PAPERS PRESENTED DURING 1922.

On the Classification of the Fulgoroidea (Homoptera).

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INTRODUCTION.

Stål has been justly styled the Father of Hemipterology, and the fourth volume of his Hemiptera Africana (1866) is still the foundation of the classification of Homoptera. Although the number of genera has increased greatly since then, yet the characters he employed in his classification of the fulgorids hold good for most cases today. The trouble has been that workers have disregarded his characters and placed genera in families where they should not be, and so they have broken down the family characters.

A contemporary of Stål's, F. X. Fieber, also laid us under a deep debt by his work. Although he based his work mainly on European species, it holds good today. In many ways he was more modern than Stål, especially in his specific work. His recognition of the value of the male genitalia for specific distinction placed the Delphacidae of Europe in a condition that no other method could have done. If we follow his lead and extend his work it will be to the advantage of Homopterology.

Another worker to whom we owe a debt of gratitude for the elucidation of the relationship of the families of Auchenorhynchous Homoptera is H. J. Hansen. His work[1] has shown the morphological distinctions between the different groups and has placed these divisions on a safe foundation. That I do not agree with him, in regarding the fulgorids as consisting of a single family, in no way implies that I do not appreciate or recognize his good work. His paper should be in the hands of every student of Homoptera.

Melichar has compiled monographs of seven of the families

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[1] Entomologisk Tidskrift XI (1890), pp. 19-76, Pls. I, II. Partly translated by Kirkaldy, The Entomologist, April, 1900, p. 116, et seq. I have not used all of Hansen's characters and must refer the reader to his work.

of Fulgoroidea, viz., Flatidae,[1] Acanaloniidae,[1] Ricaniidae,[2] Tropiduchidae,[3] Dictyopharidae,[4] Issidae,[5] and Lophopidae.[6] By so doing he has placed all Homopterists under obligation. Workers may wish at times that he had been more critical in his treatment of some groups and had used more fundamental characters for his subfamilies and tribes, but this in no way detracts from our obligations to him for his great industry.

Kirkaldy died before he had matured his views. Had he lived I feel sure he would have eventually produced a classification worthy of his labors.

Many workers have added to the number of genera and species during the last decade, but in most cases their contributions to the broader aspects of classification of the fulgorids have not been great, and in some cases their work has been inimical through their having placed many genera into wrong families.

The present paper is but an incomplete resumé of what is at present known on the subject of the families of the fulgorids. If it enables younger workers to recognize them, work upon their better characterization and to arrange more adequately the genera which compose them, then it will have served its purpose. I also hope that it will convince workers that the divisions are distinct enough to be recognized as families. This latter has a practical as well as a theoretical bearing, for workers are often more careful to place their genera into the right family than they are to place them into the right subfamily. It would also have the advantage of enabling the Recorder to segregate the genera into families in the "Zoological Record" instead of lumping them all together.

I have also used some of the information that I have accumulated on the male genitalia. The characters found in these organs are without doubt the most valuable aids to specific work. Not only do they show the specific differences, but they

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1 Ann. des K. K. natur Hofmus Vienna (1902).

2 t. c. XIII (1898).

3 Verh. Natur. Verin. Brun (1914).

4 Abh. K. K. zool. bot. Ges. Wien VII (1912).

5 t. c. (1906).

6 Ann. Mus. Nat. Hist. Hung. XIII (1915).

indicate the specific relationship better than any other characters. They are also of value for generic purposes and, so far as I have observed, are of use in the separation of families. By the study of these organs I believe that we shall eventually have a much better idea of the relationship of the families than we have at present.

The female genitalia may have equally good characters, but my knowledge of these at present is too limited to allow me to generalize upon them. I hope to be able to do so at a later date. The only generalization I can make at present is the distinction between complete and incomplete ovipositors.

Among the Fulgoroidea some of the chief characters used for generic purposes are the shape of the head and thorax and the number and arrangement of the carinae upon them. These characters, I believe, are liable to independent origin in different species, and so some of our genera may have a polyphyletic origin. Some of the families as they now stand are also likely to have a polyphyletic origin. The further study of the male genitalia is likely to show this, and will lay the foundation upon which a more natural grouping of both species and genera is likely to be erected.

The Order Hemiptera.

The Order Hemiptera or Rhynchota forms a large, homogeneous, and monophyletic group of insects characterized by the shape, position, development, and function of the mouth organs. Although there exists some difference of opinion as to the minor details of the homologies of the head and mouth parts, the fact has been established by embryological studies that they are built upon a normal, mandibular type, and that the alteration takes place during the development of the embryo. It has also been shown that the mouth parts arise in a similar manner in both the Homoptera and Heteroptera.

The mandibles form long, thin setae; the maxillae during their development divide into two parts, one forming a long, thin seta and the other amalgamates with the head capsule; the labium is long and narrow, with its lateral edges curved upward, and meet together on the middle dorsal line, thus forming a split tube in which the setae rest. In the embryo the labium arises

as paired processes, which later on amalgamate; the evidence indicates that it represents the entire labium and not the palpi only. In many adult Heteroptera there are four divisions, which, by their position, are evidently homologous to the submentum, mentum, and ligula, the latter consisting of two segments which are probably the subgalea and the amalgamated paraglossa and lacinia. In *Belostoma* there is a pair of small, simple processes on the subgalea which are considered by some to represent the palpi. From the base of the mandibles a sulcus has sunk into the head running toward the antennae, and the head capsule has grown over the base of the mouth parts. This obscures the homologies. Although the order is very large and the head undergoes great changes in the various groups, yet the shape, arrangement, and function of the mouth organs remain more constant than in any other of the larger orders of insects.

By the character of the mouth organs the Hemiptera are distinctly separated from all other insects. The Thysanoptera come nearest to them, but they are so distinct that they can have no direct phylogenetic connection, only an indirect one, through a remote common ancestor from which both may have evolved along somewhat similar but distinct lines. The Psocidae possess a semi-free maxillary rod, which may be the starting point of the maxillary seta, but they can only be related through a very distant common ancestor. The similarity between the wings of Psocidae and Psyllidae is due to convergence or parallel development, and has no phylogenetic significance. If the Mallophaga have any relationship to the Anoplura, then the latter can have no relationship with Hemiptera. The sucking mouth of the Anoplura appears to be built on a very different plan from that of the Hemiptera, and the Siphunculata most certainly are very different. I consider that the Hemiptera are the most isolated of all the large orders and their origin is obscure.

That such highly specialized mouth organs, with their special line of development going back into the embryo, could have originated independently in two or more different groups, is highly improbable, so we must, therefore, consider the Hemiptera to form a monophyletic order, very ancient and very isolated. That they are ancient is demonstrated by the fact that in the Trias of Australia the divisions of Cicadidae, Cercopidae,

Cicadellidae, and Fulgoroidea were well established; and one of the oldest fossil insects, *Prosbole* of the Permian, can be placed in the existing family Tropiduchidae.

During the course of insect evolution a number of attempts have been made to produce a piercing and sucking mouth. For perfection of mechanism none surpasses, nor even equals, that of the Hemiptera. This may account for the constancy of type through such a long period of time and in such a large group.

With the exception of the Thysanoptera and Anoplura, where the mouth parts are much more generalized, the Hemiptera is the only order of ametabolus insects with a complete piercing and sucking mouth, and the only order in which such a type of mouth arises in the embryo.

There are a number of types of venation within the order, but I know of no one character, or group of characters, by which all can be separated from all other orders.

The Two Suborders.

The two suborders, the Heteroptera and the Homoptera, are divided mainly on the shape of the head and the position of the labium. In the Heteroptera there is a well-developed gula, which is very long in some groups; the head projects forward and the proboscis is bent at its base and lies under the head when at rest. In most of the Heteroptera there are four segments to the labium, but in some the mentum and submentum are fused, thus making only three segments. In the Homoptera the gula is absent or represented only by a small membrane; the head is deflexed and inflexed so that the base of the labium is in intimate connection with the prosternum; the submentum is membraneous, and in many forms the mentum is reduced. The labium, when at rest, projects backward between the legs, more or less in line with the head, and is not bent at a sharp angle to it.

Of the two suborders the head of the Heteroptera appears to me to represent the more generalized type. Whether the primitive Hemiptera had its mouth organs deflexed beneath its head or standing straight out, it is difficult to judge. The highly developed mouth organs of the Heteroptera of today are not the primitive type of the order. This was evidently a more general-

ized type from which both suborders evolved, the Heteroptera retaining certain of the more primitive characters.

The distinction between the two suborders generally given in text-books, of the "beak" arising from the front or back of the head, is incorrect. The "beak" arises from the same place in both suborders, but in one the gula is large and the head straight out, while in the other the gula is small or absent and the head turned under.

My objection to considering these two suborders as distinct orders is that, by so doing, we divide a monophyletic group and make the same distinction between them as we do between them and Coleoptera and other orders. The characters of the tegmina, upon which the two suborders are generally based, and upon which they are named, do not hold good, for some of the Homoptera are heteropterous and some of the Heteroptera are homopterous. If we use the venation to separate the two suborders, then we must be logical and divide the Homoptera into several orders.[1]

The Two Groups of the Homoptera.

The line of evolution of the head that has divided the Homoptera from the Heteroptera has continued within the Homoptera and divided them into two groups, the Auchenorhynchi and the Sternorhynchi. In the former, the labium, while being intimately related to the prosternum, is still in close relationship with the head capsule. In the latter, a portion of the head capsule, along with the clypeus, labium and tentorial structure, is more or less detached from the head capsule; the labium is in more intimate contact with the prosternum, and an invagination at the base of the labium penetrates the thorax and forms a setal chamber or crumena, wherein the setae lie coiled when at rest. In the Aphiidae and Psyllidae the relationship of these parts can be plainly seen, but in the Coccidae and some Aleurodidae the head is greatly reduced and the true relationship is lost or very obscure.

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[1] Dr. E. Bergroth informs me that the Heteropterous family Peloridiidae has no gular region, and that the labium is not bent at the base. This is a very interesting fact and I would like to examine one of these rare insects.

That the Homopterous head has departed further from the primitive type than the Heteropterous, or is more highly specialized, is the conclusion I have arrived at after a fairly extensive study; and that the Sternorhynchi have specialized along this line further than the Auchenorhynchi is a conclusion that appears to follow as a natural sequence.

The Sternorhynchi.

It is beyond the scope of this paper to enter into a discussion of the four families, or superfamilies, forming this group. That they are highly specialized in habit and structure, and that the latter is often specialization by reduction, soon becomes evident to the student. The one or two jointed tarsi, the reduction of venation, the simplification of the genitalia, and the reduction of head and thorax are all characters in question. To a certain extent these reductions of organs coincide with reduction of size and a sedentary habit. From my present knowledge I am convinced that these simplifications are specialization by reduction and not primitive conditions. It should be realized that ideas on this point are of importance, as they influence the whole conception of the evolution of the order.

The Psyllidae, as we know them today, are too highly specialized to form the ancestor of the other three families. This ancestor must either have been a much more generalized psyllid or a generalized aphid. The Coccidae are the extreme specialization of the group.

The four families, or superfamilies, that compose this group have been treated as suborders, and there is a tendency even to consider them as orders. When we examine the characters that are used to separate them it is found that they are very slender and not of sufficient weight to justify us in so doing.

