Functional morphology of the male genitalia in Gelechiidae (Lepidoptera) and its significance for phylogenetic analysis

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Abstract. The main directions of the evolutionary transformation of some genital structures are demonstrated on the basis of morphoclines. Due to the adequate stability in position of the muscles in the copulatory apparatus the functional morphological method is sufficiently reliable in solving taxonomic and phylogenetic problems. Some important misinterpretations of the homology in genital structures and incorrect coding in matrices for cladistic analyses are discussed, highlighting the significance of functional morphological investigations for taxonomic and phylogenetic analyses.

Introduction

The present research is focused on preparatory work for any cladistic analysis based on morphological data, namely the work necessary to unravel the homology of the structures (in the present work, genital structures), the directions of their evolutionary transformations, and the coding of the character states for cladistic analysis.

In some families of Lepidoptera (Tineidae: tribe Archimeessiini; Scythrididae: species-groups within genus *Scythris* Hübner; Gelechiidae: tribe Litini*; Lasiocampidae: subfamilies Gastropachinae, Lasiocampinae, etc.) the derived taxa often represent small relatively homogeneous groups morphologically, the copulatory apparatus of which is strongly diverged and transformed during evolution. The taxonomic arrangement of these groups into a natural system of subordinated monophyletic groups encounters numerous morphological difficulties caused by the following. On the one hand, there are convergent similarities in non-homologous genital structures based on their similar functions, and, on the other hand, there are appreciable differences in homologous structures.

Without deep comparative morphological analysis of transformations in the copulatory apparatus both cases account for the misinterpretation of homologies in the genital structures. This leads to mistakes in character coding for cladistic analysis and subsequent misunderstanding of monophyletic groups.

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* The synonymy Litini Bruand, 1859 (=*Teleiodini* Piskunov, 1973; = *Exoteleiini* Омелько, 1999) was established in Ponomarenko (2005). After designation of the *Tinea nanella* Denis & Schiffermüller, 1775 as type species for *Lita* Kollar, 1832 (Nye & Fletcher 1991: 174), the genus *Recurvaria* Haworth, 1828 is treated as senior objective synonym of the last name. The genus *Recurvaria* is related to the genus *Teleiodes* Sattler, 1960 and belong to the same tribe. The family name Litidae Bruand, 1859, established on the name *Lita* Kollar, 1832 is available according ICZN, 1999, Art. 12.2.4. and Litini Bruand, 1859 must be considered as senior synonym of Teleiodini Piskunov, 1973. Besides, the results of comparative morphological analysis confirmed the absence of the morphological hiatus between groups of genera related to *Teleiodes* Sattler, 1960 (type genus for Teleiodini Piskunov, 1973) and *Exoteleia* Wallengren, 1881 (type genus for Exoteleiini Omelko, 1999). Therefore, *Exoteleiini* Omelko, 1999 was synonymized with *Teleiodini* Piskunov, 1973.

Often a simple comparison of the genitalia does not allow to solve the above-mentioned problems. The establishment of the homology of any structure (or organ) is based on three main criteria, the formulation of which can be traced back to A. Remane (1956):

(1) similarity in position (topological criterion), (2) structural similarity, and (3) presence of transitional forms.

Every genital sclerite is part of the skeleton-muscular system of the copulatory apparatus and its modification correlates with changes of other parts of that system. The functioning of genital structures is assisted by musculature and so the tracing of the skeleton's transformation is impossible without studying the musculature morphology.

The functional morphological method is based on the fact that the muscular system in genitalia is more conservative and generally has the same morphology in groups of related genera. Usually a muscle keeps the same position even after a deep transformation of the associated sclerite morphology, so the method is the key to understand the origin of genital structures and helps to trace their transformations. My studies of the skeleton-muscular apparatus of the male Gelechiidae and my comparative morphological analysis (Ponomarenko 1992, 2004, 2005) allowed to unravel the main misinterpretations of the homology of genital sclerites. The most important of them are discussed in the present work and illustrated on the morphoclines of transformation. The muscle nomenclature follows Kuznetzov & Stekolnikov (2001) with changes from Ponomarenko (2005).

Material and methods

The conclusions of the present work on the evolutionary tendencies in transformations of the genital structures are based on large material that was analyzed during slightly less than 20 years of gelechiid moths studies. At present I know the morphology of more than 400 gelechiid genera. Genera from related families were also studied (mainly Scythrididae and Cosmopterigidae) for determination of the genital character states. For the present study the material used came from the collections of Gelechiidae kept in the Zoological Institute of RAS (Sankt-Petersburg, Russia), the Zoological Museum of the Institute of systematics and ecology of animals of SB RAS (Novosibirsk, Russia), the Natural History Museum (London, UK), the Zoological Museum of Helsinki University (Finland), the Osaka Prefecture University (Japan), the National Institute of Agro-Environmental Sciences (Tsukuba, Japan), the Center for Insects Systematics (Chuncheon, Korea), the 'Muzeul de Istorie Naturala Grigore Antipa' (Bucharest, Romania), the 'Museum für Naturkunde der Humboldt-Universität' (Berlin, Germany), and my own material collected in the Far East of Russia (1989–2005), South Korea (1995, 1996), Japan (1998, 2000), Finland (1999), and Ukraine (2001, 2005). The list of species examined representing the main morphological groups within Gelechiidae and of which the genital musculature was studied, is presented as Tab. 1. Detailed descriptions of their functional genital morphology were published in the following series of papers (Ponomarenko 1992, 1995, 1997, 2004, 2005).

Tab. 1. List of the species for which the functional morphology of the genitalia was studied.

Anomologini

Deltophora korbi (Caradja, 1920)

Metzneria inflammatella (Christoph, 1851)

Isophrictis anthemidella (Wocke, 1871)

Ptocheuusa paupella (Zeller, 1847)

Apatetrini

Apatetris kinkerella (Snellen, 1876)

Apatetris elaeagnella Sakamaki, 2000

Metanarsia modesta Staudinger, 1871

Aristoteliini

Aristotelia subdecurtella (Stainton, 1859)

Chilopselaphus fallax Mann, 1867

Megacraspedus separatellus (Fischer von Röslerstamm, 1844)

Sitotroga cerealella (Olivier, 1789)

Polyhymno obliquata (Matsumura, 1931)

Xystophora psammitella (Snellen, 1884)

Caulastrocecis furfurella (Staudinger, 1870)

Psamathocrita osseella (Stainton, 1860)

Bryotropha terrella (Denis et Schiffermüller, 1775)

Pexicopiini

Pexicopia malvella (Hübner, 1805)

Platyedra subcinerea (Haworth, 1828)

Harpagidia magnetella (Staudinger, 1870)

Gelechiini

Neofriseria *peliella* (Treitschke, 1835)

Evippe albidorsella (Snellen, 1884)

Athrips mouffetella (Linnaeus, 1758)

Gelechia rhombella (Denis et Schiffermüller, 1775)

Gelechia anomorcta Meyrick, 1926

Psoricoptera arenicolor Omelko, 1999

Mirificarma eburnella (Denis et Schiffermüller, 1775)

Filatima autocrossa (Meyrick, 1936)

Holcophora statices Staudinger, 1871

Aroga velocella (Duponchel, 1838)

Gnorimoschemini

Gnorimoschema valesiella (Staudinger, 1877)

Caryocolum fischerella (Treitschke, 1833)

Litini

Recurvaria nanella (Denis et Schiffermüller, 1775)

Parastenolechia collucata (Omelko, 1988)

Protoparachronistis initialis Omelko, 1986

Exoteleia dodecella (Linnaeus, 1758)

Stenolechia gemmella (Linnaeus, 1758)

Schneidereria pistaciella Weber, 1957

Teleiodes saltuum (Zeller, 1878)

Carpatolechia fugacella (Zeller, 1839)

Anacampsini

Anacampsis populella (Clerck, 1759)

Syncopacma cinctella (Clerck, 1759)

Sophronia sicariella (Zeller, 1839)

Prolita sexpunctella (Fabricius, 1794)

Mesophleps silacella (Hübner, 1796)

Crossobela trinotella (Herrich–Schäffer, 1856)

Brachmiini

Brachmia dimidiella (Denis et Schiffermüller, 1775)

Dichomeridini

Helcystogramma triannulella (Herrich–Schäffer, 1854)

Acompsia cinerella (Clerck, 1759)

Dichomeris japonicella (Zeller, 1877)

Dichomeris rasilella (Herrich–Schäffer, 1855)

Dichomeris oceanis Meyrick, 1920

Acanthophila lucistrialella Ponomarenko et Omelko, 2003

Chelariini

Neofaculta ericetella (Geyer, 1832)

Nothris verbascella (Denis et Schiffermüller, 1775)

Encolapta tegulifera (Meyrick, 1932)

Paralida okinawensis Ueda, 2005

Hypatima rhomboidella (Linnaeus, 1758)

Faristenia quercivora Ponomarenko, 1991

Faristenia furtumella Ponomarenko, 1991.

