A PRELIMINARY REVISION OF THE FAMILIES AND SUBFAMILIES OF *ACRIDOIDEA* (ORTHOPTERA, INSECTA)

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INTRODUCTION

THE status and scope of families and subfamilies of *Acridoidea* have undergone many changes, but the general system within the group is still far from adequate. A few families are well defined, but there are others (e.g. *Eumastacidae*), and also some subfamilies (e.g. *Catantopinae*), which are highly heterogeneous assemblages and need thorough revision.

In this paper an attempt is made to establish a tentative classification of *Acridoidea* based mainly, though not exclusively, on Palaearctic and African material. Insufficiency of material, particularly from South America and from Australasia, makes a comprehensive review of the whole group impossible at present. Moreover, although as many as 1,527 valid genera have been described up to the end of 1958, this number is probably still far from the total, and one may expect possibly twice as many more to be described. Consequently, the system outlined below must be regarded as preliminary only.

In the diagnoses of the families and subfamilies below, only the most important characters are mentioned. The characters which are common to all families, and those which have not been checked for the majority of the genera of a certain family or subfamily, are omitted from the diagnoses but are mentioned in discussions or in the tables.

The keys to families and subfamilies are based on external characters only, which usually suffice for recognition of them. The distribution of both external and internal characters throughout families and subfamilies is presented in Tables II and III respectively. It will be seen that the internal and external characters often do not run parallel.

The list of genera of each family or subfamily includes only those examined by the author, arranged in alphabetical order. In many cases all the known genera were studied, and this is indicated. No lists are provided in the case of the very large and sufficiently distinct units such as *Pyrgomorphidae*, *Acridinae* and the somewhat artificial subfamily *Catantopinae*.

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STATUS AND SCOPE OF *ACRIDOIDEA*

The systematic position of *Acridoidea*, as suggested in recent leading orthoptero-logical and general entomological works, is presented in Table I. The main changes in this century have been as follows :

Handlirsch (1908) divided the order *Orthoptera* Latreille, 1793 (= *Saltatoria* Latreille, 1817), into the suborder *Locustoides*, with the families *Locustidae* (= *Tettigoniidae*), *Gryllidae*, *Tridactylidae*, and *Gryllotalpidae*, and the suborder *Acridioidea* with a single family *Acridiidae*.

Ander (1939) divided the order *Saltatoria* into the suborders *Ensifera* and *Caelifera*, the first of which corresponds to Handlirsch's *Locustoides* and the second to Handlirsch's *Acridioidea*, except that he transferred the family *Tridactylidae* to the suborder *Caelifera* as a superfamily. *Acridoidea* were regarded by him as the second superfamily of the suborder.

Some authors, however, even earlier (Jakobson & Bianki, 1904), regarded all the superfamilies of Ander as suborders. Others (Schvanwitsh, 1949) omitted the term suborder and used the term superfamily instead.

In this paper, following Handlirsch's scheme, the *Acridoidea* are regarded as a suborder of the order *Orthoptera*.

TABLE I.—*Changes in the Status of Acridoidea*

Authors	Taxonomic categories		
	Order	Suborder	Superfamily
Jakobson & Bianki, 1904	Orthoptera	Acridioidea	—
Handlirsch, 1908	Orthoptera	Acridioidea	—
Chopard, 1920	Orthoptera	Locustodea	—
Schröder, 1925	Saltatoria	Acridioidea	—
Uvarov, 1928	Orthoptera	Acridodea	—
Weber, 1938	Saltatoria	Acridoidea	—
Ander, 1939	Saltatoria	Caelifera	Acridoidea
Chopard, 1949	Orthoptera	Caelifera	Acridoidea
Shvanwitsh, 1949	Orthoptera	—	Acridoidea
Bey-Bienko & Mistshenko, 1951	Orthoptera	Caelifera	Acridoidea
Beier, 1955	Saltatoptera	Caelifera	Acridides
This work	Orthoptera	Acridoidea	—

A question concerning the scope of the suborder *Acridoidea* is the position of *Tetrigidae*, which some authors continue to regard as one of the families of *Acridoidea*, although Chopard (1920), Walker (1919–22), Snodgrass (1937), Carpentier (1932, 1936), and Ander (1939) have proved that this view is incorrect. Beier (1955) has formally established the superfamily *Tetrigides* as equal in rank to his *Acridides* (= *Acridoidea*) and consisting of the families *Tetrigidae*, *Tridactylidae* and *Cylindrachetidae*.

Beier's superfamily *Tetrigides* is here regarded as the suborder *Tetrigoidea*, equal in rank with *Acridoidea*.

A discussion of affinities of *Tetrigoidea* with other Orthopteroid groups is outside the scope of this paper, but the main characters separating them from *Acridoidea* are as follows¹ :

1. The thoracic skeletons of *Tetrigidae* and *Acridoidea* in many essential features are very different (Carpentier, 1936). The pronotum in *Tetrigidae* is strongly elongated, covering the whole or the greater part of the body, which is never the case in *Acridoidea*.

2. The structure of the phallic complex is entirely different. In *Tetrigidae* the epiphallus is absent ; the pseudosternite, described by Walker (1922), cannot be regarded as homologous with the epiphallus of *Acridoidea* and probably represents a structure of a different origin. The cingulum, in the same meaning as in *Acridoidea*, is also absent. The penis is directed towards the anterior end of the body, whereas in *Acridoidea* it is always directed towards the posterior end. The family *Trigonopterygidae* is the only exception ; in it the penis is directed towards the anterior end, as a secondary phenomenon, the whole phallic complex being in a reversed position ; the ventral part being in a dorsal position and the dorsal part ventral (see Dirsh, 1956.) The whole phallic organ in *Tetrigidae* is covered above with valves, which are absent in *Acridoidea*.

3. The elytra in *Tetrigidae* are strongly shortened, scale-like, while the wings are fully developed (though there are some apterous species). This never occurs in *Acridoidea*. The hind wing has a strongly reduced remigium, a relatively large vannus and unbranched main veins (Ragge, 1955).

4. The tympanal organ is always absent in *Tetrigidae*. In *Acridoidea*, except a few families, it is present.

5. The anterior and middle tarsi of *Tetrigidae* consist of two segments and only the hind tarsus is three-segmented, while in *Acridoidea* all tarsi are always three-segmented.

6. Arolia are absent in *Tetrigidae* but always present in *Acridoidea*.

All these characters separate *Tetrigidae* from *Acridoidea* definitely and it is probable that the internal anatomy, when studied, will provide further important features of difference.

TAXONOMIC CHARACTERS

The attitude of taxonomists of the last and the beginning of this century towards classification of *Acridoidea* was to regard the genera and species as being related if they resembled each other in general appearance. However, such resemblance, often due to convergent adaptation to habitat and mode of life, is often deceptive, and many superficially similar genera proved to be quite unrelated when their external and some internal characters were compared in detail.

For example, the genera *Acrida* and *Truxalis*, which are superficially similar and were usually regarded as closely related, actually belong to clearly distinct subfamilies. *Mesopsis* and *Mesopsera* were also regarded as related, but the first

¹ Only the family *Tetrigidae*, not the whole suborder *Tetrigoidea*, is compared here with *Acridoidea*, since it is only this family, not the whole suborder, that was regarded as belonging to the *Acridoidea*.

belongs to the subfamily *Truxalinae* and the second to *Hemiacridinae*. *Batrachotetrigini* were regarded as a part of *Oedipodinae*, to which they are superficially similar, but it is undisputed now that they belong to the family *Pamphagidae*.

The characters used for differentiation of families and subfamilies will be seen from the diagnoses and the table below, but a few explanatory remarks are necessary.

Chopard (1920) was the first to introduce the structure of the internal, mainly male, genitalia for the purpose of systematics. Since then genitalia have been used by a few other authors, as supplementary characters for the differentiation of species and genera. On a wider scale, for characterizing higher groups, male genitalia were used by Roberts (1941), Uvarov (1943) and Dirsh (1956) and the female genitalia by Slifer (1939-43) and Dirsh (1957).

It may be suggested that the male genitalia represent one of the most reliable characters for the classification of higher taxonomic units, because they are less subject to the adaptive changes of the organism in changing environmental conditions than are the external structures.

For the differentiation of families the phallic complex is certainly most reliable and can be used as a single character. Up to the present time, no intermediate forms which might suggest transition from one family to another, have been found. It serves by itself to define some subfamilies, e.g. *Euryphyminae*, *Calliptaminae*, *Eremogryllinae* and *Hemiacridinae*, or it may be used as an auxiliary character. It displays a considerable diversity at the generic level and sometimes may be used for separation of species.

Other internal characters, e.g. the Comstock-Kellogg glands, alimentary canal, malpighian tubes, nervous system, internal skeleton, muscles, chromosomes, etc., may offer characters of value, but too few species have been studied in these respects for use to be made of them for taxonomic purposes at present.

The second important character recently introduced into the systematics of *Acridoidea* is the stridulatory mechanism. The ability of some grasshoppers to produce sounds detectable by the human ear was known from time immemorial, but the relations between the types of the sound-producing mechanisms and taxonomy were not stressed until comparatively recently. A variety of structures serving for stridulation has been described (Uvarov, 1928, 1942; Chopard, 1938; Henry, 1942; Burtt, 1946; Kevan, 1953-54; Dirsh, 1955) and it is clear that they have important taxonomic value. Such structures exist in the majority of families and subfamilies, while their regular absence in others also appears characteristic.

In the majority of cases, the stridulatory mechanism provides additional taxonomic evidence for systematic groups, based on other characters. In some groups it even provides the main character when others are less adequate or are obscured by convergence, general reduction, etc.

The most important point is the principle of the structure of the stridulatory mechanism. For example: the males of *Tanaoceridae*, *Pneumoridae* and *Xyronotidae* have a combination of ridges on the sides of the third abdominal tergite with a serrated or non-serrated ridge on the internal side of the hind femora. In the majority of subfamilies of the family *Acrididae* the mechanism is based on the friction between the elytra and hind legs. In *Truxalinae* and *Eremogryllinae* this

TABLE II.—*Families and their Main*

Families	Cingulum	Internal characters						
		Valves of penis	Sacs	Epiphallus	Oval sclerites	Comstock-Kellogg glands*	Ileal caeca*	Chromosomes†
Eumastacidae	. Absent	Single sclerited	Ejaculatory sac without pockets	Variable	—	—	+	Small
Proscopiidae	. Primitive	Single sclerited	Ditto	Bridge-shaped	—	—	—	„
Tanaoceridae	. „	?	?	Plate-shaped	—	?	?	?
Pneumoridae	. „	Paired not divided	Ejaculatory sac without pockets	Ditto	—	?	?	Small
Xyronotidae	. „	?	?	„	—	?	?	„
Trigonopterygidae	„	Paired divided	Ejaculatory sac without pockets	„	—	?	?	„
Charilaidae	. Differentiated	Ditto	Ditto	„	—	?	?	?
Pamphagidae	. „	„	„	„	—	—	—	Large
Lathiceridae	. Shield-like	„	„	Bridge-shaped	+	?	?	?
Pyrgomorphidae	. Capsule-like	Paired not divided	„	Ditto	—	—	—	Large
Ommexechidae	. Differentiated	Ditto	Ejaculatory sac with pockets	Bridge-shaped with separated lateral plates	+	+	—	Small
Pauliniidae	. Ditto	Paired divided	Ditto	Ditto	+	+	?	„
Lentulidae	. „	Paired not divided	Ejaculatory sac without pockets	Bridge-shaped	+	—	?	„
Acrididae	. „	Paired divided or flexured	Ditto	Variable	+	+ or —	—	Medium

* According to Slifer (1939-43).

† According to Helwig (1958).

type of mechanism is represented by the sharpened veins of the elytra and a serration (with articulated or non-articulated pegs) on the internal side of the hind femora. In the group *Oedipodini* of *Acridinae* it consists of a serrated intercalary vein of the elytra and a sharp ridge on the internal side of the hind femora. In *Romaleinae* it is represented by serrated veinlets on the hind wings and sharpened veins on the lower surface of the elytra. In *Hemiacridinae* it is a combination of the thickened

Characters (+ Present, — Absent)

External characters

Abdomino-femoral stridulatory mechanism	Tube-like prothorax	Hind legs	Brunner's organ	Basal lobes of hind femur	Fastigial furrow	Antennal grooves	Median carina of pronotum	Elytra and wings	Tympanum
—	—	Saltatorial	+	Variable	+ or —	—	Single or absent	+ or —	—
—	+	Almost cursorial	—	Lower lobe longer	—	—	Ditto	Mainly —	—
+	—	Saltatorial	+	Ditto	—	—	Single	—	—
+	—	Almost cursorial	—	„	+	—	„	+	—
+	—	Saltatorial	+	Lower lobe shorter	+	—	„	—	—
—	—	„	+	Ditto	+	—	„	+	—
—	—	„	+	Lower lobe longer	+	—	Double	+	+
—	—	„	+	Ditto	+	—	Single or absent	+ or —	Normally +
—	—	„	+	„	+	+	Ditto	—	—
—	—	„	+	„	+	—	„	+ or —	Normally +
—	—	„	+	Of equal length	+	—	„	+ or —	+ or —
—	—	„	+	Lower lobe shorter	—	—	Single	+	+
—	—	„	+	Ditto	—	—	Single or absent	—	—
—	—	„	+	Lower lobe shorter or both of equal length	—	—	Ditto	+ or —	+ or —

veinlets of the elytra with the spines and spurs of the hind tibiae. There are other main types of the mechanism, and their modifications in some genera of the known subfamilies and families may provide useful auxiliary characters.

It is necessary to bear in mind that in some genera and species the stridulatory mechanism may be lost or reduced (particularly in females), but its loss is a secondary phenomenon often connected with the reduction or loss of wings. It should be

noted also that analogous structures may appear as an exception in unrelated genera of different subfamilies and families, but this happens with almost every external character. As an example of such analogous development, the serration on the internal side of the hind femora in the two South American genera *Atrachelacris* and *Leiotettix* of the *Catantopinae* may be cited. The serration is somewhat similar to that in *Truxalinae*, but it is not accompanied by the specialization of the veins of the elytra. The genera nearest to *Atrachelacris* and *Leiotettix* have no serration at all.

At the present stage of knowledge of *Acridoidea* it is not possible to estimate the phylogenetic value of the majority of external morphological characters; even their purpose is unknown. In consequence it is not possible to say that any external character is more, or less, important than any other. The way they are used in classification is mainly a matter of convenience. Thus although the stridulatory mechanism is not necessarily more valuable than the other external characters, it offers useful diagnostic features which cannot be ignored. The biological significance of stridulation is great, since it is largely connected with sexual activity, which makes it important for the survival of the species.

A further useful character, introduced by Uvarov (1943), is the structure of the hind femur. It is useful in differentiation of certain families and subfamilies (see Tables II and III). The lower basal lobe of the hind femur may be longer or shorter than, or equal to, the upper. This character, however, has no absolute value, since intermediate forms occur in unrelated groups, but it is valuable if considered in combination with other features.