MacGillivray[1] divides the order into three suborders, viz., Heteroptera, Homoptera, and Gularostria. He restricts the term Homoptera to the Auchenorhynchi, and the Sternorhynchi he terms Gularostria. The former he defines as follows:

"b. Antennae minute and inconspicuous, setiform or awl-shape; tarsi with three segments; prothorax large and conspicuous ..... Homoptera."

[1] MacGillivray, 1921. The Coccidae, p. 4.

The only one of these characters that will stand is the three-jointed tarsi. The antennae are never minute or setiform, and in many species the first and second segments are large, very conspicuous, and in some cases of peculiar shape. The arista or flagellum is thin, in some cases distinctly jointed, in others indistinctly or not jointed. The prothorax is sometimes small and not at all conspicuous.

Orders and suborders founded upon such trivial characters cannot take the same status as orders such as Coleoptera, Diptera, or Hymenoptera. It is, therefore, to be regretted that they are given ordinal or subordinal rank.

Some writers have derived the Psyllidae from a Psocid-like ancestor, and so, naturally, we must consider all the other Homoptera and Heteroptera as derived from the Psyllidae. In my opinion this is a reverse of the true order.

Auchenorhynchi.

This group is divided into two superfamilies, the Cicadoidea and the Fulgoroidea, upon a number of important characters. The small family Tettigometridae is of great interest, as it has a number of characters belonging to both groups.

Three ocelli are found in one family of the Cicadoidea, the Cicadidae, and also in the majority of one family of the Fulgoroidea, the Cixiidae. The latter fact is often lost sight of by systematists and phylogenists when discussing the Homoptera.

In the Cicadoidea the antennae have only a few sense-organs situated on the flagellum; in the Fulgoroidea they are numerous and generally of a complex nature, and mostly situated upon the second segment.

In the Fulgoroidea the middle coxae are articulated considerably apart and have considerable range of movement; this is similar to the condition of the front legs of most insects and of all the legs in such primitive insects as *Machilis*. In the Cicadoidea the middle coxae are much nearer together and their movements very limited, which we must consider as a specialization. In the Cicadoidea the hind coxae are mobile; in the Cicadidae and Cercopidae they are small and do not reach the lateral margins of the thorax, whereas in the Membracidae and Cicadellidae they are wide and reach the lateral margins of the

thorax. In the Fulgoroidea the hind coxae are immobile and their exterior part is coalesced with the metathorax.

In all the Cicadoidea, with the exception of the Cicadellidae, and in all the Sternorhynchi, one finds a wonderful arrangement of the alimentary tract whereby the posterior portion of the mid-gut is brought into intimate contact with part of the crop. This allows certain of the more fluid contents of the crop to pass through the walls of the crop and mid-gut by osmosis, the more solid portion passing through the intestine and undergoing digestion. The fact that the Membracidae possess a filter or colum and the Cicadellidae do not, although they are otherwise so closely related, is difficult to account for. The simplest way would be to consider that they have lost it since parting from the main stem. But we have no evidence at present that they have, so we must give this distinction weight when considering phylogeny. The Fulgoroidea and the Heteroptera possess no sign of a filter.

In the Cicadoidea and in the Delphacidae and in part of the Cixiidae the ovipositor is complete, the anterior and middle pair of processes (the latter amalgamated into one in whole or in part) are fastened together by a tongue and groove so that they work as a single organ. In the remainder of the Fulgoroidea and the Sternorhynchi the ovipositor is greatly reduced or incomplete, the anterior and middle pair are not co-ordinated, and often the three pairs are rudimentary or are entirely absent. The complete ovipositor is the primitive type among the Homoptera. The incomplete ovipositor often has secondary adaptations for cutting into plants for depositing their eggs.

The male genitalia are much more complex and difficult to understand. Our present knowledge stands as follows:

The genitalia of the sexes are homologous in so far that they arise from similar processes situated in the same position on the abdomen. Their relationship is as tabulated below, where g 1 is the anterior, g 2 the median, and g 3 the posterior processes or gonapophyses.

Female	Male
g 1. Guides of ovipositor	Genital plates, often amalgamated to pygofer
g 2. True ovipositor	Aedeagus
g 3. Ovipositor sheaths	Genital styles

The pygofer of the male is formed of the ninth tergite, together with the coxites (or endopodites) of the eighth sternite, except in the Cicadidae. In the Cercopidae, Membracidae, and Cicadellidae the anterior processes (g 1) are often free, broad plates (the genital plates of systematists). These are sometimes joined together for most of their length and amalgamated to the pygofer, but they are distinctly present in some form. In the genus *Tettigometra* g 1 are well developed and distinct as in the families above mentioned. In all other Fulgoroidea they are generally indistinguishable, having been completely incorporated into the pygofer, or they form comparatively small processes on the pygofer. In the Cicadidae the coxites and eighth sternite form a large plate, the hypandrium, below the pygofer, and the pygofer is membraneous along the median ventral surface. The genital styles (g 3) are well developed and articulate in all the families with the exception of the Cicadidae, where they are rudimentary and fixed on the sides of the pygofer. They are large and complex in some Fulgoroidea. The aedeagus in its simplest form appears to consist of a swollen basal portion, the periandrium, and a more distal portion, the penis, which is generally tubular. But this organ is the most polymorphic of all the genitalia, and in the fulgorids forms good distinctions between some of the families. In some male fulgorids the eighth abdominal sternite is distinct and free from the pygofer, in others it is closely attached to the pygofer and in still other species it is amalgamated to the pygofer and not recognizable as a separate sclerite.

The Families of the Fulgoroidea.

Although I fully recognize the value of Hansen's work, yet I am compelled to differ from his conclusion that the thousand and odd genera of the Fulgoroidea form but a single family. The external characters that separate these genera into groups are much more distinct than many ofttimes used in other orders for the erection of families, and in most cases these characters are supported by good distinctions in the male genitalia.

In discussing the venation of the Fulgoroidea, Metcalf [1] remarks: "While the wing venation of most of the insects that

[1] Ann. Ent. Soc. America, VI, 3 (1913), p. 343.

have been studied extensively so far can be reduced to a more or less uniform type for the family, in the Fulgoridae no such typical form can be given." The same might be said of any group if some fourteen families were thrown into one, and is, in itself, a sufficient reason to indicate that we are dealing with a number of families.

The classification of the Homoptera is founded upon other characters than wing venation, but a type of venation can be recognized as pertaining to most of the families. If we were to make a classification upon venation alone, without any knowledge of the rest of the insect, as we are forced to do with fossil Homoptera, it would be very different from our present one. The Sternorhynchi would have no connection with the Auchenorhynchi; the Psyllidae would be placed next the Psocidae if not with them; some of the Flatidae would be placed among the Cicadoidea because the claval veins do not form a Y; such forms as *Tessitus insignis* Walker would also be placed with them, perhaps to form a distinct family; the Tropiduchidae, as we know it now, would form several families not closely related; the Derbidae would be considered as several families and some placed with the Cixiidae; the Delphacidae would be treated as Cixiidae, and most of the other families would be changed considerably. Pterologists might maintain that such a classification would represent the natural order of things better than the present one made by entomologists. It demonstrates the great care necessary when basing conclusions upon a few fossil wings, for similar deceptions as the Psyllidae and Psocidae may have existed in the past, and we have no means of recognizing their existence.

But as fossils are the only direct evidence of the time sequence of evolution we must take every advantage of them, and for this reason a closer study of the venation in each family must be made. Except in three families of the Fulgoroidea, I have not sufficient knowledge to make a close comparative study of the venation, but there are several points which require discussing before such a task can be undertaken with any satisfaction.

The two chief points are the status of the costa and the anal veins. Unfortunately, Metcalf[1] only traced the tracheae of the

[1] Ann. Ent. Soc. Amer., VI, 3 (1913), pp. 341-352.

fore-wings down to the alar bridge in three cases. In two of them, *Amphiscepa bivittata* and *Thionia simplex,* the costal trachea is shown arising from the bridge; in the third case, *Scolops,* it arises from the subcosta. In all the genera that I have examined so far the trachea agrees with *Scolops* and arises from the subcosta. In these latter cases the question arises as to whether this trachea is homologous with the costa. Tillyard [1] has shown that the Dipteron, *Comptosia* sp., has a distinct costa arising from the alar trunk and a humeral arising from the subcosta. He has also shown good reasons for regarding the humeral and Sc′ as homologous. If Metcalf had not shown that in two cases this trachea arises from the alar trunk, I should not hesitate to consider the costa as absent and the humeral (or Sc′) as present in all the fulgorids. While I shall use the term costa for this vein, I leave its true homology an open question whose solution will influence our conception of the primitive type of venation of the group.

By calling this vein the costa we are faced by the fact that, in a large proportion of the fulgorids, the costa vein and costa margin do not coincide, but the vein lies considerably within the membrane, leaving a precostal cell or *costal area.* This is a condition recognized in no other order of insects. In certain genera, such as *Xiphidium, Conocephalus,* and some *Blattidae,* there is a trachea arising from the subcosta, which appears homologous to the vein under discussion, but Comstock refrains from calling it a costa.

The second point is the supposed movement of A1 to Cu. This has been discussed by Tillyard,[2] and I consider that his contention, that Cu does have more than two branches, is more logical than the contrary. Metcalf [3] remarks that the Cu and first anal "are united for a short distance from the body trachea and cubitus is usually two-branched," but he gives no evidence to show that a branch of A moves over to Cu, but accepts it from Comstock and Needham.

The cubital system of the Homoptera, and also of the Corrodentia, is identical with that found in neuropteroid insects such

[1] Tillyard, 1919, Pro. Linn. Soc., New South Wales, p. 548, fig. 50.

[2] t. c., p. 570.

[3] Metcalf, Ann. Ent. Soc. Amer., VI (3), pp. 341-351 (1913).

as *Sisyra flavicornis, Polystaechotes punctatus, Chauliodes pecticornis, Hemerobius humuli,* and *Sialis infumata,* to name but a few. There is neither evidence of, nor necessity for, the crossing over of A1 to the Cu system. I have stated[1] that in the Delphacidae the suture was formed by the fourth cubital and first anal. This is incorrect, as it is formed solely by the posterior branch of the cubitus, as in all Homoptera, the first and second anal forming the Y veins of the clavus. In some fulgorids, i. e., some Fulgoridae, the third anal is present.

The absence of a distinct, free R1 in the adult tegmen is characteristic of most of the living Auchenorhynchous Homoptera, but it is found in the Mesozoic Cicadid *Mesogereon* Tillyard. The R1 trachea has been found in the early nymphal stages of Cicadidae and Membracidae, and it is probable that it will be found in the early nymphal stages of some of the Cixiidae.

The amalgamation of the bases of M and Cu appears to be characteristic of all recent Cercopidae and so cannot represent a primitive type, even in those forms in which Sc is normal. The venation of the Cicadellidae and Membracidae is too specialized to represent a primitive condition, and so is that of the Sternorhynchi.

I consider that the most normal and primitive type of venation of recent Homoptera is to be found among the Cixiidae. Here we find Sc, R, M, and Cu all arising from the basal cell and M with four normal branches. The genus *Andes* Stål has a venation of this type. The tegmina are steeply tectiform, the ovipositor is complete, and there is a median ocellus. But it has a typical fulgorid head.

