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## SYNOPSIS

The family Pneumoridae of Acridoidea is revised from the taxonomic point of view. All relevant data concerning morphology, ecology, geographical distribution and phylogenetic interrelation are summarized. Nine genera and eighteen species of the family are recognized.

## INTRODUCTION

The recent discovery of male Pneumoridae (Dirsh, 1963) with a small non-inflated body has made it necessary to alter the diagnosis of the family and to a certain extent the whole conception of it from the taxonomic point of view. This has consequently led to revision of the genera and species.

This task was extremely difficult owing to the great rarity of some of the species, general lack of material and in several cases the uncertainty of conspecificity of the males and females. Some of them are placed in the same species only tentatively. A favourable factor, however, was that practically all the types of described species of the family still exist and are preserved in reasonably good condition. They have all been studied, and compared with each other and with other available material, thus allowing the establishment in several cases of correct synonymy.
This revision does not ensure that all taxonomic problems in Pneumorids are solved. Many remain unsolved, mostly because of lack of material and almost complete absence of field observations. Several species are still known by one sex only.

There is reason to believe that the family is steadily diminishing in size of populations, as Thunberg in 1772 definitely found them in abundance (Thunberg, 1795), whereas at the present time, and in the same localities, only a few specimens can be found.

It is my pleasant duty to express my sincere gratitude to Mr. H. Dick Brown, Dr. G. van Son and Dr. T. H. C. Taylor for reading the manuscript and for their opinions and suggestions towards improving it. I am also grateful to Mr. J. P. Doncaster, Keeper of the Department of Entomology, British Museum (Natural History) for his favourable attitude towards the publication of this work.

**MATERIAL USED**

Besides the types, the material used for this work was lent from the following museums and by the courtesy of the following persons. I wish to express my sincere gratitude to all the following museums and to the persons concerned with providing the material used in this study, without which this revision would have been impossible. Dr. M. Beier, Naturhistorisches Museum, Vienna; Mr. H. Dick Brown, Pretoria; Mr. R. H. Carcasson, Coryndon Museum, Nairobi; Dr. L. Chopard, Muséum National d'Histoire Naturelle, Paris; Dr. Kurt Günther, Zoologisches Museum der Universität, Berlin; Dr. B. Hanson, Naturhistoriska Riksmuseet, Stockholm; Dr. L. Hedström, Zoological Institute, University, Uppsala; Dr. A. J. Hesse, South African Museum, Cape Town; Mr. W. J. Lawson, Durban Museum, Durban; Dr. E. Morales-Agacino, Instituto Espanol de Entomologia, Madrid; Dr. E. Pinhey, National Museum of Southern Rhodesia, Bulawayo; Dr. D. R. Ragge, British Museum (Natural History); Mr. C. J. Schiff, Albany Museum, Grahamstown; and Dr. G. van Son, Transvaal Museum, Pretoria.

**TYPES STUDIED**

**Linnaeus' types**

Two species of Pneumoridae were described by Linnaeus in the tenth edition of the "Systema Naturae". They are:


Both species are denoted in the descriptions "M.L.U." (Museum Ludovicæ Ulricæ), and "Habitat in Indiis". The locality is erroneous, as Pneumoridae occur only in Africa. From the descriptions it is apparent that Linnaeus had at least two or several specimens of each species.
At present in the Lovisa Ulrika Collection in Uppsala there are several specimens of Pneumorids which should be regarded as Linnaean specimens. They are all in a rather poor state of preservation but mostly recognizable. They bear no original Linnaean labels but labels in Thunberg's handwriting are pinned in the box below them; also they have on the pins more recent labels, possibly of Aurivillius, designating them as the types. However, Aurivillius never published his type designations, so these labels have no formal significance.

   (a) A male with the wings spread and of a greenish-yellow colour, labelled by Thunberg as "unicolor Lin. immaculata β". This specimen is here selected as LECTOTYPE of *Gryllus Bulla unicolor* Linnaeus, 1758.
   (b) A male labelled by Thunberg as "immaculata α". Possibly not a Linnaean specimen.
   (c) A male with both pairs of wings spread and of a reddish coloration, labelled by Thunberg as "rubrus immaculata ruf. (unicolor Lin.)". Probably a Linnaean specimen, since he also mentioned this coloration in his description.

   (a) A male with the wings spread, labelled by Thunberg as "variolosus Lin.". This specimen is here selected as LECTOTYPE of *Gryllus Bulla variolosus* Linnaeus, 1758.
   (b) An adult female conspecific with (a), labelled by Thunberg as "variolosus Lin. Larva." possibly not a syntype.
   (c) An adult female in poor condition, labelled by Thunberg as "immaculata Larva.". Not now identifiable, but certainly not a female of *immaculata*. Probably not a syntype.

**Thunberg's types**

All Thunberg's types of Pneumoridae are still in existence and are preserved in the Uppsala Museum in "Thunberg's Collection". All are in reasonably good condition. There are no labels attached to the insects, but there are labels in Thunberg's handwriting pinned on the bottom of the box. Since the specimens correspond very well with Thunberg's descriptions and particularly with the figures published by him (Text-fig.1) it is reasonably safe to assume that these specimens are accepted as being the types and syntypes on which Thunberg based his descriptions.

1. *Pneumora immaculata* Thunberg, 1775. Three syntype male specimens present, "α, β, γ" which correspond quite well with the specimens with the same letters in Thunberg's description. The specimen mentioned by Thunberg under the letter "δ" is missing. All three specimens are conspecific. The specimen marked "β" is here selected as LECTOTYPE.

*Pneumora immaculata* was compared with the lectotype of *Gryllus Bulla unicolor* Linnaeus, 1758 and with a series of recent material of this species and was found conspecific.
2. *Pneumora rubens* Thunberg, 1810. Two male syntypes of *P. rubens* present, "α" and "β". They are conspecific with one another, and also with *Pneumora immaculata* Thunberg, and therefore with *Gryllus Bulla unicolor* Linnaeus, 1758. They differ from other specimens of the species by a general reddish coloration. Between themselves they differ in body size, the "α" specimen being larger. In the description of *Pneumora rubens* Thunberg, 1810, the "α" and "β" specimens are not mentioned. Here the "α" specimen is selected as the *LECTOTYPE* of *Pneumora rubens* Thunberg, 1810.

3. *Pneumora papillosa* Thunberg, 1810. Under this name there is one male specimen in Thunberg’s Collection. According to the description and figure, there is no doubt that it is the type. It is conspecific with the female of *Pneumora obliqua* Thunberg, 1810, the latter name having priority. It is distinguishable from the other species by the presence of two oblique, white stripes on the side of the pronotum. Kirby (1910) renamed this species as *Bulla thunbergii*, as the specific name *papillosa* was preoccupied by Fabricius, 1775.

4. *Pneumora discolor* Thunberg, 1810. One male in Thunberg’s Collection present which, according to the description and figure, is undoubtedly the type. It differs from the other specimens of the species by a slightly brownish coloration of the basal two thirds of the elytra and wings. This is a rather infrequent individual variation which occurs in this and other species of the genus.

5. *Pneumora ocellata* Thunberg, 1810. Under this name in Thunberg’s Collection there is one male specimen. From the description and the figure it is clear that the specimen is the type. It is conspecific with *Pneumora discolor* Thunberg, 1810. The only difference is that the elytra and wings are of uniformly greenish colour. This is the most common type of coloration for the species.

6. *Pneumora pupillata* Thunberg, 1810. Under this name in Thunberg’s Collection there is one male specimen. From the description and the figure there is no doubt that the specimen is the type. It is conspecific with *Pneumora discolor* Thunberg, 1810 and *Pneumora ocellata* Thunberg, 1810. The only difference is that the elytra of *P. pupillata* are sparsely covered with brownish dots. This is an individual variation which sometimes occurs in this and other species.

7. *Pneumora serrata* Thunberg, 1810. Under this name in Thunberg’s Collection there is one female specimen. According to the description and the figure there is no doubt that it is the type.

8. *Pneumora obliqua* Thunberg, 1810. In Thunberg’s Collection one female specimen is present. It corresponds very well with the description and the figure and doubtless is the type.

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**Fig. 1.** Plate of Pneumorids originally published by Thunberg in 1810. The types of Thunberg’s Collection correspond very well with the drawings.
9. *Pneumora maculata* Thunberg, 1775. In Thunberg's Collection one male specimen is present. It corresponds with the description and doubtless is the type. It is conspecific with *Gryllus Bulla variolosus* Linnaeus, 1758. It differs slightly in the pattern, but the difference does not exceed the range of individual variability.

10. *Pneumora marmorata* Thunberg, 1810. In Thunberg's Collection two male syntypes "α" and "β" present. They belong to the same species. However, in the original description they are not mentioned under the different letters. Here the male marked "β" is designated as the LECTOTYPE of *Pneumora marmorata* Thunberg, 1810. It corresponds very well with the original description and figure and could be safely considered as Thunberg's original specimen. It is conspecific with *Gryllus Bulla variolosus* Linnaeus, 1758 and differs slightly from it only in the pattern on the pronotum.

11. *Pneumora spinulosa* Thunberg, 1810. Under this name in Thunberg's Collection there is one female specimen. It corresponds with the description and the figure and is undoubtedly the type. It is conspecific with *Gryllus Bulla variolosus* Linnaeus, 1758.

12. *Pneumora sexguttata* Thunberg, 1775. Under this name there is in Thunberg's Collection one male specimen, which according to the description is without doubt the type. Comparison with the Fabricius type of *Gryllus inanis* Fabricius, 1775, proved that they are conspecific. The Fabrician name has priority.

**Fabricius' types**

1. *Gryllus inanis* Fabricius, 1775. In the Banks Collection in the British Museum (Natural History) there is one male specimen under this name. It is undoubtedly the type. Type Locality: Cape of Good Hope.

2. *Gryllus papillosus* Fabricius, 1775. Under this name in the Banks Collection in the British Museum (Natural History) there is one male specimen. It is certainly the type of the species.

**Stoll's types**

Stoll mentioned as new and figured three species of Pneumoridae:


The types of all three species are lost, but the figures and descriptions, although highly inadequate, still indicate that all of them are Pneumoridae and probably belong to the genus *Bullacris*. They have all been synonymized with *Pneumora immaculata* Thunberg, 1775 by Serville, 1888 and Kirby, 1910 (see synonymy of *Bullacris unicolor* Linnaeus, 1758). There is no reason now to consider them otherwise.

They are the only types of Pneumoridae which are lost.
Latreille's type

_Pneumora scutellaire_ Latreille, 1830. Under this name in the Muséum d'Histoire Naturelle in Paris there is one female specimen which most probably is the specimen first described by Latreille in 1830, and again in 1831 by Serville under the same name _Pneumora scutellaris_. It is conspecific with the male of _Gryllus inanis_ Fabricius, 1775.

Walker's type

_Pneumora membracioides_ Walker, 1870. Male nymph. The type is preserved in the British Museum (Natural History). It is a male nymph, probably of the last instar. After studying all available material it was concluded that _P. membracioides_ Walker is a nymph of _Bulla longicornis_ Stål, 1873. The same opinion was expressed by Péringuey, 1916.

Stål's types

Stål's types are preserved in good condition in the Stockholm Museum.

1. _Bulla longicornis_ Stål, 1873. Male type. The specimen was pinned after being preserved in spirit. All morphological characters are intact, but the integument is discoloured and partly wrinkled. Locality label "Caffraria". It is conspecific with _Pneumora membracioides_ Walker, 1870.

2. _Pneumora granulata_ Stål, 1873. Male. This type is in a very good state of preservation. Locality label: "Caffraria". The female was described as _Bulla subulata_ Péringuey, 1916.

Westwood's type

Westwood's type is preserved in the Oxford University Museum.

_Physophorina livingstoni_ Westwood, 1874. Nymph, probably of the last instar. When nymph material was studied, it became clear that _Physophorina livingstoni_ is a synonym of _Cystocoelia absidata_ Karsch, 1896.

Karsch's type

The male type of _Cystocoelia absidata_ Karsch, 1896, is preserved in the Berlin Museum in reasonably good condition. Comparison with the type of _Physophorina livingstoni_ Westwood, 1874 and all available material shows that they are conspecific.

Péringuey's types

All Péringuey's types are preserved in the South African Museum, Cape Town. All of them are in a good state of preservation.
1. *Bulla consobrina* Péringuey, 1916. Male and female are conspecific, both with the label "Type". The male is here selected as the LECTOTYPE. Type locality: "Port Elizabeth". After comparing the types and available recent material, it was found that *Bulla consobrina* Péringuey is conspecific with *Pneumora discolor* Thunberg, 1810.

2. *Bulla intermedia* Péringuey, 1916. This species was originally described from three males. The type was not designated. At present, in the South African Museum only one male remains labelled "Type". I select this specimen as the LECTOTYPE.

3. *Bulla subalata* Péringuey, 1916. Female type. It has been synonymized rightly by Uvarov, 1928 with *Pneumora granulata* Stål, 1873, which was described from one male only.

4. *Shortridgea miranda* Péringuey, 1916. Male specimen with the label "Holotype" and a conspecific female specimen with the label "Type" present. Here the male specimen is selected as the LECTOTYPE. Type locality: "Zululand, Eshowe".

5. *Cystocoelia boschimana* Péringuey, 1961. There is only the female holotype of this species, in a good state of preservation, the male is unknown. Type locality: "Bushmanland, Henkries".


**REHN’S TYPES**

Rehn’s two types are preserved in the Transvaal Museum, Pretoria.


These two species are conspecific inter se and are also conspecific with *Bullacris unicolor* Linnaeus, 1758. They were compared with the Linnaean type and all Thunberg’s types, as well as with the series of recent material of the species. The differences recorded by Rehn do not exceed the range of the individual variation.

**MORPHOLOGICAL CHARACTERS OF THE FAMILY**

**Body**

The body length of adult Pneumorids varies in males from 11.5 mm.—68 mm. and in females from 22 mm.—107 mm. The smallest is *Pneumoracris browni* and the largest *Physophorina livingstoni*.
In the majority of genera and species the male abdomen is strongly inflated and bladder-like, creating an impression of a huge bulk of roughly cylindrical shape. In males with a non-inflated abdomen, the body is slightly compressed. In females, in the majority of species, the body is compressed or in a few cases, e.g. *Pneumora*, it approximates to cylindrical.

**Head**

The head of Pneumorids is hypognathous. It is remarkable for the absence of the frontal ridge, which is present to a certain degree in all other families of Acridoidea. The face is flattened and/or slightly convex. A faint fastigial furrow is present. The compound eyes in all species are oval, comparatively small and strongly convex. The ocelli in males are very large, relatively much larger than in all other Acridoidea, in females however, the ocelli are very small (except in one species), mostly vestigial, sometimes hardly detectable. The position of the lateral ocelli may be used as a character for grouping genera, they are placed above and slightly internally to the antennal bases in *Bullacris* and related genera (Text-fig. 8), and they are above and slightly externally to the antennal bases (Text-fig. 29) in *Pneumora* and *Physophorina*, while in *Prostalia* their position is intermediate.

The maxillary palpi are five-segmented and the labial palpi four-segmented, if the palpiger is included in both cases.

The mandibles are of forbivorous type (Isely, 1944) with sharp, large, acute teeth in the incisor parts and with rather sharp, toothed edges in the molar parts (Text-fig. 8).

