaterial to the insect whether it chooses a portion of the stem covered by the leaf-sheath, or one entirely exposed (Pl. IV, fig. 1). The largest number of punctures in any one stem in the field was 40, of which 17 were in a straight line, and 23 in another line beginning one below the end of the other. Two other stems had 13 punctures each, running a slightly spiral course.

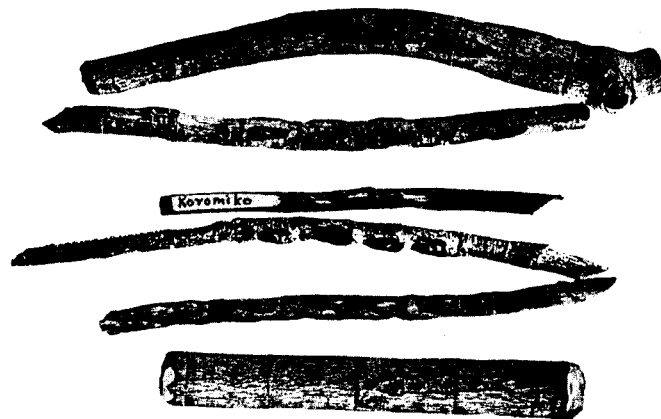
We have already mentioned the occurrence of abnormal oviposition, and before closing this section we give a few concrete examples:

"Mr. Hunter Nichols, . . . observed a female to alight on the iron rod of a bridge and attempt to insert her eggs, even extruding them to the number of seven, some of which remained attached to the rod and the others falling to the ground. Other similar cases of error on the part of the insect [*septendecim*] are noted by Mr. Davis. In one instance a female had attempted to insert her eggs in the very hard stem of catbriar (*Smilax rotundifolia*) and in another place had thrust her ovipositor entirely through the stem of a plant only to find that it was hollow" (Marlatt, 1907, p. 105).

Other cases were furnished by *Tibicen erraticus* during an irruption only to be compared with that of *Magicalada septendecim* itself. Punctures with eggs were found in abundance in the boards of a shed roof, but more remarkable were the non-Union activities of this cicada exerted on the hoe-handles during the "dinner-hour." These tools were punctured so profusely that they had to be sand-papered before use (Newell, W., 1906).



Fig. 1

Figs. 1 and 2. Egg nests of *Melampsalta* spp. in New Zealand
Reduced

H. Drake, photo

EMBRYOLOGY

Practically the only work done on cicada embryology is that of Heymons (1899), and we have nothing to add here. Buchner deals with the subject incidentally in his studies of cicada symbionts (1921, pp. 273-290). Wheeler (1889a, b) considers certain embryonal structures in *Magicicada septendecim*.

Heymons also is concerned chiefly with this species (pp. 418-423, figs. 10, 11, 35).

In the earliest stages seen by him the germinal streak was completely sunken in the yolk owing to a dorsal curvature. Two extensive head lobes, with the antennal rudiments, curved round dorsally. The other head and thoracic appendages were represented only by swellings and the segmentation of the abdomen was not complete.

At the next stage investigated the *Anlagen* of all the body segments and their appendages were much in evidence. The clypeus formed a huge helmet-shaped swelling, but all signs of a labrum were lacking. The first maxilla divided early into a lateral piece and a median peg later to form the seta. The hind maxillae in contrast to those of Heteroptera, developed very early in proximity to the prothorax. The abdomen was distinctly eleven-segmented; the first segment furnished with "Pleuropoden," in the form of conical bodies which later sink into the embryo. Spiracles were present on the meso- and metathorax and on the abdominal segments I to VIII.

At the revolution of the embryo the mandibles and maxillae have acquired their distinctive form and between them in the median line has appeared a spear-shaped, strongly developed hypopharynx (Heymons, fig. 35). The second maxillae have begun to form the labium, with its three-segmentate condition already indicated.

The peculiar body which Heymons went on to describe in the egg has been since recognized as a stage in the life-cycle of certain fungal symbionts described in a later chapter.

For the present we return to the appendages of the first abdominal segment. Heymons (p. 422) states:

"Die Gliedmaassenrudimente des I. Abdominalsegmentes sinken vollkommen unter das Körperriveau ein. In den folgenden Segmenten betheiligen sich die unscheinbaren Gliedmaassenanlagen kaum an der Bildung der Bauchplatten, indem wie bei den Heteropteren nur die unmittelbar an das Stigma angrenzende Partie des Sternites sich auf Gliedmaassenreste zurückführen lässt."

Wheeler (l.c.) carried the study of the first segment appendages further. He found that these rudiments in *M. septendecim* as in Orthoptera persist till after revolution, but instead of being evaginated as in the latter insects, they are invaginated, as indeed Heymons

would seem to imply. In this position they become glandular and secrete a glairy, much vacuolated mass, which projects between the body and the egg-envelopes. Wheeler suggests that they are primitive stink-glands. A pair of pores (fig. 69, p) in adult *M. septendecim* on the anterior margin of the IIth sternite may be connected with this gland. Their function is quite unknown, nor have they been previously recorded.

Rathvon (1869) states that the eggs increase one-third in size before hatching, and attributes this to absorption of moisture contained in the living wood. Marlatt (1907, p. 111) also believes that the egg "receives a certain nourishment from the plant."

The time occupied in embryonic development is often very long. It seems usual for eggs laid in summer to hatch the same autumn, or late summer (*M. septendecim*, Marlatt; *T. plebeia*, Fabre). In the case of the former species eggs are usually deposited about the middle of June and hatch at the end of July or beginning of August. Marlatt (1907, p. 111) notes a case in which the eggs did not hatch till the end of the year, and following Riley attributes the retardation to a gummy secretion of the plant which sealed them hermetically. Pontedera believed hatching did not take place till the following season—which is true of certain egg-parasites with which Réaumur believed the Spanish naturalist confused the young cicadas.

In the case of *Melampsalta leptomera* in New Zealand, egg nests in marram grass collected on 31st December, 1923, gave young at dates varying from 15th to 22nd of February, 1924, thus corresponding very closely with Marlatt's dates for the periodical cicada. The originally white eggs changed to salmon by the 2nd February—thus rather late in the embryonic development. In *Magiccada septendecim* this colour-change is said to take fifteen days.

The date of laying of these *Melampsalta leptomera* eggs was unknown; but a second batch, laid in cocksfoot stems in captivity on 1st January, 1924, hatched almost *en masse* between 4 and 7 p.m. on 12th April—and this in spite of the mould which had grown on the stems meanwhile.

HATCHING

Previous to hatching, the eggs, originally white, become usually salmon pink, and this is the colour of the newborn nymphs.

Hatching has been well described for *M. septendecim* by Marlatt (1907, p. 111); and inimitably by Fabre for *T. plebeia* (1921, Chap. 17). The best recent description, beautifully illustrated, is that of Snodgrass (1921, p. 405, fig. 8).

Apparently large numbers of *M. septendecim* eggs fail to hatch. We have already seen that those in twigs which have died are said to dry up. Smith (J. B., 1912) believes in an even greater mortality—perhaps 50 per cent.

Hatching may apparently occur at any hour of the day. At least it is so in captivity.

Mass-hatching is probably the rule in nature. The young nymph is enveloped in a thin glistening membrane which gives it such a distinct form that Fabre would employ the term "primary larva," as in the Meloids. Marlatt (1907, p. 111), Packard (1898, p. 584), and others have generally assumed that this investment is the amnion, but such an interpretation would appear to be incorrect. It is well ascertained that in Cicadidae the membrane we have described ensheathes the limbs separately (Snodgrass, 1921, p. 405). It is true that Fabre describes only the front legs as free, and the other four as enclosed beneath the common envelope, but it would appear more correct to describe them as fastened with their sheaths to the sides of the body. Such a condition opens up the question whether the membrane may not be an embryonic moult rather than a true amniotic envelope. Thus Williams and Buxton* argue that the hatching membrane in a species of Mantid is a first larval cuticle, and not an amnion for the following four reasons:

- (1) It envelopes limbs and antennæ every one separately.
- (2) It is furnished with spines on abdominal and thoracic tergites.
- (3) Threads from the end of the abdomen pass through it.
- (4) It resists boiling in K O H and stains like chitin.

Snodgrass (l.c.) calls the membranes in question in Cicadidae, "embryonic skins," but does not commit himself as to their interpretation. Yet he notes their difference from the Orthopteran amnion.

Withycombe† inclines to think it an embryonic moult in Neuroptera, where the limbs are likewise individually ensheathed.

Henneguy (1904, p. 492) calls it *amnion* in Cicadidae.

Imms (1925, p. 226) follows Williams and Buxton in considering it a true nymphal cuticle as far as Mantidae are concerned, and in believing

"that the shedding of it constitutes the first ecdysis. An amnion on the other hand, encloses the insect as a whole in the form of a sac and does not envelope the appendages separately."

Finally, in the same sub-order as the Cicadidae, Gimmingham describes a similar membrane in Aphididae, which most previous observers thought an amnion, though Heymons considered it an

* Williams, C. B. and Buxton, P. A., 1916. "On the Biology of *Sphodromantis guttata* (Mantidae)." *Trans. Ent. Soc., London* (1916), pp. 86-100, Pls. 7-10.

† Withycombe, C. L., 1925. "Some Aspects of the Biology and Morphology of the Neuroptera." *Trans. Ent. Soc., London* (1924), pp. 303-411, ref. p. 315, illus.

embryonic moult. (Gimingham* decides that perhaps the presence or absence of individual sheaths for the appendages should constitute a fundamental criterion.

On this basis, then, the hatching skin is really the first nymphal cuticle. It is cast almost immediately the open air is reached.

“ Revenons à la larve. Un peu plus tôt, un peu plus tard, elle tombe à terre, soit par accident, soit par elle-même, L'infime bestiole, pas plus grosse qu'une puce, a préservé ses tendres chaires naissantes des duretés du sol au moyen de son cordon suspenseur [the broken embryonic skin]. Elle s'est raffermie dans l'air, moelleux édreton. Maintenant elle plonge dans les aprêtés de la vie ” (Fabre, p. 279).

The story that the plant-tissue which is the seat of oviposition supplies nourishment to the newly hatched nymph is without foundation. Only the briefest time elapses before it reaches, usually by falling, the ground beneath.

The most characteristic features of the young nymphs are the huge size and length of the antennæ, the great width of the pronotum—the most powerful segment of the body, and the compressed form (*M. leptomera*, fig. 84).

Snodgrass (1921b, p. 409) has made observations on freshly-hatched young placed on loose earth in a small dish. We have watched *M. leptomera* nymphs, supplied immediately after hatching, with sand containing roots of marram grass. Twelve were dropped on the surface of the moist sand. In five minutes six had disappeared from view. The remaining six were walking actively round, apparently exploring. When they came to a slight depression they began to burrow, but several entered holes where others were at work and came out again. Two burrowed down by the projecting marram stalk and several at the edge of the sand next the glass. When seen they were hidden as to the head and front legs, but the middle and hind pairs were pressing sideways and backwards respectively. The last of the twelve had disappeared completely beneath the surface within ten minutes.

