Phylogeny and taxonomy of the subfamily Dichomeridinae (Lepidoptera: Gelechiidae)

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The relationships between genera within the subfamily Dichomeridinae are studied for the first time. A cladogram based on 65 analysed characters for genera of the Palaearctic fauna is given. The presumed hypothetical ancestor is reconstructed. Evolutionary changes of genital sclerites and other structures are discussed. The taxonomic composition of the subfamily Dichomeridinae of the world is proposed.

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Introduction

In a previously published work (Ponomarenko, 1992), the subfamily Dichomeridinae has been considered as consisting of three tribes (Dichomeridini, Chelariini and Anarsiini) on the basis of comparative morphological analysis. The relationships of these tribes and diagnoses of them were discussed there. The present paper, being a continuation of that work, includes the construction of a cladogram for genera within the subfamily Dichomeridinae. This subfamily numbers 20 genera in the Palaearctic fauna and 32 genera in the world. Nomenclature of the muscles is used according to Kuznetzov & Stekol'nikov (1984).

Material and methods

For this investigation, material collected mainly by the author and specimens from the collection of the Zoological Institute, St.Petersburg were examined. The skeleton and muscles of genitalia (especially of type species) are studied in 14 genera of Dichomeridinae and 18 genera of other subfamilies of Gelechiidae. The type species of *Dactylethrella* Fletch. described from India is not examined, only the morphology of Palaearctic species included in this genus is studied. Additional data on the genitalia of gelechiid genera of the world are taken from literature (Janse, 1949; Clarke, 1958, 1969; Hodges, 1986). The material available for investigation is found sufficient for solving some phylogenetic problems because all tribes and about 2/3 of world genera of Dichomeridinae and their type species are represented in the Palaearctic fauna, moths of which adequately depict the morphological diversity in this subfamily, and almost all type species of other gelechiid genera are illustrated in the literature.

The reconstruction of generic relationships in Dichomeridinae is based mainly on the characters of the male and female genitalia, so far as characters of habitus have a mosaic distribution in this group, and only more reliable of them are used in cladistic analysis. The characters of preimaginal stages for many genera of this subfamily are unknown, therefore fragmentary data from literature are taken into consideration only as additional evidence. The homology of genital structures and construction of morphological series are clarified using comparative morphological analysis. In all, 65 morphological characters are analysed. Directions of character transformation in the morphological series (polarity of morphoclines) are determined by the method of outgroup comparison with regard to general morphological regularities. The other subfamilies of Gelechiidae or other families of Gelechioidea are chosen as outgroups depending on the rank of the analysed taxon. The cladogram of generic relationships is constructed by the synapomorphy method (Fig. 1).

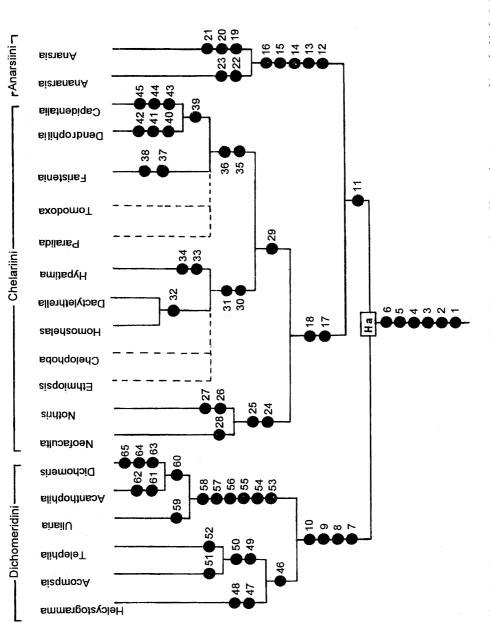


Fig. 1. Cladogram for the genera of the subfamily Dichomeridinae. Characters are denoted by numbers, symapomorphies – by black circles. Ha – hypothetical ancestor.

Phylogeny

Structures and characters used in cladistic analysis are as follows (apomorphic state denoted by *a*, plesiomorphic state denoted by *p*):

1 Parategminal sclerites: present (a); absent (p).

2 Muscles m4: arising from parategminal sclerites (Fig. 21) (a); arising from anterior part of tegumen (Figs 19, 20) (p).

