



## A contribution to knowledge of some main trends in evolutionary transformations of the male genitalia in superorder Amphiesmenoptera (Insecta, Trichoptera + Lepidoptera)

MARGARITA G. PONOMARENKO<sup>1,2</sup>

<sup>1</sup>*Institute of Biology and Soil Science, Far Eastern Branch of Russian Academy of Sciences, Vladivostok, RUSSIA*

<sup>2</sup>*Far Eastern Federal University, Vladivostok, RUSSIA. E-mail: margp@ibss.dvo.ru*

### Abstract

The general trends of evolutionary transformations in the male copulatory apparatus of the lower ditrysian Lepidoptera, family Gelechiidae, on the base of functional morphological analysis are similar to those in the order Trichoptera. Evolution of the genitalia in both groups was directed to improvement of efficiency of mating mechanisms. It is found that one of the general trends in trichopterans, reduced of gonopods, corresponds to the main direction of valvae transformation in lower ditrysian moths Gelechiidae. These structures, being of importance in grasping the female in other groups of Lepidoptera, lost this function in some genera and they completely disappeared in most advanced groups of gelechiid moths. That phenomenon is associated with transformations of other structures in copulatory apparatus, which functionally compensate for the lack of valvae. Such functional analogues are found in the course of comparative morphological analysis of the male genitalia in both groups. Similar changes and similar traits of the genital appendages in both groups, trichopterans and lower ditrysian lepidopterans, can be considered as evidence of parallel evolution. The possible parallelisms as indicators of common evolutionary trends in transformation of copulatory apparatus within the two lineages, Trichoptera and Lepidoptera, having a common ancestor, are discussed.

**Key words:** Insects, functional morphology of genitalia, parallel evolution

### Introduction

The superorder Amphiesmenoptera Kiriakoff 1948 consists of two large orders, Lepidoptera and Trichoptera. Their monophyly was established on the basis of a complex of reliable synapomorphies: wings are densely covered by setae or scales, forewings have forked  $A_1$ , larvae each have a spinneret and females are heterogametic (Kristensen 1981; Morse 1997). In the course of further investigations the monophyletic origin of these groups was confirmed by one more morphological trait, glands of sternum V. A series of publications are devoted to detailed study of glandular morphological diversification and their distribution within both groups (Davis 1975; Kristensen & Nielsen 1979; Kristensen 1984; Nielsen & Kristensen 1996; Ivanov & Melnitsky 1999, 2002; Löfstedt *et al.* 2008; Djernæs 2010; Djernæs & Sperling 2011). Molecular phylogenetic research also has confirmed the sister relationship between Trichoptera and Lepidoptera (Beutel *et al.* 2010). The lineages of lepidopterans and trichopterans diverged, probable, from the Jurassic period, and have evolved independently for a long time, during which period each group obtained a number of specific specializations. The independent development of related lineages having a common origin is defined as parallel evolution (Gould 2002). Scientific interest with parallel evolution is traced back to Darwin (1859) who wrote about parallelisms in the development of species and genera in animal and plant world. This subject arouses high interest up to the present time that is evident from numerous recently published papers on different groups of animal and plants (Rodman *et al.* 1998; Morrison *et al.* 2002; Foster & Baker 2004; Schluter *et al.* 2004; Boughman *et al.* 2005; Shapiro *et al.* 2006; Tehler & Irestedt 2007; Adams 2010; Monnet *et al.* 2011; Kidd 2012). It has been shown with numerous examples that two related taxa during development can obtain similar traits on the common genetic base inherited from their common ancestor. The number of

parallelisms is in an inverse ratio from the phylogenetic distance between the two lineages. It is known that the number of homoplasies in the most closely related taxa, of species rank, is much more than in related genera, tribes, families, etc. Furthermore, it has been confirmed that it is possible to predict the discovery of the same peculiarities in related species and genera, similar to the way that chemists anticipate the discovery of unknown chemical elements with certain peculiarities due to the empty place in the Mendeleev periodic table (Vavilov 1935). Parallel evolution is less pronounced in phyla corresponding to taxa of higher rank, e.g. of family-group rank, but in such a case the revealed similar traits can be considered as markers of common trends of morphological transformation. In addition, the morphological trends defined in one of the sister groups could help to understand similar specialization and polarity of morphological changes in the related group.

The two groups, caddisflies and moths, have been studied unequally with regard to the functional morphology of the copulative apparatus. The skeletal–muscular apparatus of the male genitalia has been studied and described in Lepidoptera much more comprehensively. There are functional morphological data on the genitalia of representatives from almost of all lepidopteran taxa of family-group ranks, although it has not been done with equal depth. Despite these differences in the level of knowledge on each order, the ground plans of the copulatory apparatus for Amphiesmenoptera and for both Trichoptera and Lepidoptera has been reconstructed (Birketh–Smith 1974; Kuznetsov & Stekolnikov 2001; Ivanov 2003b; Kristensen 2003) and probable common trends in morphological transformations in both orders have been inferred (Ivanov 2003a, 2003b). The main tasks of the present work are the detection of possible parallelisms on the basis of comparative analysis of the male genitalia in representatives of some groups of trichopterans and lepidopterans, and development of the concept of a common trend in morphological evolutionary transformations within related groups.

## Material and methods

The considered conclusions on evolutionary tendencies in transformations of the genital structures in Lepidoptera from examples of gelechiid moths are based on the great material which was analyzed during more than 20 years of study. The detailed descriptions of functional morphology of the genitalia are published in a series of publications (Ponomarenko 1992, 1995, 1997, 2004, 2005, 2006, 2008, 2009a, 2009b). Data on the genital morphology of Trichoptera were borrowed from literature (Arefina 1997; Arefina & Levanidova 1997; Vshivkova *et al.* 1997; Vshivkova 2003; Ivanov 2003a, 2003b; Chamorro-Lacayo & Holzenthal 2004; Zhong *et al.* 2006; Holzenthal *et al.* 2007) and from my own examination of specimens from various families.

**The subject of investigation.** In the order Lepidoptera, the Gelechiidae, a family of lower ditrysian moths, is selected for comparative morphological investigations. This family includes 4570 species from 509 genera in the world (Pogue 2009). Thus, this group is comparable on the generic diversity with order Trichoptera, numbering about 600 genera. The gelechiid moths are characterized by their wide morphological diversity and by the fact that they combine in their genitalia both the characters of the lepidopteran ground plan and strongly specialized ones, which are a result of deep morphological transformations. That made it possible to reconstruct the morphoclines for some genital structures and outline the main directions of their transformations. The polarity of morphological series was defined by outgroup comparison. In the order Trichoptera, representatives from both suborders, Annulipalpia (families Psychomyiidae, and Polycentropodidae) and Integripalpia (family Leptoceridae), whose genitalia possess structures considered as functional analogues, were studied.

**Methods.** The study of the skeleton of the Gelechiid copulatory apparatus was conducted according to the traditional methods in lepidopterological investigations. The maceration of the soft tissues was made by boiling the abdomens in a 10% aqueous solution of KOH followed by boiling in water. After detailed investigation of the genitalia in glycerol, they were mounted on a microscope slide in Euparal for illustration and permanent preservation. The membranous parts of the genitalia were stained with Chlorazol Black. For functional morphological study, specimens mainly fixed in 70% alcohol were used. Their dissection followed the method described by Kuznetsov & Stekolnikov (2001). Flexibility in dry specimens was obtained by the author's method (Ponomarenko 2005). Before dissection every specimen was stained with an aqueous solution of eosin. The skeletal–muscular apparatus in the male genitalia were examined using stereomicroscopes (Carl Zeiss and Nikon SMZ–10). During dissections a photo of every layer was made with a digital camera (Nikon Coolpix 8700).

The terminology in Lepidoptera follows Kuznetsov & Stekolnikov (2001), taking into account some changes for Gelechiidae by Ponomarenko (2004, 2005). The terminology for genital structures of trichopterans and lepidopterans is different. Therefore according to previously proposed homologation (Kuznetsov & Stekolnikov 2001; Ivanov 2003b) the correlated terms for homological structures in both groups are followed by a "/" [slash] in the text and in illustrations (first term for lepidopterans, second term for trichopterans). To avoid misunderstanding, a table with corresponding numerical and Latin nomenclature for muscles is proposed (Tabl. 1).

**TABLE 1.** Correspondence of numerical and Latin nomenclature for muscles (the muscles mentioned in the text and indicated on the illustrations are included only).

