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Structure of Ovipositors and Cladoendesis of Saltatoria, or Orchesopia

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Abstract—The oldest circumscriptional names of the taxon under consideration are Orchesopia Rafinesque, 1815 and Saltatoria Latreille, 1817. The recent Saltatoria are divided into two subordinate taxa whose circumscriptional names are Dolichocera Bey-Bienko, 1964 and Caelifera Ander, 1936 [= Metorthoptera Crampton, 1927 = Brachycera Bey-Bienko, 1964 (non Brachycera Zetterstedt, 1842)]. The name Ensifera Chopard, 1920, according to its original circumscription, belongs to the taxon which includes Tridactylidae; the name Caelifera Ander, 1936 originally belongs to the taxon which also includes Tridactylidae; therefore, these two circumscriptional names cannot be used in the same classification. Saltatoria belong to Tegminoptera Kluge, 2013, which belong to Rhipineoptera Kluge, 2012. Holophyly of Saltatoria is well proved by autapomorphies, the most conclusive of which are the stagnofemoral leaping specialization of the hind legs with the irreversibly reduced trochanter, and the inversed position of protoptera at the penultimolarval and ultimolarval stages. All the Saltatoria can be divided into an extinct plesiomorphon Permorchesopia **taxon n.** (characterized by primitively 5-segmented tarsi) and Neorchesopia **taxon n.** (characterized by partial or complete fusion of the 1st and 2nd tarsomeres). The structure and evolution of ovipositors are discussed. The term **kinetapophyses** is proposed as a common name for homologous abdominal appendages: the retractile vesicles on the pregenital segments of Triplura and Diplura and the 1st and 2nd ovipositor valves on abdominal segments VIII and IX of female Amyocerata. The portion of the sternum containing the muscles that extend to the kinetapophyses and styli can be referred to either as a **styliger**, a **bistyliger**, or a pair of **unistyligers**; the term "coxite" should be avoided since it implies doubtful homologization of these appendages. In the digging ovipositor of Caelifera, the shortened kinetapophyses IX are not vestiges but functionally important components. Examination of *Ripipteryx* gives insight into the origin of the peculiar lateral apodemes present in the ovipositors of the other representatives of Caelifera. Based on new hypotheses about character polarity in the ovipositor morphology and about evolution of stridulatory and hearing apparatuses, a new phylogenetic classification of Saltatoria is suggested, in which Dolichocera includes taxa with new circumscriptional names Stratensifera **taxon n.**, Acoustopoda **taxon n.**, Mesensifera **taxon n.**, Striduloptera **taxon n.**, Tettigensifera **taxon n.**, and Gryllensifera **taxon n.**, and Caelifera includes taxa with new circumscriptional names Vectocaelifera **taxon n.** and Acoustogastra **taxon n.**

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Cladoendesis is a method of phylogeny reconstruction by building a classification consisting of holophyletic taxa and plesiomorphons; it makes use of the dual nomenclature system which provides unambiguous names for taxa of any hierarchical level, regardless of whether they have formal ranks or not (Kluge, 2012a).

While working on my future book *Cladoendesis of Insects*, I discovered significant gaps in the current knowledge of some morphological and ontogenetic characters that constitute major apomorphies of large insect taxa. To fill these gaps, I had to perform original research whose results were covered in several publications. In particular, new data were obtained on the segmental composition of the insect abdomen (Kluge, 2000) and on the structure of the caudalii in Amyocerata (Kluge, 2004a); new synapomorphies were found in the thorax of Idioprothoraca (Embioptera and Notoptera) (Kluge, 2012b); new data were obtained on the metamorphosis of coccids (Gallinsecta) (Kluge, 2010b) and holometabolous insects (Metabola) (Kluge, 2005a), the homology and ontogeny of the larval mouthparts of neuropteroid insects (Birostrata and Nothomegaloptera) (Kluge, 2005a), the structure and homology of the larval legs of Nannomecoptera (Kluge, 2004b), the structure and homology of the wing vestiges of Boreidae and Aphaniptera (Kluge, 2013), and the homology and ontogeny of the mouthparts of fleas (Aphaniptera) (Kluge, 2002).

This communication presents new data on the structure of the ovipositor of Caelifera that help elucidate its origin. In this connection, the available data on the ovipositor morphology in Saltatoria are discussed, and a phylogenetic hypothesis for Saltatoria is proposed, taking into account the evolution of their ovipositors and organs of sound communication.

THE NAMES OF THE TAXA

The Principles of Nomenclature

All the names of taxa are used herein following the rules of the rank-free dual nomenclature system developed by the author, with the previous term "volumetric name" (Kluge, 1999, 2000) replaced by the term "circumscriptional name" (Kluge, 2010a). According to these rules, all the non-typified names published since 1758 are used as **circumscriptional names** with their original authorship and publication dates; each circumscriptional name can be applied only to the taxon to which its original circumscription corresponds.

Typified names of higher taxa are used herein according to the rules of the International Code of Zoological Nomenclature (ICZN) for the family-group names, as if they were extended to taxa of any rank as well as to rankless taxa. To avoid discussion of the ranks of particular taxa, the rank-free typified names are used either in the **basic format** or as **hierarchical names.** In both cases the name includes the name of the type genus followed by a slash and the letter "f" and/or "g" designating the family-group or the genus-group in the sense defined by ICZN. The hierarchical names derived from the identical genus-group names are numbered in order of subordination, starting from the highest. To designate the circumscription, such a typified name may be followed by one or several genus-group names in parentheses, with notes "incl." (including) or "sine" (without).

A drawback of the current ICZN is the presence of a separate family-group in which the principle of coordination is used independently of the principle of coordination in the genus-group. Since the formal starting point of taxonomic priority is set at 1758 for all the cases while family-group taxa came into common use in zoology only in the XIX century (Latreille, 1802–1804), the authorship of family-group names is often dubious. In some cases, changes in the status of the genus-group name lead to conflict between the ICZN rules concerning family-group names and the traditional use of these names.

In particular, in 1945 and 1954 the International Commission on Zoological Nomenclature conserved (i.e., made available) the names *Locusta* Linnaeus, 1758 with the type species *Gryllus migratorius* Linnaeus, 1758 (Opinion 158) and *Tettigonia* Linnaeus, 1758 with the type species *Gryllus viridissimus* Linnaeus, 1758 (Opinion 299). Before these acts, these names had a dubious status because in Linnaeus' classification they had been used not for genera but for rankless taxa within the genus *Gryllus*. Correspondingly, the homonymous generic names *Locusta* Fabricius, 1775 (with the type species *Gryllus viridissimus* Linnaeus, 1758) and *Tettigonia* Fabricius, 1775 (with the type species *Tibicen linnei* Smith et Grossbeck, 1907), and also family-group names derived from them were widely used in the early literature. In the modern classification, *Tettigonia* Linnaeus, 1758 and *Locusta* Fabricius, 1775 are objective synonyms and belong to Dolichocera; *Locusta* Linnaeus, 1758 belongs to Caelifera, and *Tettigonia* Fabricius, 1775 belongs to Auchenorrhyncha. The name *Tettigonia* Linnaeus, 1758 is the senior generic name in the taxon that includes *Conocephalus* Thunberg, 1815, *Bradyporus* Charpentier, 1825, *Meconema* Serville, 1831, *Phaneroptera* Serville, 1831, *Pseudophyllus* Serville, 1831, and related taxa. There is a strong tradition to refer to this taxon by a typified name derived from the generic name *Tettigonia*, namely Tettigoniidae, Tettigonioidea, etc. However, according to the ICZN rules, these family-group names have the authorship "Krauss, 1902," which is confirmed by the Commission (Opinion 647) and recorded in the Official List; therefore, they are inferior in priority to the family-group names derived from the generic names *Conocephalus*, *Bradyporus*, *Meconema*, *Phaneroptera*, and *Pseudophyllus* and having the authorship "Burmeister, 1838." Some authors (Vickery and Kevan, 1983; Gorochov, 1995a) consider the authorship of the name Conocephalidae to be an earlier one and attribute it to Kirby and Spense (1826); yet I could find no family-group name derived from *Conocephalus* in the cited book, but only the generic name *Conocephalus* and the same name erroneously used in the feminine gender as "*Conocephala*" (Kirby and Spense, 1826: p. 679). The family-group names derived from *Tettigonia* are sometimes assigned to "Stoll, 1788" (Vickery and Kevan, 1983; Gorochov, 1995a); however, the name Tettigoniae Stoll, 1788 was derived not from *Tettigonia* Linnaeus, 1758 but from *Tettigonia* Fabricius, 1775, i.e., it refers to cicadas. In the hierarchical nomenclature the taxon including *Tettigonia*, *Conocephalus*, *Brady-*

porus, *Meconema*, *Phaneroptera*, and *Pseudophyllus* may be designated as Tettigonia/g1, thus avoiding the use of a family-group name. Herein, I also propose a new circumscriptional name Tettigensifera for this taxon (see below).

Besides the circumscriptional and typified nomenclatures, some authors try to develop a new **phylogenetic** (or **cladotypic**) **nomenclature** by which they wish to replace all the existing nomenclatures. However, the currently proposed rules of phylogenetic nomenclature are totally impractical since they allow any author to give arbitrarily any name to any taxon.

An example of such inadequate use of the cladotypic nomenclature is the name for the taxon uniting katydids and crickets and characterized by the initial presence of the tegminal stridulatory apparatus. In this paper, according to the rules of circumscriptional nomenclature, I propose a new circumscriptional name Striduloptera for this taxon (see below). As for the cladotypic nomenclature, Bethoux (2012) proposed the name "Grylloptera" with the authorship "Haeckel, 1896" and a new definition which he considered to be the first phylogenetic definition of the name "Grylloptera." His definition of "Grylloptera Haeckel, 1896" included an apomorphy (the presence of the stridulatory vein) and two cladotypes (*viridissimus* Linnaeus, 1758 [*Gryllus*] and *campestris* Linnaeus, 1758 [*Gryllus*]), with new type specimens designated for each, contrary to the ICZN rules. In fact, however, it was Haeckel who introduced the terms "phylogeny" and "phylogenetic classification" and provided phylogenetic definitions for all his taxa and their names. Within the suborder Grylloptera, Haeckel distinguished families with the typified names Blattida, Mantida, Phasmida, Acridida, Locustida, and Gryllida. Therefore, if we apply the rules of cladotypic nomenclature to the name Grylloptera Haeckel, 1896, the cladotypes of this name will be the type specimens of the type species of the generic names *Blatta*, *Mantis*, *Phasma*, *Acrida*, *Tettigonia* (instead of "*Locusta*"), and *Gryllus*, of which *Blatta* was designated as the priority type (Haeckel, 1896: 710). In the phylogenetic tree (Haeckel, 1896: 711) the suborder Grylloptera with the included taxon Blattariae was shown as a single lineage forming a sister group of the suborder Dermatoptera. The holophyly of the suborder Grylloptera was not substantiated in the text of Haeckel (1896: 700, 701); but the holophyly of the taxon called "Grylloptera" by Bethoux was not substantiated, either: "should gryllacrididaeans and their kin be demonstrated to have derived from a Grylloptera and then lost the file, they would de facto belong to the Grylloptera, without need for nomenclatural emendation" (Bethoux, 2012: 56). Here, as in all the other cases of application of "phylogenetic" or "cladotypic" nomenclature, the new definition of an old name cannot be more phylogenetic than the original one, for the reason that since Darwin's time all biologists have built classifications to reflect their views of phylogeny; and even before that, since Linnaeus' time, they had built classifications to reflect the "natural system," essentially an early concept of phylogeny. Thus, the name Grylloptera Haeckel, 1896 has nothing to do with the taxon in question; instead, it is a junior circumscriptional synonym of Orthoptera Olivier, 1789 (see below).

The Names Orthoptera, Saltatoria, and Orchesopia

The taxon uniting katydids, crickets, grasshoppers, and related groups has neither a traditional common name nor a generally accepted Latin name.

Many authors consider this taxon as an order with the name "Orthoptera." The name Orthoptera Olivier, 1789 was initially proposed for the order that included the genera *Blatta*, *Gryllus*, *Mantis*, *Truxalis*, *Acrydium*, and *Tridactylus* (Olivier, 1789), which corresponds to the taxa Neoblattariae, Raptoriae, Spectra, and Saltatoria combined. The circumscriptional synonyms of the name Orthoptera are Euorthoptera Dominique, 1893 and Grylloptera Haeckel, 1896 (Dominique, 1893; Haeckel, 1896). Later, different authors have assigned the name Orthoptera to order-rank taxa widely varying in composition, i.e., they have used this non-typified name as a rank-based one without designating a type. However, the use of non-typified names as rank-based ones is not expedient (Kluge, 1996, 1999). The smallest taxon that has been referred to by the name Orthoptera is Caelifera (Vickery and Kevan, 1983), and the largest one is the taxon comprising all the Hexapoda except Arthroidignatha and Metabola (Gerstaecker, 1863). Handlirsch (1903) was the first to use the name Orthoptera for Saltatoria; later, however, the same author used the name Orthoptera in the meaning close to the original one, and used the name Saltatoria for the taxon we are dealing with herein (Handlirsch, 1925).

The name Saltatoria Latreille, 1817 is generally accepted. Its original circumscription fits the taxon for which it is currently used; therefore, the name should be regarded as correct even though it has been preoccupied (Kluge, 2010a).

