

Evolution and taxonomic significance of the copulatory apparatus in Ensifera (Orthoptera). Part 1: General concepts and origin

Эволюция и таксономическое значение копулятивного аппарата у длинноусых прямокрылых (Orthoptera: Ensifera). Часть 1: Общие положения и происхождение

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The importance of using copulatory characters in generic and higher taxonomy (not only in species taxonomy) is discussed in the light of the recent “genital clock” concept which should partly replace the old “lock-and-key” theory. This concept assumes that evolutionary changes in the copulatory apparatus (if it is sufficiently complicated) follow after genetic drift, and that these processes occur at a more uniform rate than changes in the characters of external morphology, ecological properties and many other biological traits, since structure of this apparatus is less dependent upon the situation in the ecosystem. Evolution of the copulatory apparatus in the suborder Ensifera and in its ancestors may be divided into three hypothetical stages reflected in some morphological features: 1) a highly hypothetical stage without copulation and without a copulatory apparatus in the most ancient (extinct) orthopteroid insects; 2) the appearance of different organs in early Orthoptera serving for fixation of partners during copulation and for insertion of the spermatophore in the female genital chamber; 3) the development of complicated organ with consolidation of these functions.

Важность использования копулятивных признаков в родовой и высшей таксономии (не только в видовой таксономии) обсуждена в свете современной гипотезы о «генитальных часах», которая должна частично заместить старую теорию «ключа и замка». Эта гипотеза предполагает, что изменения копулятивного аппарата (если он достаточно сложен) следуют за генетическим дрейфом, и что эти процессы идут с более равномерной скоростью, чем изменения в признаках наружной морфологии, экологических свойствах и многих других особенностях биологии, поскольку строение этого аппарата менее зависимо от ситуации в экосистеме. Эволюция копулятивного аппарата в подотряде длинноусых прямокрылых (Ensifera) и у его предков может быть подразделена на три гипотетические стадии, отраженные в некоторых морфологических чертах: 1) высоко гипотетическая стадия без копуляции и без копулятивного аппарата у наиболее древних (вымерших) ортоптероидных насекомых; 2) появление разных органов у ранних прямокрылых, служащих для фиксации партнеров при копуляции и для введения сперматофора в генитальную камеру самки; 3) развитие сложного органа с консолидацией этих функций.

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

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

INTRODUCTION

The sexual traits are among the most important characters used in biological taxonomy. In botany, they have been used for species-level and higher classifications since Linnaeus's times, whereas in zoology, the importance of these characters was realized with some delay. This delay is especially distinct in taxonomy of some groups of orthopteroid insects. Many of the old descriptions and keys to the order Dermaptera, suborder Blattina, superfamily Grylloidea, and some other groups are almost unsuitable for the species and generic identifications. Moreover, at present some specialists use the sexual characters mainly in species taxonomy but try to find mainly non-sexual characters for generic taxonomy (Otte & Alexander, 1983; Kevan & Jin, 1993; Nickle, 2003; Liu & Zhou, 2007). Their opinion may reflect the old idea that sexual characters should not be used in generic taxonomy since they are present in only one of the two sexes (Bey-Bienko, 1971). This idea has no sufficient scientific ground, but for substantiation of an opposite idea, it is necessary to propose more logical hypotheses for explanation of the following phenomena: **the presence of a certain stability** of sexual characters in the same species in many cases; **the absence of such stability** in other cases; **the presence of distinct sexual differences** between some species which are very similar in other characters; and **the absence of these differences** between some species showing distinct differences in non-sexual characters. These hypotheses must be consistent with the recent knowledge about the general regularities of evolutionary process and with the evolutionary trends revealed during the study of concrete taxa.

The paper is based on the material on this topic presented by the author at the 10th International Congress of orthopterology (21–25 June 2009, Antalya, Turkey) and briefly mentioned in the abstract of this presentation (Gorochov, 2009).

RESULTS

The primary and secondary sexual characters and intraspecific stability

The widely accepted subdivision of the sexual characters into primary and secondary ones may be based on the sequence of their historical development, on their importance in individual development or on their importance for reproduction (Zavadovskij, 1922; Ghilarov, 1989: the articles "Primary sex characteristics" and "Secondary sexual characteristics"). The first two principles force us to use the name "primary" for only characters of the gonads, some accessory sex glands, and their ducts, since all the other sexual characters (including the penis and the ovipositor) appeared later, or their appearance may have been caused by the activity of the above-mentioned glands.

Thus, these principles are not in accordance with the most common views, but consistent use of the third principle (the principle of importance for reproduction) is also not exactly congruent with these views. Reproduction is almost the only function of the genitalia, gonads and other internal sexual organs of higher animals (under the natural conditions, organisms which have lost these organs can survive but not reproduce); the characters of these organs are usually termed "primary" sexual characters. All the other morphological sexual characters of these animals are considered "secondary" ones; many of them are associated with two or more principal functions (the reproductive function being only one of them: for example, an increase in the body size of the males of some mammals reduces the pressure of predators and also helps in sexual competition) or are not critically important for reproduction (their disappearance may destroy the potential for sexual competition but not for reproduction itself: development of antlers, tusks, or a mane only or mainly in male). However, some other "secondary" sexual characters are also very important for reproduction of higher animals, as these animals cannot have any reproductive

success under natural conditions without sexual behavior and/or attractive signalization; moreover, there are special organs participating only or mainly in the actions connected with reproduction: the tail in the male of peacock, the sound-producing organs in many animals, and some others.

