Evolution and taxonomic significance of the copulatory apparatus in Ensifera (Orthoptera). Part 2: Male genitalia in Grylloidea

Эволюция и таксономическое значение копулятивного аппарата у длинноусых прямокрылых (Orthoptera: Ensifera). Часть 2: Гениталии самца у Grylloidea

A.V. Gorochov

А.В. Горохов

A.V. Gorochov, Zoological Institute, Russian Academy of Sciences, 1 Universitetskaya Emb., St Petersburg 199034, Russia. E-mail: orthopt@zin.ru

In the superfamily Grylloidea, the main trends in the evolution of the copulatory apparatus were probably connected with the transformation of simple membranous (hagloid) genitalia, characteristic of ancient groups of Ensifera, into a complicated organ with highly specialized sclerites for fixation of the female during copulation. This evolutionary process was probably accompanied by partial reduction and disappearance of paraproctal hooks or other external abdominal processes which may have been used by these ancient groups for female fixation. Sclerites in the male genitalia of Grylloidea appeared independently not less than four times: in Gryllotalpidae, Myrmecophilidae, Gryllidae and Mogoplistidae. This hypothesis, proposed by Gorochov in 1984, was one of the reasons for division of the recent Grylloidea into four families. Each of the first three families acquired sclerites in the male genitalia once, whereas Mogoplistidae possibly acquired them more than once: male genitalia of the tribe Mogoplistini are of the hagloid type, membranous; in most genera of Arachnocephalini (Mogoplistinae), in *Pseudomogoplistes* (Mogoplistinae) and in Malgasiinae, male genitalia have three types of sclerites which could have also appeared independently. Moreover, many sclerites of the male genitalia in Grylloidea are formed independently and have significant convergent similarity; this is why the nomenclature of male genital structures based partly on their function and position but not exclusively on their homology is simpler and much more suitable for descriptions and morphological investigations. This nomenclature is considered here.

В надсемействе Grylloidea главные тенденции в эволюции копулятивного аппарата были, очевидно, связаны с преобразованием простых мембранозных (хаглоидных) гениталий, характерных для древних групп Ensifera, в усложненный орган с высокоспециализированными склеритами для фиксации самки при копуляции. Возможно, этот эволюционный процесс сопровождался частичной редукцией и исчезновением парапроктальных крючков или других наружных выростов брюшка, которые могли использоваться этими древними группами для фиксации самки. Склериты в гениталиях самца Grylloidea возникают независимо не менее четырех раз: у Gryllotalpidae, Myrmecophilidae, Gryllidae и Mogoplistidae. Эта гипотеза, предложенная Гороховым в 1984 г., была одной из причин для деления современных Grylloidea на четыре семейства. Каждое из трех первых семейств приобрело склериты в гениталиях самца однажды, но Mogoplistidae, возможно, приобретали их неоднократно: гениталии самца в трибе Mogoplistini – хаглоидного типа, мембранозные; у большинства родов Arachnocephalini (Mogoplistinae), у *Pseudomogoplistes* (Mogoplistinae) и у Malgasiinae гениталии самца имеют три типа склеритов, которые могли возникнуть также независимо. Более того, многие склериты гениталий самца у Grylloidea формируются независимо и имеют значительное конвергентное сходство; вот

© 2015 Zoological Institute, Russian Academy of Sciences

почему номенклатура генитальных структур самца, частично основанная на их функции и положении, но не только на их гомологии, является более простой и более пригодной для описаний и морфологических исследований. Здесь эта номенклатура рассмотрена.

Key words: copulatory apparatus, evolution, morphology, taxonomic importance, Orthoptera, Ensifera, Grylloidea

Ключевые слова: копулятивный аппарат, эволюция, морфология, таксономическое значение, Orthoptera, Ensifera, Grylloidea

INTRODUCTION

This series of papers is the next step in the development of hypotheses on the ensiferan evolution published in a special monograph on this subject (Gorochov, 1995a, b). In the previous communication of this series, some general problems of evolution of the copulatory apparatus in Ensifera were discussed (Gorochov, 2014). These problems concerned primary and secondary sexual characters, intraspecific stability of these characters, interspecific sexual differences, the "lock-and-key" and "genital clock" hypotheses, early evolution of sexual characters in orthopteroid insects, and general trends in the evolution of the ensiferan copulatory apparatus. The present communication continues this series and contains the discussion of the structure of male genitalia in the superfamily Grylloidea and analysis of the main trends in their evolution.

The paper is based on the data presented by the author at the 11th International Congress of Orthopterology (11th–15th August 2013, Kunming, China) and briefly outlined in the abstract of that presentation (Gorochov, 2013).

RESULTS

Phylogenetic investigations of the Grylloidea and nomenclature of its male genitalia

The study of morphological evolution is closely connected with the phylogenetic study of the group in question. In the superfamily Grylloidea, the first phylogenetic scheme of families and subfamilies was proposed by Gorochov (1984, 1986). It was based on characters of the copulatory apparatus as well as of some other organs. In these works, the terminology of copulatory structures proposed by the previous authors (Randell, 1964; Alexander & Otte, 1967; Chopard, 1969) was used with some original modifications. This terminology took into account the evidence that many sclerites of the phallus (= male genitalia) were formed independently in different groups of Grylloidea and have significant convergent similarity (convergent origin of many structures in the male genitalia was also observed in Dictyoptera; Anisyutkin, 2009, 2011). Therefore, this terminology was partly based on the function and position of genital structures but not solely on their homology. Such terminology is rather simple and most suitable for descriptions and morphological investigations.