Dendrophilia mediofasciana (Park, 1991)

Bagdadia claviformis (Park, 1993)

Anarsiini

Ananarsia lineatella (Zeller, 1839)

Anarsia halimodendri (Christoph, 1877)

My studies of the skeleton of the gelechiid copulatory apparatus were conducted according to traditional methods of lepidopterological investigations. The maceration of the soft tissues was realized by boiling the abdomens in a 10% aqueous solution of KOH. The genitalia were then placed in glycerin for examination and later into euparal for permanent preservation.

My studies of the functional morphology were conducted on specimens mainly fixed in 70% alcohol. Their dissection followed the method described by V.I. Kuznetzov and A.A. Stekolnikov (2001). The flexibility in dry specimens was obtained by the author's method. The abdomens were soaked in 10% lactic acid (2-hydroxypropanoic acid, $CH_3CH(OH)COOH$) during 15–24 hours at less than 40° C. Before dissection every specimen was stained in an aqueous solution of eosin.

The skeleton-muscles apparatus of the male genitalia was studied with Carl Zeiss and Nikon SMZ-10 microscopes under magnifications of 120–160. During dissection an image of every layer was taken with a Nikon Coolpix 8700 digital camera.

Abbreviations

Muscles:	m_2	abductor muscles of valva
	m_3	muscles of median plate (juxta)
	m_4	adductor muscles of valva

Genital structures:	aed	aedeagus
	ccl	cucullus
	ejac.d	ejaculatory ductus
	gl	gland (r.gl: right gland, l.gl: left gland)
	gl.d	glandular ductus
	gld	glandiductor
	gn	gnathos
	jux	juxta
	man	manica
	pl.jn	place of junction with same process of left valva
	prt.sc	parategminal sclerite
	sacc	saccus
	scl	sacculus
	teg	tegumen
	tr	transtilla
	unc	uncus
	vlvl	valvella
	vnc	vinculum.

The homology of some "problematic" parts of the male genitalia in Gelechiidae

Transformation of the tegumen

There are two sclerites in the male genitalia of the subfamily Dichomeridinae that are placed laterally between the tegumen and vinculum and anterior of the valva (Figs 1 a–d). Hodges (1986) proposed for them the descriptive term "appendix appendicular"
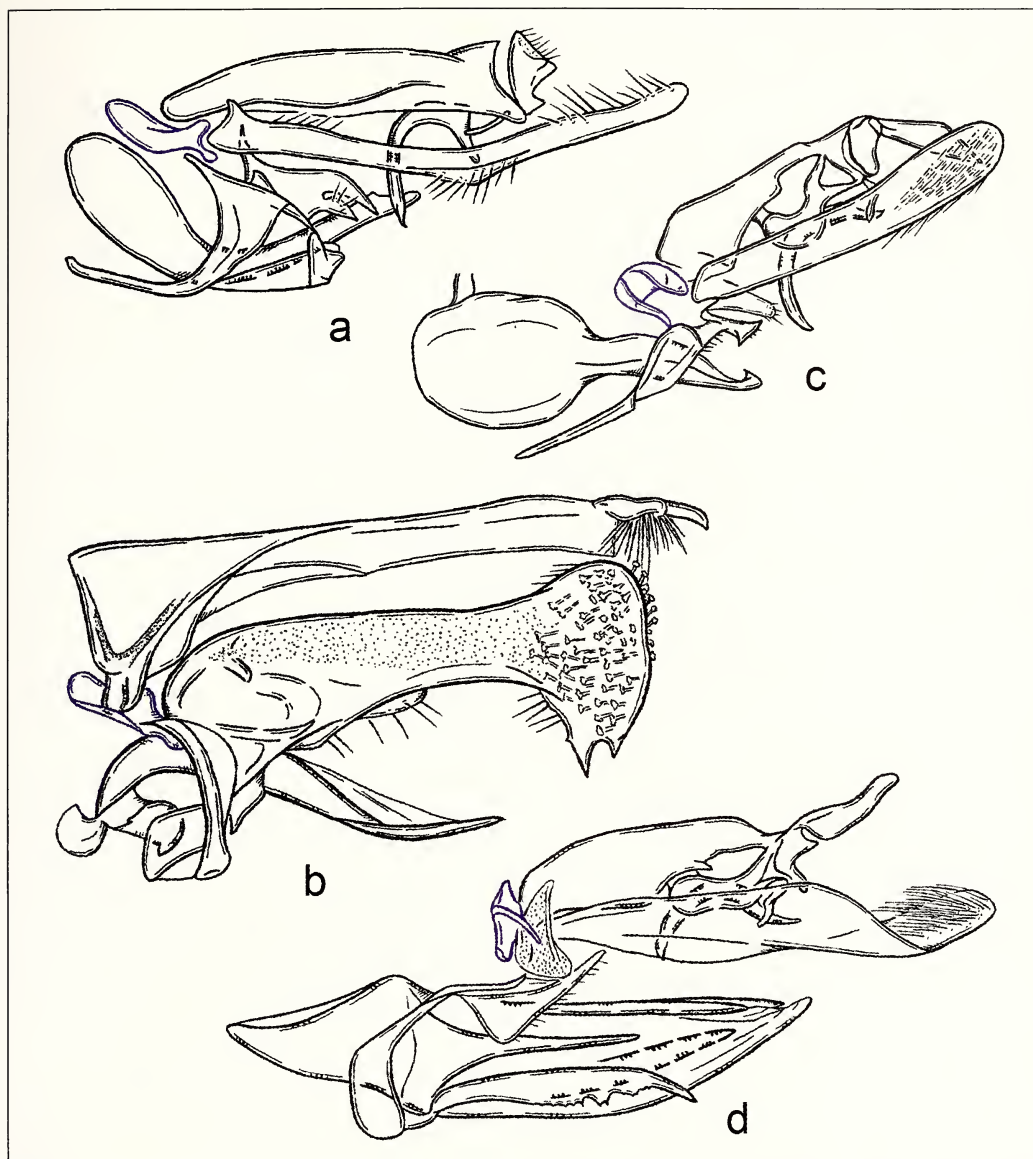
Fig. 1. Gelechiidae, male genitalia. **a.** Chelariini: *Bagdadia claviformis* (Park); **b.** Anarsiini: *Ananarsia bipinnata* (Meyrick); **c.** Dichomeridini: *Helcystogramma lutatella* (Herrich-Schäffer); **d.** Dichomeridini: *Dichomeris derasella* (Denis et Schiffermüller); parategminal sclerite shown by blue.

in the Dichomeridini, which does not indicate their origin. Omelko (1999) treated them as sacculus in tribe Chelariini and partly as tegumen and as derivative of the vinculum in Dichomeridini. Kaila (2004), commenting his cladistic analysis and character states wrote "... the appendix appendicular was interpreted to be homologous to valval costa." Summarizing the above-mentioned three opinions, one can ask: Are the "appendices appendiculares" homologous to parts of the tegumen, vinculum, or to parts of the valva?

The anterolateral parts of the tegumen are apodemes for muscle m_4, which is the adductor of the valva (Figs 2 a–d). Modifications of these parts of the tegumen are caused by the functioning of the valvae and correlated with transformations of the latter. Wide investigations in Gelechiidae allowed to trace the transformation of the anterolateral parts of the tegumen within the family (Figs 3 a–g). In many genera of Gelechiidae, as in other families, Agonoxenidae, Ethmiidae, Oecophoridae, Coleophoridae, Momphidae, Scythrididae, belonging to the superfamily Gelechioidea (after Hodges, 1998), or superfamilies Elachistoidea, Coleophoroidea and Gelechioidea (after Kuznetzov & Stekolnikov, 2001), the muscles m_4 are attached to the tegumen, therefore the state illustrated on Figs 3 a, b was treated as initial. In some groups within the family (*Caryocolum* Gregor et Povolný, *Syncopacma* Meyrick, *Mesophleps* Hübner, *Crossobella* Meyrick) the anterolateral parts of the tegumen are elongated (Fig. 3 c) and reminiscent of the pedunculi in other groups of Microlepidoptera (for example in Tortricidae). This state of the anterolateral parts of the tegumen, obviously, can be considered as intermediate between the above-mentioned initial state and separate sclerites, found in subfamily Dichomeridinae. The connection of the separate sclerites and the anterolateral parts of the tegumen with the muscles m_4 is the base for establishing their homology. These sclerites were named parategminal (Ponomarenko 1992), thus indicating their origin.