The next important character is a deep, short, median furrow on the apex of the fastigium of the vertex, which is, in most cases, a direct continuation of the sulcus of the frontal ridge. Whether it is homologous with the epicranial suture of other insects or is a secondary phenomenon is not relevant here. This furrow, first noticed by Stål (1876), and later mentioned by Rehn (1938), as characteristic for *Pamphagidae*, was introduced as a character of great value by Uvarov (1943) for that family and *Pyrgomorphidae*. Now it can be extended to *Trigonopterygidae*, *Charilaidae*, *Lathiceridae*, *Xyronotidae* and *Pneumoridae*. It is, however, not an absolute character, since in some *Pamphagidae* and others in which the head approximates to globular, it has a secondary tendency to disappear, while it occasionally appears in quite unrelated genera of *Acrididae*.

Helwig (1958) suggested, as a taxonomic character for families, the size of chromosomes, dividing the families into groups, with small, medium and large chromosomes (see Table II). It is difficult to estimate the real value of this character since too few genera have been studied.

The following general considerations are used here as a basis for the division of *Acridoidea* into families and subfamilies. A family is regarded as a group of genera possessing characters which do not occur in other groups or some of which occur in different combinations; there are no living genera intermediate between the families. A subfamily is regarded as a group of genera with one or more convenient characters, or a combination of characters, which do not normally occur in other groups of genera of the family, but are not exclusive, so that the occurrence of intermediate genera is possible.

LIST OF FAMILIES

Order *Orthoptera*

Suborder *Acridoidea*

1. Family <i>Eumastacidae</i>	8. Family <i>Pamphagidae</i>
2. „ <i>Proscopiidae</i>	9. „ <i>Lathiceridae</i>
3. „ <i>Tanaoceridae</i>	10. „ <i>Pyrgomorphidae</i>
4. „ <i>Pneumoridae</i>	11. „ <i>Ommexechidae</i>
5. „ <i>Xyronotidae</i>	12. „ <i>Pauliniidae</i>
6. „ <i>Trigonopterygidae</i>	13. „ <i>Lentulidae</i>
7. „ <i>Charilaidae</i>	14. „ <i>Acrididae</i>

KEY TO FAMILIES

The following key to families is based on external characters alone, but it must be remembered that in some cases male genitalia provide the decisive character and these are mentioned in the respective family diagnoses.

- 1 (2) Frons mostly flattened. Cubital vein of elytron and medial vein of hind wing unbranched. Antenna, on lower apical part, usually with small tubercle (antennal organ). Basal segment of hind tarsus with serrated margins, or with basal, or apical, or both external teeth or at least with a basal external tubercle *Eumastacidae*
- 2 (1) Frons of variable shape. Cubital vein of elytron and medial vein of hind wing usually branched. Antennal organ mostly absent. Basal segment of hind tarsus never serrated, never with teeth or tubercle.
- 3 (4) Body stick-like. Prothorax tube-like, with lower margins of lateral lobes of pronotum fused with prosternum. Brunner's organ absent . . . *Proscopiidae*
- 4 (3) Body usually not stick-like. Prothorax not tube-like, with lower margins of lateral lobes of pronotum not fused with prosternum. Brunner's organ present (in *Pneumoridae* vestigial or absent).
- 5 (10) Abdomino-femoral stridulatory mechanism, represented by ridges on the third abdominal tergite and a ridge on internal side of hind femur, present in males.
- 6 (7) Antenna in male longer than, in female about as long as, body. Abdominal part of stridulatory mechanism represented by curved cylindrical ridge covered with fine transverse ridgelets; ridge on internal side of hind femur not serrated *Tanaoceridae*
- 7 (6) Antenna in both sexes much shorter than body. Abdominal part of stridulatory mechanism represented by a row of short, sharp ridges; ridge on internal side of hind femur serrated.
- 8 (9) Body stout, in males strongly inflated. Head with flattened vertical frons. Brunner's organ vestigial or absent. Male macropterous, female with reduced wings *Pneumoridae*
- 9 (8) Body slender, compressed. Head acutely conical. Brunner's organ present. Completely apterous *Xyronotidae*
- 10 (5) Abdomino-femoral stridulatory mechanism absent.
- 11 (22) Fastigial furrow present.
- 12 (13) Lower basal lobe of hind femur shorter than the upper. Elytron widening towards apex *Trigonopterygidae*
- 13 (12) Lower basal lobe of hind femur longer than or as long as the upper. Elytron not widening towards apex.
- 14 (21) Lower basal lobe of hind femur longer than the upper.

- 15 (16) Antennal grooves present *Lathiceridae*
 16 (15) Antennal grooves absent.
 17 (18) Median carina of pronotum double *Charilaidae*
 18 (17) Median carina of pronotum single or absent.
 19 (20) Head of variable shape, but not acutely conical. Apical fastigial areas absent.
 Krauss's organ mostly present *Pamphagidae*
 20 (19) Head acutely conical, with regularly incurved frons. Apical fastigial areas
 mostly present. Krauss's organ absent *Pyrgomorphidae*
 21 (14) Lower basal lobe of hind femur as long as upper one *Ommexechidae*
 22 (11) Fastigial furrow absent.
 23 (24) Completely apterous. Tympanum absent. *Lentulidae*
 24 (23) Fully winged or with reduced wings, or apterous. Tympanum usually present,
 if absent, then body depressed.
 25 (26) Medial vein of elytron unbranched. Ocelli very large. Hind tibia with
 strongly expanded lateral margins *Pauliniidae*
 26 (25) Medial vein of elytron usually branched. Ocelli comparatively small. Lateral
 margins of hind tibia not expanded, slightly expanded or rarely strongly
 expanded *Acrididae*

Family *Eumastacidae*

(Text-figs. 1, 2)

Type genus : *Eumastax* Burr, 1899

Body of variable shape. Head of variable shape, with frons mostly flattened. Antenna on lower apical part usually with tubercle-like antennal organ. Prosternal process absent. Lower basal lobe of hind femur longer or shorter than upper one. Brunner's organ present. Basal segment of hind tarsus with serrated upper margins or with basal, or apical, or with both external teeth, or at least with basal external tubercle. Elytra and wings fully developed, reduced or absent; cubital vein of elytra and medial vein of hind wing unbranched. Ectophallus relatively large, not forming cingulum. Endophallus small, with single-sclerited penis. Epiphallus of variable shape. Oval sclerites absent. Ileal caeca present. Stridulatory mechanism not known.

In the structure of the phallic complex the family *Eumastacidae* differs so strongly from other families of *Acridoidea* that they can hardly be regarded of the same rank. However, temporarily, it is advisable to keep them in their present status until more data are available. A sac-like ectophallus without a cingulum is possibly a primitive feature, which does not occur in other families; on the other hand, sometimes the complicated structure of the ectophallus indicates a high specialization but in a different direction from that in other *Acridoidea*. The primitiveness is suggested also by the small, and in most cases, comparatively simple, endophallus, with penis of a single sclerite. In higher *Acridoidea* the endophallus is complicated and, except in *Proscopiidae*, always with a two-sclerited penis.

Another internal character, which according to Slifer (1944), occurs only in *Eumastacidae*, is the presence of ileal caeca in the form of six appendices attached to the hindgut of the alimentary canal.

FIG. 1. 1. *Eumastax surda* Burr, whole insect. 2. The same, elytron and wing. 3-6. Basal tarsal segment. 3. *Biroella*. 4. *Eumastax*. 5. *Pseudothericles*. 6. *Chorotypus*.

FIG. 2. Examples of the phallic complex in *Eumastacidae*. 1-3. *Moraba* sp. 1. Phallic complex from above. 2. The same in profile. 3. Penis from above. 4-6. *Euschmidtia burri* Uv. 4. Phallic complex from above. 5. The same in profile. 6. Penis from above. 7-9. *Erucius dimidiatipes* I. Bol. 7. Phallic complex from above. 8. The same in profile. 9. Penis from above. 10-12. *Biroella gracilis* C. Bol. 10. Phallic complex from above. 11. The same in profile. 12. Penis from above. 13-15. *Gomphomastax clavata* (Ostr.). 13. Phallic complex from above. 14. The same in profile. 15. Penis from above. 16, 17. *Erianthus guttatus* (Westw.). 16. Phallic complex from above. 17. The same in profile.

The external characters of value are the unbranched cubital vein of the elytron and the unbranched median vein of the hind wing (Ragge, 1955). However, the *Eumastacidae* share the former character with *Ommexechidae*, *Pauliniidae* and some *Pyrgomorphidae*, and it occurs also in some *Catantopinae* with shortened elytra.

The presence of teeth or a tooth, or at least a tubercle, on the basal segment of the hind tarsus is a character which occurs only in *Eumastacidae* and not in any other family of *Acridoidea*.

Rehn (1948) divided the family *Eumastacidae* into seventeen subfamilies. Since then, one subfamily (*Tanaocerinae*) has been removed and raised to family rank (Dirsh, 1955) and one new subfamily *Socotrellinae* Popov, 1957, described. In 1958 Rehn and Grant erected three more subfamilies. However, the main character of the family, the phallic complex, is so divergent in certain subfamilies that a wider separation than at the subfamily level appears probable, while some other subfamilies suggest closer interrelations. It would be premature to attempt a reclassification of them, because only a few of the known genera have been studied in respect of the phallic complex. At present it is more practical to regard the group temporarily as one very heterogeneous family.

LIST OF SUBFAMILIES OF EUMASTACIDAE

(Alphabetical order)

1. <i>Biroellinae</i>	11. <i>Mastacideinae</i>
2. <i>Chininae</i>	12. <i>Miraculinae</i>
3. <i>Chorotypinae</i>	13. <i>Morabinae</i>
4. <i>Episactinae</i>	14. <i>Morseinae</i>
5. <i>Eruciinae</i>	15. <i>Paramastacinae</i>
6. <i>Espagnolinae</i>	16. <i>Pseudomastacinae</i>
7. <i>Eumastacinae</i>	17. <i>Socotrellinae</i>
8. <i>Euschmidtinae</i>	18. <i>Teicophryinae</i>
9. <i>Gomphomastacinae</i>	19. <i>Temnomastacinae</i>
10. <i>Malagassinae</i>	20. <i>Thericleinae</i>

Family *Proscopiidae*

(Text-fig. 3)

Type genus: *Proscopia* Klug, 1820

Body stick-like. Basi-occipital slit of head present. Pronotum with reduced lateral lobes, lower margins of which are fused with prosternum, whole prothorax representing a tube-like structure. Prosternal process absent. Elytra and wings absent (rarely present but strongly reduced). Tympanum absent. Hind legs almost cursorial. Brunner's organ absent. External apical spine of hind tibia present. Phallic complex with differentiated ectophallus; cingulum primitive. Endophallus strongly specialized; penis single-sclerited. Epiphallus bridge-shaped; oval sclerites absent. Stridulatory mechanism not found.

All the characters of *Proscopiidae* indicate absence of close relationship with any other known family. The loss or great reduction of the wings and the reduction of

the hind legs to almost cursorial condition, and the absence of Brunner's organ, make comparisons more difficult. The phallic complex, with primitive cingulum and highly complicated endophallus, represents a blend of primitive and specialized characters but no other anatomical studies are available. The only suggestion which may be made is that the family represents a very early branch of unknown pre-acridoid stock, and is possibly remotely related to *Eumastacidae*.

Distributed in South America.

For scope of the family see Mello-Leitão, 1939.

FIG. 3. *Proscopia scabra* Klug. 1. Whole insect. 2-5. Phallic complex. 2. From above. 3. The same, but ectophallic membrane and epiphallus removed. 4. In profile. 5. The same, but ectophallic membrane and epiphallus removed.

Family *Tanaoceridae*

(Text-fig. 4)

Type genus : *Tanaocerus* Bruner, 1906

Antenna in male longer, in female only slightly shorter than body. Head subspheroidal. Prosternal process absent. Elytra, wings and tympanum absent. On the sides of third abdominal tergite of male there is thick, cylindrical ridge, densely covered with fine transverse ridgelets (part of stridulatory mechanism). Lower basal lobe of hind femur longer than upper one. External apical spine of hind tibia present. Male subgenital plate composed of several separate sclerites, connected by membrane. Poorly developed cingulum of phallic organ present. Epiphallus disc-shaped, without ancorae and lophi. Oval sclerites absent.

When the first genus of the family, *Tanaocerus* Bruner, 1906, was described it was referred to *Eremobiinae*. Later Rehn (1948) placed it and the second known genus into the family *Eumastacidae* and erected for them the subfamily *Tanaocerinae*.

When the peculiar stridulatory mechanism was found in the male *Tanaocerus*, the subfamily was raised to family rank (Dirsh, 1955).

The differences of this family from *Eumastacidae* and other *Acridoidea* are extremely striking. The peculiar stridulatory mechanism, one part of which is a ridge covered with ridgelets on the sides of the third abdominal tergite and another part is a short, sharp ridge on the internal side of the hind femur, is shared only with *Pneumoridae* and *Xyronotidae*, with which there is otherwise no relationship. The

FIG. 4. *Tanaocerus koebelei* Bruner. 1. Whole insect, male. 2. Abdominal part of the stridulatory mechanism. 3. Epiphallus.

Eumastacidae, to which *Tanaoceridae* was previously referred, have no stridulatory mechanism. A subspheroidal head, as in *Tanaocerus*, is not found in *Eumastacidae*. Such peculiarly long antennae as in *Tanaocerus* do not occur in any other family of *Acridoidea*. The peculiar structure of the male subgenital plate of *Tanaocerus* is also not found in other families.

The phallic complex of the family is not yet sufficiently studied, but the available data suggest that it is very characteristic. The presence of a primitive cingulum also suggests that *Tanaoceridae* differ widely from *Eumastacidae*, which have no cingulum. All these considerations indicate that the family *Tanaoceridae* is sharply different from other families of *Acridoidea*.

The family occurs only in the south-west part of North America.

List of known genera :

1. *Mohavacris* Rehn, 1948

2. *Tanaocerus* Bruner, 1906

Family *Pneumoridae*

(Text-fig. 5)

Type genus : *Pneumora* Thunberg, 1775

Male body strongly inflated. Head short, with shortened fastigium of vertex ; face flattened, vertical, frontal ridge absent ; fine fastigial furrow present. Ocelli located internally or externally to bases of antennae. Prosternal process absent. Venation primitive ; elytra without vannal fold, hind wing with remigium almost as large as vannus. Tympanum absent. Stridulatory mechanism in male represented by a row of transverse ridges on the sides of third abdominal tergite and serrated ridge on internal side of hind femur. Hind legs almost cursorial ; lower basal lobe of hind femur longer than upper one ; Brunner's organ vestigial or absent. Phallic complex primitive ; ectophallus sac-like ; cingulum rudimentary ; penis rudimentary, paired, valves not divided. Epiphallus plate-like, without lophi and ancorae ; oval sclerites absent.