3 Valva: divided into two sclerites, cucullus and sacculus (a); as one sclerite (p).

4 Tegumen: tube-like anteriorly, with well developed ventral wall (Fig. 3) (a); gutterlike, without ventral wall (p).

5 Muscles m₂: intrategminal, arising from dorsal side of tegumen and attached to its ventral wall (Figs 5, 6) (a); attached to basal part of valva (Fig. 4) (p).

6 Muscles m5: divided into two branches m5a and $m_{5b}(a)$; not divided into branches (p).

7 Uncus: fused with tegumen (a); separated from tegumen (*p*).

8 Lateral lobes of tegumen: present in its distal part (Fig. 25) (a); absent (p).

9 Ostium: submerged under the margin of VII segment (a); its position more distal (p).

10 Muscles m₃: reduced (a); present (p).

11 Additional wing-coupling mechanism: present (Fig. 2) (a); absent (p).

12 Genitalia: asymmetrical (a); symmetrical (p).

13 Gnathos: absent (a); present (p).

14 Setae on the cucullus: modified (a); usual (p).

15 Cucullus: with processes on the ventral margin (a); without processes on the ventral margin (p).

16 Labial palpi: with reduced third segment (a); with well developed third segment (p).

17 Valvella: various shape (conic, rounded, hook-like, etc.), but not finger-shaped (a); finger-shaped (p).

18 Vinculum: long (*a*); short (*p*).

19 Aedeagus: with comb-like process basally (a); without any process basally (p).

20 Valvella: reduced (a); well developed (p).

21 VIII tergite of female: with lobe on its anterior margin (a); without lobe anteriorly (p).

22 VIII segment: with membranous sack arising from its posterior margin (a); without membranous sack (p).

23 Aedeagus: curved ventrally (a); straight or curved dorsally (p).

24 Cucullus: narrowed distally or same width along its length (a); dilated distally (p).

25 Aedeagus: with globular inflated basal part (a); slightly dilated basally (p).

26 Uncus: curved (a): straight (p).

27 Valvella: with thorns at apex (a); only with setae at apex (p).

28 Ostial plate: present (a); absent (p).

29 Uncus: with separate basal sclerite (Fig. 12) (a); without basal sclerite (p).

30 Tegumen: with two folds on the ventral wall (Fig. 3) (a); without folds on the ventral wall (p).

31 Muscles m4: divided into two branches m_{4a} and m_{4b} (a); not divided into branches (p).

32 Valvella: stretched ventrally (a); in usual position (p).

33 Muscles m1: attached to sides of tegumen (Fig. 3) (a); attached to anterior margin of tegumen (p).

34 Muscles m6: attached to the dorsal side of aedeagus (a); attached to the ventral side of aedeagus (p).

35 Uncus: short, rounded (a); long, more or less rectangular (p).

36 Ostium: shifted mediad and covered by lateral margins of sclerite of VIII segment (a); not covered (p).

37 Basal sclerite of uncus: divided into two lateral triangular plates and dorsal one (Fig. 13) (a); not divided into plates (p).