Latin name of muscles	Abbreviation Lepidoptera/ Trichoptera	Numerical name
musculus tergalis intersegmentalis 9–10	mt. 9–10	m <sub>1</sub>
musculus gonopodalis externus dorsolateralis	mg. ed-l / mge dl	m <sub>2</sub>
musculus gonopodalis externus dorsomedialis	mg. ed-m / mge dm	m <sub>4</sub>
musculus phallicus externus posterior/ musculus phallicus externus posterior ventralis	mph. ep / mph epv	m <sub>5</sub>
musculus phallicus externus anterior	mph. ea	m <sub>6</sub>
musculus phallicus internus longitudinalis	mph. il-t / mph ilt	m <sub>21</sub>
musculus tergo-sternalis intrasegmentalis 9	mt-s. 9	m <sub>22</sub>

The abbreviations used in the text and illustrations:

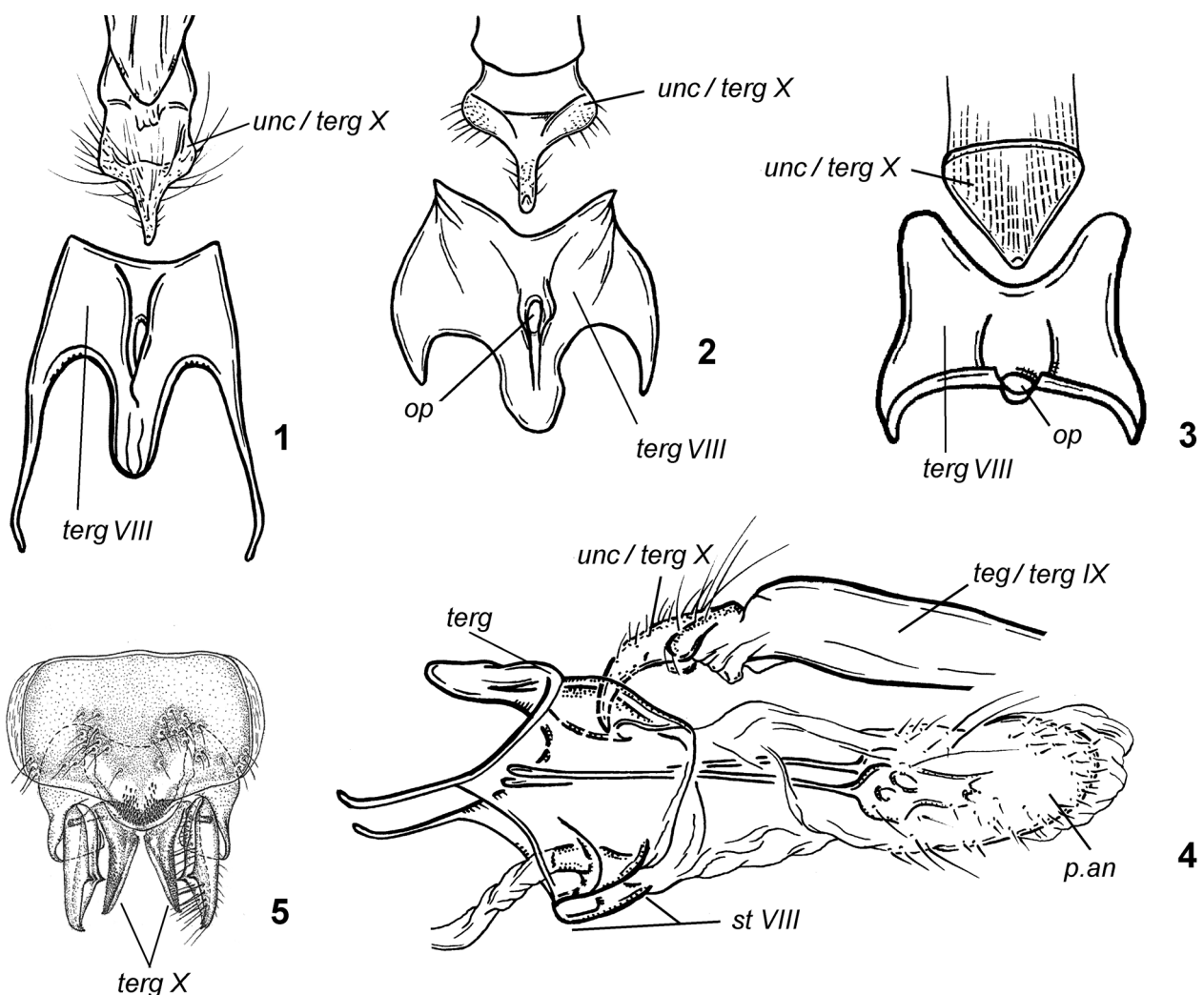
*aed/ phb*—aedeagus/ phallobase  
*c.o*—copulative organ  
*ccl/ d.p.g*—cucullus/ dorso-distal part of gonopod  
*dbp*—dorsobasal process of valva/ gonopod  
*gl*—gland  
*gl.d*—glandular ductus  
*gld*—glandiductor  
*gn*—gnathos/ derivative of sternite X  
*jux/ m.p*—juxta/ medial plate  
*op*—opening on the tergite VIII of female  
*p.an*—papilla analis  
*prm*—paramer  
*scl/ v.p.g*—sacculus/ ventral part of gonopod  
*st VIII*—sternite VIII of female  
*teg/ terg IX*—tegumen/ tergite IX  
*terg VIII*—tergite VIII  
*unc/ terg X*—uncus/ tergite X  
*vlv/ gnpd*—valva/ gonopod or inferior appendages  
*vnc/ st IX*—vinculum/ sternite IX

## Results and discussion

Analysis of the function of the copulative apparatus of the two sexes, as well as modeling of mating mechanisms and field observations allowed imaging the mechanisms of engagement of the male and female *in copula* in some gelechiid moths (Ponomarenko 2005, 2009). In most gelechiid moths, as in most Lepidoptera, terminal segments of the female are held by valvae/ gonopods (inferior appendages), uncus, and

gnathos (derivatives of segments X and XI). If valvae/ gonopods hold the terminal segments of the female laterally in all studied families of Lepidoptera, engagement by the uncus and the gnathos is accomplished differently. In the family Gelechiidae, the female is held by the male uncus and gnathos at tergite VIII, whereas for other lepidopterans, where mating mechanism is known (Tortricidae, Hesperidae, Pieridae, Lycaenidae, Saturniidae), sternite VIII or the sternal area of the female is a usual place of engagement. Gelechiid method is confirmed by the correspondence of shapes of both the uncus in the male and tergite VIII in the female. For example, in tribe Anarsiini a hook-shaped uncus and gutter-like relief of tergite VIII correspond as a “key and lock” in shape (Figs 1–4); similarly, in tribe Chelariini the females have a round, sclerotized, tergal plate at the place where they are held by the male uncus (*Faristenia* Ponom.).

It is known that most moths are positioned “tail-to-tail,” with their heads oriented in opposite directions *in copula*. The same pose has been observed in caddisflies at the end of the copulation process (Ivanov 2003a). In Ivanov’s (2003a) paper, that last stage was called a “copulative turn” and it was assumed that a similar position in the Trichoptera and Lepidoptera is probable a synapomorphy of the two orders. It is very likely that the similar position of the sexes *in copula* could be associated with similar mating mechanisms, functions, and transformations in genital structures.



**FIGURES 1–5.** Terminal segments of the male and female genitalia of Lepidoptera and the male genitalia of Trichoptera. 1–4, Uncus of male genitalia and tergite VIII of female genitalia in tribe Anarsiini (Gelechiidae): 1, *Anarsia stepposella* Ponomarenko, dorsal; 2, *A. halimodendri* Christoph, dorsal; 3, *Ananarsia lineatella* (Zeller), dorsal; 4, *A. stepposella*, locking *in copula*, female below in left lateral, male above in right lateral. 5, Male genitalia of *Limnephilus* Leach. (Limnephilidae), dorsal. 1–4, after Ponomarenko 2009b; 5, after Vshivkova 2006.

## To the ground plan of Amphiesmenoptera

The morphology of genitalia in the hypothetical ancestor of Amphiesmenoptera was discussed in a series of publications (Kristensen 1984, 2003; Kuznetsov & Stekolnikov 2001; Ivanov 2003b), and there are disagreements in ancestral state of some structures. There are two viewpoints on the primary state of the genital segment in ancestral Amphiesmenoptera. According to one of them the ring-shaped genital segment was transitional between a primarily divided tergite and sternite in the ancestor and a secondarily divided tergite and sternites in taxa of recent Amphiesmenoptera (Birket-Smith 1974; Kuznetsov & Stekolnikov 2001). Thus, in the amphiesmenopteran common ancestor, segment IX was divided into a tergite and sternite and the fusion of these sclerites into a united ring (annulus) took place in trichopterans and in lepidopterans independently. According to another view the ancestor possessed a ring-shaped genital segment and its dividing into tergite and sternite occurred within the two lineages Trichoptera and Lepidoptera independently (Kristensen 1984). The last opinion is reflected in the paper by Ivanov (2003b). There are no convincing arguments supporting or rejecting either of these hypotheses. With respect to gelechiid moths, the genital segment is divided into a tergite and a sternite in almost all groups. Only some representatives, often with specialized characters, have secondarily joined tergal and sternal sclerites, but sutures remain more or less visible where they joined. In summary, the fusion and division of the genital segment within lepidopteran groups probably occurred repeatedly.

## Transformation of valvae/ gonopods and their parts

The valvae/ gonopods are paired appendages of the genital segment. Being two-segmented in the ancestors of recent groups, valvae/ gonopods have changed into one-segmented structures in more-advanced representatives. Despite differences in details of evolutionary change, this general trend of transformation of valvae/ gonopods is shared in all above-mentioned works.

The direction of the subsequent transformation of these structures is disputable. On the basis of study of trichopterans, it has been indicated that gonopods can hold only the smooth lateral surfaces of female sternites and, after obtaining the above-mentioned mating pose, these structures became less useful; they only steer the female abdomen and therefore are reduced in most species (Ivanov 2003a). It is difficult to agree with the opinion in Ivanov's (2003a) work that the phenomenon of reduced valvae is common for both orders, Trichoptera and Lepidoptera. The valvae are the main structures holding the female during copulation and are well developed in most groups of Lepidoptera. A more or less conspicuous reduction of valvae has occurred very rarely in Lepidoptera and has been found within higher ditrysian moths in family Lasiocampidae only. As to a total disappearance of these structures, the phenomenon is known only in representatives of the lower ditrysian moths, in the family Gelechiidae, described for the first time within Lepidoptera by Ponomarenko (2005). The absence of valvae was found only in the most advanced gelechiid moths. Actually, the transformation of the valvae within Lepidoptera has occurred in several different directions.

1. Most common direction of valva transformation within order Lepidoptera is intensification of its grasping function. The result is attained in several ways, notably (Figs 6–9):

- a) by stronger sclerotization of these structures (representatives of many families in Lepidoptera);
- b) by differentiation of the valvar surface and the appearance of strong armature (Tortricidae, Choreutidae, Carposinidae, Pyraustidae, Geometridae, Bombycidae and etc.);
- c) by the differentiation of a valva into parts: a dorso-distal part (cucullus), a ventral part (sacculus), and sometimes with the presence of dorsobasal processes;
- d) by development of dense setae and thorns on the medial surface and along the valvar margins, helping to hold the female by the setose lateral sides of her terminal abdominal segments, etc.