The family *Pneumoridae* is so different from other families of *Acridoidea*, that there is no doubt of its isolated position. It shares, however, some features of stridulatory mechanism, as well as a similar type of epiphallus, with *Tanaoceridae* and *Xyronotidae*. The latter character is shared with *Charilaidae*, *Pamphagidae* and *Trigonopterygidae* also.

The primitive phallic complex and wing venation suggest that the family probably represents a surviving branch of very ancient *Acridoidea*.

By the shape of the epiphallus and spermatheca and the position of the ocelli the family is sharply divided into two groups, one consisting of the genera *Pneumora* and *Physophorina* and the other of the genera *Physemacris*, *Bullacris* and *Prostalia*.

The family is distributed in South Africa and in East Africa, as far north as Uganda.

List of known genera :

1. *Bullacris* Roberts, 1941

4. *Pneumora* Thunberg, 1775

2. *Physemacris* Roberts, 1941

5. *Prostalia* I. Bolivar, 1906

3. *Physophorina* Westwood, 1874

Family *Xyronotidae*

(Text-fig. 6)

Type genus : *Xyronotus* I. Bolivar, 1884

Body laterally compressed. Head conical. Fastigial furrow present. Prosternal process present. Elytra, wings and tympanum absent. Lower basal lobe of hind

FIG. 5. 1. *Bullacris longicornis* (St.), whole insect. 2-6. Phallic complex of *Physemacris variolosa* (L.). 2. From above. 3. Dorso-distal view. 4. In profile. 5. Endophallus in profile. 6. The same from above. 7. Epiphallus of *Pneumora inanis* (F.). 8-9. Spermatheca. 8. *Pneumora inanis* (F.). 9. *Bullacris longicornis* (St.).

femur shorter than upper one. Brunner's organ present. External apical spine of hind tibia present. Sides of third abdominal tergite of male with a row of sharp, small, transverse ridges (part of stridulatory mechanism, the other part being serrated ridge on internal side of hind femur). Ectophallus weakly differentiated; cingulum primitive. Epiphallus shield-like, without lophi and with pair of projections. Oval sclerites absent.

I. Bolivar (1909) placed the genus *Xyronotus*, which is the only one of the family, into "Sectio Xyronoti" of the family *Pyrgomorphidae*. Kevan (1952) regarded

FIG. 6. *Xyronotus aztecus* I. Bol. 1. Whole insect, female. 2. Epiphallus.

it as a tribe "... temporarily attached to the *Trigonopterygidae*". It was raised to family rank by Dirsh (1955).

As can be seen from the diagnosis, there are several characters, like the presence of the fastigial furrow and the shape of the hind femur, which *Xyronotus* shares with other families, but the stridulatory mechanism is extremely peculiar, similar to that in *Pneumoridae* and *Tanaoceridae*, to which *Xyronotidae* are not otherwise related. The mechanism and the primitive phallic complex do not permit *Xyronotus* to be placed into any known family and there is no alternative to regarding it as the only known genus of a distinct family.

The only genus, *Xyronotus* I. Bolivar, 1884, occurs in Mexico.

Family *Trigonopterygidae*

(Text-fig. 7)

Type genus : *Trigonopteryx* Charpentier, 1841

Body strongly laterally compressed. Head conical. Fastigial furrow present. Prosternal process present. Elytra widening towards apex, with radial and medial veins fused. Remigium of hind wings almost as wide as vannus. Tympanum absent. Lower basal lobe of hind femur shorter than upper one. Brunner's organ present. External spine of hind tibia present. Phallic complex in reversed position, dorsal side turned ventrad, with penis directed towards anterior end of body and epiphallus located on ventral side. Ectophallus differentiated and strongly specialized; cingulum well developed; valves of penis paired, divided. Epiphallus plate-like. Oval sclerites absent. No stridulatory mechanism known.

Westwood (1841), who described the genus *Systella*, placed it "between *Truxalides* and *Conophori*". Walker (1870) regarded the two known genera as a family which he named *Trigonopterygidae*, but I. Bolivar (1884) placed it in *Pyrgomorphinae* as a subtribe and in 1909 referred it to *Pyrgomorphinae* as "sectio *Systellae*". Dirsh (1952) restored the group as a subfamily *Trigonopteryginae* and in 1956, owing to the peculiar structure of the phallic complex, re-instated it as a family.

The very peculiar, strongly specialized and reversed phallic complex is alone sufficient to separate *Trigonopterygidae* from the other families. The unusual shape of the elytron and wings, the elytron widening towards the apex, with the radius and media fused, and the wide remigium of the hind wing, do not occur in other families except *Pneumoridae*. The combination of a distinct fastigial furrow and the lower basal lobe of the hind femur being shorter than the upper one, occurs only in *Trigonopterygidae* and *Xyronotidae*, but the latter are extremely different in all other respects. All diagnostic features indicate that the family is isolated from the others.

The family is found in Malaya, Australasian Archipelago and Philippines.

*List of examined genera :*1. *Systella* Westwood, 18412. *Trigonopteryx* Charpentier, 1841Family *Charilaidae*

(Text-fig. 8)

Type genus : *Charilaus* Stål, 1875

Body subcylindrical. Head conical. Fastigial furrow present. Pronotum with two parallel median carinae. Prosternal process present. Mesosternal furcal suture curved backwards. Elytra and wings fully developed or reduced. In fully winged forms, wing-elytron stridulatory mechanism present. Tympanum present. Lower basal lobe of hind femur longer than or equal to upper one. Brunner's organ present. External apical spine of hind tibia present. Ectophallus differentiated;

FIG. 7. *Trigonopteryx hopei* Westw. 1. Whole insect, male. 2. Fastigium of vertex from above. 3-10. Phallic complex. 3. Dorsal view. 4. The same, ventral view. 5. Ventral view, but ectophallic membrane and epiphallus removed. 6. The same, with cingulum removed. 7. Whole phallic complex, in profile. 8. The same, with ectophallic membrane and epiphallus removed. 9. Endophallus, in profile. 10. Epiphallus. 11. Epiphallus of *Systella rafflesii* Westw. 12. End of abdomen of *Trigonopteryx hopei* Westw. in profile, showing the position of penis. 13. Spermatheca of *Systella rafflesii* Westw.

FIG. 8. *Charilaus carinatus* St. 1. Whole insect, male. 2-6. Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. The same, in profile. 5. Endophallus from above. 6. Epiphallus. 7. Spermatheca.

cingulum differentiated, without zygoma and rami; with apodemes disconnected; valves of penis paired, divided; spermatophore sac dorsal. Epiphallus shield-like, without ancorae and lophi, with ventro-lateral appendices. Oval sclerites absent.

The family *Charilaidae* includes three known genera. The first, *Charilaus*, was placed by Stål (1875) in *Pyrgomorphidae*. Karsch (1896) suggested that it belongs neither to *Pyrgomorphidae* nor to *Pamphagidae* and referred it to "*Caloptenoden*". Saussure (1889) placed *Charilaus* in *Pamphagidae*, and so did I. Bolivar (1916). Uvarov (1943) suggested that it belongs to the "*Pamphaginae-Pyrgomorphinae*" complex. Dirsh (1953) erected for the group a new subfamily *Charilainae* and in 1956, mainly on the basis of the phallic complex, raised it to family rank.

The phallic complex of *Charilaidae* has very little in common with *Pyrgomorphidae* and approximates more to that in *Pamphagidae*, from which, however, it differs strongly in the disconnected apodemes of the cingulum, the absence of zygoma and rami, and the presence of ventro-lateral appendices of the epiphallus.

The external characters separating *Charilaidae* from *Pamphagidae* and *Pyrgomorphidae* are the double median carina of the pronotum, a character unique in *Acridoidea*, and the type of stridulatory mechanism, which does not occur in the two above-mentioned families.

The family is distributed in S. and SW. Africa.

List of known genera :

1. <i>Charilaus</i> Stål, 1875	3. <i>Pamphagodes</i> I. Bolivar 1878
2. <i>Hemicharilaus</i> Dirsh, 1953	

Family *Pamphagidae*

Type genus : *Pamphagus* Thunberg, 1815

Body of variable shape. Head of variable shape. Fastigial furrow present. Prosternal process present. Mesosternal furcal suture straight. Elytra and wings fully developed, reduced, or absent. Stridulatory mechanism of various types present. Tympanum usually present. Krauss's organ mostly present. Lower basal lobe of hind femur longer than upper one. Brunner's organ present. Ectophallus differentiated; cingulum differentiated; valves of penis paired, divided and articulated; spermatophore sac dorsal. Epiphallus shield-like, with ancorae and without lophi. Oval sclerites absent.

The *Pamphagidae* are a well defined family which has no clear affinity with other *Acridoidea*. In the structure of the phallic complex it has some characters in common with *Charilaidae*, such as the divided valves of the penis, the position of the spermatophore sac and the shape of the epiphallus, but other characters are very different (see *Charilaidae*).

The family is distributed throughout Africa and S. Europe and occurs in mountainous and semi-desert parts of Asia as far as the Far East.

The *Pamphagidae* are divided here into four subfamilies.

KEY TO SUBFAMILIES OF *Pamphagidae*

- 1 (6) Middle tibia without teeth or tubercles on upper side. If winged, second vannal vein of hind wing not curved and no areas of hind wing expanded
- 2 (3) Body strongly elongated, comparatively slender, cylindrical. Fastigium of vertex and upper part of frons, strongly projecting forwards. Antenna triangular in cross-section. Epiphallus mostly with deeply excised posterior margin. Krauss's organ absent *Echinotropinae*
- 3 (2) Body stout, compressed or depressed. Fastigium of vertex moderately or not at all projecting forwards. Antenna of variable shape. Posterior margin of epiphallus not excised. Krauss's organ mostly present.
- 4 (5) Costal area of elytron (in case of fully developed or shortened elytra) expanded and covered with dense, parallel, ridge-like veinlets (stridulatory specialization). Upper carina of hind femur strongly serrated *Porthetinae*
- 5 (4) Elytra never fully developed, lobiform, lateral, without stridulatory specialization. Upper carina of hind femur smooth, slightly serrated or rarely strongly serrated *Pamphaginae*
- 6 (1) Middle tibia on upper side with a row of teeth or tubercles. If winged, second vannal vein of hind wing curved and first and third vannal area expanded *Akicerinae*

Subfam. *Echinotropinae*

(Text-fig. 9)

Type genus : *Echinotropis* Uvarov, 1944

Body strongly elongated, cylindrical. Integument strongly rugose. Antenna triangular in cross-section, tapering towards apex. Fastigium of vertex and upper part of frons strongly protruding forwards. Pronotum spined or tuberculate. Prosternal process low, collar-like. Elytra fully developed, lobiform, or absent. Tympanum present or absent. Krauss's organ absent. External apical spine of hind tibia present or absent. Epiphallus mostly with deeply excised posterior margin. No stridulatory mechanism known.

The genera of this subfamily represent a natural and a very peculiar group. The most distinctive features are elongate, slender body, which is unusual for *Pamphagidae*, complete absence of Krauss's organ and a characteristic epiphallus, with the posterior end deeply excised in the middle (in two genera).

The subfamily occurs only in S. Africa.

List of known genera :

1. *Echinotropis* Uvarov, 1944
2. *Geloiomimus* Saussure 1899
3. *Thrincotropis* Saussure, 1899

Subfamily *Porthetinae* nov.

(Text-fig. 10)

Type genus : *Porthetis* Serville, 1831

Large, with body compressed or depressed. Integument rugose. Antenna compressed, differentiated or tapering towards apex, or ribbon-like. Frons, in profile, with protruding fastigium of vertex or straight. Pronotum from highly crested to flat, depressed. Prosternal process of variable shape. In most cases

FIG. 9. 1. *Echinotropis horrida* (Sauss.), female. 2-5. *Geloiomimus spinosus* (Dirsh), 2. male. 3. Head from above. 4. Wing. 5. Epiphallus. 6. Epiphallus of *Geloiomimus nasicus* Sauss.

males winged, females wingless. Costal area of elytron (except *Bolivarella* with small lobiform elytra) expanded and provided with dense, parallel, ridge-like stridulatory veinlets. Krauss's organ present. Tympanum present, open, without subtympanal

FIG. 10. *Porthetis carinata* (L.). 1. Male. 2. Female. 3. Epiphallus.

lobe. External apical spine of hind tibia present. Apical valves of penis mostly serrated.

The *Porthetinae* were regarded as a group (Dirsh, 1958), but according to all the characters and particularly owing to the peculiar stridulatory mechanism, it deserves to be accorded subfamily rank.

This subfamily is distributed from S. Africa to Angola, E. Africa, the Red Sea area and the SW. corner of Arabia.

List of known genera :

1. <i>Aphantotropis</i> Uvarov, 1924	8. <i>Porthetis</i> Serville, 1831
2. <i>Bolivarella</i> Saussure, 1887	9. <i>Puncticornia</i> Dirsh 1958
3. <i>Cultrinator</i> I. Bolivar, 1925	10. <i>Stollia</i> I. Bolivar, 1916
4. <i>Hoplolopha</i> Stål, 1876	11. <i>Trachypetrella</i> Kirby, 1910
5. <i>Lamarckiana</i> Kirby, 1910	12. <i>Transvaalana</i> Dirsh, 1958
6. <i>Lobosceliana</i> Dirsh, 1958	13. <i>Vansoniacris</i> Dirsh, 1958
7. <i>Pagopedilum</i> Karsch, 1896	14. <i>Xiphoceriana</i> Dirsh, 1958

Subfamily ***Akicerinae***

(Text-fig. 11)

Type genus : *Akicera* Serville, 1831

Of medium size ; body compressed or depressed. Integument mostly strongly rugose. Antenna from filiform to ensiform. Head from conical to subglobular. Pronotum from high crested to flat, depressed ; metazona mostly longer, sometimes slightly shorter, than prozona. Prosternal process mostly collar-like. Elytra and wings fully developed, shortened, vestigial, or absent. Second vannal vein of hind wing curved and first and third vannal areas expanded (stridulatory specialization). Krauss's organ present, sometimes poorly developed. Tympanum present. Middle tibia on upper side with row of small teeth or tubercles (second part of stridulatory specialization). External apical spine of hind tibia mostly present.

This subfamily represents a combination of several groups or tribes which were known as *Akicerini*, *Adephagini*, part of *Thrinchini* and part of *Batrachotetrigini*. They are all united by a common stridulatory specialization of the venation of the hind wing and specialization of the middle tibia. In this respect they constitute a natural group equal to the others of subfamily rank. However, their appearance is rather diverse and they can be easily subdivided into lower taxonomic units, corresponding to the groups or tribes mentioned above.

Akicerinae occur in S. and N. Africa, SE. Europe and Asia.