The presence of separate sclerites connected with muscles m_4 is one of the main diagnostic characters for Dichomeridinae, consisting of Anarsiini, Chelariini, and Dichomeridini (Figs 3 d–g, outlined by blue square).

Within Dichomeridinae the parategminal sclerites have undergone strong modification from rounded lateral plates (tribes Anarsiini and Chelariini, and genera *Acompsia* Hübner, *Scodes* Hodges, and *Helcystogramma* Zeller of tribe Dichomeridini) to complicated sclerites connected not only with muscles m_4, but also supporting androconial structures (genera *Dichomeris* Hübner, *Acanthophila* Heinemann of Dichomeridini). The modification of the parategminal sclerites in the genus *Acanthophila* Heinemann into long bands is linked to a change of the muscles m_4 function which, due to their contraction, causes sclerites rotating around their longitudinal axis and unrolling a bunch of modified, hair-like scales (Fig. 3 g).

Thus, parategminal sclerites connecting with muscles m_4 and originated from the anterolateral parts of the tegumen in tribes Anarsiini, Chelariini, and Dichomeridini, are homologous in all of these tribes. The presence of separate parategminal sclerites (apomorphy 32) allows to support subfamily Dichomeridinae as a monophyletic group (Fig. 8, shown by blue oval).

Genital glands

The valvae within Gelechiidae demonstrate a wide diversity in shape, from rounded and large to narrow and sharp, from inflated with modified setae to flat, often bearing processes and lobes with strong and long setae. Besides that, one of the evolutionary tendencies in the transformation of the valvae in the Gelechiidae is their division into separate cucullus and sacculus. Different states of the latter are found in different groups within the family. The rich morphological diversity of the valvae probably
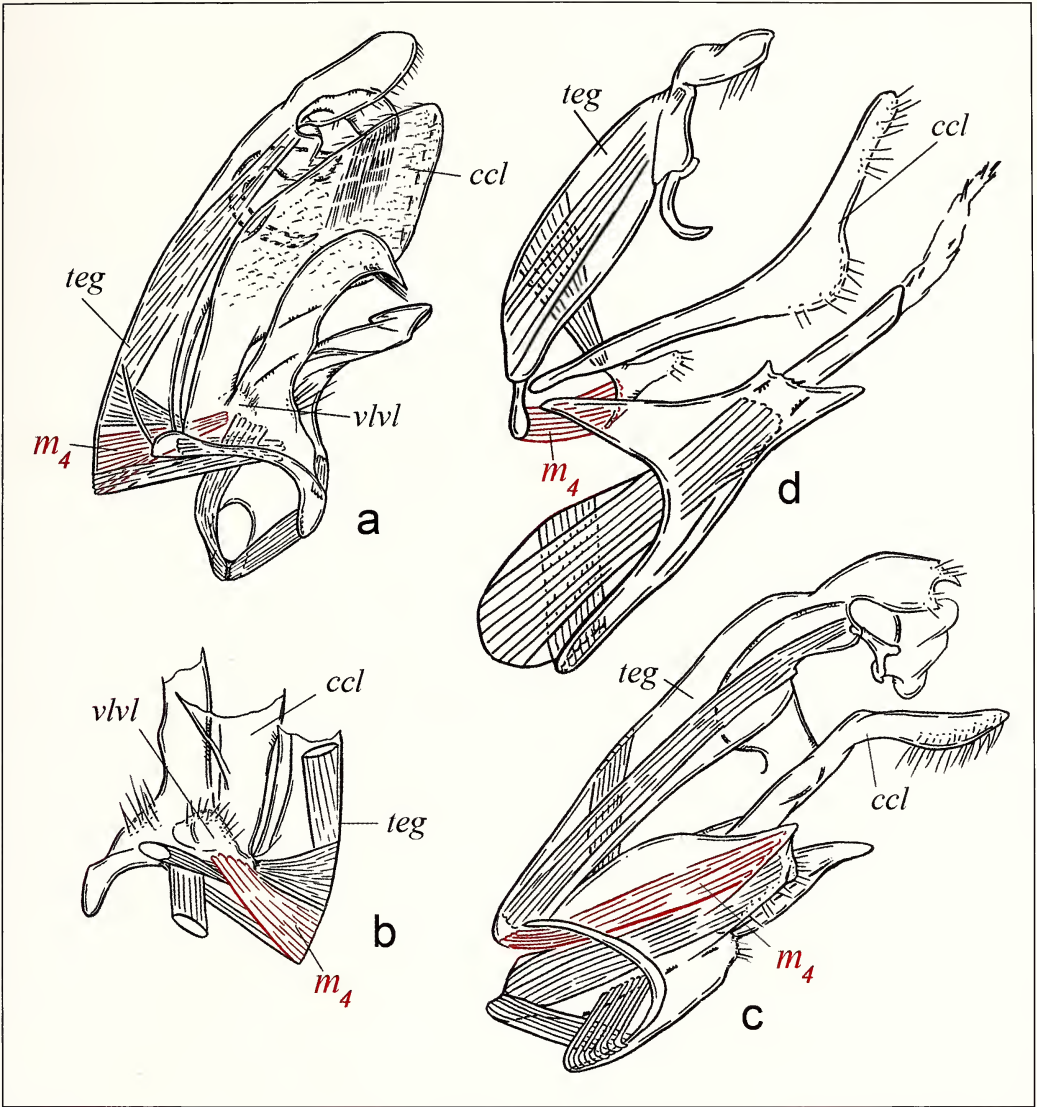
Fig. 2. Gelechiidae, male genitalia. **a, b.** *Platyedra subcinerea* Haworth (a. lateral view; b. anterior part from inner side); **c.** *Gelechia anomorcta* Meyrick; **d.** *Syncopacma cinctella* Clerck.

caused that any sclerite placed between the tegumen and vinculum was recognized as the valva or part of it.

Within a large group of genera of tribe Litini (*Recurvaria* Haworth, *Coleotechnites* Chambers, *Exoteleia* Wallengren, *Chorivalva* Omelko, *Stenolechia* Meyrick, *Parastenolechia* Kanazawa, *Nuntia* Omelko, *Schneidereria* Weber, *Teleiodes* Sattler, *Carpatolechia* Capuşe, *Pseudotelphusa* Janse, and *Altenia* Sattler) a pair of rounded formations, each connecting with a channel piercing the sclerotized structures and often strongly inflated basally have been found (Figs 4, 5). The sclerotized structures have an opening at their apex. Similar paired organs were found in *Pogochaetia* Staudinger,

Tila Povolný, and *Agonochaetia* Povolný (tribe Gnorimoschemini). The identification of this organ as gland was based on the correspondence of its general morphology (round body and ductus with opening) with that of an organ described in primitive Lepidoptera (Kristensen 1984; Scoble 1992; Hallberg & Poppy 2003).

Since the soft tissues are digested during maceration in KOH, the rounded glandular bodies and glandular ductus were never found in the genitalia and the attention of the scientists was attracted only to the sclerotized distal parts of the described glands. Before the present investigation these parts took various names in the above-mentioned genera: "valva", "cucullus", "valvella", "filament". In the course of my research I found that the discussed parts were not homologous to any part of the valva. Since these sclerotized structures support the glandular ductus the name "glandiductors" was proposed for them (Ponomarenko 2005).

During my comparative morphological analysis it was possible to reveal the tendency in the change of the glandiductors' position. Originally they probably were positioned medially to the cuculli and were fused with them basally (Figs 6 c, d, 7 a, b). Within the tribe Litini one can see the lateral removing of these structures and replacement of slightly sclerotized cuculli by them (Figs 6 b, 7 c) In some genera of the Litini the cucullus is still present (Fig. 6 c, marked by blue), but it has lost its function to hold the female during copulation. The described transformation is closely linked with the main evolutionary tendency in the valva's transformation within Gelechiidae. This tendency is directed toward the loss of the basic valva's role of holding the female during copulation which is caused by the fusion of the valvae with other structures of the genitalia and often accompanied by a reduction of the valval musculature (Ponomarenko 2005).