Names of large taxa included in Saltatoria

<table>
<tr><th>Typified rank-free names</th><th>Gryllus/fg (incl. <i>Tettigonia</i>)</th><th>Tridactylus/fg1</th><th>Acrida/fg (incl. <i>Tetrix</i>)</th></tr>
<tr><td rowspan="2">Circumscriptional names</td><td colspan="2">Digastria = Diplogastera Graber, 1875
= Ensifera Chopard, 1920</td><td></td></tr>
<tr><td>Dolichocera Bey-Bienko, 1964</td><td colspan="2">Metorthoptera Crampton, 1927
= Caelifera Ander, 1936
= Brachycera Bey-Bienko, 1964
(non Brachycera Zetterstedt, 1842)</td></tr>
</table>

The senior name Orchesopia Rafinesque, 1815 corresponds to the same taxon by its original circumscription. It was probably derived from the Greek ὀρχηστής *dancer* (the same root occurs in *orchestra*). This is the preferred name for the taxon in question but it has almost never been used until recently.

The junior circumscriptional synonyms of Orchesopia Rafinesque, 1815 and Saltatoria Latreille, 1817 are the names Salientia Claus, 1868 (non Salientia Laurenti, 1768), Orthopterida Pearce, 1936, and Orthopteroida Kevan et Knipper, 1961.

The Names Ensifera, Caelifera, Dolichocera, and Brachycera

The two subordinate taxa within Saltatoria are commonly named Ensifera Chopard, 1920 and Caelifera Ander, 1936. The names Dolichocera Bey-Bienko, 1964 and Brachycera Bey-Bienko, 1964 are regarded as junior synonyms of Ensifera and Caelifera, respectively (Bey-Bienko, 1964). However, the name Ensifera Chopard, 1920 was originally introduced for the taxon that comprised, among other groups, also pygmy mole crickets as the subfamily Tridactylinae (Chopard, 1920); this name is a junior circumscriptional synonym of Digastria (or Diplogastera) Graber, 1875. The name Caelifera Ander, 1936 was originally introduced for the taxon that also included pygmy mole crickets as the superfamily Tridactyloidea, while the alternative taxon was referred to as “Ensifera.” This usage of the name Ensifera is at variance with the principles of circumscriptional nomenclature: according to the original circumscriptions of the names Ensifera and Caelifera, pygmy mole crickets (Tridactylus/fg1) would belong to both Ensifera and Caelifera, which is impossible within the same classification.

Bey-Bienko (1964) introduced new names Dolichocera and Brachycera and indicated the names Ensifera and Caelifera as their respective synonyms. Since he used the same classification as Ander (1936), the name Brachycera is indeed a circumscriptional synonym of Caelifera, while the name Dolichocera is not a circumscriptional synonym of Ensifera (see table).

Thus, if we follow the classification in which pygmy mole crickets belong to Caelifera, the valid circumscriptional names of the taxa in question will be Dolichocera Bey-Bienko, 1964 and Caelifera Ander, 1936.

The name Metorthoptera Crampton, 1927 is a senior circumscriptional synonym of Caelifera because the taxon named Metorthoptera originally included pygmy mole crickets as the family Tridactylidae. Of the two valid circumscriptional names Metorthoptera and Caelifera, the latter is to be preferred since it is widely used in the literature while the name Metorthoptera is little known. The junior circumscriptional synonym Brachycera Bey-Bienko, 1964 should not be used as a valid name since its senior homonym Brachycera Zetterstedt, 1842 is broadly used as a valid name of a taxon within Diptera.

APPROACHES TO PHYLOGENETIC RECONSTRUCTION

The only valid approaches to understanding phylogeny are traditional systematics and cladoendesis as its improved variant; the alternative matrix-based methods make no scientific sense (Kluge, 2000, 2012a).

Some authors believe that in order to reconstruct phylogeny it is sufficient to build a dendrogram by applying a certain arbitrary formula to the taxon/character matrix with arbitrarily selected characters. In the course of compiling such a matrix, all the characters appear to be formulated by the dialectic principle and, as a result, are stripped of their original phylogenetic meaning. The matrix is then used to build the most “parsimonious” tree, in spite of the fact that Darwin’s theory, which these authors accept, disclaims the possibility of parsimony in evolution

(Kluge, 2000, 2004a). Besides, an arbitrarily selected species is used by these authors as an "outgroup."

In reality, however, the outgroup-based approach to determining character polarity would make sense only if the outgroup comprised not any particular taxon but all the living organisms outside the phylogenetic lineage being analyzed. In this case, the apomorphic state of a given character would be supported by its absence in the outgroup and by the presence of the alternative plesiomorphic character in some representatives of the outgroup. This approach is based on the assumption of unique origin of the character in question. By contrast, if some arbitrarily selected taxon is taken as an outgroup, the absence of a given character in that taxon gives no indication of its polarity and such an approach to determining character polarity is not based on any scientific assumption.

Relying solely on the matrix method, Gwinne (1995) and Desutter-Grandcolas (2003) computed "parsimonious" trees of Dolichocera based on an arbitrary set of morphological characters in which, for instance, such a simple character as "forecoxa longer than broad" and such a complex one as the presence of the tibial tympanal organ were given equal significance. The resulting trees were different, but both the cited authors concluded that the tibial tympanal apparatus and the tegminal stridulatory apparatus must have appeared independently in different groups of Dolichocera. Their "outgroup" comprised only Phasmatodea and Acrididae, in which such artificial characters as the proportions of the fore coxa happened to match some taxa within Dolichocera.

If instead we consider all the living organisms outside the Dolichocera as the outgroup, it becomes evident that the tibial tympanal apparatus and the tegminal stridulatory apparatus do not occur anywhere in the whole outgroup; therefore they are autapomorphies which have appeared only once within Dolichocera.

Numerous recent publications are devoted to reconstruction of phylogenies based on molecular data. Since molecular trees are also computed according to the "parsimony" principle with arbitrary "outgroups," they cannot be considered phylogenetic, either. They are mere dendrograms reflecting, to a certain extent, similarities in individual genes or gene sets. Some branches of such molecular trees may correspond to actual phylogenetic lineages, in the same manner as some taxa formally established on the basis of morphological characters may eventually prove to be holophyletic. Flook and co-authors (1999) analyzed ribosomal and mitochondrial DNA sequences and built a dendrogram in which Grylloidea were opposed to all the other Dolichocera. Jost and Shaw (2006) proposed a different dendrogram, also based on ribosomal DNA, in which Caelifera did not form a single branch while Grylloidea were consecutively grouped with Schizodactylidae, Rhaphidophoridae, and Tettigoniidae. These authors did not propose any explanation for the discrepancy between their results and the conclusions of Flook and co-authors (1999). Legendre and co-authors (2010) used the same data to produce another tree, in which Caelifera was a paraphyletic group and Rhaphidophoridae was opposed to the rest of Dolichocera. Fenn and co-authors (2008) built a separate "phylogeny" of Saltatoria based solely on mitochondrial DNA sequences and pointed to a specific trait of the transfer RNA as a possible autapomorphy of Caelifera; this trait may be useful for true phylogenetic analysis.

THE TAXONOMIC POSITION OF SALTATORIA

Earlier, saltatorians used to be classified within Polyneoptera Martynov, 1923. Since the taxon Polyneoptera does not have a single autapomorphy and its status is obscure (Kluge, 2012b), I suggest that two holophyletic taxa should be considered instead of it, namely Idioprothoraca Kluge, 2012 and Rhipineoptera Kluge, 2012. The first taxon unites webspinners (Embioptera) and grylloblattids (Notoptera) and is characterized by a specific modification of the prothorax, two-segmented cerci at least in the first instar, and primitively homonomous wings. The taxon Rhipineoptera is characterized by the presence of the anal fan in the hind wing, i.e., the character which used to be erroneously attributed to all the Polyneoptera. Within Rhipineoptera, saltatorians belong to the taxon Tegminoptera Kluge, 2013, which approximately corresponds to the taxon named Dermaptera De Geer, 1773 and Ulonata Fabricius, 1775 but, unlike it, includes termites (Isoptera) that have secondarily lost the characters of this taxon. The taxon Tegminoptera comprises the subordinate taxa Pandictyoptera Crampton, 1917 (cockroaches, termites, and mantids), Dermatoptera Burmeister, 1838 (earwigs), Spectra Latreille, 1802 (phasmids), and Saltatoria. The phylogenetic relations between these four taxa remain obscure; none of the variants proposed has been supported by reliable apomorphies.

The taxonomic position of Saltatoria among the winged insects can be described as follows (Kluge, 2000, 2010a, 2012b, 2013); the abbreviation "nom. hier." designates the hierarchical typified name.

1. Pterygota Gegenbaur, 1878; nom. hier.: Scarabaeus/fg5
1.1. Ephemeroptera Hyatt et Arms, 1890; nom. hier.: Ephemera/fg1
1.2. Metapterygota Börner, 1909; nom. hier.: Scarabaeus/fg6
1.2.1. Odonata Fabricius, 1793; nom. hier.: Libellula/fg1
1.2.2. Neoptera Martynov, 1923; nom. hier.: Scarabaeus/fg7
1.2.2.1. Idioprothoraca Kluge, 2012; nom. hier.: Embia/fg1
1.2.2.1.1. Embioptera Lameere, 1900; nom. hier.: Embia/fg2
1.2.2.1.2. Notoptera Crampton, 1915; nom. hier.: Grylloblatta/fg1
1.2.2.2. Rhipineoptera Kluge, 2012; nom. hier.: Gryllus/f1=Forficula/g1
1.2.2.2.1. Plecoptera Burmeister, 1839; nom. hier.: Perla/fg1
1.2.2.2.2. Tegminoptera Kluge, 2013; nom. hier.: Gryllus/f2=Forficula/g2
1.2.2.2.2.1. Pandictyoptera Crampton, 1917; nom. hier.: Mantis/f1=Blatta/g1
1.2.2.2.2.2. Dermatoptera Burmeister, 1838; nom. hier.: Forficula/f1=g3
1.2.2.2.2.3. Spectra Latreille, 1802; nom. hier.: Phasma/fg1
1.2.2.2.2.4. Orchesopia Rafinesque, 1815, or Saltatoria Latreille, 1817; nom. hier.: Gryllus/f3=g1
1.2.2.3. Eumetabola Hennig, 1953; nom. hier.: Scarabaeus/fg8
1.2.2.3.1. Parametabola Crampton, 1938; nom. hier.: Cimex/f1=Cicada/g1
1.2.2.3.2. Metabola Burmeister, 1832; nom. hier.: Scarabaeus/fg9

THE STATUS AND AUTAPOMORPHIES OF SALTATORIA

The Background

Despite obvious similarity between katydids, crickets, and grasshoppers, their placement in one taxon has long been a matter of dispute. The oldest names of this taxon are dated by only 1815 and 1817 (see above), whereas many other insect taxa were established much earlier. The holophyly of the taxon Saltatoria has been contested by the leading entomologists at least until the 1980s.

G.C. Crampton, who made a great contribution to the development of insect phylogeny, refused to consider Saltatoria a natural taxon: "The fact that the 'Acridiidae', Gryllidae and 'Locustidae' are all saltatorial should have no great weight, for on this basis, we would have to group together the flea-beetles, Psyllidae, and any other forms which happened to have developed the power of leaping" (Crampton, 1915: 345).

Chopard (1920) established the artificial taxon Ensifera (see above) and treated it as one of the four subordinate taxa within the so-called "Orthoptera"; he arranged these taxa in such a way that representatives of Saltatoria were not even placed together: (1) "Dictyoptera" (i.e., Notoptera + Oothecaria); (2) Ensifera; (3) Phasmodea; (4) "Locustodea" (i.e., Acrida/fg).

Handlirsch (1925) and Beier (1969) accepted the order Saltatoria (or Saltatoptera Beier, 1955) as a taxon distinct from phasmids, earwigs, cockroaches, and mantids but including grylloblattids (Notoptera).

Sharov (1968) formally accepted the taxon Saltatoria (under the name "Orthoptera") but considered it paraphyletic because he regarded phasmids as a sister group of Caelifera (Sharov, 1968: fig. 10).

In the different variants of Hennig's phylogenetic classification, the taxon Saltatoria was either present (Hennig, 1962) or absent; in the latter case "Ensifera" (i.e., Dolichocera) and Caelifera had the same status as phasmids within "Orthopteria" (non Orthopteria Rafinesque, 1815) or "Orthopteroidea" (non Orthopteroidea Handlirsch, 1903) (Hennig, 1953, 1969, 1981).

So far, the authors who accept Saltatoria as a holophyletic taxon have not provided clear arguments in support of their view. Hennig, who introduced the term "apomorphy," doubted the holophyly of Saltatoria and therefore mentioned no apomorphies for this group (see above). Boudreaux (1979) indicated only two apomorphies ("advanced features"): (1) "an expanded pronotum" and (2) "elongate hind legs fitted for leaping." The same definitions were repeated by some other authors as well. These two characters are indeed inherent in the common ancestor of Saltatoria and are therefore apomorphies of the taxon, but in this particular wording they are clearly not sufficient to distinguish Saltatoria from many other insects.

In the widely cited monograph of Grimaldi and Engel (2005), the autapomorphies of Saltatoria included the same two characters: (1) "A cryptopleuron, developed from the lateral extension of the pronotum over the pleural sclerites and desclerotization of the latter, is typical of Orthoptera, though this feature is lost in Proscopiidae," (2) "the possession of saltatorial (i.e., jumping) hind legs, with straightening of the femur-tibia articulation for maximal leg extension, and a thick femur packed with muscles," and also some "additional defining features of the order": (3) "the hind tibia with paired, longitudinal rows of teeth or spines on the dorsal surface," (4) "a horizontal division of the prothoracic spiracle," (5) "wings inclined over the abdomen during rest," and (6) "a reversal in the orientation of nymphal wings during later instars."