List of known genera :

1. <i>Akicera</i> Serville, 1831	15. <i>Haplotropis</i> Saussure, 1888
2. <i>Adephagus</i> Saussure, 1887	16. <i>Iranotmethis</i> Uvarov, 1943
3. <i>Asiotmethis</i> Uvarov, 1943	17. <i>Melanotmethis</i> Uvarov, 1943
4. <i>Atrichotmethis</i> Uvarov, 1943	18. <i>Mongolotmethis</i> Bey-Bienko, 1948
5. <i>Batrachornis</i> Saussure, 1884	19. <i>Pezotmethis</i> Uvarov, 1943
6. <i>Batrachotetrix</i> Burmeister, 1838	20. <i>Prionotropis</i> Fieber, 1853
7. <i>Eotmethis</i> Bey-Bienko, 1948	21. <i>Pseudotmethis</i> Bey-Bienko, 1948
8. <i>Eremocharis</i> Saussure, 1884	22. <i>Rhinotmethis</i> Sjöstedt, 1933
9. <i>Eremopeza</i> Saussure, 1884	23. <i>Strumiger</i> Zubowsky, 1896
10. <i>Eremotettix</i> Saussure, 1888	24. <i>Thrinchus</i> Fischer v. Waldheim, 1833
11. <i>Eremotmethis</i> Uvarov, 1943	25. <i>Tmethis</i> Fieber, 1853
12. <i>Filchnerella</i> Karny, 1908	26. <i>Tuarega</i> Uvarov, 1943
13. <i>Glyphanus</i> Fieber, 1853	27. <i>Utubius</i> Uvarov, 1936
14. <i>Glyphotmethis</i> Bey-Bienko, 1948	

FIG. 11. 1-4. *Akicera fusca* (Thunb.). 1. Male. 2. Middle tibia, with dorsal serration. 3. Wing. 4. Epiphallus. 5. Epiphallus of *Tmethis cisti* (F.)

Subfamily *Pamphaginae*

(Text-fig. 12)

Type genus : *Pamphagus* Thunberg, 1815

From small to large size ; body compressed to depressed. Integument rugose, sometimes shiny. Antenna filiform, ribbon-like or weakly ensiform. Fastigium of

FIG. 12. *Pamphagus elephas* (L.). 1. Male. 2-5. Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. The same in profile. 5. Epiphallus. 6. Spermatheca.

FIG. 13. 1-3 *Batrachidacris tuberculata* (Rehn). 1. Male, in profile. 2. The same, from above. 3. Face (antennal grooves painted black). 4-7. Phallic complex of *Batrachidacris rubridens* (Uv.). 4. Whole phallic complex from above. 5. The same, but ectophallic membrane and epiphallus removed. 6. Penis, from above. 7. Endophallus, in profile. 8. Epiphallus of *Batrachidacris tuberculata* (Rehn). 9. Spermatheca of *Lathicerus cimex* Sauss.

vertex slightly projecting forwards. Pronotum from crest-like to flat, depressed; metazona always much shorter than prozona. Prosternal process of variable form. Elytra and wings lobiform, lateral, vestigial or absent. Tympanum present or absent. Krauss's organ mostly present. External apical spine of hind tibia present.

Of all the subfamilies of *Pamphagidae* this is probably the most heterogeneous. It contains genera of widely diverse appearance, which are united by the retrogression of characters connected with the loss or great reduction of wings; genera which cannot be placed into other, well defined subfamilies. Nevertheless, the characters (see key and diagnosis) are sufficient to differentiate the *Pamphaginae*, even if it is a rather artificial assemblage.

The subfamily is distributed in N. Africa, S. Europe and W. Asia.

List of known genera :

1. <i>Acinipe</i> Rambur, 1838	16. <i>Ocnerodes</i> Brunner, 1882
2. <i>Acrostira</i> Enderlein, 1929	17. <i>Ocneropsis</i> Uvarov, 1942
3. <i>Ananothrotres</i> Mistshenko, 1951	18. <i>Oronothrotres</i> Mistshenko, 1951
4. <i>Araxiana</i> Mistshenko, 1951	19. <i>Pamphagus</i> Thunberg, 1815
5. <i>Bufonocarodes</i> Mistshenko, 1951	20. <i>Paraemigus</i> I. Bolivar, 1914
6. <i>Eunapiodes</i> I. Bolivar, 1907	21. <i>Paranocaracris</i> Mistshenko, 1951
7. <i>Eunothrotres</i> Adelung, 1907	22. <i>Paranocarodes</i> I. Bolivar, 1916
8. <i>Euryparyphes</i> Fischer, 1853	23. <i>Paranothrotres</i> Mistshenko, 1951
9. <i>Finotia</i> Bonnet, 1884	24. <i>Pseudamigus</i> Chopard, 1943
10. <i>Glaivia</i> I. Bolivar, 1912	25. <i>Pseudonothrotres</i> Mistshenko, 1951
11. <i>Glaugarovia</i> Morales, 1949	26. <i>Prionosthenus</i> I. Bolivar, 1878
12. <i>Iranacris</i> Mistshenko, 1951	27. <i>Purpuraria</i> Enderlein, 1929
13. <i>Nocaracris</i> Uvarov, 1928	28. <i>Savalania</i> Mistshenko, 1951
14. <i>Nocarodes</i> Fischer v. Waldheim, 1846	29. <i>Tropidauchen</i> Saussure, 1887
15. <i>Ocneridia</i> I. Bolivar, 1912	30. <i>Znojikiana</i> Mistshenko, 1951

Family *Lathiceridae*

(Text-fig. 13)

Type genus : *Lathicerus* Saussure, 1888

Body robust, depressed. Head mostly prognathous. Fastigial furrow present. Antenna short, 7-13 segmented, closely fitted into deep antennal groove on sides of frontal ridge. Ocelli absent. Prosternal process present. Metasternal interspace short and very wide. Elytra, wings and tympanum absent. Lower basal lobe of hind femur longer than upper one. Brunner's organ present. External apical spine of hind tibia absent. Ectophallus differentiated; cingulum shield-like, without apodemes; valves of penis paired, divided; spermatophore sac ventral. Epiphallus bridge-shaped, with lophi and without ancorae. Oval sclerites present. Stridulatory mechanism not known.

The first two genera of the family, *Lathicerus* and *Crypsicerus*, when described by Saussure in 1888, were placed by him in "*Thrincites*" of *Oedipodinae*. In 1943 Uvarov transferred the three then known genera of the group to the tribe *Thrinchini* of *Pamphagidae*. Dirsh, after study of the phallic complex, raised the group to subfamily rank (1954) and later (1956) to family rank.

The reasons for regarding this group as a family are obvious from the diagnosis. Such a striking character as the antennal grooves is not known in other families. The cingulum and penis are also quite unique.

Lathiceridae occur in S. and SW. Africa only.

List of known genera :

1. <i>Batrachidacris</i> Uvarov, 1939	3. <i>Crypsicerus</i> Saussure, 1888
2. <i>Crypsiceracris</i> Miller, 1932	4. <i>Lathicerus</i> Saussure, 1888

Family *Pyrgomorphidae*

(Text-fig. 14)

Type genus : *Pyrgomorpha* Serville, 1838

Body of variable shape. Head acutely conical. Fastigial furrow present. Prosternal process present. Elytra and wings fully developed, reduced or absent. Tympanum normally present. Lower basal lobe of hind femur normally longer than upper one. Brunner's organ present except few genera, with thin, almost cursorial hind legs. External apical spine of hind tibia present or absent. Ectophallus differentiated ; cingulum capsule-like ; valves of penis paired, undivided ; spermatophore sac in dorsal position. Epiphallus bridge-shaped, with dorso-lateral appendices ; ancorae absent ; lophi hook-like. Oval sclerites absent. No stridulatory mechanism known.

The name *Phymateidae* was used for this family by Jakobson & Bianki (1904) and earlier as a group name by various authors, but for the last fifty years and more it was known as *Pyrgomorphidae* and this usage should be retained as less likely to cause confusion.

The *Pyrgomorphidae* are a very well defined family, with a peculiar phallic complex which is rather uniform through the family.

The relationship with other families is rather obscure and no close affinities exist. They have some common features with *Lentulidae*, such as the undivided, paired valves of the penis and the dorsal position of the spermatophore sac, and others with *Ommexechidae*, such as the presence of a fastigial furrow and the paired undivided valves of the penis. All other characters, however, are so distinct that the relationship is a very remote one.

Pyrgomorphidae are represented in all the tropical and subtropical parts of the world by a large number of genera, a list of which appears unnecessary.

Family *Ommexechidae*

(Text-fig. 15)

Type genus : *Ommexecha* Serville, 1831

Body of variable shape. Head of variable shape. Fastigial furrow present. Prosternal process present. Elytra and wings fully developed, shortened or absent. Cubital vein of elytron unbranched. Tympanum present or absent. Stridulatory

FIG. 14. 1. *Phymateus viridipes* St., male. 2. Head of *Pyrgomorphella arachidis* Dirsh (Ff. fastigial furrow. Fa. fastigial area). 3-6. Phallic complex of *Phymateus morbillosus* (L.). 3. Whole phallic complex from above. 4. The same, in profile. 5. Endophallus, in profile. 6. Penis, from above. 7. Epiphallus of *Phymateus purpurascens* Karsch.

FIG. 15. 1-7. *Ommexecha servillei* Blanch. 1. Female. 2-7 Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. Endophallus from above. 5. In profile. 6. The same, with ectophallic membrane removed. 7. Endophallus in profile.

mechanism (elytron-femur) sometimes present, but very imperfect. Lower basal lobe of hind femur as long as, or slightly longer than, upper one. Brunner's organ present. External apical spine of hind tibia absent. Ectophallus differentiated; cingulum differentiated, forming apodemes; valves of penis paired, not divided; ejaculatory sac with additional pockets. Epiphallus bridge-shaped, with lateral plates joined by membrane; ancorae absent; lophi present. Oval sclerites present.

This family is very insufficiently studied. Very remote affinity with the *Pyrgomorphidae* is suggested by the presence of the fastigial furrow and by the undivided valves of the penis; the latter, which were described (Dirsh, 1956) as flexured owing to the presence of a very long and thick flexure, may be better regarded as not divided, but rather as having a very elongate and rather thin medial part. The peculiar joining of the lateral plates of the epiphallus by membrane is found elsewhere only in *Pauliniidae*.

The *Ommexechidae* occur in S. America only.

List of known genera :

1. <i>Graea</i> Philippi, 1863	4. <i>Parossa</i> Bruner, 1911
2. <i>Ommexecha</i> Serville, 1831	5. <i>Spathalium</i> I. Bolivar, 1884
3. <i>Pachyossa</i> Rehn, 1913	

Family ***Pauliniidae***

(Text-fig. 16)

Type genus : *Paulinia* Blanchard, 1843

Body subcylindrical. Head subconical. Fastigial furrow absent. Ocelli very large. Prosternal process absent. Elytra and wings fully developed or shortened. Medial and cubital veins of elytron unbranched. Tympanum present. Lower basal lobe of hind femur shorter than upper one. Brunner's organ present. Hind tibia strongly expanded; external apical spine present; basal tarsal segment expanded. Ectophallus differentiated; cingulum differentiated; valves of penis paired, divided; ejaculatory sac with lateral pockets. Epiphallus bridge-shaped, with ancorae and lophi; lateral plates connected with bridge by membrane. Oval sclerites present. Ovipositor strongly reduced, shorter or hardly exceeding sub-genital plate. Stridulatory mechanism not found.

The family *Pauliniidae* is insufficiently studied and its position is rather doubtful. The structure of the epiphallus and ejaculatory sac approximate it to *Ommexechidae*, but the lobes of the hind femur, the lower lobe being shorter than the upper, and the absence of the fastigial furrow and of the prosternal process, suggest some affinity with *Acrididae*. However, the whole phallic complex, with its complicated structure, the divided valves of the penis, the complicated ejaculatory sac, and the peculiar epiphallus, isolate it from *Acrididae*. According to the size of chromosomes (Helwig, 1958), the *Pauliniidae* cannot be placed in *Acrididae*.

The family at present contains two genera: *Paulinia* Blanchard, 1843, and *Marellia* Uvarov, 1929, but the latter genus probably does not belong here. Its affinity needs further study.

The family occurs in S. America only.

FIG. 16. 1-8. *Paulinia acuminata* (DeGeer). 1. Male. 2. Right elytron. 3-8. Phallic complex. 3. Whole phallic complex from above. 4. The same, but ectophallic membrane and epiphallus removed. 5. Endophallus, from above. 6. As 4, but in profile. 7. Endophallus, in profile. 8. Penis, in profile. 9. Left hind tibia from above.

Family *Lentulidae*

(Text-fig. 17)

Type genus : *Lentula* Stål, 1878

Body of variable shape. Head of variable shape. Fastigial furrow absent. Pronotum short. Prosternal process present. Elytra, wings and tympanum absent. Lower basal lobe of hind femur shorter than upper one. Brunner's organ present. External apical spine of hind tibia present or absent. Ectophallus differentiated ; cingulum differentiated ; valves of penis paired, undivided ; spermatophore sac dorsal. Epiphallus bridge-shaped, with ancorae and lophi. Oval sclerites present. Stridulatory mechanisms not found.

This recently erected family (Dirsh, 1956) consists of genera with highly retrogressive external characters. They have lost wings and tympanum, and the pro-, meso- and metathorax are reduced. As a result they have a nymphal appearance and are externally similar to the wingless and tympanum-less representatives of other families. The phallic complex, however, provides an excellent character. Its structure is only remotely similar to that of *Pyrgomorphidae* (Dirsh, 1956) and quite different from that in all other families. It is not possible to relate this family closely to any known family. The most difficult problem presented by the *Lentulidae* is that there are no reliable external characters, and for identification of its representatives it is necessary to investigate the phallic complex. The only external character which is consistent in this family is the complete absence of wings and tympanum, while in the other families this state occurs only as a retrogression. Moreover, in the only species of the family studied with regard to the anatomy, the indirect flight muscles are completely absent in the adult, while they are present in other wingless acridoids (Ewer, 1958).

Lentulidae are distributed in South Africa and part of East Africa.

