

**Phylogenetic position of the tribe Azelinini
(Lepidoptera, Geometridae, Ennominae)
based on functional morphology of the male genitalia**

**Филогенетическое положение трибы Azelinini
(Lepidoptera, Geometridae, Ennominae)
на основании функциональной морфологии гениталий самцов**

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Key words: Lepidoptera, Geometridae, Ennominae, Azelinini, functional morphology, male genitalia, apomorphies, phylogeny.

Ключевые слова: Lepidoptera, Geometridae, Ennominae, Azelinini, функциональная морфология, гениталии самцов, апоморфии, филогения.

Abstract. Based on the functional morphology of the male genitalia the relationships and genetic composition of the endemic American geometrid tribe Azelinini are considered. A sister relationship of the Azelinini with the tribe Ennomini s.l. and a more remote relationship with the tribe Prosoplophini are proposed. The tribe is limited to the genus *Pero* Herrich-Schäffer, 1855 alone.

Резюме. На основании функциональной морфологии гениталий самцов рассмотрены родственные связи и родовой состав эндемичной американской трибы пядениц Azelinini. Обосновано сестринское родство Azelinini с трибой Ennomini s.l. и более отдалённое родство с трибой Prosoplophini. В составе трибы Azelinini оставлен только род *Pero* Herrich-Schäffer, 1855.

Introduction

The Azelinini Forbes, 1948, is currently considered to be a strictly American tribe of the Ennominae, and includes only 3 genera — the nominotypical genus *Pero* (= *Azelina* Guenée, 1857), consisting of more than 300 species in the Nearctic and Neotropical Regions, the Nearctic monotypical genus *Stenaspilatodes* Franclemont et Poole, 1972, and the genus *Nepitia* Walker, 1866, with 2 Neotropical species [Franclemont, Poole, 1972; Poole, 1970, 1987; Pitkin, 2002].

In the systems of American Geometridae the tribe Azelinini was placed between the Angeronini and the Nacophorini [Forbes, 1948; Ferguson, 1983], between the Campaeini and the Ennomini [McGuffin, 1987, in the text] or between the Campaeini and the Baptini [McGuffin, 1987, Fig. 250]. Forbes [1948] first noted

the presence of similar pupal antennal tubercles in the Azelinini and Nacophorini. Heitzman [1985, cit. from Holloway, 1994, and Young, 2006] noted this character also in North American species of *Ennomos* Treitschke, 1825, and linked the Azelinini, Nacophorini and Ennomini s.str. Heitzman [1985] and Poole [1987] also suggested most close affinities between the Azelinini and the Nacophorini based on the sharing of multiple lateral setae on the A6 larval prolegs. Holloway [1994] noted a similar setal pattern on the prolegs in the Odontoperini, and placed the Azelinini on the common stalk between the Nacophorini and the Odontoperini in his tentative phylogeny for the Geometridae [Holloway, 1997, Fig. 2]. I treated both the latter tribes as closely related and proposed to subordinate the junior name Nacophorini to the older name Odontoperini [Beljaev, 1997, 2006a, b]. Therefore the opinions of Poole and Holloway on the relationships of the Azelinini may be considered as coincident. Commenting on the opinions of Poole and Holloway, Young [2006] notes that multiple lateral setae on the A6 larval prolegs occur in many ennomines, and that not all American nacophorines have multiple lateral setae on the A6 larval prolegs. This larval character therefore has low phylogenetic value.

I stated earlier that, based on the unique structure of the skeleton of the male genitalia, the Azelinini cannot be linked to any other ennomine tribe. This conclusion was based on the absence of a basal process [following Kuznetsov, Stekolnikov, 2001] on the transtilla, and assumes the absence of crossing of the genital muscles m_2 and m_4 (nomenclature following [Kuznetsov,

Stekolnikov, 2001)), and on my incorrect belief that the stellate mushroom-like signum, typical for ennomines, was absent in the Azelinini. Consequently I proposed to place the Azelinini, together with other problematic ennomine tribes, the Campaeni, Cheimoptenini and Diptychini, into a basal, probably paraphyletic, supertribe Azelinidii [Beljaev, 1994, 2006a, b].