**Antenna**

The antennae are relatively short in all genera and species, shorter or much shorter than the pronotum, the scape and pedicel are short, the flagellum filiform or in a few cases slightly club-like. The number of segments varies from 18 to 23; in most cases there is the same number in both sexes of a species, but sometimes in females there are one or two segments less than in males. This number fits very well into the range of antennal segments of Acridoidea generally (Mason, 1954). The segments are well defined and rather sharply separated.

**Thorax**

The pronotum in Pneumorids varies between highly crest-shaped and low tectiform. It is crossed by four, usually well developed transverse sulci. In the first instar, the pronotum is relatively larger, covering the whole body from above. In subsequent instars it becomes relatively smaller, but is still very large even in the adults.

The sternal part of the thorax in general outline is similar to that on all other Acridoidea, but a detailed morpho-anatomical study is necessary to ascertain the homology of the parts. The prosternum is without a process or tubercle. The meso- and metasternum have deep furcal sutures and very deep foveolae (sternal apophyseal pits). The mesosternal lobes (sternellum of anatomists) are relatively small. In males with an inflated abdomen the whole thorax is inflated as well.
ABDOMEN

The segmentation of the abdomen in Pneumorids is of the usual Acridoidea type. In the males of the majority of genera, however, the first five or six abdominal segments form a bladder-like inflation. The first, second and third abdominal segments in the inflated species are partly fused and sometimes it is difficult to distinguish them. The third abdominal tergite bears a crescent-like row of small strongly sclerotized ridges, which represent part of the stridulatory mechanism. The non-inflated distal segments of the abdomen are of usual narrow cylindrical shape. The inflation of the male body apparently appears only at the last moult; the male nymphs of the last instar have the normal, compressed body.

The terminal abdominal segments are represented by a pair of paraprocts and by a supra-anal plate (epiproct of anatomists), which are regarded as the eleventh abdominal tergite. The paraprocts in Pneumorids are large and frequently exceed the length of the supra-anal plate. The supra-anal plate in both sexes of all genera and species of the family is simple, elongate and angular. The cerci in both sexes also simple, short and conical. The subgenital plate, which in the male is regarded as the ninth abdominal sternite, is short or moderately elongated, conical or acutely conical. In the female the subgenital plate is regarded as the eighth abdominal sternite; it is always simple with a widely obtuse-angular apex.

The ovipositor in all genera and species is a rather simple, uniform structure, with straight valves, which are subacute and slightly curved at the apices, without external sculpture (Text-fig. 8).

LEGS

The structure of the legs of Pneumorids does not deviate markedly from other Acridoidea. The front and middle pair have no unusual specialization, except that the femora are sometimes tuberculate. The hind legs, however, differ in the respect that functionally they have lost or are losing saltatorial ability and approximate to cursorial. Morphologically they are short and rather slender. They are adapted for walking and also for producing sounds as a part of the sound-producing mechanism. The shape of the hind femur suggests that the lower basal lobe is longer than the upper one. In the middle of the internal side of the male femur there is a short, strongly sclerotized longitudinal carina with a series of strong, short, transverse ridges (Text-fig. 8) for stridulatory purposes (see description of the stridulatory mechanism).

Brunner's organ in most cases is absent, but sometimes it can be traced as a vestigial formation, and in other cases as in Pneumora and Parabullacris, it is fairly well developed.

The reduction and disappearance of Brunner's organ is probably connected with the lack of saltatorial specialization of the legs. It is observed that in the whole family Proscopiidae it is absent, and the hind legs in that family are also weak and approximating to cursorial. The same is also applicable to the genus Psednura of the family Pyrgomorphidae; the hind legs in this genus are very thin and look
almost cursorial. Brunner's organ in this genus also is vestigial. Thus, probably the Pneumorids are losing Brunner's organ as the result of the reduced saltatorial ability.

Wings

All known Pneumorids possess wings. The males with inflated bodies are all macropterous. The males with non-inflated bodies have vestigial elytra and wings completely hidden under the pronotum.

Females have micropterous elytra and wings completely or partly hidden under the pronotum (Bullacris, Physemacris), or strongly shortened brachypterous elytra and wings (Physophorina, Prostalia and Pneumora). In the genera Parabullacris and Pneumoracris the elytra and wings in the females are vestigial and completely hidden under the pronotum.

![Diagram of wings](image)

Fig. 2. Wings of the male Bullacris unicolor. For lettering of venation see text.
The elytra and wings in the Pneumorids have certain peculiarities which separate them from all other Acridoidea.

The elytra of the macropterous males are comparatively wide: they possess a large remigium (terminology after Snodgrass, 1935) and very small vannus; there is no vannal flex (vannal fold, Snodgrass, 1935) of the elytra.

The main venation of the elytron (Text-figs. 2–5) is described below. (The terminology used is a combination of that of Snodgrass, 1935, which is the most adequate for Acridoidea and that of Ragge, 1955, who attempted to homologize the venation of all Orthopteroids.)

Costa (C) (Snodgrass, 1935; Ragge, 1955): the first main vein, well defined from the basal articulation of the elytron. It is located posteriorly to the anterior or costal margin and reaches about half the length of the elytron.

Subcosta (Sc) (Snodgrass, 1935; Ragge, 1955): the second main vein after the costa. It is very well defined from the basal articulation. It runs almost to the apex of the elytron and is unbranched.

Radius (R) (Snodgrass, 1935; Ragge, 1955): the third main vein, which is very well defined from the basal articulation, runs next to the subcosta, and forms a branch, the Radial sector (Rs), which itself forms three or four branches.

Media (M) (Snodgrass, 1935; Ragge, 1955), the fourth main vein, is derived from the basal articulation. It is two or sometimes three branched in the apical half.

Cubitus (Cu) (Snodgrass, 1935; Ragge, 1955): the fifth main vein emerges from the basal articulation and near the base is branched into cubitus (Snodgrass, 1935) or cubitus one Cu₁ (Ragge, 1955) and to postcubitus (Snodgrass, 1935) or cubitus two Cu₂ (Ragge, 1955). The cubitus one is unbranched in the genera Bullacris, Physemacrïs, Peringueyacrïs and Prostalia (Text-fig. 2) and two branched in the apical half in Physophorina and Pneumora (Text-fig. 4).

Next to the fifth vein is the dividing vein, vena dividens (Snodgrass, 1935) or the first anal vein A (Ragge, 1955). Along this vein the elytron is flexed in all Acridoidea except Pneumoridae. The next vein after the vena dividens is the first vannal vein (Snodgrass, 1935) or the second anal vein (Ragge, 1955).

The wing in the macropterous males is remarkable for its large remigium, of almost the same size as the vannus. The vannal flex (vannal fold, Snodgrass, 1935) is present and the venation is not different from other Acridoidea (Text-figs. 2, 4). The Costa forms the margin of the wing, and the Subcosta almost reaches the apex. The Radius and Media are fused in the basal part; in the apical half they are both branched, the Radius into Radial sectors and the Media into Media anterior and Media posterior. Cubitus one and Cubitus two are unbranched. The vena dividens (Snodgrass, 1935) or first anal vein (Ragge, 1955) is well pronounced and the wing is flexed along it; all veins posterior to it are vannal veins (Snodgrass, 1935) or anal veins (Ragge, 1955).

In the brachypterous females (Physophorina, Pneumora and Prostalia) the venation of elytron and wing is essentially the same as in the males of this group (Text-fig. 5), but the first cubital vein of all female elytra is unbranched. All the veins, however, are less developed than in the males and show definite signs of reduction.
In the micropterous females (*Bullacris, Physemacris*) the elytron is thickened and strongly sclerotized and in a few, greatly reduced, but the main veins can be traced (costa, subcosta, radius-media and probably the first anal vein) (Text-fig. 3). The wing in these females is completely hidden under the pronotum. It is much larger

![Diagram of Bullacris unicolor](image)

**Fig. 3.** *Bullacris unicolor*, female. 1, right elytron and wing in normal position; hind wing folded, r, remigium; v, vannus. 2, venation of the right elytron. 3, venation of the right wing (for lettering see text).
than the elytron, and its venation is quite detectable (Text-fig. 3), consisting of all the veins as in the males, but reduced and unbranched (Text-fig. 3). The wing is folded singly only (Text-fig. 3) along the vannal flex. Its reticulation is rather strong and is possibly part of the sound producing mechanism (q.v.)

The net-like reticulation of elytra and wings (archedictyon of some authors) exists in both sexes, but is obscure in the sclerotized elytra of micropterous females. It is well pronounced, however, in the micropterous type of wings.

The main differences between the elytra and wings of Pneumoridae and those of the rest of the Acridoidea are, in macropterous species, as follows:

<table>
<thead>
<tr>
<th>Pneumoridae</th>
<th>Acridoidea</th>
</tr>
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<tbody>
<tr>
<td>Elytron:</td>
<td>Elytron:</td>
</tr>
<tr>
<td>Relatively very wide.</td>
<td>Relatively narrow (except</td>
</tr>
<tr>
<td></td>
<td>Trigonopterygidae).</td>
</tr>
<tr>
<td>Vannal flex absent.</td>
<td>Vannal flex present.</td>
</tr>
<tr>
<td>Main veins, in apical half,</td>
<td>Main veins comparatively</td>
</tr>
<tr>
<td>curved towards posterior</td>
<td>straight and very little or</td>
</tr>
<tr>
<td>margin.</td>
<td>not at all curved</td>
</tr>
<tr>
<td>Remigium relatively large.</td>
<td>Remigium relatively much</td>
</tr>
<tr>
<td>Vannus very small and narrow.</td>
<td>smaller.</td>
</tr>
<tr>
<td>Radial vein and radial sector</td>
<td>Radial vein and radial sector</td>
</tr>
<tr>
<td>in basal two thirds fused.</td>
<td>close together in basal</td>
</tr>
<tr>
<td>Intercalary veins absent.</td>
<td>half, but not fused (except</td>
</tr>
<tr>
<td>Wing:</td>
<td>in Trigonopterygidae).</td>
</tr>
<tr>
<td>Remigium relatively very</td>
<td>Intercalary veins mostly</td>
</tr>
<tr>
<td>large, almost as large as</td>
<td>present.</td>
</tr>
<tr>
<td>vannus.</td>
<td>Wing:</td>
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<tr>
<td>Vannus relatively very small.</td>
<td>Remigium relatively small,</td>
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<tr>
<td>Archedictyon well developed</td>
<td>much smaller than vannus.</td>
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<td></td>
<td>Vannus large.</td>
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<td></td>
<td>Archedictyon poorly</td>
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Ragge (1963) investigated venation and tracheation of the nymph’s wing pads. He showed one more character which distinguishes wings of Pneumorids from those of other Acridoidea. The bases of the tracheae of the elytron and wing, which are branched from the transverse basal trachea, are further apart in Pneumorids than in the rest of the Acridoidea. In the latter, they are more clustered together, particularly those which correspond to the median, cubital and vannal veins (Ragge, 1963). The remoteness of the bases of the tracheae from each other is generally more pronounced in Tettigonioidae, Gryllidoidea and Gryllacridoidea than in Acridoidea.

It can be definitely asserted that the venation of Pneumorids is the simplest in all the Acridoidea.
Fig. 4. Elytron and wing of the male Physophorina livingstoni. For lettering of venation see text.

Stridulatory Mechanism

The male stridulatory mechanism consists mainly of strongly sclerotized ridges on the third abdominal tergite (Text-figs. 8, 12, 14, 16, 18, 20, 22, 24, 25, 27, 29, 31, 33). The ridges form a crescent-like row, and are smaller at the ends, becoming gradually larger in the median part. At the upper end of the row there is a small, tubercle-like inflation of the body wall of unknown function. The lower part of the row gradually diminishes to the point of obliteration. In Physophorina and Pneumora the row is represented in the upper half by large, rough ridges and in the lower half, with a small gap between them, by small, slender and more densely placed ridges (Text-figs. 29, 33). The number of ridges may be used as an additional taxonomic character, sometimes of specific value.
The second part of the stridulatory mechanism is a short high carina, bearing a small row of strong, transverse ridges on the internal side of the hind femur (Text-fig. 8). The sound is produced by rubbing the ridges of the abdomen with the ridges of the hind femur. It is assumed that the inflation of the male abdomen represents a further specialization for sound production, its function being a resonator amplifying the sounds. It is true that the inflation increases the sound greatly, but whether this inflation is a primary specialization for sound production or developed for different purposes and became a secondary adaptation for the sound, remains a matter for speculation.

The structure of the inflated abdomen, however, may suggest that it was primarily a sound producing specialization. The abdominal segments, particularly the tergites, are strongly enlarged in width and partly in length, and the connecting intersegmental membrane almost disappears, acquiring almost the same texture as the segments themselves. The integument of the whole inflated part is very thin and semi-transparent; the tracheae can be seen through it very clearly. All the inflated part, although thin, is sufficiently firm to maintain a definite form of this part of the body. Inside this empty "bladder" only a thin length of the alimentary canal can be seen through the semi-transparent walls. It is difficult to imagine any function of this inflation other than as a resonator.

It seems that the males with a non-inflated body cannot produce sounds unless they possess some kind of mechanism not yet discovered. It should be noted, however, that in the species with the non-inflated body, the same kind of stridulatory mechanism is present as in those with the inflated body, but in a highly reduced, vestigial form and most probably not functional.

The sounds produced by Pneumorids was first mentioned by Thunberg, 1795 in his narrative of the "journey into Caffraria, 1772". He described it as follows: "After sunset they begin to make a singular noise, by rubbing their barbed hind legs against their empty and transparent stomach".

Périnęguey, 1916 described the sound produced by the males as . . . "A long and very deep and loud rasping noise, a stop, and a second noise shorter, but occasionally longer than the first, and something as if it were produced by exhalation."

Van Son (in litt. 1963) described the sounds produced by the males of Bullacris and Prostalia as follows: "it consists of a 'preliminary' short series of clicks or chirps, followed by a protracted 'main' sound". He also stated that in Pneumora inanis "there is a long preliminary screech, followed by a series of very human-like 'khonia - khonia - khonia'," that the "Physemacris variolosa call has no preliminary sound, and is like the word 'hatchigeeee' emitted in a rather high screeching note", and that "in Physophorina miranda the call starts with a prolonged screech (not unlike that of Pneumora) followed directly by the four sharp metallic "pings", the first accentuated, the other three in quick succession, thus like the Morse telegraph code letter — · · ·".

It should be noted that the male of both Physophorina miranda and Pneumora inanis males possess similarly shaped rows of abdominal ridges.
Fig. 5. Pneumora inanis. Female. Right elytron and wing. For lettering of venation see text. Below, left, highly magnified part of the wing, showing supposed stridulatory mechanism (diameter of the circle = 1 mm.).
The females do not possess the same kind of sound producing mechanism as the males, but according to many direct observations can produce sounds. Van Son, 1958 described these sounds for Bullacris longicornis as follows: "... peculiar squeak, somewhat like that produced by a disturbed Death-Head Moth"... When taken in the hand it produced louder squeaks... "rather resembling the hiss-like sounds emitted by an angry scorpion".

Péringuey, 1916 described the sounds produced by the females of Bullacris and Physemacris as follows: "When alarmed she raises the pronotum at a high angle, and produces an extremely sharp stridulation, nearly equal in intensity to that of a Decticid".

It is still not definitely known by what mechanism the sounds are produced by females. There is a possibility that they are produced by rubbing the folded vannus of the wing against the abdominal wall. In Pneumora inanis the posterior part of the vannus of the wing (Text-fig. 5), is covered with a net of rather strong veinlets between the main vannal veins and both these main veins and the veinlets in this region are covered with small, rather strong teeth (Text-fig. 5). The purpose of these teeth could be stridulatory.