A short time later, a new phylogenetic scheme of the Grylloidea and a new nomenclature of its phallus were proposed in some of the first publications by Desutter (1987, 1988). Her opinion was based solely on the study of the phallus; therefore she could not discover the numerous cases of convergence in male genital structures. The nomenclature of Desutter suggested that any single term should refer only to homologous (not convergent) structures, so that a great number of terms would need to create for all structures of convergent origin. These cases of convergence were not taken into account in her phylogenetic scheme of Grylloidea: the principal division of Gryllidae into "Diplosclerophalles" (Oecanthinae and part of Phalangopsinae) and "Monosclero-

phalles" (all the other subfamilies of Gryllidae except Pteroplistinae), separation of the phalangopsid tribe Paragryllini from all the other taxa of "Monosclerophalles", and unification of Mogoplistidae with Myrmecophilidae in a holophyletic clade were unsuccessful and later rejected by Desutter-Grandcolas (1992) or not supported by later morphological (Gorochov, 1995) and molecular (Jost & Shaw, 2006) studies. In her subsequent publications, no new phylogenetic scheme of Grylloidea was proposed.

An additional nomenclature for structures of the cricket phallus was also proposed by Mesa et al. (1997, 1999a, b, c). This nomenclature had no phylogenetic explanation: it seems that these authors used their terms for homologous structures, but their homologizations were often erroneous [for example, their terms "PECS" and "DECS" were used in Nemobiinae for epiphallus and rami, respectively (Mesa et al., 1999c: Figs 8–15); but in Gryllinae, these terms were used in the opposite sense: "PECS" for rami, and "DECS" for epiphallus (Mesa & Garcia, 1999a: figs 4–11 and 20–27)].

The first phylogenetic scheme and earlier terminology of genital structures were corrected by Gorochov (1995, 2001, 2002, 2010). This corrected phylogenetic scheme was partly supported by the molecular data of Jost & Shaw (2006), except for the position of the Gryllinae subfamily group. Thus, at present there is only one phylogenetic scheme for all the higher taxa of Grylloidea; and for the majority of species, genera, and higher taxa of crickets with the phallus described, the genital terms of Randell and Gorochov are used. Therefore, it is reasonable to continue to use this phylogenetic scheme (Fig. I) and this terminology of copulatory structures (Fig. II).

Main trends in the evolution of male genitalia in Grylloidea

The main trends in the evolution of the cricket copulatory apparatus were probably related to the transformation of a simple membranous (hagloid) phallus, characteristic of ancient groups of Ensifera and preserved in many recent representatives of the infraorder Tettigoniidea (Hagloidea, Stenopelmatoidea and Tettigonioidea), into a complicated organ with highly specialized sclerites for fixation of female during copulation. This evolutionary process was probably accompanied by partial reduction and disappearance of hooks or other external processes of the male abdomen which could be used by these ancient groups for female fixation (preservation of the tendency to form the latter copulatory structures can be observed in many other groups of Orthoptera). Sclerites in the phallus of Grylloidea independently appeared not less than 4 times: in Gryllotalpidae, Myrmecophilidae (including Bothriophylacinae), Gryllidae and Mogoplistidae. This hypothesis (Gorochov, 1984) was one of the reasons for division of the recent Grylloidea into four families (Fig. I). Each of the first three families acquired sclerites in the phallus once, but Mogoplistidae possibly acquired them more than once.

There were two main ways of emergence of sclerites in the phallus of Ensifera: [1] appearance of a sclerite or sclerites in a small area of the dorsal fold (plica dorsalis) of the hagloid phallus or very close to it (such a type of genitalia is named "tettigonioid", since it is usual in katydids but rare in other ensiferans; Figs III: 2, 12); [2] development of sclerotization on most part of the dorsal fold, usually with a simultaneous increase of this fold (such a type of genitalia is named "grylloid", since it is characteristic of most Grylloidea and sometimes developed in some other ensiferans; Figs III: 4, 7). In the grylloid genitalia, the ventral surface of the dorsal fold often additionally forms a special median process (Fig. III: 4, 8, 15) named "rachis" (= "guiding rod" *sensu* Alexander & Otte, 1967) and probably providing insertion of the spermatophore apex (with the spermatophore aperture) into the female spermathecal opening during copulation.