In some cases these early burrows were only an eighth to a quarter of an inch deep; in others they were already three inches deep at the end of twenty-four hours and impinging on the bottom of the tube.

* C. T. Gimingham, 1926. “ On the Presence of an Egg-burster in Aphididae.” *Trans. Ent. Soc. London* (1925), pp. 585-590, 2 figs.

CHAPTER X

LATER LIFE-HISTORY

Are you not he, cicada,
Of whom I have heard told you can transform
Your body, magically moulding it
To new estate? Are you not he who, born
Upon the dung-heap, coveted the sky,
The clean and open air;
Found wings to mount the wind, yet skyward sailing
Upon a leafy tree-top checked your flight,
Pleased with its trim retreat?

OU-YANG HSIU (A.D. 1056). Translated by Arthur Waley.

WE have seen that the family Cicadidae, as exemplified by the imagos, is a remarkably homogeneous one. Shall we not seek the root of this uniformity in the unvarying feeding-habits and monotonous habitat of the often excessively prolonged pre-adult stages? Be this as it may, the nymphs are even more alike than the adults.

A newly-hatched nymph of *Melampsalta leptomera* is shown in figure 84 and a final instar, drawn from the exuviae, in figure 85.

Incidentally it may be mentioned that the nymphal exuviae, found adhering to tree-trunks and fences wherever cicadas are numerous, are delightful objects of study, not only from the viewpoint of cicada anatomy, but also from that of general insect morphology. They possess all the advantages of caustic potash preparations for the study of exoskeletal structures, and none of their disadvantages.

We have seen that the Greeks early realized the earthly origin of cicadas and recognized the nymph as τερτίγομήτρα or cicada-mother.* The first description of a nymph is perhaps that of Putius in 1721. A few words on this uncle if not father of tettigology may not be out of place. It appears that Girolamo Laurenti (Hieronymus Laurentus) made observations on the sound-organs and habits of the adults, and deputed Pozzi (or Puzzi, or Putius) to study the eggs and nymphs (worms), which he did in considerable detail, communicating both his own and Laurenti's results to the Real Accademia delle Scienze dell' Istituto di Bologna as early as 1721. Apparently they were not however published until ten years later;

* Kolenati (1857, p. 428), with unexpected incomprehensibility, would attempt to derive the second element from μέτρον, mensura.

when F. M. Zanotti incorporated them in a paper appearing in the *Commentarii* of the Accademia.

Numerous later authors have described the nymph of the European species (chiefly *Tibicen plebeia*), notably Réaumur (1740) and Fabre. Swammerdam (1737) was perhaps the first to see that *Tettigometra* "vera Cicadarum *Nympha* est" (p. 215)—that is to say, he went further than a recognition of the first as an instar of the second, to an attempt to classify the type of metamorphosis involved.

Marlatt has given a very detailed study to the nymphs of *Magiccicada septendecim* (1907, p. 118 *et seq.*) while Silvestri (1921) has well described and figured these of *plebeia* and *orni*. Lyle (1910) does likewise for *Melampsalta montana*. Schumacher describes in detail the last nymphal exuviae of the Oriental *Huechys sanguinea* (de Geer), (1917a). Packard (1873) illustrates the "pupa" of *Tibicen pruinosa* (fig. 144) and of *Okanagana rimosa* (Say), (fig. 145). The first and last nymphal instars of *Tibicen viridifascia* (Walk.) have been excellently described and figured by Osborn and Metcalf (1920). *Melampsalta argentata* (Ol.) has received some attention in its nymphal stage, from Brown (R., 1900), while Kuhlitz describes very exactly intermediate and full-grown nymphs of *Ueana dahli* (Kuhlg.) from the Bismarck Archipelago. Kirkaldy (1909a, p. 181) remarks that nymphs of *Cryptotympana* show clearly the metasternal tubercle so characteristic of the adults in this genus. Kirby (W. F., 1889, p. 554) does little more than mention an extremely hairy "pupa" from Christmas Island, belonging probably to *Platypleura calypso* (Kirby). Froggatt (1907), Musgrave, Tillyard (1926) and Myers (1921a) figure between them the nymphs of two Australian and one New Zealand species.

The nymph of *Tettigarcta* was figured with the type of the genus at the time of its erection (A. White, 1845), and illustrations of nymphs of a few other cicada species occur in the literature. Gadd (1908b) gives a few notes on the last stage nymphs of *Cicada orni*, *Cicadatra hyalina*, and *C. atra*, as well as on those of *Tibicen plebeia* and *Cicada orni*. An undetermined Cameroon species is described and figured by Melichar (1914a), and the nymphs of *Huechys sanguinea* are described by Maki.

This is a remarkably poor list when we consider the abundance of the nymphal exuviae whenever cicadas are at all plentiful. Two factors have, however, militated against the advantageous treatment of this material—firstly, the usual impossibility of ascribing it to a known species and secondly the paucity, supposed or actual, of taxonomic characters. We have been delighted to find very good characters in the armature of the fore-femora (figs. 89–97), which we feel confident will enable us to separate all the New Zealand species, congeneric though they be. It is difficult, however, to catch an example of every species in the act of emerging, and yet this is the only way by which authentication can be rendered exact.

A cicada nymph at any stage may be recognized by the following general characters: The form is characteristic as shown in the figures (84, 85); and the colour very pale. The head is conical, much more produced than the adult's, and the rostrum long and

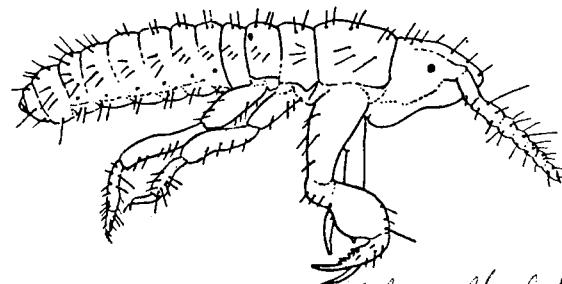


Fig. 84. *Melampsalta leptomera*

stout. The antennæ are long and stouter than those of the adult, being proportionately very large in the first instar, and in all lacking differentiation into peduncle and flagellum. Ocelli, or rather their future position, are marked in the later stages by faint reddish spots.

The thorax shows greatest development in the prothorax, probably in correlation with the powerful fossorial fore-legs. In later

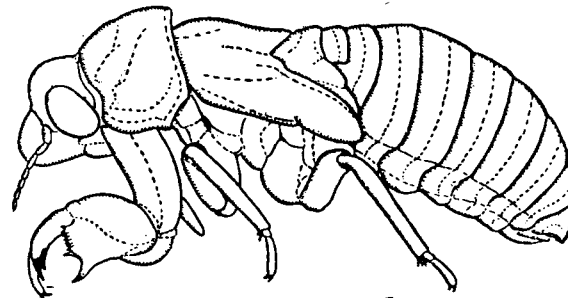


Fig. 85. *Salm...*

instars the wing pads are conspicuous. The abdomen is much swollen save in newly-hatched young, and very distinctly segmented. The spiracles are visible laterally in the first instar, but later are completely hidden by "pleural" flaps (fig. 86), which are apparently an adaptation to subterranean life. These flaps are well-developed in *Melampsalta leptomera* and in most other species examined, but are absent in *Tettigarcta crinita*. Heymons would appear to refer to them on page 422 (1899) in discussing *Magiccicada septendecim*.

Long hairs beset not only the head and body but also the legs. Of these latter, the second and third pairs are relatively unspecialized

while the first are highly modified. The tarsi of the second and third pairs are two-segmented, but the basal joint is extremely short.

The claws (figs. 87, 88) are fused basally and one is shorter than the other.

In *Tettigarcta* (fig. 87) the smaller claw appears only a process of the other. The fore-legs shows a very great lengthening of coxa

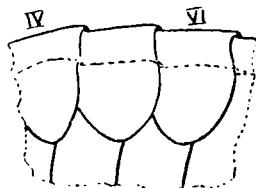


Fig. 86.

and trochanter, and a huge development of the femur, which is supplied ventrally with a long, often toothed spine and distally with a toothed, sharp, laminate edge which meets the equally sharp ventral edge of the tibia with a scissor-like action; in fact, Berlese (1909, p. 215) believes it actually functions as such an instrument. I have not seen the record of an eye-witness. Similarly the femoral spike meets the tip of the tibia to form a pincer-like organ. In the newly-hatched young (first instar unless we count the embryonic

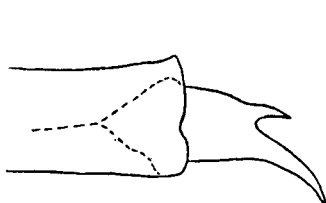


Fig. 87.



Fig. 88.

moult) the fore-legs have well developed and actively functional tarsi, and the same may be said of the ultimate instar. The intermediate stages, however, show only the merest rudiments of an organ which would probably be of little use in the burrows. In the first and last nymphal instars on the contrary, clawed tarsi are an essential for climbing. Kunckel d'Herculais (1879) claims to have been the first to describe the tibial groove in which this tarsus is folded back before the last instar emerges from the earth. His species was *Tibicen plebeia* (Scop.), (*fraxini*), which would appear to have a greater developed groove for this purpose than other cicadas since in *Magicicada septendecim* (Marlatt) and in the New Zealand *Melampsaltae* the tarsus is merely bent back against the face of the tibia.

The number of the antennal segments varies in the different species, even in the same genus. Thus *Magicicada septendecim* has seven, while *Tibicen linnei* S. and G. has eight (Marlatt, 1907, p. 118). In *Tettigarcta crinita*, last nymph, there are nine, and in *Melampsalta ochrina* there are signs of a ninth, but in *M. cingulata*, *M. sericea*, and *M. scutellaris* there are eight, in *M. leptomera*, and the closely-allied *M. cruentata* only seven.

The best character for separating the instars of a given species and the species of a given genus lies in the armature of the fore-femora, as recognized by Marlatt for two or three North American species and as shown in our figures (89-97), where all the species of which

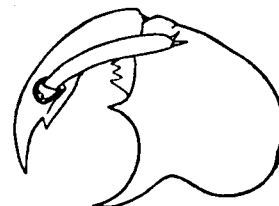


Fig. 89.

authentic nymphs are known in New Zealand are readily distinguished. Fabre has noticed, and we have confirmed the fact, that the eyes in exhumated nymphs are dull, opaque white, but in the nymph which rises of its own accord for the last ecdysis they are black and apparently functional. This change has nothing to do with the effect of light since it occurs in captivity sometimes a month before emergence (see later).



Fig. 90.

During the whole of the pre-imaginal development after hatching the cicada nymph stays beneath the surface of the ground. It is true that individuals in captivity will sometimes leave their cells and wander on the surface, afterwards burrowing again *de novo*, but such behaviour is probably occasioned only by artificial conditions since we have no record of it in nature, save as an immediate preparation for the last ecdysis.