In most Fulgoroidea the Y vein is present, but in some it is not; in the Cicadoidea it is never distinctly present. When not present in fulgorids they can be distinguished from Cicadoidea by the two claval veins passing out of the end of the clavus and not entering the hind margin before the apex of clavus, as they do in most Cicadoidea.

The interesting Mesozoic fossil genus *Ipsvicia* Tillyard has a Y vein, but otherwise it might be placed among some of the existing Cercopidae. I consider that it is closely related to the

[1] Muir, Pro. Haw. Ent. Soc., II (1913), p. 269, Pl. 6, figs. 1, 2.

Tettigometridae, and it cannot be considered as more primitive than some existing fulgorids. Handlirsch placed *Prosbole hirsuta* Koken in the Palaeohemiptera. Tillyard considered that it is not on the direct line of descent of the Heteroptera, but on a side line, nearly allied to *Dunstania* Tillyard, which he considered as in the direct line. In *Prosbole* the Sc and R are amalgamated to slightly before the node, a condition common in the Homoptera, but, so far as I know, not found in the Heteroptera. There is no sign of a median furrow, and the anal furrow is behind the cubitus in the normal homopterous position, whereas in the Heteroptera it is normally before the cubitus. As we have only the venation to judge by, I should place *Prosbole* among the Homoptera in the Tropiduchidae. The heteropterous condition found in *Prosbole* occurs in several genera of the Tropiduchidae, especially among the Tambiniini.

Fossil Homoptera are not very numerous, but the few we know, especially the Mesozoic, are of great interest. They demonstrate beyond any doubt the great antiquity of the order. In the Mesozoic Homoptera of Australia we find the two great superfamilies of the Auchenorhynchi completely established. The Cercopidae, Ciccadellidae, and Cicadidae are completely differentiated, and the Fulgoroidea are also represented. This indicates that we must go back far beyond that period for the origin of the order, or believe that evolution proceeded at a very much greater rate before than after the Trias.

The following table is not considered final, as further study in some of the families may change my views; and in the process of time, and with accumulated knowledge, some of them are sure to be divided. Neither is the table completely satisfactory, as the division between one or two of the families may not prove to be complete. Such a case is that between those Cixiidae without a median ocellus and with lateral carinae on the clypeus, and the Dictyopharidae. But the student soon becomes familiar with the facies of these insects and recognizes them at once.

TABLES OF THE FAMILIES OF THE FULGOROIDEA.

1. (2) Antennal flagellum segmented. No mobile spur on hind tibiae. Lateral ocelli not outside the lateral carinae of frons; lorae plainly visible in full view forming a continuous curve with clypeus ..... *Tettigometridae*

2. (1) Antennal flagellum not segmented. Lateral ocelli outside the lateral carinae of frons, generally beneath the eyes; lorae not visible in full view or forming an angle with clypeus.

3. (4) Hind tibiae with a mobile spur at apex. Tegmina without a costal area ..... *Delphacidae*

4. (3) Hind tibiae without a mobile spur.

5. (6) Three ocelli present..... *Cixiidae* in part

6. (5) Two or no ocelli.

7. (8) Posterior angle of mesonotum restricted off by a groove or fine line. Costal area present or absent..... *Tropiduchidae*

8. (7) Posterior angle of mesonotum not restricted off by a groove or fine line.

9. (10) Anal area of wings reticulate. Lateral carinae of frons continued on to clypeus. No costal area, or only a very narrow one without cross-veins. Clavus open, the Cu 2 (Claval suture) and claval veins continuing to apical or hind margin and often branched ..... *Fulgoridae*

10. (9) Anal area of wings not reticulate or, if so, then lateral carnae of frons not continued on to the clypeus.

11. (12) Face transverse or nearly as long as wide, lateral edges angular. Anal area of wings sometimes reticulate, in which case no lateral carinae on clypeus. With or without costal area. Clavus often roundly closed; claval veins reaching apex of clavus, the suture (Cu 2) and claval veins continuing to the apical or hind margin, and sometimes branched..... *Eurybrachidae*

12. (11) Lateral edges of face not angular or, if so, then face distinctly longer than wide.

13. (26) Tegmina without a costal area, or only a small one without transverse veins.

14. (19) Claval vein not entering apex of a closed clavus, but joining the commissure or suture before apex, or the clavus is open.

15. (16) Apical segment of labium short or very short (*Venata* an exception) ..... *Derbidae*

16. (15) Apical segment of labium much longer than wide, sometimes very long.

17. (18) Sides of clypeus acute or with carinae. Apart from the lateral edges, frons generally with two or three carinae.
Dictyopharidae

18. (17) Apart from the lateral edges, the frons with not more than one (median) carina. Sides of clypeus rounded, without carinae.
Cixiidae in part

19. (14) Claval vein entering apex of clavus.

20. (21) Base of abdomen with one or more appendages bearing three hemispheroidal depressions ..... *Achilixiidae*

21. (20) Base of abdomen without lateral appendages.

22. (23) Tegmina when at rest nearly horizontal or but slightly tectiform. Hind margin beyond clavus generally expanded, and when at rest overlap.....*Achilidae*

23. (22) Tegmina when at rest steeply tectiform; hind margin beyond clavus not expanded, and do not overlap when at rest.

24. (25) Tegmen large, tectiform. Hind edge of pronotum slightly roundly emarginate; mesonotum large, long. No spines on hind tibiae. *Acanaloniidae*

25. (24) Tegmina generally smaller. Head as wide, or nearly as wide, as the thorax. Posterior edge of pronotum straight, rarely slightly concave; mesonotum short. Hind tibiae with spines. Tegmina often coriaceous or subcoriaceous.....*Issidae*

26. (13) Tegmina with a distinct costal area with transverse veins.

27. (30) Clavus not granulate.

28. (29) Head wider than pronotum, seldom a little narrower, sides of clypeus often without carinae. Pronotum without carinae or with an obscure median carina; mesonotum very large; front legs simple.....*Ricaniidae*

29. (28) Head narrower than pronotum. Sides of clypeus with carinae. Pronotum with carinae. Front legs expanded.....*Lophopidae.*

30. (27) Clavus granulate. Apex of clavus sometimes blunt and closed, sometimes open. Claval veins separate or joined together at apex ..... *Flatidae*

I. Tettigometridae.

Tettigometridae Germar (1821), Magaz, Entom.; type **Tettigometra** Latreille (1804), Hist. Nat. Ins., 12, p. 312.

From the viewpoint of morphology and the relationship of the various fulgorids this family is the most interesting and important, although it is one of the smallest. Its synthetic characters make it hard to say whether it should be placed in the Cicadoidea or the Fulgoroidea, or whether it should be placed in a group by itself. For systematic purposes I have kept it in the Fulgoroidea because the majority of its characters indicate that to be its correct position.

Its cicadoidean characters are as follows: The arista of the antenna is segmented; the shape of the head is typically cicadoidean, the frons reaches from eye to eye without any lateral carinae dividing off a small area around the eyes (a continua-

tion of the genae) on which both the lateral ocelli and the antennae are situated; the lateral ocelli are present on the frons; the antennae are situated nearer together than the eyes and not distinctly beneath them; the lorae are plainly visible in full view and form a curve with the clypeal region; the middle coxae allow of very little movement in a transverse direction and, in some species, the male genitalia have the genital plates (g 1) well developed and free.

The fulgoroidean characters are as follows: The second segment of the antenna is large and bears large and comparatively complex sense-organs; tegulae are present and well developed; the posterior coxae are fixed; the spiracles are on the lateral areas of the abdomen; the empodium is free for the greater portion of its length, and its apex is not deeply emarginate; the tegmina have a Y claval vein.

The tegmina are small, convex, coriaceous and have a resemblance to the tegmen of Cercopidae. The subcosta and radius are joined to beyond the middle, the claval veins form a Y, and there are irregular cross-veins in the apical area.

In *Hilda breviceps* (fig. 2) the genital plates (g 1) are amalgamated to the pygofer, but are recognizable; the periandrium is semibulbous, large, and in contact with the base of the anal segment, which is very short; the penis is short and tubular, the apodeme of the penis is large. In *Tettigometra* sp. (fig. 1) the genital plates are large and free; the periandrium forms a large ring which touches the base of the anal segment; the penis is long, angular in middle, and has a large membraneous "sac" at apex; the anal segment is large.

With the exception of the female external genitalia, which are abortive, and the venation, all the characters of this family are primitive. Whether it represents the direct line of evolution from the precicadoidean type to the fulgoroidean, or whether it only represents an offshoot from the lower stem, it is difficult to say. But its cicadellian characters and the fact that the Cicadellidae have no intestinal filter, support the idea that the primitive cicadellian type was the starting point of the splitting of the group into two, and that the Cicadellidae are the more direct descendants from the primitive type, but do not now

contain all the primitive characters, and are highly specialized in certain directions.

It is interesting to note that the two types of male genitalia found in the Cixiidae are represented in the Tettigometridae by generalized forms, and so may go back beyond the Cixiidae.

II. Cixiidae.

Cixoides Spinola (1839), Soc. Ent. Fra., VIII, p. 202; type **Cixius** Latreille (1804), Hist. Nat. Crus. Ins., XII, p. 310.

This family contains from ninety to one hundred genera. Except in a limited manner in faunistic works, it has not been revised since 1866, when Stål tabulated thirteen genera. From a point of view of morphology and phylogeny it is of great interest, as from it, according to my views, the other families of the Fulgoroidea, with the exception of Tettigometridae, have most likely evolved.

The chief characteristic of most of the Cixiidae, but not all, is the presence of a third ocellus. Apart from this, the absence of certain characters separates them from other families. The tegmina have no costal area, or only a small one at the base, and then it has no transverse veins. The claval vein runs into the hind margin of the clavus or, in a few cases, into the suture near the apex; the clavus is closed. There is no mobile spur on the hind tibia. The apical segment of labium is distinctly longer than wide, generally of considerable length. When no median ocellus is present the clypeus is often destitute of lateral carinae. The frons never has more than three carinae, viz., the median and lateral.

At present I divide the family into two subfamilies, one of which can be divided into two tribes.

1. (4) Clavus not granulate.....*Cixiinae*
2. (3) No subantennal process and antennae not sunk into pits...*Cixiini*
3. (2) Subantennal process present or antennae sunk into pits. *Bothriocerini*
4. (1) Clavus granulate .....*Meenoplinae*

In many of the genera of the Cixiini the ovipositor is complete; in these cases the abdomen is generally considerably flattened laterally, the tegmina steeply or fairly tectiform, the pygofer longer than wide, with a depression down the middle

in which the ovipositor rests, and the hind tibia seldom has spines. In the other genera the ovipositor is incomplete and often considerably reduced, the abdomen is not flattened laterally but often flattened horizontally; the pygofer is flat, broader than long and covered with wax glands; the tegmina very slightly tectiform, and the hind tibiae often have spines.