List of known genera :

1. <i>Bacteracris</i> Dirsh, 1956	11. <i>Mecostiboides</i> Dirsh, 1957
2. <i>Basutacris</i> Dirsh, 1953	12. <i>Mecostibus</i> Karsch, 1896
3. <i>Betiscoides</i> Sjöstedt, 1923	13. <i>Nyassacris</i> Ramme, 1929
4. <i>Devylideria</i> Sjöstedt, 1923	14. <i>Paralentula</i> Rehn, 1944
5. <i>Eremidium</i> Karsch, 1896	15. <i>Qachasia</i> Dirsh, 1956
6. <i>Gymnidium</i> Karsch, 1896	16. <i>Shelfordites</i> Karny, 1910
7. <i>Helwigacris</i> Rehn, 1944	17. <i>Swaziacris</i> Dirsh, 1953
8. <i>Karruacris</i> Dirsh, 1958	18. <i>Sygrus</i> I. Bolivar, 1889
9. <i>Karruia</i> Rehn, 1945	19. <i>Usambilla</i> Sjöstedt, 1909
10. <i>Lentula</i> Stål, 1878	

Family *Acrididae*Type genus : *Acrida* Linnaeus, 1758

Body and head of extremely variable shape. Fastigial furrow absent (rarely present, but apparently as a secondary formation). Prosternal process present or absent. Elytra and wings fully developed or reduced, or absent. Tympanum

normally present. Stridulatory mechanisms of various structure found in the majority of subfamilies. Lower basal lobe of hind femur mostly shorter than or equal to upper one. Brunner's organ present. External apical spine of hind tibia

FIG. 17. 1-7. *Lentula callani* Dirsh. 1. Male. 2-6. *L. obtusifrons* St. phallic complex. 2. From above. 3. From below. 4. Penis from above. 5. Whole phallic complex, in profile. 6. Endophallus, in profile. 7. Spermatheca.

present or absent. Ectophallus differentiated; cingulum differentiated; valves of penis paired, flexured or divided. Epiphallus mostly bridge-shaped, sometimes disc-shaped, sometimes divided; ancorae and lophi present (sometimes lost). Oval sclerites present.

The family *Acrididae* is the most numerous, most heterogeneous and probably most recent and advanced family. It is divided below into seventeen subfamilies of unequal value and probably of different phylogenetic status. It is possible that further study, particularly of the so-called aberrant genera, would demand a revision, and the present arrangement of the subfamilies should be regarded as tentative and practical rather than natural.

As a family the *Acrididae* show remote affinity with *Pauliniidae* but no close relationship with the other families.

TABLE III.—*Subfamilies of Acrididae and their Main Characters*

Subfamily	Valves of penis	Epi- phallus	Comstock- Kellogg glands*	Basal lobes of hind femur	Stridulatory mechanism	Tym- panum
Dericorythinae	. Paired flexured	. Bridge- shaped	. —	. Equal length	. — or +	. Normally present
Chilacridinae .	. Ditto	. Ditto	. ?	. Ditto	. —	. Ditto
Romaleinae .	. „	. „	. + or —	. „	. +	. „
Lithidiinae .	. Paired divided	. „	. ?	. Lower lobe shorter	. —	. Absent
Hemiacridinae	. Ditto	. „	. +	. Ditto	. + or —	. Normally present
Tropidopolinae	. Paired flexured	. „	. +	. „	. — or +	. Ditto
Oxyinae .	. Ditto	. Divided or with tendency to be divided	. +	. „	. —	. „
Coptacridinae .	. „	. Divided	. +	. „	. —	. „
Calliptaminae	. „	. Plate-like	. +	. „	. —	. „
Euryphyminae	. „	. Divided	. +	. „	. —	. „
Eyprepocnemidinae .	. „	. Bridge- shaped	. +	. „	. —	. „
Catantopinae .	. „	. Bridge- shaped sometimes divided	. + or —	. „	. —	. „
Cyrtacanthacri- dinae	. „	. Bridge- shaped	. +	. „	. —	. „
Egnatiinae .	. „	. Ditto	. +	. „	. + or —	. „
Acridinae .	. „	. „	. —	. „	. + or —	. „
Eremogryllinae	. „	. Divided	. ?	. „	. +	. „
Truxalinae .	. „	. Bridge- shaped	. —	. „	. +	. „

* According to Slifer (1939-43).

KEY TO SUBFAMILIES OF *Acrididae*

- 1 (6) Lower basal lobe of hind femur as long as upper one or only insignificantly longer or shorter.
- 2 (5) First vannal area of hind wing (if present) without stridulatory specialization.
- 3 (4) Hind tibia curved. Median carina of pronotum raised in prozona. Cingulum of ectophallus with long apodemes. (Asia, Africa) *Dericorythinae*
- 4 (3) Hind tibia not curved. Median carina of pronotum not raised. Cingulum of ectophallus with short, plate-like apodemes. (S. America) *Chilacridinae*
- 5 (2) First vannal area of hind wing with series of parallel, transverse, finely serrated stridulatory veinlets; medial, cubital and second vannal areas expanded, with row of parallel thickened, transverse veinlets. Hind tibia not curved. Median carina of pronotum of variable shape or absent *Romaleinae*
- 6 (1) Lower basal lobe of hind femur distinctly shorter than upper one.
- 7 (8) Body depressed. Tympanum absent even in fully winged species. Mesosternal interspace very large and wide, often separated from metasternal only by suture *Lithidiinae*
- 8 (7) Body not depressed or if depressed, then tympanum present. Sometimes tympanum absent, but then body compressed or cylindrical. Mesosternal interspace variable, but well distant from metasternal.
- 9 (10) Radial area of elytron with a series of regular, parallel stridulatory veinlets (Text-fig. 22). If apterous, then body compressed and tympanum absent *Hemiacridinae*
- 10 (9) Stridulatory veinlets of radial area of elytron absent. If apterous, then tympanum (at least rudimentary) present.
- 11 (26) Prosternal process, or collar present.
- 12 (13) Lower external lobe of hind knee with spine-like apex (Text-fig. 24) *Oxyinae*
- 13 (12) Lower external lobe of hind knee with apex rounded, angular or subacute, but not spine-like.
- 14 (15) Last abdominal tergite in male (in majority of genera) with well developed furcula; supra-anal plate mostly with attenuate or trilobate apex; subgenital plate with transverse fold *Coptacridinae*
- 15 (14) Last abdominal tergite in male without well developed furcula; supra-anal plate variable; subgenital plate without transverse fold.
- 16 (17) Mesosternal interspace closed *Tropidopolinae*
- 17 (16) Mesosternal interspace open.
- 18 (25) Mesosternal lobes rounded or obtusangular.
- 19 (20) Male cerci pincers-like, strong, regularly incurved. Epiphallus discoidal, without lophi *Calliptaminae*
- 20 (19) Male cerci variable, but not pincers-like. Epiphallus variable, but always with lophi.
- 21 (22) Male cercus with large basal articulation; posterior margin of the last abdominal tergite strongly sclerotized. Epiphallus divided, with large, mostly angular, lophi *Euryphyminae*
- 22 (21) Basal articulation of male cerci small. Posterior margin of the last abdominal tergite not strongly sclerotized. Epiphallus not divided, or if divided, then with comparatively small, lobiform lophi.
- 23 (24) Dorsum of pronotum flat or weakly tectiform, with median and lateral carinae linear (lateral carinae sometimes obliterated). Male cercus with strongly compressed lobiform or subacute apex *Eyprepocnemidinae*
- 24 (23) Dorsum of pronotum of variable shape; lateral carinae, if present, not linear. Male cercus variable, but not with strongly compressed lobiform or subacute apex *Catantopinae*
- 25 (18) Mesosternal lobes rectangular *Cyrtacanthacridinae*

- 26 (11) Prosternal process or collar usually absent ; if present, then antenna ensiform and body strongly elongated.
- 27 (30) Stridulatory serration on internal side of hind femur absent.
- 28 (29) Furcal suture of mesosternum curved backwards in the middle, thus shortening the mesosternal interspace (Text-fig. 31). Sides of abdominal tergites often with transverse (stridulatory) ridges *Egnatiinae*
- 29 (28) Furcal suture of mesosternum of normal shape. No stridulatory specialization on sides of abdominal tegites *Acridinae*
- 30 (27) Stridulatory serration on internal side of hind femur present.
- 31 (32) Male cercus strongly thickened in basal part with strongly incurved apex *Eremogryllinae*
- 32 (31) Male cercus simple, mostly conical *Truxalinae*

Subfamily *Dericorythinae*

(Text-fig. 18)

Type genus : *Dericorys* Serville, 1838

Size large, medium or small. Head variable. Pronotum with strong crest or at least hump in prozona only. Prosternal process or collar present. Mesosternal interspace open. Elytra and wings fully developed, shortened, lobiform or absent.

FIG. 18. 1. *Dericorys albidula* Serv., female. 2. Epiphallus of *Dericorys tibialis* (Pall.).

Tympanum present or (in apterous species) absent. Lower basal lobe of hind femur as long as, or slightly longer than, upper one. Hind tibia curved ; external apical spine present. Basal and apical valves of penis connected by flexure. Epiphallus bridge-shaped, with ancorae and lophi. Stridulatory mechanism not found, except in one species, in which it is represented by inflated part of subcostal area of hind wing.

This subfamily was erected by Jakobson (Jakobson & Bianki, 1904), but was disregarded by the later authors, who placed the subfamily into *Catantopinae*.

Dericorythinae are remarkable in that the shape of the lower basal lobe of the hind femur is of the same length as or slightly longer than the upper one, a condition found also as a normal feature in *Romaleinae* and *Chilacridinae* only amongst other subfamilies of *Acrididae*. It is not possible to retain *Dericorythinae* in *Catantopinae* because of the shape of the basal lobes of the hind femur, nor is it possible to regard them as a family, since all the families with this type of femur are characterized by other features, such as the phallic complex, fastigial furrow, and stridulatory mechanism.

Dericorythinae are distributed in SW. and central Asia and Northern Africa.

List of examined genera :

1. <i>Anamesacris</i> Uvarov, 1934	4. <i>Dericorys</i> Serville, 1838
2. <i>Bolivaremia</i> Morales-Agacino, 1949	5. <i>Pamphagulus</i> Uvarov, 1929
3. <i>Corystoderes</i> I. Bolivar, 1936	

Subfamily *Chilacridinae*

(Text-fig. 19)

Type genus : *Chilacris* Liebermann, 1943

Of medium size, integument rugose. Antenna filiform. Head subglobular ; fastigium of vertex mostly with faint trace of fastigial furrow. Three sulci crossing dorsum of pronotum. Prosternal process present. Meso- and metasternal interspace short and wide. Elytra and wings fully developed, reduced or absent. Tympanum normally present. Lower basal lobe of hind femur as long as or slightly longer than upper one. External apical spine of hind tibia absent or present. Ectophallus membranous ; cingulum poorly sclerotized, plate-like, with apodemes wide, short, plate-like, poorly differentiated ; sheath of penis wide, covering whole apical valves of penis. Endophallus strongly sclerotized ; basal valves of penis form long posterior projections, distal ends of which meet distal ends of apical valves of penis, proximal part of them plate-like, widened ; proximal ends of apical valves of penis close to lower part of basal valves ; they are connected by short flexure. Spermatophore sac placed in space between posterior projections of basal valves and apical valves of penis ; ejaculatory sac partly below, partly between proximal parts of basal valves of penis. Epiphallus bridge-shaped, with strong, non-articulated ancorae and strong, hook-shaped lophi. Oval sclerites present. Spermatheca variable, with widened single distal end or forming apical and preapical diverticula.

This subfamily was erected by Liebermann and called *Chilacrinae* in 1942, but the name has to be amended to *Chilacridinae*. He included in it four genera : *Aucacris* Hebard, 1929, *Chilacris* Liebermann, 1943, *Philippiacris* Liebermann, 1943, and *Elasmoderus* Saussure, 1888. Later the genus *Uretacris* Liebermann, 1943, was included in the subfamily and *Elasmoderus* was excluded (Liebermann, 1959, in litt.). *Bufonacris* Walker, 1871, should also be included here.

Dr. J. Liebermann kindly sent me the types of his genera and I was able to study the phallic complex and spermatheca. The phallic complex proved to be of

peculiar structure, which was not found in other families and subfamilies of *Acridoidea*. The most striking features are: firstly, the poorly developed cingulum, which resembles that in the primitive families *Tanaoceridae*, *Xyronotidae* and *Pneumoridae*; secondly, the peculiar shape of the endophallus, with the basal valves of

FIG. 19. *Chilacris maculipennis* Lieb., male type. 2-5. *Philippiacris rubiosus* Lieb.
 2. Ectophallus, from above (whole proximal part of ectophallic membrane and epiphallus removed). 3. Endophallus, from above. 4. Endophallus, lateral view.
 5. Epiphallus. 6. *Chilacris maculipennis*, spermatheca.

the penis forming long posterior projections, which extend to the point of meeting of the apices of the apical valves of the penis, with the spermatophore sac located between them. These general features of the phallic complex are similar in all studied genera of the subfamily, though they vary in details. The phallic complex of

Philippiacris is figured (Text-fig. 19), since the several specimens of this genus were in the best condition for dissecting and drawing.

It is difficult to suggest the position and relationship of *Chilacridinae* with other groups of *Acridoidea*. Their genitalia are quite peculiar without a close parallel in the rest of *Acridoidea*. The shape of the basal lobes of the hind femur suggest a possible link with *Romaleinae* and *Dericorythinae*. Tentatively, *Chilacridinae* are placed in the family *Acrididae*, but further detailed studies of South American *Acridoidea* are needed to establish their exact position.

List of known genera :

1. <i>Aucacris</i> Hebard, 1929	4. <i>Philippiacris</i> Liebermann, 1943
2. <i>Bufonacris</i> Walker, 1871	5. <i>Uretacris</i> Liebermann, 1943
3. <i>Chilacris</i> Liebermann, 1943	

Subfamily ***Romaleinae***

(Text-fig. 20)

Type genus : *Romalea* Serville, 1831

Size mostly large or medium. Body of variable shape. Head of variable shape. Prosternal process present. Mesosternal interspace open. Highly specialized stridulatory mechanism present : first vannal area of hind wing narrow, convex, forming tube-like fold, when the wing is folded ; this area has arched, parallel, finely, but strongly serrated, transverse veinlets—sometimes adjoining longitudinal veins are serrated as well ; cubital, second vannal and sometimes medial area are expanded, with thickened, regular, transverse veinlets. Lower basal lobe of hind femur about as long as upper one. External apical spine of hind tibia present or absent. Basal and apical valves of penis connected by strong, thickened flexure. Epiphallus robust, bridge-shaped, with short ancorae and lophi.

The subfamily *Romaleinae* was established by Roberts (1941) on the basis of the phallic complex, but although this character alone is not sufficient for separating the subfamily, several other characters support its status, in particular the peculiar stridulatory mechanism which occurs only in this subfamily and may be traced even in the strongly reduced wings of micropterous species. Sometimes it may be reduced as in *Aplatacris* or strongly reduced as in *Munatia*, in which only weak traces of the serration may be observed. Another character, which occurs elsewhere in *Acrididae*, as a stable normal character, only in *Dericorythinae* and *Chilacridinae* is the lower basal lobe of the hind femur being as long as the upper one. Yet another character is the flexure of the valves of the penis being more robust than is usual in other *Acrididae*.

Members of the *Romaleinae* present the same extreme diversity in the shape of the body and in general appearance as the other large subfamilies. There are amongst them some forms strikingly similar to certain representatives of the *Pamphagidae* (*Phrynotettix*, *Dracotettix*), and of the *Acridinae* (such as *Legua*, which superficially resembles *Acrida* ; *Callonotacris*, which superficially resembles *Pyrgodera*) ; and *Tropidacris* and allied genera which are very similar to *Cyrtacanthacridinae*.