In reality, however, the first of these characters is not lost in Proscopiidae; judging by the specimens of *Apioscelis bulbosa* (Scudder, 1869) from Peru examined by me, their cryptopleurites are merely fused with the pronotum; similar fusion can be found in many other representatives of Saltatoria (Gorochov, 1995a). Besides Saltatoria, more or less pronounced cryptopleurites are present in some other insects, in particular Idioprothoraca (Kluge, 2012b: figs. 1, 2, 4) and Coleoptera.

The "prothoracic spiracle" in character (4) actually refers to the stenothoracic, i.e., anterior thoracic spiracle, true prothoracic spiracles being absent in insects; what is meant here is the bridge separating the tracheal openings, which are present in the number of two or more in the stenothoracic spiracle of Saltatoria (Gorochov, 1995a). In fact, modification of the stenothoracic spiracle is related to the development of the tibial tympanal hearing organs and is typical of Striduloptera within Acoustopoda within Dolichocera, rather than of Saltatoria as a whole (see the section *Transformations of Sound Communication in Dolichocera* below).

Character (5) does not seem to be an autapomorphy of Saltatoria, either, if we assume that the enveloping mode of wing folding, typical of Stratensifera and Mesensifera (see below), is initial for Saltatoria.

In the collective monograph *History of Insects*, the following characters were named by Gorochov and Rasnitsyn (2002) as apomorphies of Saltatoria ("Orthoptera"): (1) a hypognathous head; (2) saltatorial hind legs; (3) hind tibiae dorsally bearing two regular rows of robust spines; (4) fore wings folding longitudinally, with their anterior parts freely hanging on the body sides; (5) the anterior branch of *2A* in the hind wing without a bundle of branches; (6) a simple *CuP* in both wings; (7) the inversed nymphal protoptera. In reality, however, character (1) is initial for arthropods as a whole but the head position has changed from hypognathous to prognathous and vice versa many times in many taxa including Saltatoria; judging by the stable absence of the gula, the hypognathous position is initial for Saltatoria. Character (4) was considered above. Character (5) is in fact a plesiomorphy and differentiates Saltatoria only from phasmids (Spectra), whose autapomorphy is the specific vein branching pattern in the anterior part of the anal fan. Character (6) is shared with most insects; it can differentiate Saltatoria only from the extinct taxon Titanoptera Sharov, 1968.

Although the morphological details typical of the common ancestor of Saltatoria (the saltatorial hind legs with two rows of spines on the tibia, etc.) have been described in detail in the literature, it is still not clear from the above diagnoses, as well as from the other published diagnoses of Saltatoria, which characters are invariably retained in all the representatives of Saltatoria and which are initial for the taxon but have been lost in some of its representatives. Therefore, the available diagnoses of Saltatoria do not allow one to prove the holophyly of this taxon or outline its boundaries.

Autapomorphies Supporting the Holophyly of Saltatoria

The diagnosis of Saltatoria rejecting the earlier assumptions about inclusion of grylloblattids, phasmids, and other insects in this phylogenetic lineage comprises, among other features, two autapomorphies: the peculiar specialization of the hind legs and the position of the protoptera.

1. Stagnofemoral leaping specialization of the hind legs with a reduced trochanter. I propose a special term "stagnofemoral" (i.e., leading to immobilization of the femur during the leap) to differentiate this particular specialization from other saltatorial modifications of the hind legs and to avoid misunderstandings similar to the one showed by Crampton (1915) in the above quotation. Stagnofemoral specialization of the hind leg includes: (1) shortening of the trochanter to a narrow welt between the coxa and the femur (Fig. 3); this welt is often concealed inside the articular fossa, so that the femur appears to be articulated directly to the coxa; (2) elongation of the femur, thickening of its proximal portion, and enlargement of its internal muscle abducing the tibia; (3) the presence of two longitudinal rows of hypoderm-containing spines or spurs on the outer surface of the tibia; (4) the inner side of the tibia usually bearing 4 or 6 apical hypoderm-containing spurs (unlike 2 spurs on the fore and middle legs and on the legs of most insects). The leap is powered by only one muscle, namely the tibial abductor: before the leap the femur apex is directed posteriorly and the tibia is pressed against the femur; during the leap the tibia turns by 180° and extends posteriorly in line with the femur while the femur itself remains immobile. In some Saltatoria (Eumastacidae, Gryllidae) the immobile femora are directed laterally rather than posteriorly during the leap.

Unlike the hind legs, the fore and middle legs retain their usual morphology: the trochanter is fairly well developed (Fig. 2); the femur has no proximal thickening while the adductor and abductor of the tibia are equally developed; the tibial spines and/or spurs do not form two regular rows on the outer surface. The fore and middle tibiae, unlike the hind ones, sometimes bear two regular longitudinal rows of hypoderm-containing spines and/or spurs on the inner surface (Fig. 1).

The leaping ability is weak or lost in some saltatorians; in such cases the above differences between the different pairs of legs may be leveled to a certain degree or lost, but the difference between the hind trochanters and those of the fore and middle legs is invariably retained (Figs. 2, 3). The shape of the trochanters reliably differentiates all the Saltatoria from representatives of other taxa.

2. The inversed position of protoptera in the penultimonymph and ultimonymph. The terms "ultimonymph" and "penultimonymph" (or "ultimolarva" and "penultimolarva") refer to the nymphs (or larvae) of the last two instars; the term "protopteron" designates the external outgrowth on the thorax of the nymph (larva) which is a precursor of the imaginal wing. These terms were introduced in my papers on the insect metamorphosis, where they were needed for description of the intricate molting processes (Kluge, 2005, 2010b). The penultimonymph and ultimonymph of Saltatoria are sometimes referred to as "protonymph" and "deuteronymph," respectively, but this is inconsistent with the use of the term "nymph" as applied to most insects (in which the protoptera are not inversed in all the nymphal instars).

In the representatives of Saltatoria which possess either functional wings or stridulatory organs derived from wings, or nonfunctional but still articulated wing vestiges at the adult stage, the protoptera are inversed in the ultimonymph and the penultimonymph while in the preceding instar they overlap the thoracic pleurites with their apices directed ventrally. This character is absent only in those representatives of Saltatoria whose imaginal wings have been completely lost or reduced to immobile outgrowths of the notum (i.e., retain the structure of the larval protoptera).

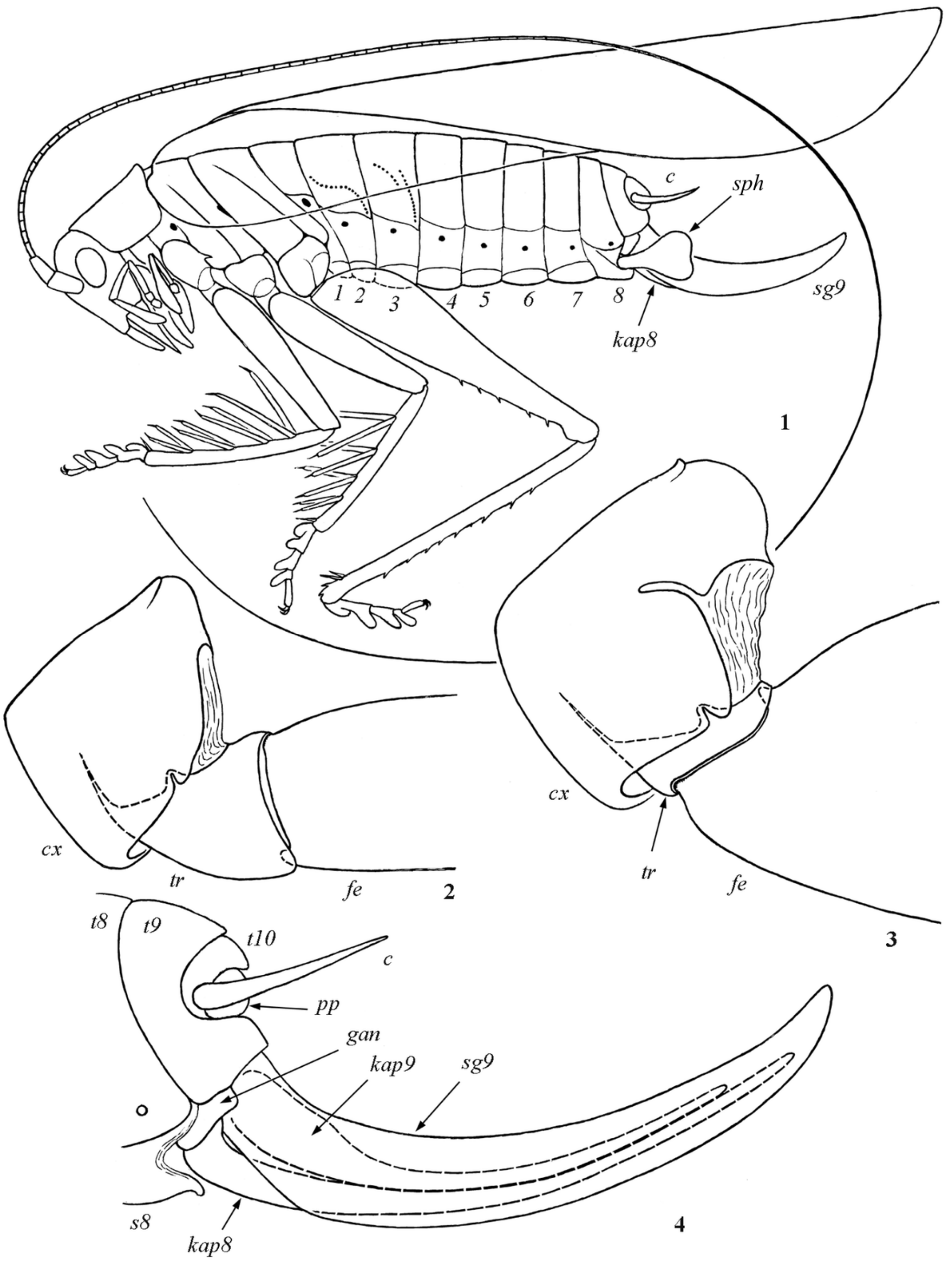
Apart from Saltatoria, the inversed position of the protoptera is known only in Odonata, in which, unlike in Saltatoria, protoptera are inversed since they appear.

CLASSIFICATION OF SALTATORIA AND THE BOUNDARIES OF THE TAXON DOLICHOCERA

All the Saltatoria are traditionally subdivided into two subordinate taxa: Dolichocera and Caelifera (the names were discussed above). This division appears perfectly justified when applied to the recent representatives of the group, because the holophyly of either taxon can be proved by unique apomorphies in its ovipositor morphology (see below).

The extinct representatives of Saltatoria belonging to the families Oedishiidae Handlirsch, 1906, Pruvostitidae Zalessky, 1929, Tcholmansvissiidae Zalessky, 1934, Proparagryllacrididae Riek, 1956, and Permelcanidae Sharov, 1962 are commonly placed in the taxon named "Ensifera" (whose valid circumscriptional name is Dolichocera; see above). However, the characters of these taxa do not correspond to the general characteristic of Saltatoria based on the recent representatives. In all the recent Saltatoria at least the 1st and 2nd tarsomeres are immovably fused; if the boundary between them is retained the 1st tarsomere is usually relatively short. In contrast with all the recent taxa, the tarsi of some fossil forms retain all the five distinct segments, the 1st tarsomere being relatively long. Such tarsi have been described for the Permian species with the original names *Metoedischia longipes* Martynov, 1940, *Uraloedischia permiensis* Sharov, 1968, *Jubilaeus beybienkoi* Sharov, 1968, *Gryllacrimima perfecta* Sharov, 1968, *Permelcana kukalovae* Sharov, 1968, and also for the fossils probably belonging to Silvoedischiinae Gorochov, 1987 (Sharov, 1968; Gorochov, 1995a).

The placement of these fossil saltatorians into Dolichocera ("Ensifera") is based on the presence of long setiform antennae and a saber-shaped ovipositor. The setiform antennae are plesiomorphic; besides Dolichocera, antennae of this type occur in Triplura, larvae of Ephemeroptera, larvae and adults of Plecoptera, Palaeoblattariae, and Neoblattariae, and seem to be initial for Amyocerata (Kluge, 2012a).



Figs. 1–4. Stratensifera-Gryllacridinae: *Hyperbaenus* sp., fertilized female with folded wings (fore wing venation and hind wings not shown): (1) total view; (2) coxa, trochanter, and base of femur of the middle leg; (3) the same, of the hind leg; (4) ovipositor (valves concealed between the 3rd valves shown in dashed lines): *1–8*, abdominal segments (uromeres); *c*, cercus; *cx*, coxa; *fe*, femur; *gan*, gonangulum; *kap8*, *kap9*, kinetapophyses of VIII and IX pairs (the 1st and 2nd ovipositor valves); *pp*, paraproct; *s8*, urosternite VIII; *sg9*, styliger of IX pair (the 3rd ovipositor valve); *sph*, spermatophore; *t8*, *t9*, *t10*, urotergites VIII–X; *tr*, trochanter.