**Phallic complex**

The phallic complex in Pneumoridae is rather uniform in structure throughout the family. It differs strongly from that of all the other families of Acridoidea. The main feature is its simplicity and a very low degree of sclerotization. Schematically it could be described as a structure relatively small for the size of the body, membranous, consisting of a very simple endophallus, simple ectophallus and weakly sclerotized epiphallus. The ectophallus and endophallus are partly and weakly sclerotized.

The membranous parts of the ectophallus are so soft that on the basis of dry specimens, it is difficult to reconstruct their natural shape. Accordingly, the figures of the phallic complex given below must be regarded only as a near approximation, giving the notion of the shape in its principal parts. They have been drawn as they are and do not look symmetrical because some parts are creased and cramped, and more or less folded. As can be seen from the figures every species has its characteristic features, but it must be remembered that in Pneumoridae the ectophallus may be stretched like a concertina, or more telescoped than is shown on the figures, thus changing the visual picture considerably. This stretching and collapsing is a matter of preparedness for copulation and is a natural feature of the organ. The post-mortem position may be of any degree between the two extremes mentioned above. Preparing a specimen for study by maceration or boiling in potassium hydroxide makes it soft, but the natural position of the parts is a matter for conjecture.

The phallic complex of Bullacris unicolor is described and figured below in detail, with as much reconstruction as possible of the supposed natural shape. The parts described are present in all the species of the family and differ only in relative sizes and slightly in shape. Since the Pneumorid phallic complex is rather different from
that of other Acridoidea, the terminology used for it (Dirsh, 1956) is restricted to a few terms and instead a descriptive procedure is employed.

The phallic complex (Text-fig. 9) of *Bullacris unicolor* (Linnaeus) is a relatively small, membranous structure, some of the parts of which are weakly sclerotized. The epiphallus (A) is large, discoidal, without ancorae, lophi or oval sclerites, but with three tooth-like median projections at the anterior end and with lateral plates (in the same meaning as in other Acridoidea), as well as the posterior projections; the posterior part of the epiphallus is a weakly sclerotized membrane (B), which should be considered as a part of the epiphallus. The major part of the phallic organ is covered at the dorsal side by the epiphallus (Text-fig. 9). The epiphallus is connected by a membranous fold with the ectophallic membrane, which posteriorly forms a sclerotized transverse part (C); the distal end of this part has a folding membranous continuation which is connected by the fold at the distal end with the weakly sclerotized disc-like part of the membrane (D). This disc has been considered as a rudimentary cingulum (Dirsh, 1956), but in fact there is no certainty that it is a homologous or even analogous structure. Accordingly, in this paper, it is referred to as discoidal sclerotization of the ectophallic membrane. The distal part of the discoidal sclerotization forms a membranous fold and is connected with a pair of dorsal, slightly sclerotized lateral valves (E); the lateral part of these valves is inflated and the dorsal part protrudes upwards and forms a pair of lobes (F). The E valves at the distal end are joined with a thin-walled sac (H) of undefined form. This sac is a continuation of the pair of ventro-posterior valves (G). The proximal end of these valves produces a plate-like membranous continuation (I). The endophallus is represented by a banana-shaped membranous tube (L), on the sides of which there is a pair of longitudinal, rod-like sclerotizations (M); at the apex its edges merge with the edges of the ectophallus sac, and form a pair of laterally protruding small lobes (J), between which is the opening of the endophallus. Ejaculatory duct (K) is rather wide.

The structure of the endophallus is extremely simple, without definite division on the ejaculatory and spermatophore sacs, but if the longitudinal sclerotizations are considered as homologous with the penis valves of other Acridoidea then it is possible to consider one of the parts of the sac as the ejaculatory sac and another part as the spermatophore sac.

It may be concluded that the Pneumoridae have the same general plan of structure of the phallic complex as all other Acridoidea but in much simpler form with an undifferentiated ectophallus and endophallus.

Snodgrass, 1957 generalized the phylogenetic development of the male genitalia of insects on the basis of their ontogeny. He offered the theory that all male genital structures were derived from the small ectodermal outgrowth, the primary phallic lobes, which are in fact continuations of the ampullae of the vasa deferentia. They develop later into terminal parts of the internal genitalia.

The study of the phallic complex of adult Pneumorids suggests that their endophallus could be interpreted rather as a simple widening of the vasa deferentia. The ectophallus then represents a secondary external invagination of the endophallus.
which has acquired a certain degree of differentiation. The epiphallus may be a
derivative of this invagination. However, the possibility that it may be derived
from the tergal metamere is not excluded.

**Spermatheca**

The spermatheca in Pneumorids, judging from the species in which it was studied,
may be divided into two groups. In the first group it is a narrow vermicular tube,
with several vermicular diverticula (*Bullacris, Physemacris, Parabullacris* and
*Pneumoracris*). In the second group (*Physophorina, Pneumora*) it is a sac-like
formation with several large, pocket-like diverticula. These two groups correspond
very well with the division of the Pneumorids on the basis of other taxonomic
characters.

The spermatheca is structurally one of the simplest in Acridoidea but in Euma-
stacids it is even simpler. In the latter family the end of the spermatheca, so far
as it is known, is a simple pear-shaped widening. It should be noted that the relative
size of the spermatheca in Pneumoridae is very large. It is of the same length or
longer than the phallic complex of males. In other Acridoidea it is usually smaller.

**Chromosomes**

According to Helwig, 1958, the karyotype of the males of Pneumoridae is \(2n = 23\). He does not indicate what genera and species were investigated.

This number of chromosomes of the Pneumoridae is shared with the following
families of Acridoidea: Xyronotidae, Trigonopterygidae, Ommexechidae, Paulinii-
dae, Lentulidae and Acrididae (Helwig, 1958). White (1963) showed that Charilaiaidae
also possesses the same number.

However, Eumastacidae have 17, 19, 21 and 23 chromosomes. Proscopiidae
have 17 and Pyrgomorphidae and Pamphagidae both have 19. From this account
it is difficult to draw a conclusion concerning the phylogenetic inter-relation of the
families. It seems that the families can be divided into three groups: firstly one
with 17 to 23 chromosomes, the Eumastacid group; secondly one with 19, the
Pamphagoid group, and thirdly one with 23, the Acridoid group. According to the
number of chromosomes the Pneumorids belong to this last group.

**Eggs and Eggpods**

There are no data concerning the eggs or eggpods (if any) and nothing is known
about the mode of egg deposition.

The only information available is that in a dry collection a female of *Bullacris
discolor*, ready for oviposition, was found in the course of dissection. The eggs were
of the usual Acridoid shape. In the dry condition the length of the egg was 7.5 and
the width 1.9 mm. After soaking in 10 per cent solution of potassium hydroxide
the length of the egg increased to 10.5 and the width to 2.7 mm.

Nothing is known concerning embryonic development.
REVISON OF THE PNEUMORIDAE

NYMPHAL STAGES

It is not known how many nymphal instars the Pneumorids have. The scanty material available in museums does not permit one to place nymphal specimens definitely into a species and frequently not even into a genus. Neither can the instars be definitely distinguished. The only case in which the first and last instars are definitely known is Physophorina livingstoni (Text-fig. 29). The first instar of this species is 9.5 mm. in length which shows a great difference between the first instar and adult (70–107 mm.).

In the first and subsequent instars, in all observed Pneumorids, the whole body in both sexes is covered above by the relatively huge, crest-like, strongly compressed pronotum. In the later instars the pronotum becomes relatively smaller and the end of the abdomen protrudes posteriorly from it. Sexual dimorphism in wing development was not observed. The pads of male wings, in macropterous species, are hidden under the pronotum as in the females and cannot be detected without dissection.

The inflation of the bodies of the males probably takes place at the last moult. In a few observed nymphs, males of the last instar had bodies of the usual nymphal appearance, being compressed laterally.

The carina on the inner side of the hind femur in stridulating males is readily detectable in the last instar, but the transverse ridges on it are weakly developed. The stridulatory ridges on the abdomen are not detectable in the last instar; probably they appear at the last moult.

SEXUAL DIMORPHISM

Sexual dimorphism in most genera of Pneumorids is enormous. Males in most genera possess an inflated body, fully developed wings, large ocelli, high and strongly crest-shaped pronotum, and a peculiar sound-producing mechanism; they are also of smaller size.

In the corresponding females the body is of normal shape, elytra and wings are reduced or strongly reduced, ocelli are vestigial, the pronotum is mostly tectiform or comparatively slightly crested, the sound-producing mechanism is of an entirely different type and the body is larger.

In the group of genera with the male body not inflated, the sexual dimorphism is not so great, but the sexes differ to a greater extent in body size, the males being much smaller than the females; they differ also in the shape of the pronotum and in the size of the ocelli. The other characters are the same in both sexes.

There is no great sexual dimorphism in coloration or in pattern. In some cases (Pneumora) the females are more ornamental than the males, in other cases the females are more uniform than the males (Bullacris), but both sexes may be of the same uniform colour (Physophorina) or of the same pattern (Pneumoracris).

It is interesting to note that in the nymphs, even of the last instar, sexual dimorphism is hardly pronounced at all except in the external genital appendages. The wings in both sexes are hidden under the pronotum; the body is of the same com-
pressed shape; the pronotum is the same crest-shaped, strongly compressed structure and more resembles that of the adult males than the adult females. The most striking features of the sexual dimorphism appear only after the last moult.

**BEHAVIOUR**

Almost nothing is known about the behaviour of Pneumorids. It was observed, first by Thunberg in 1772 and confirmed later, that they are nocturnal. The males are attracted towards light. Sometimes they fly into an open camp-fire and their inflated bodies characteristically explode in the flames.

They were heard and observed on bushes, trees and low ground vegetation.

Thunberg's observations in 1772 and the observations of later authors suggest that Pneumorids, particularly the males, in day time are confined to the trees and descend at night to the ground and lower vegetation.

It is possible that the males and females differ in their daily regimes, and also that their habits and the development of the ocelli are connected; the ocelli in the males are exceptionally large, while in females they are vestigial.

The song or call of males begins, in the case of *Physemacris variolosa*, at 10–11 o'clock p.m. Other species usually begin to call after midnight (Van Son, 1963, in litt.). Females emit an answering call. Unfortunately no other activities of their life have been observed.

**FOOD**

As the structure of the mandibles suggest, the Pneumoridæ are forbivorous, i.e. feed on comparatively soft leaves of herbs.

The existing records are: *Physophorina miranda* was observed feeding on *Berkheya amplexicaulis* Hoffman, 1891, Compositæ (Van Son, 1958); *Bullacris* sp. and *Physemacris variolosa* on *Elytropappus rhinocerotis* Lessing, 1832, Compositæ; and *Bullacris longicornis* on *Plectranthus* sp., Labiatae (Van Son, 1963, in litt.).

**GEOGRAPHICAL DISTRIBUTION**

Pneumoridæ are confined chiefly to Southern Africa. They are distributed in the coastal areas in the west, south of the Orange River, along the western coast, and also along the southern and eastern coasts. There are no reliable records from inland* and it seems that almost all existing records for Southern Africa are confined to Cape Province and Natal. Only one genus (*Physophorina*) is recorded as far north as Nyasaland, Tanganyika and Uganda (Map 7). There is also a single record for *Bullacris membracioides* from Nyasaland (Map 7).

Is this peculiar distribution the result of ecological selectiveness of the insects or is it that the area is poorly explored in this respect? A definite answer cannot be given. It is clear that the Pneumorids are highly localized, but little is known about their ecological requirements. Judging from the meagre material available, they are probably difficult to detect in nature.

* There is one record by Rehn 1941, of a nymphal specimen of *Bullacris* from Pretoria (Transvaal). However, the record is doubtful and may be the result of wrong labelling.
Only one species, *Physophorina livingstoni*, reaches as far as Uganda and few records of it are from East Africa. Most probably this species penetrated northwards from the main area of the family.

From the geographical distribution it is clear that the family can be regarded as primarily endemic in South Africa.

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**Fig. 7. Geographical distribution.**
- ■ *Physophorina livingstoni*.
- ● *Physophorina miranda*.
- ♦ *Pneumora inanis*.
- ▲ *Physemacris variolosa*. 

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REVISION OF THE PNEUMORIDAE

NOTE ON THE GROUP OF GENERA WITH NON-INFLATED MALE BODY

When the first species of the Pneumorids with a non-inflated male body was studied, it was of great interest to compare it with the species which possess an inflated male body. A second and third species increased the interest and the riddle of this unusual male character.

The males of the species with non-inflated bodies differ from those with inflated bodies not only in the shape of the body but also in the absence, or reduction to a highly vestigial form, of the stridulatory mechanism, the reduction of elytra and wings to vestigial form, the shape of the pronotum and the structure of the phallic complex.

However, in one case in which the males are not inflated the females are so similar to those of another species, in which the male has an inflated body, that it is extremely difficult to distinguish them. These species are Parabullacris vansoni Dirsh and Bullacris unicolor Linnaeus, respectively.

Pneumoracris browni Dirsh could be regarded as parallel to Peringueyacris namaqua (Péringuey) in the characteristic pattern of the pronotum, but the female of the latter species is unknown.

In Paraphysemacris spinosus Dirsh only the male is known. In its pattern and the shape of the pronotum it is very similar to Physemacris variolosa Linnaeus. They may be regarded as parallel species. The females of these two species may be indistinguishable.

The interrelation of this group of genera with other genera and species with inflated bodies is not yet understood. However, the possibility could be considered that these species are not parallel to the species with inflated bodies, but represent neotenic forms of them.*

AFFINITIES OF THE FAMILY

There is no fossil evidence which can help to establish the relationship of the Pneumorids with the other families of Acridoidea or with the other groups of Orthoptera. At present only the study of the comparative morphology of the group can provide some indirect clues.

There is very little concerning this question in the literature. Rehn, 1941 expressed the opinion that the Pneumorids are an ancient group, equivalent to the Tettigoida. Smart, 1953 stated that the wing venation of Pneumorid males is "remarkably primitive", implying primitiveness of the family. Ragge, 1955 considered the wing venation of Pneumorids as the most primitive of all Acridoidea. He considered them as derived from the general Acridoidea stock even earlier than Locustopsidae, and earlier than the other branches of Acridoidea.

*Dr. G. van Son, of Transvaal Museum, who has observed the species in nature and with whom I discussed the possibility of the existence of neoteny in the above mentioned species, wrote to me that it is his "firm opinion that they (the species with non-inflated bodies) did represent nymphal forms of males in which the genitalia had apparently reached full development in advance of the remainder of the morphological characters".

Not dismissing entirely the possibility of the existence of neoteny in the species, I think that there is still not enough material to prove it sufficiently.
It seems that most authors consider the Pneumorids as a group more primitive than other Acridoidea. However, the term "primitive" is greatly misused. In the case of the Pneumorids it can be stated that some of their characters are extremely simple, but whether they are primitive or just simple, or are the result of secondary simplification, is a matter for speculation.

One can consider the Pneumorids as members of the suborder Acridoidea, since their characters fit into it very well. They have the same head sclerites as the other Acridoidea; the same short antennae; principally the same wing venation; the same three-segmented tarsi; the same arolia, and the same four-valved, short ovipositor. From the morphological point of view at present there is no doubt that they have the same characters as the taxon named Acridoidea (sensu Dirsh, 1961).

However, there are several characters which separate Pneumorids from other Acridoidea, making them a distinctly isolated group.