In the normal type of aedeagus of the Cixiinae the periandrium is tubular, membraneous or chitinous, and often bears spines or other processes; the penis is often complex and large (figs. 7 and 8), or it is greatly reduced and difficult to separate as a distinct part of the aedeagus (fig. 25). There is a tubular apodeme from the base of the penis, passing through the periandrium and connected with the apodemes of the genital styles. The ejaculatory duct passes through this apodeme and opens on the penis. In the genus *Mnemosyne* Stål the periandrium and apodeme of penis are amalgamated into one and form a strong, chitinous mass, with, in some species, a small membrane at apex to represent the penis (fig. 3). The genus *Kinnara* (fig. 4) is the exception to this type.

In the Meenoplinae (fig. 6) and in the genus *Kinnara* (fig. 4) the periandrium is large, more or less funnel-shape, and the penis is drawn into it, the base of the penis often projecting through and beyond the base of the periandrium. The penis is sometimes also funnel-shape.

The Delphacidae, Derbidae, Tropiduchidae, and Achilixiidae have the aedeagus as in the Cixiinae, or modifications of it, while the other nine families have the aedeagus on the Meenoplinae type.

The fact that the Tettigometridae contain representatives of the two types of genitalia in generalized conditions indicates that the two subfamilies may have arisen among the precixiids, and should be regarded as distinct families.

Unfortunately for systematists we cannot use the absence or presence of spines on the hind tibiae, or the complete or incomplete ovipositor, to divide the Cixiini, as there are too many intermediate stages.

The family will be greatly enlarged by a slight amount of collecting in the tropics.

III. Delphacidae.

Delphacoides Spinola, Ann. Soc. Ent. Fr., VIII, p. 329 (1839); type **Delphax** Fabricius (1798), Ent. Syst. Suppl., p. 500.

This family has been neglected by most collectors, especially in the tropics, but at present it contains over ninety genera. It is recognizable from all other fulgorids by the presence of a movable spur on the apex of the hind tibia. It has been divided into two subfamilies and three tribes.

1. (2) Posterior tibial spur subulate, with cross-section either circular or angular, apex acuminate, without teeth on sides.....*Asiracinae*
2. (1) Posterior tibial spur cultrate, subcultrate or thin, with or without teeth on the hind margin.....*Delphacinae*
3. (4) The tibial spur cultrate, solid, both surfaces convex, distinct teeth along the hind margin.....*Alohini*
4. (3) Tibial spur thin, or if solid, then with the inner surface concave.
5. (6) Spur cultrate, solid but with inner surface concave, no teeth on hind margin .....*Tropidocephalini*
6. (5) Spur thin or foliaceous, sometimes tectiform, with or without teeth along the hind margin.....*Delphacini*

The female is furnished with a well-developed, complete ovipositor, and the eggs are laid in the tissues of the food plant. The base of the ovipositor is situated considerably anterior of the middle of the abdomen, and the pygofer is long and narrow, with a groove along the middle for the reception of the ovipositor. This makes the more posterior abdominal sternites more or less V-shape. The male has a well-developed pygofer, one pair of genital styles and an aedeagus consisting of a single tube which in some forms (Delphacinae) is simple (fig. 9) and in others (Asiracinae) complex, with a distinct penis and large periandrium (fig. 10). In most species there is no evidence of the anterior gonapophyses (g 1), but in others these are quite evident. The venation is of a simple form, very uniform, and similar to that of many Cixiidae. In many species brachypterous forms are known.

IV. TROPIDUCHIDAE.

Tropiduchidae Stal (1866), Hem. Afr., IV, p. 130; type **Tropiduchus** Stal (1854), Afr. Vet. Ak. Forh., p. 248.

This family was monographed by Melichar in 1914, at which date he recognized sixty-nine genera. Since then several new ones have been added.

With few exceptions the claval vein reaches to the apex of the clavus, which is acutely closed. In a few cases it joins the suture near its apex, and in a few it joins the claval margin near the apex. In many genera there is a distinct costal area with cross-veins; in others the costal area is entirely missing. The genus *Alcestis* is of interest on account of its peculiar venation. What Melichar considers the subcosta I consider to be the costa, so that in some species there is a very small costal area; Sc and R are joined for some distance at their bases, and Sc gives out branched veins which reach the costal margin.

Melichar uses the presence of a suture that divides the posterior angle of the mesothorax from the disc as the distinguishing character of the family. If the forms it brings together can be retained in one family, then it is of great service and relieves systematists of considerable trouble.

We know little about the genitalia at present. The ovipositor appears always to be of the incomplete form. The aedeagus shows considerable variation in the different groups. In *Ommatissus loufouensis* Muir (fig. 11) the periandrium forms a small ring with two long, slender processes; the penis is long, slender, tubular and slightly sinuate; the genital styles are separate. In *Tabinia formosa* (fig. 27) the genital styles are connected together at their base, the periandrium is like a semitube on the dorsal aspect of the penis (an epiandrium), and the penis is tubular. In *Vanua poyeri* Muir (fig. 20) the genital styles are amalgamated together and form a single, asymmetrical organ; the periandrium is a long, slender, chitinous tube, and the penis is complex and large. There is a large apodeme connecting the base of the periandrium with the apodemes of the genital style. It is possible that what I term the periandrium in this genus is, in reality, the penis, and that the periandrium is absent. It recalls the type found in Derbidae, but it is curved in an opposite direction and there is an apodeme. It is necessary to do

considerable more work in this family before we can follow the connection of the groups of genera. It is highly probable that it will be divided into two or more families.

The following is a slight modification of Melichar's table. I treat the groups as representing two subfamilies and seven tribes.

1. (4) Costal area present with cross-veins.....*Tropiduchinae*
2. (3) Antennae very short, globose.....*Tropiduchini*
3. (2) Antennae longer, double as long as the width of the eye. *Catulliini*
4. (1) Costal area absent or very small and without cross-veins. *Tambiniinae*
5. (6) Costal area absent or very short; subcosta with many branches, some furcate, reaching costal margin.....*Alcestisini*
6. (5) Subcosta without furcate branches reaching to costal margin.
7. (12) Tegmina not leathery.
8. (9) Cross-veins absent .....*Tripetimorphini*
9. (8) Cross-veins present.
10. (11) Cross-veins distad of the middle of tegmin.....*Tambiniini*
11. (10) Cross-veins basad of middle of tegmen, apical area longer than corium .....*Paricanini*
12. (7) Tegmina leathery, reaching but little beyond apex of abdomen. *Hiraciini*

I consider that the Upper Permian fossil *Prosbole* can be placed within this family. It is very similar in venation to the living insect *Neommatissus* Muir, and to *Trobolophya* Mel. I cannot consider it in any way ancestral to the Heteroptera. It has no median furrow, and the posterior furrow (suture) is behind the cubitus and not between it and the media.

V. Derbidae.

Derboides Spinola, Ann. Soc. Ent. Fra., VIII (1839), p. 205; type **Derbe** Fabricius (1803), Syst. Rhyng., p. 80.

This family contains about ninety genera. Every collection of any extent received from the tropics contains new species and genera, and when the tropics of Africa and America are explored for these insects the number of species will soon be doubled.

The eggs are unknown, but they must be laid in rotten wood, or under bark, for that is where the nymphs are found. In some genera the ovipositor is absent or represented by mere

rudiments; in others the gonapophyses are fairly well developed, but never coadapted or developed for cutting, so that the eggs are most likely all laid on the surface.

The family is recognized by the very short joint of the labium, except in a very few cases, together with the absence of other characters. The male genitalia are also quite distinctive. There is great diversity of form within the family; the head in several genera is more bizarre than in any other family of fulgorids, and the tegmina and wings run from quite normal cixiid-like forms to long, narrow tegmina and wings reduced to mere stumps and used as stridulating organs. There is no costal area except in a few forms, and then it is at the base and has no cross-veins. Many species have the claval area granulate.

I divide the family into two subfamilies and six tribes.

1. (4) Tegmina long and narrow. Wings very small or not more than half the length of the tegmina, narrow, the costal and posterior margins subparallel or converging to a pointed apex, the cubital and claval areas greatly reduced, with the claval veins missing or reduced, the posterior basal area large, corrugated and used as a stridulating organ.....*Zoraidinae*
2. (3) Eyes in front not reaching to base of clypeus, subcostal cell long, sometimes very narrow.....*Zoraidini*
3. (2) Eyes in front, reaching to the base of the clypeus; subcostal cell very short or absent; female genital styles abortive..*Sikaianini*
4. (1) Tegmina not long and narrow; wings nearly always more than half the length of tegmina, the anal area large and the cubital and anal veins normally developed.....*Derbinae*
5. (10) Claval cell closed or only narrowly open for a short distance, the extended claval vein not joining cubitus and not forming part of a contiguous series of submarginal cross-veins; cubitus generally proceeding straight to hind margin.
6. (7) Cubitus apparently with four or more veins, reaching to the hind margin .....*Derbini*
7. (6) Cubitus with less than four veins reaching to the hind margin.
8. (9) Cubitus simple or furcate, reaching the hind margin direct, not running into the basal median sector.....*Cenchreini*
9. (8) Cubitus connected with the basal median sector, forming an angular or quadrate cell; sometimes with a cross-vein near the base of the basal median sector, forming a triangular cell; tegmina broad .....*Rhotanini*
10. (5) Clavus open, the cubital veins bent and touching and, together with the extended claval, forming part of the submarginal row of apical cross-veins.....*Otiocerini*

The Cenchreini are the most generalized tribe, and such genera as *Vekunta* approach the Cixiidae very closely. In the genus *Symidia* we have an approach toward the Zoraidinae and in the genus *Phaciocephalus* toward the *Otiocerini.*

So far no fossil forms have been recognized. The present distribution is over the entire tropics in forest country, with a few straying into temperate regions. The Zoraidinae and the Rhotanini are only known from the Eastern Hemisphere, while the two genera *Derbe* and *Mysidia* are confined to the Western Hemisphere.

The aedeagus is quite typical of the family and can be recognized from all other fulgorids. The pygofer and anal segment are normal; the latter is often large and produced into one or two spines at the apex; the former is generally produced into the middle of the ventral margin. The genital styles vary in size and shape, their apodemes are fairly large and free from all connection (except muscular) with the aedeagus, and thus differ from most other fulgorids. The aedeagus is long, subtubular, slender, and curved upward, with a complex structure at the apex; the base is in contact with the base of the anal segment and has a large surface connection with the body membrane. The curved basal section I am inclined to regard as the periandrium (fig. 28, pa.) and the apical section as the penis. Under this interpretation there is no apodeme of the penis, but only a small, strong apodeme on the base of the periandrium for the attachment of muscles. This type of genitalia, with slight modification among the Zoraidini, is found all through the family. The genus *Venata* Distant has this type of genitalia and must be included in the family.

VI. Achilixiidae.

Type **Achilixius** Muir. Philippine Jour. Sci., 22 (5) (1923), p. 483.

This family is easily recognized by the two processes on each side of the base of the abdomen, the anterior larger than the posterior. The larger bears two hemispheroidal depressions and the smaller bears one. There is a somewhat similar appendage at the base of the abdomen in the genera *Benna* and *Bennaria* of the Cixiidae. The posterior margins of the tegmina beyond the clavus are not produced and do not overlap when at rest, the tegmina

being considerably tectiform. The male genitalia are very different from those of other families, but the nature of the aedeagus places it in the Cixiine group, although otherwise it might be placed near the Achilidae in the Meenopline group.