We are therefore concerned to know the habits during subterranean life and the *modus operandi* of digging. Earlier mention has been made of the behaviour of freshly-hatched young. Nymphs of nearly all ages of *Melampsalta leptomera* have been kept without much difficulty in separate glass vials of sand, either sown with wheat or other grass-seed, or supplied periodically with fresh stems

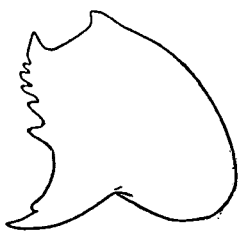


Fig. 91.

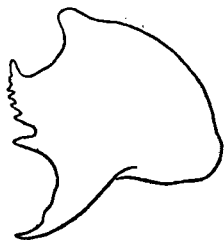
Melampsalta ochrina

Fig. 92.

Melampsalta scutellaris

or roots of marram grass. In several cases the imago was reared from fairly advanced nymphs. The insects were obtained in the fore-dunes at Wellington, New Zealand, at depths varying from four inches to two feet, but most were in the second foot, in pure, somewhat moist sand. Placed in tubes as described above, by the next morning all had burrowed to the bottom of the sand and were sitting in sometimes very spacious cells in many cases in contact with the root supplied.

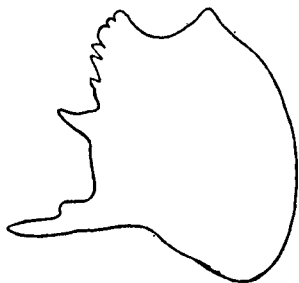


Fig. 93.

Melampsalta septendecim

Fig. 94.

Melampsalta septendecim

The above depths agree with those generally observed for *M. septendecim* (Marlatt, 1907, p. 124), but the same author records specimens on odd occasions taken at much greater depths, and instances one case where the "pupae" are reported to have "worked their way through a hard mass of cinders about 5 feet in thickness, which had been firmly compacted."

A female *M. leptomera* in last nymphal instar collected thus on 16th August was less active than some of the others. It would

sit for days in exactly the same position, in its cell, with the head nearly touching the root of marram, and the rostral setae inserted in this. The huge fore-femora were placed, and seemed to clasp, the root on each side of the rostrum. Later this cell was abandoned

Fig. 95. *Melampsalta crinita*

and another made, to tap the same root elsewhere. On 17th September it had begun to take on a slight brownish tinge, but the final ecdysis did not occur until 5th January, or some twenty weeks after collecting.

A male *M. leptomera* nymph, likewise in the last stadium and



Fig. 96.

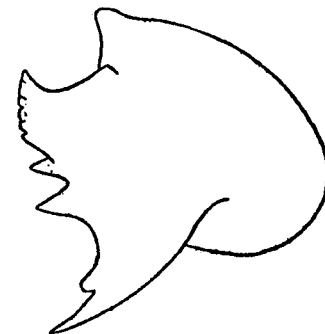
Melampsalta crinita

Fig. 97.

Melampsalta circinata

collected on the same date, emerged on the 4th December, and interested us by singing on the morning of ecdysis, a song different from that of the species in the field and later sung by this same one. This nymph showed a change in eye-colour from white to deep reddish on 7th November, or nearly a month before emergence.

Frequently the confined nymphs would build several cells connected by tunnels in which they were often seen moving—whether backwards, forwards, upside down or right way up seemed quite immaterial. No amount of shaking the tube would cause the cells or tunnels to collapse. Often there was a completely different set of burrows on two successive days.

The colour changes and times of emergence of the two nymphs already described and of a third may be tabulated thus :

- a. collected 18 August ; slightly brownish 17 September ; emerged as adult 5 January.
- b. collected 18 August ; deep brownish cream 17 September ; emerged as adult 20 December.
- c. collected 18 August ; deep reddish 7th November ; emerged as adult 4 December.

In digging the fore-tibia is used as a pickaxe and also as a rake for the loosened material. The strokes, as observed through glass, in *M. leptomera*, are surprisingly powerful and rather quickly repeated. Snodgrass (1921b, p. 385) describes the tarsus of the last nymph bent forward and used as a rake, but such usage would appear to be unessential since the intermediate nymphs lack functional tarsi. The same writer (l.c., p. 385) well describes the most characteristic part of the cicada's method :

“The little pile of rakings is grasped between the tibia and the femur, the former closing up against the ventral spines of the latter, the leg strikes forcibly outward, and the fistful of loosened earth is mashed back into the surrounding earth. The process is repeated, first with one leg, then with the other. The digging cicada looks like a pugilist training on a punching-bag. Now and then the worker stops and rubs its legs over the front of its head to clean them on the rows of bristles which cover each side of the face.—Thus, the secret is out, the cicada excavates a closed cavity by crowding the earth back into the surrounding earth.”

Fabre (ed., 1921, Chap. 14) devotes a fascinating chapter to the same process, showing, moreover, by very ingenious experiments, that in dry soil, the cicada secures the moist condition necessary for its peculiar method by means of the liquid stored in its swollen abdomen.

“Sous ses deux formes, la Cigale, malgré son tempérament sec, est un irrigateur émérite.”

Fabre (l.c.) describes the carefully constructed burrow in which the nymph of *Tibicen plebeia* awaits the moment when it shall emerge for its final ecdysis. This building of waiting shelter to serve until, as it has been suggested, meteorological conditions are favourable, is a peculiarity of cicada biology and takes extreme forms in *M. septendecim* and in some Oriental species.

Marlatt (1907, p. 91, Pl. II) gives a summary of observations on the peculiar “huts” or “cones” which the famous American species, under certain circumstances, little understood, builds as a sub-aerial extension of its waiting burrow. More recently Snodgrass has dealt with them. They were first mentioned by Potter (N., 1839), and later described by Rathvon, Riley, Davis, Lintner, Lander, and Lowe, all of whose reports have been admirably summarized by Marlatt and need not be discussed further here. Suffice it to say that these turrets may be as much as six inches high, built as mason-work, of pellets of moist earth brought up with the fore-feet. The exit-hole is at the base, but the cicada may often be surprised within the closed top. The structures may be extraordinarily numerous—as many as twenty-five to the square foot. They have occurred in especially great numbers on the floors of cellars and sheds, and over burnt areas following a forest fire. As we have had no experience of these structures we quote Marlatt's summing-up of the explanatory evidence (l.c., p. 96).

“A complete hypothesis, therefore, seems to be in a union of the explanations offered, namely, that the cone-building habit is induced either by a shallow soil, proximity of the pupae to the surface, or conditions of unusual warmth which brings the pupae to the surface in advance of their normal time, and more rarely to unfavourable conditions of excessive moisture. The mud caps are to protect the burrow from cold until the time of issuing arrives.”

Apparently similar turrets are described by F. Mason in Burma (1860, p. 355).

“One of the first objects that attracts the attention of an observer in some localities of the Karen jungles, is a clay tube several inches high, raised above a shaft sunk two or three feet in the ground, over which may be often seen a Karen, bending and inserting the extremity of a long branch of a thorny ratan, which after a few twists is withdrawn, bringing with it a grub that is deemed a great luxury. The natives have a distinct name for the grub, and seem to be ignorant that it is the larva of the cicada. This I was enabled to verify on one occasion by observing the exuviae of many of their pupae adhering by claws to the serrated back of trees, with rents in their backs out of which the perfect insect had escaped.”

H. M. Pendlebury (in Moulton, 1923, p. 107) describes similar cones in peninsular Siam.

"I noticed a number of little mounds of earth cast up on the jungle floor which at first sight resembled the beginnings of a termite mound. The average height of these was from 4" to 6", and their diameter at the base from 3" to 3½". These structures which were either shaped more or less like an inverted tumbler, or else like an inverted test-tube, were composed of earth to which apparently some secretion had been added to hold it together, and frequently fallen leaves and twigs were mixed up in its composition."

Beneath each was a hole some two to four feet deep and an inch in diameter. The passage, internally very smooth, was continued up into the mound to within about an inch of the top. Pendlebury ascribes these to the authorship of *Pomponia* spp., and notes that those still inhabited presented a fresh appearance, while old ones had an emergence hole at the top—not at the base as in *Septendecim*.

Schultze, as described in Melichar (1914a) found peculiar tubular earth structures made by cicada nymphs of unknown species, in inundated forest in South Cameroons. These were about 15 centimetres long, with an inner smooth canal, and reached above the surface of the water in the rainy season. Beneath the ground level they extended sometimes as much as a metre vertically downwards, to end in a simple or branched more or less horizontal canal.

ECDYSIS

Folliculos ut nunc teretes aestate cicadae
Linquunt sponte sua victumque petentes . . .

LUCRETIUS, *de Rerum Natura*, lib. 5.

Yo no naka yo
Kaëru no hadaka,
Sémi no kinu !

Naked as frogs and weak we enter
this life of trouble ;
Shedding our pomps we pass ; so
sémi quit their skins.

Japanese Buddhist poem, Hearn, 1900.

Concerning the final ecdysis of the Cicadidae much has been written: the process is fascinating, easily observed, and in the periodical cicada, highly spectacular when thousands are engaged in it at once. Aristotle was the first to record the fact that the newly emerged nymphs are moderately pale and rapidly become darker. Reichel's statement (1804, p. 54) is no advance on Aristotle. He says the "aurelias," when they first issue from the earth,

"are moist, soft, and of a whitish colour; but by the heat of the sun, they soon become brown, dry, and consistent; and after a few days (!), expand and produce the locusts."

Since Reichel almost countless descriptions have been published of ecdysis in *M. septendecim*, but the latest, by Snodgrass (1921b, p. 387, fig. 3, Pl. 2) is one of the most interesting.

Fabre deals with *Tibicen plebeia* (1921, Chap. 15), as also do most of the European observers. Gadd (1908a, b) observed this and several other species in the Crimea, notably *Cicada orni* and *Cicadatra hyalina*. Lyle (1913) carefully timed the emergence of *Melampsalta montana*—the only species available to English naturalists. Moulton (1911) gives notes on *Huechys sanguinea* in Borneo, while Dracott (1914) describes ecdysis in an undetermined species in Sikkim. Bell-Marley (in Distant, 1906b, p. 174) discusses *Pycna semiclara*, finding in one case a nymph cuticle thirty-five feet up in a tree, and others on stones and stems of herbs. Felt (1905, p. 237) gives a very good account of the emergence of *Tibicen linnei* S. & G. (*T. tibicen*). Froggatt (1903, p. 339) observed *Cyclochila australasiae*.

In perusing the available records one finds that in most countries and for most species observed the time of issuance from the ground, preparatory to the ecdysis itself, is evening, and the crucial period is passed under cover of darkness. This is abundantly testified, among the above observers, by American workers on *M. septendecim*; by Froggatt; by Pendlebury for *Pomponia* (in Moulton, 1923, p. 108); by Bell-Marley (Distant, 1906b, p. 174) for *Pycna semiclara*; and is also the rule for the Zew Zealand species so far studied. It is true that Hyatt and Arms mention one emergence (probably of *Tibicen linnei*=*tibicen* auctt. nec L.) at 1.40 p.m., but the only real exceptions to the above rule outside of Europe are furnished by Moulton in Borneo (1911b) who found *Huechys sanguinea* in process of ecdysis at 11.45 a.m. (though Maki saw emergence usually in the very early morning), and Dracott (1914) who discusses an unknown species in Sikkim. This Indian form was observed to emerge in thousands every year from the same plot of ground beneath a tree. All emerge at once, "one follows the other, with clock-like regularity, . . . when the sun is bright." (Italics mine.) Dracott states that the entire time from the issuance of the nymph out of the earth to the flying of the imago is only thirty minutes—a time so much shorter than that recorded for any other species that we wonder whether it is in any way, direct or indirect, associated with emergence "when the sun is bright," though *plebeia* emerging in daylight takes much longer.