These characters are discussed below:— The wing venation as already explained is extremely simple in the Pneumorids. Ragge, 1955 showed that morphologically they are extremely close to the fossil Palaeodictyoptera—Stenodictya lobata Brongniart (Fam. Dictyoneuridae). But it is not conceivable that they were derived directly and primarily from the Palaeodictyoptera stock, as they have too many other characters in common with Acridoidea in the recent concept of this suborder. In 1963 Ragge considered that the "wing venation of the Pneumoridae suggests a close relationship with the remaining Acridoidea".

Thus, on the one hand the venation of the Pneumorids is very similar to that of the Dictyoneuridae and on the other hand it is closely related to that of Acridoidea. This can lead to only two possibilities: firstly, that the Pneumorids retained the characters of the ancient Palaeodictyoptera during their phylogeny and branched independently from the Acridoidea, but developed a parallel set of characters; and secondly that the wings of Pneumorids are the result of the secondary simplification. In the latter case the Pneumorids may have branched early from the common Acridoidea stock and possibly lost or reduced the function of the wings. As a result the wings would degenerate to a simplified form, very similar to the primitive Palaeodictyoptera Dictyoneuridae.

Neither explanation can be verified. However, in other Acridoidea there are cases where, in generally micropterous species (e.g. females of Chrysochraon, and Rubellia), freak specimens occur with long wings, which are of the same type as other species of the group to which they belong, but possess simplified venation. These cases may be considered to some extent as parallel to the Pneumorids, with the difference that macropterous forms may appear in some genera of other families sporadically, whereas in the Pneumorids they appeared and persisted and the simplification may have become fixed genetically. In any case, there is no doubt now that wing venation is not an extremely rigid arrangement. The idea that the main veins are formed around the tracheae has been questioned recently (Whitten, 1962).

The phallic complex of Pneumorids is extremely uniform for the whole group. It indicates that as a taxon they do not diverge very much between themselves. It
might also indicate that the group is comparatively young; but this is not a permissible conclusion. Some characters are very persistent and remain unchanged for a long time during the phylogeny of a group or branch. We are reminded of the simple and very persistent character of the five branched extremities which persist in Amphibia, Reptilia, Aves and Mammals to Man. Many other examples of this kind can be found in any branch of the Animal Kingdom.

The structure of the phallic complex is also extremely simple. It is simple so that one almost involuntarily regards it as primitive. However, in this case also there is no positive proof. It is true that the phallic complex of Pneumorids is very different from that of other Acridoidea studied to date, and the family may be distinguished by this character alone. But there are several characters of similarity: the presence of the epiphallus, similar differentiation into ectophallus and endophallus, and traces, if correctly interpreted, of a rudimentary cingulum and penis or analogous structures. These characters connect Pneumorids with the rest of Acridoidea in their general features. It is interesting to note, however, that the Pneumorid phallic complex is remotely similar to the corresponding structure in Tettigonioida and Gryllacridoidea (Snodgrass, 1937). If one considers that Tettigonioida and Gryllacridoidea are more primitive than Acridoidea, then it may be inferred that the Pneumorids are more primitive than the other Acridoidea.

Although very simple in respect of wings and genital structures Pneumorids, however, display a very high degree of specialization in their sound-producing mechanism. In fact, it is unique in that the whole body of the male, being inflated, is adapted for this purpose. There are similar abdominal-femoral stridulatory mechanisms in Tanaoceridae (Dirsh, 1955) and Xyronotidae (Kevan, 1952, Dirsh, 1955), but they are less specialized, not having inflated bodies. This specialization in the Pneumorids is probably of very ancient origin, as the males without inflated bodies still retain in vestigial form the same stridulatory mechanism.

When and how the sound-producing mechanism originated in the Pneumorids can be solved only on the basis of fossil material, which at present is lacking. It should be noted that analogous stridulatory mechanisms exist in certain groups of Gryllacridoidea, but this could, however, be coincidental and an independent parallel development. A second possibility is that this character was primarily developed in a common ancestral stock of Orthopteroid insects and was retained in Pneumoridae, Tanaoceridae and Xyronotidae, reaching the highest point of specialization in the Pneumoridae.

Another interesting point is that although Pneumorids produce much noise, they do not possess a tympanal organ, which is considered as an organ of sound perception. Probably they have some other kind of organ for sound perception, as yet unknown. It is known, however, that there is a great variety of these organs in various groups of insects (Haskell, 1961). The tympanal organ exists only in Orthopteroids, in Hemiptera and Lepidoptera. In Acridoidea it is present in six out of fourteen families of the suborder.

It is absent in all the families with an abdomino-femoral sound producing mechanism. In Gryllacridoidea, the group possessing the abdomino-femoral mechanism,
the tympanal organ (on the front tibia) is absent, while in some groups without the mechanism the tympanal organ is present. As the tympanal organ is present in Acridoidea in the more advanced families and subfamilies, it is possible to deduce that the groups that lack it are primitive.

There is another character which is common to all Acridoidea, except those groups of which the hind legs approximate to the cursorial type. This is the Brunner’s organ. It is absent completely in Proscopiidae and greatly reduced in the genus Psednura (Pyrgomorphidae), which have also hind legs functionally approximating to the cursorial type. In Pneumorids in some species the Brunner’s organ is absent, in some it is hardly detectable and in others it is fairly well developed. This indicates that primarily the Pneumorids possessed the Brunner’s organ, and that it has undergone reduction in some species in connection with the lessening of jumping ability. According to this character they are nearer to the Acridoid stock than to the earlier Orthopteroid stock, Brunner’s organ being found in Acridoidea only.

As is shown above, the Pneumorids have several characters which are rather contradictory phylogenetically. Almost every character may be considered from more than one point of view and there is no direct verification of any of them owing to lack of fossil data.

From the indirect considerations presented above, it can be concluded that Pneumorids branched very early from the same stock as the rest of Acridoidea and approximately at the same time as Locustopsidea and Acridoidea.

Family PNEUMORIDAE

Antennae short. Head short, with shortened fastigium of vertex; face vertical, frontal ridge absent; fine fastigial furrow present. Ocelli large or vestigial. Prosternal process absent. Venation simple; elytra without vannal flex, wing with remigium almost as large as vannus. Tympanum absent. Stridulatory mechanism mostly present in male, consisting of a row of transverse ridges on 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; Brunner’s organ present, vestigial or absent. Phallic complex simple; ectophallus sac-like, with rudimentary sclerotizations; endophallus simple, tube-like; epiphallus plate-like, without lophi and ancorae; oval sclerites absent. Spermatheca large, with several verricular or pocket-like diverticula.

Type genus: Pneumora Thunberg, 1775.

Key to Genera

1 12 Body of males strongly inflated, bladder-like. Elytra and wings fully developed. Females micropterous with elytra sclerotized, or brachypterous with elytra membranous.
2 9 Anterior cubital vein of male elytron unbranched. Lateral ocelli placed above and slightly internally to antennal bases.
3 8 Lower lobe of hind knee without tooth on lower margin. Females micropterous, with elytra sclerotized.
4 5 Pronotum in profile regularly arcuate (Text-figs. 10, 11, 13, 15, 17, 19.)

BULLACRIS (p. 353)
Pronotum in profile not regularly arcuate, with deep constriction at posterior transverse sulcus.

Median carina in prozona forming two or three large teeth (Text-fig. 22).

Median carina of pronotum low, in prozona with tubercle-like thickening (Text-fig. 25).

Lower lobe of hind knee with large tooth on base of lower margin. Female brachypterous, with elytra membranous (Text-fig. 26).

Anterior cubital vein of male elytron branched. Lateral ocelli above and slightly externally to antennal bases.

Pronotum high arcuate and strongly inflated, particularly in females (Text-fig. 28).

Pronotum low arcuate and not inflated in both sexes. (Text-fig. 32).

Body of males not inflated, of usual acridoid shape in both sexes. Elytra and wings vestigial in both sexes and completely hidden under pronotum.

Pronotum in profile regularly arcuate (Text-fig. 34).

Pronotum in profile not regularly arcuate, with constriction at posterior transverse sulcus.

Median carina of pronotum at posterior end of prozona and anterior end of metazona tubercle-like widened (Text-fig. 36).

Pronotum with three large teeth in prozona, median carina serrated in metazona (Text-fig. 38).

**BULLACRIS** Roberts, 1941

_Bulla_ Stål, 1873 : 137 (nec Linnaeus, 1758)

_Bullacris_ Roberts, 1941 : 18 [n.n.]

Anterior part of body of male down to seventh abdominal segment strongly bladder-like, inflated; end of abdomen of usual cylindrical shape. In female, body normal, compressed laterally. Antenna filiform or slightly club-like, widened at apex. Face slightly convex or flat. Frons angularly or roundly merging with vertex. Lateral ocelli placed above and slightly internally to antennal bases; in male all three ocelli very large, in female small, vestigial. Compound eyes in both sexes small, oval, moderately convex. Pronotum highly arcuate, crest-like or low arcuate, crossed by four transverse sulci; median carina sharp, in females roughly serrated; prozona much shorter than metazona; metazona elongated with angular posterior margin; episternum toothed. Mesosternal interspace deeply concave. Male fully winged; anterior cubital vein of elytron unbranched. Female elytra and wings strongly shortened, covered by pronotum or slightly protruding from under lateral margins of metazona; costal and subcostal area of elytron strongly sclerotized; wing about twice as long as elytron, weak, longitudinally folded once only along vannal flex. Third abdominal tergite of male with crescent-like row of strong stridulatory ridges. Anterior and middle femora often strongly tuberculate; hind femur weak, short, almost cursorial; in male, internal side of hind femur with short, high carina, bearing row of transverse ridges, forming second part of stridulatory mechanism; Brunner's organ absent or vestigial, hardly detectable. Arolium large. Suprannal plate in both sexes simple, angular, with deep transverse sides. Cerci short, conical. Subgenital plate in male short, acutely conical, at apex excised or truncate; in female with angular apex. Ovipositor moderately short, with straight valves, obtuse at apices.

Phallic complex weakly sclerotized; lateral parts of ectophallus slightly sclerotized; dorsal part consisting of a pair of lateral, inflated valves; ventro-posterior part sac-like, membranous; between these parts, opening of endophallus is located. Endophallus with a pair of lateral,
Fig. 8. *Bullacris unicolor*. 1, mandibles: Right mandible—A, outside; C, inside. Left mandible—B, outside; D, inside. 2, face of male, showing position of the ocelli in relation to the antennal bases. 3, end of female abdomen, lateral view. 4, spermatheca. 5, end of male abdomen, lateral view. 6, the same from above. 7, abdominal stridulatory ridges (semi-schematic). 8, stridulatory ridges of the internal side of hind femur.
narrow, longitudinal sclerotizations. Ephiphallus short and wide, with long lateral plates and three strong median apical teeth.

Spermatheca with several narrow, vermicular, irregularly twisted diverticula.

Type species: *Gryllus Bulla unicolor* Linnaeus, 1758.

**Key to Species**

**MALES**

1. (2) Antenna slightly club-like widened at apical part (Text-fig. 10). Supra-anal plate comparatively short and widely angular (Text-fig. 8) *unicolor* (Linnaeus)
2. (1) Antenna filiform. Supra-anal plate comparatively long and narrow, angular.
3. (6) Pronotum in profile highly arcuate (Text-figs. 11, 13).
4. (5) Pronotum in profile regularly arcuate (Text-fig. 11). Third episternum with brown patch. Size smaller (44–49 mm.) *intermedia* (Péringuey)
5. (4) Arc of pronotum, in profile, lower in prozona (Text-fig. 13). Third episternum without brown patch. Size larger (47–59 mm.) *membracioides* (Walker)
6. (3) Pronotum in profile low arcuate.
7. (10) Pronotum in profile regularly arcuate (Text-figs. 15, 17). Third abdominal tergite with 9–10 stridulatory ridges. Size larger (44–58 mm.).
8. (9) Pronotum without callosities. Veinlets of reticulation of elytra of the same colour as membrane. Sides of abdomen with ocellate pattern (Text-fig. 15) *discolor* (Thunberg)
9. (8) Pronotum with whitish callosities. Veinlets of reticulation of elytra darkened. Sides of abdomen with ocellate and marble pattern (Text-fig. 17) *serrata* (Thunberg)
10. (7) Arc of pronotum in profile lower in prozona. Third abdominal tergite with 13 stridulatory ridges. Size smaller (41–46 mm.) *obliqua* (Thunberg)

**FEMALES**

1. (4) Arc of pronotum in profile comparatively high (Text-figs. 11, 13).
2. (3) Smaller size (42 mm.) (Text-fig. 11) *intermedia* (Péringuey)
3. (2) Larger size (48–55 mm.) (Text-fig. 13) *membracioides* (Walker)
4. (1) Arc of pronotum in profile comparatively low.
5. (6) Pronotum narrow, slender (Text-fig. 10) *unicolor* (Linnaeus)
7. (8) Pronotum without dorsal callosities or with only traces of them (Text-fig. 15) *discolor* (Thunberg)
8. (7) Pronotum with dorsal callosities forming oblique whitish stripes.
9. (10) Dorsum of pronotum with convex sides and comparatively low obtuse median carina (Text-fig. 17) *serrata* (Thunberg)
10. (9) Dorsum of pronotum with slightly concave sides and sharp median carina.
11. (12) General coloration greenish; sides of abdomen with four rows of small whitish, oblique spots (Text-fig. 19) *obliqua* (Thunberg)
12. (11) General coloration pale brownish; sides of abdomen with two rows of large, whitish spots of irregular form (Text-fig. 21) *boschimana* (Péringuey)

**Bullacris unicolor** (Linnaeus, 1758)

(Text-figs. 8–10)

*Gryllus Bulla unicolor* Linnaeus, 1758: 427. ♂.

*Pneumora immaculata* Thunberg, 1775: 256. ♀, *syn. n.*


*Mantis paradoxa* Stoll, 1813: 79. ♂ [Syn. Serville, 1838: 716.]

*Gryllus Locusta pulicarius* Stoll, 1813: 37. ♂ [Syn. Serville, 1838: 716].
Bullacris unicolor (Linnaeus) Roberts, 1941: 19.
Bullacris thalassina Rehn, 1941: 141. ♂ syn. n.
Bullacris namaquensis Rehn, 1941: 144. ♂, syn. n.

Fig. 9. Bullacris unicolor. Phallic complex. 1, whole phallic complex from above. 2, the same, lateral view. 3, phallic complex from above, but epiphallus removed. 4, the same, lateral view. 5, endophallus, lateral view. 6, schematic saggital section of the phallic complex. (For lettering for this and all following figures of the phallic complex—see text. The phallic complex and spermatheca are drawn under the same magnification.)
♂. Large. Integument on head and thorax rugose, granulose and slightly hirsute, on abdomen smooth. Antenna 18–20-segmented, at apex slightly club-like widened, with segments shortened and deeply separated. Head relatively small, strongly rugose, granulose and hairy; frons slightly convex, roundly merging with vertex; fastigial furrow faint. Pronotum in profile moderately arcuate, with shallow depression between prozona and metazona, median carina in profile downcurved at posterior sulcus; anterior margin of prozona angularly protruding forwards, its median carina between sulci with transverse wrinkles; metazona in posterior part, at sides of median carina, depressed, median part compressed; lateral carinae in anterior part of metazona weak, gradually fading backwards. Third abdominal tergite with 11–13 stridulatory ridges. Anterior and middle legs without tubercles. Hind femur short and weak; Brunner’s organ undetectable. Supra-anal plate short, widely angular; subgenital plate short, angular with bilobate apex.