The transformation of the glandiductors within the Gelechiinae is not limited to the example considered above and should be subjected to a special investigation. The illustrations of the male genitalia of *Chionodes* Hübner, *Sattleria* Povolný, and *Tila* Povolný (Sattler 1947: figs 7–18; Pitkin & Sattler 1991: fig. 66; Povolný 2002: figs 473, 474) allow to imagine several directions of glandiductor transformation within the subfamily: their replacement dorsally and junction over the aedeagus, their ankylosis with the cuculli, or their reduction to perforated plates in the anellus zone.

In genus *Mirificarma* Gozmány the glandular body is unpaired and asymmetric and the glandular ductus, arising from it, penetrates the long so-called filament with two small lobes outlining the excretory opening (Fig. 5 c).

In *Gelechia* Hübner and *Psoricoptera* Stainton, which are very close to *Mirificarma* in genitalic morphology, the glands have not been found. However, in some species of *Gelechia* the membranous sac is placed where the medial valvar processes (transtilla) are fused. The similarity of the membranous sac in these genera was already noted by Pitkin (1984).

The homology of these new organs (genital glands) cannot be doubted; they not only occupy the same position, but they are also connected with the abductor muscles of the valvae (m_2) in all mentioned genera, as the transtilla in *Gelechia* and *Psoricoptera* (Figs 6 a, b). Genus *Neofriseria* Sattler, which is related to genus *Gelechia*, attracts the attention by its long twisted processes on the medial side of each valva (Figs 5 d, e, marked in green). The abductor muscles of the valvae (m_2) arise from the dorsal arched part
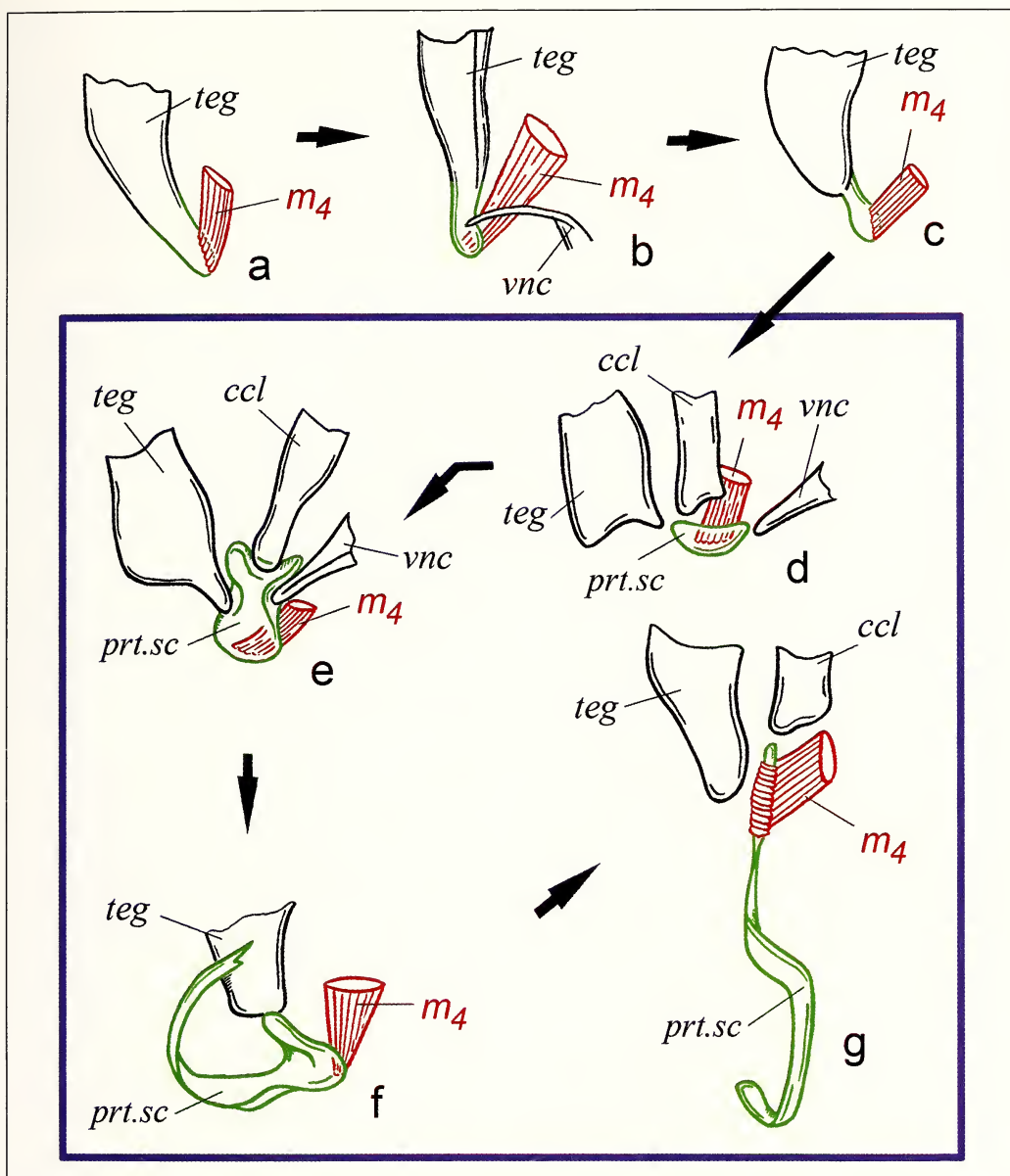
Fig. 3. Transformation of the anterolateral parts of tegumen within family Gelechiidae. **a.** *Gelechia* Hübner, **b.** *Psoricoptera* Stainton; **c.** *Syncopacma* Meyrick, **d.** *Neofaculta* Gozmány, **e.** *Hypatima* H Hübner, **f.** *Dichomeris* Hübner, **g.** *Acanthophila* Heinemann. Direction of transformation is shown by arrow. Genera belonging to Dichomeridinae are outlined by blue square.

of these processes, which is evidence for their homology with the medial processes of the valvae in other genera close to *Gelechia*, including genus *Mirificarma*, which has a well-developed gland. The distal part of the processes in *Neofriseria* is dilated, with a gutter-like concavity and both are joined medially by a membranous sac. The peculiarities of the long twisted processes on the medial side of the valvae in *Neofriseria*

allow to hypothesize on the genesis of the above-described glands. I presume that they originated from the ectoderm by invagination of the wall in processes like those of *Neofriseria*, and that there were originally two of them. The confirmation of this hypothesis is the presence of the paired glandular bodies and ducti in most of the genera in which they were found. Genus *Tila*, with its basally joined glandular bodies and two glandiductors, probably holds a transitional position to *Mirificarma*, which has an asymmetric unpaired gland, as a result of the fusion of the originally paired glandular bodies.

The position of muscles m_2, enclasping the inflated bases of the glandiductors (Fig. 7 b), allows to presume their performance of two functions. The first of them (mentioned above) is supporting the glandular ductus. The second function of the glandiductors is implied also by their position: in many genera they are placed over the aedeagus and positined in the same direction. Being inserted in the ductus bursae along with the aedeagus, they take part in the fixation of the female during copulation by moving outwardly due to the traction of muscles m_2. Thus, the glandiductors not only support the glandular ductus but functionally compensate for rudimentary or reduced cuculli.

In summary, the presence of glands in the genitalia should be estimated to be a common specialization of tribes Gelechiini, Gnorimoschemini, and Litini inherited from a common ancestor and secondarily lost by some of their representatives. Thus, the presence of the described glands could be considered as a basal synapomorphy for the subfamily Gelechiinae (Fig. 8, shown by green oval).

The transformation of the juxta

The ground plan of the skeleton-muscular apparatus of the genitalia in Lepidoptera, analysed in details by Kuznetzov & Stekolnikov (2001) and Kristensen (2003), is characterized by the presence of a sclerotized median plate (juxta) in the ventral part of the anellus and connected with muscles m_3. The position of this ventral sclerite and its connection with muscles m_3 are characteristic for many families of Microlepidoptera. Therefore, the homology of the separate median plate (juxta) connected with muscles m_3 in the gelechiid genera related to *Apatetris* Staudinger and *Brachmia* Hübner and in genera of the Chelariini and Anarsiini (Figs 9 a–c, 10 a), and the juxta in other families of Microlepidoptera is obvious.

The juxta belongs to the phallic functional morphological complex (Ponomarenko 2004, 2005). It is impossible to consider the function and transformation of any structure of this complex separately from the other ones, especially the most important of them, the aedeagus. The general tendency in evolutionary transformation of the aedeagus within Gelechiidae is its junction with the ventral part of the genitalia (with vinculum and juxta; or with vinculum, juxta, and sacculi) till their ankylosis into one sclerite. The later stage is typical for most specialized groups within the family. Such groups were used for introducing new terminology in lepidopterological morphology and the source of misinterpretations of the structures' homology.