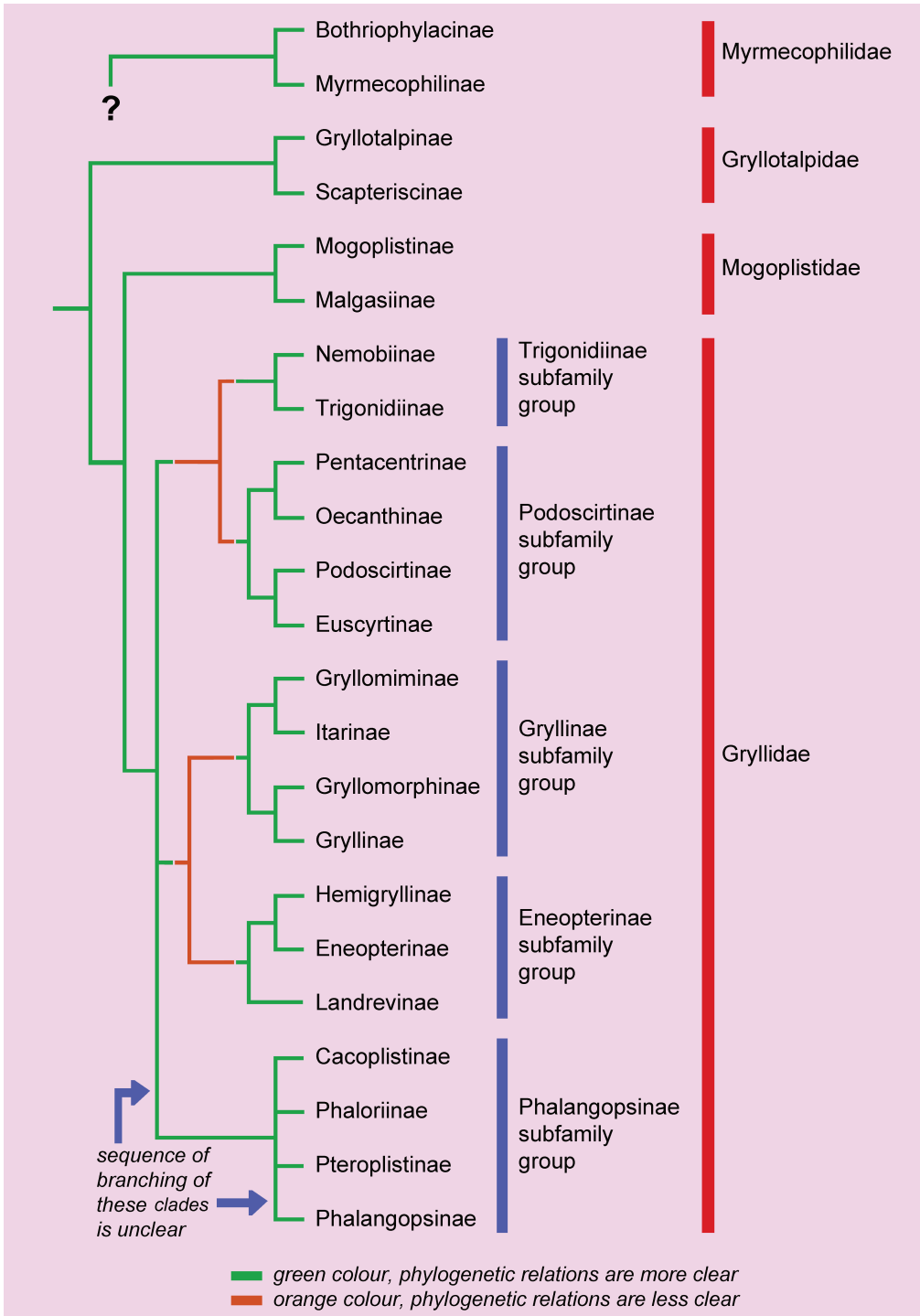


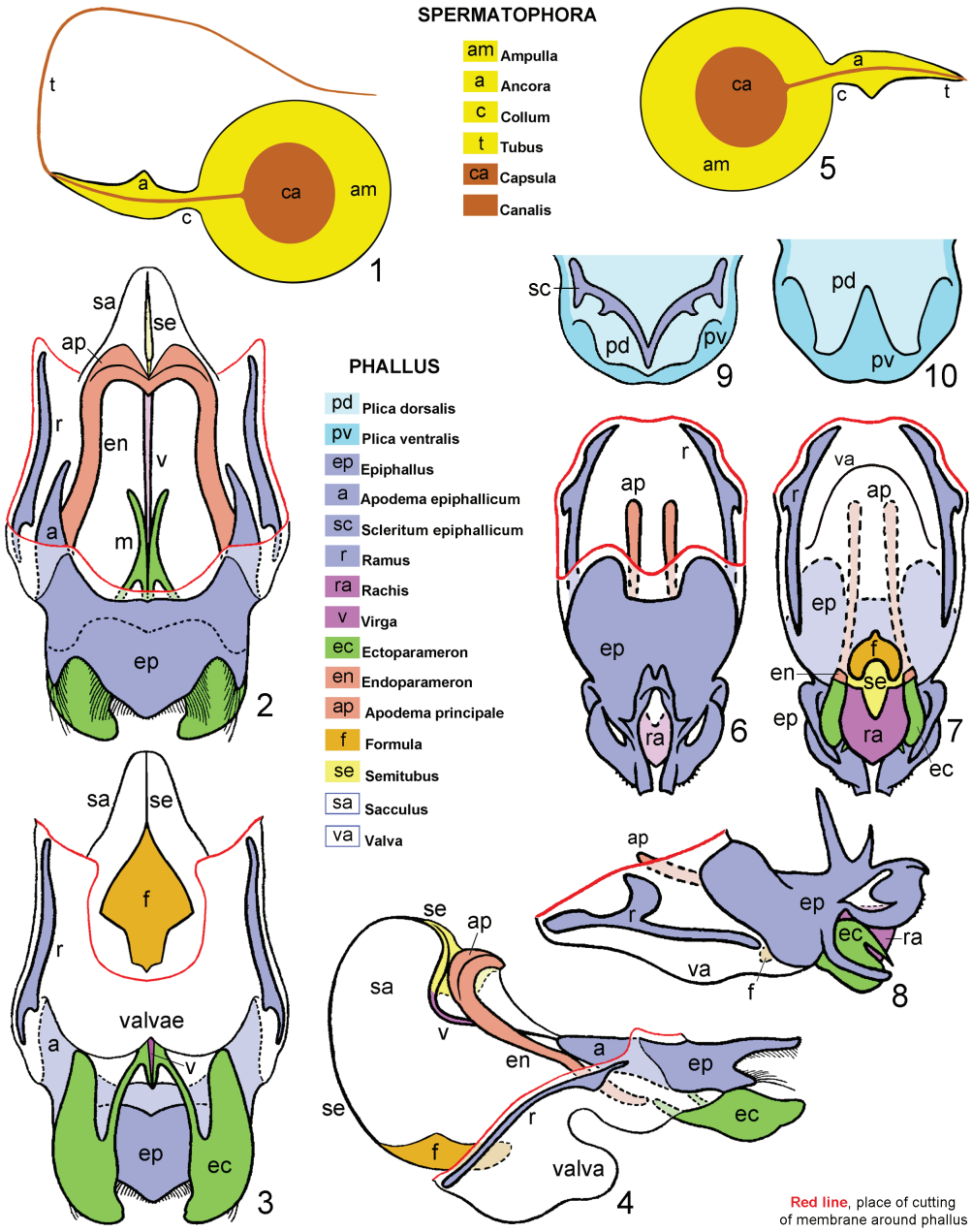
Fig. I. Phylogenetic scheme of Grylloidea [after Gorochov (1995b) with later changes: Gorochov (2001, 2010a, b)]

A structure similar to rachis may also appear sometimes in the tettigonioid male genitalia. Such a complicated type of phallus is characteristic of the both subfamilies of Gryllotalpidae. Their epiphallus was possibly formed as a rather small epiphallic sclerite on the dorsal surface of the dorsal fold (Fig. III: 2); later this sclerite somewhat increased in size, and the apex of the dorsal fold was changed into an additional sclerite (or two such sclerites) which may be a certain analogue of the rachis in other Grylloidea (Fig. III: 3). The main body of spermatophore in Gryllotalpidae is probably formed between the dorsal and ventral folds, as in the hagloid and tettigonioid phallus.

Myrmecophilidae, especially Bothriophylacinae, have a more complicated phallus. Such a phallus probably appeared as a primitive grylloid phallus from the ancestral hagloid phallus (Fig. III: 4). Its epiphallus could acquire an anterior median projection (forming a large unpaired apodeme), a median membranous area, and lateral arms articulated with the 9th and 10th abdominal sternites; the rachis and an unpaired endoparameral sclerite with a large apodeme, as well as membranous lobe-like ectoparameres also appeared (Fig. III: 5). Such a condition of the phallus is characteristic of Myrmecophilinae, but in Bothriophylacinae, some additional modifications have appeared (Fig. III: 6): partial reduction