Pitkin [2002], giving the most recent diagnosis of the Azelinini, noted that the tribe is defined primarily by male genital characters, and although not a definitive character of the tribe, it is worth noting that the subscaphium (=subanal plate) is often strongly developed [loc. cit., p. 130]. Subsequently she noted that the shape of the juxta in the male genitalia is a synapomorphy of the genera *Nepitia* and *Pero*, and putatively for the tribe Azelinini. Relationships of the Azelinini were not discussed, except for citation of the opinions of Poole and Holloway, already mentioned.

Data on the molecular phylogenetic relationships of the Azelinini are controversial. Based on ribosomal fragment 28S D2, the Azelinini (*Pero honestaria* (Walker, 1860)) is grouped with part of the American Nacophorini (*Oratha significata* Walker, 1863), but based on EF-1a, the Azelinini are placed as sister group to the common stalk (Ennominae + Geometrinae + Oenochrominae), in both cases with low bootstrap values [Young, 2006].

To clarify the phylogenetic relationships of the Azelinini an examination of the musculature of the male genitalia of *Pero occidentalis* (Hulst, 1896) was made. Two dry specimens were dissected using the technology described in Ponomarenko [2006] and Beljaev [2008b]. The names of the male genitalia skeleton structures follow Klots [1970] and Kuznetsov, Stekolnikov [2001], with additions proposed by Minet [2002] and Beljaev [2008b].

Pero occidentalis (Hulst, 1896)

Material examined. 2♂♂ — USA, Wyoming, Park Co, Shoshone National Forest, T56N, R106W, Sec. 3, 6.vii.1983, R. Lavigne, S. Katovich et J. Littlefield leg. (In the Collection of the Zoological Institute, Saint Petersburg).

Skeleton of the male genitalia. Annulus comparatively narrow and long, distinctly subdivided laterally by deep narrowing on tegumen and vinculum. Tegumen almost half length of vinculum, comparatively strong, with broad lateral branches, subdivided dorsally almost up to base of uncus; sagittal plate of tegumen lacking. Paratergal plates small, rounded, more closely associated with tegumen, than with vinculum. Vinculum long, narrow, saccus not developed. Uncus separate from tegumen, with wide, triangular basal part, laterally with pointed claw-like extensions. Distal process of uncus long, narrow, moderately arched. Socii large, membranous. Gnathos long, narrow, separated basally from tegumen and uncus, medianly with long and narrow, pointed hook-like process. Subanal plate (=subscaphium of Poole [1987]) long and broad, heavily sclerotized, groove-like with tongue-like posterior portion. Valva broad, moderately long, with strong broad costa, comparatively small cucullus (=costal fold of Poole [1987]) having at its base a large lobe-like setose ampulla. Sacculus large, heavily sclerotized, with a raised longitudinal rib medially. Clasper shaped

as dorsoventral prominent folded rib between the base of ampulla and distal part of sacculus (cuiller). Costulae (following Weller [1990], and Minet [2002]) form transtilla which consists of two broad lateral lobes with a weakly developed ventral process, connected to each other by a narrow but firm «bridge». Juxta complete: consisting of a broad ventral triangular plate with narrow median groove-like depression and dorsal funnel-like sclerotization, which could be considered as a caulis. However in many species of *Pero* the caulis laterally forms more or less prominent processes and may have its origin from an initially free distal process of the juxta, fused with the ventral wall of the anellus. Ventral plate of juxta laterally completely fused with sacculi, and can be delimited from them by well developed cristae. Dorsally near base of caulis juxta produced into a pair of dorsolaterally directed narrow, long, moderately sclerotized plates — labides (sensu Beljaev [2006a, 2008b]). Aedeagus simple, tube-like, with moderately long finger-like basal process and wedge-like sclerotized apex; vesica with single massive inflated cornutus. For the shape of eighth abdominal sternite see McGuffin [1987].

Musculature of the male genitalia. Muscles m_1 strong and lying from anterior margin of tegumen to ventral edge of distal process of uncus. Muscles m_{10} also strong, stretching ventrally from most posterior median point of anterior margin of tegumen to anterolateral sides of sibanal plate. Muscles m_2 stretching from dorsolateral extensions of anterior margin of tegumen to slightly developed anteroventral dilations on transtilla (basal processes sensu Kuznetsov, Stekolnikov [2001] well mediad of m_4). Muscles m_4 short, going from paratergal plates to base of transtilla. Muscles m_7 strong and long, going to base of clasper by 2 moderately separated branches: m_{7a} , which stretches from base of sacculus near juxta, and m_{7b} , which begins from dorsolateral side of juxta ventrad of cristae. Muscles m_3 paired, but not entirely separated one from another, the muscles going from ventral side of vinculum to median depression at middle of juxta. Muscles m_5 broad, stretching from dorsolateral sides of vinculum to top of basal process of aedeagus, muscles m_6 going from ventrolateral sides of vinculum to ventrolateral sides at middle of aedeagus.