Phallic complex with comparatively strongly sclerotised lateral parts of ectophallus and comparatively strongly sclerotised dorsal part of membrane.

General coloration light green, straw-yellowish, pinkish or reddish. Third episternum in upper two thirds, brown; side of abdomen uniformly coloured or with three or four brown spots with white centres.

♀. Large. Integument not hairy. Antenna 17–19-segmented, scarcely club-like at apex. Head relatively large; face flattened; fastigial furrow hardly detectable. Pronotum in profile very low arcuate, without depression between prozona and metazona; prozona without transverse wrinkles; metazona strongly elongated, narrow angular. Elytra and wings shortened, completely covered by pronotum; elytron half the length of wing, of elliptical shape with costal area sclerotized. Subgenital plate with angular apex.

Spermatheca with three long, narrow, vermicular diverticula.

General coloration green or olive-green; posterior margin of metazona in region where it is merging with lateral lobe of pronotum whitish or yellowish, with blackish stripe in adjoining part of pleuron; sclerotized part of elytron bright red, with blackish stripe along subcostal area; abdomen sometimes with three or four faint yellowish spots.

Length of body ♂ 35–45; ♀ 38–44; pronotum ♂ 15–21, ♀ 22–24; elytron ♂ 29–36, ♀ 4–5; hind femur ♂ 11–12.5, ♀ 10.5–12 mm.

Variability: Body size varies little in both sexes (see measurements). Pronotum varies in its length, in height of arcuated part of dorsum, deepness of depression of median carina at posterior transverse sulcus and deepness of lateral depression of metazona in males. Supra-anal plate in males may be more or less acutangular. Incision at apex of subgenital plate varies in deepness. Coloration in males green, greenish, yellowish, pinkish to reddish; median carina of pronotum sometimes yellowish; abdomen uniformly coloured or more frequently on sides with three or four brown spots with white centres; elytra sometimes sparsely covered with brownish dots. In females general coloration more uniform, mostly olive-green; pronotum uniformly coloured, but stripe on lower margin of metazona varies from white to yellow and sometimes almost disappears; spots on both sides of abdomen vary in their intensity, sometimes undetectable.

Material examined. 67 ♂, 12 ♀. Lectotype, ♂. Type locality according to description: “Habitat in Indiis” (erroneous). (Lovisa Ulrika Collection in Uppsala). Syntypes 2♂. As above.

The Thunberg types and syntypes mentioned in the synonymy are without locality labels.

CAPE PROVINCE: Kuils River, Stellenbosch; Saldanha Bay; Tygerberg Hills; Somerset West; Langebaan; Port Elizabeth, Redhouse; Still Bay; Eland Bay, Leipoldtville; Cradock; Alicedale; Robben Isl.; Darling; Doornbosch, between
Calvinia and Clanwilliam; Calvinia; Clanwilliam; Matjesfontein; Willowmore; Steinkopf; Fishhoek; Grahamstown; Wallekraal; Kleinzee; Gelykwerk; Richtersveld; Nababiep; Springbok; Hondeklip Bay; Port Nolloth; O'okiep; O'ograbies. December to May.

**Fig. 10.** *Bullacris unicolor.* 1, male. 2, female. 3, male face. 4, female face.
**Bullacris intermedia** (Péringuey, 1916)

(Text-figs. 11, 12)


♂. Integument of head and pronotum rugose and sparsely hairy. Antenna 20-segmented, filiform, with segments slightly or not at all elongated. Head relatively small; frons slightly convex, roundly merging with vertex; fastigial furrow faint. Pronotum in profile highly and

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**Fig. 11.** *Bullacris intermedia.* 1, male. 2, female. 3, male face. 4, female face.
regularly arcuate on whole length, with slight lateral depressions; anterior margin of prozona angularly protruding forwards, its median carina between sulci with transverse wrinkles; sides of metazona convex; lateral carinae weak. Third abdominal tergite with 9–10 stridulatory ridges. Anterior and middle legs without tubercles. Hind femur weak. Brunner's organ vestigial, hardly detectable. Supra-anal plate narrow angular; subgenital plate short, angular, with incised apex.

Phallic complex with comparatively weakly sclerotized lateral parts of ectophallus and comparatively weakly sclerotized dorsal part of membrane.

General coloration green. Third episternum with brown patch; sides of abdomen with three or four small brownish spots or uniformly coloured.

♀. Integument of head and pronotum rugose, of abdomen smooth. Antenna filiform. Head large; face flat, frons angularly merging with vertex. Pronotum highly and regularly arcuate; sides of dorsum with four oblique callosities; median carina, in profile, roughly serrated, particularly in prozona; anterior margin of prozona not protruding forwards; lateral carinae well pronounced. Elytra and wings strongly shortened, covered by pronotum, except narrow margin of elytron, which protrudes slightly from under lateral margin of metazona; elytron much shorter than wing, of oval form, with strongly sclerotized costal and subcostal areas. Anterior and middle femora slightly tuberculate; hind femur weak; Brunner's organ not detectable. Apex of subgenital plate angular.

General coloration green; callosities of pronotum whitish; posterior margin of lateral lobe of pronotum whitish; sclerotized part of elytron bright red; sides of abdomen with three rows of whitish oblique spots.

Fig. 12. *Bullacris intermedia*. 1, phallic complex from above. 2, end of male abdomen, lateral view. 3, the same, from above. 4, abdominal stridulatory ridges (semi-schematic).
Length of body ♂ 44-49, ♀ 42; pronotum ♂ 20-22, ♀ 24; elytron ♂ 36-37; hind femur ♂ 13-14, ♀ 16 mm.
Variability: Only a few male specimens are known; they are rather uniform in appearance. One specimen has venation and reticulation in basal part of elytra brownish.

This species is very near to B. membracioides (Walk.) and also, but to a lesser extent, to B. unicolor L. Since only a few males are available, it is difficult to decide if it is a good species or merely a local race of B. membracioides.


CAPE PROVINCE: Kowie River 2 ♂; Port Alfred 1 ♀; "Natal" 1 ♀.

**Bullacris membracioides** (Walker, 1870) comb. n.
(Text-figs. 13, 14)

*Pneumora membracioides* Walker, 1870: 800. ♂ nymph.
*Bulla longicornis* Stål, 1873: 139. syn. n.

♂ type. Integument of head and thorax rugose and granulose. Antenna comparatively long, 23-segmented, filiform, with elongated segments. Head relatively large, strongly granulose, frons almost flat, slightly convex, angularly merging with vertex; fastigial furrow sharp. Pronotum in profile highly and regularly arcuate in metazona, and lowered in prozona, without depression between prozona and metazona; anterior margin of prozona slightly angularly protruding forwards, its median carina, between sulci with transverse wrinkles; sides of metazona convex; only traces of lateral carinae exist. Second abdominal tergite with 9 stridulatory ridges. Anterior femur tuberculate; hind femur moderately short; Brunner's organ undetectable. Supra-anal plate narrow angular; subgenital plate moderately long, angular, with slightly excised apex.

Phallic complex with weakly sclerotized lateral parts of ectophallus and moderately sclerotized dorsal part of membrane.

General coloration from green to straw-yellowish, mostly uniform, sometimes on sides of abdomen 3-7 brownish spots.

♀. Integument on head and pronotum rugose. Antenna 23-segmented, filiform. Head large granulose, frons flat, angularly merging with vertex. Pronotum highly and regularly arcuate, rugose and granulose; median carina in profile serrated; anterior margin of prozona not protruding forwards, prozona without transverse wrinkles between sulci; lateral carinae rather strong. Anterior femora tuberculate. Elytra and wings completely covered by pronotum; elytron half the length of wing, of oval form, its costal and subcostal area strongly sclerotized. Subgenital plate with angular apex.

Spermatheca, with three or four narrow, vermicular diverticula.

General coloration green or greenish; pronotum sometimes with oblique, whitish, granulose stripes; sclerotized part of elytron bright red; sides of abdomen sometimes with row or three rows of whitish oblique spots.

Length of body ♂ 47-59, ♀ 48-55; pronotum ♂ 19-23, ♀ 26-32; elytron ♂ 38-44, ♀ 7-8; hind femur ♂ 15-16, ♀ 17-21 mm.

Variability: this species varies slightly in body size, curvature and height of pronotum, acuteness of male supra-anal plate and coloration as described above.
Material examined. 32 ♂, 4 ♀. Type ♂ nymph. Type locality: "Natal". (British Museum (Natural History).)

Type of *Bulla longicornis* Stål 1873. 1 ♂, "Caffraria". (Naturhistoriska Riksmuseet, Stockholm).

**Natal**: Pinetown; Port Shepstone; Pietermaritzburg; Durban; Uvongo Beach; Amanzimtoti; Stanger; Inchanga; Umkomaas; Richmond. **Zululand**: Eshowe. **Nyasaland**: Road, Mlanje to Zomba. **Cape Province**: Port St. John. From November to May.

**Fig. 13. Builacris membracioides.** 1, male. 2, female. 3, male face. 4, female face.
Bullacris discolor (Thunberg, 1810)  
(Text-figs. 15, 16)

Pneumora discolor Thunberg, 1810 : 59. ♂.
Pneumora ocellata Thunberg, 1810 : 60. ♂. syn. n.
Pneumora pupillata Thunberg, 1810 : 60. ♂. syn. n.
Bullacris discolor (Thunberg) Johnston, 1956 : 27.

♂. Integument of head and pronotum rugose, abdomen smooth. Antenna filiform, 22–23-segmented, all, except six apical segments, elongated. Head relatively large; frons slightly convex, gradually merging with vertex; fastigial furrow faint. Pronotum in profile very low, regularly arcuate, with weak depression between prozona and metazona; anterior margin of prozona angular, median carina in prozona, between sulci, with transverse wrinkles; metazona with convex sides; lateral carinae weak. Third abdominal tergite with 9–10 stridulatory ridges. Anterior femur with large tubercles; hind femur short and weak; Brunner’s organ undetectable. Supra-anal plate acutely angular, moderately elongated. Subgenital plate short acutangular with obtuse apex.

Phallic complex with moderately well sclerotized lateral parts of ectophallus and with elongated dorsal valves.

General coloration green, straw-yellowish or less frequently reddish; median carina of pronotum reddish or yellowish; posterior margin of lateral lobe of pronotum yellowish, sides of abdomen with four or five brown spots with centres of lighter shade; three middle spots large, marginal ones small.

♀. Integument more rugose and granulose. Antenna 23-segmented. Head large; frons flat; fastigial furrow well pronounced. Pronotum more tectiform than in male; depression between prozona and metazona less pronounced than in male; median carina in prozona, in

Fig. 14. Bullacris membracioides. 1, phallic complex, from above. 2, spermatheca. 3, end of male abdomen, lateral view. 4, the same from above. 5, abdominal stridulatory ridges (semi-schematic).
profile, slightly serrated; lateral carinae more strongly developed than in male. Elytra and wings strongly shortened, completely covered by pronotum; elytron half as long as wing, of oval shape, with costal area sclerotized. Subgenital plate with acutangular apex.

Spermatheca vermicular, with three or four vermicular diverticula.

General coloration green or olive-green; posterior margin of lateral lobe of pronotum and merging part of margin of metazona yellowish; sclerotized part of elytron bright red.

Length of body ♂ 44–58, ♀ 43–51; pronotum ♂ 21–24, ♀ 25–29; elytron ♂ 37–45, ♀ 8; hind femur ♂ 14–15, ♀ 15–18 mm.

Variability: This species varies in body size, shape of pronotum, which in profile varies in height of arc; number of stridulatory ridges in males (9 or 10); and supra-anal plate which may be elongated and acute or less elongated. Coloration varies from green or yellowish to red; pronotum in both sexes uniformly coloured or with whitish, oblique stripes; elytra

Fig. 15. Bullacris discolor. 1, male. 2, female. 3, male face. 4, female face.
mostly uniformly coloured, but sometimes basal part brownish, owing to brown venation and reticulation, sometimes whole elytra sparsely covered with small brown dots; spots on sides of abdomen in males vary in size and in size of their lightish central area, spots sometimes entirely lacking; in females, spots whitish and sometimes obliterated.

Material examined. 26♂, 6♀. Type ♂. Type locality: “South Africa”. (Zoologiska Institutionen, Uppsala University.)

None of Thunberg’s types mentioned in synonymy bear locality labels.

CAPE PROVINCE: Pearly Beach; Alice, Nutwoods; Knysna; Swellendam; Somerset West; Port Elizabeth; Kalk Bay; Lemoens Hoek, Heidelberg; Noordhoek; East London; Cape Town, Kirstenbosch; Stellenbosch; Zoetendals Valley, Bredasdorp Dst. From October to January.

**Bullacris serrata** (Thunberg, 1810)
(Text-figs. 17, 18)

*Pneumora serrata* Thunberg 1810: 64. ♀.

♂. Integument of head and pronotum rugose, abdomen smooth. Antenna filiform, 23-segmented. Head relatively large; frons slightly convex, roundly merging with vertex; fastigial furrow faint. Pronotum in profile low and regularly arcuate; between prozona and metazona on sides of median carina there are moderately deep depressions; median carina rather sharp, in prozona in profile roughly serrated; lateral carinae well pronounced in anterior part of metazona; dorsum of metazona on sides of median carina slightly depressed. Third abdominal tergite with ten stridulatory ridges. Anterior femur tuberculate; hind femur weak; Brunner’s organ not detectable. Supra-anal plate narrow acutangular; subgenital plate short, acutangular, at apex shallowly incised.

![Fig. 16. Bullacris discolor. 1, phallic complex, from above. 2, end of male abdomen, lateral view. 3, the same, from above. 4, spermatheca. 5, abdominal stridulatory ridges (semi-schematic).](image-url)
Phallic complex with weakly sclerotized lateral parts.

General coloration green, olive-green; pronotum covered with small, whitish spots; membrane and main veins of elytra light olive green, veinlets of reticulation dark olive-green; reticulation of wing also much darker than membrane; sides of abdomen with four brown and white spots and second to seventh tergites each with several whitish spots.

♀. Integument of head and pronotum rugose, of abdomen moderately smooth. Antenna filiform, 23-segmented. Head large; frons almost flat, roundly merging with vertex; fastigial furrow faint. Pronotum in profile very low arcuate; depressions between prozona and metazona hardly exist. Median carina rather sharp, in prozona in profile slightly serrated; lateral carinae well pronounced in prozona and metazona; metazona at sides of median carina

Fig. 17. *Bullacris serrata*. 1, male. 2, female. 3, male face. 4, female face.
convex. Elytra and wings strongly reduced and covered by pronotum; elytron of oval shape, slightly more than half of length of wing, its costal area sclerotized. Anterior femur strongly tuberculate and toothed; middle femur tuberculate; hind femur weak; Brunner’s organ undetectable. Subgenital plate with angular apex.

Spermatheca vermicular, with several vermicular diverticula.

General coloration olive-green; median and lateral carinae of pronotum yellowish, sides of dorsum of pronotum with three to five whitish oblique stripes of callosities; sclerotized part of elytron bright red; tergites on each side of abdomen with whitish oblique spots forming four parallel rows; a similar row of spots in upper part of sternites.

Length of body $\delta$ 49-53, $\Omega$ 45-55; pronotum $\delta$ 18-20, $\Omega$ 24-27; elytron $\delta$ 38-47, $\Omega$ 9; hind femur $\delta$ 14-15, $\Omega$ 15-18 mm.