2. The less frequently distributed direction of valva transformation within order Lepidoptera is a loss of its grasping function. This trend is common with the outlined direction of genitalia transformation in trichopterans (Ivanov 2003a) and a general tendency of valva transformation in gelechiid moths. There are several transformations as follows:

- a) *Fusion of valva with the tergal part of the genital segment* (tegumen/ tergite IX) that causes complete or partial loss of valval mobility.

In the course of comparative morphological analysis, it was discovered that the depth of the tegminal and valvar transformation is directly dependent on the degree of their fusion. In the case of a point or small area of fusion, the abductors of the valva *mg. e-dll/ m<sub>2</sub>* are kept almost in the initial state but are attached to the place of fusion (Fig. 10). As result of the extensive fusion of the valvae with the tegumen (till ankylosed sclerite) the muscles have disappeared. The latter disappearance is correlated with a dilation of the intersegmental muscles *mt. 9-10/ m<sub>1</sub>*, compression of their lateral branches and subsequent partial or complete division into two separate muscles *m<sub>1a</sub>* and *m<sub>1b</sub>*. If the first muscles keep the original function typical for muscles *mt. 9-10/ m<sub>1</sub>*, the last ones become a functional analogue of muscles *mg. e-dll/ m<sub>2</sub>* (Fig. 11).

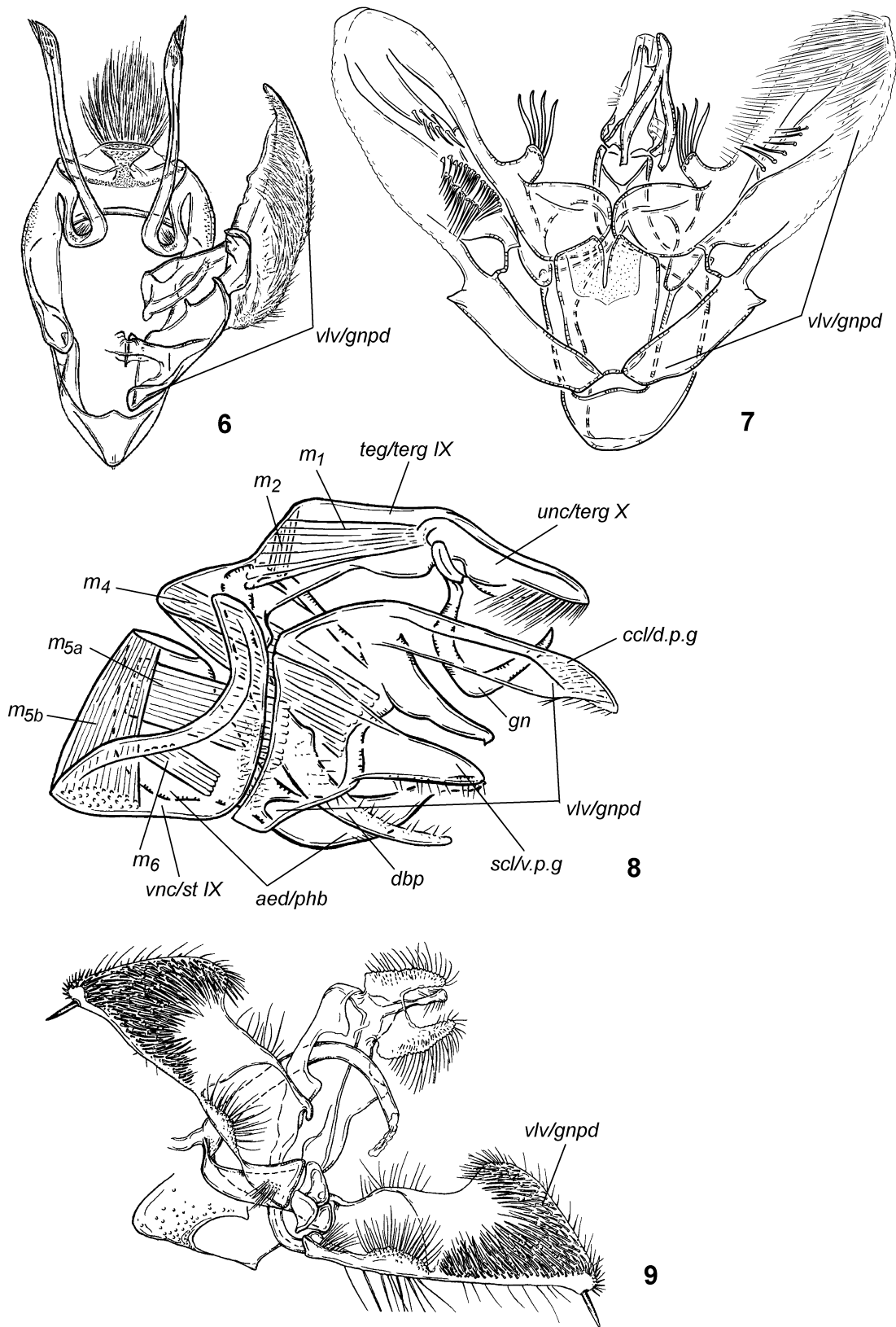
- b) *Fusion of valvae with the sternal part of the genital segment* (vinculum/ sternite IX) that causes full or partial loss of valval mobility. Further transformation is directed to the deep integration of skeletal structures (valvae and sternite) till their full ankylosing. As result of this fusion the valval and phallic muscles partly disappear. The extreme state of this morphocline is found in tribe Litini, where 1 or 2 pairs from 4 pairs of phallic muscles are kept and no one pair of muscles is attached to aedeagus/ phallobase in some genera (*Pseudotelphusa* Janse) (Fig. 15).

- c) *Division of the valvae by distal excavating towards the base*. The continuation of that process leads to complete separation of the dorsal part of a valva (cucullus) from the ventral part of the valva (sacculus) along the lateral side of the valva (Fig. 12). The ventral part of the valva (sacculus) almost always integrates with the vinculum, whereas the dorsal part of the valva (cucullus) has two ways of transforming that are traced within family Gelechiidae. The first of them is demonstrated by the morphocline in the subfamily Dichomeridinae, where the originally well-sclerotized cuculli, bearing strong setae, are shifted dorsally, fused with the tergal part of the genital segment (tegumen), and modified into semimembranous structures, losing their main role in holding the female during copulation (Figs 13, 14). This described transformation of the cuculli is coupled with a reduction of the abductor muscles of the valvae (*mg. e-dll/ m<sub>2</sub>*) (Fig. 13c). The second direction of cucullus transformation is revealed in the tribe Litini, where cuculli are kept as thin membranous structures only in some representatives (Fig. 16) and in most genera they have fully disappeared (Figs 17, 28). In the tribe Litini, functional analogues to valvae (or cuculli) were found: The sclerotized distal parts of the glands of the genital segment take part in grasping the female during copulation instead of the absent dorsal parts of the valvae. These sclerotized parts of the glands in the genital segment are the one of the points of present work.