The use of this classification of sexual characters for lower animal (invertebrates) leads to additional difficulties. The male copulatory apparatus of some insects is rather complex; it includes the structures adapted to insertion of the spermatophore tube into the spermathecal duct (somewhat analogous to the penis in mammals) as well as the structures used for fixation of the female during copulation (the epiphallus and ectoparameres in the genitalia of Gryllidae, the cerci in most Tettigoniidae, hooks on the paraprocts and abdominal tergites in many representatives of Stenopelmatoidea, the characteristic claspers formed from distinctly curved hind tibiae and strong ventral teeth of the hind femora in some Ensifera and Phasmatoptera, and specialized attachment organs of the fore legs in diving beetles). If one classified all the characters of the structures mainly adapted to this fixation as "secondary" ones (because in higher animals, this function is usually performed by unspecialized organs), then the characters of gryllid male genitalia would be divided into "primary" and "secondary" ones; moreover, in some cases parts of the same structure participating in the female fixation as well as in the spermatophore tube insertion (the ectoparameres of some gryllids) would have to be classified as "secondary" and "primary" characters at the same time. Another problem appears if one attempts to divide the characters of the fixing devices into "secondary" or "primary", as it is necessary to find an objective criterion for establishing a sufficient (for this division) level of reproductive importance of these characters.

One of these criteria may be the value of variability in sexual characters within the same species. A certain stability of the most important sexual characters allows differ-

ent individuals to have the widest choice of sexual partners and to form their posterity with the minimal breach of its development during the most vulnerable early stages (for example, the stability of the ovipositor structure ensures the most similar conditions for oviposition and thus for egg development). This stability is so important for the reproductive success of the species that natural selection supports such stability, although in many cases this selection supports certain diversity in other structures (such diversity allows species to have certain preadaptations to different changes of the environment). Diversity in sexual characters may also be useful since some of these characters belong to the special structures participating in sexual competition, and their strong development in some individuals may disrupt their cryptic appearance and reduce their survival during increasing predator pressure. So, it seems to me that it is reasonable to divide all sexual characters into primary and secondary ones on the basis of their stability within the same species. Such a classification is somewhat different from the most commonly accepted one, but it may more exactly reflect the importance of these characters for reproduction. This approach still faces some problems, as it permits the presence of intermediate variants; for example, the characters of the male stridulatory apparatus in many representatives of Grylloidea and Tettigonioidea are usually stable and may be considered primary sexual characters, but in some of them having two or three morphological forms (f. macroptera, f. brachyptera and intermediate one) there are certain differences in the size of the sound-radiating areas within the same species (due to some reduction of the tegmina in the latter forms).

Interspecific sexual differences: the "lock-and-key" and "genital clock" hypotheses

In many animals (including most insects), the sexual characters having a certain intraspecific stability and distinct interspecific differences at the same time

belong mainly to the copulatory apparatus. To explain these characteristics of the copulatory apparatus, the “lock-and-key” hypothesis was proposed. This hypothesis supposes that this apparatus functions as one of the isolation mechanisms preventing interbreeding of sympatric species (for additional information about this hypothesis see Rentz, 1972). The absence of any distinct differences in the copulatory apparatus of many sympatric species may be explained by the presence of some other isolation mechanisms (behavioral, acoustic, visual, and others). However, this hypothesis cannot explain the presence of distinct differences in the copulatory apparatus of many closely related allopatric species and of many closely related species which possess additional isolation mechanisms (for example, acoustic ones) preventing inter-specific copulation. Moreover, although the presence of copulatory isolation mechanisms must be especially important for the most closely related species, these species usually do not have any distinct differences in copulatory apparatus; also, although copulatory isolation mechanisms seems to be less important for remotely related species (for example, from different genera) because they usually have greater differences in their behavior and ecological preferences strongly reducing the possibility of inter-specific copulation even without special copulatory isolation mechanisms, but such species have more distinct differences in the copulatory apparatus.

These facts have allowed me to propose a somewhat other explanation for the above-mentioned characteristics of the copulatory apparatus (Gorochov, 2005) which is referred to herein as the “genital clock” hypothesis. It does not reject the “lock-and-key” hypothesis but distinctly limits its application. The “genital clock” hypothesis supposes that the rate of changes in the complex of primary (stable) sexual characters (if this complex is sufficiently complicated: for example, in the compound copulatory apparatus) and the rate of genetic drift are rather

similar and may be considered more or less constant as compared to the rate of changes in many non-sexual or secondary sexual characters. In the environment highly competitive for a concrete species, the change of its life form is very difficult because all accessible adaptive areas are occupied by numerous species with high competitive ability. The adaptive evolution under such conditions proceeds slowly, without quick changes in important adaptive characters, and the genetic drift is reflected mainly in the change of characters less closely associated with the environment, for example, in the structure of the male genitalia (Gorochov, 2001a). In the less competitive environment, this species may have quick adaptive radiation, since change of its life form can happen easily (because of the absence or a small number of serious competitors). At the same time, the characters less closely connected with the environment (for example, the structure of the copulatory apparatus) have a more stable rate of changes, similar to that of the genetic drift, and therefore this rate may be distinctly slower than that of the characters more closely connected with the environment. These two types of evolution correspond to the “coherent evolution” and “non-coherent evolution” concepts, respectively (Krassilov, 1969).