The variety of opinions on the homology of the "ventral sclerite" in the male genitalia of gelechiid moths requires to consider this problem in detail. The descriptive term
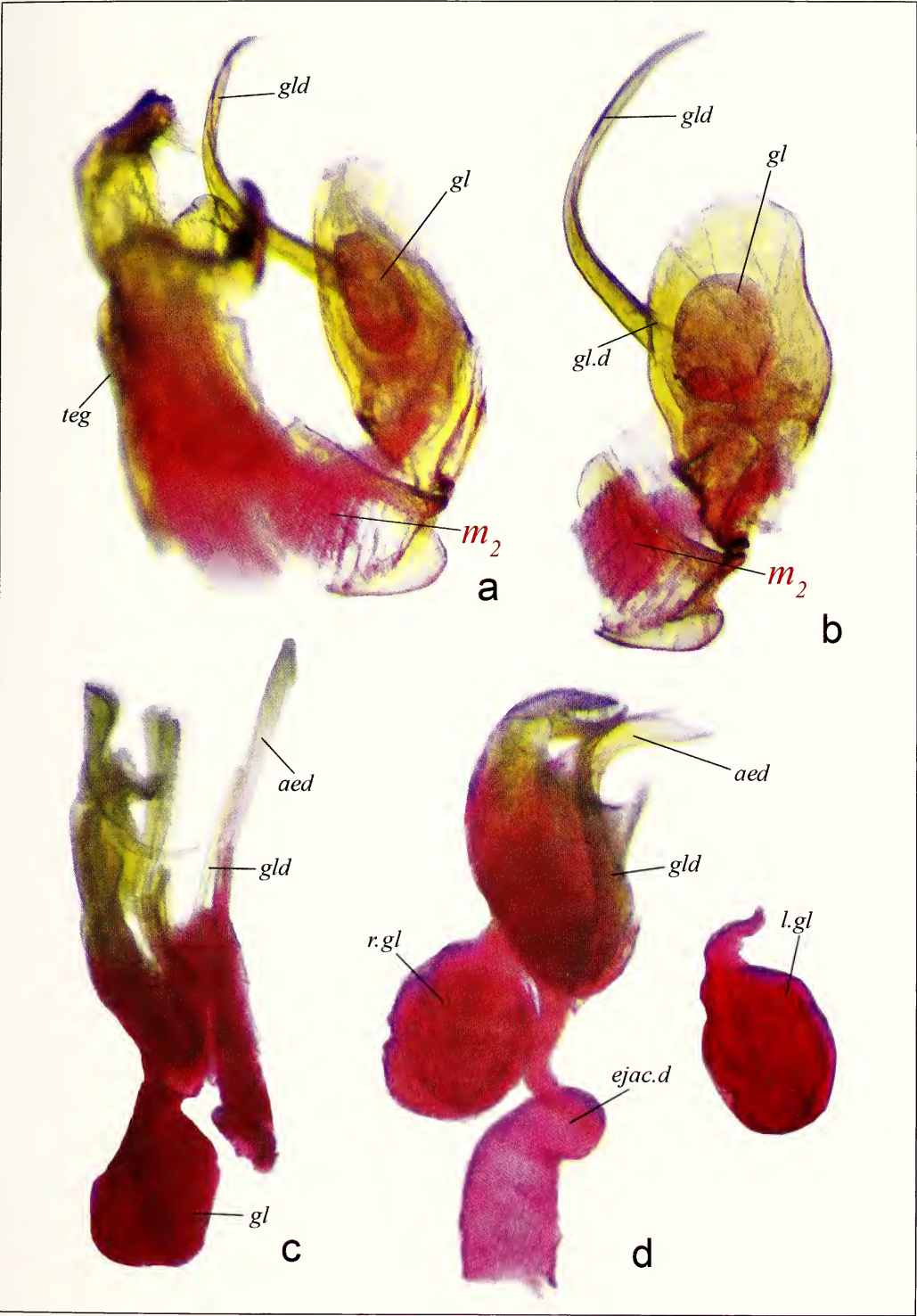
Fig. 4. Photo of male genitalia with glands of genital segments. **a, b.** *Teleiodes saltuum* (Zeller) (a. genitalia in lateral view, b. gland); **c.** *Mirificarma eburnella* (Denis et Schiferrmüller); **d.** *Schneidereria pistaciella* Weber.

"ventral sclerite" was used by V.I. Piskunov (1981) in the tribe Dichomeridini. Ronald H. Hodges (1986) used the traditional term "juxta" in the same tribe. Omelko (1991) treated the ventral sclerite as a "juxta" in tribes Chelariini and Anarsiini only, but in tribe Dichomeridini he associated this sclerite with the distal processes of the sacculi. The term "sicae" was used by Park (1994) and later by Hodges (1998) following Heinrich (1920). Kaila (2004) in his cladistic analysis of Gelechioidea mentioned "… the sicae were not coded separately from the modification of the sternum 8 of Cosmopterigidae and Scythrididae" thus associating the term "sicae" to parts of the abdomen that do not belong to the genitalia. This conclusion was based on the genital morphology of *Pexicopia malvella* Hübner, belonging to the Pexicopiini (Gelechiidae).

The origin of the sclerite placed ventrally in the male genitalia of the Dichomeridini is unravelled in an analysis of the evolutionary transformation of the ventral part of the male genitalia in the subfamily Dichomeridinae. One of the directions of transformation of the juxta within this subfamily consists in its fusion with the median side or posterior margin of the vinculum, which is revealed in more specialized genera of the Chelariini (*Dendrophilia* Ponomarenko, *Empalactis* Meyrick, *Bagdadia* Amsel) and genera from of the Dichomeridini with more generalized morphology (*Helcystogramma* Zeller) (Figs 9 e, 10 b). The juxta, as a result of its fusion with the vinculum, loses its ability to the free mobility correlated with a weakening and reduction of muscles m_3. This transformation is shown on Fig. 10. On the base of this morphocline the homology of the ventral sclerite, fused with the posterior margin or median surface of the vinculum in specialized genera of Dichomeridini and with the juxta in other representatives of the subfamily is established.

The described transformation also takes place in other groups of Gelechiidae and it is possible to find examples with different stages of this process: juxta joined with vinculum and still connected with muscles m_3; juxta fused with vinculum with reduced muscles m_3 (Fig. 9 d) and presence of muscles m_3 with absence of juxta. A study of the functional morphology in genus *Pexicopia* Common shows that the "ventral sclerite" should be considered as the fused vinculum+juxta, of which the homology is confirmed by the position and attachment of muscles m_3 (Fig. 9 f) and phallic muscles m_{5a}, m_{5b} and m_6 (Ponomarenko 2005: 110, fig. 28), originally arising from those sclerites in genera with a more generalized morphology. The separate vinculum and juxta as well as the derivative vinculum+juxta are parts of the 9th genital segment and cannot be treated as homologous to the modified 8th sternum in Cosmopterigidae and Scythrididae.

Incorrect homologies of the genital structures in cladistic analyses of Gelechioidea