38 Tegumen: strongly narrowed in distal part (a); same width along its length (p).

39 Juxta: connected with vinculum (a); separate from vinculum (p).

40 Vinculum: divided into two sclerites (a); as one sclerite (*p*).

41 Saccus: consists of two long narrow sclerites (a); as one sclerite (p).

42 Priostial lobes: present (a); absent (p).

43 Uncus: curved dorsally at a right angle (a); straight or curved ventrally (p).

44 VIII segment of female: with membranous tergal part (a); with sclerotized tergal part (p).

45 Gnathos: with rhomboidal apex (a); narrowed towards apex (p).

46 Juxta: absent (a); present (p).

47 Sacculus: triangular, beaked (a); lobelike, rounded (p).

48 Aedeagus: with hook-like apex (a); with rounded plate at apex (p).

49 Sacculi: with stretched apices and superposed ventrally (a); not stretched ventrally (p).

50 Aedeagus: with separate dorsal plate (a); without separate plate dorsally (p).

51 Ductus bursae: with sclerites near bursa copulatrix (a); without sclerites (p).

52 Sacculus: curved medially in distal part (a); not curved medially (p).

53 Saccus: absent (a); present (p).

54 Muscles m₂: reduced (*a*); well developed (*p*).

55 Ostium: covered by quadrangular plate (a); not covered by plate (p).

56 Antrum: sclerotized and flattened dorso-ventrally (a); membranous, not flattened (p).

57 Bursa copulatrix: sclerotized distally (a); membranous (p).

58 Anellus: sclerotized (a); membranous (p).

59 Anellus: with ventral processes (a); without ventral processes (p).

60 Parategminal sclerites: with androconial hairpencils (a); without androconial hairpencils (p).

61 Juxta: fused with anellus (a); separate from anellus (p).

62 Parategminal sclerites: stretched longitudinally, band-like (*a*); rounded, lobe-like (*p*).

63 Antrum: wide, with rounded prominences (a); relatively narrow (p).

64 Cucullus: shifted dorsad and fused with anterior margin of tegumen (a); placed laterally, not joined with tegumen (p).

65 Parategminal sclerites: shifted dorsad and turned perpendicularly to longitudinal axis of body (*a*); placed laterally (*p*).

Hypothetical ancestor

As a result of comparative morphological analysis of genitalia of Dichomeridinae, the complex of plesiomorphic characters has been found, on the basis of which the presumed hypothetical ancestor for this group is reconstructed. Probably, males of this ancestor were characterized by a stretched tegumen with lobe-like uncus and hook-like gnathos, valva with separate cucullus dilated distally and small sacculus fused with vinculum laterally, well developed juxta, tube-like aedeagus, vinculum with saccus. Anterior part of tegumen, basal part of cucullus and arms of vinculum were joined with the parategminal sclerites laterally. Probably, VIII segment in females was with a ventral membranous part.

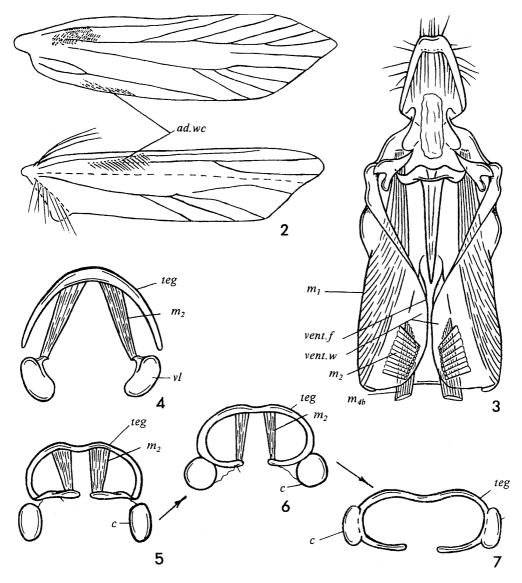
Discussion

Monophyly of the subfamily Dichomeridinae is based on synapomorphies 1-6, which have been estimated as reliable. Presence in this subfamily of separate parategminal sclerites functionating as apodemes of muscles m4 and the intrategminal position of muscles m₂ are unique characters not only in the family Gelechiidae, but in the whole superfamily Gelechioidea. All genera of Gelechioidea are characterized by muscles m4 arising from anterior part of tegumen. The morphological series reflecting the separation of this part of tegumen with muscles m₄ within Gelechiidae was shown earlier (Ponomarenko, 1992), here the transformation of parategminal sclerites from lobe-like to band-like, joining with androconial hairpencils is illustrated (Figs 21-24). In all gelechiids, except for Dichomeridinae, the tegumen is gutter-like with muscles m₂ arising from its dorsal side to basal part of valvae (Fig. 4). The formation of the ventral wall of the tegumen caused the change of the position of muscles m_2 to intrategminal. Within the subfamily, it is found out that the cuculli shifted dorsad and as slightly sclerotized structures connected to the sides of tegumen. They lose their active function in fixation of the female during copulation, and, as a result, the muscles m₂ are reduced (Figs 5-7). A similar transformation occurs in the ventral part of genitalia (Figs 8-10), where in consequence of connecting of juxta with vinculum the first of them loses active function in movement of aedeagus, resulting in the reduction of muscles m₃.