FIG. 20. 1. *Romalea microptera* (Beauv.), male. 2. Wing of *Colpolopha obsoleta* Serv. 3. Part of the stridulatory mechanism under large magnification. 4. Epiphallus of *Romalea microptera*.

Romaleinae occur mainly in S. America with a few in N. America, but several genera are known from NE. Africa and S. Asia.

List of examined genera :

1. <i>Acrostegastes</i> Karsch, 1896	21. <i>Lophacris</i> Scudder, 1869
2. <i>Aeolacris</i> Scudder, 1875	22. <i>Lyrotyloides</i> Bey-Bienko, 1956
3. <i>Agriacris</i> Walker, 1870	23. <i>Lyrotylus</i> Uvarov, 1923
4. <i>Alcamenes</i> Stål, 1878	24. <i>Munatia</i> Stål, 1875
5. <i>Alophonota</i> Stål, 1873	25. <i>Pelecinotus</i> I. Bolivar, 1881
6. <i>Antandrus</i> Stål, 1878	26. <i>Phrynotettix</i> Glover, 1872
7. <i>Aplatacris</i> Scudder, 1875	27. <i>Prionacris</i> Stål, 1878
8. <i>Brachystola</i> Scudder, 1876	28. <i>Prionolopha</i> Stål, 1873
9. <i>Callonotacris</i> Rehn, 1909	29. <i>Procolpia</i> Stål, 1873
10. <i>Chariacris</i> Walker, 1870	30. <i>Robecchia</i> Schulthess, 1898
11. <i>Chromacris</i> Walker, 1870	31. <i>Romalea</i> Serville, 1831
12. <i>Cibotopteryx</i> Rehn, 1905	32. <i>Taeniopoda</i> Stål, 1873
13. <i>Colpolopha</i> Stål, 1873	33. <i>Teratodes</i> Brulle, 1835
14. <i>Coryacris</i> Rehn, 1909	34. <i>Titanacris</i> Scudder, 1869
15. <i>Draconata</i> Pictet & Saussure, 1887	35. <i>Tropidacris</i> Scudder, 1869
16. <i>Dracotettix</i> Bruner, 1889	36. ? <i>Tropidostethus</i> Philippi, 1863
17. <i>Eurynotacris</i> Ramme, 1931	37. <i>Tytthotyle</i> Scudder, 1897
18. <i>Eutropidacris</i> Hebard, 1923	38. <i>Xestotrachelus</i> Bruner, 1913
19. <i>Kabulia</i> Ramme, 1928	39. <i>Xyleus</i> Gistel, 1848
20. <i>Legua</i> Walker, 1870	40. <i>Zoniopoda</i> Stål, 1873

Subfamily *Lithidiinae* nov.

(Text-fig. 21)

Type genus : *Lithidium* Uvarov, 1925

Small or medium size, robust, body depressed. Male much smaller than female. Antenna filiform or slightly thickened in apical part. Head subglobular. Fastigium of vertex short, wide. Pronotum short, wide, depressed. Prosternal collar present or absent. Mesosternal interspace very large, close or fused with the metasternal or separated from it only by suture. Elytra and wings present or absent. Tympanum absent. Lower lobe of hind femur shorter than upper one. External apical spine of hind tibia present or absent. Valves of penis paired, divided ; apical ones being thin and reduced. Epiphallus bridge-shaped, with short ancorae and short, hook-shaped lophi. Stridulatory mechanism not found.

Only four genera of this family are known. The first one, *Eneremius* was placed by Saussure in the "Strips *Eremobia*", then of the subfamily *Oedipodinae*. Uvarov (1925) removed it, with *Lithidium*, to the tribe *Thrinchini*, then of *Oedipodinae*, but in 1943 he transferred the tribe to *Pamphagidae*. Dirsh (1956) referred these two genera and *Lithidiopsis* tentatively to the family *Lentulidae*. The only winged genus, *Microtmethis*, was described by Karny as a member of the *Oedipodinae*. The males of *Lithidium* and of *Microtmethis* have only recently become available. In the phallic complex they proved to be very similar to one another, but strongly different from the *Lentulidae* and from all other known subfamilies of *Acrididae*, except perhaps *Hemiacridinae*.

In the divided valves of the penis the *Lithidiinae* approximate to *Hemiacridinae*,

FIG. 21. 1-4. *Lithidium bushmanicum* Dirsh. 1. Female, in profile. 2. The same, from above. 3. Face. 4. Meso- and metasternum. 5-9. Phallic complex of *Lithidium pusillum* Uv. 5. From above. 6. From below. 7. In profile. 8. Penis, in profile. 9. Epiphallus.

but the apical valves are strongly reduced. The epiphallus is rather simplified, with narrow bridge and simple, small ancorae and lophi. The latter character, the shape of the meso- and the metasternum and the absence of the tympanum even in winged species, preclude placing the *Lithidiinae* in *Hemiacridinae*.

The subfamily is found in S. and SW. Africa only.

List of known genera :

1. <i>Lithidium</i> Uvarov, 1925	4. ? <i>Eneremius</i> Saussure, 1888. (Known
2. <i>Lithidiopsis</i> Dirsh, 1956	from females and its subfamily
3. <i>Microtmethis</i> Karny, 1910	position is uncertain)

Subfamily *Hemiacridinae*

(Text-fig. 22)

Type genus : *Hemiacris* Walker, 1870

Body of variable shape. Head prognathous, orthognathous or opisthognathous. Prosternal process present. Mesosternal interspace open or closed. Elytra and wings fully developed, reduced or absent; radial area of elytron with series of regular, thickened, transverse, stridulatory veinlets. Tympanum present, in apterous forms absent. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia present or absent. Basal and apical valves of penis disconnected, but sometimes there is a tendency to form flexure. Epiphallus bridge-shaped, sometimes with divided bridge; ancorae and lophi present.

The subfamily was established recently by Dirsh (1956) on the basis of divided valves of the penis and the presence of a peculiar stridulatory mechanism. The first character is shared with *Lithidiinae* and also links them to some extent with *Tropidopolinae*, which have a tendency towards disappearance of the flexure. The peculiar stridulatory mechanism does not occur in other subfamilies of *Acrididae*.

The subfamily is distributed in the tropics and subtropics of Africa, Asia, the Australasian Archipelago and Australia, and there are two genera in S. America.

List of examined genera :

1. <i>Acanthoxia</i> I. Bolivar, 1906	20. <i>Merehana</i> Kevan, 1957
2. <i>Aleuas</i> Stål, 1878	21. <i>Mesopsera</i> I. Bolivar, 1908
3. <i>Bermius</i> Stål, 1878	22. <i>Oraistes</i> Karsch, 1896
4. <i>Calviniacris</i> Dirsh, 1956	23. <i>Parahieroglyphus</i> Carl, 1916
5. <i>Castetsia</i> I. Bolivar, 1902	24. <i>Paraspathosternum</i> Ramme, 1929
6. <i>Clonacris</i> Uvarov, 1943	25. <i>Pareuthymia</i> Willemse, 1930
7. <i>Diademacris</i> Ramme, 1929	26. <i>Perakia</i> Ramme, 1930
8. <i>Dirshacris</i> Brown, 1959	27. <i>Phalinus</i> Rehn, 1944
9. <i>Gesonula</i> Uvarov, 1940	28. <i>Pristocorypha</i> Karsch, 1896
10. <i>Glauningia</i> Ramme, 1929	29. <i>Pseudocarsula</i> Kirby, 1914
11. <i>Hemiacris</i> Walker, 1870	30. <i>Spathosternum</i> Krauss, 1877
12. <i>Hemipristocorypha</i> Dirsh, 1952	31. <i>Sudanacris</i> Uvarov, 1944
13. <i>Hieroglyphus</i> Krauss, 1877	32. <i>Tarbaleus</i> Brunner, 1898
14. <i>Kassongia</i> I. Bolivar, 1908	33. <i>Tauchira</i> Stål, 1878
15. <i>Leatettix</i> Dirsh, 1956	34. <i>Uvarovidium</i> Dirsh, 1956
16. <i>Leptacris</i> Walker, 1870	35. <i>Willemsella</i> Miller, 1934
17. <i>Lopheuthymia</i> Uvarov, 1943	36. <i>Xenippa</i> Stål, 1878
18. <i>Loryma</i> Stål, 1878	37. <i>Zygoclistron</i> Rehn, 1905
19. <i>Malagasacris</i> Rehn, 1944	

FIG. 22. *Hemicrisis fervens* Walk. 1. Male. 2-6. Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. Penis, from above. 5. As the fig. 3, but in profile. 6. Penis, in profile.

Subfamily *Tropidopolinae*

(Text-fig. 23)

Type genus : *Tropidopola* Stål, 1873

Body cylindrical, elongated (sometimes strongly). Head from strongly elongated and acutely conical to subglobular. Median and lateral carinae of pronotum present or absent. Prosternal process beak-like or cylindrical or with widened, flat or concave

apical surface. Mesosternal interspace closed. Elytra and wings fully developed or reduced. Tympanum present. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia present. Male cercus of variable shape. Flexure between basal and apical valves of penis has tendency to disappear. Epiphall-

FIG. 23. 1-4. *Afroxyrrhopes acuticercus* Dirsh. 1. Male. 2. Meso- and metasternum. 3. End of abdomen, in profile. 4. The same, from above. 5-8. Epiphalli. 5. *Tropidopola cylindrica* (Marsh.). 6. *Tristria lacerta* St. 7. *Homoxyrrhopes punctipennis* (Walk.). 8. *Afroxyrrhopes procera* (Burm.).

us bridge-shaped, sometimes divided; ancorae and lophi present. Stridulatory mechanism sometimes present (thickened veinlets in costal and subcostal areas of elytron).

There are four features, the combination of which characterizes this subfamily. These are the closed mesosternal interspace, the presence of an external apical spine

on the hind tibia, a tendency towards losing the flexure between the basal and apical valves of the penis, and the shape of the prosternal process. None of these characters could be regarded as absolute, since they can be found separately in other subfamilies of *Acrididae*. However, their combination defines the *Tropidopolinae* as a natural group.

This subfamily is distributed in S. Asia and Africa, and with one genus reaching S. Europe.

List of examined genera :

1. <i>Afroxyrrhepes</i> Uvarov, 1943	8. <i>Musimoja</i> Uvarov, 1953
2. <i>Bambusacris</i> Henry, 1933	9. <i>Oxyrrhepes</i> Stål, 1873
3. <i>Calamippa</i> Henry, 1940	10. <i>Petamella</i> Giglio-Tos, 1907
4. <i>Chloroxyrrhepes</i> Uvarov, 1926	11. <i>Tinnevellia</i> Henry, 1940
5. <i>Homoxyrrhepes</i> Uvarov, 1926	12. <i>Tristria</i> Stål, 1873
6. <i>Limnippa</i> Uvarov, 1941	13. <i>Tropidopola</i> Stål, 1873
7. <i>Mesopsilla</i> Ramme, 1929	

Subfamily *Oxyinae*

(Text-fig. 24)

Type genus *Oxya* Serville, 1831

Size small or medium. Head subconical ; fastigium of vertex short. Pronotum cylindrical or subcylindrical ; median carina weak, linear or absent ; lateral carinae absent. Prosternal process conical. Mesosternal interspace open. Elytra and wings fully developed, shortened or absent. Tympanum present. Two or three distal abdominal sternites (in the majority of genera) with brush-like lateral groups of hairs. Lower basal lobe of hind femur shorter than upper one ; lower lobe of hind knee spine-like. Hind tibia (in the majority of cases) expanded ; external apical spine (except *Gerista*) present. Valves of ovipositor and female subgenital plate (in most genera) with teeth, spines or serration. Basal and apical valves of penis flexured. Epiphallus bridge shaped, with bridge divided or with tendency to division, with ancorae and lophi. Stridulatory mechanism not found.

Members of the subfamily *Oxyinae* form a natural assemblage which differs from the other subfamilies of *Acridoidea* in the presence of a spine-like lower lobe of the hind knee, the more or less divided bridge of the epiphallus and the hairy distal sternites of the abdomen. These characters are found in other subfamilies also, but their combination defines the *Oxyinae* reasonably well.

The subfamily *Oxyinae* is distributed in Africa, Asia and Australia.

List of examined genera :

1. <i>Austiniella</i> Ramme, 1931	10. <i>Genditia</i> I. Bolivar, 1911
2. <i>Badistica</i> Karsch, 1891	11. <i>Gerista</i> I. Bolivar, 1905
3. <i>Caledonia</i> Willemse, 1923	12. <i>Lucretilis</i> Stål, 1878
4. <i>Caryanda</i> Stål, 1878	13. <i>Oxya</i> Serville, 1831
5. <i>Cercina</i> Stål, 1878	14. <i>Pterotiltus</i> Karsch, 1893
6. <i>Chitaura</i> I. Bolivar, 1918	15. <i>Quilta</i> Stål, 1860
7. <i>Dapperia</i> Sjöstedt, 1921	16. <i>Racilia</i> Stål, 1878
8. <i>Dibastica</i> Giglio-Tos, 1907	17. <i>Zulua</i> Ramme, 1929
9. <i>Digentia</i> Stål, 1878	

FIG. 24. 1-3. *Oxya hyla* Serv. 1. Male. 2. Hind knee, external side. 3. Ovipositor. 4-6. Epiphallus. 4. *Oxya hyla* Serv. 5. *Dibastica major* I. Bol. 6. *Pterotiltus inuncatus* (Karsh).

Subfamily *Coptacridinae*

(Text-fig. 25)

Type genus : *Coptacra* Stål, 1873

Size small or medium. Head subconical; occiput forming angle with vertex, mostly separated by ridge. Pronotum without lateral carinae. Prosternal process conical. Mesosternal interspace open. Elytra and wings fully developed or reduced. Tympanum present. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia absent. Last abdominal tergite of male mostly with furcula; supra-anal plate mostly with attenuate apex; subgenital plate with transverse fold. Male cercus widened in basal and compressed in apical half, with downcurved or complicatedly shaped apex. Basal and apical valves of penis flexured. Epiphallus bridge-shaped, with divided bridge; ancorae and lophi present. Stridulatory mechanism not found.

The subfamily *Coptacridinae* was regarded as a group (Brunner, 1893), later as a tribe (Mistshenko, 1952), of *Catantopinae*, but when the characters were studied in more detail, it became necessary to separate it as a subfamily. The combination of characters is as follows: the divided bridge of the epiphallus; the presence, in the majority of genera, of a furcula on the last abdominal tergite of the male; the peculiar shape of the supra-anal plate and male cercus; a transverse fold in the subgenital plate of the male, and the separation of vertex and occiput. The two last characters are apparently peculiar to the *Coptacridinae*.

FIG. 25. 1-3. *Cyphocerastis laeta* Karsch. 1. Male. 2. End of abdomen from above. 3. Left cercus. 4. *Eucoptacra anguliflava* (Karsch), left cercus. 5-7. Epiphalli. 5. *Coptacra ensifera* I. Bol. 6. *Poecilocerastis striata* Ramme. 7. *Eucoptacra praemorsa* St.