The male pygofer is normal, with a transverse bar across the middle to which the base of the aedeagus is attached (fig. 5, t. b.); the aedeagus shows no sign of division into periandrium and penis, but is cultrate, the ventral margin being double and curved, the dorsal margin straight and single. The ovipositor is incomplete.

The family is erected for a single genus containing four species. I hesitated before erecting the family, but as the genus cannot be placed in any recognized family without doing violence to the family characters it is best placed by itself.[1]

VII. Dictyopharidae.

Dictiophoroides Spinola (1839), Ann. Soc. Ent. Fra., VIII, pp. 202, 283; type **Dictyophara** Germar, Silb. Revue Ent., I, p. 175 (1833).

This family was monographed by Melichar in 1912, at which time he recognized seventy-six genera. He divided it into five groups, which I shall consider as two subfamilies with five tribes.

1. (6) A distinct suture dividing clavus from corium; tegulae and ocelli present ..... *Dictyopharinae*
2. (3) No cross-veins in the clavus..... *Dictyopharini*
3. (2) Clavus with a cross-vein between first claval and suture.
4. (5) Tegmina with narrow costal area..... *Dichopterini*
5. (4) Tegmina without costal area..... *Cladyphini*
6. (1) No suture dividing the clavus from corium..... *Orgerinae*
7. (8) Tegmina entirely or almost covering the abdomen..... *Lynciini*
8. (7) Tegmina very short, not nearly covering the abdomen... *Orgeriini*

Melichar called his Group IV Bursini, although he placed the genus *Bursinia* Costa in his Group V, Orgerini. The above classification is likely to be modified with further study.

The tegmen has no costal area, or a very narrow one without transverse veins; the claval vein does not reach the apex of clavus. Besides the lateral margins the frons generally has two

[1] The writer has received from Dr. F. X. Williams specimens from Ecuador, representing two species of an undescribed genus which goes into this family. There is only one rounded process bearing three depressions.

or three median longitudinal carina. The family is closely connected with the Fulgoridae. At present it contains a number of aberrant forms which make it difficult to define. It is also difficult to separate from those Cixiidae without a median ocellus.

The periandrium is large, often funnel-shape, membraneous or semi-membraneous, and often has the apical margin divided into lobes (fig. 29). The penis is a short tube or ring with two long processes (fig. 18, 29 a) very similar to the type found in the Fulgoridae (fig. 16).

VIII. Fulgoridae.

Fulgorellae Latreille (1807), Ger. Crust. Ins., VII, p. 163; type **Fulgora** Linn., Syst. Nat. (1767), I, p. 703.

Kirkaldy [1] considered that the type of the genus *Fulgora* is *europaea* Linn. and, therefore, should be used in place of *Dictyophara* Germ. For *Fulgora* auctt. (type *Laternaria* Linn.) he used *Laternaria* Linn., which agrees with Stål. The question appears to stand upon whether Sulzer's fixation of the type in 1776 be valid. Van Duzee does not follow Kirkaldy, and as I am not in a position to follow the history of this name I shall place myself with the majority and not make the alteration.

The family stands with about one hundred or more generic names. It needs a modern revision, as nothing has been done to it since Stål's time except in local faunistic works where a number of genera have been described. It contains the largest and most showy species of the superfamily, and so has attracted more attention from collectors than any of the others. In some species the head is greatly elongated and enlarged, and has been stated by some to be luminous. The controversy on this subject is old, but an explanation may be found in Kershaw's discovery that the prolongation of the head is filled by a diverticulum from the crop. The head at times may be filled with bacteria from the stomach and be in the same condition as the silkworm larva when attacked by luminous bacteria.

The reticulation of the anal area of the hind-wings appears to be a constant character of this family, and cross-veins are numerous on the tegmina, which are comparatively narrow. The costal area is absent or forms but a narrow area without trans-

[1] Haw. Sug. Planters' Exp. Sta. Ent. Bull., XII, p. 11, 1913.

verse veins. The Sc is free to the basal cell in some genera, the bases of R and M are generally joined together for a short distance. The clavus is open, the suture (Cu2) continues as an independent vein and is often branched and enters the apical margin. The first and second claval veins form a Y and often continues as a free, branched vein to the apical margin; the third claval (An3) is sometimes present as a free vein in the apical portion of the clavus.

The lateral margins of the frons are generally straight, or if they are angular then the frons is longer than wide.

The female ovipositor is incomplete and is often abortive. The eggs are laid on the surface, in some cases in double rows, and covered with wax. The aedeagus is very similar to that found in the Dictyopharidae. The periandrium is large, funnel-shape, and membraneous, the penis short and produced into two slender processes (fig. 16). The penis is sometimes greatly reduced.

IX. Eurybrachidae.

Eurybrachydida Stal (1866), Hem. Afr., IV, p. 129; type **Eurybrachys** Guer. (1834) Voy. Belang. Ind. Orient, p. 475.

This small family of some two dozen genera is a fairly difficult one to place. In certain characters it approaches the Fulgoridae, in others the Achilidae.

The female has an incomplete ovipositor. The male genitalia are complex and at present not fully understood. In *Gelastopsis insignis* Kirk. (fig. 24) the male pygofer is simple and the genital styles large but normal. The aedeagus is unique, so far as my knowledge extends; it forms a short tube flattened horizontally, on each side arises a large, strong spine-like process, dorsally and ventrally there is a semi-membraneous flap. In *Olonia picea* Kirk. (fig. 12) there is a large plate attached to the ventral margin of the pygofer produced posteriorly into two curved spines; this may represent a development of g 1. The genital styles are large and complex; the aedeagus is peculiar and consists of a membraneous area in which the genital opening is situated, with three pairs of sclerites, the basal pair being the largest, triangular and projecting as two large, broad spines; internally there is a membraneous tube to which the apodeme is

attached (fig. 12 b). The genitalia require much further study before we can place the family with any certainty.

The frons is broad, generally broader than long, and the lateral margins angular. In some genera there is a costal area with cross-veins, in others it is absent. The claval vein runs to the apex of the clavus, which is generally roundly closed; the vein proceeds beyond the clavus and ends in the hind margin and is sometimes branched. The third claval vein (An3) is sometimes present as a free vein in the apical half of the clavus; Cu2 or claval suture continues beyond the clavus, branches and terminates in the apical margin. The anal area of the hind-wing is reticulate in a few species.

X. Achilidae.

Achilida Stal (1866), Hem. Afr., IV, p. 130; type **Achilus** Kirby (1818), Trans. Linn. Soc., Lond., XII, 475.

This is a very homogeneous family of about sixty genera. The chief characteristics of the family are the claval vein reaching the apex of clavus, which is closed; the hind margin produced beyond the apex of clavus; the tegmina, when at rest, very slightly tectiform or nearly horizontal, and the areas beyond the clavus overlapping. In only a few genera is there any sign of a costal area, and then there are no cross-veins.

The female has an incomplete ovipositor. In the male the pygofer is considerably flattened horizontally, there is generally a pair of processes on the medio-ventral margin; the genital styles are large and complex; the aedeagus in *Eurynomeus granulatus* (fig. 23) consists of a periandrium which is produced into three pair of processes, and a penis which is a small tube with two long, flat processes (fig. 23 a). In a large Philippine Achilid at present undetermined (fig. 26) the periandrium and penis are fairly normal, but the apodeme forms a long, semi-chitinous tube, the nature of which I do not understand. A great deal more work must be done upon the family before its correct position in the superfamily can be demonstrated. Certain points place it near the Eurybrachidae and Fulgoridae, but there are others which separate it very decidedly.

XI. Acanaloniidae.

Acanonides Amyot and Serville (1843), Hemip., pp. LVIII, 520; type **Acanalonia** Spinola, Ann. Soc. Ent. Fra., VIII (1839), p. 447.

This small family, which contains only five or six genera, was monographed by Melichar in 1902. It comes very close to some of the Issidae by which it appears to be separated by the absence of spines on the hind tibiae.

The head is about as wide as the thorax and the clypeus lacks lateral carinae. The posterior margin of the pronotum is straight or but slightly concave, the pronotal carinae absent or obscure; the mesonotum is large. The tegmina are steeply tectiform. This family differs from the Flatidae by having no costal area, or if there be one then it is obscure and has no transverse veins.

The ovipositor is incomplete. The aedeagus is complex, the penis and periandrium appear to be amalgamated into a complex tube with appendages (figs. 30, 31), a condition found in some Issidae.

XII. Issidae.

Issites Spinola (1839), Ann. Soc. Ent. Fr., VIII, p. 204; type **Issus** Fabricius (1803), Syst. Rhyng., p. 99.

This is a difficult family to characterize. With the exception of a few cases the head is as wide as the thorax, or wider. The hind margin of the pronotum is straight or but slightly concave or convex; the mesonotum is short, not more than twice the length of the pronotum, with a transverse carina across it parallel to the hind margin of the pronotum, which divides it into two parts; the anterior portion is covered by the pronotum and is generally of a different sculpturing to the posterior portion. This character is also found in some Dictyopharidae and Lophopidae.

The tegmen is without a costal area, or if one be present then it is small, obscure, and without cross-veins. The tegmen is often very short or very narrow and the venation obscured. The legs are generally thick and the hind basitarsus short and thick.

The ovipositor is incomplete. The male genitalia are considerably diverse, even in the few species that I have examined.

In *Hemisphaerius moluccanus* Kirk. (fig. 33) the periandrium is large and semi-membraneous; the penis forms a fairly large tube produced into two processes with a median process in the middle. This aedeagus is like the type found in the Ricaniidae. In *Danepteryx* sp. (fig. 21) the periandrium forms a small tube which fits tightly around the large, semi-cylindrical, curved penis. In *Gelastissus histrionicus* Kirk. (fig. 35) the periandrium is a short, wide tube with the dorsal edge curved over at its apex; the penis is smaller and has two large, curved spines at the apex. In *Aphelonema vespertina* Kirk. (fig. 34) the periandrium is large and membraneous, while the penis is thin and curved. These few examples show the diversity to be found in the family, and indicate the necessity for a great amount of work before we shall be able to understand the relationship of the genera included within it.

Melichar monographed the family in 1906, when he recognized ninety-five genera; since then several new ones have been added. The following division of the family is based on Melichar's work.

1. (2) Tegmina short and only reaching slightly beyond the base of the abdomen, or exceedingly narrow, parchment-like, thick or opaque, seldom hyaline; wings absent or rudimentary.....*Caliscelinae*
2. (1) Tegmina entirely covering the abdomen or the greater portion of it.
3. (4) Clavus and corium not separated by a suture. Tegmina generally convex, thick, and the venation obscure.....*Hemisphaerinae*
4. (3) Clavus separated from corium by a suture.....*Issinae*
5. (6) Wings absent or rudimentary, not folded.....*Hysteropterini*
6. (5) Wings present, entire.
7. (8) Wings with margins entire.....*Issini*
8. (7) Wings with a deep cleft in the apical margin, the anal area very large .....*Thioniini*

The genus *Augila* Stål would come into the Issini. It might be as well to make a separate tribe, or even subfamily of it. *Danepteryx* Uhler and *Gamergomorphus* Melichar would go into the Caliscelinae near to *Alleloplasis* Waterh. It might be more natural to consider the Caliscelinae as a tribe of the Issinae.