European observers, however, report a surprising divergence which has been discussed by Gadd (1908a). *Tibicen plebeia* (Gadd, l.c.; Fabre; Krumbach; LaBonne), *Melampsalta montana* (Lyle, 1910 (testé Colthrop), 1913), *Cicada orni* (Gadd, 1908b), other unspecified Crimean species (Gadd, 1908b)—all these appear normally to emerge in the morning—*T. plebeia* usually about 9 a.m. and sometimes earlier, *M. montana* somewhat later in the morning. Gadd suggests that *Cyclochila* in Australia and *Magi-*

cicada septendecim in North America emerge at night as a protection from enemies in the open country which they frequent; but do they live in open country? Whatever the explanation, the fact is certainly remarkable that the time most frequently given for the emergence of *M. septendecim* (Marlatt and others) and for an Australian form—namely, 9 p.m.—should be exactly the opposite time of the day from that commonly mentioned for *T. plebeia* in parts of Europe as separated as Provence and the Crimea.*

The issuing nymphs require a firm perch for their final ecdysis. Fabre (1921, p. 243) has shown, with *T. plebeia*, that unless this is secured, the process cannot take place. From the accounts of eye-witnesses (e.g. Riley, 1885) the scurrying rush of thousands of *M. septendecim* nymphs to the bole of an especially isolated tree is a most remarkable sight. They swarm up the trunk and larger branches and come to rest finally even on the leaves. When the area occupied by a given brood has been more or less deforested since the last appearance, interesting developments may take place. Thus Claypole (1883) found emerging nymphs in a meadow, buried in grass knee-high, all making their convergent way to the stump of a solitary oak, *cut close to the ground* since their hatching. He claims that they could not see the remains of the tree and invokes "instinct." The case is unexplained but solitary.

The split usually—perhaps invariably—occurs along the mid-longitudinal line of the thoracic nota and along the arms of the epicranial suture. We describe subsequent events in *Melampsalta cinzulata*, from field notes made on 22nd January, 1924. The nymph was found between five and six feet up a tree-fern trunk, at 9.15 p.m. The head and thorax were already protruding at right angles from the vent in the nymphal cuticle, and were beautifully opalescent, pink on the future pale areas (hypoderm colours) and green on the dark ones (cuticular colours). The insect seemed to rise steadily from the case and the wings appeared, not as shapeless bags but as stiff-looking projections which lengthened imperceptibly, but yet with surprising rapidity, if the paradox may be excused. The latter showed green with pink tips. After a time they appeared to shorten instead of lengthening further, but this was caused by a folding of the wing upon itself. Much later, this fold disappeared and the wing extended again. Meanwhile the legs were gradually, very slowly, pulled out, or rather forced out in the upward progress which was caused apparently by the alternate swelling and contracting of the abdomen. The first pair of legs, when freed, were deliberately and frequently waved, bent and extended very symmetrically and rhythmically as though for exercise. As the legs became free the head and thorax leaned further and further backward and downward

* Since the above was written, Musgrave (1926) has described the emergence of another large Australian cicada, *Thopha saccata* which, in the two cases observed in detail, occurred during the morning.

until only the tip of the abdomen remained within the exuviae, and it seemed impossible that such a small purchase could sustain the weight at such an angle. The cicada hung thus for the longest stationary period observed, and the integument continued perceptibly to harden—the head particularly becoming conspicuously less tumescent. Finally, with surprisingly little apparent effort, the body began to rise again until the legs could reach and grip the exuviae somewhere about the head. Then the tip of the abdomen was quickly withdrawn and allowed to hang in a natural position, the pygophor fully exerted and the genitalia extended. The still opalescent but now plane and much lengthened wings were held flat in one dorsal plane over the back, like those of a Pyralid, and quivered at intervals. One hour had elapsed. In twenty minutes more the wings assumed the usual stegopterous position, and the process was virtually complete.

Mr. T. Cockcroft found *Melampsalta scutellaris* emerging in several cases at 9.50 p.m., the nymphs clinging to tree-trunks at a height of about four feet. One specimen observed at the time mentioned to have just released itself from the exuviae showed the wings fully extended at 11.25, but very damp and with a large drop of liquid retained at the adjacent tips. *M. muta* also emerges at night.

Snodgrass (1921b, p. 391) gives 45 to 72 minutes for the time in *M. septendecim* from the first split to the folding of the wings over the back. Riley (1885) gives 20 minutes from splitting to "full stretching of the wings in the flat position," but states that, under "precisely similar conditions," it may be five or six times as long. *T. plebeia* can fly three and a half hours after the beginning of ecdysis (Fabre, 1921, p. 242). For the same species Gadd (1908a) records complete pigmentation in three hours and ability to fly in twelve. La Bonne (1904) found an emerging cicada at 7 a.m. By 9 a.m. the wings reached the end of the abdomen, and at midday the insect could fly; but the full black pigmentation was not achieved till 3 p.m. Dracott (1914), as we have seen, records an undetermined Indian species as able to fly in 30 minutes; an observation which perhaps needs confirmation. Finally Lyle, studying *Melampsalta montana* in England (1913) noticed one example splitting at 11.42 a.m., folding its wings normally in 44 minutes and attaining full pigmentation at 2.20 p.m.; but a second, splitting at 12.5, folded its wings in only 29 minutes. These periods are much shorter in this form than in the New Zealand species which, as we have seen, emerge at night.

Cicadas of open country must necessarily dispense with tree-trunks and such supports at ecdysis, and we have found that *M. leptomera* will emerge successfully on a plane surface—sand or floor. *M. septendecim* sometimes chooses a queer support: as witness the pigs which Butler (A. W., 1886) records as returning from the woods

in the morning with nymphal exuviae securely fastened to the bristles of their back.

In only one case—that of *M. septendecim*—is there any information as to the number of moults. Riley originally postulated 25 to 30 changes largely to account for the wear and tear especially on the fore-legs, during nearly seventeen years of supposedly active digging. Marlatt examined the material which Riley had separated to illustrate these hypothetical stadia, and found that on sound morphological criteria, especially those based on the fore-femora, not more than six distinct instars can be recognized. Henneguy (1904, p. 497) repeats Riley's statement and numerous other writers (e.g. Folsom, 1909, p. 165; Packard, 1898, p. 616) have subscribed to the same opinion. Marlatt (1907, p. 116) recognizes four "larval" and two "pupal" stages, the pupa being distinguished by the perfectly developed fore-tarsus. Of the "second pupal stage" (l.c., p. 121) Marlatt writes:

"This stage does not present any differences from the last except in the greater size of the specimens, which is noticeable in the relative dimensions of the parts hitherto measured for comparison."

These differences are, however, by no means of the same order of magnitude as those separating Marlatt's other instars, and we believe that the "second pupal stage" is not distinct. There is no indication whatever that *M. septendecim* differs from the vast majority of other Hemiptera by undergoing more than five ecdyses. (N.B.—In this discussion we have not considered the embryonic moult described earlier in this chapter.)

Marlatt has admirably described and figured the earlier instars in the periodical cicada, of which an uninterrupted breeding record was secured by "sowing" literally cartloads of "darted twigs" beneath the oaks and other trees in the grounds of the Department of Agriculture at Washington, and digging up samples of nymphs at regular intervals. The only other successfully complete record we know is that of W. P. Fisher and his son as reported by Surface (1906a). Young from eggs laid in 1889 were reared in a zinc box sunk in the ground. In 1894 the five-year-old nymphs were the size of a grain of wheat, and in 1901 about half-grown. In February, 1906, the year of their expected emergence, the nymphs were apparently full-grown and bore well-developed wing-pads.

Actual observation of any of the first to fourth moults has apparently not been made in any species of cicada. An intermediate instar of *M. leptomera* kept for nearly five months as described above, changed its system of burrows, in the sand of its small vial, almost every day. In the whole period there was one intermission of four days, during which no alteration was made in the burrows, nor did the nymph appear in any of those visible from outside. On

the fourth day it appeared, looking somewhat larger, and immediately resumed its active habits. A moult may have intervened.

It is frequently stated that the Cicadidae exhibit a "quiescent, pre-imaginal instar" (Carpenter, 1921, pp. 181, 258; Henneguy, 1904, p. 420); but there would appear to be no foundation in fact for such a belief, and the term "pupa" should be deleted from Hemipterous horismology. Certain species build cones which have been interpreted as watch-towers, and perhaps all others remain for some time just beneath the surface awaiting a moment favourable for final emergence; but though perhaps not feeding, they remain active, upon occasion during this period, which, on all the evidence, is to be interpreted as influenced by external rather than by internal conditions.

That external conditions operate powerfully to influence the time of emergence is attested by several observations. Thus:

Schwarz (1890, pp. 230-231) found *Magiccada septendecim* emerging in a glade, strongly insolated, when none were yet doing so in the surrounding woods. He thinks it possible such a natural forcing might cause an emergence even a year earlier than usual.

Krumbach (1917), working in Istria, especially on *plebeia*, has a table showing soil temperatures at depths of 100, 60, 30 cm., air temperatures at the surface and at a height of 100 cm. These were correlated day by day with Cicadid activity. The first nymph emerged when the gradually increasing soil temperature, at the above depths, was 18.7° C., 21.6°, and 23.3° respectively, as compared with previous maxima, as it happened on the previous day, of 18.5°, 21.3°, and 23.2°. The last nymph for the season emerged the day succeeding the highest soil temperature observed at the 100 cm. depth. The peak of the air temperature at 100 cm. above the surface had been reached a week earlier. Marlatt (1907, p. 24) instances the appearance of *septendecim* a full year ahead of its time in green-houses which had been built over its usual area of emergence.

Krumbach has made (1917) interesting quantitative observations on *T. plebeia* during development. A freshly-emerged adult at 11.10 a.m. weighed 2.5 gm. At 1.15 great drops of liquid were shed, weighing in the aggregate .06 gm. The total loss in weight by 7.15 p.m. was .44 gm. A second example lost .41 gm. (initial weight 2.63), a third .45 (initial weight 2.46). The empty nymph case weighed .21 gm. Captured males weighed 1.03-1.75 gm. and females 1.50-1.80; a male dried in air, .5 to .6 gm.

SEASONAL AND CYCLICAL APPEARANCE

"Cicada aestatem praesagit certo," writes Aldrovandi. The swallows and the butterflies are much less reliable prophets; vigorous and tempestuous weather may yet occur after their

arrival, but "cum post Cicadae adventum, nunquam frigus rediisse visum est."

The close association of the cicada with the hottest days of summer and with the flowering of the scolymus, has been noticed in our opening chapter. "Phoebus himself loves thee" (Anacreon, Ode 43):

Soko no nai
Atsusa ya kumo ni
Sémi no koé.
SAREN.