Thus, changes in the compound complex of primary sexual characters as well as the molecular changes may be considered a certain kind of biological clock. This conclusion is important for taxonomy since it means that bigger differences in these characters are evidence of older divergence between species. This regularity is certainly not absolute, but it allows one to imagine (very roughly) the process of species divergence as the following sequence: (1) subdivision of a single species into several very closely related ones having indistinct (invisible) changes in the complex of their primary sexual characters and using the isolation mechanisms not connected with this complex (this stage is present in many species of the cricket subgenus *Thliptoblemmus*

Saussure, 1898 and in all species from many genera of Acrididae); (2) gradual formation of small but distinct interspecific differences between such complexes in the descendants of the above-mentioned species with simultaneous stabilization of these complexes in each of these species (this stage is characteristic of most species from many genera of Gryllidae and from some genera of Tettigoniodea and Stenopelmatoidea; it is possible that the copulatory apparatus may begin to function as an additional isolation mechanism only at this stage); (3) slow development of big and very big differences between the complexes of primary sexual characters accompanied by their intraspecific stabilization (such differences characterize related subfamilies, families, orders, etc.; for very high-ranked taxa, establishment of homologies in these complexes is often very difficult or even practically impossible). If this hypothesis is correct or even partly correct, the primary sexual characters (for example, those of the copulatory and stridulatory devices if the latter device is specialized to sexual communication) must be necessarily used in the generic and higher taxonomy, as the total value of their differences may indirectly reflect a total value of genetic differences between the species more adequately than most of the other characters often used in taxonomy.

However, the latter conclusion is only valid for compound complexes of these characters or their significant parts, because such complexes and parts are less subjected to parallel evolution than many other complexes (for example, less compound complexes or complexes of adaptive characters). The combination of all the primary sexual characters (including the stable sexual characters of the stridulatory apparatus, different attractive glands, and devices for fixation of partners during copulation) in dioecious species may be regarded as a certain system, which is comparable to the digestive, nervous or circulatory systems but differs from them in being divided into two unequal parts: one belonging to the male,

and one belonging to the female. The copulatory and communicative components of this system are also divided into two parts, which may be very unequal. Usually the male has the more significant part of these components which include numerous and often compound structures; in this case, the female may have only one simple structure or a few ones (many representatives of Tettigoniodea and Grylloidea). The latter structure (or structures) has a limited ability to form of different modifications, as many of them almost inevitably recur (including partial return to the ancestral condition). Such simple structures (for example, the copulatory papilla in Gryllidae) do not provide any good characters for generic and higher taxonomy. If the female has only simple copulatory and communicative devices, it is necessary to use mainly the male sexual characters; but if these devices are rather simple in both sexes (some Stenopelmatoidea), the use of characters of these devices in generic and higher taxonomy is rather difficult owing to numerous parallelisms.

It should be added that the simple structure of such devices may create the illusion of little divergence between species, since the evolutionary drift of the characters of these devices may be imagined as prolonged fluctuations ("Brownian motion") near the once established successful variant. Some compound complexes of primary sexual characters may remain stable for longer time than some others (for example, the gonads and sometimes the stridulatory apparatus in comparison with the copulatory apparatus). This situation is possibly connected with the usefulness of stability in such complexes, if their characters are in highly balanced condition with respect to each other and to the non-sexual complexes of high adaptive significance. For example, the male tegmina of the gryllid genus *Trellius* Gorochov, 1988 have two main functions (one of them is highly adaptive to the environment and thus important for preservation of the life form, while the other is sexual, communicative), and changes in its com-

pound tegminal stridulatory apparatus are strongly slowed down since these changes would be practically impossible without corresponding changes in the structure of other parts of the tegmina and thus in their adaptive characteristics.

Early evolution of sexual characters in orthopteroid insects

The spermatophore of Arthropoda, in accordance to the widely known theory by Giljarov (1970), appeared independently in different groups during their adaptation to life on land. It is most probable that the spermatophore was initially transferred from male to female without copulation. This method of spermatophore transfer is preserved in very primitive apterous insects (Thysanura) and in some terrestrial representatives of other classes of Arthropoda. There are also indirect evidences suggesting that the copulatory apparatus was originally absent in some earliest representatives of Pterygota and independently formed in some oldest branches of this subclass. One such evidence is the development of a "secondary penis" from processes of the second and third abdominal sternites in the male of Odonata (the male transfers sperm to this copulatory device from its own gonopore). It is considered (Bechly et al., 2001) that such a copulatory device could have appeared only in case of the original absence of copulation in an ancestor of the recent taxa of Odonata (possibly the male of this ancestor began to attach its spermatophore not to any surrounding substrate but to its own body surface).