of the epiphallus (also in some species of Myrmecophilinae); strong increase of the endoparameral apodeme; development of heavy sclerotization of the rachis and sometimes of the semitubus with the formula; appearance of rather numerous smaller sclerites supporting the soft ectoparameres; and others.

The phallus of Gryllidae is most diverse. It is also distinctly modified in comparison with the primitive grylloid phallus and may have originated independently from the ancestral hagloid phallus (Figs III: 7, 8). A moderately complicated phallus is present in all the subfamilies of Trigonidiinae, Eneopterinae and Phalangopsinae subfamily groups as well as in Pentacentrinae, Podoscirtinae, Gryllomiminae and Gryllomorphinae; this phallus usually has a diverse rachis, short semitubus, small formula (Fig. III: 9), and a pair of endoparameres (each with a large apodeme) connected with the base of the rachis and/or bases of the pair of ectoparameres. In the above-mentioned subfamilies, such a phallus may have very diverse unique or convergent modifications: appearance of ectoparameres from the paired processes of the epiphallus and / or rachis; strong increase or disappearance of the rachis, development of its mobility; development of diverse processes and lobes on the epiphallus; its division into a few separate plates or hooked sclerites; lengthening or fusion of endoparameres; fusion of the rachis with the semitubus and formula (formation of one larger sclerite from these structures); development of a large apodeme on the formula; appearance of additional sclerites; and much more.