(Fathomless deepens the heat; the ceaseless shrilling of sémi—
Mounts, like a hissing of fire, up to the motionless clouds.

HEARN, 1900.)

As a general rule, the further one leaves the Equator the shorter the season during which cicadas are seen. There is considerable variation among the species. Thus, for instance, in North America, the already anomalous periodical cicada has appeared, mated, oviposited, and disappeared almost before the larger forms, *Tibicen* spp., have entered the scene. In northern states the latter do not extend their seasonal range outside July, August, and September. In Florida the cicada season ranges from March to November inclusive. At least in a part of that state, then, cicadas are heard during all but three months, as in New Zealand. In Southern California they appear early, but often disappear in the dry season, even though it is warm (Mr. Wm. T. Davis, *in litt.*, 12 June, 1922).

St. George (1920) has given a very detailed table of phenological events accompanying the sub-aerial activities of *M. septendecim*. No adults sang until the daily temperature reached 60° F. The period from the first appearance of nymphs to the sound of the last adult male extended from 22nd May till 1st July. The observations were made in the District of Columbia.

In the tropics it would appear that the adults are confined in their activities chiefly to the rainy season, but how far this generalization may be extended I do not know.

In New Zealand the following data are available:

Melampsalta cingulata: November–April.
M. strepitans: October (J. F. Tapley)–February.
M. sericea: October–March.
M. cruentata: November–March.
M. leptomera: November–March.
M. muta: October–June.
M. m. subalpina: December–March.
M. m. cutora: November–May.
M. fuliginosa: February.
M. ochrina: December–June.
M. scutellaris: October–May.

M. cauta: November–March.
M. nigra: January.
M. mangu: December–January.
M. oromelaena: January–March.
M. iolanthe: November–January.
M. campbelli: December–March.
M. hamiltoni: November–January.
M. cassiope: December–February (Otago).
M. lindsayi: November–December.
M. maorica: December.

July, August, and September are thus the only three months during which no cicadas may be found in New Zealand.

It appears that the only definitely ascertained life-cycle in the Cicadidae is that of *M. septendecim*, with its famous seventeen-year period, believed to constitute a record in the Insecta. The very distinct broods into which the individuals of this species are divided, facilitated the accumulation of strong circumstantial evidence in favour of a seventeen-year cycle, and this was substantiated by two successful breeding records as previously mentioned.

Pontedera was responsible for the statement that one of the European species underwent a two-year cycle. This statement was repeated by Jaeger (1854), who used it in an attempted refutation of the theory that *M. septendecim* required seventeen years; and Jaeger's statement, according to Davis and to Ball (1920) is the foundation of the popular opinion that the North American species of *Tibicen* take only two years to complete their cycle. However, yearly observations by Davis (1925, p. 38) render it evident that a much longer period must be assigned to them.

Fabre states somewhat dogmatically with reference to *Tibicen plebeia*, "La Cigale reste quatre années en terre" (1921, p. 234), and Coupin (1898, p. 119), among others, has followed him, but there would seem no experimental foundation for the belief.

Schumacher (1924) mentions that there is sometimes a ten-year period in Cicadidae, but mentions neither species nor further data.

In New Zealand there is at least evidence for *M. cingulata* that the cycle requires more than one year (Hudson, 1919), while in Australia, Froggatt (1903, p. 339) believes that *Cyclochila australasiae* has a three-year period.

Innes (1915) gives circumstantial evidence that in Egypt *Cicadatra foveicollis* [*flavicollis*?] and *Hymenogaster planiceps* undergo a five-year cycle.

Finally there are several interesting references to phenomenal swarms of cicadas in Afghanistan and Baluchistan possibly indicating a long life-cycle. Hay (1840) described a tremendous irruption in treeless country in the Turnuk Valley about fifty miles from Kandahar. He believed three undetermined species were chiefly concerned.

"The prevailing colour was a deep orange, and the stems and branches of the tamarisk [bushes] were covered with them as hardly to be able to distinguish a particle of green, and their noise all day was unceasing. The jewassee bushes being at the same time covered with the empty scales of the pupae, and showing at once that these insects were bred on the spot: otherwise I should have conceived they were only migrating. Our tents and tent ropes as soon as pitched, were covered by these insects, in fact everything looked yellow. They continued in equal numbers for several days' march through the Ghiljie country, and I saw in all eight or nine different species."

At Quetta, in Baluchistan, McMahon (1910) saw in 1909 immense swarms of *Cicadatra (Psalmocharias) querula*, and stated that similar irruptions recur at intervals of about six years. Lastly, in 1918, at the same place, F. B. Scott (1919) observed a plague of cicadas (species undetermined).

"The trunks and branches of these trees were so closely studded with the cicadas that they appeared gnarled and discoloured. When a motor-car passed along the road the insects continually rose in a swarm, resembling a swarm of large bees. The ground on either side of the road was pitted with the holes of the pupae, and the empty pupal cases clung in dozens to every plant and shrub. In the evening the noise near the trees was deafening. . . . At about the end of June they began to die off, and the ground under the trees was littered with their bodies. Some of the smaller trees were so damaged by their attacks that they lost their leaves."

It would be extremely interesting to know whether the cicadas observed by these observers were the same species.

Kershaw (1897) records large numbers of *Cyclochila australasiae* and of *Psaltoda moerens* in the vicinity of Melbourne in the summer of 1896; but apparently not so extensive as those in Afghanistan and Baluchistan.

Champion (1911) saw *Melampsalta cantans* in Algeria, "so abundant as to remind one of the migratory swarms of a locust. They seemed to be travelling about the wastes, alighting in large numbers on our clothes and the seats of the carriage . . ."

We are concerned now to say a few words on the origin of broods in such a species as *M. septendecim*. American entomologists, and especially Riley and Marlatt have devoted much energy and research to the study of broods in this species—their distribution, limitation, and chronology. The result forms a chapter unique in entomological literature. Marlatt's enumeration, which recognizes thirty broods, is now generally accepted. The areas occupied by these have been mapped in the greatest detail and the time of their appearance can be predicted any number of years previously, with absolute exactitude. On pages 22 to 25 of his now classic bulletin on the periodical

cicada Marlatt (1907) discusses the origin of the broods. It appears that especially in the larger broods, odd individuals, owing apparently to slightly differential retardation or acceleration of development, appear in the season immediately before and that just after the main swarm.

"It is not difficult to imagine, therefore, that under exceptional conditions some of the earlier appearing individuals or the later ones may occur in sufficient numbers to establish a well-marked peculiarity in this direction and form a new brood appearing a year earlier or a year later than the original one" (Marlatt, l.c., p. 23).

"It is possible to conceive also of conditions which would result in the acceleration or retardation in the development of an entire brood or broods of the Cicada, such as variation in climatic conditions, geological changes, or changed conditions of the topography of the country, including the character of the vegetation" (l.c., p. 25).

F. M. Webster (1897) had a "suspicion . . . that a glacial period may have had its influence in retarding the development of the species for different periods of time, in different localities."

Perhaps the most interesting contribution on this puzzling question is that of Gossard (1917) who has made an attempt to show that the distribution of the broods in Ohio is directly influenced or even determined by the character of the soil. The first appeared probable from a comparison of a cicada-brood map with that of the soil survey of the state. Gossard writes:

"While their distribution may sometimes depend wholly or in part on other than the soil factor, I cannot escape the conclusion that this has been a potent cause in determining the limits of several of our Ohio broods. An alternative conclusion is that the causes that fixed the soil areas at the same time directly operated to determine the cleavage lines between the broods—to my mind a more improbable supposition" (p. 555).

A line drawn roughly down the middle of the state divides off three large soil areas on the west and two on the east. The same line forms the boundary between the Brood V of Marlatt (most recent appearance, 1914) and Brood X of Marlatt (most recent appearance, 1919). Thus the western boundary of Brood V coincides with surprising exactitude with that of the Volusia silt loam and the DeKalb silt loam. "In other words, this brood flourishes on the last two soil areas named and disappears abruptly and completely at the border" of the three western soil areas. This same western boundary of the brood agrees also with the western limit of the Waverly and Maxville shales, sandstones and limestones.

"The brood ceases abruptly at the eastern boundary of the dolomitic limestones which underlie the western half of the State."

Unfortunately for the explanation, however,

"there is no outstanding factor of difference between the soils on either side of the dividing line except that those east of the line are more likely to be acid than those west of it, and the underground drainage east of the line is somewhat poorer than west of it, producing a colder soil in spring. However, there are spots east of the line underlain with limestone just as west of it; and, so far as present knowledge enables us to speak, the cicadas appear over these at the same time and in the same numbers as over the surrounding sandstones" (Gossard, l.c., p. 558).

It seems to us that the influence, if any, is far more likely to be indirect, and exerted especially through the character of the vegetation. Gossard himself admits

"the fact that certain trees and plants are characteristic of each area. The chestnut tree is common over the sandstones but will scarcely grow in the western limestone section. Alfalfa and the clovers grow more readily in the western half than in the eastern" (l.c., p. 559).

SLEEP AND DEATH

Yagaté shinu
Keshiki wa miézu
Sémi no koé.

BASHŌ.

(Never an intimation in all those voices of sémi,
How quickly the hush will come,—how speedily all must die.

HEARN, 1904.)

We have tried to trace the life and activities of cicadas from the time of the fertilization of the ovum to the season of their appearance in the sub-aerial world. Leaving for consideration in a later chapter the song and the more complex elements of cicada behaviour, we deal here with their sleep and death.

Cold seems to be the chief factor in the torpidity which cicadas as a general rule take on after sunset. St. George (1920) showed that no singing occurred among *M. septendecim* until the daily temperature reached 60° F. Ordinarily this, like other species, sings only during the day, but when the temperature reached 60° in the night there were frequently full choruses then also—and song denotes the acme of cicada activity.

As early as 1801 Herr Kanonicus Trost observed the sluggishness of cicadas in the very early morning and attributed it to sleep. After discoursing on the difficulty of capturing *Melampsalta tibalis* he says:

"Wer aber Zeit und Gelegenheit, die ich in meinem Stifte nicht

habe, benutzen kann, dasselbe in der Morgendämmerung aufzusuchen, der kann es leicht und häufig noch schlummernd finden und fangen" (Trost, 1801, p. 65).

On a far other horizon Morrill (1915, p. 35) dealing with *Tibicen cinctifera* (Uhl.), a serious cicada pest of olives, citrus and cotton in Arizona, recommends hand-picking of the insects in the orchards in the early morning.

In New Zealand, the usually very wary *Melampsalta cingulata* has been found at dusk on an autumn day (25 March, 1921) to allow handling without attempting to fly. The evening was cool.

Whether such a comatose state should be called "sleep" is a question.

We have seen that the season of the adults is sometimes very short, but concerning the individual span of life in the imago there appears to be no information in the literature. It is possible that the individual cicada lives throughout the period of imaginal appearance.