XIII. Lophopidae.

Lophopida Stal (1866), Hem. Afr., IV, p. 130; type **Lophops** Spinola (1839), Ann. Soc. Ent. Fra., VIII, p. 387.

This small and homogeneous family was monographed by Melichar in 1915, and twenty-seven genera were then recognized. The head is narrower than the thorax and there is a tendency for the middle portion of the frons to be produced; the front legs are flattened and expanded in most cases; the hind margin of pronotum is truncate; the clypeus is keeled laterally: the hind basitarsus is short and generally swollen; there is a distinct costal area with cross-veins.

I do not follow Melichar's tribes, as the characters he uses do not hold true, and he has placed some of his genera into the wrong tribes, according to his own characters.

The ovipositor is incomplete. The aedeagus has a large periandrium (figs. 15, 17, 19), often considerably complex; the penis forms a short tube with a pair of processes, often of a complex nature. It is a specialization upon the *Dictyophara* type near to the Ricaniidae.

XIV. Ricaniidae.

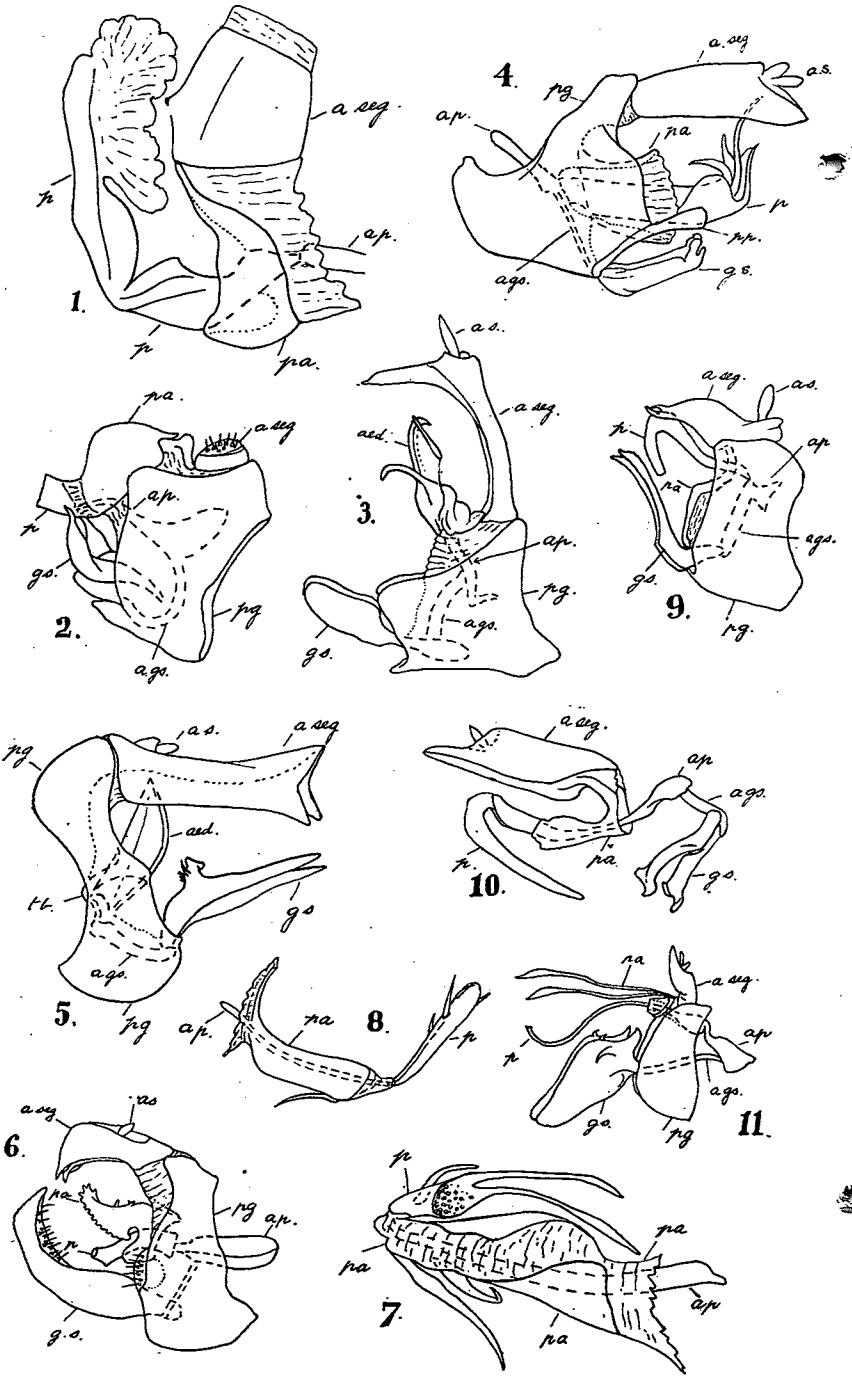
Ricaniida Stal, Hem. Afr., IV, p. 219 (1866); type **Ricania** Germ. Mag. Ent., III, p. 221 (1818).

Head wide, in a few cases narrower than the pronotum. Pronotum slightly roundly emarginate on hind margin; mesonotum very large. Tegmina large, steeply tectiform when at rest, a costal area with transverse veins always present, which is quite distinct even when narrow; clavus not granulate, apex closed, pointed, claval vein reaching apex, the costal veins joining before the middle or shortly beyond the middle. Posterior tibiae with spines; hind basitarsi short.

In 1898, when Melichar monographed the family, he recognized thirty-one genera. A few more have been added since. He divided the family into two groups.

1. (2) Frons wider than long, or as wide as long; the sides of clypeus without carinae ..... *Ricaniini*
2. (1) Frons distinctly longer than wide or as wide as long; in the latter case the clypeus has lateral carinae..... *Nogodini*

I believe a better classification can be made on the venation,



Male Genitalia of Fulgoroidea.

but my present knowledge of the family is too limited to allow me to carry out such a scheme.

In the few genera which I have examined the male genitalia are all built on the same type. The periandrium (figs. 13, 22) forms a large and comparatively simple tube; the penis forms a more or less short tube or ring from which arises a pair of processes more or less narrow and with ample apices; within the penis there is a small process which is sometimes trilobed, and on which the gonopore appears to be situated, and which may represent the true penis.

Most species of this family are comparatively large and often gaily colored, and so they have been given more attention by collectors than the more obscure fulgorids. The family is a very homogeneous one.

XV. Flatidae.

Flatoides Spinola, Ann. Soc. Ent. Fr., VIII, pp. 204, 387 (1839); type **Flata** Fabricius, Ent. Syst. Suppl., 511, 517 (1798).

Head generally narrower than thorax. Pronotum with the posterior margin generally roundly emarginate, in some case subangularly and in a few cases straight; mesonotum fairly

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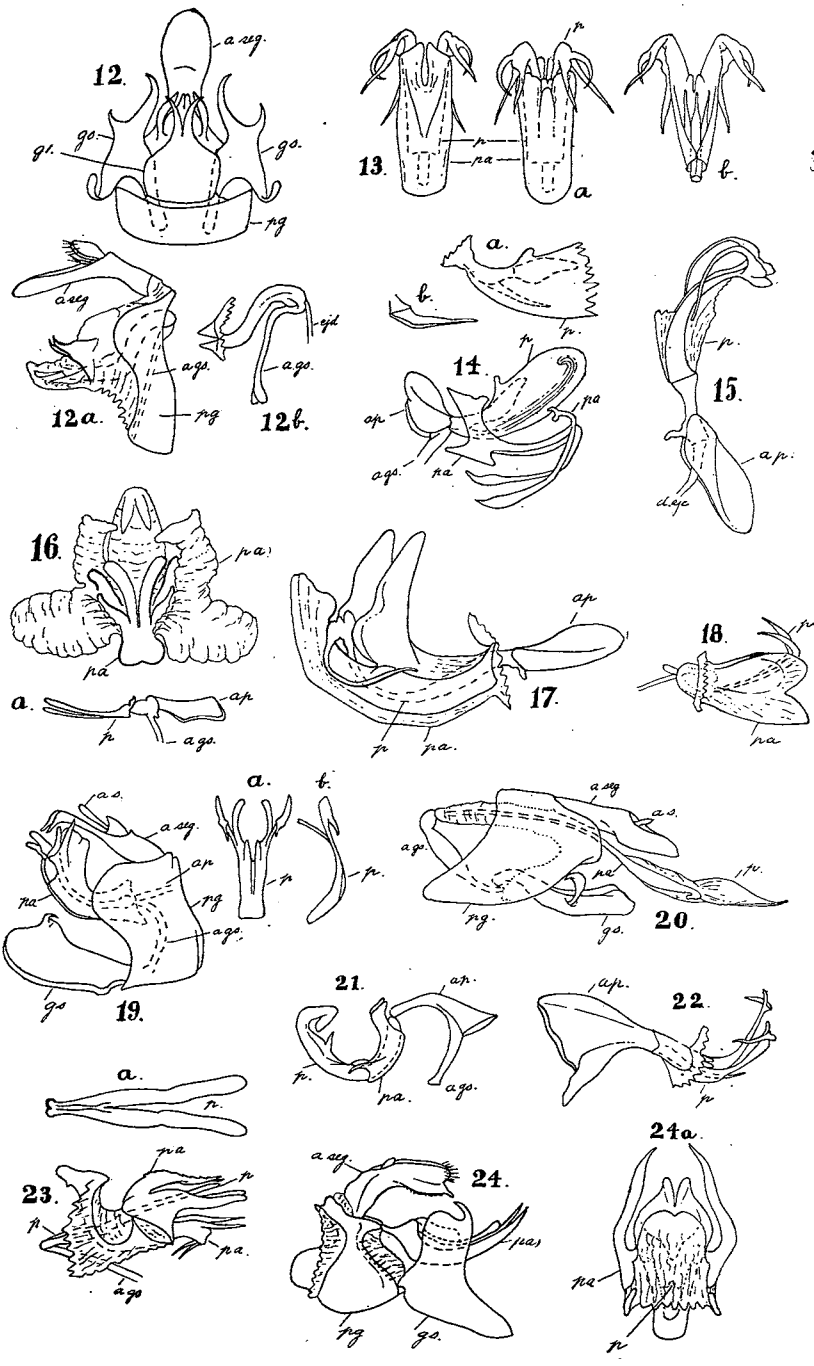
PLATE IV.

1. *Tettigometra* sp. (Tettigometridae). Right side view of aedeagus and anal segment.
2. *Hilda breviceps* (Tettigometridae). Right side view of male genitalia.
3. *Mnemosyne efferatus* (Cixiidae). Right side view of male genitalia.
4. *Kinnara maculata* (Cixiidae). Left side view of male genitalia.
5. *Achilixius singularis* (Achilixiidae). Left side view of male genitalia.
6. *Phaconura froggatti* (Cixiidae). Right side view of male genitalia.
7. *Borysthenes fasciolatus* (Cixiidae). Right side view of aedeagus.
8. *Myndus caligineus* (Cixiidae). Left side view of aedeagus.
9. *Stenocranus seminigrifrons* (Delphacidae). Right side view of male genitalia.
10. *Ugyops kellersi* (Delphacidae). Right side view of anal segment, aedeagus and genital styles.
11. *Ommatissus loufouensis* (Tropiduchidae). Right side view of male genitalia.