The subfamily is distributed in tropical Africa and Asia.

List of examined genera :

1. <i>Apalacris</i> Walker, 1870	8. <i>Exochoderes</i> I. Bolivar, 1881
2. <i>Bocagella</i> I. Bolivar, 1889	9. <i>Opharicus</i> Uvarov, 1940
3. <i>Coptacra</i> Stål, 1873	10. <i>Paracoptacra</i> Karsch, 1896
4. <i>Cyphocerastis</i> Karsch, 1891	11. <i>Parepistaurus</i> Karsch, 1896
5. <i>Dubitacris</i> Henry, 1938	12. <i>Poecilocerastis</i> Ramme, 1929
6. <i>Epistaurus</i> I. Bolivar, 1889	13. <i>Ruwenzoracris</i> Rehn, 1914
7. <i>Eucoptacra</i> I. Bolivar, 1902	14. <i>Traulia</i> Stål, 1873

Subfamily *Calliptaminae*

(Text-fig. 26)

Type genus : *Calliptamus* Serville, 1831

Size small to medium. Head subconical to subglobular ; frons in majority of genera vertical ; fastigium of vertex roundly merging with frontal ridge ; interocular distance wide. Pronotum with median and lateral carinae (lateral ones

FIG. 26. 1-3. *Calliptamus italicus* (L.). 1. Male. 2. End of abdomen from above. 3. Male left cercus. 4-6. Epiphalli. 4. *Calliptamus italicus* (L.) 5. *Sphodromerus tuareg* Uv. 6. *Caloptenopsis glaucopsis* (Walk.).

sometimes obliterated) ; dorsum crossed by three sulci. Prosternal process cylindrical, conical or antero-posteriorly compressed. Mesosternal interspace open. Elytra and wings fully developed or reduced. Tympanum present. Hind femur usually wide, its lower basal lobe shorter than upper one. External apical spine of hind tibia absent. Two last abdominal tergites of male fused, inflated and upcurved. Cercus large, strong, incurved, bilobate, adapted for gripping. Basal and apical

valves of penis flexured. Epiphallus plate-like, mostly trapezoidal, with ancorae and without lophi. Stridulatory mechanism not found.

The subfamily *Calliptaminae* was erected by Jakobson (Jakobson & Bianki, 1904), but was disregarded as such by the majority of later authors; Mistshenko (1952) treated it as a tribe of *Catantopinae*. The representatives of this subfamily have a very characteristic plate-like epiphallus, not known in other subfamilies of *Acrididae*. The pincer-like male cerci also are peculiar, without close parallel in other subfamilies.

Calliptaminae are distributed in Europe, Africa and Asia.

List of known genera :

1. <i>Acorypha</i> Krauss, 1877	8. <i>Palaciosia</i> C. Bolivar, 1930
2. <i>Bosumia</i> Ramme, 1929	9. <i>Paracaloptenus</i> I. Bolivar, 1876
3. <i>Bothrocaracris</i> Uvarov, 1954	10. <i>Peripolus</i> Martinez, 1902
4. <i>Brachyxenia</i> Kirby, 1914	11. <i>Sphodromerus</i> Stål, 1873
5. <i>Caloptenopsis</i> I. Bolivar, 1889	12. <i>Sphodronotus</i> Uvarov, 1943
6. <i>Calliptamus</i> Serville, 1831	13. <i>Stobbea</i> Ramme, 1929
7. <i>Indomerus</i> Dirsh, 1951	

Subfamily *Euryphyminae*

(Text-fig. 27)

Type genus : *Euryphymus* Stål, 1873

Size small to medium. Antenna filiform. Head subconical to subglobular. Frons vertical or slightly oblique. Median and lateral carinae of pronotum present. Prosternal process present. Mesosternal interspace open. Elytra and wings fully developed, reduced or vestigial. Tympanum present. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia absent. Posterior margin of last abdominal tergite of male strongly sclerotized and slightly upcurved, with serrated or toothed edge. Male cercus of variable, mostly complicated shape, with expanded basal articulation. Ectophallic membrane with secondary sclerotization. Basal and apical valves of penis flexured. Epiphallus bridge-shaped, with divided bridge, lobiform ancorae and very large, tooth-shaped or elongate-lobiform lophi. Stridulatory mechanism not found.

The subfamily *Euryphyminae* was erected (Dirsh, 1956) mainly on the basis of the structure of the epiphallus, which is divided and has peculiar lophi, and the characteristic structure of the male cerci, with specialized basal articulation, which allows a wider range of movement of the cerci than in other groups. In both respects the subfamily is so well separated from all other subfamilies of *Acrididae* that it might be regarded as a family. However, the flexured basal and apical valves of the penis suggest that the *Euryphyminae* belong to the family *Acrididae*.

The subfamily *Euryphyminae* is distributed in S., SW., and E. Africa.

FIG. 27. 1. *Euryphymus haematopus* (L.), male. 2. *Amblyphymus rubripes* Uv., posterior end of male abdomen in pre-coital position, showing position of supra-anal plate (dotted), epiphallus (black) and cerci. 3-5. Cerci. 3. *Brachyphymus vylteri* St. (Ba, basal articulation). 4. *Amblyphymus miniatus* Uv. 5. *Acrophymus ocreatus* Uv. 6-8. Epiphalli. 6. *Brachyphymus vylteri* St. 7. *Amblyphymus miniatus* Uv. 8. *Acrophymus ocreatus* Uv. 9. Posterior margin of the last abdominal tergite and supra-anal plate of *Amblyphymus miniatus* Uv., showing strong sclerotization.

List of known genera :

1. <i>Acoryphella</i> Giglio-Tos, 1907	12. <i>Pachyphymus</i> Uvarov, 1922
2. <i>Acrophymus</i> Uvarov, 1922	13. <i>Phymeurus</i> Giglio-Tos, 1907
3. <i>Amblyphymus</i> Uvarov, 1922	14. <i>Platacanthoides</i> Kirby, 1910
4. <i>Anabibia</i> Dirsh, 1956	15. <i>Plegmapteroides</i> Dirsh, 1959
5. <i>Aneuryphymus</i> Uvarov, 1922	16. <i>Plegmapteropsis</i> Dirsh, 1956
6. <i>Brachyphymus</i> Uvarov, 1922	17. <i>Plegmapterus</i> Martinez, 1898
7. <i>Calliptamicus</i> Uvarov, 1922	18. <i>Rachitopis</i> Uvarov, 1922
8. <i>Calliptamuloides</i> Dirsh, 1956	19. <i>Rhodesiana</i> Dirsh, 1959
9. <i>Calliptamulus</i> Uvarov, 1922	20. <i>Somaliacris</i> Dirsh, 1956
10. <i>Euryphymus</i> Stål, 1873	21. <i>Surudia</i> Uvarov, 1930
11. <i>Kevanacris</i> Dirsh, 1961	

FIG. 28. 1-2. *Eyprepocnemis plorans* (Charp.). 1. Male. 2. Dorsum of pronotum, showing characteristic pattern. 3-5. Male cerci. 3. *Phyllocercus bicoloripes* Uv. 4. *Heteracris herbacea* (Serv.). 5. *Eyprepocnemis plorans* (Charp.). 6-8. Epiphalli. 6. *Heteracris calliptamoides* Uv. 7. *Phyllocercus bicoloripes* Uv. 8. *Eyprepocnemis plorans* Charp.

Subfamily *Eyprepocnemidinae*

(Text-fig. 28)

Type genus : *Eyprepocnemis* Fieber, 1853

Size small to large. Head subconical to subglobular. Fastigium of vertex merging roundly with frontal ridge ; inter-ocular distance wide. Pronotum with median and lateral carinae (lateral sometimes obliterated) ; dorsum crossed by three sulci. Prosternal process cylindrical or antero-posteriorly compressed. Mesosternal interspace open. Elytra and wings fully developed or reduced. Tympanum present. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia absent. Male cercus at apex flattened, widened or subacute and down curved. Basal and apical valves of penis flexured. Epiphallus bridge-shaped, mostly with poorly sclerotized bridge ; ancorae and lophi present. Stridulatory mechanism not found.

The subfamily *Eyprepocnemidinae* was established by Jakobson (Jakobson & Bianki, 1904), but was disregarded by later authors and considered as part of the subfamily *Catantopinae* and recently (Mistshenko, 1952) as a tribe of it.

The subfamily is defined by the following combination of characters : a weakly sclerotized and rather wide bridge of the epiphallus, with curved and sometimes rather complicated ancorae ; slender hind femur (with few exceptions) ; rounded and rather wide fastigium of the vertex ; presence of lateral carinae on the pronotum (rarely obliterated) ; and apically compressed male cerci. These characters are not confined to the *Eyprepocnemidinae*, but their combination defines the *Eyprepocnemidinae* as a natural group.

Eyprepocnemidinae are distributed in Africa, S. Europe, Asia and Australia.

List of examined genera :

1. <i>Amphiprosopia</i> Uvarov, 1921	15. <i>Heteracris</i> Walker, 1870
2. <i>Asmara</i> I. Bolivar, 1914	16. <i>Horaeocerus</i> Saussure, 1899
3. <i>Belonocnemis</i> I. Bolivar, 1914	17. <i>Jucundacris</i> Uvarov, 1921
4. <i>Brownacris</i> Dirsh, 1958	18. <i>Macrocara</i> Uvarov, 1930
5. <i>Burmacris</i> Ramme, 1941	19. <i>Navasia</i> Kirby, 1914
6. <i>Cataloipus</i> I. Bolivar, 1890	20. <i>Oxyaidea</i> I. Bolivar, 1914
7. <i>Choroedocus</i> I. Bolivar, 1914	21. <i>Paraeyprepocnemis</i> Brunner, 1893
8. <i>Cyathosternum</i> I. Bolivar, 1881	22. <i>Parathisoicetrus</i> Ramme, 1929
9. <i>Cyclopternacris</i> Ramme, 1928	23. <i>Phyllocercus</i> Uvarov, 1941
10. <i>Macrotona</i> Brunner, 1893	24. <i>Taramassus</i> Giglio-Tos, 1907
11. <i>Eyprepocnemides</i> I. Bolivar, 1914	25. <i>Thisoicetrellus</i> Uvarov, 1921
12. <i>Eyprepocnemis</i> Fieber, 1853	26. <i>Thisoicetrinus</i> Uvarov, 1921
13. <i>Eupreponotus</i> Uvarov, 1921	27. <i>Tropidiopsis</i> I. Bolivar, 1911
14. <i>Habrocnemis</i> Uvarov, 1930	28. <i>Tylotropidius</i> Stål 1873

Subfamily *Catantopinae*

(Text-fig. 29)

Type genus : *Catantops* Schaum, 1853

Size from small to large. Head of variable shape. Median carina of pronotum present or absent ; lateral carinae only rarely present. Prosternal process present.

FIG. 29. *Catantops melanostictus* Schaum. 1. Male. 2-6. Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. Penis, from above. 5. As fig. 3, but in profile. 6. Endophallus, in profile.

Mesosternal lobes rounded. Elytra and wings fully developed, reduced or absent; intercalary vein of medial area of elytron absent (rarely present). Tympanum normally present, rarely absent. Lower basal lobe of hind femur normally shorter than upper one. External apical spine of hind tibia present or absent. Basal and apical valves of penis flexured. Epiphallus bridge-shaped, sometimes with divided bridge; ancorae mostly present; lophi of variable form, mostly present. Stridulatory mechanism not found.

The *Catantopinae* are closely related to *Cyrtacanthacridinae* and *Acridinae*, but may be separated from *Cyrtacanthacridinae* by the rounded mesosternal lobes; and from *Acridinae* by the presence of a prosternal process, the absence of an intercalary vein in the medial area of the elytron and the non-articulated ancorae of the epiphallus, although these three characters do occur in certain *Acridinae*.

The subfamily urgently needs further study. It would be premature to attempt to subdivide it now, since there must be a large number of undescribed genera, particularly in the tropics.

The large subfamily *Catantopinae*, even in its present reduced scope, still represents a highly heterogeneous assemblage. It was usual to put into the subfamily any genus which would not fit elsewhere. As a result, the subfamily not only contains the basic group *Catantopini* but has also been a dumping ground for everything which needs further investigation.

The subfamily *Catantopinae* is distributed in the whole world, and includes a large number of genera. No list is given for obvious reasons.

Subfamily *Cyrtacanthacridinae*

(Text-fig. 30)

Type genus: *Cyrtacanthacris* Walker, 1870

Size large or medium. Antenna filiform. Head subglobular; frons vertical. Pronotum without lateral carinae; dorsum crossed by three sulci. Prosternal process large. Mesosternal interspace open; mesosternal lobes rectangular. Elytra and wings fully developed or reduced. Tympanum present. Lower basal lobe of hind femur shorter than upper one. External apical spine of hind tibia absent. Basal and apical valves of penis flexured. Epiphallus robust, bridge-shaped, with small or without any ancorae; lophi large lobiform or tooth-like. Stridulatory mechanism not found.

The main characteristic features of *Cyrtacanthacridinae* are the rectangular mesosternal lobes, the large size of the body, the strong epiphallus, with the ancorae shortened or absent, and the absence of lateral carinae on the pronotum.

It might be possible to regard *Cyrtacanthacridinae* as a group or a tribe within the subfamily *Catantopinae*, but their characters are sufficiently definite for them to be regarded as a separate subfamily.

The subfamily is distributed over the tropical, subtropical and temperate zones of the whole world.

List of known genera :

1. <i>Acanthacris</i> Uvarov, 1924	15. <i>Nomadacris</i> Uvarov, 1924
2. <i>Acridoderes</i> I. Bolivar, 1889	16. <i>Ootua</i> Uvarov, 1927
3. <i>Adramita</i> Uvarov, 1936	17. <i>Ornithacris</i> Uvarov, 1924
4. <i>Anacridium</i> Uvarov, 1923	18. <i>Orthacanthacris</i> Karsh, 1896
5. <i>Austracris</i> Uvarov, 1924	19. <i>Pachyacris</i> Uvarov, 1923
6. <i>Bryophyma</i> Uvarov, 1923	20. <i>Pachynotacris</i> Uvarov, 1923
7. <i>Chondracris</i> Uvarov, 1924	21. <i>Patanga</i> Uvarov, 1923
8. <i>Congoa</i> I. Bolivar, 1911	22. <i>Phyxacra</i> Karny, 1907
9. <i>Cyrtacanthacris</i> Walker, 1870	23. <i>Rhadinacris</i> Uvarov, 1923
10. <i>Finotina</i> Uvarov, 1924	24. <i>Rhytidacris</i> Uvarov, 1923
11. <i>Gowdeya</i> Uvarov, 1923	25. <i>Schistocerca</i> Stål, 1873
12. <i>Kinkalidia</i> Sjöstedt, 1931	26. <i>Valanga</i> Uvarov, 1923
13. <i>Kraussaria</i> Uvarov, 1924	27. <i>Willemsea</i> Uvarov, 1923
14. <i>Melicodes</i> Uvarov, 1923	

FIG. 30. 1. *Cyrtacanthacris tatarica* (L.), male. 2. Meso- and metasternum of *Schistocerca gregaria* Forsk. 3-5. Epiphalli. 3. *Cyrtacanthacris tatarica* (L.). 4. *Ornithacris cyanea* (Stoll). 5. *Anacridium aegyptium* (L.).