This is corroborated by the large numbers of dead or dying cicadas which appear relatively suddenly towards the end of the season. Such have been abundantly described by writers on *M. septendecim*, where, however, the phenomenon is so much associated with *Massospora* fungus infestation that the element of natural death may be obscured.

We have, however, already seen that F. B. Scott (1919) described the ground littered with dead bodies at the end of the cicada swarm observed by him in Baluchistan. This, for lack of evidence to the contrary, may be considered natural death—the termination of the cicadan equivalent of three-score and ten. In New Zealand, where startling irruptions of cicadas do not occur, the phenomenon is less remarkable. Nevertheless in March (in the Wellington district) it is a common occurrence to find cicadas on the road, lying apparently helpless, sometimes with one or more wings torn, but often quite perfect. We note *Melampsalta ochrina* as occurring frequently in this condition; *M. muta* much more rarely and *M. scutellaris* often. With regard to *M. cingulata*, on 28th March, 1921, the road along the west shore of Lake Wairarapa, overhung with trees, was strewn with large numbers of both sexes, for several miles. The night had been cold, and the cicadas were in a comatose state, but recovered in our boxes later in the morning. A little later in the season, and a little colder the night and doubtless the coma becomes death itself. Thus Figuiet (1872, p. 107) writes, probably of *Tibicen plebeia*:

"When one walks along the outskirts of woods as early as the month of October, in the South of France, one finds the soil covered with dead Cicadas."

CHAPTER XI DISTRIBUTION

“Der Aufschwung der ökologischen und biologischen Forschung hat uns gelehrt, die Zusammensetzung der Tierverbände einer Gegend nicht bloß als Zufallsspiel zu betrachten, sondern in der Gegenseitigkeit von Lebensgemeinschaften, Biocönosen, eine Vereinigung von Lebewesen zu sehen, die ihre Zusammengehörigkeit durch ihr Zusammenleben dokumentiert und die überall dort wieder in gleicher Zusammensetzung anzutreffen ist, wo äusserlich die gleichen Faktoren der Umwelt sich zusammen finden.”

E. HANDSCHIN, *Schweiz. Entom. Anz.*, Nr. 6-8, 1923.

OF the some 1500 species of cicadas the *Oriental region* contains the most, but it is extremely difficult to draw a line between this region and on the one hand, the Australian, on the other the Palaearctic. A very characteristic group is formed by *Dundubia* and its allies, a very highly specialised but dominant type, with the sound-organs completely covered, the opercula reaching their maximum length and the tegmina with the nodal line reduced to a minimum. The largest (*Pomponia*, *Tacua*) and most brilliantly coloured cicadas in the world occur in this region. Distinct and peculiar groups are typified by *Tosena* and its allies, with opaque brightly coloured tegmina; by *Huechys*, remarkable for its “warning” colouration and peculiar odour; and by *Mogannia*, with its narrowly-produced head, and usually well-marked nodal line.

Breddin (1901) postulates a system of land-bridges by which predominantly Australian forms have filtered into the Oriental region even as far north as the Philippines. He instances one supposed chain of related forms, beginning in Australia with *Cystosoma* and leading northward via Thursday Island, New Guinea, Mysol, and the Celebes, in the shape of insular species of *Prasia*. Representative Oriental genera are: *Cosmopsaltria*, *Platylomia*, *Gaeana*.

The *Australian region* is remarkable for two features—the presence of a great wealth of primitive (*Tettigarcta*) and highly specialized forms (*Chlorocysta*, *Cystosoma*, etc.) and for the dominance of the small cicadas of the genus *Melampsalta*, the most widespread genus in the family, here reaching its maximum. *Melampsalta*, in a confounding wealth of species, is the cicada par excellence of the xerophytic plains of Australia. The same genus extends to New Zealand, where several species have become thoroughly adapted to rain-forest conditions.

The New Zealand cicada fauna is wholly endemic and it has been

suggested that this fauna is derived from an immigrant species resembling *Melampsalta sericea*, entering the north. So far as the cicadas are concerned New Zealand must be considered only a subregion of the Australian, from which it differs negatively in the paucity of species and especially of genera, as compared with the extraordinarily rich and varied cicada fauna of Australia, and positively in the development of two types which are found in *Melampsalta* nowhere else in the world. The first type is exemplified by *M. cutora* and *M. ochrina*, vivid green species closely associated with the evergreen shrubs in which the New Zealand flora is so remarkably rich, e.g. *Veronica* (*Hebe*), *Coprosma*, *Olearia*, *Metrosideros*. The second type is furnished by the high mountain cicadas associated with conditions which do not recur anywhere else in the Australian region save possibly in the mountains of New Guinea.

Other representative Australian genera, are *Thopha*, *Cyclochila*, and *Macrotristria*, which represent an Oriental element in the fauna. The highly anomalous *Heteropsaltria* belongs to the Solomon Islands, while *Moana* is peculiar to Samoa.

The *Neotropical region* is in many respects the converse of the Oriental. It is poor in those forms with completely covered sound-organs which are dominant in the latter, but it is extremely rich in the subfamily Cicadinae (Gaeaninae Dist.), and furnishes also the most primitive cicadas outside Australia. These form the subfamily Tettigadinae, the members of which, remarkable for the possession of an accessory stridulatory area on the mesonotum, are predominantly open country (pampas and steppe) forms, while the characteristic neotropical Cicadinae—*Fidicina* and its relatives—reach their highest development in the rain-forest. *Melampsalta* is absent. Representative genera are *Tettigades*, *Chonosia*, *Dero-tettix*, *Fidicina*, *Proarna*, *Quesada*, *Zammara*.

The *Nearctic region*, with *Tibicen* and *Okanagana* dominant, is not rich in cicadas. It is remarkable chiefly for *Magicicada septendecim*, with its unexampled cycle of 17 years.

The *Ethiopian region* is characterized by the dominance of *Platycleura* and related genera with a strong tendency to platyptery and a corresponding broadening of the body. *Tettigomyia*, *Xosopsaltria*, *Inyamana*, *Saticula*, and *Gazuma* form a peculiar group. The Malagasy cicada fauna is extremely rich and peculiar, and perhaps supports the view that Madagascar should be considered a separate region. Jacobi (1904c) remarks that the Ethiopian cicada fauna is remarkably homogeneous, so that one cannot even make a division between south and tropical Africa. The same author discusses the northern limits of this region. North of the Sahara, of course, Palaearctic genera and even species predominate. Egypt, nevertheless, has several peculiar forms, e.g. *Hymenogaster*.

The *Palaearctic region* is not difficult to divide from the Ethiopian, but from the Oriental the demarcation is very indistinct. The

cicadas of Japan have a very Oriental flavour, as exemplified by the presence of *Platypleura*, *Cosmopsaltria*, *Cryptotympana*, *Pomponia*, *Terpnosia*. Yet *Melampsalta* is present—a genus almost lacking from the Malayan subregion of the Oriental region. The dominant and only widespread genera of the Palaearctic region as a whole are *Melampsalta* and *Cicadatra*. *Tibicina* is well-represented, while the three species, *T. haematodes*, *Tibicen plebeia*, and *Cicada orni*, are the cicadas of settled country throughout southern Europe. *Melampsalta montana* extends the furthest north (61°), (Sahlberg), and breaks the family record for distance from the Equator. In North America the northward range is nothing like so great, and cicadas are rare in Canada. *M. montana* is the only species of the family to reach England, where it is confined to several localities in the New Forest, with one record for Surrey.

Ethological distribution : Within a given area or within the range of a given species, the distribution of cicadas is by no means continuous. Their ethological distribution is far more clear-cut and specific than a non-specialist in the group is apt to expect. But Dufour nearly a century ago drew attention to the sedentary habits of cicadas, while classical literature affords several explanations ranging from purely mythological to semi-scientific, why “*ubi non sint et ubi sint*.” Thus the silent or more probably absent cicadas of the Rhegian bank of the River Halex were attributed by one account to the curse of Hercules, whom they kept awake by their song (Solinus) and by another (Strabo *et al.*) to the dense shade which prevented their singing “membranes” from becoming dry enough to operate. Such is perhaps the first recorded problem in the ethological distribution of insects.

Aristotle (*Hist. anim.*, lib. V., cap. 30) says that cicadas cannot breed where there are no trees; and of these they love olives best because they cast less shade.

Aelian (*De natura animalium*, lib. V., cap. 9) is much interested in cicada distribution :

In Cephalenia fluvius est, qui inter cicadarum sterilitatem et copiam medius interfluit.

He would give the mute cicadas of Rhegium a more naturalistic explanation than the story of the Heracleian curse :

Fluvii igitur ersi inter Rheginos et Locros medii ripae non dimidio jugeris spatio distant, tamen neutrae transvolant cicadae.

One of the fathers of American entomology, Asa Fitch, observed under rather exasperating circumstances the predilection for trees in the case of *Tibicen superba* Fitch. The misrelated participles of his account reproduce the confused emotions of the occasion so forcibly that we are impelled to a fuller quotation than is scientifically necessary. This new species

“occurred upon two small elm trees growing two rods apart, beside a brook in the middle of a prairie, with no other trees near. . . . On climbing one of these trees the cicadas, of which there were a number of individuals, all flew to the other tree; on climbing this last they all flew back; so that on climbing one tree three times and the other twice, but a single specimen could be captured, so shy were they.” (Fitch, 1856, p. 41, footnote).

The literature on this side of cicada natural history is scanty and random in the extreme. So far as concerns other species than the periodical cicada of North America, the only workers to deal with it systematically have been Gadd in the Crimea (1908a, b), Krumbach in the Istrian Peninsula and Marshall (1897) in Mashonaland. Matsumura has given a few brief notes on Japanese cicada ethology (1898, 1907), while single species have been studied in this regard by Lyle (*Melampsalta montana*), and by Osborn and Metcalf (*Tibicen viridifascia*). Apparently the first to deal with ethological distribution of Homoptera at all intensively was Sahlberg (1871) in the introduction to his *Ofversigt*, but unfortunately this careful observer was largely outside the geographical range of cicada distribution. We have followed especially the distribution of New Zealand cicadas.

In the light of such fragmentary knowledge it is useless to attempt a systematic review of the species on which observations have been made. We may rather arrange the scattered data according to the distributional factors concerned. Of these the nature of the vegetation would appear to exert the most powerful influence. We shall discuss the character of this influence later. Essentially tree-haunting species are the following :

Tibicen olympusa (Walk.) sings commonly in the tops of young pine seedlings, Florida (Dozier, 1920, p. 359; listed as *Cicada sordidata* Say).

Meimuna opalifera (Walk.) has a predilection for willows in Japan (Matsumura, 1898).

Tanna japonensis (Dist.) occurs often, in Japan, in dense forests where but little sunlight penetrates (Matsumura, 1898). So also does the related *Pomponia fusca* (Ol.), (Matsumura, 1907, p. 100).

Terpnosia vacua (Ol.) is so restricted to pines that its Japanese name—*Matsumushi*—is based on the association (Matsumura, 1898).

Tibicen flammata (Dist.) in Japan, on the other hand, prefers oaks.

Cosmopsaltria bivocalis Mats., in Formosa, sits under *Pandanus* bushes—a position which renders its capture with a net extremely difficult (Matsumura, 1907, pp. 97–98).