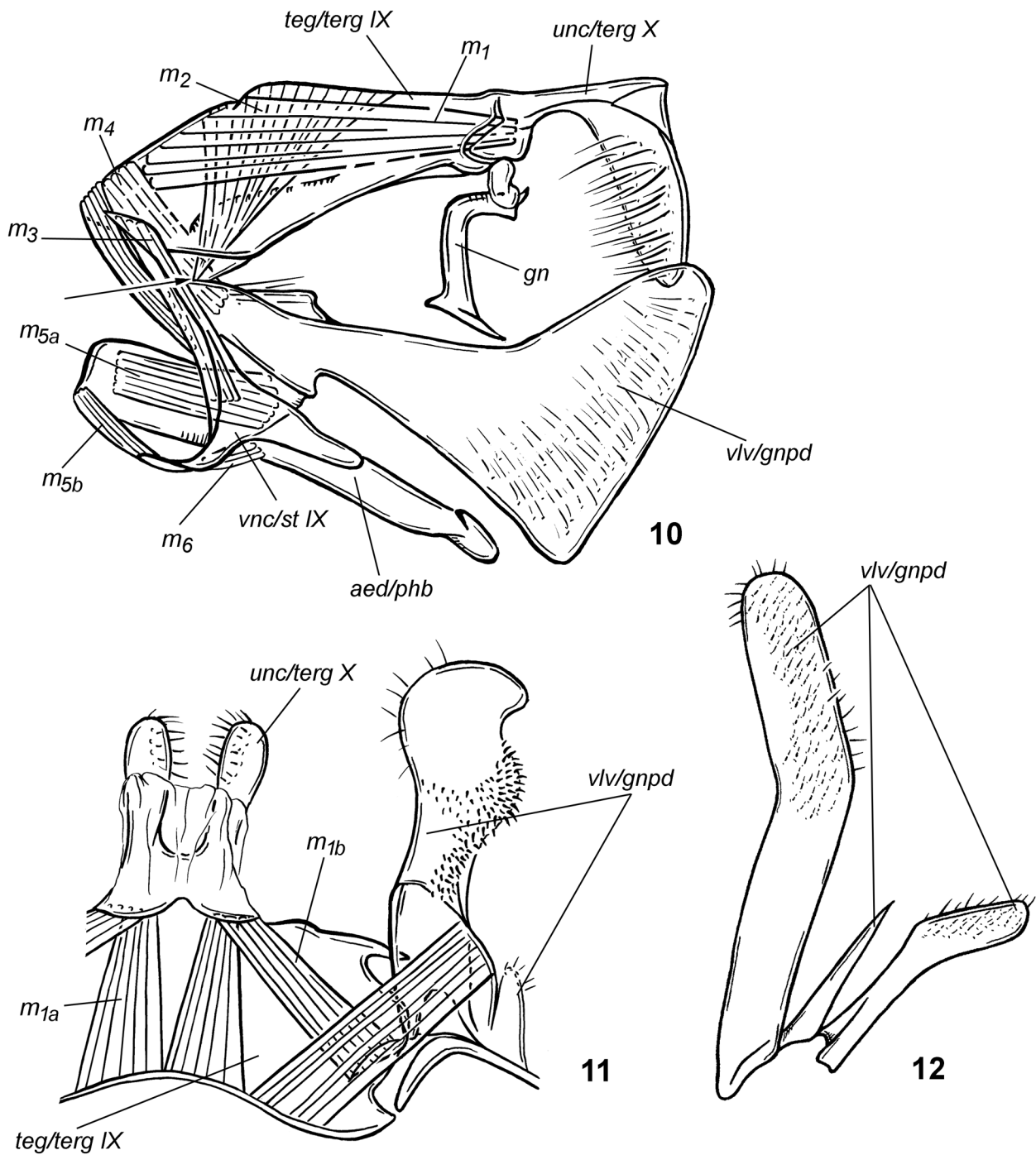
## Glands of genital segment

In the male genitalia of tribe Litini (lower ditrysian moths, family Gelechiidae), the glands of the genital segment have been discovered and described (Ponomarenko 2005, 2008, 2009b). They consist of paired (rarely unpaired) bodies and ducti (or ductus) penetrating sclerotized conic or horn-shaped structures. These sclerotized structures were named as glandiductors in those above-mentioned papers. In previously published papers, the glandiductors were wrongly considered as strongly transformed valvae/ gonopods. What is the reason of such misinterpretation? The glandiductors were found in the genera where the valvae/gonopods are completely absent. The glandiductors have shifted from a medial position to a lateral one, and have taken the place of the missing valvae. As result of comparative morphological analysis within Litini, the glandiductor transformation was traced, passing through the following stages: In the male genitalia the glandiductors are placed initially dorsal of the aedeagus and the valvae are present (*Agonochaetia intermedia* Sattler, fig. 22); subsequently the male glandiductors became placed laterally and genitalia with a slightly sclerotized thin valvae (*Exoteleia dodecella* L., fig. 16); and finally the male glandiductors are in their lateral position and genitalia with the valvae completely absent (*Schneidereria pistaciella* (Weber), fig. 17). The homology of the glandiductors (their paired and unpaired states) and their origin were established on the basis of a functional

morphological study within the gelechiid moths. The glanductors of all genera, wherever they are found, are homologous because they are attached with the same muscle *mg. e-dl/ m<sub>2</sub>*.

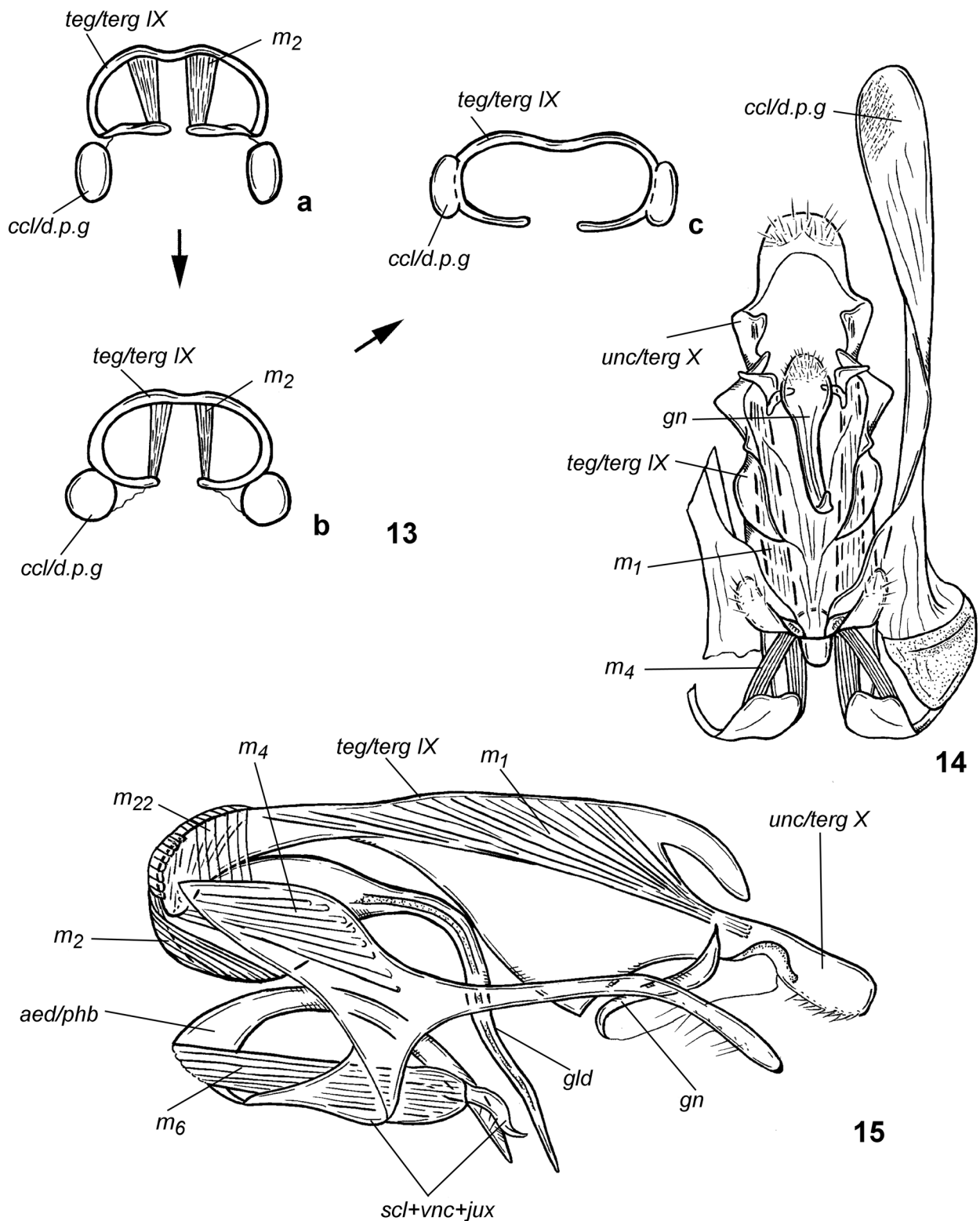


**FIGURES 6–9.** Male genitalia of Lepidoptera. 6, *Carposina sasakii* Matsumura (Carposinidae), caudal; 7, *Ctenognophos grandinaria* (Motschulsky) (Geometridae), caudal; 8, *Neofriseria peliella* (Treitschke) (Gelechiidae), left lateral; 9, *Rhopalovalva pulchra* (Butler, 1879) (Tortricidae), left caudolateral. 6, 8, after Ponomarenko 1999, 2005; 7, after Beljaev 1994; 9, after Kuznetsov 2001.

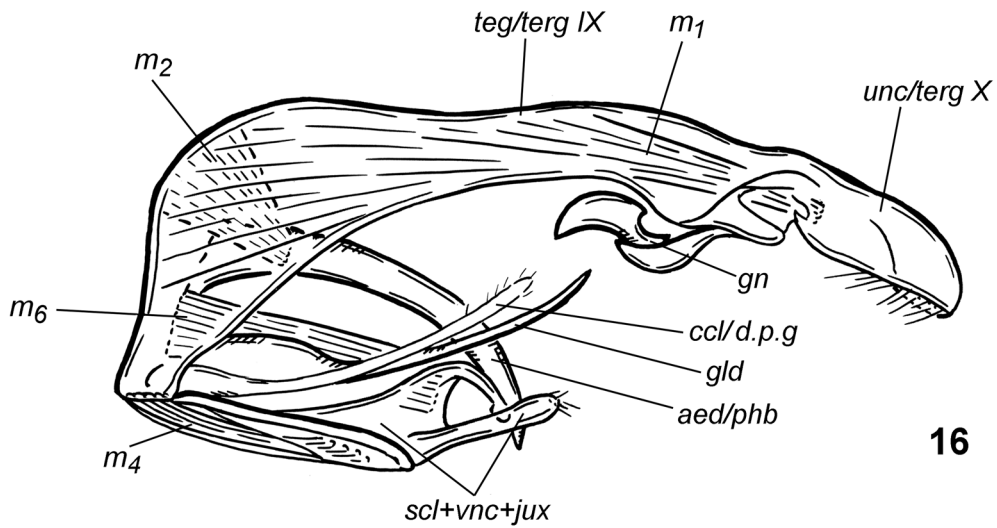


**FIGURES 10–12.** Male genitalia of Gelechiidae. 10, *Pexicopia malvella* (Hübner), left lateral; 11, *Ptocheuusa paupella* (Zeller), uncus, tegumen and valva, view from medial side; 12, *Neofaculta ericitella* (Geyer), valva, left lateral. 10–12, after Ponomarenko 2004, 2005.