Subfamily ***Egnatiinae***

(Text-fig. 31)

Type genus : *Egnatius* Stål, 1876

Small. Head subconical. Median and lateral carinae of pronotum present. Prosternum with low convexity. Mesosternal interspace very short, mesosternal furcal suture being strongly curved backwards. Elytra and wings fully developed or

reduced; weak intercalary vein of medial area of elytron present or absent. Tympanum present. Abdominal tergites of male, on sides, often with transverse stridulatory ridges. Arolium very small. Basal and apical valves of penis flexured. Epiphallus bridge-shaped; ancorae articulated with bridge; lophi present.

The affinities of the subfamily *Egnatiinae* are rather obscure. Not long ago the genera concerned were regarded as members of the *Oedipodinae*. Bey-Bienko (1951) recognized them as a separate subfamily on the basis of the peculiar shape of the mesosternal furcal suture, the peculiar stridulatory mechanism in some of the genera

FIG. 31. 1-2. *Egnatius apicalis* St. 1. Male. 2. Meso- and metasternum. 3-6. Epiphalli. 3. *Charora crassivenosa* Sauss. 4. *Egnatius apicalis* St. 5. *Egnatiella cabrerai* I. Bol. 6. *Leptoscirtus isphahanicus* Uv.

and the poor development or absence of a vena intercalata in the medial area of the elytron. Slifer (1939) noticed that they possess Comstock-Kellogg glands, which are otherwise believed to occur only in *Catantopinae*. Bryantseva (1953) studied the foregut in *Egnatiinae*, and found that the folds and sculpture of its internal surface are similar to those in *Catantopinae* and different from those of *Oedipodinae*. On this basis it can be suggested that they are nearer to the *Catantopinae* than to any other subfamily.

The *Egnatiinae* are distributed in N. Africa and SW. Asia.

List of known genera :

1. <i>Charora</i> Saussure, 1888	4. <i>Egnatiella</i> I. Bolivar, 1914
2. <i>Egnatius</i> Stål, 1876	5. <i>Leptoscirtus</i> Saussure, 1888
3. <i>Egnatioides</i> Vosseler, 1902	6. <i>Paregnatius</i> Uvarov, 1933

FIG. 32. *Acrida turrita* L. 1. Male. 2-6 Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. Penis from above. 5. As fig. 3, but in profile. 6. Penis, in profile. 7. Serrated intercalary vein of *Oedipoda miniata* (Pall.).

Subfamily *Acridinae*

(Text-fig. 32)

Type genus : *Acrida* Linnaeus, 1758

Size small to large. Head of variable shape. Median and lateral carinae of pronotum mostly present. Prosternal process mostly absent. Elytra and wings fully

developed, reduced or absent; intercalary vein of medial area of elytron sometimes strong and serrated, sometimes weak, disappearing, but mostly present. Stridulatory mechanism, consisting of variable serration of elytra or wings, often present. Tympanum normally present. Lower basal lobe of hind femur shorter than upper one. Basal and apical valves of penis flexured. Epiphallus bridge-shaped; ancorae mostly present, articulated with bridge; lophi mostly present.

The subfamily *Acridinae* is related on the one hand to *Catantopinae*, on the other to *Truxalinae*.

The presence in some genera of a prosternal process connects them with *Catantopinae*, from which they differ, however, in the combination of other characters (see *Catantopinae*). From *Truxalinae* they differ clearly in the absence of stridulatory serration on the internal side of the hind femur. In the case of wingless genera and species, however, it is extremely difficult to decide to what subfamily they belong, since the phallic complex of *Acridinae* and *Truxalinae* does not provide clear separating features. The subfamily may be divided into several groups or tribes and one of them could be *Oedipodini*, which has been in the past regarded as a subfamily, mainly on the grounds of general appearance. Dirsh (1956) reduced it to a group. The only diagnostic character of *Oedipodini* suggested by Uvarov (1942), the serrated intercalary vein of the medial area of the elytra, is not reliable since there is a full transition to the *Acridinae*, the intercalary vein of which may be serrated, irregular, or altogether absent.

The *Acridinae* are distributed throughout the world and include a vast number of genera, a list of which would be superfluous.

Subfamily *Eremogryllinae*

(Text-fig. 33)

Type genus: *Eremogryllus* Krauss, 1902

Small. Head subconical or subglobular. Pronotum with median and lateral carinae. Prosternum with low, transverse convexity and slightly raised anterior margin. Mesosternal interspace short and wide. Elytra and wings fully developed; elytron with sharp radial vein (stridulatory specialization); intercalary vein of medial area absent. Tympanum present. Stridulatory serration, consisting of articulated pegs on internal side of hind femur present; lower basal lobe of hind femur shorter than upper one. Male cercus short, thickened, with incurved, acute apex. Subgenital plate shortened, transverse. Phallic complex relatively very small. Basal and apical valves of penis flexured. Epiphallus with divided bridge; ancorae small, incurved; lophi tooth-like, with strongly acute apices.

The subfamily *Eremogryllinae* was established recently (Dirsh, 1956) mainly on the basis of the peculiar structure of the epiphallus and the external genital appendages of the male. It shares the type of stridulatory mechanism with *Truxalinae* but the structure of the phallic complex is very different. There is no close relationship between *Eremogryllinae* and the other subfamilies of *Acrididae*.

The *Eremogryllinae* occur only in N. Africa.

List of known genera:

1. *Eremogryllus* Krauss, 1902

2. *Notopleura* Krauss, 1902

FIG. 33. 1-4. *Eremogryllus hammadae* Kr. 1. Male. 2. Stridulatory serration on internal side of hind femur. 3. End of male abdomen from above. 4. Epiphallus. 5. Epiphallus of *Notopleura saharica* Kr.

Subfamily *Truxalinae*

(Text-fig. 34)

Type genus : *Truxalis* Fabricius, 1775

Size from small to large. Head of variable shape. Median and lateral carinae of pronotum mostly present. Prosternal process absent, rarely present. Elytra and wings fully developed or reduced ; radial or radial and medial vein of elytron sharp (stridulatory specialization) ; intercalary vein of medial area absent. Tympanum present. Lower basal lobe of hind femur shorter than upper one ; stridulatory serration with articulated or not articulated pegs on internal side of hind femur present. Basal and apical valves of penis flexured. Epiphallus bridge-shaped ; ancorae articulated with bridge ; lophi present.

FIG. 34. *Truxalis grandis* Klug. 1. Male. 2-6. Phallic complex. 2. Whole phallic complex from above. 3. The same, but ectophallic membrane and epiphallus removed. 4. Penis from above. 5. As fig. 3, but in profile. 6. Penis in profile. 7. Stridulatory serration on internal side of hind femur (not articulated). 8. *Gomphocerus sibiricus* (L.), stridulatory serration (articulated).

The name *Truxalinae* has been used by many authors for the complex which is now divided into *Acridinae* and *Truxalinae*. Externally, representatives of both subfamilies present a series of parallel forms, but *Truxalinae* possess a stridulatory mechanism of a definite structure, found elsewhere only in *Eremogryllinae*. A somewhat similar structure is found in two South American genera of *Catantopinae* (see p. 358).

It might be argued that a single character is insufficient for separating the *Truxalinae* from the *Acridinae*, but it consists of a complicated structure of articulated or non-articulated stridulatory pegs, combined with the second part of the mechanism comprising sharp veins for friction and often widened areas of the elytron which serve as resonators. This highly specialized stridulatory mechanism constitutes a character so well defined that no confusion between winged members of the two subfamilies can possibly arise. There are no intermediate forms between *Truxalinae* and other subfamilies.

The *Truxalinae* are distributed throughout the world except Australia and Madagascar.

List of examined genera:

1. *Acantherus* Scudder, 1902
2. *Achurum* Saussure, 1861
3. *Acocksacris* Dirsh, 1958
4. *Acridarachnea* I. Bolivar, 1908
5. *Acrolophitus* Thomas, 1871
6. *Afrohippus* Uvarov, 1941
7. *Ageneotettix* McNeil, 1897.
8. *Amblytropidia* Stål, 1873
9. *Amesotropis* Karsch, 1893
10. *Amphitornus* McNeil, 1897
11. *Anablepia* Uvarov, 1938
12. *Anaptygus* Mistshenko, 1951
13. *Arcyptera* Serville, 1839
14. *Aswatthamanus* Kirby, 1914
15. *Aulacobothrus* I. Bolivar, 1902
16. *Aulocara* Scudder, 1876
17. *Azarea* Uvarov, 1926
18. *Baidoceracris* Chopard, 1947
19. *Bodenheimerella* Uvarov, 1933
20. *Bootettix* Bruner, 1890.
21. *Brachycrotaphus* Krauss, 1877
22. *Brainia* Uvarov, 1922
23. *Capulica* I. Bolivar, 1918
24. *Clinocephalus* Morse, 1896.
25. *Chloealtis* Harr, 1841
26. *Chorthippus* Fieber, 1852
27. *Chromotraxalis* Dirsh, 1951
28. *Chrysochraon* Fischer, 1853.
29. *Cophohippus* Uvarov, 1953
30. *Cordillacris* Rehn, 1901
31. *Dhimbama* Henry, 1940
32. *Diablepia* Kirby, 1902
33. *Dichromorpha* Morse, 1896
34. *Dnopherula* Karsch, 1896
35. *Dociostaurus* Fieber, 1853
36. *Eleutherotheca* Karny, 1907.
37. *Eremiacris* Hebard, 1929
38. *Eremippus* Uvarov, 1926
39. *Eritettix* Bruner, 1890
40. *Ermia* Popov, 1957
41. *Euchorthippus* Tarbinsky, 1925
42. *Euplectrotettix* Bruner, 1902
43. *Eupnigodes* McNeil, 1897
44. *Euthystira* Fieber, 1853
45. *Faureia* Uvarov, 1921
46. *Gomphocerippus* Roberts, 1941
47. *Gomphocerus* Thunberg, 1815
48. *Goniatron* Bruner, 1905
49. *Goniocara* Uvarov, 1953
50. *Heliaula* Caudell, 1915
51. *Kirmania* Uvarov, 1933
52. *Komandia* Uvarov, 1953
53. *Krausella* I. Bolivar, 1909
54. *Leuconotus* Bruner, 1904
55. *Leva* I. Bolivar, 1909
56. *Ligurotettix* McNeil, 1897
57. *Lounsburya* Uvarov, 1922
58. *Macneillia* Scudder, 1898
59. *Madurea* I. Bolivar, 1902
60. *Mermiria* Stål, 1873
61. *Mesochloa* Scudder, 1898
62. *Mesopsis* I. Bolivar, 1906
63. *Milleriola* Uvarov, 1953
64. *Mizonocara* Uvarov, 1912

65. *Mongolotettix* Rehn, 1928
66. *Morseiella* Hebard, 1925
67. *Myrmeleotettix* I. Bolivar, 1914
68. *Napaia* McNeil, 1897
69. *Notostaurus* Bey-Bienko, 1933
70. *Ochrlidia* Stål, 1873
71. *Omocestus* I. Bolivar, 1878
72. *Opeia* McNeil, 1897
73. *Oxytruxalis* Dirsh, 1950
74. *Paragonista* Willemse, 1932
75. *Paragymnobothrus* Karny, 1910
76. *Pararcyptera* Tarbinsky, 1930
77. *Paropomala* Scudder, 1899
78. *Pedioscirtetes* Thomas, 1873
79. *Peruvia* Scudder, 1890
80. *Phlibostroma* Scudder, 1875
81. *Phonogaster* Henry, 1940
82. *Phorenula* I. Bolivar, 1909
83. *Platypternodes* I. Bolivar, 1908
84. *Pnorisa* Stål, 1861
85. *Podismopsis* Zubowsky, 1899.
86. *Primnia* Stål, 1873
87. *Pescrocnemus* Henry, 1940
88. *Pseudegnatius* Dirsh, 1956
89. *Pseudoaracyptera* I. Bolivar, 1909
90. *Pseudogmothela* Karny, 1910
91. *Pseudopomala* Morse, 1896
92. *Psoloessa* Scudder, 1875
93. *Ptygonotus* Tarbinsky, 1927
94. *Quangula* Uvarov, 1953
95. *Ramburiella* I. Bolivar, 1906
96. *Raphotitta* Karsch, 1896
97. *Scyllina* Stål, 1873
98. *Silvitettix* Bruner, 1904
99. *Sinipta* Stål, 1860
100. *Sporobolius* Uvarov, 1941
101. *Stauroderus* I. Bolivar, 1897
102. *Staurorhectus* Giglio-Tos, 1897.
103. *Stenobothrus* Fischer, 1853
104. *Stenohippus* Uvarov, 1926
105. *Stirapleura* Scudder, 1876
106. *Syrbula* Stål, 1873.
107. *Thyridota* Uvarov, 1925
108. *Tinaria* Stål, 1861
109. *Truxalis* Fabricius, 1775
110. *Truxaloides* Dirsh, 1950
111. *Xenotruxalis* Dirsh, 1950
112. *Xerohippus* Uvarov, 1942
113. *Yendia* Ramme, 1929
114. *Zapata* Brunner, 1902

EXPLANATION OF SYMBOLS USED IN THE FIGURES OF THE PHALLIC COMPLEX

<i>Ap</i> , apical valves of penis.	<i>Fx</i> , flexure.
<i>Apd</i> , apodemes.	<i>Gpr</i> , gonopore processes.
<i>Art</i> , articulation.	<i>Gprs</i> , gonopore sclerite.
<i>Bf</i> , basal fold.	<i>m</i> , membrane.
<i>Bp</i> , basal valves of penis.	<i>Op</i> , opening.
<i>Cng</i> , cingulum.	<i>Os</i> , oval sclerites.
<i>Cv</i> , valves of cingulum.	<i>P</i> , penis.
<i>Da</i> , dorsal appendices of penis.	<i>Pht</i> , phallotreme.
<i>Ect</i> , ectophallus.	<i>Po</i> , pouch of phallus.
<i>Ectm</i> , ectophallic membrane.	<i>Rm</i> , ramus of cingulum.
<i>Ectv</i> , ectophallic valves.	<i>Scl</i> , sclerites of indefinite meaning.
<i>Ejd</i> , ejaculatory duct.	<i>Sh</i> , sheath of penis,
<i>Ejs</i> , ejaculatory sac.	<i>Sps</i> , spermatophore sac.
<i>End</i> , endophallus.	<i>Va</i> , ventral appendices of penis.
<i>Eph</i> , epiphallus.	<i>Zyg</i> , zygoma.

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