Variability: This species varies in body size, height of arc of pronotum, degree of depression between prozona and metazona, and in degree of the rugosity of pronotum; pattern on pronotum may be covered with callosities forming whitish stripes disintegrated into spots or almost disappearing completely; intensity of the pattern on sides of abdomen in both sexes also variable and in females may almost disappear.

This species is very near to Bullacris discolor Thunberg, 1810. It differs in the pattern of the pronotum and of the sides of abdomen, and also in the dark coloured reticulation of the elytron. It is possible that it represents a local race of discolor, but the material is so scanty that temporarily it is advisable to regard it as a separate species.

Material examined. 10 $\delta$, 2 $\Omega$. Type $\Omega$. Type locality: “South Africa”. (Zoologiska Institutionen, Uppsala University.)

CAPE PROVINCE: East London; Carl’s Rust; Swartberg Pass, Great Karroo; Knysna; Grahamstown. November–December.

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**Fig. 18. Bullacris serrata.** 1, phallic complex, from above. 2, end of male abdomen, from above. 3, the same, lateral view. 4, spermatheca. 5, abdominal stridulatory ridges (semi-schematic).
Bullacris obliqua (Thunberg, 1810)
(Text-figs. 19, 20)

Pneumora obliqua Thunberg, 1810: 65. ♂.
Bulla thunbergii Kirby, 1910: 63. [n. n.]. syn. n.
Bullacris thunbergii (Kirby) Rehn, 1941: 152.

♂. Integument of head and pronotum moderately rugose and granulose, abdomen smooth. Antenna filiform, 21-segmented. Head of medium size; frons slightly convex, roundly merging with vertex. Pronotum in profile low arcuate; between prozona and metazona with lateral depressions; median carina in prozona lowered, and in profile roughly serrated; anterior margin of prozona angular; sides of metazona convex; lateral carinae weak.

Fig. 19. Bullacris obliqua. 1, male. 2, female. 3, male face. 4, female face.
Third abdominal tergite with 13 stridulatory ridges. Anterior femur tuberculate; middle femur slightly tuberculate; hind femur weak; Brunner’s organ vestigial, hardly detectable. Supra-anal plate elongate, narrow angular; subgenital plate short, angular, with apex excised.

Phallic complex with small inflated lateral valves and weakly sclerotized lateral parts.

General coloration green or greenish; pronotum with two or three oblique, lateral, white stripes; posterior margin of lateral lobe of pronotum with whitish stripe; median carina reddish; sides of abdomen with three or four white spots with narrow brown margins.

♀ Integument of head and pronotum rugose and granulose, abdomen smooth. Antenna filiform, 23-segmented. Head relatively large; frons almost flat, angularly merging with vertex. Pronotum in profile moderately low arcuate, regular in shape, rather high tectiform; between prozona and metazona shallow lateral depressions; median carina rather sharp, in prozona in profile slightly incised at transverse sulci; anterior margin of prozona slightly angular; sides of metazona convex; lateral carinae strong. Elytra and wings strongly shortened almost completely covered by pronotum; elytron of oval shape, slightly more than half length of wing, its costal area strongly sclerotized. Anterior femur moderately tuberculate; middle femur almost smooth, hind femur weak; Brunner’s organ not detectable. Subgenital plate with obtusangular apex.

General coloration greenish; pronotum with four or five oblique, whitish lateral stripes; median carina of pronotum reddish; sclerotized part of elytron bright red; sides of abdomen with four rows of whitish spots.

Length of body ♂ 41–46, ♀ 45–51; pronotum ♂ 16–18, ♀ 22–24; elytron ♂ 32–37, ♀ 7; hind femur ♂ 13–14, ♀ 14–15 mm.

Variability: Too few specimens of this species are known to judge its variability. However, even in a few specimens, in both sexes, it was observed that the pronotum varies slightly in the shape of the arcuate part. The general coloration varies in its intensity; the described pattern may be strongly developed, with large well defined spots or the spots may be reduced in size and intensity; this is particularly noticeable on the pronotum and the sides of the abdomen.

This species is very near to Bullacris discolor Thunb. and Bullacris serrata Thunb. Possibly they are local races of the same species. Unfortunately the available material is too small to reach a definite conclusion.

Material examined. 3 ♂, 4 ♀. Type ♀. Type locality: “South Africa”. (Zoologiska Institutionen, Uppsala University.)

CAPE PROVINCE: Saldanha Bay; Wallekraal; Tygerberg Hills; Eland’s Bay, Leipoldtville. October.

Fig. 20. Bullacris obliqua. 1, phallic complex, from above. 2, end of male abdomen, from above. 3, the same, lateral view. 4, abdominal stridulatory ridges (semi-schematic).
Bullacris boschimana (Péringuey, 1916)
(Text-fig. 21)

Bullacris boschimana (Péringuey) Johnston, 1956 : 27.

♀. Integument of head and pronotum strongly granulose, with three callosities on pronotum; abdomen smooth. Antenna filiform, 23-segmented. Head moderately large, frons slightly convex, angularly merging with vertex. Pronotum tectiform, in profile almost non-arcuate; anterior margin of prozona angular; median carina slightly raised towards posterior sulcus and roughly serrated in prozona, in middle of metazona slightly lowered; a pair of lateral depressions on sides of median carina, at posterior sulcus well pronounced; in anterior part of metazona a pair of shallow lateral depressions on sides of median carina present as well; lateral carinae marked by row of granules. Elytra strongly shortened, not reaching second abdominal tergite, with sclerotized costal area and coarse reticulation, protruding from under lateral margin of metazona of pronotum. Anterior and middle femora slightly tuberculate; hind femur weak. Subgenital plate with acutangular apex.

General coloration pale brownish; callosities of pronotum form three pairs of irregular, oblique, white spots; posterior margin of lateral lobe of pronotum and adjoining part of lateral margin of metazona white; costal area of elytron, protruding from under pronotum, pinkish; sclerotized reticulation dark brown, shiny; second episternum whitish; sides of abdomen with two rows of large sharply defined whitish spots on second to fifth tergites; on dorsal part of abdomen every tergite also with small whitish spot.

Only female known.
Length of body 54; pronotum 25; elytron (visible part) 6; hind femur 14 mm.

This species, known by the female type only, is rather remote from the other known species of the genus. By the low, almost non-arcuate pronotum and the peculiar pattern of the integument it resembles slightly the genus Pneumora; however, the position of the ocelli is quite characteristic of the Bullacris group of genera. It was not possible to study the spermatheca, since no other specimen except the type is available. Further study of this species, particularly of a male, may establish its true position.

Material examined: Cape Province: Bushmanland, Henkries, 1 ♀ type. (South African Museum.)

Fig. 21. Bullacris boschimana. 1, female (type). 2, face.
**PHYSEMACRIS** Roberts, 1941

*Gryllus (Bulla)* Linnaeus, 1758 : 427.

*Pneumora* Stål, 1873 : 143. (nec Thunberg, 1775).

*Physemacris* Roberts, 1941 : 12, 19 [n. n.].

Body of male down to seventh abdominal segment strongly inflated, bladder-like; end of abdomen of normal cylindrical shape. In female, body normal, slightly compressed. Antenna filiform almost throughout length, slightly widening towards apex. Face slightly convex. Lateral ocelli placed above and slightly internally to antennal bases; in male all three ocelli very large, in female vestigial. Compound eyes comparatively small. Pronotum crossed by four transverse sulci; prozona much shorter than metazona, in middle with strong teeth or with teeth and tubercles; at posterior transverse sulcus, prozona separated from metazona by a rather deep constriction on sides of median carina; metazona elongated, low arcuate, with sides convex, covered with oblique callosities; median carina rather sharp. Mesosternal interspace deeply concave. Male macropterous; anterior vein of elytra unbranched. Female elytra and wings strongly shortened, covered by pronotum; elytra sometimes slightly protruding from under lateral margins of metazona; anterior two-thirds of elytron strongly sclerotized; wings, almost twice as long as elytron, weak, longitudinally folded, once only, along vannal fold and completely hidden under pronotum. Third abdominal tergite of male with crescent-like row of stridulatory ridges. Anterior and middle femora tubercululate; hind femur weak, short, almost cursorial; in male, internal side of hind femur with short high carina, bearing row of sharp transverse ridges, forming second part of stridulatory mechanism; Brunner’s organ not detectable. Arolium large. Supra-anal plate, in both sexes, simple, angular, with transverse sulcus; cerci short, conical in both sexes; subgenital plate in male short, acutely conical, with apex excised; in female with angular apex. Ovipositor moderately short, with straight valves; lower valves slightly curved at apices.

Phallic complex membranous, lateral parts of ectophallus slightly sclerotized; dorsal part consisting of a pair of lateral inflated valves; ventro-posterior part sac-like, membranous; between these two parts the opening of endophallus is located. Epiphallus short and wide, with long lateral plates and three strong median, apical teeth.

Spermatheca with several narrow vermicular, irregularly twisted diverticula.

Type species: *Gryllus Bulla variolosus* Linnaeus, 1758.

**Key to Species**

1 (2) Vertex, above compound eyes, with a pair of small tubercles. Third abdominal tergite of male with 12–14 stridulatory ridges. Median carina of pronotum in prozona forming 3–4 large teeth. Tessellated pattern of male elytron strong **variolosus** (Linnaeus)

2 (1) Vertex, above compound eyes, with a pair of large pyramidal tubercles. Third abdominal tergite of male with 8 stridulatory ridges. Median carina of pronotum in prozona forming a large tubercle-like projection and two small teeth. Tessellated pattern of male elytron weak . . . . . **papillosus** (Fabricius)

**Physemacris variolosus** (Linnaeus, 1758)

(Text-figs. 22, 23)

*Gryllus Bulla variolosus* Linnaeus, 1758 : 427. ♀.

*Pneumora maculata* Thunberg, 1775 : 257. ♀ syn. n.

*Pneumora marmorata* Thunberg, 1810 : 63. ♀ [Syn. Stål, 1873 : 143].

*Pneumora spinulosa* Thunberg, 1810 : 64. ♀ syn. n.

*Physemacris variolosus* (Linnaeus) Roberts, 1941 : 19.
Fig. 22. *Physemacris variolosus*. 1, male. 2, female. 3, male face. 4, female face.
♂. Of medium size. Integument of head and pronotum rugose and granulose. Antenna 23-segmented, longer than face, but much shorter than head and pronotum together. Frons roundly merging with vertex, above compound eyes with a pair of small tubercles. Median carina of pronotum in prozona forming three or four large teeth, which are sometimes fused, and one or two smaller teeth; a few smaller lateral teeth scattered on lateral lobes; metazona low arcuate, with median carina low, sharp and lateral carinae irregular, wrinkle-like, present in anterior part; lower margin of lateral lobe of pronotum sinuate, episternum comparatively large, with smooth edges. Elytra and wings reaching or slightly exceeding end of abdomen. Third abdominal tergite with 12–14 stridulatory ridges.

General coloration green to olive-green; head and pronotum with numerous small, white or whitish spots of irregular form sometimes fused into oblique, longitudinal patches on dorsum of pronotum; elytra green, with white tessellated pattern; sides of abdomen with numerous white or whitish spots.

♀. Large. Integument rugose and granulose. Antenna 22-segmented, about as long as face. Frons roundly merging with vertex, above compound eyes with a pair of small tubercles. Median carina of pronotum in prozona forming two or three large teeth, which are sometimes fused, and a few smaller teeth; several smaller teeth scattered on dorsum and lateral lobes; metazona low arcuate, with low, sharp median carina; lateral carinae irregular, callous and tuberculate, present in anterior part of metazona and partly in posterior part of prozona; lower margin of lateral lobe of pronotum sinuate; episternum with tooth on upper part of anterior margin. Elytra and wings hidden under pronotum; elytron sometimes slightly protruding from under lateral margin of metazona.

General coloration light green; whole body covered with small silvery-white spots of irregular form; on pronotum spots sometimes fused into elongate, oblique patches; on sides of abdomen spots form two or three regular longitudinal rows, with smaller spots scattered between them; ventral side with two rows of similar spots. Protruding part of elytron bright red.

Length of body ♂ 39–51, ♀ 40–50; pronotum ♂ 15–17, ♀ 18–20; elytron ♂ 31–42, ♀ about 6; hind femur ♂ 13–16, ♀ 16–17.5 mm.

Fig. 23. Physemacris variolosus. 1, phallic complex, from above. 2, end of male abdomen, from above. 3, the same, lateral view. 4, spermatheca. 5, abdominal stridulatory ridges (semi-schematic).
This species varies very much in body size and in shape and sculpture of the pronotum, which bears three and sometimes four teeth, while sometimes the teeth are fused or partly obliterated. The pattern on the pronotum and the whole body also varies very much, sometimes there are small white spots forming an indefinite pattern and sometimes the spots are fused into patches forming oblique stripes.

Material examined. 43 ♂, 13 ♀. Type ♂. Type locality “In Indiis” (erroneous). (Lovisa Ulrika Collection in Uppsala.)

Cape Province: Cape Town, Kirstenbosch; De Wet; Moshameer; Cape Peninsula; Garcias Forestry; Still Bay; Worcester; Fishhoek; Swartberg Pass; East London; Swellendam; Montagu; Stellenbosch; Riversdale; Hermanus; Willowmore; Stanford; Seven Weeks Port; Jonkersberg; Knysna; Jeffreys Bay; Oudtschoorn; Tradow Pass; Somerset West; Arniston; Zoetendals Valle. October–January.

**Physemacris papillosus** (Fabricius, 1775)

(Text-fig. 24)

*Gryllus papillosus* Fabricius, 1775: 827. ♂ [nec Thunberg, 1810: 61].

*Physemacris papillosus* (Fabricius) Johnston, 1956: 32.

♂. Of medium size. Integument of head and pronotum moderately rugose (antennae broken). Frons roundly merging with vertex, above compound eyes with a pair of large, pyramidal tubercles. Median carina of pronotum in prozona forming large fold projecting upwards; posteriorly to projection are two small teeth; metazona low arcuate, with sharp, moderately high median carina; lateral carinae strong, covered with callosities, strongly

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**FIG. 24. Physemacris papillosus.** 1, male. 2, male face. 3, abdominal stridulatory ridges. (semi-schematic).
protruding forwards and upwards, forming large "shoulders"; lower margin of lateral lobe sinuate; episternum with small tooth on anterior margin. Elytra and wings slightly exceeding end of abdomen. Third abdominal tergite with eight stridulatory ridges.

General coloration greenish; dorsum of pronotum with oblique, irregular, branched white spots; elytra greenish, with green venation and reticulation and weak tessellated pattern; side of abdomen with three longitudinal rows of irregular, large spots; ventral side of abdomen with two rows of white spots.

Female unknown.
Length of body 42; pronotum 15.5; elytron 34.6; hind femur 13 mm.

Material examined. Type ♂. Type locality; Cape of Good Hope. (Banks Collection, British Museum (Natural History).)
Cape Province: Uniondale, 1 ♂; Rusten Vrede, Oudtshoorn Distr., 1 ♂ nymph.