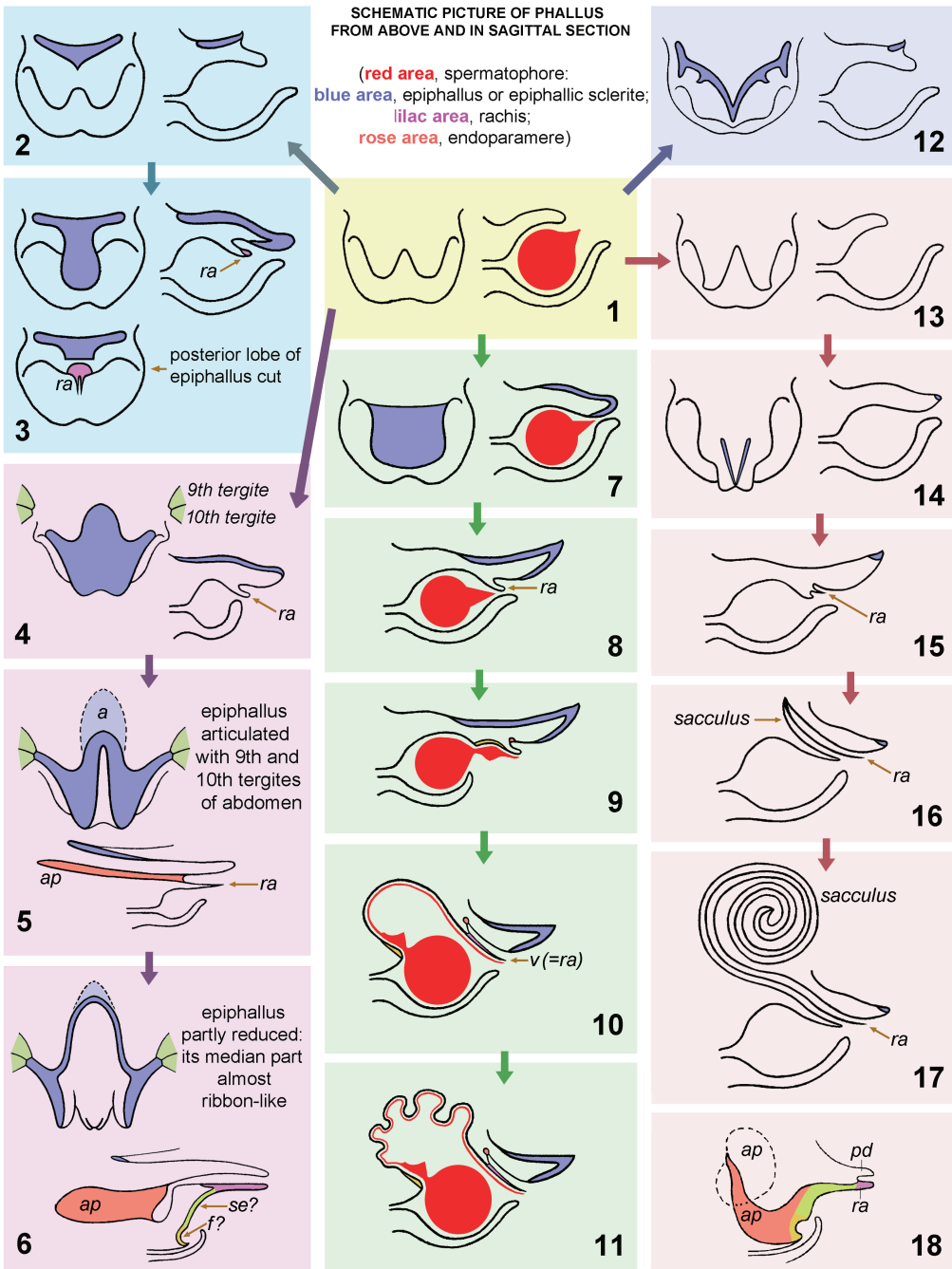
However, the most important changes in the phallus of Gryllidae are related to the development of a large sacculus, having a long semitubus (for the formation of a long spermatophore tube), and the appearance of a partly reversed position of the spermatophore in the phallus (Fig. III: 10). This type of phallus is present in all the species of Gryllinae and Itarinae, in many representatives of Gryllomorphinae, Oecanthinae and Euscyrtinae, and in some taxa of Podoscirtinae (Aphonoidini and Hapithini) and Phalangopsinae (Luzaropsini). In some taxa, the sacculus may be festoon-like or have loops; such a structure allows them to form an extremely long semitubus for an extremely long spermatophore tube (some species of Gryllinae and Gryllomorphinae; Fig. III: 11). During copulation, Gryllidae may use the strong and movable ectoparameres for crasping the female copulatory papilla (many of Gryllinae) or for anchor-like fixation in the female genital chamber (the majority of Podoscirtinae and some Pentacentrinae); for the latter type of fixation, processes or hooks on some other structures, including the rachis, may be used.



© 2015 Zoological Institute, Russian Academy of Sciences, *Zoosystematica Rossica* 24(1): 31–41

Fig. II. Scheme of spermatophore and male genitalia in Grylloidea with nomenclature of their structures: **1**–**4**, grylloid type, *Acheta* F. (Gryllinae); **5**–**8**, grylloid type, *Zvenella* Gor. (Podoscirtinae); **9**, tettigonioid type, *Malgasia* Uv. (Malgasiinae); **10**, hagloid type, *Paramogoplistes* Gor. (Mogoplistinae). Spermatophore from side (**1**, **5**); genitalia from above (**2**, **6**, **9**, **10**), from below (**3**, **7**) and from side (**4**, **8**).