Another evidence is the characteristic structure of abdominal sexual organs in the male and especially in the female visible on some oldest (Carboniferous) imprints of Pterygota from the orders Palaeodictyoptera and Meganeurida (Brauckmann, 1991; Bechly et al, 2001). The long and possibly segmented styli of these insects may have functioned as sensory organs serving in the male for assessment of the substrate conditions and spermatophore position during its

attachment to the substrate (Fig. 1, a), and in the female, for searching the spermatophore on the substrate and for controlling its fixation in or near the female gonopore (Fig. 1, g). Among the later representatives of Pterygota, such styli were found in the males of Ephemeroptera and ancient roaches (Vishnjakova, 1971); however, in the first order these styli have changed into copulatory hooks (Fig. 1, b), and in the latter insects, the styli possibly had a different sensory function associated with the presence of the copulatory structures (Fig. 1, c). The shortened remnants of such styli were also preserved in some taxa of Pterygota: as copulatory sensory structures in the male (many recent representatives of Dictyoptera and Orthoptera), as sensory structures participating in control over the position of the ovipositor apex during oviposition in the female (Fig. 1, h, i), and as rudiments in female nymphs (Fig. 1, j, k). The latter nymphal rudiments are now present in Grylloblattida and in some other groups of Polyneoptera, but they are absent in adult females of all the known (recent and fossil) representatives of Polyneoptera (with the only exception of *Tarragoilus* Gorochov, 2001, one of the recent hagloid genera with a reduced, almost nymphal ovipositor; Gorochov, 2001b); nevertheless their preservation may be explained by the great importance of sensory styli for the females of the earliest orthopteroid insects.

The recent hypothesis about early evolution of the infraclass Polyneoptera (=orthopteroid insects) (Gorochov, 2004), based on analysis of recent and fossil materials, supposes that the common ancestor of Polyneoptera may have had the following sexual characters: the coxopodites of the 9th abdominal sternite of the male were approximately the same as those of Grylloblattida, ancient roaches (Vishnjakova, 1971), and the possible representatives of Eoblattida (Vilesov & Novokshonov, 1993), i.e. not fused with this sternite and with one another (Figs 1, c–f); the styli situated on these coxopodites were long and segmented