In addition to the specializations discussed here, the monophyly of this subfamily is corroborated by similarity in pupae of all tribes of Dichomeridinae, especially of their caudal part and cremaster (Patocka, 1987). Also the resting position in all moths of Dichomeridinae is the same. Moths sit with high raised head, flatly laid wings and antennae closely pressed along the dorsal margin of wings. These two characters are not included in the synapomorphies of the subfamily because pupae have not been in all genera of Dichomeridinae and Gelechiidae examined, and resting position in moths of tropical genera is not known to the author.

Tribe Chelariini

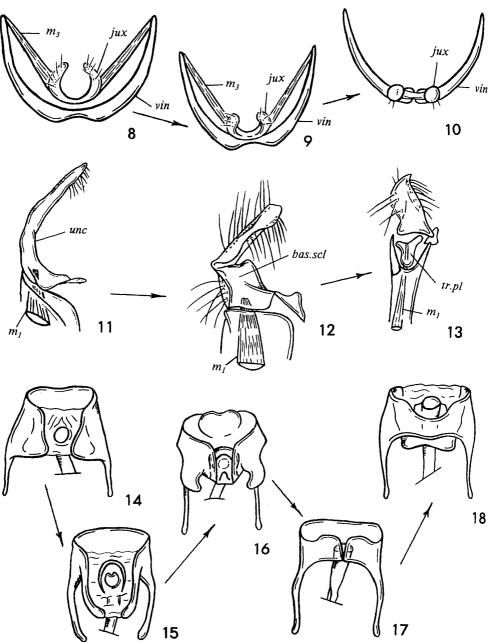
This tribe has more generalized characters than other tribes in the subfamily. There are three directions in the evolution of Chelariini, corresponding to three groups of genera. The genera *Neofaculta* Gozm. and *Nothris* Hbn. belong to the first of them. In both genera, the evolutionary trends are narrow-



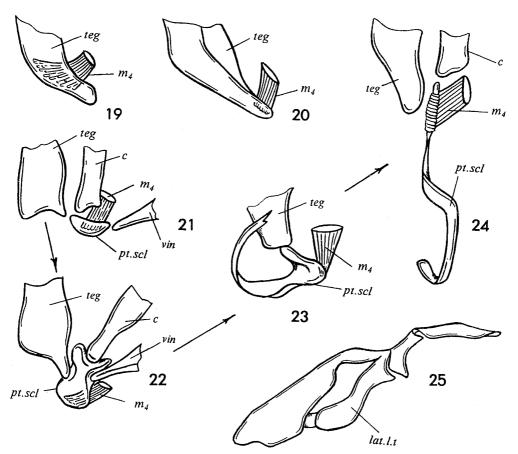
Figs 2-7. 2, additional wing-coupling mechanism; 3, *Hypatima* Hbn., tegumen and uncus; 4, *Gelechia* Hbn., position of muscles m_2 ; 5-7, transformation of cucullus position and reduction of muscles m_2 in Dichomeridinae (5, *Hypatima* Hbn.; 6, *Helcystogramma* Z.; 7, *Dichomeris* Hbn.), *ad.wc* – additional wing-coupling mechanism, *c* – cucullus, *teg* – tegumen, *vent f* – ventral folds of tegumen, *vent w* – ventral walt of tegumen, *vl* – valva, m_1 , m_2 , m_{4b} – muscles.

ing of cucullus distally, stretching of aedeagus apex and turning it in a spiral. These two genera keep some plesiomorphic characters of genitalia, such as large sacculus with rounded apex, weakly formed ventral wall of tegumen in male, and membranous sternal part of VIII segment in female.