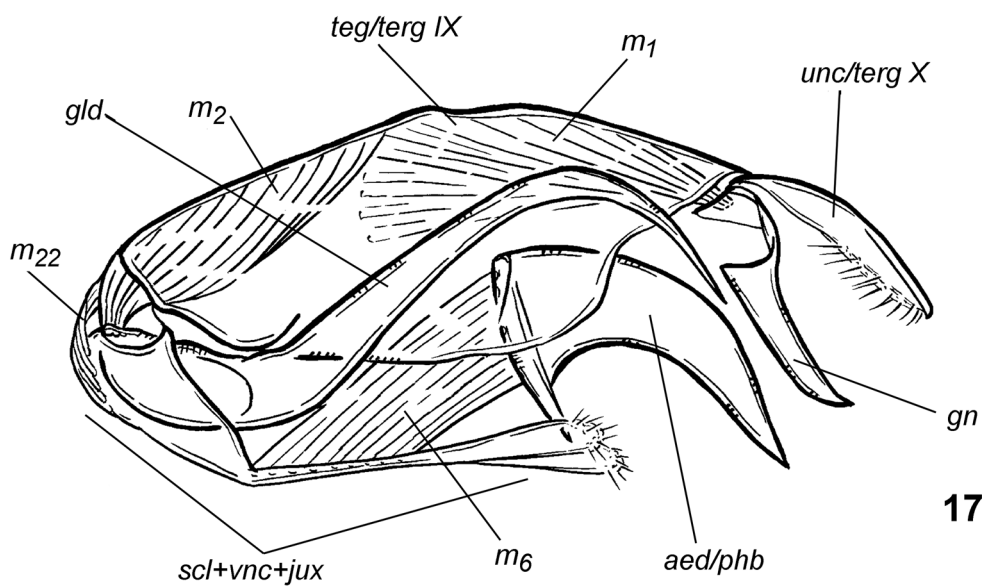




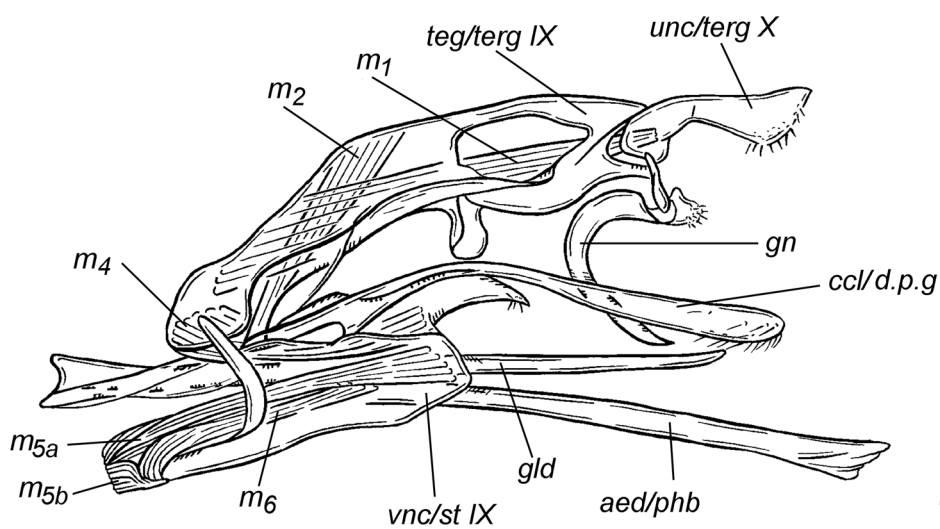
**FIGURES 13–15.** Male genitalia of Gelechiidae. 13, morphocline of cuculli transformation in Gelechiidae, dorso-ventral plane: a, *Hyatima* Hübner, b, *Helcystogramma* Zeller, c, *Dichomeris* Hübner; 14, *Dichomeris oceanis* Meyrick, tegminal part of skeletal–muscular apparatus, from medial side; 15, *Parastenolechia collucata* Omelko, skeletal–muscular apparatus, left lateral. 13–15, after Ponomarenko 2004, 2005.



16

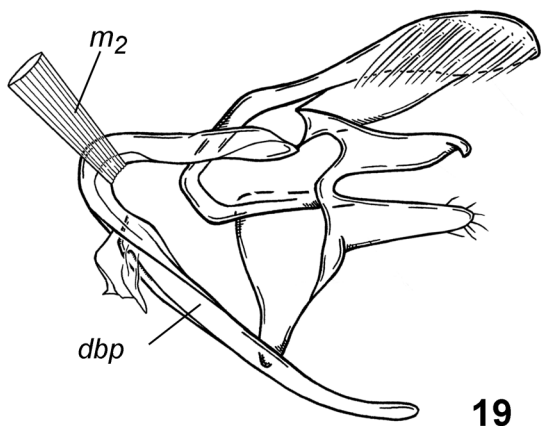


17

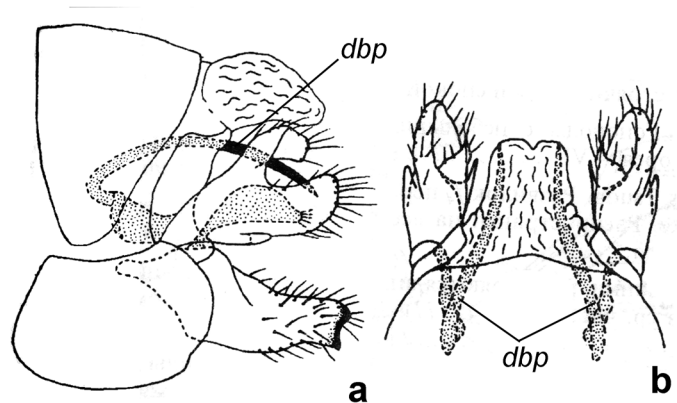


18

**FIGURES 16–18.** Skeletal–muscular apparatus of the male genitalia of Gelechiidae, left lateral. 16, *Exoteleia dodecella* (Linnaeus); 17, *Schneidereria pistaciella* (Weber) (Gelechiidae); 18, *Mirificarma eburnella* ([Denis & Schiffermüller]). 16–18, after Ponomarenko 2005.