Abbreviations (from top to bottom). **SPERMATOPHORA** (= SPERMATOPHORE): *am* – **Ampulla**, largest globular or almost cylindrical part of spermatophore body; *a* – **Ancora** (= attachmnent plate), widened part of spermatophore used for its attachment to female genitalia; *c* – **Collum** (= neck), thin part of spermatophore between ampulla and ancora; *t* – **Tubus** (= tube), very thin and often long, or not very thin and short distal part of spermatophore inserted in female spermathecal duct during copulation; *ca* – **Capsula**, small globular reservoir with sperm situated inside ampulla, and **Canalis**, duct for sperm eruption leading from capsula and piercing part of ampulla, ancora and tubus. **PHALLUS** (= MALE GENITALIA): *pd* – **Plica dorsalis** (= dorsal fold) and *pv* – **Plica ventralis** (= ventral fold), upper and lower membranous folds in primitive phallus of hagloid type (in Hagloidea, most Stenopelmatoidea, many Tettigonioidea and some Grylloidea) usually consisting of two or three lobes; *ep* – **Epiphallus**, large and more or less flat sclerite covering most part of dorsal surface of plica dorsalis in phallus of grylloid type (in many Grylloidea, some Tettigonioidea and some Stenopelmatoidea) often having diverse processes and sometimes divided into several sclerites; *a* – **Apodeme epiphallicum** (= epiphallic apodeme), large paired apodeme situated at anterolateral corner of epiphallus or along anterior edge of epiphallus (in most Gryllidae), but sometimes absent or forming unpaired apodeme; *sc* – **Scleritum epiphallicum** (= epiphallic sclerite), small sclerite on dorsal surface of plica dorsalis in phallus of tettigonioid type (often in Tettigonioidea, sometimes in Grylloidea and Stenopelmatoidea); *r* – **Ramus**, paired ribbon-like anterolateral projection of epiphallus often separated from it by small membranous area (only in Gryllidae) but sometimes completely disappearing; *ra* – **Rachis** (= guiding rod), membranous or sclerotized unpaired process of ventral surface of plica dorsalis directed backwards or downwards and adapted for insertion of spermatophore tube into female spermathecal duct, but sometimes also for fixation of phallus in female genital chamber (in Grylloidea, sometimes in Tettigonioidea with grylloid or complicated tettigonioid phallus); *v* – **Virga**, spine-like (thin and rather long) sclerotized rachis with acute or almost acute apex (often in Gryllidae and Mogoplistidae, sometimes in Myrmecophilidae); *ec* – **Ectoparameron** (= ectoparamere), sclerotized or membranous, movable (articulate) or almost movable paired process of epiphallus or rachis used for grasping female copulatory papilla, for anchor-like fixation of phallus in female genital chamber, or for orientation of phallus in this chamber (often in Gryllidae and Myrmecophilidae; seldom more than one pair of ectoparameres developed); *en* – **Endoparameron** (= endoparamere), paired or unpaired sclerotized part of ventral surface of plica dorsalis situated at base of rachis and/or ectoparamere for attachment of strong muscles (in Gryllidae and Myrmecophilidae; left and right endoparameres often partly fused); *ap* – **Apodema principale** (= endoparameral apodeme), largest paired apodeme present in phallus of almost all recent ensiferans and connected with ventral surface of plica dorsalis (in most Grylloidea, this apodeme connected with plica dorsalis via endoparamere); *f* – **Formula** (= mold or mould of spermatophore attachment plate), distinctly or weakly sclerotized plate (or several plates situated near each other) used for formation of spermatophore ancora (in most Gryllidae) and often having unpaired apodeme; *se* – **Semitubus**, unpaired sclerotized or semimembranous groove between rachis and formula used for formation of short or long spermatophore tube (in most Grylloidea; sometimes semitubus with small or rather large apodeme, or with semisclerotized ligament connecting semitubus near base of rachis with median part of fused endoparameres); *sa* – **Sacculus** (= spermatophore sac), large unpaired invagination of ventral membranous surface of plica dorsalis in region of rachis base for placing of long semitubus necessary for formation of long spermatophore tube (some Gryllidae and Mogoplistidae); *va* – **Valva** (= valve), paired membranous lobe of plica ventralis in phallus of Grylloidea serving for formation of spermatophore ampulla or part of this ampulla (right and left valves sometimes fused with each other).


SCHEMATIC PICTURE OF PHALLUS
FROM ABOVE AND IN SAGITTAL SECTION
(red area, spermatophore:
blue area, epiphallus or epiphallic sclerite;
lilac area, rachis;
rose area, endoparamere)
1
2
3
ra
ra
posterior lobe of epiphallus cut
4
9th tergite
10th tergite
ra
5
a
epiphallus articulated with 9th and 10th tergites of abdomen
ap
ra
6
epiphallus partly reduced: its median part almost ribbon-like
ap
se?
f?
7
8
ra
9
10
v (=ra)
11
12
13
14
15
ra
16
sacculus
ra
17
sacculus
ra
18
ap
pd
ap
ra

However, the type of phallus fixation in this chamber is often not evident, and these structures (usually not very strong ones) possibly help in orientation of the phallic parts inside this chamber, or perform some unknown function.