The ovipositors of the fossil saltatorians with five-segmented tarsi are generally considered to be similar to the ovipositors of Dolichocera, since they consist of long closed valves and in this respect clearly differ from those of Caelifera. However, it is impossible to determine by the fossil remnants whether these insects possessed the secondary olistheter which constitutes an autapomorphy of Dolichocera (see below). It is quite possible that the ovipositors of these primitive Saltatoria had the same morphology as the ovipositors of other insects (such as Odonata, Hemelytrata, and Hymenoptera), i.e., they consisted of the primary ovipositor formed by two pairs of coupled valves and movable relative to the third pair of valves, which form the sheath (see below). I have examined the type specimens of *Metoedischia longipes* and *Gryllacrimima perfecta* deposited at the Paleontological Institute of the Russian Academy of Sciences but could not solve this problem.

The modification of the tarsus typical of the recent Saltatoria can be found in many other insects; therefore it must have appeared more than once in the evolution of insects. However, the fact that this modification is present in all the recent Saltatoria without exception suggests its origin in their common ancestor. Based on this assumption, all the Saltatoria can be subdivided into the extinct plesiomorphon Permorchesopia **taxon n.** characterized by the plesiomorphic retention of the primitive five-segmented tarsus with the long 1st segment, and the holophyletic taxon Neorchesopia **taxon n.** characterized by immobile fusion of the 1st and 2nd tarsomeres. In its turn, the taxon Neorchesopia is subdivided into Dolichocera and Caelifera.

Permorchesopia appeared in the Paleozoic and existed until the Paleogene. Judging by the published photograph (Zompro, 2005: fig. 4), *Ensiferophasma velociraptor* Zompro, 2005, described from the Baltic amber and placed in Mantophasmatodea, is in fact a young larva of Permorchesopia (Kluge, 2013).

EVOLUTION OF THE OVIPOSITOR
(Figs. 4–16)

The Abdominal Appendages and Ovipositor of Insects

Each of abdominal segments I–IX of Hexapoda initially bears two pairs of ventral appendages movably articulated to the posterior margin of the sternite (Fig. 16). The lateral appendages are commonly referred to as styli while the median ones are named differently depending on their structure and specialization on particular segments: "retractile vesicles," "coxal appendages," "subcoxal appendages," "gonapophyses," "valves," and "pseudoparameres." The numbering of these appendages depends on their names: for example, the appendages called "gonapophyses" or "ovipositor valves" are numbered starting with abdominal segment VIII, i.e., gonapophyses I occur on segment VIII, and gonapophyses II, on segment IX. I suggest that all these serially homologous appendages should be termed **kinetapophyses** (in the singular, kinetapophysis) and numbered by the abdominal segments (uromeres) to which they belong, i.e., from I to IX.

The kinetapophyses of the pregenital abdominal segments (I–VII) are usually represented by retractile vesicles: they are small, membranous, and can be inverted and retracted into the body. Such vesicles are present on all or some of the pregenital segments in many apterous insects: Triplura (Zygentoma and Microcryphia) and Diplura (Rhabdura, Prodicellura, and Dicellurata). In many Microcoryphia, some abdominal segments have two pairs of kinetapophyses in the form of retractile vesicles, the more lateral pair being a secondary modification. In Rhabdura and Prodicellura kinetapophyses of the first pair are sclerotized and non-retractable; therefore they cannot be called retractile vesicles.

The kinetapophyses of the genital abdominal segments (VIII and IX) of the females are long and sclerotized ovipositor valves that cannot be inverted or retracted. Some authors use the term "gonapophyses" exclusively for these structures, but this does not exactly agree with its original meaning. The term "gonapophyses" was used for the first time in a morphological description of the cockroach *Blatta orientalis*, where it referred to all the three pairs of ovipositor valves (Huxley, 1878: 349). The same meaning of the term was recorded in later morphological reviews. Snodgrass (1909: 575) gave the following definition: "Gonapophyses (Gon.)—The chitinous processes of the eighth and ninth abdominal sterna which form the ovipositor or sting. Two arise from the eighth segment and four from the ninth. Gonapophyses Huxley (1878)." Thus, the term "gonapophyses" was originally applied not only to the kinetapophyses of abdominal segments VIII and IX but also to the styligers of segment IX (see below).

The kinetapophyses of the genital abdominal segment (i.e., uromere IX) of the males of some Triplura (Zygentoma and Microcoryphia) are non-retractable structures termed pseudoparameres; they may resemble the ovipositor valves of the female (in Microcoryphia) or retractile vesicles on the pregenital abdominal segments (in some Zygentoma), or they may have some specific shape.

In the initial variant, the muscles moving the styli and kinetapophyses extend to these appendages from the sternite of the same uromere. In some cases, the posterior portion of the sternite including the attachment sites of these muscles becomes morphologically separated and/or delimited by a suture from the rest of the sternite. This portion is often referred to as "coxites," which reflects the idea of its origin from the reduced abdominal legs. However, these "coxites" have nothing in common with legs in terms of their morphology, and their origin from legs is doubtful. Therefore, this portion of the uromere should be designated by the neutral term **styliger.** This term is commonly used for the corresponding part of the male genital segment of mayflies (Ephemeroptera), whose styli have been transformed into the genital appendages, or gonostyli. If the styliger exists as an unpaired plate to which a pair of styli is articulated, it may be referred to as a **bistyliger**; if the segment has a pair of distinct styligers, each bearing one stylus (on the pregenital abdominal segments of Microcoryphia and partly Zygentoma, and on the genital segments of various insects), each styliger may be called a **unistyliger** (Kluge and Novikova, 2011). The portion of the sternite lying in front of the styliger or the pair of unistyligers is often called the "sternite," which implies that the styliger is not part of the sternite proper but a derivative of the legs. Since this assumption is dubious, this portion of the segment may be designated by the neutral term **prestyliger.**

Thus, the urosternite may be either entire (the pregenital segments of part of Zygentoma and all the Pterygota, and all abdominal segments I–IX of Diplura), or divided by the transverse **styligeral suture** into the prestyliger and styliger (bistyliger) or into the prestyliger and a pair of styligers (unistyligers).

The primary ovipositor of insects consists of two pairs of valves: kinetapophyses VIII (the first pair of valves) and kinetapophyses IX (the second pair of valves); on each side (left and right), kinetapophysis VIII is coupled with kinetapophysis IX by a sliding interlock, or olistheter, formed by a groove (aulax) on the dorsal side of the 1st valve and a matching ridge (rhachis) on the ventral side of the 2nd valve. The most primitive ovipositor morphology occurs in all the Triplura, being identical in Zygentoma and Microcoryphea: their styligers IX retain some similarity to the styligers of the preceding abdominal segments, while their primary ovipositor consisting of the coupled 1st and 2nd valves can move relative to the styligers. In pterygotes styligers IX form the 3rd pair of ovipositor valves, which do not usually participate in the functioning of the ovipositor but serve as its sheath: in the resting state the primary ovipositor consisting of two pairs of coupled valves is concealed between the valves of the 3rd pair, and in the active state it is turned downwards and released from the sheath. Such an ovipositor with a sheath is present in the remotely related taxa Odonata, Hemelytrata, and Hymenoptera, which indicates its primitiveness for Pterygota. In Notoptera (which some authors united with Saltatoria; see above) styligers IX do not serve as a sheath but instead move together with the primary ovipositor, so that all the three pairs of valves form the functional part of the ovipositor. In this respect the ovipositor of Notoptera resembles that of Dolichocera; however, it essentially differs from the latter in the mode of coupling between the 3rd and the other valves: in Notoptera the articulation of the kinetapophyses and styligers IX (i.e., the 2nd and 3rd ovipositor valves) has become immobile, whereas in Dolichocera this articulation remains mobile while the valves are coupled by secondary olistheters (see below). In most insects the primary ovipositor has lost its function and has been reduced, down to total disappearance.

The Ovipositor of Saltatoria

In Saltatoria the sliding interlocks between kinetapophyses VIII and IX of the primary ovipositor (i.e., the primary olistheters) are retained, but the mode of interaction of kinetapophyses with styligers IX has changed in opposite directions in Dolichocera and Caelifera. The primary ovipositor of Dolichocera has acquired sliding interlocks (secondary olistheters) with styligers IX, so that the ovipositor can no longer be detached from styligers IX, and all the three pairs of ovipositor valves move together and form a single canal for the egg transfer (see below). By contrast, in Caelifera the primary ovipositor can move away from styligers IX with a greater force and is used for digging, while its function of egg transfer has been lost (see below).

Despite the opposite directions of specialization of ovipositors in Dolichocera and Caelifera, they share common characters in the muscle morphology: there is a powerful paired muscle extending from the base of the 1st valve (kinetapophysis VIII) to the internal ridge on the lateral side of urotergite IX (muscle 3 in Figs. 5 and 13); the other side of the same ridge serves for insertion of the powerful muscle extending from the base of the 3rd ovipositor valve (muscle 9 in the same figures). Since in Dolichocera all the ovipositor valves are coupled by olistheters, these two pairs of muscles work as antagonists; by contrast, in Caelifera the same two pairs of muscles contract simultaneously to move the valves apart (see below).

Morphology and Evolution of the Ovipositor in Dolichocera

Besides the primary olistheter coupling kinetapophyses VIII and IX, the ovipositor of Dolichocera also has a secondary olistheter which couples styliger IX with either kinetapophysis IX or kinetapophysis VIII (Figs. 5–12). The ovipositor of the larvae resembles that of the adults but has no olistheters (Fig. 9). The secondary olistheter can be found in no other insects, and its presence is the autapomorphy of Dolichocera proving the holophyly of this taxon. It is obvious that the secondary olistheter appeared in the common ancestor of Dolichocera and changed its position in the course of subsequent evolution. The initial structure of the secondary olistheter and the directions of its change remain, however, a matter of debate.

I consider the secondary olistheter of Rhaphidophoridae as the most primitive (Figs. 5, 6). In this variant, styligers IX enclose kinetapophyses VIII and IX from the sides (similar to those insects in which styligers IX serve as the ovipositor sheath); the rhachis of the secondary olistheter is a compact protrusion on the inner side of styliger IX coupling with the aulax on the lateral side of kinetapophysis IX. In Stenopelmatidae (including Gryllacridinae), styligers IX also enclose kinetapophyses VIII and IX from the sides and are coupled with kinetapophyses IX (Figs. 4, 7, 8), but the rhachis of the secondary olistheter is shaped not as a compact protrusion but as a long ridge similar to that of the primary olistheter. Stenopelmatidae and Rhaphidophoridae can be united in a taxon with a non-typified circumscriptional name Stratensifera **taxon n.**, characterized by styligers IX coupling with kinetapophyses IX and laterally overlapping kinetapophyses VIII. The name "Stratensifera" (from stratum *layer* and ensifer *sword bearer*) reflects the "layered" structure of the sword-shaped ovipositor caused by overlapping of the 3rd valves. Stratensifera is a plesiomorphon since its paraphyly cannot be excluded. The idea of primitiveness of Stratensifera is consistent with the invariable absence of the tympanal hearing organs and the tegminal stridulatory apparatus, and also with retention of the femoro-abdominal stridulatory apparatus, initial for Saltatoria, in some representatives of this taxon (see below). Besides, Stratensifera should probably include Schizodactylidae, in which the tympanal organs and the tegminal stridulatory apparatus are absent and the ovipositor is reduced.

In Anostostomatidae, styliger IX remains coupled with kinetapophysis IX but does not overlap kinetapophysis VIII laterally; instead, its ventral margin fits into the groove on the dorsal side of kinetapophysis VIII (Figs. 10, 11). For this taxon I propose a non-typified circumscriptional name Mesensifera **taxon n.**, reflecting the ovipositor morphology intermediate between the variants of Stratensifera and Tettigensifera (see below).

In Tettigonia/g1 (erroneously referred to as "Tettigoniidae" or "Tettigonioidea"; see the section *The Names of the Taxa* above), the groove on the dorsal side of kinetapophysis VIII, which had appeared in Mesensifera, has been transformed into the aulax of the secondary olistheter, while the aulax of kinetapophysis IX has disappeared. Thus, the secondary olistheter couples styliger IX with kinetapophysis VIII rather than with kinetapophysis IX (Fig. 12; Cappe de Baillon, 1919: figs. 34–49). For this taxon I propose a non-typified circumscriptional name Tettigensifera **taxon n.** This name is reminiscent of the diagnosis given by Linnaeus to the fifth subordinate taxon within the genus *Gryllus*: "TETTIGONIA. *Cauda ensifera feminis*" (Linnaeus, 1758: 429).

All the three pairs of valves are needed for the functioning of the ovipositors of Stratensifera and Mesensifera, because the antagonistic muscles lowering and raising the ovipositor (muscles 3 and 9 in Fig. 5) are attached to the bases of the 1st and 3rd valves, and these valves are coupled only indirectly, via the 2nd valves. In the ovipositor of Tettigensifera the 1st and 3rd valves are coupled directly, so that the 2nd valves become unnecessary for the functioning of the ovipositor. Further transformation of the ovipositor is observed in Grylloidea, in which the 2nd valves (kinetapophyses IX) have been reduced. For this taxon I propose a non-typified circumscriptional name Gryllensifera **taxon n.**

An alternative hypothesis states that the evolution of the ovipositor proceeded not from Stratensifera via Mesensifera to Tettigensifera but from Mesensifera in two opposite directions, to Stratensifera and to Tettigensifera; it is assumed that the ancient Haglidae had the same ovipositor morphology as in Mesensifera, and they were the ancestors of all the recent Dolichocera (Gorochov, 1995a). It follows from this assumption that the secondary olistheter originated in its most complex variant with the rhachis on styliger IX, the aulax on kinetapophysis IX, and the groove on kinetapophysis VIII; moreover, these three structures were perfectly matched both in cross-section and lengthwise, and the whole construction was simplified in the subsequent evolution. This assumption can be neither proved nor disproved because the ovipositor is reduced in all the known recent Haglidae and its original structure is unknown.