**PERINGUEYACRIS gen. n.**

Small; anterior part of body of male, to seventh abdominal segment, bladder-like, inflated; end of abdomen of normal cylindrical shape. Antenna filiform, slightly widening at apical part. Face slightly convex; frons roundly merging with vertex. Lateral ocelli placed above and slightly internally to antennal bases; in male all three ocelli very large; compound eyes small, oval, strongly convex. Pronotum low arculate, crossed by four transverse sulci; prozona much shorter than metazona; at posterior sulcus there are deep lateral depressions; median carina of prozona low, tubercle-like, widening in posterior part, in metazona sharp and slightly serrated; posterior margin of metazona elongate angular; episternum granulose, with small projection on anterior margin. Mesosternal interspace deeply concave. Male macropterous; anterior cubital vein of elytron unbranched. Third abdominal tergite of male with long row of fine stridulatory ridges. Anterior and middle femora slightly tuberculate; hind femur weak, moderately short; in male, internal side of hind femur with short high carina, bearing row of small transverse ridges, forming second part of stridulatory mechanism. Brunner's organ hardly detectable. Arolium large. Supra-anal plate of male elongate angular, with transverse sulcus. Cercus short, conical. Subgenital plate short, acutely conical.

Phallic complex. Ectophallus membranous; lateral valves weakly sclerotized, posterior sac-like formation large. Endophallus banana-shaped, with a pair of weak lateral sclerotizations. Epiphallus with large medium and pair of smaller lateral, apical teeth; lateral plates comparatively wide.

Type species: *Pneumora namaqua* Péringuey, 1916.

**Peringueyacris namaqua** (Péringuey, 1916) **comb. n.**

(Text-fig. 25)


♂. Small. Integument of head and pronotum rugose and granulose and slightly hairy. Antenna 22-segmented, slightly longer than face and much shorter than head and pronotum together. Prozona of pronotum with convex folds between sulci; lateral carinae of pronotum weak, noticeable in posterior part of prozona and anterior part of metazona as granulated wrinkles; lower margin of lateral lobes slightly sinuate. Male elytra reach well beyond end of abdomen. Third abdominal tergite of male with 28–30 fine stridulatory ridges.

General coloration green; pronotum with two or three pairs of white, longitudinal, oblique patches; elytra greenish, with yellowish main veins; sides of abdomen with two rows of white spots, which are sometimes obliterated; ventral part of abdomen sometimes also with two rows of whitish spots.
♀. Unknown.
Length of body 25–26; pronotum 12.4–12.5; elytron 25–26; hind femur 10–11 mm.

Material examined. Type ♂. Type locality: Springbok Fontein. (South African Museum.)

CAPE PROVINCE: Nababiep, 1 ♂; Springbok, 1 ♂. August, October.

Fig. 25. *Peringueyacris namaqua*. 1, male. 2, male face. 3, phallic complex, from above. 4, end of male abdomen, lateral view. 5, the same, from above. 6, abdominal stridulatory ridges (semi-schematic).
PROSTALIA I. Bolivar, 1906

_Pompholyx_ Stål, 1873: 144, [nec Gosse, 1851].
_Prostalia_ I. Bolivar, 1906: 396 [n. n.].

Anterior part of body in male, to sixth segment, strongly inflated, bladder-like; end of abdomen of usual cylindrical shape. In female, body of normal shape, slightly compressed. Antenna thin, filiform, much shorter than pronotum. Face slightly convex. Lateral ocelli placed slightly above and internally to antennal bases; in male all three ocelli large, in female smaller. Compound eyes, in both sexes, small, oval, strongly convex. Pronotum low arcuate, crossed by four transverse sulci; median carina sharp and deeply serrated, particularly in prozona; lateral carinae sharp, tuberculate; metazona three or four times as long as prozona, its posterior margin elongate angular. Episternum with angular, tooth-like anterior end. Male fully winged; anterior cubital vein of elytron unbranched; reticulation sparse. Female brachypterous, elytra reaching end of pronotum and protruding from under sides of metazona; venation reduced, reticulation moderately sparse. Third abdominal tergite of male with a row of transverse stridulatory ridges. Anterior and middle femora moderately slender, slightly tuberculate; hind femur comparatively short and weak, on internal side with short high carina, bearing a row of transverse ridges, which form second part of stridulatory mechanism; in female, on internal side of hind femur there is a longer row of small teeth but not ridges on abdomen. Brunner's organ absent. Lower lobe of hind knee narrow with subacute apex, in basal part of lower margin with large, acute tooth. Arolium large. Supra-anal plate, in both sexes, elongate angular. Cerci short, conical. Subgenital plate of male short, acutely conical, in female with acutangular apex; ovipositor short, robust, with straight valves.

Phallic complex. Almost wholly membranous; lateral and proximal dorsal parts of ectophallus slightly sclerotized; dorsal part with pair of lateral, inflated valves; ventro-posterior part sac-like, membranous; opening of endophallus located between valves and sac-like part; endophallus with a pair of lateral, narrow, longitudinal sclerotizations. Epiphallus approximately bridge-shaped, with elongated posterior projections and, in anterior projecting part, with numerous small teeth.

Type species: _Pneumora granulata_ Stål, 1873.

_Prostalia granulata_ (Stål, 1873)

(Text-figs. 26, 27)

_Pneumora granulata_ Stål, 1873: 53. ♂.
_Pompholyx granulata_ (Stål) I. Bolivar, 1906: 396.
_Prostalia granulata_ (Stål) I. Bolivar, 1906: 341.

♂. Large; body strongly inflated. Integument of head and pronotum strongly granulose and rugose, abdomen smooth. Antenna slightly longer than face, 21-segmented. Frons roundly merging with short vertex. Crest of pronotum low; median carina sharp throughout length, in prozona more strongly serrated than in metazona; all four sulci deep, across whole width of dorsum; lower margin of lateral lobe of pronotum sinuate. Elytra and wing exceeding end of abdomen. Third abdominal tergite with 15 stridulatory ridges. Stridulatory ridges on internal side of hind femur forming a rather short row.

General coloration green; elytra and wings transparent, venation and reticulation light green.

♀. Large. Integument of head and pronotum strongly granulose and rugulose, abdomen smooth. (Antennae broken.) Frons roundly merging with moderately short vertex. Crest of pronotum low; median carina sharp throughout length, in prozona much more strongly serrated than in metazona; all four sulci deeply crossing dorsum and carina; lower margin of
lateral lobe of pronotum slightly sinuate. Elytra and wings strongly shortened and scarcely reaching end of pronotum, but roundly and considerably protruding from under lateral margins of metazona. Internal side of hind femur with moderately long row of small teeth, which probably forms part of stridulatory mechanism, another part of which is probably the rather convex costal vein of elytron.

General coloration uniformly green.

Length of body ♂ 58–64, ♀ 60; pronotum ♂ 25–28·5, ♀ 30; elytron ♂ 47·5–56, ♀ 17·5; hind femur ♂ 16–18·5, ♀ 18 mm.

Material examined. Type ♂. Type locality: "Caffraria". (Stockholm Museum.)

Natal: Richmond ♀ (Type of P. subalata); "Natal" i ♂. Transvaal: Lochiel, i ♂.

Fig. 26. Prostalia granulata. 1, male. 2, female. 3, male face. 4, female face.
**Physophorina** Westwood, 1874

_**Physophorina**_ Westwood, 1874: 175.


Anterior part of body in male, to sixth segment, strongly bladder-like, inflated; end of abdomen of usual cylindrical shape. In female, body of normal shape slightly compresses, except pronotum which is strongly inflated. Antenna thin, filiform, much shorter than pronotum. Face flat. Lateral ocelli placed above and slightly externally to antennal bases; in male all three ocelli large, in female vestigial. Compound eyes, in both sexes, small, oval, moderately convex. Pronotum arcuate, inflated, in female strongly inflated; three transverse sulci present; median carina sharp; lateral carinae present in metazona only, sharp, covered throughout length with small tubercles; metazona six or seven times as long as prozona, elevated and forming deep fold at posterior sulcus; its posterior margin elongate angular. Episternum small, angular, with several teeth. Mesosternal interspace deeply concave. Male macropterous; anterior cubital vein branched; reticulation sparse. Female brachypterous, elytra reaching middle of fourth abdominal tergite; venation reduced, reticulation dense. Third abdominal tergite of male with a row of transverse stridulatory ridges, which in lower part are slender and closely placed, in upper part robust and sparsely placed. Anterior and middle femora slender, tuberculate; hind femur comparatively short, weak, on internal side with short high carina, bearing row of transverse ridges, which forms second part of stridulatory mechanism; in female, on internal side of hind femur there is a longer row of small teeth, but no ridges on abdomen. Brunn's organ moderately well developed or vestigial. Arolium large. Supra-anal plate in both sexes elongate angular. Cerci short, conical. Subgenital plate in male conical, with obtuse apex; in female with acutangular apex; ovipositor short, robust, with straight valves.

Phallic complex. Almost wholly membranous; lateral parts of ectophallus slightly sclerotized; dorsal part with a pair of lateral, inflated valves; ventro-posterior part sac-like, membranous; opening of endophallus located between valves and sac-like part; endophallus with a pair of lateral, narrow, longitudinal sclerotizations. Epiphallus approximately shield-or bridge-shaped, dorsal surface covered with numerous small teeth.

Spermatheca large, sac-like, with several pocket-like diverticula.

Type species: _Shortridgea miranda_ Péringuey, 1916.

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**Fig. 27. Prostalia granulata.** 1, phallic complex, from above. 2, endophallus, lateral view. 3, end of male abdomen, from above. 4, the same, lateral view. 5, left hind knee, external view. 6, abdominal stridulatory ridges (semi-schematic).
KEY TO SPECIES

MALES

1 (2) Pronotum with high, narrow, sharp crest. Subgenital plate elongate, acutely conical .................. *livingstoni* Westwood

2 (1) Pronotum with moderately high, comparatively wide and less sharp crest. Subgenital plate short, conical .................. *miranda* (Péringuey)

Females

1 (2) Pronotum strongly inflated, with high crest, convex on sides. Elytra reaching or slightly exceeding end of pronotum. **livingstoni** Westwood

2 (1) Pronotum less inflated, crest moderately high, with sides concave. Elytra considerably exceeding end of pronotum, reaching seventh abdominal tergite. **miranda** (Péringuey)

**Physophorina livingstoni** Westwood, 1874

(Text-figs. 28, 29)


♂. Very large; body strongly inflated. Integument of head and pronotum moderately rugose, abdomen smooth. Antenna slightly longer than face, 22-segmented. Frons angularly merging with short vertex. Pronotum with narrow, sharp, very high crest; median carina in prozona almost linear, crossed by posterior and pre-posterior sulci; first sulcus not reaching median carina; lateral lobe of pronotum comparatively small, at lower margin rounded. Elytra and wings exceed end of abdomen. Third abdominal tergite with 8 large upper and 19 small lower striulatory ridges. Subgenital plate elongate, acutely conical, from above with excised apex. Hind femur on internal side with short row of small, transverse sharp ridges.

Phallic complex comparatively large; dorsal lateral valves large and comparatively strongly inflated, their dorsal, lobe-like parts large. Epiphallus with very deep incision in middle of anterior part and with well developed lateral plates; small teeth cover anterior margin and are sparsely distributed along the lateral convexities of the epiphallus.

General coloration green; median and lateral carinae of pronotum brownish or yellowish; elytron and wing transparent with light green venation and reticulation, in apical part of median area of elytron there is a small, round yellow spot.

♀. Very large. Integument of head and pronotum moderately rugose, abdomen smooth. Antenna 22-segmented about as long as face. Frons angularly merging with very short vertex, which hardly protrudes from under pronotum. Pronotum strongly inflated, with high crest and convex sides, median carina sharp throughout length, crossed by posterior sulcus only, lateral carinae sharp, covered with small tubercles. Elytra not reaching or only slightly exceeding posterior end of pronotum and widely protruding from under lateral margins of metazona. Hind femur on internal side with a row of small, teeth-like tubercles (presumably part of a striulatory mechanism, the other part being the rather convex radial vein of the elytron).

General coloration light green; metazona of pronotum, in angle formed by lateral carina and lateral margin, mostly with triangular white spot; apical part of costal area of elytron with larger, silvery white triangular spot.

Length of body ♂ 70–81, ♀ 89–107; pronotum ♂ 38–43, ♀ 62–67; elytron ♂ 65–71, ♀ 33–38; hind femur ♂ 16.5–18, ♀ 22.5–24.5 mm.

Material examined. 20 ♂, 9 ♀ and 12 nymphs. ♀ nymph type. Type locality "Zambezi". Hope Dept. of Entomology, University Museum, Oxford.

**Zululand**: "Zululand". **Mozambique**: Mutuale; Prov. du Mozambique. **Nyasaland**: Zomba; Chileka aerodrome, 2,000 ft.; Mbidi; Namiwawa. **Tanganyika**: Handeni, 350 m.; Kilosa; Tendaguru; Chidya (16° 38 S 39° 04 E); Liwale; Mikindani; Tendaguin; Mpwapwa (Type locality of **Cystocoelia absidata** Karsch, 1896). **Uganda**: "Uganda".

The specimens (2 ♂, 1 ♀) from Uganda, which is the northernmost locality for the whole family, were collected by Dr. Baxter. Unfortunately no other particulars concerning these specimens are available.
**Physophorina miranda** (Péringuey, 1916) **comb. n.**

(Text-figs. 30, 31)

*Shortridgea miranda* Péringuey, 1916: 412. ♂.

♂. Large. Body strongly inflated. Integument of head and pronotum slightly rugose, abdomen smooth. Antenna about as long as face, 22-segmented. Frons angularly merging

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**Fig. 29. Physophorina livingstoni.** 1, first instar nymph. 2, phallic complex, from above. 3, endophallus, lateral view. 4, end of male abdomen, from above. 5, the same, lateral view. 6, spermatheca (in natural state 4.5 mm. length). 7, abdominal stridulatory ridges (semi-schematic). 8, face of adult male.
Fig. 30. Physophorina miranda. 1, male. 2, female. 3, male face. 4, female face.
with very short vertex. Pronotum with crest moderately high, narrow and sharp; metazona in front, at posterior sulcus, forming deep fold and overhanging prozona, sometimes almost completely; three transverse sulci present; median carina in prozona hardly noticeable, in metazona sharp; lateral carinae sharp, covered with small tubercles; lateral lobe of pronotum small with lower margin rounded. Elytra and wings exceed end of abdomen. Third abdominal tergite with 7 large irregularly shaped ridges and 13 small regular stridulatory ridges. Subgenital plate short, acutely conical, from above with slightly excised apex. Hind femur on internal side with short high carina, bearing row of small transverse ridges.

Phallic complex comparatively small; dorsal lateral valves comparatively small, their dorsal, lobe-like parts small. Epiphallus with shallow excision in middle of anterior part, with lateral plates large, but not very well defined. Small teeth cover anterior and middle part of epiphallus.

General coloration green; median carina of pronotum yellowish; elytron and wing transparent, with green venation and reticulation, in apical part of median area of elytron a small, oblique, silvery white spot.

♀. Larger than male. Integument of head and pronotum slightly rugose, abdomen smooth. Antenna 22-segmented, slightly shorter than face. Frons angularly merging with short vertex. Pronotum moderately strongly inflated, with comparatively moderately high crest and concave sides; median carina in prozona obtuse, in metazona sharp; lateral carinae sharp, covered with small tubercles. Elytra shortened, exceeding end of pronotum and reaching sixth abdominal tergite. Hind femur on internal side, with a row of small, tooth-like tubercles (presumably part of stridulatory mechanism, the other part possibly being the rather convex radial vein of the elytron).

General coloration green; median carina of pronotum sometimes yellow; lateral carinae white with reddish tubercles; metazona of pronotum, in angle formed by lateral carina and lateral margin, with silvery white, triangular spot; elytron in region of base of radial vein with small white spot, in apical part of costal area with large, triangular white spot.