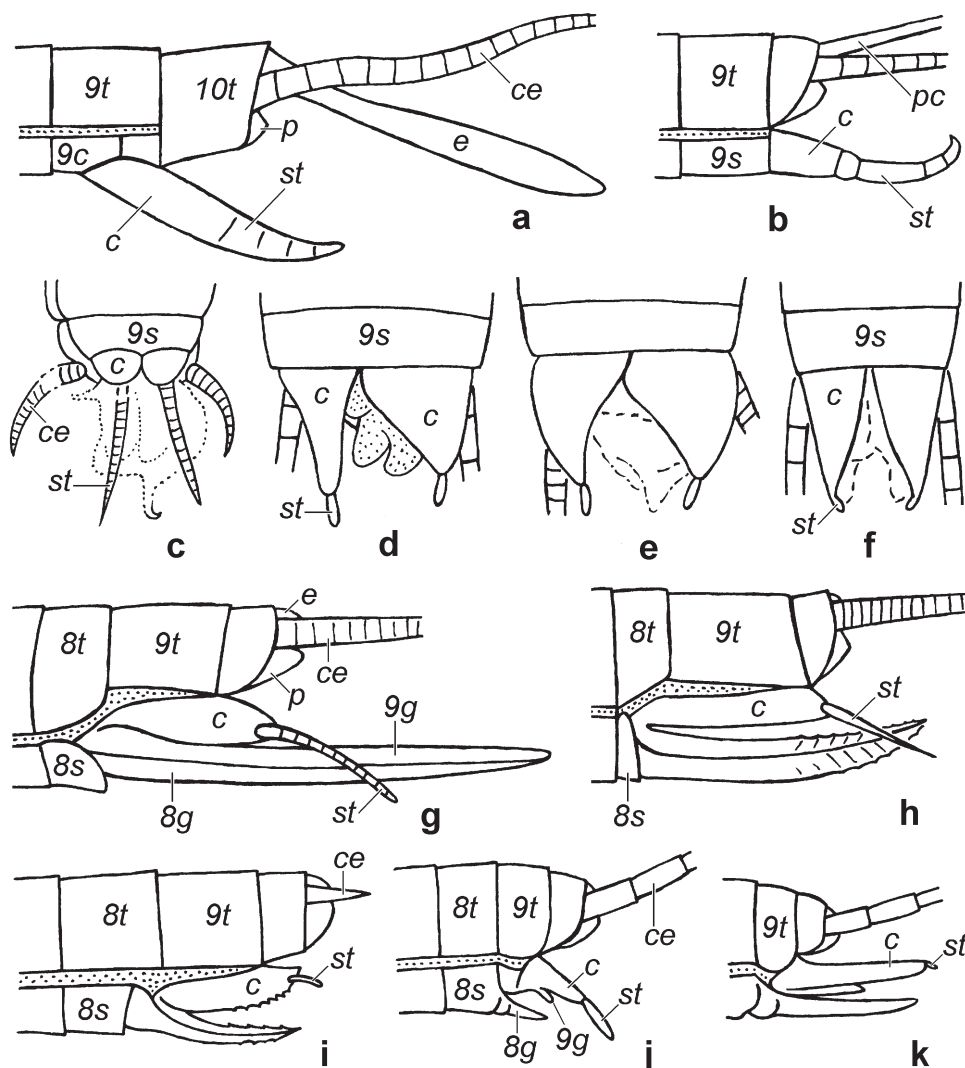


Fig. 1. Scheme of abdominal apex in some fossil and recent Pterygota (after Gorochov, 2004). **a, b**, male, lateral view: (**a**, *Namurotypus* (Meganeurida), Carboniferous; **b**, recent Ephemeroptera); **c–f**, male, ventral view: (**c**, *Aktassoblatta* (Dictyoptera), Jurassic; **d**, recent Grylloblattida; **e**, *Blattogryllus* (Grylloblattida), Jurassic; **f**, *Tillyardembia* (Eoblattida?), Permian); **g–i**, female, lateral view: (**g**, *Homioptera* (Palaeodictyoptera), Carboniferous; **h**, *Permuralia* (Diaphanopterida), Permian; **i**, recent Odonata); **j, k**, recent Grylloblattida, lateral view: (**j**, protonymph of female; **k**, deutonymph of female).

Abbreviations: 8g, 9g, gonapophyses of 8th and 9th abdominal segments; 8s, 9s, 8th and 9th abdominal sternites; 8t–10t, 8th–10th abdominal tergites; c, coxopodite of 9th abdominal segment; ce, cercus; e, epiproct; p, paraproct; pc, paracercus; st, stylus.

(as in Fig. 1, c); the male genitalia consisted of only membranous folds around the gonopore (the name “genitalia” is used here only for the structures originating from these

folds or areas near them and for structures of female genital chamber), participated mainly in the formation of the spermatophore, and were probably more or less ho-

mologous to the “penis” of Thysanura; in the female, the 8th abdominal sternite was well developed (it is absent or strongly reduced in the recent females of Polyneoptera except Grylloblattida and probably Mantophasmatodea), the operculum was absent (this structure is often named “genital plate” or “subgenital plate”, but these names are also used for a different structure in the male), and the 9th abdominal sternite and its coxopodites were presented by the parts of the ovipositor which was more or less similar to that of Grylloblattida; the upper valves of ovipositor were shorter than other valves (gonapophyses) and had free, rather long, and articulated styli at the apex; the copulatory structures for fixation of the partner and stridulatory organs for its attraction were absent in both sexes. The sexual characters listed above are mainly the primary ones; they belong to the organs which may provide the formation and non-copulative transfer of the spermatophore as well as oviposition. There are no other grounded ideas about the sexual characters in the earliest orthopteroid insects.

The hypotheses about the origin and phylogeny of the orders of Polyneoptera proposed in the same publication (Gorochov, 2004) provide an additional morphological basis for the old idea of holophyly of this infraclass (this idea was also supported by the recent paleontological and molecular data: Rohdendorf & Rasnitsyn, 1980; Rasnitsyn & Quicke, 2002; Whiting et al., 1997; Whiting, 2002) and show that these orders diverged from each other during or around the Carboniferous (Fig. 2), with the possible exception of two smaller taxa with a very obscure origin: the “order” Embioptera and the enigmatic taxon Mantophasmatodea (in Fig. 2, the latter taxon is tentatively included in Titanoptera). Thus, the great age of these (large) orders allows one to suppose that in each of them (or in each superorder at least), the copulatory apparatus appeared independently. Some support of this opinion comes from the structure of this apparatus in the different polyneop-

teran orders: their copulatory structures are very different, and no homologies between many of them (Dictyoptera, Dermaptera, Phasmatoptera, etc.). Moreover, even within a single order Orthoptera (which is one of the old orders known since the Late Carboniferous) it is possible to propose three variants of the appearance of copulation and the copulatory apparatus: they could have appeared (1) in the ancestors of this order before its separation, (2) in an ancient species of Orthoptera ancestral to all the recent taxa of this order, or (3) independently in a few extinct representatives of Orthoptera ancestral to the different recent higher taxa of this order.