In my opinion, the scenario of evolution from Stratensifera to Tettigensifera is more plausible since it assumes that the most primitive secondary olistheter was the simplest, and in the course of evolution its morphology gradually deviated from the ancestral variant. In the primitive state (in all insects having primary ovipositors, except Dolichocera), styliger IX has no rhachis and its margin does not precisely match any part of the primary ovipositor. In Stratensifera, styliger IX acquired a rhachis matching in cross-section the secondary aulax that appeared on kinetapophysis IX; in Rhaphidophoridae the rhachis is compact and much shorter than the secondary aulax on kinetapophysis IX (Fig. 5). In all the Stratensifera the margins of styliger IX do not match the outlines of the primary ovipositor (Fig. 4). The exact match between the ventral margin of styliger IX and the groove on kinetapophysis VIII appeared only in Mesensifera, Tettigensifera, and Gryllensifera.

The ovipositor morphology of Tettigensifera is more rational than that of Stratensifera, because the coupling of the 1st and 3rd valves is ensured by one pair of olistheters in Tettigensifera and by two pairs in Stratensifera; the primary olistheter is a necessary element of the ovipositor of Stratensifera, whereas in Tettigensifera its significance is lost.

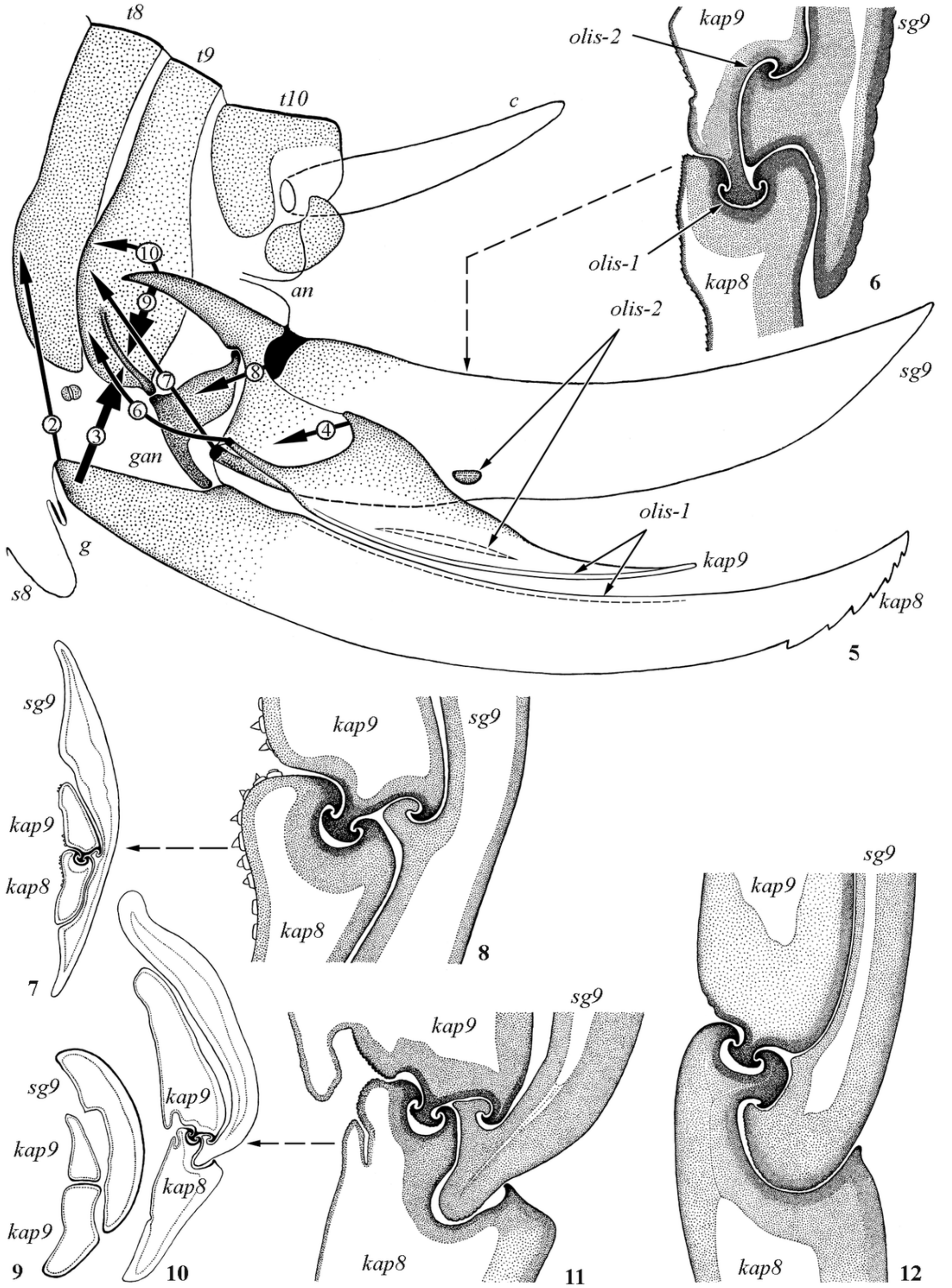
This view of the ovipositor evolution agrees well with the scenario of the evolution of stridulatory and hearing organs considered below: the taxon Acoustopoda, characterized by the emergence of the tibial tympanal organ, is also characterized by the emergence of the groove on kinetapophysis VIII accommodating the margin of styliger IX; the taxon Striduloptera, characterized by the emergence of the tegminal stridulatory apparatus, is also characterized by the establishment of coupling between styliger IX and kinetapophysis VIII and by the loss of coupling between styliger IX and kinetapophysis IX.

Analysis of the ovipositor morphology allows us to completely reject such phylogenetic hypotheses as the uniting of Grylloidea with Rhaphidophoridae into a group opposed to Tettigensifera (Jost and Shaw, 2006): the ovipositor of Gryllensifera with reduced kinetapophyses IX could have originated only from the ovipositor of Tettigensifera but not from that of Rhaphidophoridae in which these kinetapophyses participate in the coupling.

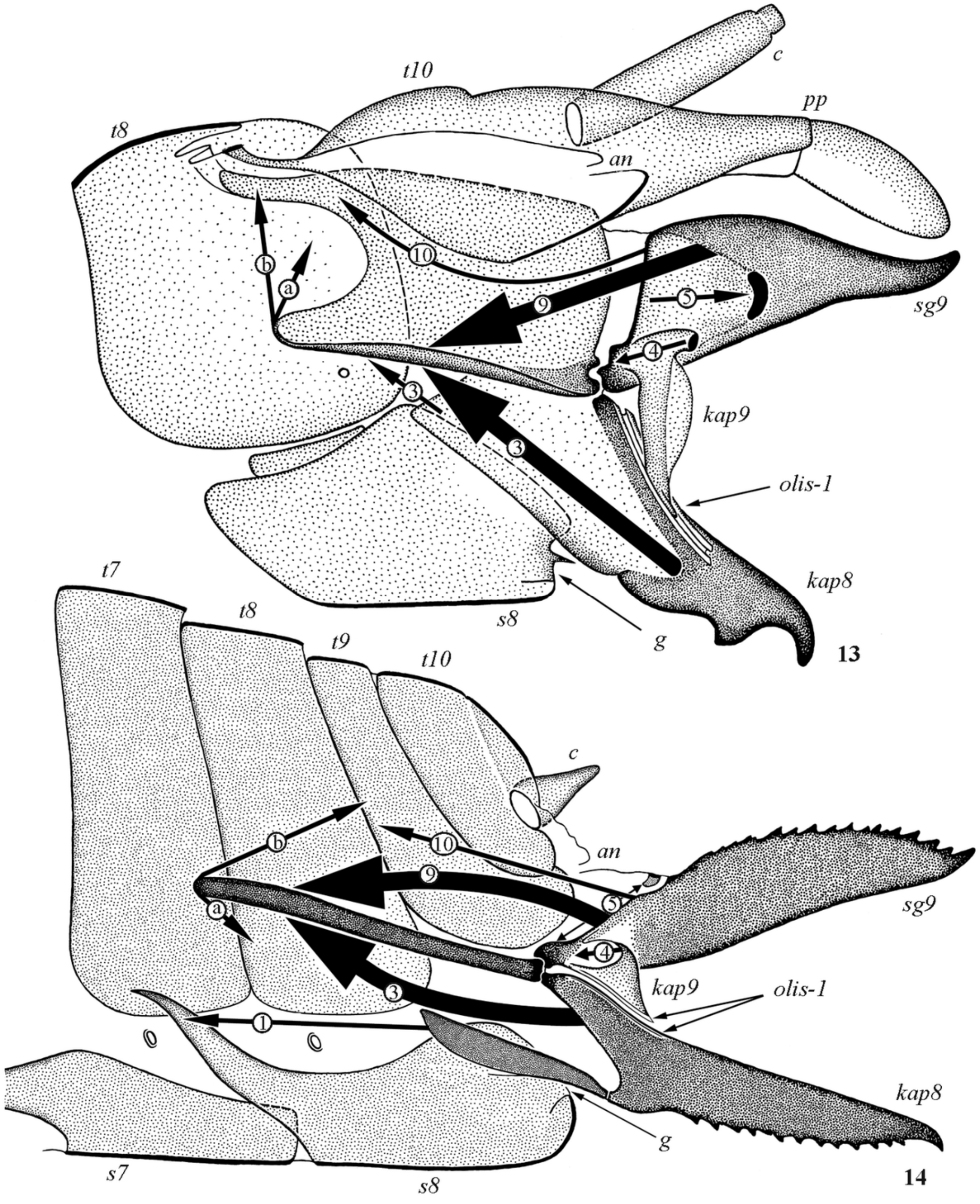
The Ovipositor of Caelifera

Until recently, it has been assumed that the ovipositor of all the Caelifera consists of two pairs of valves used for digging (the 1st and 3rd valves, i.e., kinetapophyses VIII and styligers IX) and a pair of nonfunctional valves between them (the 2nd valves, i.e., kinetapophyses IX), while the bases of the digging valves are always articulated to a pair of long and movable lateral apodemes. Such an interpretation leaves open the following questions: (1) what muscles close the digging valves of the ovipositor, if all the muscles extending from the valves to the lateral apodemes and to the body walls are only capable of drawing them apart, and (2) what are the homologs of the apodemes and the muscles inserted on them. I was able to answer these questions having examined the ovipositor morphology of several species of Caelifera.

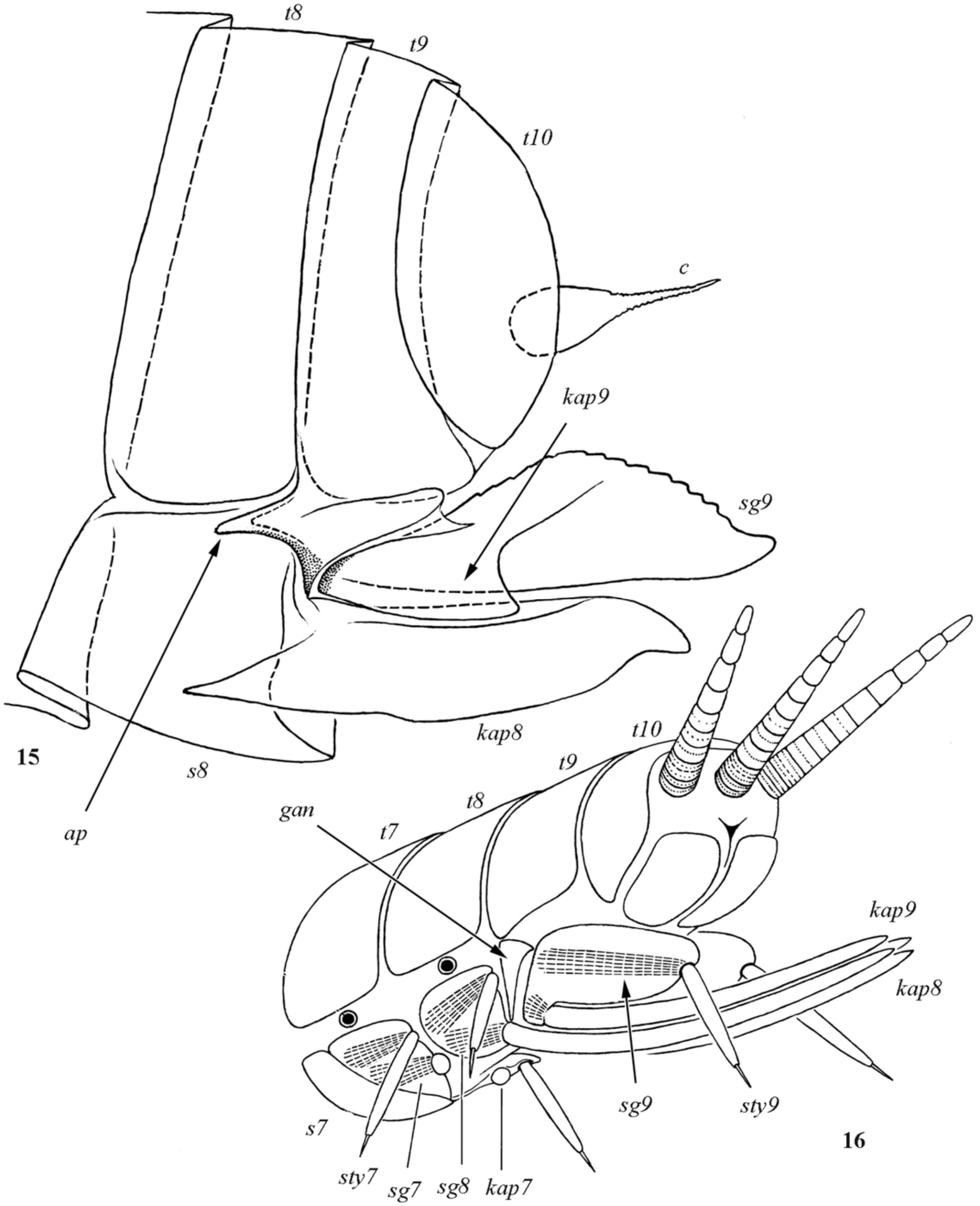
The functions of ovipositor valves in Caelifera. There is an erroneous opinion that the functioning of the digging ovipositor of Caelifera involves only two pairs of valves which can move apart with a great force in the dorso-ventral plane: kinetapophyses VIII form the ventral component of this digging apparatus, and styligers IX form its dorsal component, whereas kinetapophyses IX positioned between them are believed to be reduced and nonfunctional. In this case, since styligers IX and kinetapophyses VIII are articulated to the lateral apodemes at immediately adjacent sites (Fig. 14), all the muscles attached to them would draw the valves apart, and no muscle would be able to close them. Snodgrass assumed that the valves were pulled together by some indirect action: "The closing of the valvulae evidently is produced by muscles of the anterior intervalvula, there being no muscles inserted