Fig. 31. *Physophorina miranda*. 1, phallic complex, from above. 2, endophallus, lateral view. 3, end of male abdomen, lateral view. 4, the same, from above. 5, spermatheca. 6, abdominal stridulatory ridges (semi-schematic).
Too few specimens were studied to judge the variability of the species, except the coloration. It is mostly green or brownish (but the latter may be a postmortem change). Sometimes the pronotum in both sexes is covered with sparsely scattered, small, blackish dots.

Material examined. 5 ♂️, 2 ♀️. Type ♂️. Type locality: Zululand, Eshowe. (South African Museum.)

CAPE PROVINCE: Port St. Johns. NATAL: Annerley; Eshowe; Nkandhla Forest. TANGANYIKA: Liwale. January, April, October, November.

**PNEUMORA** Thunberg, 1775

*Pneumora* Thunberg, 1775: 255.

*Pneumora (Cystocoelid)* Serville, 1838: 713 [Syn. Kirby, 1910: 65].

Anterior part of body in male, to sixth abdominal segment, strongly inflated, bladder-like, end of abdomen of normal cylindrical shape. In female, body of normal shape, cylindrical. Antenna thin, filiform, much shorter than pronotum. Face flat. Lateral ocelli placed above and slightly externally to antennal bases; in male all three ocelli large, in female vestigial. Compound eyes in both sexes small, oval, moderately convex. Pronotum low arcuate; three transverse sulci present; median carina in male absent in prozona, low and sharp in metazona; in female, low and sharp in prozona and comparatively high and sharp in metazona; with small tubercles on whole length; metazona much longer than prozona, forming deep fold at posterior sulcus and overhanging above prozona, in male almost covering it, in female covering only small part of it; posterior margin of metazona elongate, angular. Episternum with large anterior tooth. Mesosternal interspace deeply concave. Male fully winged; anterior cubital vein of elytron branched; reticulation sparse. Female brachypterous, elytron reaching fifth abdominal tergite; venation reduced; reticulation dense. Third abdominal tergite of male with a row of transverse stridulatory ridges, which in upper part of row are large and robust, sparsely placed, in lower part small, slender, closely placed. Anterior and middle femora slender, slightly tuberculate; hind femur short and weak; on internal side with short high carina, bearing a row of transverse ridges which forms second part of stridulatory mechanism; in female, on internal side of hind femur there is a longer row of small teeth, but no ridges on abdomen. Brunner's organ present, sometimes reduced. Arolium large. Supra-anal plate angular in both sexes. Cerci short, conical. Subgenital plate in male short, conical, from above with angularly excised apex; in female with acutangular apex. Ovipositor moderately short, robust, with straight valves.

Phallic complex. Almost wholly membranous; lateral part of ectophallus slightly sclerotized; dorsal part with a pair of lateral, inflated valves and in proximal part with slight sclerotization; ventro-posterior part sac-like membranous; opening of endophasus located between valves and sac-like posterior part; endophasus with a pair of lateral, narrow longitudinal sclerotizations, protruding in distal part at opening of endophasus. Epiphallus approximately shield-like, its dorsal surface covered with numerous small teeth.

Spermatheca large, sac-like, with several pocket-like diverticula.

Type species: *Pneumora sexguttata* Thunberg, 1775.

**Pneumora inanis** (Fabricius, 1775)

(Text-figs. 32, 33)

*Gryllus inanis* Fabricius, 1775: 827. ♂️.

*Pneumora sexguttata* Thunberg, 1775: 258. ♂️. [Syn. Fabricius, 1781: 363].


*Pneumora inanis* (Fabricius) Roberts, 1941: 19.

General coloration green; posterior margin of pronotum whitish, sometimes with reddish-brown narrow line between whitish border and green basic colour of pronotum; dorsum often

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**Fig. 32. Pneumora inanis.** 1, male. 2, female. 3, male face. 4, female face.
with three pairs of oblique longitudinal white lateral stripes; elytra and wings greenish transparent with green venation and reticulation; on elytron two silvery white, short, oblique spots; abdomen uniformly green or with several whitish spots.

♀. Very large. Body subcylindrical, not inflated. Integument of head and pronotum granulose and slightly hairy, abdomen smooth. Antenna about as long as face, 23-segmented. Frons angularly merging with short vertex. Pronotum with sharp, granulose carina; lateral carinae strong, with teeth covering almost whole carina; strong teeth on lateral lobes and smaller teeth on dorsum of pronotum present. Hind femur on internal side with short carina, bearing a row of small, tooth-like tubercles. No ridges on abdomen.

General coloration green; posterior margin of pronotum silvery white, with reddish-brown border line between white and basal green of pronotum; carinae brown-reddish; below posterior half of lateral carina a silvery-white stripe; dorsum with three to five oblique, elongate, lateral silvery-white stripes, with brown-reddish borders; elytron green; base of costal area blackish; middle of elytron with two large, silvery white spots of irregular form with reddish borders; costal area with similar stripe, forming two narrow angular projections; side of abdomen with two rows of large and two rows of small silvery-white spots with reddish borders.

Length of body ♂ 62-67, ♀ 70-86; pronotum ♂ 23·5-27, ♀ 30-38; elytron ♂ 61-67·5, ♀ 25-36; hind femur ♂ 16-17·5, ♀ 20-21·5 mm.

This species varies in body size and in pattern and coloration. The silvery stripes and spots may be larger or smaller and on the pronotum from three to five. Coloration from brown-reddish to greenish.

Material examined. 20 ♂, 16 ♀. Type ♂. Type locality: Cape of Good Hope. (Banks’ collection, in British Museum (Natural History).)

CAPE PROVINCE: East London; Grahamstown; Alexandria; Somerset East; Hogsback. NATAL: Yellowwoods, Karkloof; Balgowan; Hilton Rd; Bulwer: Nottingham Road. TANGANYIKA: Lukuledi.

Fig. 33. Pneumora inanis. 1, phallic complex, from above. 2, endophallus, lateral view. 3, end of male abdomen, lateral view. 4, the same, from above. 5, spermatheca. 6, abdominal stridulatory ridges.
Parabullacris Dirsh, 1963


Compared to the Parabullacris Dirsh, 1963, they are comparatively small and slender; appearance nymph-like. Male body not inflated. Integument granulose. Antenna short, slightly widening towards apex. Head comparatively narrow; frons flat, angularly merging with vertex. Ocelli large in male, vestigial in female, lateral ocelli placed above and slightly internally to antennal bases; compound eyes moderately

Fig. 34. Parabullacris vansonii. 1, male. 2, female. 3, male face. 4, female face.
large, oval and moderately convex. Pronotum strongly elongate, in profile regularly arcuate, in female low arcuate; four transverse sulci present; metazona about three times as long as prozona, its posterior margin acutangular; lateral carinae not strongly developed. Vestigial elytra and wings present and completely hidden under pronotum. Abdomino-femoral stridulatory mechanism highly reduced: a few stridulatory ridges on third abdominal tergite and serration on internal side of hind femur being hardly detectable. Hind femur moderately short; Brunner's organ present. Arolium large. Abdomen slender, of usual acridoid shape. Supra-anal plate in both sexes elongate angular, with transverse furrow; cercus in both sexes short, conical; subgenital plate in male conical, at apex slightly excised; in female obtusangular; ovipositor moderately short, with straight valves.

Phallic complex of usual Bullacris group type, membranous, on dorsal side with a pair of lateral inflated valves and ventro-posterior membranous, sac-like formation; endophallus with a pair of elongated lateral sclerotizations. Epiphallus shield-like, with protruding posterior projections and three median teeth at anterior margin.

Type species: Parabullacris vansoni Dirsh, 1963.

This genus differs from Bullacris in the non-inflated abdomen of the male, the vestigial elytra and wings, vestigial stridulatory mechanism and the more compressed pronotum. The females of both genera could easily be confused.

Parabullacris vansoni Dirsh, 1963
(Text-figs. 34, 35)

Parabullacris vansoni Dirsh, 1963: 179.

♂ (Type). Antenna about one quarter length of head and pronotum together, 20-segmented. Fastigial furrow very weak; vertex short. Median carina of pronotum sharp, regular; crossed by all four deep transverse sulci; lateral carinae weakly pronounced. Anterior and middle femora moderately slender; hind femur short, comparatively thick; lower lobes of hind knee angular, with rounded apices.

General coloration olive-brownish; lateral margin of metazona whitish; four white spots on sides of abdomen.

♀. Much larger than male. Antenna 20-segmented. Ocelli vestigial. Pronotum less arcuate than in male, approximating to tectiform, with metazona more elongate. Coloration and pattern as in male, but white spots and the sides of the abdomen fading and sometimes completely disappearing.

Length of body ♂ 17.7–22, ♀ 32–39; pronotum ♂ 12–15, ♀ 19–21.5; hind femur ♂ 8.6–9.8, ♀ 9–11 mm.

Material examined. Type ♂. Type locality: Cape Province, Nababiep. (Transvaal Museum).


Pneumoracris Dirsh, 1963


Comparatively small and slender; appearance nymph-like. Male body not inflated. Integument of head and pronotum strongly granulose, abdomen smooth. Antenna comparatively long, slightly widening towards apex. Head narrow; frons slightly convex, roundly merging with vertex; ocelli very small in both sexes, lateral ocelli placed above and slightly
internally to the antennal bases; compound eyes large, oval, strongly convex. Pronotum elongate, tectiform and slightly saddle-shaped; four transverse sulci present; prozona forming tubercle-like median projection in front of posterior sulcus and, in anterior part of metazona, another similar tubercle-like median projection; metazona two or more times as long as prozona, the posterior part with a pair of lateral depressions, its posterior margin acutangular; all pronotal characters more sharply expressed in males than in females. Elytra and wings vestigial and completely hidden under pronotum. Abdomino-femoral stridulatory mechanism absent. Hind femur comparatively long and strong; Brunner's organ not detectable. Arolium large. Abdomen slender, of usual acridoid shape. Supra-anal plate in both sexes elongate angular, with transverse furrows; cercus in both sexes short, conical, subgenital plate in male conical, at apex slightly excised; in female obtusely angular; ovipositor moderately long, with straight comparatively robust valves.

Phallic complex of usual Bullacris group type, membranous, dorsally with a pair of lateral inflated valves, and ventro-posteriorly of membranous, sac-like form; endophallus with a pair of elongated lateral sclerotizations. Epiphallus shield-like, with slightly protruding posterior projections and with three median teeth at anterior margin.

Type species: Pneumoracris browni Dirsh, 1963.
This genus superficially may be compared with Pneumora namaqua Péringuey, 1916. It shares similar structure of the pronotum and similar pattern, but differs in all the other essential characters mentioned in the description. On the basis of similarity of the pronotum Péringuey described a female of Pneumoracris browni as the female of Pneumora namaqua. This error is corrected now, since a good series of both males and females of Pneumoracris browni is available.

Fig. 35. Parabullacris vansoni. 1, phallic complex, from above. 2, end of male abdomen, lateral view. 3, the same, from above. 4, spermatheca.
Pneumoracris browni Dirsh, 1963
(Text-figs. 36, 37)


♂ Type. Antenna slightly more than half length of head and pronotum together, 21-segmented. Fastigial furrow weak, vertex short. Median carina of pronotum wide and thick, forming tubercles in posterior part of prozona and anterior part of metazona; lateral carinae

Fig. 36. Pneumoracris browni. 1, male. 2, female. 3, male face. 4, female face.
represented by convex lateral margins of metazona. Anterior and middle femora comparatively robust, widening towards apex; hind femur rather thick; lower lobes of hind knee angular, with obtuse apices.

General coloration greenish, with brown spots and silvery scale-like patches and spots; frons brownish; vertex and genae green; vertex with median yellowish stripe; a pair of yellowish postocular stripes present; pronotum greenish, median part above brownish, lateral lobes brownish, with four patches of silver-white of irregular form, forming definite pattern; pleura with large silvery white spot, becoming yellowish; abdomen with three rows of lateral spots, yellowish white with blackish margins.

♀ Paratype. As the male, but larger. Antenna 20-segmented. Ocelli vestigial. Pronotum with less developed lateral impressions, less pronounced tubercles of median carina and more elongate metazona.

Length of body ♂ 11·5-14, ♀ 22-29; pronotum ♂ 8-8·2, ♀ 15-16·5; hind femur ♂ 9·1-9·6, ♀ 11·5-12 mm.

Material examined. Type ♂. Type locality: Cape Province, 5 m. East Kamieskroon. (Transvaal Museum.)


Fig. 37. Pneumoracris browni. 1, phallic complex. 2, end of male abdomen, lateral view. 3, the same, from above. 4, spermatheca.

PARAPHYSEMACRIS Dirsh, 1963


Comparatively small and slender; appearance nymph-like; male body not inflated. Integument of head and pronotum strongly tuberculate and spiny, with silvery white scale-like flattened tubercles. Antenna moderately long, slightly widening towards apex. Head moderately wide; frons slightly convex, roundly merging with vertex; ocelli in male moderately large, lateral ocelli placed above and slightly internally to antennal bases; compound eyes small, oval, strongly convex. Pronotum elongate, tectiform: median carina in prozona
forming three large, upwardly protruding teeth and numerous small teeth on sides; in metazona median carina serrated and slightly arcuate; four transverse sulci present; at posterior sulcus dorsum constricted; metazona about twice as long as prozona, its posterior margin angular. Elytra and wings vestigial and completely hidden under pronotum. Abdomino-femoral stridulatory mechanism absent, but vestige of serration on internal side of hind femur is detectable. Hind femur comparatively long; Brunner's organ absent. Arolium large. Abdomen slender, of usual acridoid shape. Supra-anal plate elongate angular, with transverse furrow; cercus short, conical; subgenital plate acutely conical, at apex slightly excised.

Fig. 38. Paraphysemacris spinosus. 1, male. 2, male face. 3, phallic complex, from above. 4, end of male abdomen, lateral view. 5, the same, from above.
Phallic complex of usual *Bulacris* group type, membranous, on dorsal side with a pair of lateral, inflated valves, and in ventro-posterior part is a membranous sac-like formation; endophallus with a pair of elongate, lateral sclerotizations. Epiphallus shield-like, with protruding posterior projections and three teeth at anterior margin.

Type species: *Paraphysemacris spinosus* Dirsh, 1963.

In shape and pattern this genus superficially resembles *Physemacris*. However, it probably has only remote relationship with that genus. The non-inflated abdomen, absence of stridulatory mechanism and vestigial wings are sufficient characters to place *Paraphysemacris* into an entirely different group.

**Paraphysemacris spinosus** Dirsh, 1963

(Text-fig. 38)


♂ Type. Antenna 22-segmented, about half as long as head and pronotum together. Fastigial furrow weak; vertex short and broad. Prozona of pronotum with three large, median teeth and numerous lateral teeth and tubercles; metazona tuberculate; lateral carinae detectable as elongate tubercle-like formations. Anterior and middle femora tuberculate, moderately slender; hind femur long, slender but strong; lower lobes of hind knee angular, with obtuse apices.

General coloration greenish; scale-like flattened tubercles and spots scattered on pronotum, pleura and abdomen, spots of irregular form, silvery white or slightly yellowish.

Only males known.


Material examined. Type ♂. Type locality: Cape Province: Kuyana, (British Museum (Natural History); "South Africa"). 1 ♂ paratype. (Stockholm Museum).

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