General trends in the evolution of the ensiferan copulatory apparatus

The suborder Ensifera is an oldest suborder of the order Orthoptera; it is considered as ancestral for the suborder Caelifera (Sharov, 1968; Gorochov, 1995). The structure of the copulatory apparatus in the most ancient, Carboniferous ensiferans is unknown. Their abdominal sexual characters were possibly more or less similar to those of the above-mentioned hypothetical ancestor of Polyneoptera. However, the Early Permian representatives evidently had a copulatory apparatus similar to that of some primitive recent ensiferans: the male genital plate consisted of the coxopodites and the 9th abdominal sternite fused together; the styli were short and unarticulated; the male cerci were unspecialized, lacking hooks and processes; the male genitalia were probably membranous, consisting of membranous folds for spermatophore formation (Gorochov, 1995). Some females of that time, judging by the material of Sharov (1968) and my original data, probably had a developed 8th abdominal sternite (as in recent grylloblattids) and no genital plate (this plate in Orthoptera and the operculum in Phasmatoptera evidently have independent origins), but their imaginal ovipositor had the upper valves (the coxopodites of the 9th abdominal sternite) not shorter than

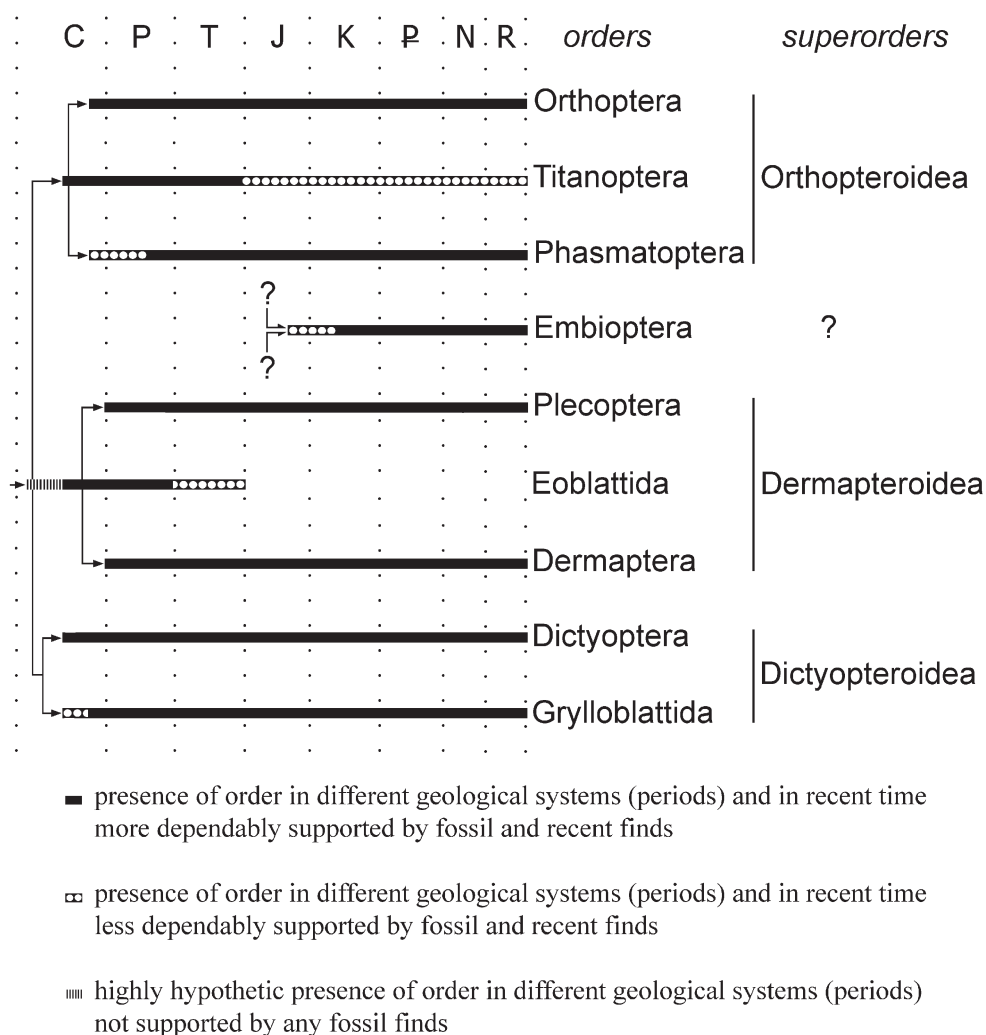


Fig. 2. Paleophylogram of Polyneoptera (after Gorochov, 2004) [order of isolation of two superorders and four orders from Eoblattida and Titanoptera is not clear].

the other valves of the ovipositor and was lacking the styli.

Based on the morphological study of numerous recent ensiferans, Gorochov (1984) supposed that the male genitalia originally consisted of only two main membranous folds around the gonopore: *dorsal fold* and *ventral fold* (Fig. 3, a, b). These folds participated in spermatophore formation which took place inside the cavity between them. This *hagloid type* of male genitalia is present in all the recent species of the primi-

tive superfamily Hagloidea and in many recent groups in all the other main phylogenetic lineages (Tettigonioidae, Stenopelmatoidea, and Grylloidea) which probably originated from Hagloidea. If the common ancestor of all these taxa had copulation, its male copulatory device may have originated from some structures other than genital ones: from specialized processes or hooks of the hind abdominal tergites (as in some recent representatives of Stenopelmatoidea), from processes of the paraprocts (as