As a result of functional morphological analysis, the homology of some genitalic structures has been reconsidered and evolutionary transformations within the family were revealed. Investigations on the homology of genital sclerites would be incomplete without an overview of the use of these characters in recently published cladistic analyses and their coding.
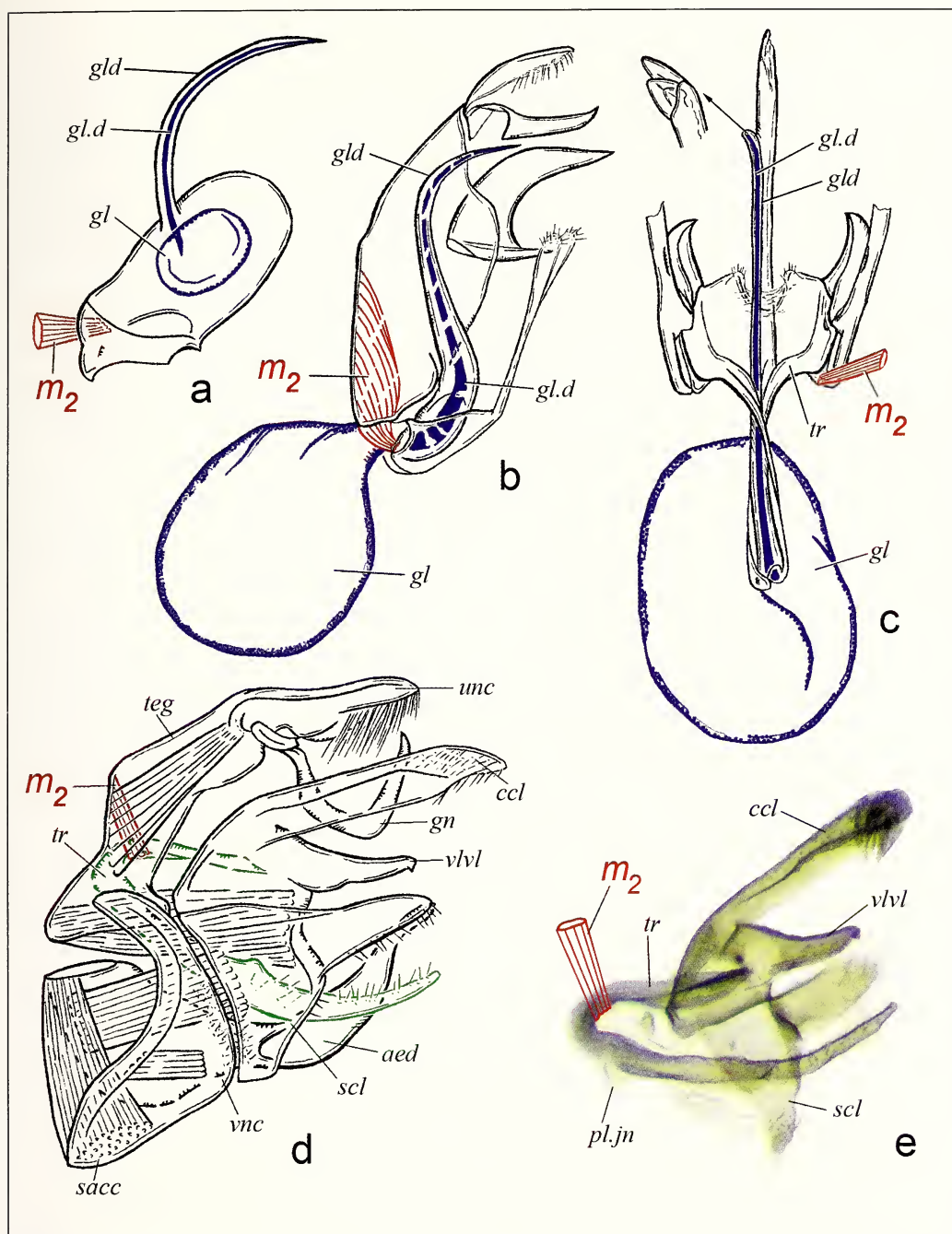
Figs 5 a–e. Glands of genital segments. **a.** *Teleiodes saltuum* (Zeller), **b.** *Schneidereria pistaciella* Weber, **c.** *Mirificarma eburnella* (Denis et Schiferrmüller). **d, e.** *Neofriseria peliella* (Treitschke), skeleton-muscular apparatus of the male genitalia. **d.** lateral view, **e.** right valva, view from inner side.

As shown above, the parategminal sclerites of the Dichomeridinae, consisting of tribes Anarsiini, Chelariini, and Dichomeridini, have a common origin. They are homologous

to the anterolateral parts of the tegumen in other Gelechiidae and were separated from them along with muscles m_4 during their evolutionary transformation. The parategminal sclerites are equal to the "appendix appendicular" in the Dichomeridini (only!).

The term "appendix appendicular" introduced by Hodges (1986) for Dichomeridinae sensu stricto (Dichomeridini in my understanding) was used for any sclerites placed anterolaterally in the male genitalia of many groups within Gelechiidae, not only by the term's author, but by other researchers as well. According to the functional morphological data the sclerites named "appendix appendicular" were not homologous structures; most often they are the transtilla in Apatetrini, Gelechiini and Gnorimoschemini, the anterolateral parts of the tegumen in Gelechiini and Pexicopiini, or the parategminal sclerites in Anarsiini and Dichomeridini. If the anterolateral parts of the tegumen and parategminal sclerites are both apodemes of muscles m_4 and states of the same morphocline (see above, Fig. 3), the transtilla being the apodeme of m_2 is not homologous to the anterolateral parts of the tegumen and parategminal sclerites.

This misinterpretation was the basis for an additional mistake in Kaila (2004), where characters 1 (valva without/with developed costa as free lobe) and 29 (appendix appendicular present/absent) of Hodges (1998) were fused and "the appendix appendicular was interpreted to be homologous to valval costa".

As a result of the misinterpretation of the homology of these genital sclerites the character "appendix appendicular" was scored as present in the matrix for three subfamilies Gelechiinae, Dichomeridinae and Pexicopiinae and finally received the status of parallelism in Hodges (1998: character 29). In its reconsidered version and broadened interpretation that character found a place in the cladogram of Gelechioidea as an homoplastic synapomorphy for the branches Gelechiidae+Cosmopterigidae, Scythrididae and Coleophoridae (Kaila 2004: 329, character 101).

There is probably no reason to discuss the coding of this character in the matrix of Gelechioidea in Bucheli & Wenzel (2005), where, on the one hand, complexes of characters were uncritically used following previous authors, and, on the other hand, the matrix was filled in error. Referring to Hodges (1998), the authors indicated an absence of the appendix appendicular in Dichomeridinae instead of a presence, but no group was given that state of character in their matrix.

The next point of the present study is that the "ventral sclerite" of the vinculum in Dichomeridini was formed as a result of the evolutionary transformation of the typical juxta in other gelechiid moths (see morphocline on Fig. 10). Both states, free juxta and joined with vinculum correspond to the definition of the term "juxta" in Klots (1970): Juxta is a "sclerotized plate, often shield-shaped, ventrad of aedeagus, which it helps to support; strongly fastened to or fused with bases of sacculi and ventral part of vinculum; sometimes connected with anellus by a median rodlike process, which is often forked dorsally so as to surround aedeagus". Hodges (1998), referring to Klots, reduced this definition and divided the states of this character into two: "free juxta present/absent" and "sicae (joined juxta and vinculum) absent/present". This would not be a subject for discussion if every author using these states would be consistent in their coding. Firstly, it is necessary to emphasize that the term "sicae" was used by Hodges for the subfamily
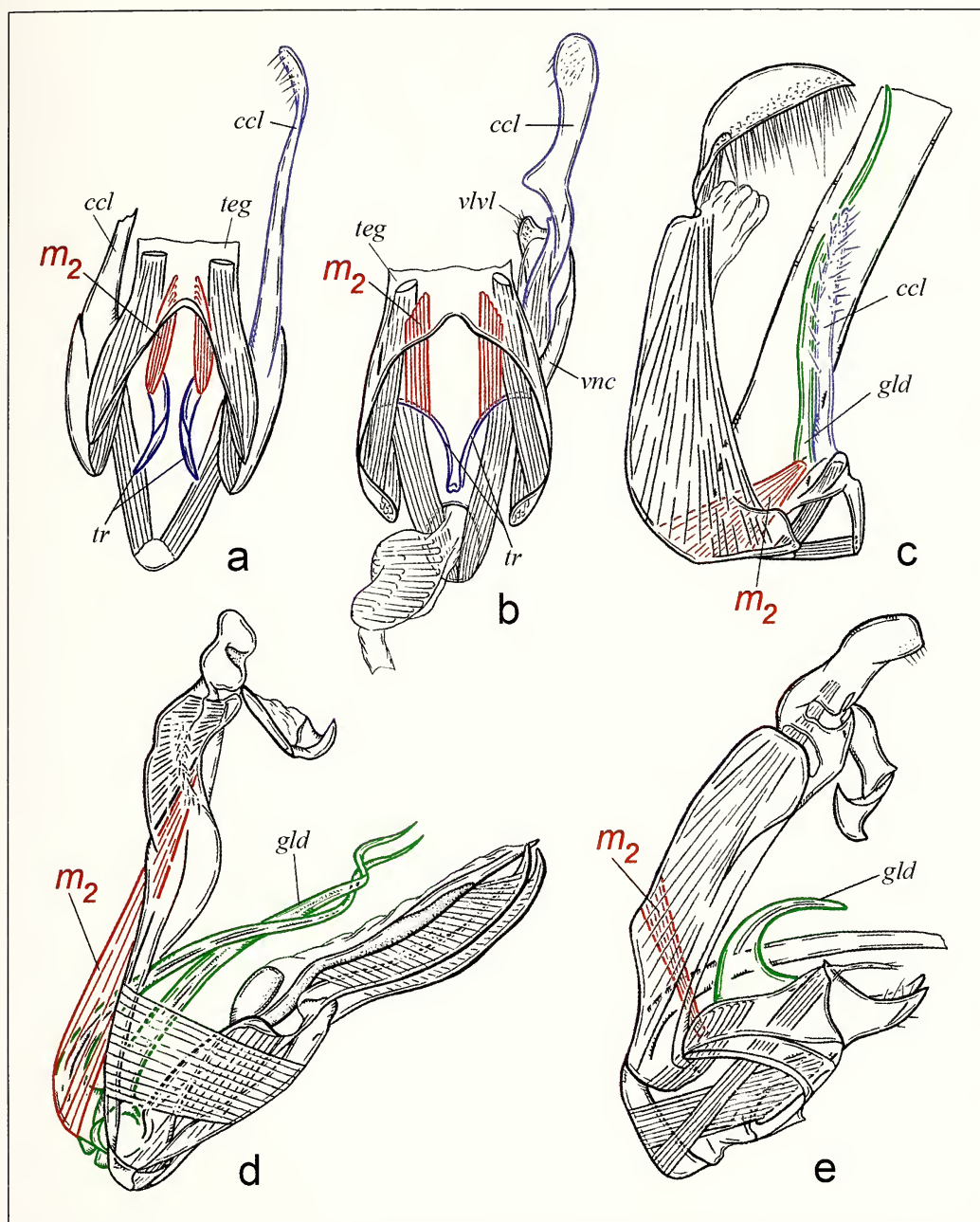
Figs 6 a–e. Position of muscle m_2 in the genera of Gelechiinae. **a.** *Psoricoptera arenicolor* Omelko; **b.** *Gelechia rhombella* (Denis et Schiferrmüller); valva, base of tegumen and aedeagus, dorsal view. **c–e.** Position of glandiductors in Litini. **c.** *Carpatolechia fugacella* (Zeller), **d.** *Recurvaria nanella* (Denis et Schiffermüller), **e.** *Stenolechia gemmella* (Linnaeus). Glandiductors are shown by green, cucullus and transtilla marked by blue.