Discussion

Phylogenetic position of the tribe Azelinini. The male genitalia of *P. occidentalis* do not differ strongly from those of the type species of the genus, *Pero rectisectaria* (Herrich-Schäffer, [1855]) [Pitkin, 2002: Figs 265, 513], except for the shape of the cucullus and the arming of the aedeagus. Therefore the described structure of the male genitalia musculature of *P. occidentalis* in its main characters may be extrapolated to the type species of the genus, and also to other members of the genus *Pero*, to judge from the figures of the genitalia in Poole [1987]. In spite of a wide diversity in the shapes of the distal part of the valva, most species of the genus *Pero* have similar structures which serve for the attaching of muscles. This indicates a similar arrangement of genital musculature.

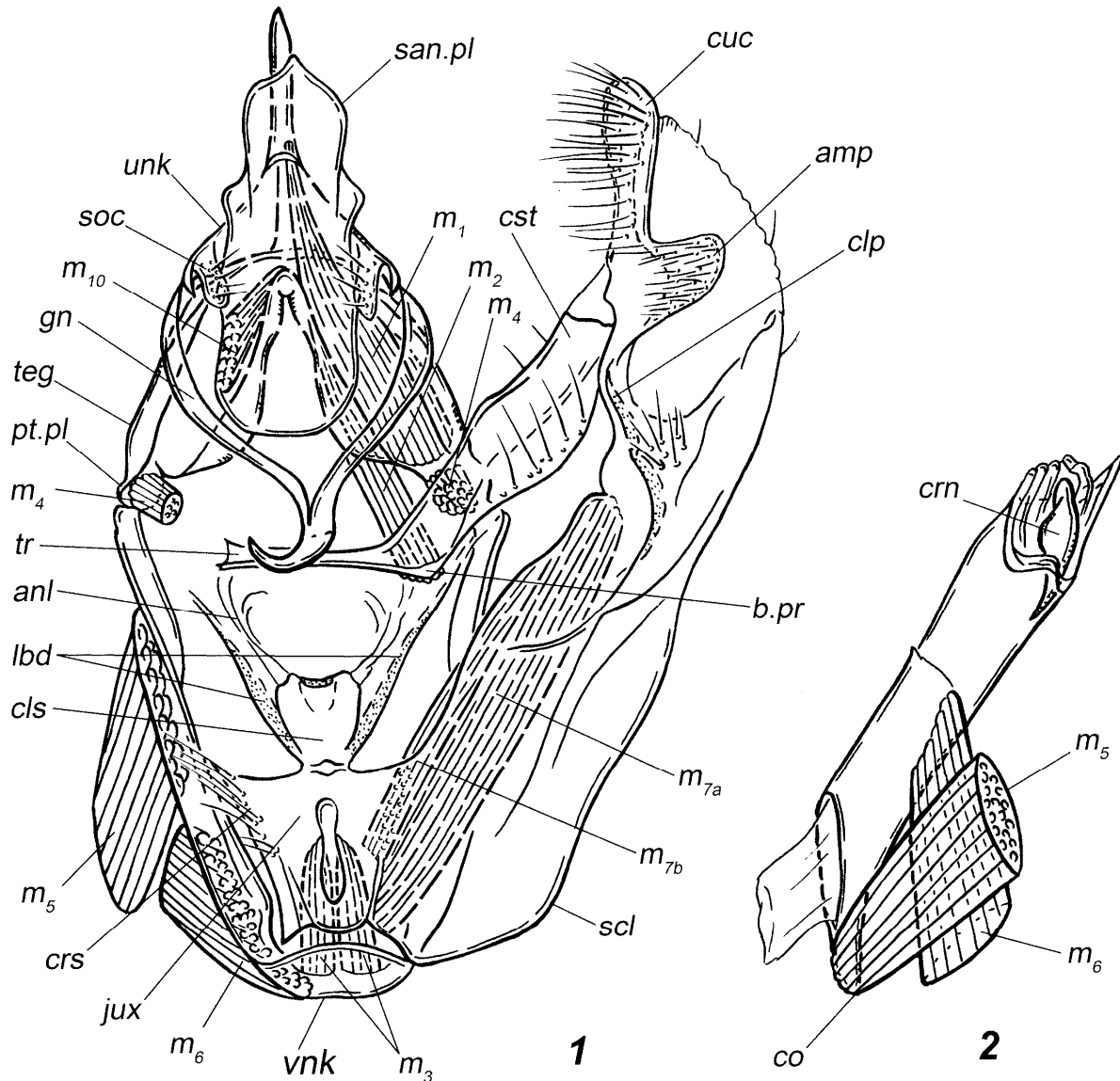
In spite of marked differences in general shape of the genitalia skeleton, the musculature of the genitalia and some of the skeleton characters clearly indicate a