The second group is represented by 5 genera. In *Dactylethrella* Fletch. and *Hypatima* Hbn., the ventral wall has two folds in anterior part of tegumen and the muscles m_4 are divided into two branches (m_{4a} and m_{4b}), latter attached to the inner side of the ventral wall (Fig. 3). The two apomorphies, 30 and 31, have been estimated as unique because such characters are unknown in other Gelechiidae. Unfortunately, the functional morphology of genitalia in *Ethmiopsis*



Figs 8-18. Morphological series. 8-10, transformation of juxta position and reduction of muscles m₃ in Dichomeridinae (8, *Hypatima* Hbn.; 9, *Dendrophilia* Ponom.; 10, *Dichomeris* Hbn.); 11-13, transformation of uncus in Chelariini (11, *Neofaculta* Gozm.; 12, *Hypatima* Hbn.; 13, *Faristenia* Ponom.); 14-18, transformation of ostial area in Chelariini (14, Dactylethrella Fletch.; 15, *Hypatima* Hbn.; 16, *Faristenia* Ponom.; 17, *Dendrophilia* Ponom.; 18, *Capidentalia* Park). *bas.scl* – basal sclerite, *jux* – juxta, *tr.pl* – triangular plate, *unc* – uncus, *vin* – vinculum, m₁, m₃ – muscles.



Figs 19-25. 19-20, anterior part of tegumen (19, Bryotropha Hein.; 20, Gelechia Hbn.); 21-24, transformation of parategminal sclerites in Dichomeridinae (21, Neofaculta Gozm.; 22, Hypatima Hbn.; 23, Dichomeris Hbn.; 24, Acanthophila Hein.; 25, Helcystogramma Z., tegumen and uncus). lat.l.t – lateral lobe of tegumen, pt.scl – parategminal sclerite, m4 – muscles.

Meyr., *Chelophoba* Meyr. and *Homoshelas* Meyr. has not been examined. Therefore the relationships of these genera are deduced on the basis of genital skeleton only (Clarke, 1969, p. 76, figs 1-1d; p. 187, figs 1-1d; p. 437, figs 1-1d), and the position of *Ethmiopsis* and *Chelophoba* is shown in the cladogram as a dotted line.

Between genera included in the first and second groups, some similarities have been found. So, the valvella in *Nothris* Hbn. and *Hypatima* Hbn. bears thorns on the apex, and the valvella in *Neofaculta* Gozm. and *Dactylethrella* Fletch. is stretched ventrally. These characters have been considered as pseudapomorphies, because of the unique synapomorphies of *Hypatima* and *Dactylethrella* mentioned above. The correctness of this conclusion is corroborated by a synapomorphy (29) of the second group and the third group including *Faristenia* Ponom., *Dendrophilia* Ponom. and *Capidentalia* Park.

The evolution of the third group was accompanied with correlated shortening of the uncus and gnathos, dividing of uncus into lateral triangular plates and dorsal one (Fig. 13), narrowing of cucullus, connection of juxta and vinculum and great morphological changes of ostial area in female (approaching of lateral margins of sclerite of VIII segment ventrally and complete cover of ostium, which is shifted mediad, as illustrated in morphological series in Figs 14-18). These three genera are the most specialized in the tribe Chelariini.

The genera *Tornodoxa* Meyr. and *Paralida* Clarke are very similar to *Faristenia* Ponom. Since their morphology is deduced from

photographs of genitalia only (Clarke, 1958; 1969, p. 488, figs 1-1d), their relationships are shown as a dotted line.

Tribe Anarsiini

This tribe is a sister-group of the tribe Chelariini because of synapomorphy 11 (Fig. 2). On the basis of a complex of characters, including profound morphological changes of genitalia of both sexes (synapomorphies 12-16), the early deviation of Anarsiini from an ancestor common with Chelariini and its independent evolution over a long time are presumed. On the basis of several synapomorphies (19-21) *Anarsia* is considered more specialized than *Ananarsia* Ams.

Tribe Dichomeridini

Undoubtedly this tribe, having synapomorphies 7-10, is monophyletic. In the tribe two groups of genera are revealed. The genera Helcystogramma Z., Acompsia Hbn. and Telephila Meyr., forming the first of them (synapomorphy 46), have more generalized morphology. Their female genitalia are similar to the ancestral state for the subfamily. Many characters, such as presence of saccus and intrategminal muscles m₂, aedeagus without cornuti, membranous anellus in the male, genitalia, and membranous narrow antrum, bursa copulatrix without sclerotization in female, characterize these genera as close to the genera of the tribe Chelariini and allows this group to be considered as transitional between Chelariini and more specialized genera of Dichomeridini.