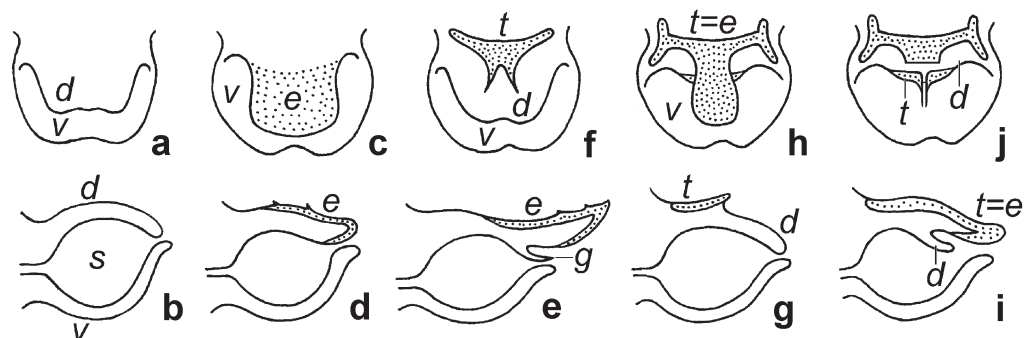


Fig. 3. Scheme of male genitalia (partly after Gorochov, 1984, 1995), dorsal view (upper row) and sagittal section (lower row) [sclerotized parts dotted]: **a, b**, hagloid type; **c–e**, grylloid type (**c, d**, simple variant; **e**, complicated variant); **f–j**, tettigonioid type (**f, g**, simple variant; **h, i**, complicated variant characteristic of *Gryllotalpa* and partly convergent to complicated variant of grylloid type; **j**, same but without distal part of epiphallus).

Abbreviations: *d*, dorsal fold; *e*, epiphallus; *g*, rachis (= guiding rod); *s*, spermatophore cavity; *t*, titillators (= small sclerites of dorsal fold; in *Gryllotalpa*, larger proximal titillator is named epiphallus, and smaller titillators on apical part of dorsal fold together with this apical part form rachis); *v*, ventral fold.

in recent species of Hagloidea and some recent groups of Stenopelmatoidea and Grylloidea) or of the subgenital plate (as in some recent species of Hagloidea, Tettigonioida, and Grylloidea), from the specialized epiproct (as in many species of Tettigonioida), and/or from the cercal hooks (as in most Tettigonioida and some genera of Grylloidea). The latter origin of the male copulatory device is less probable for this ancestor, as the cerci of all the ancient fossil ensiferans with known abdominal apex are not hooked. The female of this ancestor may have had some copulatory cavities, processes, rough areas, and other catches on the external part of its abdominal apex serving for fixation of the male copulatory structures. However, no visible traces of these hooks and other catches in the rare Palaeozoic imprints of the ensiferan abdomen.

Such a copulatory apparatus may have appeared once or more than once, but in either case, it is most probable that in the male, it was originally represented only by the structures of the dorsal half of the abdominal apex, i.e. by tergal, paraproctal, and/or epiproctal specializations. This assumption follows from the preservation of

short sensory styli at the male subgenital plate of many ensiferan taxa (from all recent superfamilies except Grylloidea) lacking any special device for exact orientation of the spermatophore aperture opposite female spermathecal opening, since a possible function of such styli is the control over the position of the ventral half of the male abdominal apex during copulation (this control is necessary for the exact orientation of the spermatophore aperture; Fig. 4, a, b). This function of the male styli in the ancestor (ancestors) of all the recent ensiferans appeared probably to ensure copulation, and the establishment of contact between the copulatory structures of the partners led to the shortening of these styli and possibly whole subgenital plate (its shortening could be one of reasons of fusion of its components: the sternite and coxopodites). If male genitalia acquire fixing devices providing such orientation of the spermatophore aperture, or if additional structures for fixation of the ventral half of the male abdominal apex appear, the sensory styli usually become reduced or disappear (the ventral fixation of the male abdominal apex and its dorsal fixation in two places create

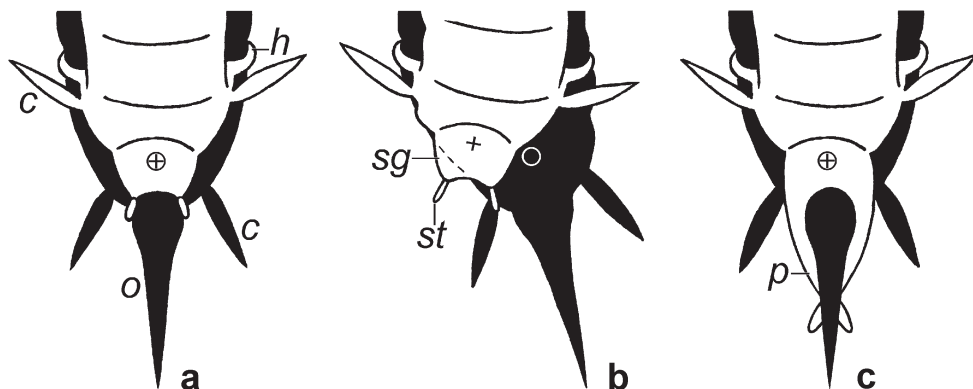


Fig. 4. Scheme of abdominal apices of male (white) and female (black) during copulation, ventral view (position of spermatophore aperture is designated by small cross; position of spermathecal opening, by small circle): **a**, normal copulative position with styli touching base of ovipositor (position of aperture of spermatophore located within male genitalia and position of spermathecal opening coinciding with one another); **b**, possible displacement of ventral half of male abdominal apex in relation to female one (positions of above-mentioned aperture and opening not coinciding with one another); **c**, rigid attachment of ventral half of male abdominal apex to ovipositor base by lateral processes of genital (=subgenital) plate (styli disappear).