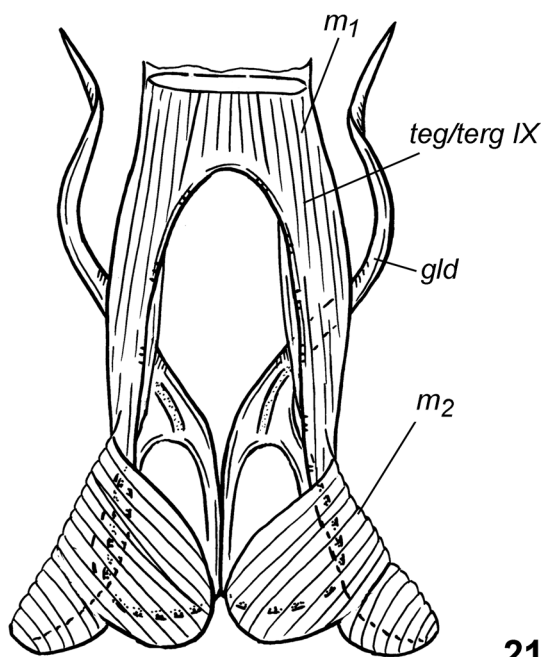
19



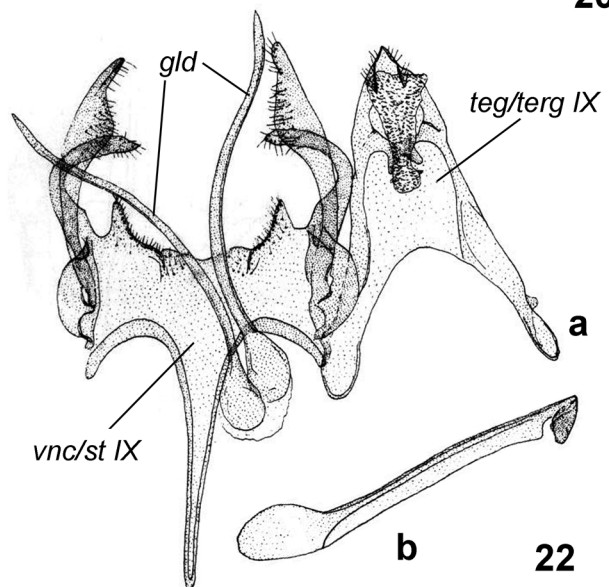
a

b

20



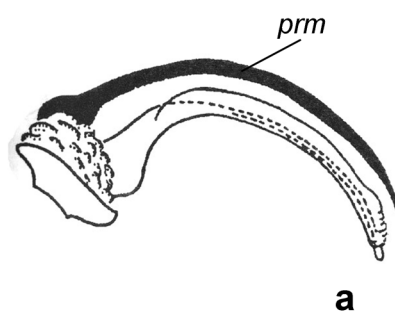
21



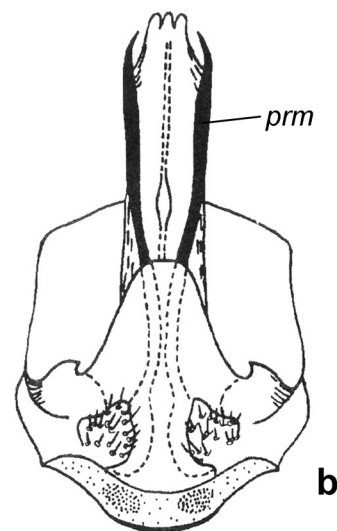
a

b

22



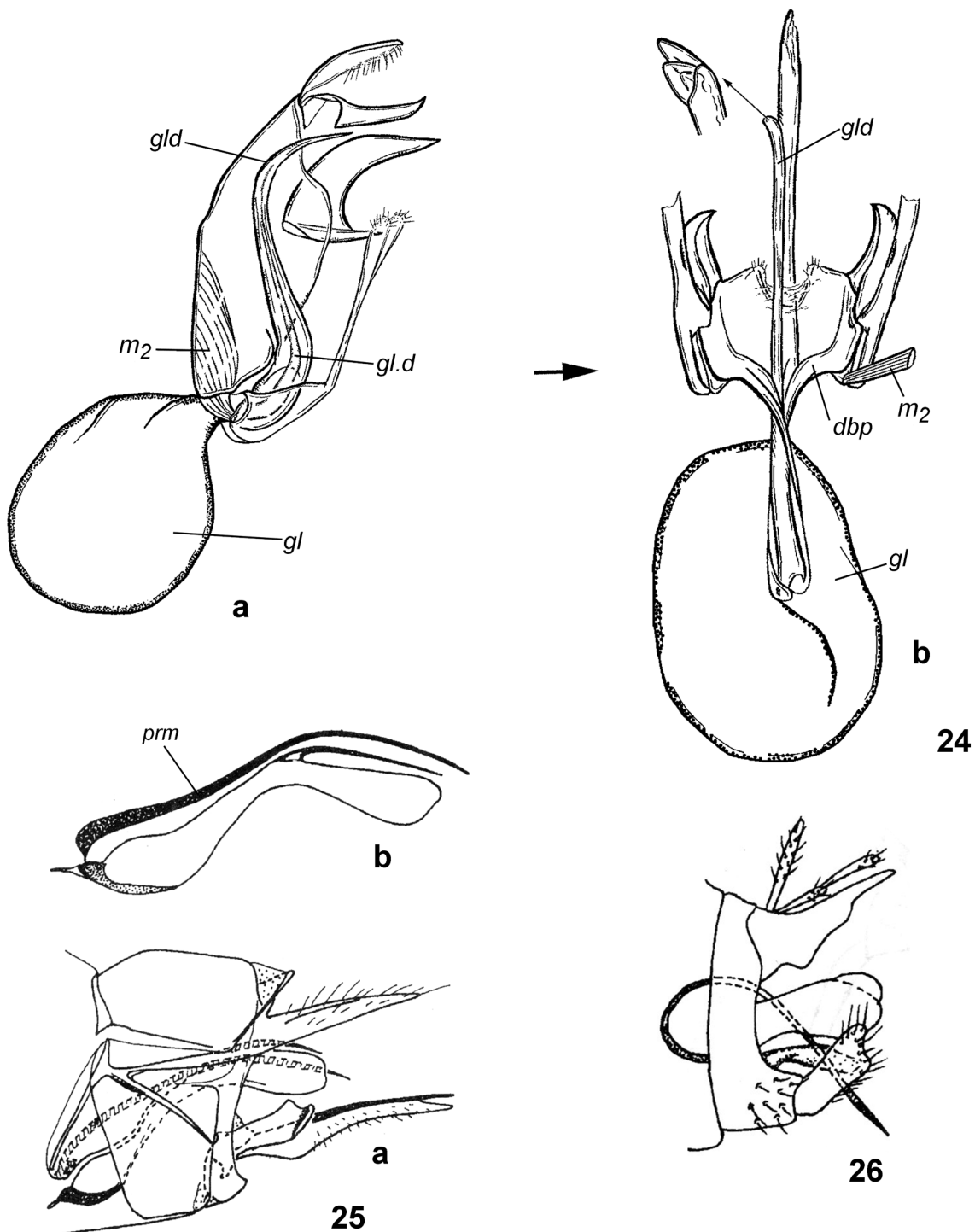
a



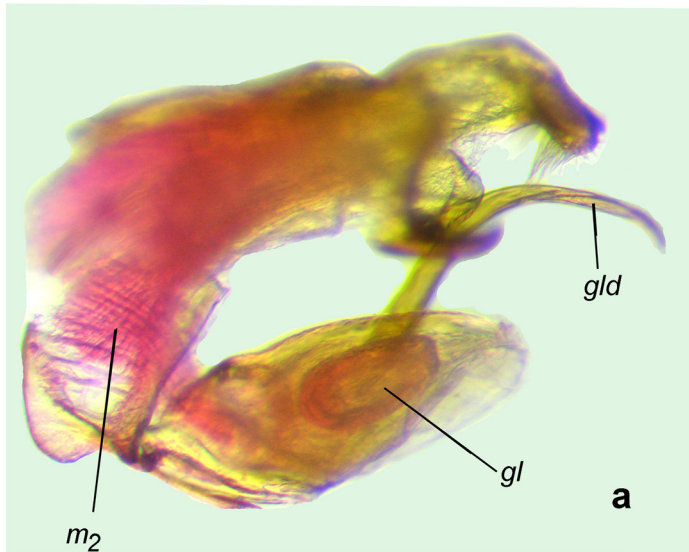
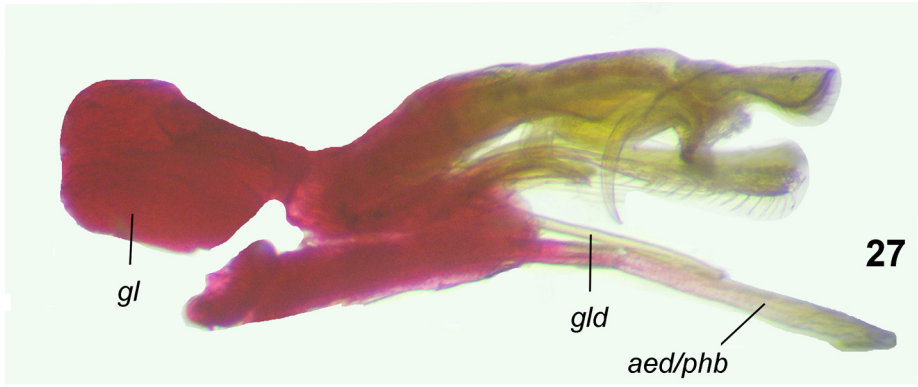
b

23

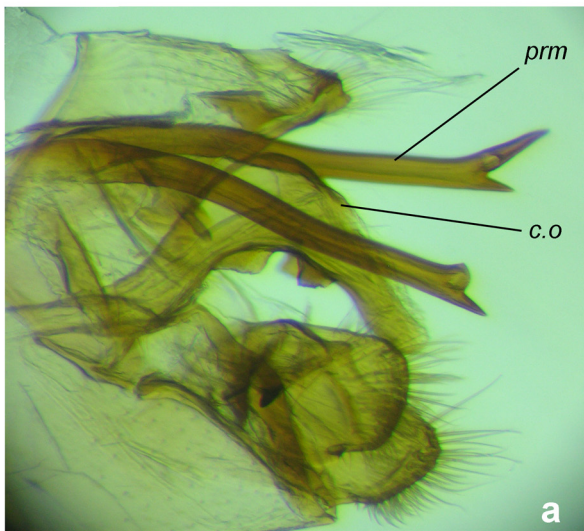
**FIGURES 19–23.** Male genitalia and their details in Gelechiidae (Lepidoptera) and Polycentropodidae (Trichoptera). 19, *Neofriseria peliella* (Treitschke) (Gelechiidae), valva, medial; 20, *Polyplectropus nocturnus* Arefina (Polycentropodidae), male genitalia: a, left lateral, b, dorsal; 21, *Parastenolechia collucata* Omelko (Gelechiidae), skeletal–muscular apparatus (part), dorsal; 22, *Agonochaetia intermedia* Sattler (Gelechiidae): a, tergum and sternum separated and illustrated together, dorsal/ventral; b, aedeagus, left lateral; 23, *Setodes punctatus* (Fabricius) (Leptoceridae), a, phallus, left lateral; b, male genitalia, dorsal. 19, 21, after Ponomarenko 2005; 22, after Povolný; 20, after Arefina 1997; 23, after Vshivkova *et al.* 1997.



**FIGURES 24–26.** Male genitalia and their details in Gelechiidae (Lepidoptera) and Psychomyiidae and Leptoceridae (Trichoptera). 24, transformation of glands of the genital segment in Gelechiidae: a, paired glands in *Schneidereria pistaciella* (Weber), left lateral; b, unpaired gland in *Mirificarma eburnella* ([Denis & Schiffermüller]), genitalia, medial; 25, *Paduniella amurensis* (Martynov) (Psychomyiidae), left lateral: a, male genitalia; b, phallus with unpaired paramere; 26, *Ylodes jakutanus* (Martynov) (Leptoceridae), left lateral. 24, after Ponomarenko 2005; 25, 26, after Martynov 1910, 1934.



28



29

**FIGURES 27–29.** Glands of genital segment in Gelechiidae (Lepidoptera) and male genitalia of Leptoceridae (Trichoptera). 27, *Mirificarma eburnella* ([Denis & Schiffermüller]) (Gelechiidae), genital segment and gland with unpaired body, left lateral; 28, *Teleiodes saltuum* (Zeller) (Gelechiidae): a, genital segment and paired glands, left lateral; b, inflated basally glandiductor with glandular body inside, left lateral; 29, *Setodes obscurus* Schmid & Levanidova (Leptoceridae): a, left lateral; b, parameres and phallus, left dorsolateral. 27, 28, after Ponomarenko 2008; 29, original.

As to probable origin of glandiductors, the following scenario is inferred: The same muscles (*mg. e-dll m<sub>2</sub>*) extended from a pair of long processes in the genus *Neofriseria* Sattler (Figs 8, 19) and the two processes joined each other in the middle and became supplied in that place with a membranous sac. These processes could be considered as homologous with glandiductors. On the base of genital morphology of *Neofriseria* the hypothetical origin was initiated. It was supposed that the ectodermal origin of the glandiductors was by invagination of the wall into processes like those in *Neofriseria* genus; also their primary paired condition is assumed. More advanced (secondary) state were found in the genus *Mirificarma* Gozmány, where the rounded glandular body is unpaired, and the channel arising from it penetrates the long glandiductor with two small lobes on the apex, surrounding the excretory opening (Figs 18, 24b). This long glandiductor is positioned dorsally and is codirected with the copulative organ.

What is the function of these glands and glandiductors?

The morphology of the described glands (rounded body, ductus, and opening, surrounded by lobes) is similar to the glands of segment V, which are known in Trichoptera and primitive Lepidoptera (see cited papers above). The peculiarities of the connection of the muscles *mg. e-dll m<sub>2</sub>*, which surround the inflated base of the glandiductors (Fig. 21), make it possible to presume the performance of two functions by these glandiductors. The first of them is to support the glandular ductus, and second one is participation in grasping the female. The sclerotized glandiductors are inserted in genital tract of female and moved outward due to muscular traction. Thus, glandiductors are functional analogues of valvae and functionally compensate weak or disappeared valvae.