Lettering on figures: *aed*, aedeagus; *ags*, apodeme of genital styles; *ap*, apodeme of penis; *as*, anal style; *a seg*, anal segment; *ejd*, ejaculatory duct; g_1, anterior gonopophyses; *p*, penis; *pa*, periandrium; *pg*, pygofer.



Male Genitalia of Fulgoroidea.

large. Tegmina large, in a few genera narrow, with a distinct costal area with cross-veins; the clavus granulate, often open and the claval veins separate, or the claval veins joined near apex.

The family was monographed in 1902 by Melichar, who included the Acanaloniidae. By excluding these we have a homogeneous group of about eighty to ninety genera which can be divided into two subfamilies of strikingly different facies.

1. (2) Body considerably compressed laterally, the tegmina steeply tectiform, the apical portion of the costal margins and the apical margins meeting together, or approaching very closely when at rest ..... *Flatinae*
2. (1) Body not compressed laterally or only slightly so; tegmina horizontal or only slightly tectiform, the apical portion of costal margins not meeting together beneath the abdomen.. *Flatoidinae*

In the few genera in which I have examined the male genitalia they appear to be very uniform. The periandrium forms a short tube or ring and from each side a long, narrow appendage arises which generally has the apex enlarged or complex. The penis forms a large tube, often funnel-shape and flattened

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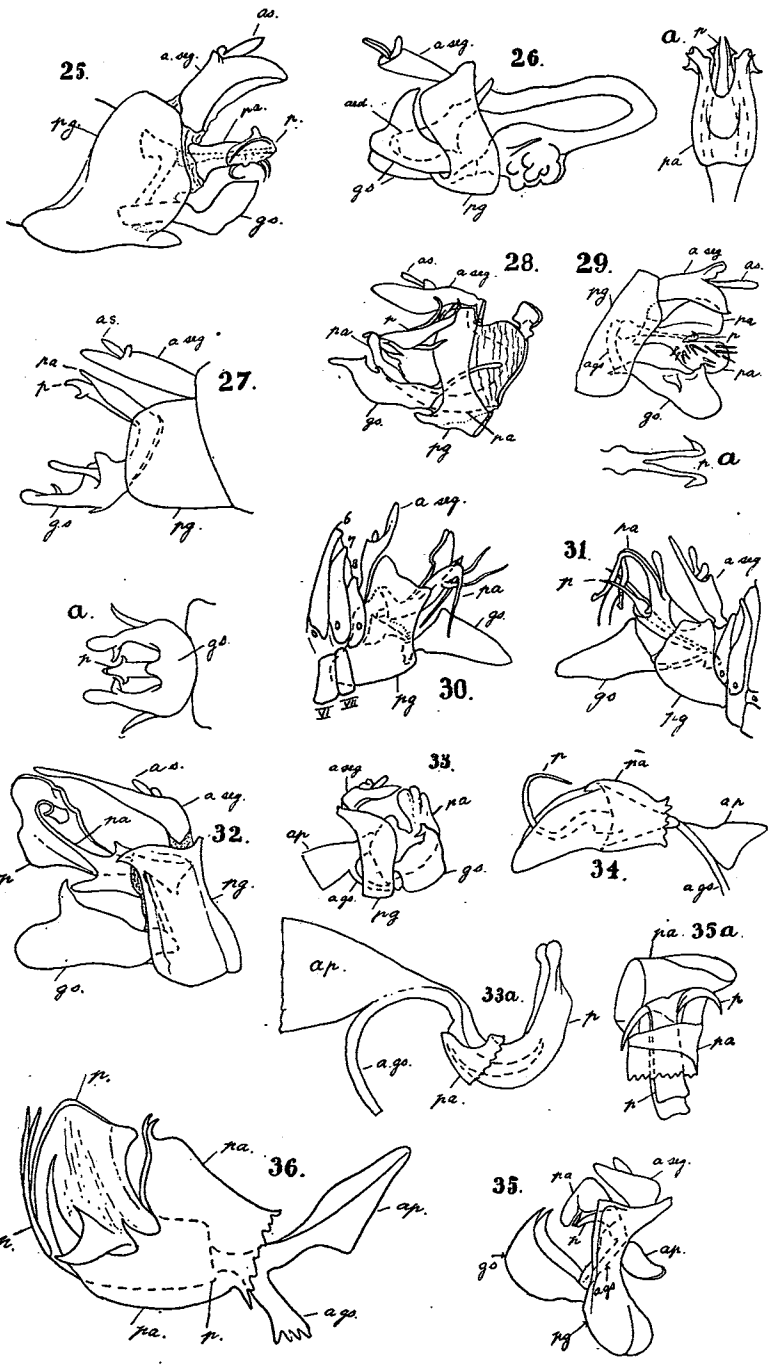
PLATE V.

12. *Olonia picea* (Eurybrachidae). Ventral view male genitalia; *a*, right side view male genitalia with styles and g^1 cut away; *b*, aedeagus.
13. *Pochaza fuscata* (Ricaniidae). Ventral view of aedeagus; *a*, dorsal view of aedeagus; *b*, dorsal view of penis.
14. *Neomelicharia guttulata* (Flatidae). Left side view of aedeagus; *a*, basal portion of penis; *b*, process bearing gonopore.
15. *Pyrella aberrans* (Lophopidae). Right side view of penis.
16. *Aphana* sp. (Fulgoridae). Ventral view of periandrium; *a*, lateral view of penis.
17. *Pyrella aberrans* (Lophopidae). Right side view of aedeagus.
18. *Dictyophara nerides* (Dictyopharidae). Left side view of aedeagus.
19. *Virgilia nigropicta* (Lophopidae). Right side view of male genitalia; *a*, dorsal view; *b*, lateral view of penis.
20. *Vanua poyeri* (Tropiduchidae). Left side view of male genitalia.
21. *Danepteryx* sp. (Issidae). Right side view of aedeagus.
22. *Mindura obscurus* (Ricaniidae). Left side view of penis.
23. *Eurynomeus granulatus* (Achilidae). Left side view of aedeagus; *a*, dorsal view of penis.
24. *Gelastopsis insignis* (Eurybrachidae). Left side view of genitalia; *a*, dorsal view of aedeagus.



Male Genitalia of Fulgoroidea.

laterally, the apical margin being cleft for some distance; on each side of the penis there is often a depression into which the process of the periandrium fits when at rest. Within the penis at its base there is a process on which the gonopore appears to be situated (figs. 14, 32). In the Flatoidinae the periandrium is large, forming a short, thick funnel, and the processes are shorter; the penis is also shorter and wider (fig. 36). The ovipositor is always incomplete.

PHYLOGENY.

The classification of animals started early in the history of mankind, most likely with the dawn of speech. It was started for convenience and was empirical, and has continued down the ages on the same lines. With the dawn of biological science it was continued scientifically, and a natural order of arrangement became evident. Since Darwin made evolution a living force with biologists the natural arrangement, or natural order, has become predominant, in some cases even to the detriment of utility.

The living species of animals represent the terminal twigs of the tree of insect life of which we examine but the surface.

PLATE VI.

25. *Myndus musivus* (Cixiidae). Left side view of male genitalia.
26. gen. sp. ? (Achilidae). Right side view of male genitalia; *a*, dorsal view of aedeagus.
27. *Tambinia formosa* (Tropiduchidae). Right side view of male genitalia; *a*, ventral view of same.
28. *Phaciocephalus* sp. (Derbidae). Right side view of male genitalia.
29. *Dictyophara europeae* (Dictyopharidae). Left side view of male genitalia; *a*, dorsal view of penis.
30. *Acanalonia* sp. (Acanaloniidae). Left side view of male genitalia.
31. *Amphiscepa bivittata* (Acanaloniidae). Right side view of male genitalia.
32. *Siphanta acuta* (Flatidae). Right side view of male genitalia.
33. *Hemisphaerius moluccanus* (Issidae). Left side view male genitalia; *a*, left side view of penis.
34. *Aphelonema vespertina* (Issidae). Right side view of aedeagus.
35. *Gelastissus histrionicus* (Issidae). Right side view of male genitalia; *a*, ventral view of aedeagus.
36. *Uxantes* sp. (Flatidae). Right side view of aedeagus.

What lies below that surface—the branches, limbs, and trunk—we can only speculate about, using for our guides the arrangements of the terminal twigs and such little evidence as is given us by paleontology. Such speculation we term phylogeny, and its existence entirely depends upon our belief in evolution; the form it takes is moulded by the nature of that belief.

To the phylogenist the cut and dried dichotomous characters, which are such a boon to systematists, are often of little value. On the other hand, those organs showing a graduate series, which are anathema to the systematist, are generally the phylogenist's best friends. It is upon these lines that the following speculations proceed.

The Hemiptera existed before the Heteroptera or Homoptera, and were characterized by the nature and function of the mouth parts. They were more generalized that either of these suborders are today, but they approached nearer to the former. The head would have possessed a gula region, and the beak may have been carried out straight. When not in use this position would be inconvenient, and it was possibly to avoid this that the main dichotomy came about. In the Heteroptera the gula region persisted and even became greatly developed and the beak bent at its base so that it packed away under the head and thorax. In the Homoptera the gula was reduced and the head became inflexed so that the beak when at rest lay straight out beneath the thorax without a bend at its base, thus the base of the labium was brought into intimate relationship with the prosternum. This turning under of the head led to a flattening and widening of the head capsule, especially the more apical portions such as the genae and lorae. This line of evolution of the head was carried to its greatest extent in the Cicadoidea, more especially in the specialized Cicadellidae. The Tettigometridae of the Fulgoroidea retains this type of head, but it is modified slightly along the fulgorid lines. It is possible that in the Fulgoroidea the vertex lengthened and curved downward. In this case the lateral carinae of the frons would represent the ridge above the antennae in the Cicadoidea.