The last evolutionary branch includes the genera Uliaria Dum., Acanthophila Hein. and Dichomeris Hbn. and is based on six synapomorphies (53-58). The genitalia of the genus Uliaria differ from those of other two genera in the presence of some plesiomorphic characters. Dichomeris and Acanthophila, combined in a monophyletic group after synapomorphy 60, on the basis of profound morphological changes in genitalia of both sexes are considered most specialized not only in this tribe but in the whole subfamily.

Taxonomy

On the basis of external characters, Meyrick (1925) divided the family Gelechiidae into 9 groups. For two of them, *Chelaria*

Hw. and Dichomeris Hbn., were fixed as type genera. 21 genera were placed in the Hypatima Hbn. (=Chelaria) group, many of them still remaining poorly known. Only the genus Anarsia Z. was said to be related to Hypatima more often than other genera (Heslop, 1938; Kloet & Hincks, 1945; Gozmány, 1958; Leraut, 1980; Moriuti, 1982; Hodges, 1983; Kuznetzov & Stekolnikov, 1984; Park, 1983; Vives, 1985; Karsholt, 1985; Bradley & Fletcher, 1986). Later, Anarsia Z. and Ananarsia Ams. were considered as a separate family (Amsel, 1977) or tribe (Ponomarenko, 1992). The taxonomic rank and composition of the tribe Anarsiini here are the same as in the last cited paper.

The tropical genera *Apotactis* Meyr., *Metatactis* Janse (Janse, 1949), and *Crasimorpha* Meyr. (Zimmerman, 1978) had been considered as related to *Hypatima* Hbn. The photographs of the genitalia of their type species in the catalogue by Clarke (1969) allow us to support the opinion of mentioned authors and to consider these genera as belonging to the tribe Chelariini.

It is necessary to include in this tribe the tropical genera Anthistarcha Meyr., Axyrostola Meyr., Encolapta Meyr., Haplochela Meyr., Pessograptis Meyr., Pilocrates Meyr., Porpodryas Meyr., and Syncratomorpha Meyr., genitalia of which are very similar to those of Dactylethrella Fletch., the closest relative of Hypatima Hbn.

It is difficult to determine the taxonomic position of the South American monotypic genera *Metabolaea* Meyr. and *Sclerograptis* Meyr. The male genitalia of the first of them are unknown, and the female genitalia are very different from those in Chelariini. In the published photographs of the male genitalia of *Sclerograptis*, important taxonomic characters are not shown.

As to other genera included before in "*Chelaria*-group" by Meyrick, some of them have been transferred to different subfamilies. For example, *Pectinophora* Bsk., *Platyedra* Meyr. and *Pexicopia* Common are in the Pexicopeinae now, their exclusion from Chelariini is corroborated by the following differences: the male genitalia lacking parategminal sclerites, muscles m₂ attached to valva, muscles m₄ arising from anterior part of tegumen; female genitalia have quite different ostial area, and bursa copulatrix has two signa. The genus *Psoricoptera* Stt. is closely related to *Gelechia* Hbn., and this opinion is shared by many authors.

The position of the genera *Mesophleps* Hbn. and *Holcophora* Stgr. within the Gelechiidae is disputable. Both of them were placed near *Hypatima* Hbn. or with *Dichomeris* Hbn., but according to present morphological investigation the genus *Holcophora* is more related to Gelechiinae, and *Mesophleps* to the Stomopteryginae.

The position of the genus *Epilechia* Bsk. placed near *Hypatima* Hbn. by Hodges (1983) is not clear. The male genitalia of this genus (Sattler, 1960) have characters similar to those of the subfamily Gelechiinae and it cannot be included in Chelariini.

Three genera, *Protomeus* Bsk., *Tituacia* Meyr. and *Holcophoroides* Mats., are known from external characters only. Therefore they are not considered here in the tribe Chelariini.