In Mogolistidae, male genital sclerites possibly appeared three times. The tettigonioid phallus of Malgasiinae may have evolved from the hagloid type independently but in the way similar to that of Gryllotalpidae; it also has an initial stage of rachis development (convergence; Fig. III: 12). Among Mogoplistinae, the phallus of the tribe Mogoplistini is hagloid, membranous (Fig. III: 13). But in most genera of Arachnocephalini (from the same subfamily), the dorsal fold (plica dorsalis) forms a single large lobe with a pair of narrow sclerites (this type of phallus looks as intermediate between the grylloid and the tettigonioid types); in the genus *Arachnocephalus*, this phallus is very simple (without distinct additional structures), but its very simple construction may be the result of reduction (Fig. III: 14). In other genera of Arachnocephalini (*Ornebius* and some others), strong development of a long and virga-like rachis as well as a large and flattened sacculus are observed (Fig. III: 16). The extremely long rachis of *Discophallus* (another genus of Arachnocephalini) is situated inside the extremely long, spiral-shaped sacculus (Fig. III: 17). The third way of possible convergent appearance of the phallic sclerite is demonstrated by the genus *Pseudomogoplistes* (probably also belonging to Arachnocephalini): its phallus has one large and heavily sclerotized structure possibly analogous to the rachis, semitubus and formula together but with a very large unpaired apodeme bifurcated anteriorly (each of the paired disc-like lateral parts of this apodeme are possibly ho-

Fig. III. Scheme of evolution of male genitalia in Grylloidea: **1**, hypothetical hagloid phallus (ancestral for all recent Grylloidea); **2**, hypothetical tettigonioid phallus of ancient representatives of Gryllotalpidae; **3**, complicated tettigonioid phallus (with rachis) of *Gryllotalpa* (Gryllotalpidae: Gryllotalpinae); **4**, hypothetical primitive (but weakly complicated, with rachis) grylloid phallus of ancient representatives of Myrmecophilidae; **5**, more complicated grylloid phallus with large unpaired epiphallic apodeme (*a*), with large unpaired endoparameral apodeme (apodema principale), and with lateral arms of epiphallus articulated with tergites (Myrmecophilidae: Myrmecophilinae); **6**, strongly complicated phallus with very large and rather high endoparameral apodeme, modified epiphallus, and sclerotized semitubus and formula (Myrmecopnilidae: Bothriophylacinae); **7**, hypothetical most primitive grylloid phallus of ancient representatives of Gryllidae; **8**, hypothetical primitive (but weakly complicated, with rachis) grylloid phallus of Gryllidae; **9**, more complicated (with formula) phallus of Gryllidae usual in Podoscirtinae, Nemobiinae, etc; **10**, strongly complicated phallus (with large sacculus and long semitubus, and with reversed spermatophore having long tube) of Gryllidae (Gryllinae, Itarinae, usually in Gryllomorphinae, Oecanthinae and Euscyrtinae, and sometimes in Podoscirtinae and Phalangopsinae); **11**, strongly complicated phallus of Gryllidae but additionally with festoon-like sacculus and with extremely long semitubus and tube of spermatophore (sometimes in Gryllinae and Gryllomorphinae); **12**, tettigonioid phallus of *Malgasia* (Mogoplistidae: Malgasiinae); **13**, hagloid phallus of *Paramogoplistes* (Mogoplistidae: Mogoplistinae: Mogoplistini); **14**, grylloid-tettigonioid (looking primitive but possibly secondary simplified) phallus of *Arachnocephalus* (Mogoplistidae: Mogoplistinae: Arachnocephalini); **15**, hypothetical primitive (but weakly complicated, with small rachis) phallus of ancient representatives of Arachnocephalini; **16**, more complicated (with flattened sacculus and long rachis) phallus of *Ornebius* and some other genera of Arachnocephalini; **17**, strongly complicated (with very long spiral-like sacculus and extremely long rachis) phallus of *Discophallus* (Arachnocephalini); **18**, possibly significantly complicated hagloid phallus having one large sclerite corresponding to several structures of grylloid phallus: rachis, semitubus, formula and paired apodema principale (?Arachnocephalini: *Pseudomogoplistes*). Position of spermatophore inside phallus in Gryllotalpidae, Myrmecophilidae and Mogoplistidae is insufficiently clear or unclear; abbreviations as in Fig. II.

mologous to apodema principale); however, its dorsal fold is completely membranous (Fig. III: 18). Thus, this phallus may be a unique, very complicated variant of the hagloid type.

ACKNOWLEDGEMENTS

This study was partly supported by the Presidium of the Russian Academy of Sciences (Program "Biosphere Origin and Evolution of Geo-biological Systems"). The study was performed in the frames of the state research project No. 01201351189 (Russian Federation).

REFERENCES

Alexander R.D. & Otte D. 1967. *The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera*. Miscellaneous publications, Museum of Zoology, University of Michigan, **133**: 1–62.

Anisyutkin L.N. 2009. New representatives of the genus *Nahublattella* Bruijning, 1959 (Dictyoptera, Blattellidae) from Central and South Americas. *Entomologicheskoe obozrenie*, **88**(3): 603–624. [In Russian. English translation in *Entomological Review*, 2009, **89**(7): 820–838].