After the departure of the Fulgoroidea from the main stem, or perhaps even before that, there arose the peculiar arrangement of the intestine whereby the "filter" or "colum" was

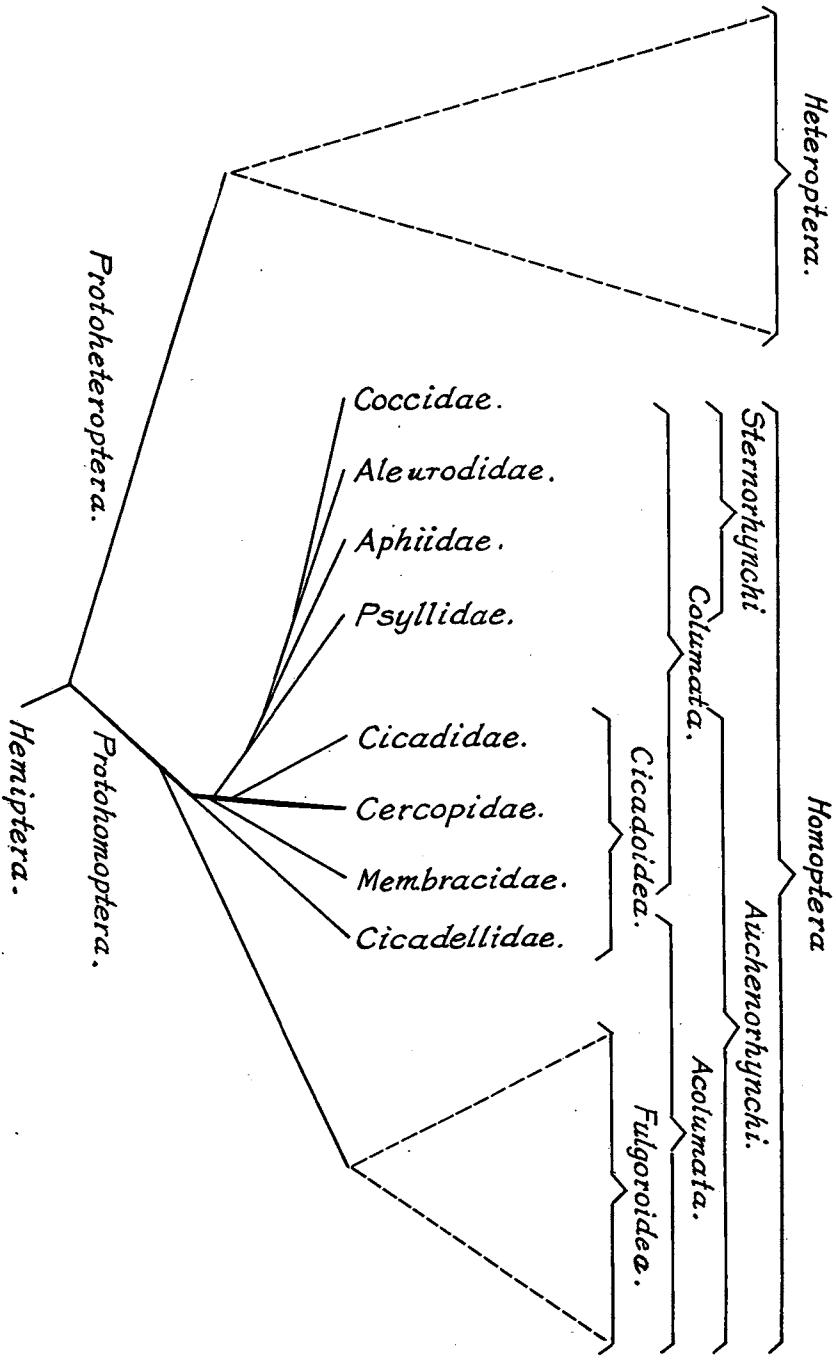


Diagram 1, showing the morphological affinity of the Homoptera.

formed. This must have been on a side branch and it gave rise to the Cicadidae, Cercopidae, and Membracidae, as well as to the Sternorhynchi. The latter followed certain lines of evolution of their own, such as specialization by reduction, the formation of a setal chamber or crumena and the detachment of part of the head capsule from the rest of the head. This reduction may be due to their decrease in size together with their sedentary habits. The formation of the setal chamber may be for a mechanical perfection for controlling the long setae when in use, as well as for a place of protection when at rest. This line of evolution of the Sternorhynchi culminates in the Coccidae, which are in general the smallest and most sedentary of the group.

The venation of the early Hemiptera approached Comstock's theoretical wing very closely, and a somewhat similar type of venation is found in the more generalized of each of the larger groups. The tendency for the bases of the four chief systems to amalgamate one with another is traced through all the groups, especially with the reduction of the width of the wings. This is carried to its greatest extent among the Sternorhynchi and is possibly a result of reduction of size and disuse.

According to my interpretation of the evolution of the Fulgoroidea, the Tettigometridae represent the *modified descendants* of the most primitive fulgorids. They descended from a form having small hind coxae, as in Cercopidae, and not from a form having the present membracid-cicadellid type. The Cixiidae represent a branch from the early stem which have retained certain primitive characters, such as the three ocelli, a simple venation and the complete ovipositor. At an early period the Cixiidae divided into two groups, Cixiinae and the Meenoplini.[1] From the former the Delphacidae arose by the acquisition of a mobile spur on the hind tibia; they carried over and retained the complete ovipositor and the more generalized male genitalia. The modification of the venation in the family is by reduction. The Tropiduchidae evidently came from a Cixiinae stock and have undergone considerable evolution within the family (if all the genera contained in it represent a monophyletic group).

[1] It is possible that this dichotomy goes back to a pre-cixiidae form, and that they should be regarded as distinct families.

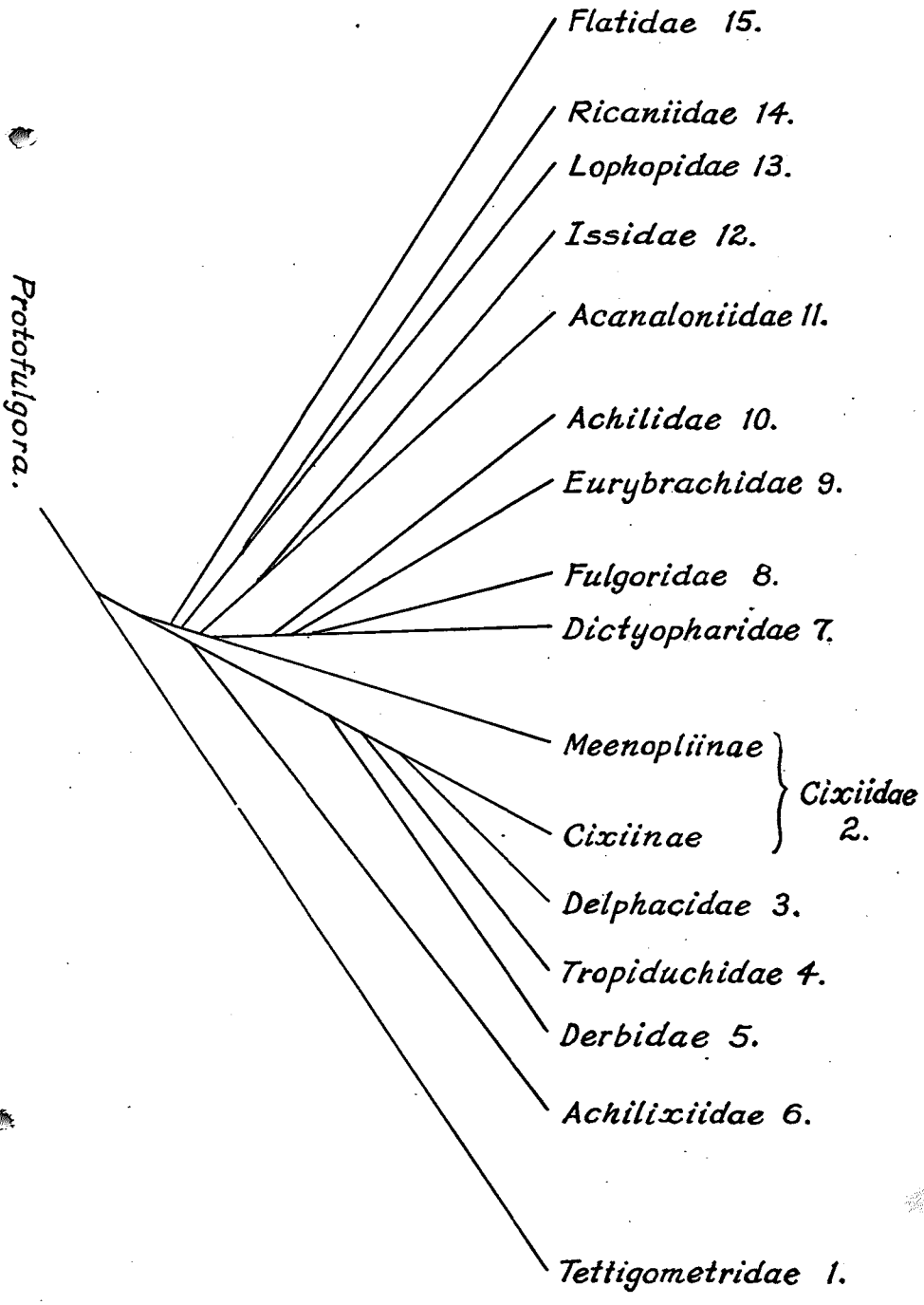


Diagram 2, showing the morphological affinity of the families of the Fulgoroidea.

Platygenesis has taken place in one group and stenogenesis in another. The aedeagus has undergone considerable evolution within the family, but, so far as present knowledge enables us to judge, it is of the Cixiinae type. The generalized Derbidae approach so closely to the Cixiidae that some genera have been shifted from one to another, but they possess distinct male genitalia. The Achilixiidae belong to the Cixiinae group, but they are difficult to place as they have some synthetic characters. The other nine families arose from the Meenoplinae stock or from genera having their type of genitalia. Our knowledge is too slight to allow us to speculate on their relationship with any hope of being correct. The Dictyopharidae and Fulgoridae are closely allied. The Eurybrachidae show some affinities to the Fulgoridae, and so do the Achilidae. The other five families may have arisen from the generalized Dictyopharidae or from a more direct Meenoplinae stem. The Issidae and Acanaloniidae are closely allied, but the possibility of the Issidae being a composite group must not be overlooked. The Lophopidae and the Ricaniidae have affinities, and the Flatidae come close to them. With the exception of the Issidae, one of whose characteristics is a reduction and thickening of the tegmina, the last five families show considerable platygenesis, the last three often having a wide costal area containing cross-veins; the Tropiduchidae in part share this characteristic, and other families show it to some extent. Stenogenesis also appears in several families quite independently, so that neither of these characters can be used for the grouping of the families.

It is to paleontology that we must look for information to fill in our time elements so as to round out our speculations in phylogeny. So far the evidence fits in with the above conclusions. The Tropiduchidae, Cixiidae, and Tettigometridae (if the latter are allied to *Ipsvichia*) are found in Mesozoic times or earlier, along with Cercopidae, Cicadidae, and Cicadellidae; whereas Fulgoridae, Flatidae, Ricaniidae and, perhaps, the Derbidae have only been found in much more recent formations.

While paleontology gives us some positive data as to the presence of certain forms at certain periods, yet the geological record is not nearly complete enough to allow us to accept negative evidence as indicating that other forms did not exist at

those periods. We must use other evidence to support such a proposition. We cannot expect to find much evidence of Coccidae in the geological records, but we can reason from their high specialization that they appeared later than the more generalized Sternorhynchi.

When considering the problems of phylogeny the possibilities and probability of parallel and convergent evolution must be constantly borne in mind. In every large group of animals there is evidence of such, and it is the first work of the phylogenist to decide where this has taken place. For this reason we must not base our conclusions upon one structure alone. But we must base our conclusions upon evidence, even if it be inconvenient. If evidence can be shown that the "filter" was once present in the Cicadellidae and has since been lost, then our task would be simplified; the Membracidae would then come off the same base and the Cercopidae would represent the more direct line. This is indicated by the thickened line in the diagram. But until such evidence can be produced we must take things as we find them and arrange our diagram accordingly.

In drawing up diagrams Nos. 1 and 2 (Plates VII and VIII) I have tried to take the above remarks into consideration. They do not indicate the time element, but simply try to express my conceptions of the morphological affinity of the families dealt with. As such they are liable to alterations and repairs, as they give way beneath the weight of accumulated knowledge.