#### **Tentative parallelisms in lineages Trichoptera and Lepidoptera**

There is major background for development of parallel traits in the related lineages Trichoptera and Lepidoptera. The origin from a common ancestor and the underlying patterns of genetic variation define similarity in evolutionary changes. That has become apparent from the similar ground plan of the musculoskeletal apparatus of the male genitalia and similar the mating mechanism in these two groups.

*New compensatory formations.* The development of armature in the copulative organ and sclerotized periphallallic processes are common phenomena for different groups in Trichoptera and Lepidoptera, as has already been indicated (Ivanov 2003a).

*Hook-shaped segment X/ uncus.* Transformation of tergite X into hook-shaped processes in higher representatives of family Limnephilidae (Fig. 5) in Trichoptera and the hook-shaped uncus (derivative of tergite X) in moths from tribe Anarsiini (Figs 1–4, subfamily Dichomeridinae) are considered here as a parallelism resulting in morphological and functional analogues. Both structures play a role in grasping the female during copulation.

*Processes of gonopods/ valvae and processes of superior appendages.* The ancestral valvae/ gonopods of lower ditrysian moths, probably were rounded, each with a relatively wide base and moderately divided into parts. The valvae and its parts in the genus *Neofriseria* Sattler (Figs 8, 19) are most complete and in accordance with the valvae described above. Caddisflies of the genus *Polyplectropus* Ulmer (Polycentropodidae) have appendages similarly divided into parts. Besides, these structures are each with a long dorsobasal process (Fig. 20) (Arefina 1997; Chamorro-Lacayo & Holzenthal 2004; Zhong *et al.* 2006), and these processes are directed in the same direction as the copulatory organ. Also in genus *Tinodes* Curtis (Psychomyiidae), the superior appendages with long dorsal parts (Li & Morse 1997). It has been established that in *Neofriseria* these processes play a role in grasping the female. Presumably the processes of the appendages in *Polyplectropus* and in related genera are functional analogues of those of *Neofriseria*.

*Glandiductors in moths and parameres in caddisflies as functional analogues.* In the copulative apparatus of Trichoptera there are structures which have been called parameres. Their position in genitalia is different within Trichoptera, and described in detail by Vshivkova (2006).

The male genitalia of *Setodes* Rambur (Leptoceridae) have paired parameres placed over the copulatory organ (Figs 23, 29). Unfortunately, wide functional morphological analysis within Trichoptera was not conducted and homology of mentioned parameres is unknown. However, it is possible to suppose that they, being inserting into genital tract of female, take part in its fixing. A similar hypothesis was stated by Vshivkova (2006) in her PhD Dissertation, where the morphological diversity of parameres and their possible function in some limnephilids were considered: “Usually small-sized limnephiloids possess simple stick-like,

weakly armed parameres, whereas large-bodied limnephilids (including even some advanced Dicosmoecinae) possess long, strong and well-armed parameres. In *Limnephilus*, they are extremely strong, apically widened, very often well-sclerotized, covered with strong setae and even have strong sclerotized tooth/teeth on the proximal paramere branch. Probably, one of the male paramere functions is to anchor itself in the female at copulation." Thus, the parameres in *Setodes* could be considered as functional analogues of the processes in *Neofriseria*. Their position over the aedeagus is the same as the sclerotized parts (glanductors) of glands in the genital segment described in gelechiid moths (Figs 15–18, 22, 27, 28).

Are there glands of the genital segment in trichopterans? The glands of segment V described in Trichoptera and in primitive Lepidoptera are considered as one of the synapomorphies supporting their monophyly. These glands independently disappear in many groups of Trichoptera and Lepidoptera. Therefore the study of a few representatives from order Trichoptera is not enough to answer this question. A narrow channel is visible inside parameres with broken apices in *Setodes obscurus* Schmid & Levanidova (Figs. 29a, b). However, the base of these parameres is inflated and the distinct glandular bodies were not found in examined trichopteran specimens. The confirmation or rejection of the presence of similar glands in genital segment is possible only after more thorough investigation within the group.

Within gelechiid moths paired glanductors became unpaired in advanced groups, relocated over copulative organ and shaped as a long and slender filament (Figs 24a, 24b). The homology of these processes is affirmed on the basis of their connection with the same muscles  $m_2/mg. e-dl$ . All of them play a role in holding the female by being inserted into its genital tract and they also support the glandular ductus in many gelechiid genera. One of the genera where an unpaired glanductor (filament) was found is the genus *Mirificarma*, which is one of the more-advanced groups in tribe Gelechiini. The long unpaired parameres in species from the more-advanced trichopteran family Leptoceridae can be considered as functional analogous with similar structures in Gelechiidae. The family Leptoceridae, belonging to suborder Integripalpia, is treated as one of the more-advanced trichopterans (Holzenthal *et al.* 2007). The direction of paramere transformation is in accordance with that of glanductors in lower ditrysian moths, Gelechiidae. Earlier, Nielsen (1970) had already assumed that paired parameres became unpaired secondarily in both Annulipalpia and Integripalpia.

Summarizing the above data, it can be concluded that similar traits observed in the genitalia may be considered as evidence of a parallel evolutionary transformation in the sister groups of trichopterans and lower ditrysian moths. Their evolutionary changes were co-directed into improving of grasping of females *in copula*. From the general tendencies in the transformations of the male genitalia, it can be inferred that the weakening of valvae (or cuculli) / gonopods and partial or complete loss by them of the function of female holding is a parallel development. The process of weakening, reduction and disappearing of genital structures correlated, on the one hand, with changes in the muscles, often with complete disappearance of muscles, and on the other hand, with the appearance of special compensatory morphological complexes consisting of functional analogues and new formations, partly or completely substituting for the structures which lost their function.

## Acknowledgements

I am grateful to Dr. T. Vshivkova for invitation to take part in discussion of evolutionary problems in Amphiesmenoptera in the 14th International Symposium on Trichoptera and for material from different groups of caddisflies for the present study. The study was supported by the RFBR, grant 14–04–000649, and the Grant of the President of the Russian Federation for the state support of leading scientific schools of the Russian Federation number HIII-150.2014.4.

## References

- Adams, D.C. (2010) Parallel evolution of character displacement driven by competitive selection in terrestrial salamanders. *BMC Evolutionary Biology*, 10 (72), 1–10.  
<http://dx.doi.org/10.1186/1471-2148-10-72>
- Arefina, T.I. (1997) Fam. Polycentropodidae. In: Lerh, P.A. (Ed.), *Key to the insects of Russian Far East. Vol. 5 (1) Trichoptera and Lepidoptera*. Dalnauka, Vladivostok, pp. 69–76. [in Russian]
- Arefina, T.I. & Levanidova, I.M. (1997) Fam. Psychomyiidae. In: Lerh, P.A. (Ed.), *Key to the insects of Russian Far East. Vol.*