Koma bombifrons (Karsch) is a tree-haunting species in Mashonaland which does not greatly discriminate between the plants it frequents (Marshall, 1897); but several other species, according to the same author, are strictly confined to special kinds of trees. We

may instance the following, while regretting that the author gave only the native names of the trees concerned :

Taipinga nigricans (Stål) is confined to the smoother trunks of the *mosassa* tree ;

Platyleura marshalli (Dist.) occurs only on the smaller branches of *mopai* trees, where it is extremely difficult to see ;

Platyleura centralis Dist. prefers the main trunk of the *mfuti* tree, where it is very cryptically coloured ;

Ioba leopardina (Dist.) is more catholic in its tastes, but frequents chiefly *machabel* ; while the next species,

Ioba horizontalis (Karsch) sits high in the branches of the same tree.

Psaltoda moerens (Germ.), a black Australian cicada, seems to prefer the white trunks of the "apple gum," *Angophora lanceolata* (Froggatt, 1903, p. 340).

Cicada orni L. ; olive gardens (Krumbach ; Lucas, H., 1849, p. 102 ; Swinton, 1908, p. 380, and other observers), pines (Krumbach, Swinton), (Byron's "people of the pine,") *Juniperus excelsus* (Gadd, 1908a, in Crimea), ash (Fabre, and numerous other observers), poplars (Swinton, 1880, p. 26), carobs, and "agaves" (Lucas, H., 1849, p. 102).

Cicada orni sits very high up the trunk and is strongly protectively coloured on old olive branches with their numerous peeling bark-flakes (Krumbach) and on juniper bark (Gadd). Schugurov (1906) lists it as ampelophagous in Russia.

Magiccicada septendecim (L.) is, of course, essentially a forest species, with perhaps a preference for oaks.

Okanagana rimosa (Say) was found by Van Duzee in California (1916, p. 245) usually perched at least 15 feet up in trees ; but Osborn (1896) records it as sometimes very plentiful in the Middle West, on prairie land remote from timber.

Melampsalta montana (Scop.) would seem to favour pine trees, usually the lower branches (Lyle, 1910, 1911, 1913). Nymph cases have been found attached to grass blades or more often to bracken stems, where also copulation has been observed. Gadd (1908b) collected it on trees of moderate height in the Crimean forest—as also the next species, **Melampsalta adusta** (Hagen).

Melampsalta radiator Uhl. is confined to the stems of pines in Japan (Matsumura, 1898) ; and finally

Melampsalta argentata (Ol.) occurs in Southern Tyrol almost only on oaks (Milde, 1865). In New Zealand **M. cingulata** (F.), **M. scutellaris** (Walk.), and **M. cauta** Myers are essentially forest species.

Cystosoma saundersi Westwood in Australia, occurs especially in orange orchards but also on weeping willows (*Salix Babylonica*), (Froggatt, 1903, p. 422 ; Bennett, A. W. Scott).

Large tropical cicadas are usually recorded as singing from trees,

but such records are not often specific for the cicada and still less for the tree concerned.

Graptosaltria colorata Stål shows a *penchant* for telegraph poles and fence posts—a habit derived from tree-haunting (Matsumura, 1898).

A transition to the cicadas of the open country is furnished by the shrub and low bush-frequenting forms which we consider now :

Tibicen plebeia (L.), the cicada of antiquity, though recorded by Fabre and others as singing on trees, is a much less arboreal species than *Cicada orni*. Krumbach (1917) found it especially on hill slopes in the Istrian Peninsula covered with evergreen bush-woods and with vineyards. But Gadd (1908b) states that it does not occur in vineyards in the Crimea. The oviposition hosts would appear to be almost entirely herbaceous. Krumbach (l.c.) notices a habit of perching on low posts and dry twigs, where it is quite conspicuous. Virgil's remark concerning probably this species, is ethologically sound—*et cantu querulae rumpent arbusta cicadae*—especially as the term *arbusta* is applied particularly to trees planted as vine-props. *T. plebeia* is listed as ampelophagous in Russia by Schugurov (1906).

But the true vineyard cicada is undoubtedly **Tibicina haematodes** (Scop.). References to this association are as numerous in European literature as those which characterize *orni* as the cicada of the olive gardens and pine plantations (Vogel, 1923, Tübingen ; Leydig, Würzburg ; Swinton, 1908, Southern Europe, and many other observers). *Tibicina haematodes* is listed by Schugurov as ampelophagous in Russia, where it is said to be widely distributed (1906). On the Istrian Peninsula it is the cicada of the summer-green bush-woods (Krumbach, 1917). Fabre (1921, p. 259) found it on hawthorn hedges in Provence.

Mogannia hebes (Walk.) frequents low bushes in Formosa (Matsumura, 1907, p. 102).

Cicadatra atra (Ol.), listed in Russia generally, as an ampelophagous species (Schugurov, 1906), in the Crimea, according to Gadd (1908b), occurs among the grasses round the vineyards, but not in the latter themselves.

Huechys sanguinea (de Geer) in the Malay Peninsula (Annandale, 1900 ; Gravely, 1915) flies about among low bushes in the open. In China it is fond of the tree, **Ailanthus foetida** (Porter Smith), and in Formosa of two species of **Glochidion** (Maki, 1921). In New Zealand **Melampsalta muta** vars. **cutora** and **subalpina** and **M. ochrina** are typical shrubland cicadas.

Melampsalta tibialis (Panz.) occurs on hazel bushes in the Southern Tyrol (Milde, 1806). Krumbach (1917) characterizes it as the cicada of hedges and waysides.

A cicada of unknown species was found in phenomenal swarms on

the tamarisk and "jewassee" bushes of treeless country in Afghanistan (Hay, 1840).

Chlorocysta vitripennis Westw. frequents low scrub and is easily captured by shaking the bushes (Goding and Froggatt, 1904, p. 660).

Cicadas of open country have been mentioned as follows :

Tibicen chiricahua Davis frequents treeless plateaux in Navajo county, Arizona, perching almost only on or near the tops of clumps of a large, heavy grass (Davis, 1925, p. 40).

Tibicen viridifascia (Walk.), the salt-marsh cicada, occurs commonly on the coast of the south-eastern United States on the "tall dense grasses" of the beach itself.

"They were especially common on the so-called Sea Oats (*Uniola paniculata*) which grows luxuriantly on the higher sand dunes on the Wrightsville Banks (North Carolina) . . . one male observed singing was clinging to a stem of the sea oats about five feet from the ground, head up and abdomen well elevated. Several other males were flushed from a coarse, densely matted, short grass which grows near the edge of the water at low tide. . . . All the females collected were found in this latter locality. . . . A close examination of the stems of the sea oats revealed characteristic cicada egg punctures. . . . The nymphal cast skins were found in various situations, clinging to the sea oats on the higher sand-dunes, clinging to the short grass at water edge during low tide and in the drift cast up by the waves. Some, if not most, of the nymphs must pass their underground life in the between tide zones and be subject periodically to submersion during the incoming tide" (Osborn and Metcalf, 1920, pp. 248-249).

In another paper the same observers note that

"in many instances the specimens taken were at points evidently below the high tide level. Pupae were found in considerable numbers attached to the grasses well below the level of high tide and very evidently where they had been attached for the emergence of the adults. Holes were observed at points well below the high-tide level which had every appearance of being the openings from burrows which had been occupied by nymphs as they were in the same localities where exuviae were clinging to the stems of grass. Further, there were many pupal cases in the drift and these would appear much more likely to have come from a level below tide than above as otherwise it would have been necessary for the cases to have been dislodged from the grass and blown to the surface of the water. From these observations we feel warranted in the conclusion that the nymphal stages of this species are passed in soil that is for a large part of the time under water, in fact only exposed at times of low tide" (Metcalf and Osborn, 1920, p. 109).

Okanagana synodica (Say) frequents grassy plains in Colorado (Putnam, 1881).

In Formosa the little cicadas of the genus *Mogannia* are largely taken by sweeping herbage (Esaki, Maki).

Platypleura stridula (L.). This South African species, belonging to a genus almost exclusively tree-frequenting, is plentiful on the Rand (Transvaal) on plains where trees are completely absent (Pead, 1910). It would be interesting to know whether elsewhere this species perches on trees. Dr. E. D. Ball, well known for his intimate acquaintance with the habits of North American Homoptera, informs me that the various species of prairie cicadas in the Middle West never settle on trees even in areas where these have been extensively planted.

Taipinga consobrina Dist. is similarly very plentiful in the Transvaal in areas completely destitute of trees (Pead, l.c.).

Okanagana gracilis Davis occurs on bare rocks, Gulf of California (Van Duzee, 1923, p. 168).

Cicadatra hyalina (Fabr.), in the Crimea, frequents grasses and other herbs, such as *Scrophularia* sp. in pastures and woods, and on the borders of vineyards (Gadd, 1908a, b).

Cicadatra querula (Pall.), in the Crimea as elsewhere, is essentially a member of the steppe fauna, entering the mountains hardly at all, even where conditions appear relatively similar (Gadd, 1908a).

Melampsalta leptomera Myers and to a less extent *M. cruentata* (F.) are New Zealand sand-dune species. *M. strepitans* haunts rocky coasts and river-beds; *M. muta* open country generally, as does *M. sericea* in the north.

Melampsalta cantans (Fabr.) and

Melampsalta aestuans (Fabr.), (*algira*), in Algeria show a predilection for thistle stems (Lucas, H., 1849, p. 103).

Froggatt (1901, p. 7) mentions that

"in the coastal districts [of Australia], the most prominent forms [of Homoptera] are the large Cicadas, or 'Screech Bugs,' as the Americans call them, but they disappear inland, only the smaller species belonging to the genus *Melampsalta* being common."

The coastal regions are of course more or less forested, while the central areas are largely arid.

Data on altitude as a factor in cicada distribution are scanty. Hopkins (1898) found in West Virginia about three and a half days' difference in the time of the first general appearance of *Magiccicada septendecim* for each degree of difference in the average summer temperature between any two points in the state, whether the difference be due to latitude or to elevation. In West Virginia it appears confined to the Upper Austral and Transition life-zones; occurring very rarely in the Canadian life-zone which lies in this state above 3000 feet elevation.

Tettigarcta crinita Dist. is found on Mt. Kosciusko, the highest mountain in Australia, at an elevation of 5000 feet, which is still within the limits of large trees (Ashton, *in litt.*).

The highest record in New Zealand is that of *Melampsalta cassiope* taken on Mt. Ruapehu between 6000 and 7000 feet elevation (coll. T. R. Harris). This is over 1000 feet above the alpine line, and some 3000 feet higher than the upper limit of forest. In the South Island *M. nigra* has occurred at 5000 feet, which is ethologically, owing to higher latitude, the same altitude.

In South America *Carineta basalis* Walk. is met with in the Andes of Venezuela at an elevation of 9000 feet, while *C. fimbriata* Dist. ranges from 3000 to 10,000 feet in Ecuador (Distant, 1891b, p. 119).

Tettigades dumfriesi Dist. occurs on the Argentine side of the Andes at an elevation of about 6000 feet (Distant, 1920e, p. 169).