Figs. 5–12. Ovipositors of Dolichocera: (5) Rhaphidophoridae gen. sp., median section of ovipositor, median view; ovipositor valves uncoupled and moved apart from their natural position to expose the rhachis of secondary olistheter on 3rd valve (muscles powering the ovipositor are shown as thick arrows with encircled numbers; sections of transverse bridges connecting the paired valves are shown in black); (6–12) cross-sections of right ovipositor valves and enlarged sections through right olistheters: (6) the same ovipositor as in Fig. 5 but with coupled valves (level of cross-section marked with dashed arrow); (7, 8) Stenopelmatidae-Gryllacridinae: *Papuogryllacris* sp.; (9–11) Anostostomatidae: *Cratomelus armatus* Blanchard, 1851: (9) larva; (10, 11) adults; (12) Tettigensifera: Mecopodinae gen. sp. Homologous muscles are designated by identical numbers in Fig. 5 and in Figs. 13, 14. Muscles shown in Fig. 5: 2, 1st valve—urotergite VIII; 3, 1st valve—urotergite IX; 4, 2nd valve—3rd valve; 6, ventral bridge between bases of 2nd valves—urotergite IX; 7, ventral bridge between bases of 3rd valves—urotergite IX; 8, 3rd valve—gonangulum; 9 and 10, 3rd valve—urotergite IX. *an*, anal opening; *g*, genital opening; *olis-1*, rhachis and aulax of primary olistheter; *olis-2*, those of secondary olistheter; other designations as in Figs. 1–4.



Figs. 13, 14. Caelifera: median section of ovipositor, median view (muscles powering the ovipositor are shown as thick arrows with encircled numbers; sections of transverse bridges connecting the paired valves are shown in black): (13) *Ripipteryx* (*Mirhipipteryx*) *peruviana* Saussure, 1896; (14) *Tetrix subulata* (Linnaeus, 1758) (the 1st and 2nd ovipositor valves are uncoupled and moved apart from their natural position). Homologous muscles are designated by identical numbers in Figs. 13, 14 and in Fig. 5. Muscles shown in Figs. 13, 14: 1, 1st valve—urosternite VIII; 3, 1st valve—urotergite IX; 4, 2nd valve—3rd valve; 5, 3rd valve—bridge between 3rd valves; 9 and 10, 3rd valve—urotergite IX. Designations as in Figs. 1–12.



Figs. 15, 16. (15) vestige of ovipositor in larva of *Tetrix subulata* (Linnaeus, 1758) (median section of apical abdominal cuticle, median view); (16) scheme of the apical portion of abdomen and the ovipositor in Amyocerata: *ap*, precursor of lateral apodeme; *kap7*, kinetapophyses VII; *s7*, urosternite VII; *sg7*, *sg8*, styligers VII and VIII; *sty7*, *sty8*, *sty9*, styli of uromeres VII–IX; *t7*, urotergite VII; other designations as in Figs. 1–14.

on the valvulae that directly oppose the opening muscles" (Snodgrass, 1935: 42). The error lies in the fact that in all the drawings of ovipositors of Caelifera, kinetapophyses IX are shown sticking out between styligers IX and kinetapophyses VIII (Walker, 1919: pl. XX, figs. 22–28; Snodgrass, 1935: figs. 17A, B, 18B, 20A, etc.). In fact, the ovipositor valves assume this position only in improperly fixed specimens, whereas in the natural state kinetapophyses VIII and IX are strongly coupled by means of olistheters.

In reality, not two but all the three pairs of valves are the necessary components of the digging ovipositor of Caelifera. Its ventral component is formed not by one pair of kinetapophyses VIII but by the whole primary ovipositor consisting of kinetapophyses VIII and IX coupled together (Figs. 13, 14). The dorso-ventral opening of the valves during digging is the movement inherent in the insect ovipositor. In insects with primitive ovipositors, such as dragonflies, cicadas, and hymenopterans, the same movement (the dorso-ventral parting of the valves) releases the ovipositor proper (the coupled kinetapophyses VIII and IX) from its sheath (styligers IX). The reverse movement, i.e., the closing of the valves, is powered by a pair of muscles that extend from kinetapophyses IX to styligers IX (muscle 4 in Figs. 13 and 14), both in Caelifera and in insects with the primitive ovipositor morphology. Since kinetapophyses IX are coupled with kinetapophyses VIII by the primary olistheters, contraction of this pair of muscles shifts both styligers IX and kinetapophyses VIII.

In Caelifera the ventral margins of kinetapophyses IX are inserted between kinetapophyses VIII; the olistheters are oriented in such a way that the aulax on kinetapophysis VIII opens medially rather than dorsally, while the rhachis on kinetapophysis IX is directed laterally rather than ventrally (Fig. 13), providing a stronger coupling during the dorso-ventral movements of the valves.

Since kinetapophyses VIII and styligers IX in Caelifera are heavily sclerotized and bear digging teeth while kinetapophyses IX are reduced in size, it may seem that the digging apparatus consists only of kinetapophyses VIII and styligers IX. However, its function would be impossible without kinetapophyses IX, their muscles, and a fully developed olistheter.

The ovipositor of *Ripipteryx* and homology of ovipositor parts in Caelifera. Based on examination of *Ripipteryx forceps* Saussure, 1896 (under the name "*R. forcipata*"), Walker (1919) described the ovipositor of Tridactylidae as "… a prominent, shelf-like apodeme (ap 9), extending from the angle between the valvulae along the ventral edge of the ninth tergite and projecting a short distance under the eighth. This ridge is quite similar in relation to the valvulae to the free rod of the Acridoidea, but is a true ninth tergal apodeme, like that of the Gryllidae and Tettigoniidae. It is in this feature that the genitalia of the Tridactylidae differ most from those of the Acridoidea" (Walker, 1919: 288). His drawing of this ovipositor (Walker, 1919: fig. 19) is correct but too small and therefore not exactly clear; the muscles are not shown. Snodgrass (1935) studied a different species, *Ripipteryx biolleyi* Saussure, 1896, and made an opposite conclusion: "The writer, however, finds no tergal connection of the apodemes in *R. biolleyi*, in which the structures appear to be identical with the intervalvular apodemes of Acrididae." His drawings (Snodgrass, 1935: fig. 19) are more detailed but show the following inconsistency: in figure 19C (abdominal segment IX from the left) the tergite of segment IX has exactly the same shape as in Walker's drawing, i.e., with a long ventral margin jutting out into segment VIII, whereas in figure 19E (abdominal tergite IX in ventral view) the ventral margins of this tergite are very short and rounded. Figure 19D shows a free apodeme of an unusual spatulate shape, kinetapophyses VIII articulated to it, and the muscles connecting them, but it is not clear from this drawing where styliger IX is articulated and where its muscles are inserted. This is not clear from the text, either: "The lateral apodemes of the ovipositor of *Ripipteryx* are long spatulate plates arising between bases of the valvulae, but each is more specifically connected with the corresponding ventral valvula, rather than with the dorsal valvula as in Acrididae."

My examination of the ovipositor of *Ripipteryx* (*Mirhipipteryx*) *peruviana* Saussure, 1896 allows me to conclude that the ovipositor morphology should be the same in all these species; the description made by Walker is correct while that made by Snodgrass is not; figure 19C by Snodgrass is correct while his figure 19E is erroneous; figure 19D shows not the whole apodeme but only its ventral layer serving for attachment of kinetapophysis VIII and its muscles.

Thus, the lateral apodemes in *Ripipteryx* are not separated from abdominal tergite IX (Fig. 13). Such an apodeme is a flat internal ridge, i.e., an invagination of the integument along the margin of urotergite IX. The powerful muscle "9" extends from styliger IX to the dorsal side of this internal ridge; the powerful muscle "3" extends from kinetapophysis VIII to the ventral side of the ridge.

In the initial state, the gonangulum is movably articulated at three different points to urotergite IX, kinetapophysis VIII, and styliger IX; in all the Caelifera, the gonangulum is completely fused with the portion of urotergite IX incorporated into the lateral apodeme, and the places of articulation of the gonangulum with kinetapophysis VIII and styliger IX are positioned close together.

All the remaining Caelifera except Tridactyloidea form a holophyletic taxon which may be referred to by the non-typified circumscriptional name Vectocaelifera **taxon n.** (from vectis *lever*, caelum *chisel*, and fero *carry*). In this taxon, the lateral apodemes have been completely detached from urotergite IX and from all the outer body walls and remain connected to them by an elastic membrane only near the articulations with the ovipositor valves (Fig. 14). Each apodeme is a tubular cylindrical ingrowth covered on all sides by muscles “3” and “9” inserted on it. The pair of lateral apodemes, the ovipositor valves security articulated with them, and the connecting muscles “3” and “9” form an integral digging apparatus movable relative to the remaining parts of the abdomen. This apparatus can be protruded posteriorly by the muscles extending from the tips of the apodemes to urotergites VIII and IX (muscles a and b in Fig. 14). In the last-instar larva the precursors of the lateral apodemes exist as invaginations at the boundary of urotergite IX and styliger IX (Fig. 15), which are transformed during the imaginal molt into long apodemes separated from the tergite (Fig. 14).

The taxon corresponding to Vectocaelifera by circumscription exists in many classifications; it was generally accepted before its inclusion into Caelifera. This taxon has been referred to as Acrydiana (sensu Latreille, 1802), Acridina (sensu MacLeay, 1821), Locustidae (sensu Stephens, 1829), and many other typified names derived from the generic names *Acrydium* Geoffroy, 1768, *Acrida* Linnaeus, 1758, and *Locusta* Linnaeus, 1758. However, I could not find any non-typified name for this taxon which may be used as a circumscriptional name.

EVOLUTION OF STRIDULATION AND HEARING IN SALTATORIA

Most representatives of Saltatoria can emit and hear sounds. In most species of Dolichocera, sounds are produced by the tegminal stridulatory apparatus and perceived by the tibial tympanal hearing apparatus; by contrast, in most species of Caelifera sounds are produced by femoro-tegminal stridulation and perceived by the abdominal tympanal hearing apparatus. The tegminal and femoro-tegminal types of stridulation have nothing in common and require essentially different movements: during tegminal stridulation the overlapping tegmina perform lateral movements while the legs remain immobile, and during femoro-tegminal stridulation the hind legs perform dorso-ventral movements while the tegmina remain immobile. The morphological adaptations to these two types of stridulation are also completely different, and they obviously have independent origins. The tibial and abdominal tympanal hearing apparatuses are positioned in totally different places and have also appeared independently. Therefore, it may seem that the ability for sound communication was acquired independently in Dolichocera and Caelifera and had been absent in their common ancestor.

However, this is probably not so; adaptations to sound communication appeared in the common ancestor of Saltatoria and then underwent various evolutionary changes in different taxa. The evolution of sound communication in Saltatoria can be seen as follows.

The Initial State

The initial variant for Saltatoria is the femoro-abdominal type of stridulation. Saltatorians with this type of stridulation possess arched rows of tubercles on the sides of abdominal segment III (Fig. 1) and longitudinal ridges on the inner surface of the hind femora; during dorso-ventral movements of the hind legs the ridges on the femora rub over the tubercles on the abdomen and generate sounds. The primitiveness of this stridulatory apparatus is indicated by its occurrence in both Dolichocera and Caelifera: among Dolichocera it is present in Stenopelmatidae (including Gryllacridinae and Schizodactylinae), and among Caelifera, in Pneumoridae, Tanaoceridae, and Xyronotidae. In Stenopelmatidae, besides rows of tubercles on the sides of abdominal segment III, similar rows are present on the adjacent segments II and/or IV (Fig. 1). Among Dolichocera, femoro-abdominal stridulation also occurs in Anostostomatidae, which have no regular rows of tubercles but only irregular tubercles or rugosities. Among Caelifera, besides the taxa mentioned above, femoro-abdominal stridulation is also retained in Pamphagidae, which possess a rugose field on the sides of urotergite II instead of a row of tubercles on the sides of urotergite III.