- 5 (1) *Trichoptera and Lepidoptera*. Dalnauka, Vladivostok, pp. 78–82. [in Russian]
- Beljaev, E.A. (1994) *Geometrid moths of the subfamily Ennominae (Lepidoptera, Geometridae) of Russian Far East*. Candidate of Biology (PhD) Dissertation, Zoological Institute of RUS, Sankt-Petersburg, 145 pp. [in Russian]
- Beutel, R.G., Friedrich, F., Hornschmeyer, T., Pohl, H., Hunefeld, F., Beckmann, F., Meier, R., Misoff, B., Whiting, M.F. & Vilhelmsen, L. (2010) Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Cladistics*, 26, 1–15.
- Birket-Smith, S.I.R. (1974) Morphology of the male genitalia of Lepidoptera. II. Monotrysia, Zeugloptera and discussion. *Entomologica Scandinavica*, 5 (2), 163–183.  
<http://dx.doi.org/10.1163/187631274x00209>
- Boughman, J.W., Rundle, H.D. & Schluter, D. (2005) Parallel evolution of sexual isolation in sticklebacks. *Evolution*, 59 (2), 361–373.  
<http://dx.doi.org/10.1111/j.0014-3820.2005.tb00995.x>
- Chamorro-Lacayo, M.L. & Holzenthal, R.W. (2004) Seven new species of *Polyplectropus* Ulmer (Trichoptera: Polycentropodidae) from Costa Rica. *Proceedings of the Entomological Society of Washington*, 106 (1), 202–216.
- Darwin, C.R. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. 1<sup>st</sup> Edition. John Murray, London, xxxi + 703 pp.
- Davis, D.R. (1975) Systematics and zoogeography of the family Neupseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). *Smithsonian Contributions to Zoology*, 210, 1–45.
- Djernæs, M. (2010) *Morphology, function and evolution of the sternum V glands in Amphiesmenoptera*. A thesis for the degree of Doctor of Philosophy. Edmonton, Alberta. 343 pp.
- Djernæs, M. & Sperling, F.A.H. (2011) Evolutionary riddles and phylogenetic twiddles: The ground plan and early diversification of the sternum V gland in Amphiesmenoptera (Trichoptera + Lepidoptera). *Zoosymposia*, 5, 83–100.
- Foster, S.A. & Baker, J.A. (2004) Evolution in parallel: New insights from a classic system. *Trends in Ecology and Evolution*, 19 (9), 456–459.  
<http://dx.doi.org/10.1016/j.tree.2004.07.004>
- Gould, S.J. (2002) *The structure of evolutionary theory*. 6<sup>th</sup> Edition. Harvard University Press, Cambridge, Massachusetts, 1932 pp.
- Holzenthal, R.W., Blahnik, R.J., Prather, A.L. & Kjer, K.M. (2007) Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. In: Zhang, Z.-Q. & Shear, W.A. (Eds.), *Linnaeus Tercentenary: Progress in Invertebrate Taxonomy*. *Zootaxa*, 1668, pp. 639–698.
- Ivanov, V.D. (2003a) Ground plan and basic evolutionary trends of male terminal segments in Trichoptera. *Proceedings of the 11th International Symposium on Trichoptera (2003, Osaka)*. Tokai University Press, Kanagawa, 207–218.
- Ivanov, V.D. (2003b) Ground plan and nomenclature of muscles in the male terminalia of the Amphiesmenoptera (Insecta: Trichoptera and Lepidoptera). *Entomologicheskoe Obozrenie*, 82 (1), 17–32.
- Ivanov, V.D. & Melnitsky, S.I. (1999) Structure of sternal pheromone glands in caddisflies (Trichoptera). *Entomological Review*, 79, 926–942. [translated from *Entomologicheskoe Obozrenie*, 78, 505–526]
- Ivanov, V.D. & Melnitsky, S.I. (2002) Structure of pheromone glands in Trichoptera. *Nova Supplementa Entomologica (Proceedings of the 10th International Symposium on Trichoptera)*, 15, 17–28.
- Kidd, M.R., Duftner, N., Koblmüller, S., Sturmbauer, C. & Hofmann, H.A. (2012) Repeated parallel evolution of parental care strategies within *Xenotilapia*, a genus of cichlid fishes from Lake Tanganyika. *PLoS ONE*, 7 (2), e31236.  
<http://dx.doi.org/10.1371/journal.pone.0031236>
- Kiriakoff, S.G. (1948) A classification of the Lepidoptera and related groups with some remarks on taxonomy. *Biologisch Jaarboek*, Antwerpen, 15, 118–143.
- Kristensen, N.P. (1981) Amphiesmenoptera. Trichoptera. Lepidoptera. [Revisionary notes]. In: Hennig, W. (Ed.), *Insect Phylogeny*. John Wiley & Sons, New York, pp. 325–330, 412–415.
- Kristensen, N.P. (1984) The pregenital abdomen of the Zeugloptera (Lepidoptera). *Steenstrupia*, 10 (4), 113–136.
- Kristensen, N.P. & Nielsen, E.S. (1979) A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). *Steenstrupia*, 5 (7), 69–147.
- Kuznetsov, V.I. (2001) Superfamily Tortricoidea. In: Lerh, P.A. (Ed.), *Key to the Insects of Russian Far East. Vol. 5. Trichoptera and Lepidoptera. Part 3*. Vladivostok, Dalnauka, Vladivostok, pp. 11–472.
- Kuznetsov, V.I. & Stekolnikov, A.A. (2001) *New approaches to the system of Lepidoptera of world fauna (on the base of the functional morphology of abdomen)*. Nauka, St. Petersburg, 462 pp.
- Li, Y.J. & Morse, J.C. (1997) *Tinodes* species (Trichoptera: Psychomyiidae) from The People's Republic of China. *Insecta Mundi*. Paper 275. Available from: <http://digitalcommons.unl.edu/insectamundi/275> (accessed 29 November 2013)
- Löfstedt, C., Bergmann, J., Francke, W., Jirle, E., Hansson, B.S. & Ivanov, V.D. (2008) Identification of a sex pheromone produced by sternal glands in females of the caddisfly *Molanna angustata* Curtis (Trichoptera, Molannidae). *Journal of Chemical Ecology*, 34 (2), 220–228.  
<http://dx.doi.org/10.1007/s10886-007-9418-7>
- Monnet, C., De Baets, K. & Klug, C. (2011) Parallel evolution controlled by adaptation and covariation in ammonoid cephalopods. *Evolutionary Biology*, 11, 1–21.



- <http://dx.doi.org/10.1186/1471-2148-11-115>
- Morse, J.C. (1997) Phylogeny of Trichoptera. *Annual Review of Entomology*, 42, 427–450.  
<http://dx.doi.org/10.1146/annurev.ento.42.1.427>
- Morrison C.L., Harvey, A.W., Lavery, S., Tieu, K., Huang, Y. & Cunningham, C.W. (2002) Mitochondrial gene rearrangements confirm the parallel evolution of the crab-like form. *Proceedings of the Royal Society B: Biological Sciences*, 269, 345–350.  
<http://dx.doi.org/10.1098/rspb.2001.1886>
- Nielsen, A. (1970) 19. Trichoptera. In: Tuxen, S.L. (Ed.), *Taxonomist's glossary of genitalia in insects. 2<sup>nd</sup> Edition*. Munksgaard, Copenhagen, 104–115.
- Nielsen, E.S. & Kristensen, N.P. (1996) The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera–Glossata. *Invertebrate Taxonomy*, 10, 1199–1302.  
<http://dx.doi.org/10.1071/IT9961199>
- Pogue, M. (2009) Biodiversity of Lepidoptera. In: Foottit, R.G. & Adler, P.H. (Eds.), *Insect biodiversity: Science and society*. Wiley-Blackwell, West Sussex, pp. 325–356.  
<http://dx.doi.org/10.1002/9781444308211.ch13>
- Ponomarenko, M.G. (1992) Functional morphological analysis of male genitalia of the gelechiid moths of the subfamily Dichomeridinae *sensu novo* (Lepidoptera, Gelechiidae). *Entomologicheskoe Obozrenie*, 71 (1), 160–178. [in Russian]
- Ponomarenko, M.G. (1995) Review of the genus *Capidentalia* Park (Lepidoptera: Gelechiidae, Dichomeridinae) with the description of two new species. *Actias*, 2 (1–2), 45–51.
- Ponomarenko, M.G. (1997) Phylogeny and taxonomy of the subfamily Dichomeridinae (Lepidoptera, Gelechiidae). *Zoosystematica Rossica*, 6 (1/2), 305–314.
- Ponomarenko, M.G. (1999) Family Carposinidae. In: Lerh, P.A. (Ed.), *Key to the Insects of Russian Far East. Vol. 5. Trichoptera and Lepidoptera. Part 2*. Dalnauka, Vladivostok, pp. 579–583.
- Ponomarenko, M.G. (2004) Gelechiid moths from the subfamily Dichomeridinae (Lepidoptera, Gelechiidae): functional morphology, evolution and taxonomy. *A. I. Kurentzov's Annual Memorial Meetings*, 15, 5–88. [in Russian]
- Ponomarenko, M.G. (2005) Gelechiid moths (Lepidoptera, Gelechiidae) of the Palaearctics: functional morphology of the male genitalia, phylogeny and taxonomy. *Meeting in memory of N.A. Cholodkovsky*, 58 (1), 1–139. [in Russian]
- Ponomarenko, M.G. (2006) *Phylogeny and taxonomy of the Gelechiid moths (Lepidoptera, Gelechiidae) from the subfamily Dichomeridinae (Lepidoptera, Gelechiidae)*. Doctor of Sciences Dissertation, Zoological Institute of RUS, Sankt-Petersburg, 469 pp. [in Russian]
- Ponomarenko, M.G. (2008) Functional morphology of the male genitalia in Gelechiidae (Lepidoptera) and its significance for phylogenetic analysis. *Nota Lepidopterologica*, 31 (2), 193–212.
- Ponomarenko, M.G. (2009a) Functional morphology of the male genitalia in the gelechiid–moth genera *Holcophora* Stgr., *Ananarsia* Ams. and *Nothris* Hbn. (Lepidoptera, Gelechiidae: Gelechiini, Dichomeridini). *Entomologicheskoe Obozrenie*, 88 (1), 135–142. [in Russian]
- Ponomarenko, M.G. (2009b) *Gelechiid Moths of the Subfamily Dichomeridinae (Lepidoptera: Gelechiidae) of the World Fauna*. Dalnauka, Vladivostok, 389 pp. [in Russian]
- Rodman, J., Soltis, P., Soltis, D., Sytsma, K. & Karol, K. (1998) Parallel evolution of glucosinolate biosynthesis inferred from congruent nuclear and plastid gene phylogenies. *American Journal of Botany*, 85 (7), 997–1006.  
<http://dx.doi.org/10.2307/2446366>
- Shapiro, M.D., Bell, M.A. & Kingsley, D.M. (2006) Parallel genetic origins of pelvic reduction in vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 13753–13758.  
<http://dx.doi.org/10.1073/pnas.0604706103>
- Schluter, D., Clifford, E.A., Nemethy, M. & McKinnon, J.S. (2004) Parallel evolution and inheritance of quantitative traits. *The American Naturalist*, 163 (6), 809–822.  
<http://dx.doi.org/10.1086/383621>
- Tehler, A. & Irestedt, M. (2007) Parallel evolution of lichen growth forms in the family Roccellaceae (Arthoniales, Ascomycota). *Cladistics*, 23, 432–454.  
<http://dx.doi.org/10.1111/j.1096-0031.2007.00156.x>
- Vavilov, N.I. (1935) Law of homologous series in hereditary variability. In: Vavilov, N.I. (Ed.), *Theory of plant selection. Vol. 1*. Moscow, Leningrad, pp. 75–128.
- Vshivkova, T.C., Morse, J.C. & Yang, L.F. (1997) Fam. Leptoceridae. In: Lerh, P.A. (Ed.), *Key to the insects of Russian Far East. Vol. 5(1) Trichoptera and Lepidoptera*. Dalnauka, Vladivostok, pp. 69–76. [in Russian]
- Vshivkova, T.C. (2006) *Phylogeny of Family Limnephilidae (Insecta: Trichoptera) with Emphasis on Tribe Limnephilini (Subfamily Limnephilinae)*. PhD Dissertation, Clemson University, Clemson, South Carolina, 690 pp.
- Zhong, H., Yang, L.F. & Morse, J.C. (2006) Six new species of the genus *Polyplectropus* (Insecta, Trichoptera, Polycentropodidae) from China. *Acta Zootaxonomica Sinica*, 31 (4), 859–866.