Abbreviations: *c*, cercus; *h*, copulatory hook of dorsal half of male abdominal apex; *o*, ovipositor; *p*, lateral process of genital (=subgenital) plate; *sg*, genital (=subgenital) plate; *st*, stylus.

a rather rigid triangle preventing displacement of the spermatophore aperture during copulation; Fig. 4, c). Such dependence of the presence or absence of styli on the structure of the male copulatory apparatus is not absolute; it is only one of the general trends in the evolution of this apparatus, and some other variants are possible (for example, control over the position of ventral half of the male abdominal apex may be ensured by the sensory hairs of the subgenital plate, in which case reduction and disappearance of the styli are also possible; another example is one species of *Cyphoderris* Uhler, 1864 which has partly duplicating devices at the male subgenital plate: the normal sensor styli and copulatory hook between them).

The first variant of reduction and disappearance of the styli is often forced by development of the *grylloid type* of male genitalia, and the second one is sometimes observed in the male genitalia of the *tettigonioid type*. The grylloid type is characterized by general sclerotization of the dorsal fold (Fig. 3, c–e) which is membranous in the hagloid geni-

talia. This sclerotization is named “epiphallus”. It is probable that the grylloid type of genitalia (and thus of the epiphallus) appeared independently in different families of Grylloidea and in some representatives of Stenopelmatoidea and Tettigonioidae. In the primitive grylloid genitalia (Fig. 3, d), this lobe may be almost semimembranous and have more sclerotized small structures not isolated from the epiphallic main body and not articulated with it (some species of Meconematinae, Gryllacridinae, and Rhaphidophoridae). In the more specialized grylloid genitalia, the epiphallus is more sclerotized, and the ventral surface of the dorsal fold forms a special median process (Fig. 3, e) named the “guiding rod” (Alexander & Otte, 1967) and probably ensuring of the insertion of the spermatophore apex (with the aperture) into the female spermathecal opening (such genitalia are characteristic of some primitive representatives of Gryllidae and Arachnocephalini, but also of the specialized genus *Euanisous* Hebard, 1922 from Meconematinae). The

highly specialized grylloid genitalia have articulated sclerites for the fixation of the female copulatory structures, and/or a very long guiding rod for the deep insertion of the spermatophore tube into the female spermathecal duct (such genitalia are present in many gryllids, in some non-primitive genera of Mogoplistidae, and possibly in Myrmecophilidae). The development of the grylloid genitalia is often accompanied by replacement of all the non-genital fixing devices by the genital ones. Independent appearance and improvement of grylloid genitalia is the second general trend in the evolution of the ensiferan copulatory apparatus (the first highly hypothetical trend is the appearance of the copulatory apparatus with a non-genital fixing device in the ancient ancestors of the recent ensiferans).

The tettigonioid type of male genitalia is more or less similar to the hagloid one, but it differs in the appearance of a sclerite or sclerites on a small area (areas) of the dorsal fold or near it (Figs 3, f, g); usually such sclerotizations originate from the proximal part of the dorsal surface of this fold, from its lateral parts, from the apex of its lateral projections, and/or from the areas between them. These sclerotizations may bear diverse processes, hooks and denticles, and represent fixing devices additional to those of the dorsal half of the male abdominal apex; they usually do not eliminate the need for the styli. In Tettigoniidae, some of these sclerotizations as well as the paraproctal hooks in Mogoplistidae are sometimes named "titillators" (Love & Walker, 1979; Storozhenko, 2004), but it may be more reasonable to use this name for a certain kind of genital sclerites only. The tettigonioid type has independently appeared in very many genera from different subfamilies of Tettigoniidae (or even in one subgenus within a genus), in some genera and tribes of Stenopelmatoidea (*Diaphanogryllacris* Karny, 1937 and *Aemodogryllini*) and possibly in some higher taxa of Grylloidea. Sometimes this type may be transformed into a complicated variant (Figs 3, h–j) more or less

similar to the grylloid type (*Gryllotalpidae* and possibly *Malgasinae*). Appearance and complication of tettigonioid genitalia, i.e. appearance and complication of small fixing structures of male genitalia which usually do not replace the non-genital ones (exceptions occur: for example, the male fixing apparatus in some genera of *Aemodogryllinae* is presented by only one small denticulate plate of the genitalia), is the third general trend in the evolution of the ensiferan copulatory apparatus.

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