Summarizing, 23 genera of the world fauna are included in the tribe Chelariini: Antistarcha Meyr., Apotactis Meyr., Axyrostola Meyr., Capidentalia Park, Chelophoba Meyr., Crasimorpha Meyr., Dactylethrella Fletch., Dendrophilia Ponom., Encolapta Meyr., Ethmiopsis Meyr., Faristenia Ponom., Haplochela Meyr., Homoshelas Meyr., Hypatima Hbn., Metatactis Janse, Neofaculta Gozm., Nothris Hbn., Paralida Cl., Pessograptis Meyr., Pilocrates Meyr., and Tornodoxa Meyr.

Meyrick uniked 60 genera of Gelechiidae in the Dichomeris-group. Of them Rhynchopacha Stgr. (=Atrips Billb.), Oxycrytis Meyr., and Eunebristis Meyr. are similar to Gelechia Hbn. in the genitalia. Also Aulidictis Meyr. and Sphagiocrates Meyr. (Clarke, 1969) must be excluded from Gelechiidae according to the genitalia of their type species.

Neochrista Meyr. and Plocamosaris Meyr. are junior synonyms of *Noeza* Walk. (Clarke, 1955), and Brochometis Meyr. is a junior synonym of Dichomeris Hbn. (Diakonoff, 1941). As to other genera, there are different opinions about their position. On the one hand, Acanthophila Hein. and Acompsia Hbn. were allied with Anacampsis Curt. (Kloet & Hincks, 1945; Vives, 1985) and Uliaria Dum. in the latter paper was included in the subfamily Autostichinae. On the other hand, these genera were included in one group with Dichomeris Hbn. (Povolný, 1980; Piskunov, 1981; Ivinskis, Piskunov & Emeljanov, 1984), which is supported by the author.

In the last-mentioned paper also the genus *Thiotricha* Meyr. was placed in Dichomeridi-

nae, but it is difficult to agree with this decision. Its male genitalia differ from those of Dichomeridinae in the shape of tegumen with muscles m_4 arising from its anterior part (they are intrategminal in Dichomeridinae), shape of vinculum, modified sternite of VIII segment, and position of muscles m_5 and m_6 .

In 1986, 80 genera had been united in one genus *Dichomeris* Hbn. by Hodges, of them 51 were synonymized for the first time and for 9 synonymy was confirmed. As result of examination of the functional morphology of genitalia, it was found that *Uliaria* Dum. and *Acanthophila* Hein. must be considered separate genera. Probably, after thorough investigation many other genera united with *Dichomeris* will be restored.

Hodges (1986) restored the genus Helcystogramma Hein. and transferred to it many species placed before in the genus Brachmia Hbn. The differences between these two genera were indicated as early as by Janse (1954). His opinion is corroborated by examination of the skeleton and muscles of genitalia of the type species B. dimidiella Den. & Schiff. and *H. lutatella* Hbn. But inclusion of the genus Brachmia Hbn. in the subfamily Dichomeridinae is not supported by author. On the one hand, free and functioning juxta connecting with muscles m₃ clearly differentiate this genus from the monophyletic group Dichomeridini. On the other hand, its similarity to the tribes Chelariini and Anarsiini is based on obviously plesiomorphic characters. Probably, a well developed and freely functioning juxta connecting with muscles m₃ was an ancestral character for all Gelechiidae. This opinion is corroborated by the presence of rudimentary juxta (small setaceous lobes on ventral part of vinculum) in many representatives of other subfamilies: Gelechia rhombella Den. & Schiff., Caryocolum fischerellum Tr., Bryotropha oppositela Thub. (Gelechiinae), Metzneria metzneriella Stt. (Metzneriinae), Syncopacma vorticella Scop. (Stomopteryginae). So, the morphology of genitalia of Brachmia Hbn. (absence of parategminal sclerites and valvella, shape of uncus, shape of anterior part of tegumen, with muscles m₄ arising from it) clearly differentiate this genus from genera of Dichomeridinae.

Summarizing, 7 genera of the world fauna are included in the tribe Dichomeridini: *Acanthophila* Hein., *Acompsia* Hbn., *Dichomeris* Hbn., *Helcystogramma* Z., *Scodes* Hodges, *Telephila* Meyr., and *Uliaria* Dum.

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