The primitive representatives of Saltatoria have no external tympanal hearing organs and use only the internal chordotonal organs (Staaden et al., 2003) to perceive sounds produced by the femoro-abdominal apparatus. Among the taxa capable of femoro-abdominal stridulation, external tympanal hearing organs are absent in Stenopelmatidae, Pneumoridae, Tanaoceridae, and Xyronotidae.

Further evolution of stridulatory and hearing organs proceeded in different directions in Dolichocera and Caelifera.

Transformations of Sound Communication in Dolichocera

In Stenopelmatidae (including Gryllacridinae and Schizodactylinae) and Rhaphidophoridae the external tympanal hearing organs are primitively absent, so that sounds can be perceived only by the internal sensory organs.

A holophyletic taxon with a non-typified circumscriptional name Acoustopoda **taxon n.** may be distinguished within Dolichocera. This taxon is characterized by the emergence of the tibial tympanal hearing apparatus positioned in the proximal portion of the fore tibia. Its resonator consists of two areas of thin cuticle shaped as two oval windows on the sides of the tibia, and its receptor is the subgenual chordotonal organ (which is present in all the leg pairs in various insects). Some representatives of Acoustopoda have secondarily lost both sound communication and the tibial tympanal hearing apparatus. The taxon Acoustopoda comprises Mesensifera, Tettigensifera, and Gryllensifera.

The most primitive taxon within Acoustopoda is Mesensifera (i.e., Anostostomatidae), which retains the femoro-abdominal stridulation initial for Saltatoria. The primitiveness of Mesensifera is also indicated by the fact that their stenothoracic spiracles (i.e., spiracles of the anteriormost pair positioned at the boundary of the pro- and mesothorax) are not modified, even though they are used for filling the tracheal sacs of the tibial hearing apparatus. Unlike those of Mesensifera, the stenothoracic spiracles of Tettigensifera and Gryllensifera are more or less modified: each of them is divided into two parts, and there is a separate tracheal tube extending from the anterior opening into the fore leg (Zeuner, 1939: 73).

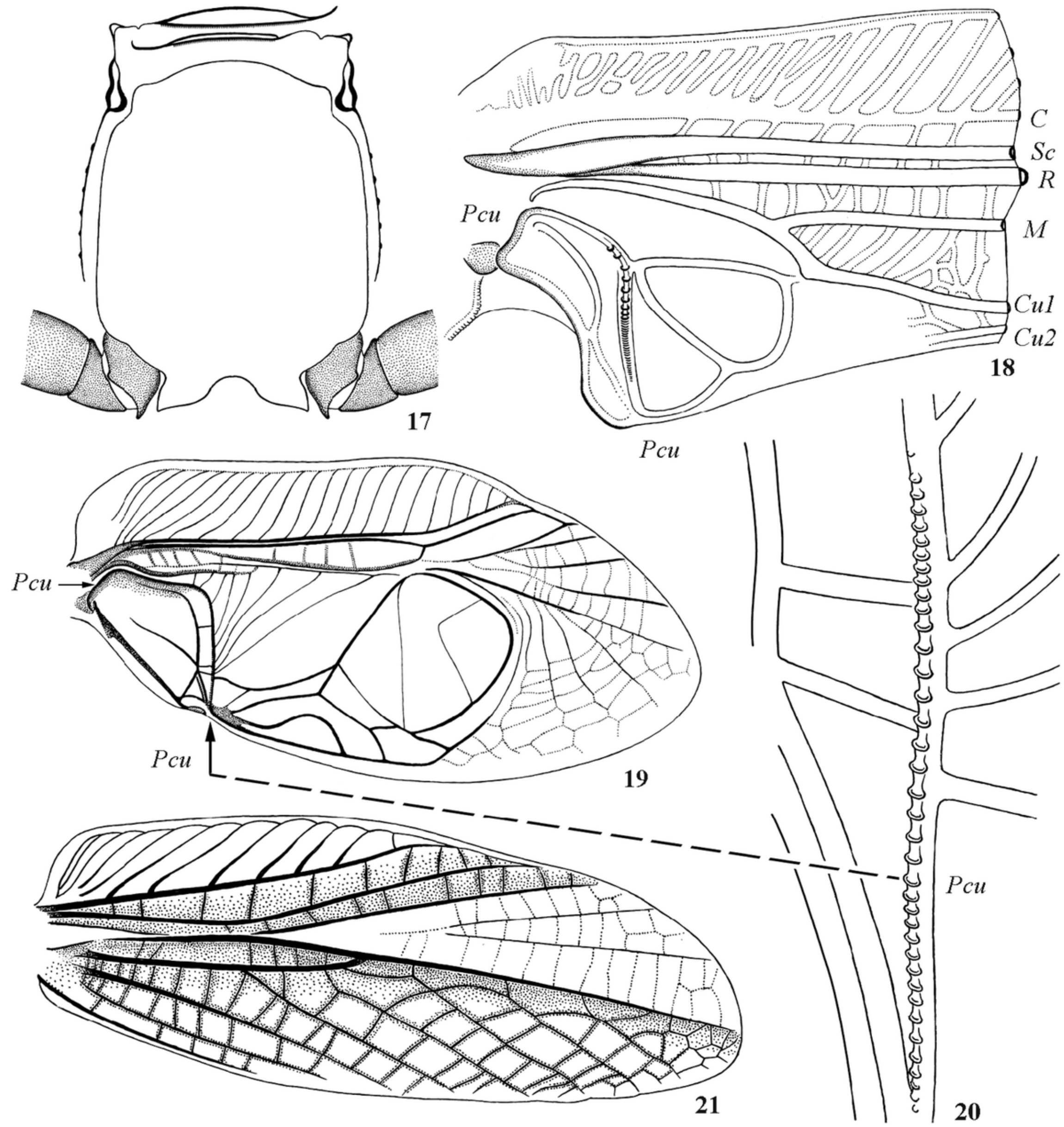
Tettigensifera and Gryllensifera form a holophyletic taxon within Acoustopoda with a non-typified circumscriptional name Striduloptera **taxon n.**, characterized by the emergence of the tegminal stridulatory apparatus. Bethoux (2012) used for this taxon the name "Grylloptera Haeckel, 1896," which is in fact a junior circumscriptional synonym of the name Orthoptera Olivier, 1789 (see the section *The Names of the Taxa* above).

The tegminal stridulatory apparatus is positioned on the fore wings of the male and consists of the stridulatory vein, the plectrum, and the resonator. The stridulatory vein is the transverse portion of the S-shaped postcubitus (*Pcu*) bearing numerous transverse ridges on its ventral side (Figs. 18, 21); during lateral movements of the tegmina, this vein portion acts as a file scraping against the plectrum, which is the elevated and sclerotized posterior margin of the other tegmen (Fig. 17). The resonator is formed by one or several fields positioned on the tegmen distally to the stridulatory vein (Figs. 18, 19). Some representatives of Striduloptera have secondarily lost both sound communication and the tegminal stridulatory apparatus.

It was supposed that the stridulatory vein and tegminal stridulation evolved independently in Tettigensifera and Gryllensifera (Ander, 1939; Sharov, 1968). This opinion was based on the interpretation of the stridulatory vein of katydids as the postcubitus ($Pcu = 1A$) and that of crickets, as the posterior branch of the cubitus (Cu_2). Errors in vein homologization may be caused by the fact that some authors believe all the veins to extend from the wing base and branch similar to a growing tree. In reality, however, during individual development all the veins appear simultaneously at an early stage of the protopteron formation. The places of proximal and distal attachment of the same vein may shift, appear, and disappear both in evolution and as the result of individual variation.

Gorochov (1995a) and Bethoux (2012) have shown that the stridulatory vein is homologous in all the Striduloptera; they consider it as the posterior branch of the cubitus (*CuP* or *CuPb*). It is possible, however, that the stridulatory vein of both katydids and crickets is the continuation of the postcubitus ($Pcu = 1A$), i.e., the longitudinal vein positioned directly behind the claval furrow (Figs. 18–20).

According to a different scenario, the tegminal stridulatory apparatus and the tibial hearing apparatus were initially present in Dolichocera; their absence in all the Stenopelmatidae and Rhaphidophoridae, and also the absence of the tegminal stridulatory apparatus in all the Anostostomatidae are explained by secondary reduction (Gorochov, 1995a). This version is supported by the assumption that the similarity in the venation pattern and the mode of folding of the tegmina in Stenopelmatidae and Anostostomatidae represents their synapomorphy. In the macropterous representatives of these taxa the veins of the posterior part of the tegmen run parallel to its posterior margin, and



Figs. 17–21. Tegminal stridulatory apparatus of Striduloptera: (17) *Tettigonia cantans* (Fuessly, 1775), cross-section of mesothorax of adult male with folded wings at the level of stridulatory veins and plectra of folded tegmina (the parts of the leg behind the section plane are punctated); (18) Tettigensifera: *Conocephalus* sp., proximal part of the left tegmen, ventral view; (19–21) Gryllensifera: *Phaloria* (*Papuloria*) *aspersa* Gorochov, 1996: (19) fore wing of adult male, ventral view; (20) the same, stridulatory vein *Pcu*; (21) fore wing of female.

the folded tegmina envelope the body (Fig. 1); this type of folding prevents the lateral movements of the tegmina and makes tegminal stridulation impossible. This scenario implies that Stenopelmatidae have retained the tegmina but lost the tegminal stridulatory apparatus (which had been present in their ancestors) and instead acquired the femoro-abdominal stridulatory apparatus morphologically identical to that of some representatives of Caelifera. In my opinion, this assumption is less feasible than the hypothesis of the initial absence of the tegminal stridulatory apparatus in Dolichocera and the initial presence of the femoro-abdominal apparatus inherited from their common ancestor with Caelifera.

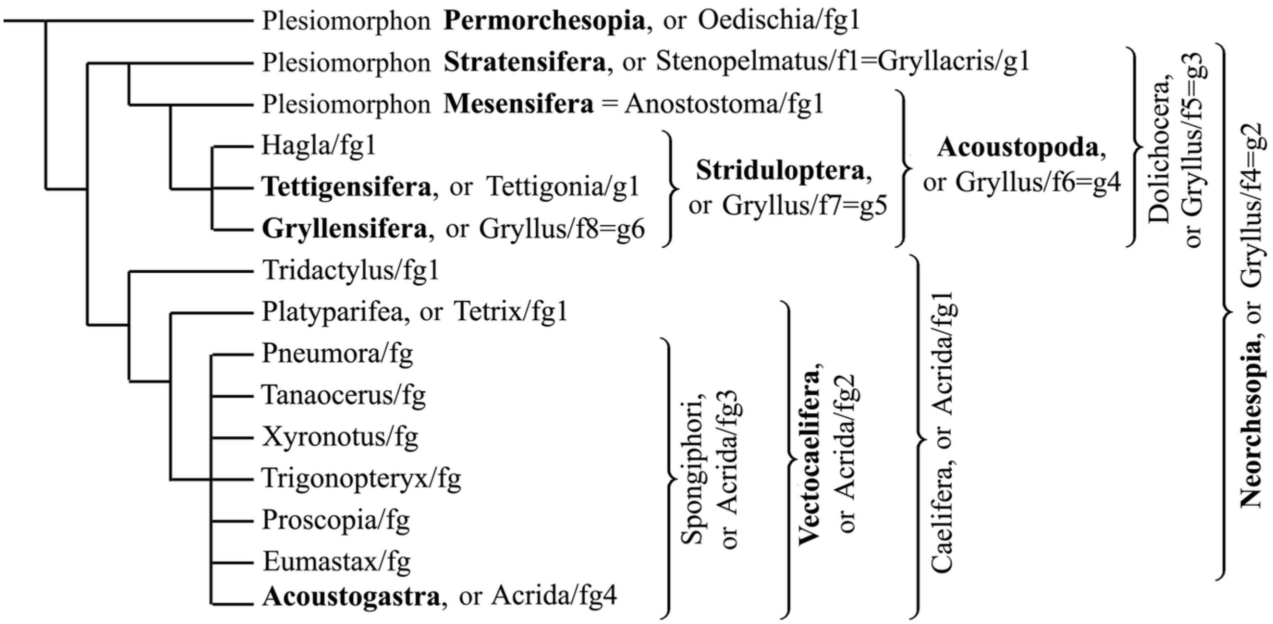


Fig. 22. Phylogeny of Saltatoria. The new circumscriptional names are shown in bold.

Apart from the morphology of the hearing and stridulatory apparatuses, the holophyly of the taxa Acoustopoda and Striduloptera is confirmed by the structure of their ovipositors: only in Acoustopoda the 1st valve has a groove accommodating the margin of the 3rd valve, and only in Striduloptera the secondary olistheter couples the 3rd valves not to the 2nd but to the 1st valves (see above).

The nature of the stridulatory vein. Most veins in insects have a smooth semi-cylindrical surface, but some bear regular semicircular transverse ridges outwardly resembling the taenidia of the tracheae. The term "taenidium" was introduced by Packard (1886) for the filiform convexities forming the characteristic rings or spirals on the inner cuticular lining of the tracheae. Unlike those of the tracheal taenidia, the transverse ridges of the wing veins are positioned not on the inside but on the outside of the cylindrical surface of the vein; they do not form complete rings or spirals because the vein itself is not a tube but only a relief element on the wing surface. By analogy with taenidia, these external transverse ridges may be termed **exotaenidia.** They are usually present on elastic veins which have no longitudinal rigidity. In some insect taxa, certain exotaenidia on certain veins are modified and perform special functions. The transverse ridges on the ventral side of the stridulatory vein of Striduloptera seem to be modified exotaenidia of that vein. The presence of exotaenidia in other insects makes no evidence against the idea of a single origin of the tegminal stridulatory apparatus in Dolichocera, since the specific design of the stridulatory apparatus in which the transverse portion of the S-shaped postcubitus acts as a file during the opening and closing of the tegmina is not found in any other taxon outside Dolichocera (i.e., in the outgroup).