Dichomeridinae following Heinrich (1920), who had introduced it for unrelated groups (*Recurvaria* Haworth, *Tosca* Heinrich) and for nonhomologous structures. As for cod-
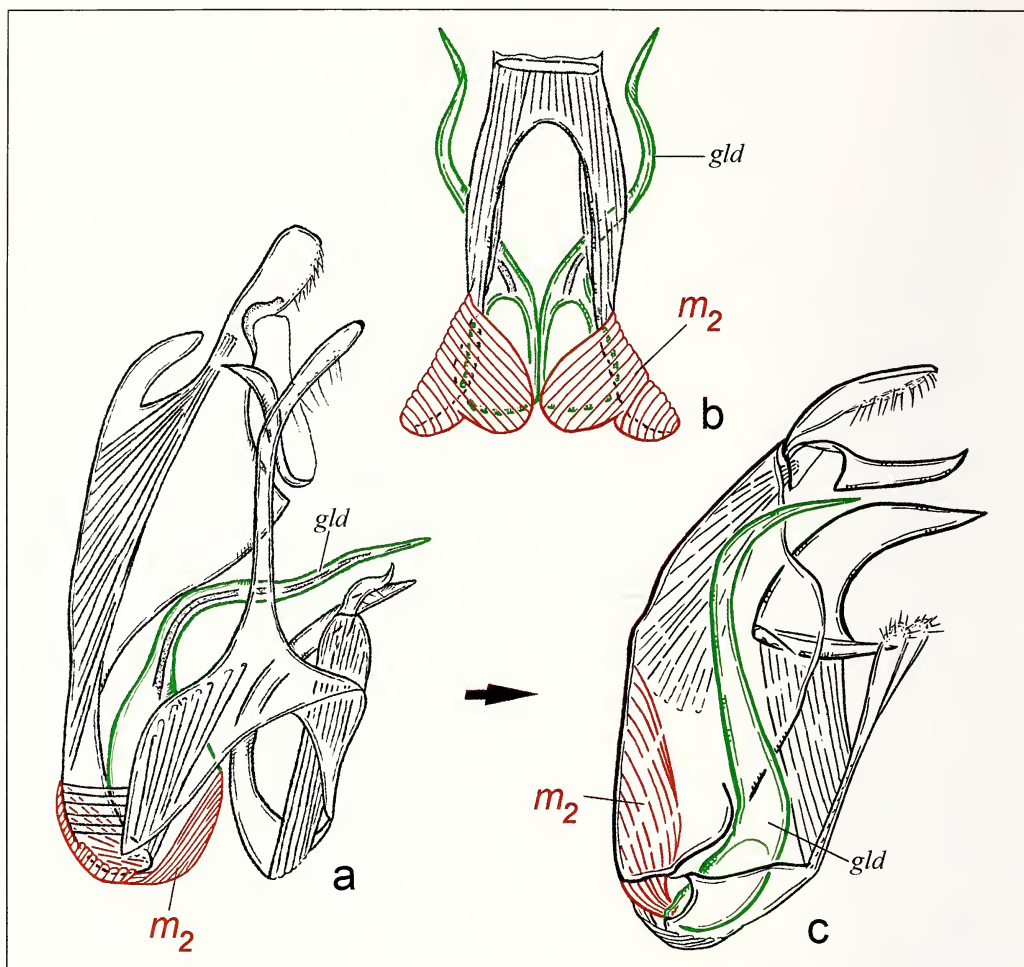
Fig. 7. Transformation of glandiductor position. **a, b.** *Parastenolechia collucata* Omelko (a. lateral view, b. dorsal view), **c.** *Schneidereria pistaciella* Weber. Glandiductors are shown by green. Direction of transformation is shown by arrow.

ing, the character state "juxta absent" (Hodges 1998: character 2 (1)) was indicated for subfamily Gelechiinae, in which the tribes Chelariini (including the *Anarsia*-group) and Anomologini (including *Apatetris* Staudinger and *Metanarsia* Staudinger) were included. All these groups have a free juxta with well developed muscles m_3 (Figs 9 a, b; 10 a). On the other hand, the character state "sicae present" (Hodges 1998: character 7 (1)) in the matrix was indicated for subfamily Dichomeridinae only, whereas the term was introduced by Heinrich for the tribe Litini (=Teleiodini). Besides that, Hodges (1998) included genus *Brachmia* Hübner in his Dichomeridinae whereas it possesses a typical free juxta with well-developed muscles m_3 (Fig. 9 c). The processes on the posterior margin of the vinculum in *Helcystogramma* Zeller are homologous to sacculi, not to the juxta. The juxta in this genus is represented by a bridle-like sclerite with attached muscles m_3 and lacking any processes (Fig. 9 e). The so-called "sicae" in this
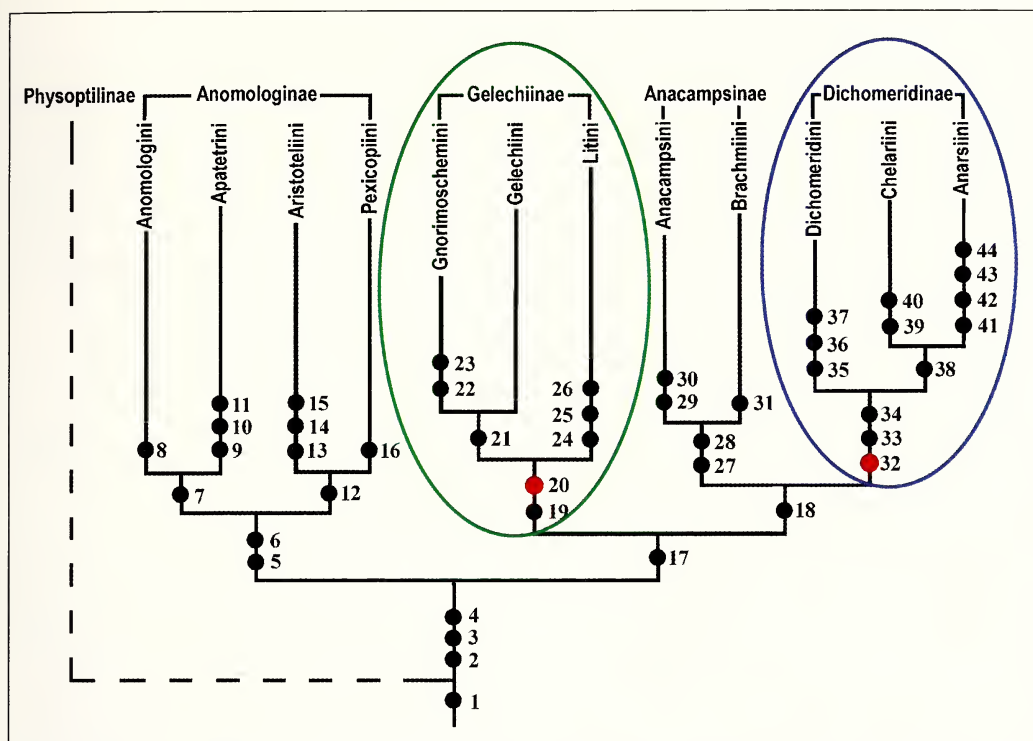
Fig. 8. Cladogram of the family Gelechiidae. Monophyletic groups, subfamilies Gelechiinae and Dicho-meridinae, are shown by green and blue ovals. Synapomorphies marked by red: 20: presence of glands of the genital segment; 32: muscles m_4 attached to separate parategminal sclerites. For remaining apomor-phies see Ponomarenko (2005).