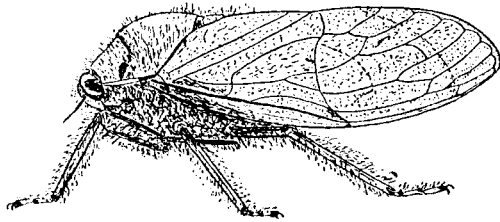


Fig. 98. *Tettigarcta crinita* Dist. from Australia.
J. G. M. del.

In North America *Tibicen chiricahua* Davis, already mentioned, is found in Arizona between 6000 and 6500 feet above sea-level (Davis, 1925, p. 40).

In Europe, the range is much lower. Thus in Southern Tyrol the highest altitudinal distribution is that of *Cicada orni*, at 3800 feet (Milde, 1866, p. 15).

Turning to Northern India we again soar to the heights. In the Himalayas Hooker (1854, II, p. 96), the botanist, found at least one of the large tropical species (undetermined) at an altitude of over 9000 feet. This, be it noted, was below the upper limit of heavy timber. In the same great range Hingston found a cicada ranging from "low lying valleys" to an elevation of 10,000 feet (1922). Thus the highest records known, one from the Andes and the other from the Himalayas, are identical—namely, 10,000 feet.

Another factor that may engage our attention a moment is that of sunshine and heat varying for other than geographical reasons. Captures of the larger cicadas, such as *Tibicen plebeia* and *Tibicina haematodes*, in the more northern portions of Europe are usually chronicled with considerable exactitude and many such records in German literature show that such stragglers are usually located in

sheltered districts with a predominantly southern aspect—spots where other southern insects, as, for instance, *Mantis religiosa* L., are occasionally taken. There is about such records, none of that appearance of accident which ordinarily accompanies the occurrence of a bird or even a butterfly species outside its normal geographical range (see Hueber, 1903; Kolbe, 1923; Scherdlin, 1910; Lienhardt, 1914).

Another, and somewhat specialized factor is considered by Forshey (1846) who found no periodical cicadas (*Magiccada*) in the alluvial lands of the Mississippi, and attributed their absence to long-continued inundations. This may well be the true explanation, since the ability of the salt-marsh cicada (*Tibicen viridifascia*) to withstand submergence (Metcalf and Osborn, l.c.) is no indication of a similar power in a normally dry land form like *M. septendecim*.

The only species in which some data are available on a combination of various ethological factors in distribution is *Magiccada septendecim*, which appears very irregular in local distribution, i.e. within the limits of a swarm.

"This variation in abundance is due in some cases to differences in the character of the soil and in others, perhaps, to varying surface conditions, as of timber growth, etc. They prefer, apparently, white-oak groves, and are most abundant where the land is high and well-drained and the subsoil a rich, sandy loam, with a sandy or soft clay subsoil . . . on Staten Island . . . the cicadas were very rare in sandy districts, while in districts less sandy they appeared by thousands" (Marlatt, 1907, p. 100; evidence of Wm. T. Davis and others).

We do not regard it as proved that the soil has a direct influence other than that exerted through the plant-associations.

CONCLUSIONS

It behoves us now to consider the possibility of drawing from the foregoing miscellaneous data general conclusions concerning the ethological distribution of Cicadidae and the factors influencing it.

Most of our information concerns the imagines only, or the nymphs indirectly through these. The subterranean life of the nymphal instars renders systematic observation almost impossible and we have no means of knowing whether the nymph exercises any selection among the roots of the plant species it encounters in its burrows. There is no evidence to indicate that its host-plants are more restricted in species than the flora of the immediate vicinity of oviposition. Most of the ethological distributional facts are doubtless to be explained by the habits and preferences of the adult.

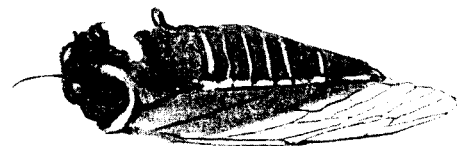
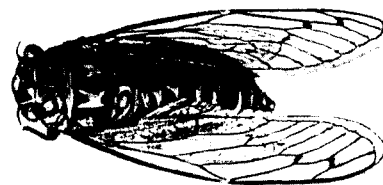
Here there is the difficulty of ignorance concerning the feeding-habits—such potent factors in many other insects. The discussion

in a previous chapter has indicated the mystery which from highest antiquity has surrounded the nourishment of adult cicadas. It is a considerable time since the dew hypothesis was seriously re-suggested, but barely twenty years have elapsed since it was believed for at least one species that the digestive tract of the adult was atrophied, while it is still claimed in certain quarters that the seventeen-year cicada, for one, takes practically no food in the imaginal state. There is proof, however, that numerous species feed regularly, and this coupled with the highly specialized and complex alimentary system and the very efficient mouth parts in all species dissected must render very strong evidence necessary to show that a given species does not feed.

Before it is possible to decide how great an influence is exerted on distribution by feeding-habits, the factors determining the latter must be considered. A discussion of this question occurs in the section on feeding habits, where the conclusion was reached that in Homoptera more than in Heteroptera and in Cicadidae perhaps more than in any other Homoptera, the environmental element in the choice was far greater than the botanical factor—i.e. the influence of the taxonomic relationships of the plant host or hosts. In other words, Cicadas choose places rather than plants; plant-associations rather than plant species. It might be suggested that given a selection or accidental adoption of a certain association by the ancestor of a species, the descendants remain in it because they were born there. This is really the naive explanation put in the mouth of *M. cingulata* by the Maori, "I cling to my ancestor, *Tane-mahuta*" (the personified form and tutelary deity of trees), and is not satisfying because under New Zealand conditions the associations are frequently so numerous in a small area, that the emerging adult has in many cases several different stations at hand, and it requires something more than mere location of emergence to explain the extraordinarily close restriction to some one of these. This "something more" has all the appearance of active and definite choice—instinctive if you will—but exerted not once nor twice in the life of the adult but crystallized into habitual preference.

This choice is influenced by at least two other imaginal activities besides feeding. The common perching place is not only a source of food; it is in fact predominantly a singing-stand for the males and a meeting-ground for the sexes. In the case of rock-living species it can in fact necessarily subserve only the second and third activities. Such species must leave the common perch to feed just as a trunk-haunting form like *M. cingulata* must depart to the thinner twigs to oviposit.

Unfortunately the oviposition habits are known only in *Melampsalta muta*, *leptomera*, *cingulata*, and possibly *ochrina*. Both the two former appear to be confined to herbaceous oviposition-hosts, while *M. cingulata* and probably *M. ochrina* are restricted to woody plants.



a. *Melampsalta muta subalbina* (Huds.) New Zealand, attacked by a giant dragonfly, *Uropetalala carotzi* Wh.
 b. *Cicada orni* L. Europe. Male.
 c. *Huechys sanguinea* (de Geer). Female. The Chinese medicinal cicada.
 All enlarged.

How far oviposition-hosts are constant in a given cicada species, whether botanically or ethologically the data are lacking to establish. The largest list is that of *Magicicada septendecim*, which, while preferring woody plants and using them in the vast majority of cases, descends also to herbaceous plants of every type; but too much emphasis should not be given to data regarding this species, in which the phenomenal swarms of its septendecennial irruptions produce strong competition and give scope for the appearance of every abnormality.

The occurrence in New Zealand of nineteen species of one genus filling every suitable ethological niche; and more forcibly, the converse case deduced from the literature, showing that tree-haunting species, open country forms and xerophilous types respectively may be drawn from almost any of the taxonomic divisions of the family Cicadidae, indicate that ethological station is not correlated save to the remotest degree with systematic affinity. There is perhaps a general tendency, both within a given genus, and in the family as a whole, for tree-haunting species to be larger than open country forms. The most highly specialized of modern cicadas, forming the subfamily Platyleurinae, are predominantly tree-dwellers, yet even here there is a xerophilous *Tibicen* in North America and a South African *Platyleura* living far from trees.

The Cicadidae are decidedly adaptive, but they have in no degree accomplished that conquest of freshwater stations credited to them by an enthusiastic if somewhat uncritical student of the group (Buckton, 1890). The Australian "aquatic cicada" mentioned by him as exhibited at the Entomological Society of London (Proc., pp. ii-iii, 1886) is an Orthopteron, *Tettix australis* (Walk.)!

The dependence of the various cicada species on definite plant-formations render them singularly susceptible to the changes brought about by colonization. In New Zealand I have shown that while the high mountain cicadas have been so far unaffected by settlement, the lowland ones have felt considerably the changed conditions. Thus the cicadas of open country have—in a country originally so heavily forested as New Zealand—had their range very materially extended, while that of the forest-dwelling species has been commensurately reduced. The shrublands cicadas, however, find conditions greatly to their liking in the large areas of cut-over land, second-growth, and scrub—not to mention gardens and plantations.

The only references I have been able to find on this topic concern the periodical cicada, which is apparently doomed to extinction with the disappearance of forests (F. M. Webster, 1897; Marlatt, 1907—summary) and two others (Goding and Froggatt, 1904, p. 570; and Leydig, 1902, p. 112), one in Australia, and the other in Central Europe. Goding and Froggatt state that the large *Cyclochila australasiae* is common in Sydney suburban gardens and has thus apparently in large measure adapted itself to altered conditions.

Leydig mentions the former abundance of *Tibicina haematodes* in the vineyards of Würzburg and adds :

“ Jetzt ist das Thier zur Seltenheit geworden und auch der volksthümliche alte Name ‘ Lauer ’ fängt an sich zu verlieren.”

This he attributes partly to the altered method of vine-cultivation, possibly to

“ allgemeine kosmische Einflüsse, da das Auftreten der Cikade immer mit wirklich guten Weinjahren zusammen fiel, solche aber seit Längerem ausgeblieben sind.”

A dismal picture is painted of the future of the famous periodical cicada. Will it too, disappear, like that other swarming inhabitant of the North American forests—the passenger pigeon? Wherever the woods are cleared it seems certain this cicada must go—and it is in just such places that the work of destruction is most assisted by the English house sparrow. Some of the well-recognized earlier broods appear now to be practically extinct—and each brood represents a definite and almost calculable proportion of the total strength of the species.

“ To the lover of nature there is something regrettable in this slow extermination of an insect which presents, as does the periodical Cicada, so much that is interesting and anomalous in its habits and life history. During the long periods of past time the species has recurred with absolute regularity except as influenced by notable changes in the natural topographical conditions and the despoliation of forests which has followed the path of settlement of the white man. It is interesting, therefore, in thought to trace the history of this species backward, taking, as time measures, its periodic recurrences, until in retrospect it is possible to fancy its shrill notes jarring on the ears of the early colonists or listened to in the woodlands bordering the ocean by the still earlier discoverers and explorers. Still more remotely one can picture its song causing wonderment to the savage Indians who attributed to it baleful influences, and yet, less dainty than their white followers, used the soft, newly emerged cicadas as food; or further back in time, when it had only wild animals as auditors. With these long-time measures our brief periods of days, weeks, months, and years seem trivial enough ” (Marlatt, 1907, p. 14).