Transformations of Sound Communication in Caelifera

The femoro-abdominal stridulatory apparatus, initial for Saltatoria, is retained in Pneumoridae, Tanaoceridae, and Xyronotidae, while the external tympanal hearing organs are absent in these groups. In such taxa as Tridactyloidea, Tetrigidae, Trigonopterygidae, Proscopiidae, and Eumastacidae femoro-abdominal stridulation has been secondarily lost.

A holophyletic taxon with a non-typified circumscriptional name Acoustogastra **taxon n.** may be distinguished within Caelifera. This taxon is characterized by the emergence of the unique tympanal hearing apparatus on the sides of the first abdominal segment. The taxon Acoustogastra comprises Acrididae, Pamphagidae, Pyrgomorphidae, and related taxa. It corresponds to the family Acrididae sensu Gorochov (1995b), whereas some authors use the family name Acrididae for a smaller taxon.

Among Acoustogastra, the femoro-abdominal stridulatory apparatus is retained in Pamphagidae, in which it is positioned not on uromere III but on uromere II and consists of a rugose field rather than of regular rows of tubercles. In other members of Acoustogastra the femoro-abdominal mode of stridulation is replaced by a similar femoro-tegminal mode, in which the legs also move up and down but they rub not against the sides of the abdomen but against the veins of the folded tegmina.

THE CLASSIFICATION OF SALTATORIA

The phylogeny of Saltatoria is shown in Fig. 22. The classification in which the polarity of characters of ovipositor morphology is consistent with the scenarios of evolution of the stridulatory and hearing apparatuses is presented below; the abbreviation "nom. hier." designates the hierarchical typified name.

1\. Orchesopia Rafinesque, 1815, or Saltatoria Latreille, 1817; nom. hier.: Gryllus/f3=g1 [f:1781; g:1758]. Autapomorphies: (1) hind legs initially saltatorial, always with reduced trochanter (see above); (2) protoptera in penultimolarva and ultimolarva inversed (see above).

1.1. † Plesiomorphon Permorchesopia **taxon n.**; nom. hier.: Oedischia/fg1 [f:1906; g:1885]. Plesiomorphy: tarsi clearly 5-segmented, 1st tarsomere longer than 2nd (see above).

1.2. Neorchesopia **taxon n.**; nom. hier.: Gryllus/f4=g2 [f:1781; g:1758]. Autapomorphy: 1st and 2nd tarsomeres immovably fused; if boundary between them retained, then 1st tarsomere shorter than 2nd.

1.2.1. Dolichocera Bey-Bienko, 1964 (non Dolichocera Latreille, 1829); nom. hier.: Gryllus/f5=g3 [f:1781; g:1758]. Autapomorphy: emergence of coupling of 3rd ovipositor valves with primary ovipositor (initially coupled with 2nd valves of primary ovipositor) (see above).

1.2.1.1. Plesiomorphon Stratensifera **taxon n.**; nom. hier.: Stenopelmatus/f1=Gryllacris/g1 (incl. *Rhaphidophora*) [f:1838; g:1831]. Plesiomorphy: 3rd ovipositor valves remain coupled with 2nd valves [see Dolichocera] and overlap 1st valves laterally (see above).

1.2.1.2. Acoustopoda **taxon n.**; nom. hier.: Gryllus/f6=g4 [f:1781; g:1758]. Autapomorphies: (1) emergence of tibial tympanal hearing organs (see above); (2) ventral margins of 3rd ovipositor valves inserted in grooves on 1st valves (see above).

1.2.1.2.1. Plesiomorphon Mesensifera **taxon n.**; nom. hier.: Anostostoma/fg1 [f:1859; g:1837]. Plesiomorphy: 3rd ovipositor valves [with their ventral margins inserted in grooves on 1st valves; see Acoustopoda (2)] remain coupled with 2nd valves (see above).

1.2.1.2.2. Striduloptera **taxon n.**; nom. hier.: Gryllus/f7=g5 [f:1781; g:1758]. Autapomorphies: (1) emergence of tegminal stridulatory apparatus (see above); (2) 3rd ovipositor valves [with their ventral margins inserted in grooves on 1st valves; see Acoustopoda (2)] lost coupling with 2nd valves and acquired coupling with 1st valves (see above).

1.2.1.2.2.1. Hagla/fg1 [f:1906; g:1856] (incl. *Prophalangopsis*).

1.2.1.2.2.2. Tettigensifera **taxon n.**; nom. hier.: Tettigonia/g1 [g:1758]. Autapomorphy: in tegminal stridulatory apparatus [see Striduloptera (1)] mirror on right tegmen shaped as small, distinctly outlined translucent field edged with curved vein; plectrum better developed on right tegmen, and file, on left tegmen. Plesiomorphy: 2nd ovipositor valves retained [being coupled only with 1st valves while coupling with 3rd valves is lost; see Striduloptera (2)].

1.2.1.2.2.3. Gryllensifera **taxon n.**; nom. hier.: Gryllus/f8=g6 [f:1781; g:1758]. Autapomorphy: 2nd ovipositor valves reduced.

1.2.2. Caelifera Ander, 1936; synn. circ.: Metorthoptera Crampton, 1927; Brachycera Bey-Bienko, 1964 (non Brachycera Zetterstedt, 1842); nom. hier.: Acrida/fg1 [f:1821; g:1758]. Autapomorphy: 1st and 2nd ovipositor valves digging, articulated with gonangula close together; gonangula fused with lateral apodemes of urotergite IX (see above).

1.2.2.1. Tridactylus/fg1 [f:1835; g:1789] (incl. *Ripipteryx*, *Cylindacheta*). Autapomorphy: pretarsus and claws on hind leg lost, tarsus not divided into segments, probably due to loss of walking function and enhancement of leaping specialization of hind legs; in *Cylindacheta*, in connection with subterranian mode of life, hind legs secondarily became walking, though with vestigial tarsus. Plesiomorphy: lateral apodemes of ovipositor [fused with gonangula; see Caelifera] not separated from urotergite IX (see above) (Fig. 13).

1.2.2.2. Vectocaelifera **taxon n.**; nom. hier.: Acrida/fg2 [f:1821; g:1758]. Autapomorphy: lateral apodemes of ovipositor [fused with gonangula; see Caelifera] totally separated from urotergite IX (see above) (Fig. 14).

1.2.2.2.1. Platyparyphea Fieber, 1852; nom. hier.: Tetrix/fg1 [f:1838; g:1802]. Probable plesiomorphy: arolium absent (among Saltatoria, the same state found in Tridactylus/fg1 and Dolichocera).

1.2.2.2.2. Spongiphori Audinet-Serville, 1838; synn. circ.: Choeratotrachela Fieber, 1852; Acridomorpha *sensu* Dirsh, 1966; nom. hier.: Acrida/fg3 [f:1821; g:1758]. Probable apomorphy: arolium present (the same state found in many other insects).

1.2.2.2.2.1–3. Taxa Pneumora/fg [f:1845; g:1775], Tanaocerus/fg [f:1948; g:1906], and Xyronotus/fg [f:1909; g:1884]. Plesiomorphy: femoro-abdominal stridulatory apparatus retained as rows of tubercles on uromere III (see above).

1.2.2.2.2.4–6. Taxa Trigonopteryx/fg [f:1870; g:1841], Proscopia/fg [f:1838; g:1820], and Eumastax/fg [fg:1899].

1.2.2.2.2.7. Acoustogastra **taxon n.**; nom. hier: Acrida/fg4 [f:1821; g:1758]. Autapomorphy: emergence of tympanal hearing organs on uromere I (see above).

DISCUSSION

Some authors (Beier, 1955; Dirsch, 1961; Sharov, 1968) united Tridactylidae with Tetrigidae based on similarity in the wing morphology and the absence of the arolium. However, the ovipositor of Tetrigidae (Fig. 14) has the same, completely separated lateral apodemes as in the rest of Vectocaelifera, which disproves the close relation between Tetrigidae and Tridactylidae.

The above classification of Dolichocera is at variance with the traditional schemes in which Tettigensifera are united with Stratensifera and the two taxa are opposed to Gryllensifera; the reason for this lies in a different interpretation of the directions of evolution of the ovipositor and the types of sound communication (see above).

The Opposite View on the System of Dolichocera

The above analysis of the character polarity and phylogeny of Saltatoria does not include many characters, in particular those of wing venation, which have been studied in the greatest detail and are most commonly used in systematics and phylogenetic reconstructions. For most fossil forms, wing venation is the only source of data shedding light on their phylogenetic position; this is perfectly true of Dolichocera as well. Considerable discrepancies exist between the above classification and the system of Dolichocera based largely on wing venation (Gorochov, 1995a):

Infraorder Tettigoniidea
  Superfamily Hagloidea
  Superfamily Tettigonioidea
    (corresponds to Tettigensifera)
  Superfamily Stenopelmatoidea
    (corresponds to Stratensifera + Mesensifera)
Infraorder Gryllidea (corresponds to Gryllensifera)

The autapomorphies of the taxon referred to as the infraorder Tettigonioidea were not mentioned in the literature; technically, this taxon can be differentiated from Gryllidea only based on the plesiomorphic retention of four tarsomeres. According to A.V. Gorochov (pers. comm.), the autapomorphies of this taxon are (1) the divided spermatophore capsule (see Fig. 1) and (2) the emergence of an additional vein between $MP + CuA_1$ and CuA_2 in the anal fan of the hind wing; this vein is fused distally with CuA_2 (Gorochov, 1995a: fig. 90). The origin of this additional vein was related to a change in the position of the folding line along which the anal fan is tucked under the remigium: this line is shifted forwards and crosses CuA_2 and $MP + CuA_1$ (Gorochov, 1995a: 53). This additional vein is developed in some representatives of Hagloidea, Tettiginioidea, and Stenopelmatoidea.

The autapomorphy of the taxon Stenopelmatoidea (uniting Stratensifera and Mesensifera) is believed to be the parallelization of venation of the fore wing, in which the posterior veins CuA_2, CuP, and PCu run a considerable distance along the posterior wing margin and end in the distal quarter of the wing (Gorochov, 1995a: 186). Correspondingly, in some representatives of this taxon the folding line of the fore wing is shifted forwards in such a way that the posterior margin of the folded wing leans over onto the opposite side (Fig. 1). Such an enveloping mode of wing folding is typical of macropterous representatives of Stratensifera and Mesensifera. However, the same parallelized venation of the fore wing can also be found among Permorchesopia, in particular in *Gryllacrimima perfecta* Sharov, 1968 (Sharov, 1968: fig. 33); it may be assumed that the folded wings of such species enveloped the body (Gorochov, 1995a: fig. 207).

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Material Used in Preparation of Figures 1–15 and 17–25

Figs. 1–4. *Hyperbaenus* sp. Peru, Loreto, Ucayali Province, 17 km NNE of Contamana, thermal springs (Aguas Termales), 26.VII–4.VIII.2013 (N. Kluge, L. Sheiko), 1 ♀ adult.

Figs. 5, 6. Rhaphidophoridae gen. sp. Chile, X Region—Los Lagos, Llanquihue Province, Petrohue, lago de Todos los Santos, 3.II.2012 (N. Kluge, L. Sheiko), 1 ♀ adult.

Figs. 7, 8. *Papuogryllacris* sp. Indonesia, Papua Province (New Guinea Island), Jayapura, env. of Depapre, 25–28.VIII.2012 (N. Kluge, L. Sheiko), 2 ♂ and 2 ♀ adults, 1 ♂ larva.

Figs. 9–11. *Cratomelus armatus* Blanchard, 1851. Chile, VII and X Regions, 30.XII.2011–11.II.2012 (N. Kluge, L. Sheiko), ♂♂ and ♀♀ adults and larvae.

Fig. 12. Mecopodinae gen. sp. Indonesia, Papua Province (New Guinea Island), Jayapura, env. of Depapre, 25–28.VIII.2012 (N. Kluge, L. Sheiko), 1 ♀ adult.

Fig. 13. *Ripipteryx* (*Mirhipipteryx*) *peruviana* Saussure, 1896. Peru, Loreto, Ucayali Province, 17 km NNE of Contamana, thermal springs (Aguas Termales), 26.VII–4.VIII.2013 (N. Kluge, L. Sheiko), 9 ♂ and 7 ♀ adults.

Figs. 14, 15. *Tetrix subulata* (Linnaeus, 1758). Russia, Leningrad Province, Lodeinopolsky District, Zaostrovie, VI.2001, adults and larvae.

Fig. 17. *Tettigonia cantans* (Fuessly, 1775) (*Gryllus*). Russia, Belgorod Province, Borisovka: 1 ♂ adult.

Fig. 18. *Conocephalus* sp. Indonesia, Papua Province (New Guinea Island), Baliem Valley, Elagaima, 15–19.VIII.2012 (N. Kluge, L. Sheiko), 1 ♂ adult.

Figs. 19–21. *Phaloria* (*Papuloria*) *aspersa* Gorochov, 1996. Indonesia, Papua Province (New Guinea Island), Jayapura, Waena, 9–13.VIII.2012 (N. Kluge, L. Sheiko), ♂♂ and ♀♀ adults.

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