Anisyutkin L.N. 2011. A review of the genus *Euphyllodromia* Shelford, 1908 (Dictyoptera: Ectobiidae), with description of three new species. *Trudy Zoologicheskogo instituta RAN* [Proceedings of the Zoological Institute, Russian Academy of Sciences], **315**(4): 369–398.

Chopard L. 1969. *Grylloidea. The fauna of India and adjacent countries. Orthoptera*, 2. Calcutta: Baptist Mission Press. 421 p.

Desutter L. 1987. Structure et évolution du complexe phallique des Gryllidea (Orthoptères) et classification des genres Néotropicaux de Grylloidea. Première partie. *Annales de la Société entomologique de France (nouvelle série)*, **23**(3): 213–239.

Desutter L. 1988. Structure et évolution du complexe phallique des Gryllidea (Orthoptères) et classification des genres Néotropicaux de Grylloidea. Deuxieme partie. *Annales de la Société entomologique de France (nouvelle série)*, **24**(3): 343–373.

Desutter-Grandcolas L. 1992. Les Phalangopsidae de Guyane française (Orthoptères, Grylloidea): systématique, éléments de phylogénie et de biologie. *Bulletin du Muséum national d'Histoire naturelle (4e série)*, **14**(section A, 1): 93–177.

Gorochov A.V. 1984. On the classification of recent Grylloidea (Orthoptera) with description of new taxa. *Zoologicheskij Zhurnal*, **63**(11): 1641–1651.

Gorochov A.V. 1986a. System and morphological evolution of crickets from the family Gryllidae (Orthoptera) with description of new taxa. Communication 1. *Zoologicheskij Zhurnal*, **65**(4): 516–527. [In Russian].

Gorochov A.V. 1986b. System and morphological evolution of crickets from the family Gryllidae (Orthoptera) with description of new taxa. Communication 2. *Zoologicheskij Zhurnal*, **65**(6): 851–858. [In Russian].

Gorochov A.V. 1995a. System and evolution of the suborder Ensifera (Orthoptera). Part 1. *Trudy Zoologicheskogo instituta RAN* [Proceedings of the Zoological Institute, Russian Academy of Sciences], **260**: 1–224. [In Russian].

Gorochov A.V. 1995b. System and evolution of the suborder Ensifera (Orthoptera). Part 2. *Trudy Zoologicheskogo instituta RAN* [Proceedings of the Zoological Institute, Russian Academy of Sciences], **260**: 1–213. [In Russian].

Gorochov A.V. 2001. Preliminary notes on the history of South American Ensifera (Orthoptera). *Acta Geologica Leopoldensia*, **24**(52/53): 81–86.

Gorochov A.V. 2002. Taxonomy of Podoscirtinae (Orthoptera: Gryllidae). Part 1: the male genitalia and Indo-Malayan Podoscirtini. *Zoosystematica Rossica*, **10**(2): 303–350.

Gorochov A.V. 2010a. New and little-known orthopteroid insects (Polyneoptera) from fossil resins: communication 3. *Paleontologicheskij Zhurnal*, 4: 70–87.

Gorochov A.V. 2010b. New and little-known orthopteroid insects (Polyneoptera) from fossil resins: communication 4. *Paleontologicheskij Zhurnal*, 6: 56–71.

Gorochov A.V. 2013. Evolution of the copulatory apparatus in Ensifera (Orthoptera): Grylloidea. *Metaleptea*, special conference issue (11th International Congress of Orthopterology, 11–15 August 2013, Kunming, China): 64.

Gorochov A.V. 2014. Evolution and taxonomic significance of the copulatory apparatus in Ensifera (Orthoptera). Part 1: General con-

cepts and origin. *Zoosystematica Rossica*, **23**(2): 197–209.

Jost M. S. & Shaw K. L. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution*, **38**: 510–530.

Mesa A. & Garcia P. 1999. *Paranurogryllus*, a new genus of cricket with two new species (Orthoptera, Grylloidea, Gryllidae). *Journal of the Orthoptera Research*, **8**: 65–72.

Mesa A., Garcia P. & Zefa E. 1999. *Strinatia brevipennis* Chopard 1970 and *S. teresopolis* sp. n.: descriptioin of new species and comparative study of their chromosomes and male and female genitalia sclerites (Grylloidea, Phalangopsidae). *Journal of the Orthoptera Research*, **8**: 73–82.

Mesa A. & Garcia-Novo P. 1997. *Endecous onthophagus*: a new combination. Phallic sclerites and karyology of the species (Orthoptera: Grylloidea). *Journal of the Orthoptera Research*, **6**: 117–120.

Mesa A., Ribas Ch.C. & Garcia P.C. 1999. *Phoremia nigrofasciata* and *P. circumcincta*: two new species of cricket of the subfamily Nemobiinae (Orthoptera, Grylloidea, Trigonidiidae). *Journal of the Orthoptera Research*, **8**: 59–64.

Randell R.L. The male genitalia in Gryllinae (Orthoptera: Gryllidae) and a tribal revision. *Canadian Entomologist*, **96**(12): 1565–1607.

Received December 22, 2014 / Accepted April 26, 2015