genus are absent. Additionally, the genera *Scodes* Hodges and *Acompsia* Hübner have neither juxta and processes on the vinculum. The large setaceous lobes in both genera are sacculi, which is confirmed by the position of the phallic muscles. Thus, really only one genus, *Dichomeris* Hübner, possesses "sicae" in male genitalia, but not in all spe-cies. This does not allow to treat the character state "sicae present" as a synapomorphy for the Dichomeridinae.

Bucheli & Wenzel (2005) did not reconsider the states of these characters and in coding them they completely followed Hodges (1998). The extrapolation of the term "sicae" to sternum 8 of the visceral segments of the abdomen could be interpreted as an un-fortunate misinterpretation, which found place in Kaila's cladogram (2004) as a single "unique" synapomorphy for the Scythrididae+Gelechiidae+Cosmopterigidae (Kaila 2004: character 81 (1)).

The last point is the newly discovered gland of the male genitalia. The sclerotized structures which support glandular ductus (or insert it) in the Gelechiinae were named glandiductors. They are not homologous to parts of the valva. One of the directions in the evolutionary transformation of the glandiductors was the lateral removing of these structures and replacement of the slightly sclerotized cuculli by them. The numerous
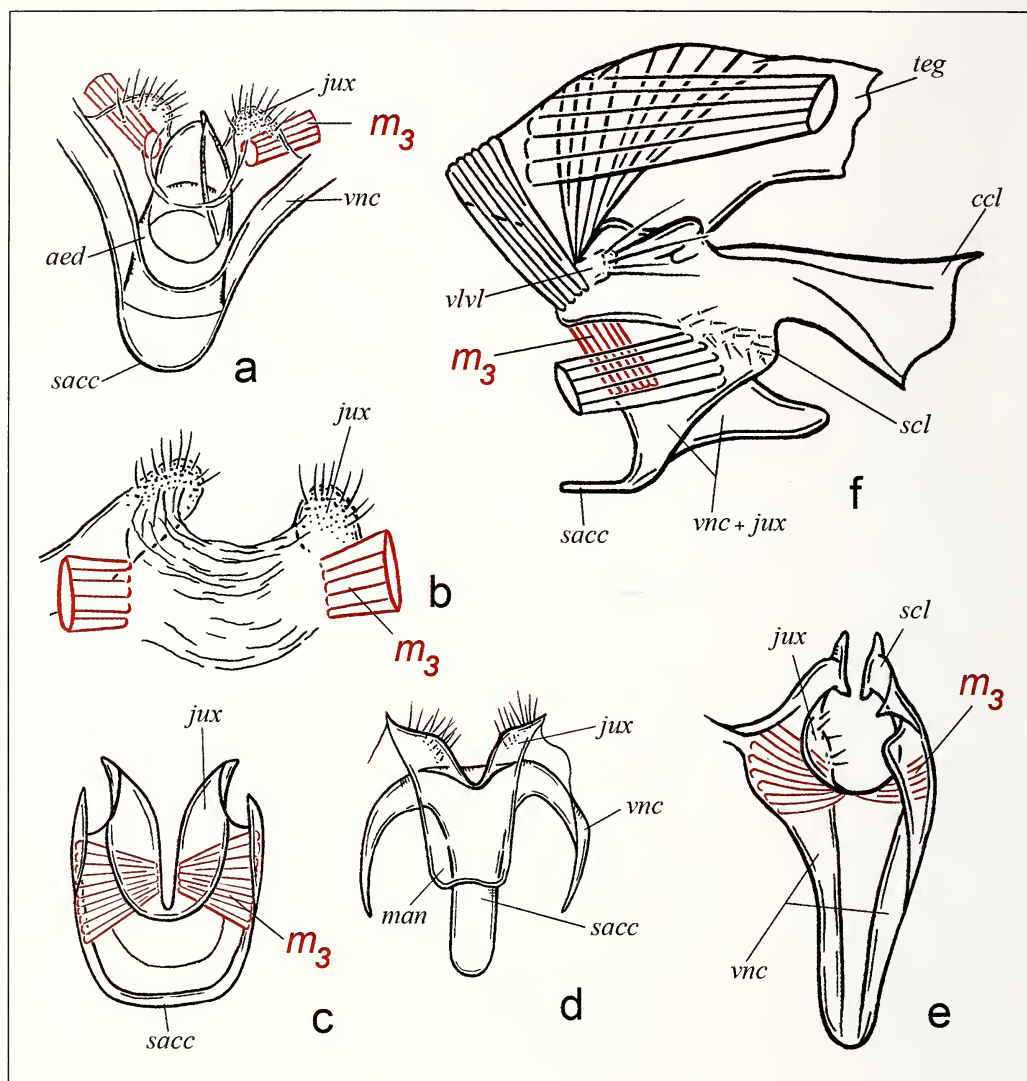
Fig. 9. Position of the juxta in Gelechiidae. **a.** *Apatetris kinkerella* (Snellen); **b.** *Metanarsia modesta* Staudinger; **c.** *Brachmia dimidiella* (Denis & Schiferrmüller); **d.** *Gelechia rhombella* (Denis et Schiffermüller); **e.** *Helcystogramma triannulella* (Herrich-Schäffer); **f.** *Pexicopia malvella* (Hübner).

misinterpretations of the homology of the glandiductors are simply caused by their occupation of a lateral position in the male genitalia.

In summary, it is reasonable to conclude that the final results of any cladistic analysis directly depend not from the number of included characters, but from their quality. A careful comparative morphological analysis to understand the genital sclerites' homology and, as consequence, to correctly code the states of the characters and to critically select the characters to analyze represent a good guarantee to achieve believable results.
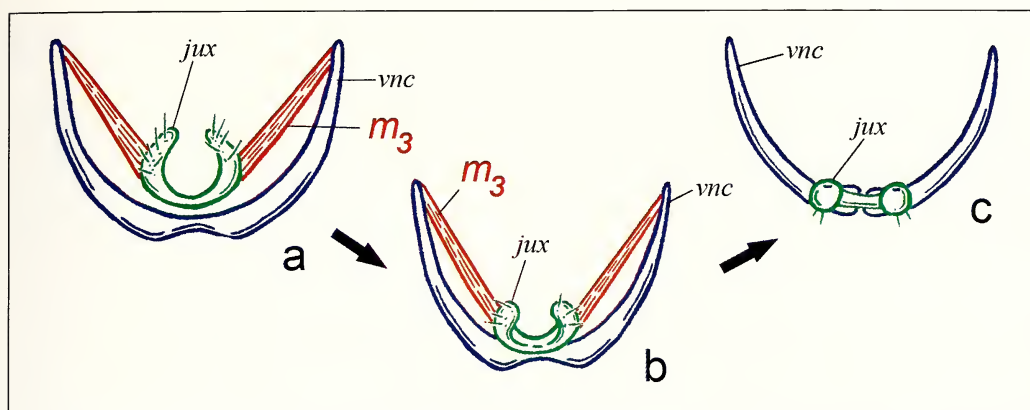
Fig. 10. Transformation of juxta position and reduction of the muscle m_3. **a.** *Hypatima* Hübner; **b.** *Dendrophilia* Ponomarenko; **c.** *Dichomeris* Hübner.

Acknowledgements

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