sister relationship between *Pero* and the tribe Ennomini s.l. (sensu Beljaev [2008a]). The characters are as follows:

1. Presence of characteristic labides shaped as elongated sclerites forming a pair of narrow folds on anellus ventrolaterad of aedeagus. This character is a synapomorphy for Ennomini s.l. and Prosoplophini

(sensu Beljaev [1994, 2006a, b], and clearly indicates that *Pero* belongs to the supertribe Ennomidii. This last point was determined earlier as the apomorphy «labides shaped as narrow sclerotized bridges' between juxta and base of transtilla» [Beljaev, 2006a, Fig.1].

2. Presence of paired m_3 which are distally attached to the median depression of the juxta. This character



Figs 1–2. The male genitalia of *Pero occidentalis* (Hulst). 1 — male genitalia, ventral view, left valva and aedeagus are removed, left muscles m_1 , m_2 , m_a and m_b , and right muscles m_3 , m_6 and m_{10} are not illustrated; 2 — aedeagus, lateral view, internal muscle m_{2i} is not illustrated. *amp* — ampulla; *anl* — anellus; *b.pr* — basal process; *clp* — clasper; *cls* — caulis; *co* — coecum (basal process of aedeagus); *crn* — cornutus; *crs* — cristae; *cst* — costa; *cuc* — cucullus; *gn* — gnathos; *jux* — juxta; *lbd* — labides; m_1 — depressor of uncus; m_2 — abductor of valva; m_3 — muscles of medial plate (juxta); m_4 — adductors of valva; m_a — protractors of aedeagus; m_b — retractors of aedeagus; m_{7a} — dorsal bunch of flexors of valva; m_{7b} — ventral dorsal bunch of flexors of valva; m_{10} — protractors of anal cone; *pt.pl* — paratergal plate; *san.pl* — subanal plate; *scl* — sacculus; *soc* — socius; *teg* — tegumen; *tr* — transtilla; *unk* — uncus; *vnk* — vinculum.

Рис. 1–2. Гениталии самца *Pero occidentalis* (Hulst). 1 — гениталии самца, вид снизу, левая вальва и эдеагус удалены, левые мускулы m_1 , m_2 , m_a и m_b и правые мускулы m_3 , m_6 и m_{10} не изображены; 2 — эдеагус, вид сбоку, внутренний мускул m_{2i} не изображен. *amp* — ампулла; *anl* — анеллюс; *b.pr* — базальный отросток; *clp* — класпер; *cls* — каулис; *co* — цекум (базальный вырост эдеагуса); *crn* — корнутус; *crs* — кристы; *cst* — коста; *cuc* — кукулулус; *gn* — гнатос; *jux* — юкста; *lbd* — лабиды; m_1 — депрессоры ункуса; m_2 — абдукторы вальв; m_3 — мышцы медиальной пластинки (юксты); m_4 — аддукторы вальв; m_a — протракторы эдеагуса; m_b — ретракторы эдеагуса; m_{7a} — вентральный пучок флексоров вальвы; m_{7b} — дорсальный пучок флексоров вальвы; m_{10} — протракторы анального конуса; *pt.pl* — паратергальная пластинка; *san.pl* — субанальная пластинка; *scl* — саккулус; *soc* — соция; *teg* — тегумен; *tr* — транстилла; *unk* — ункус; *vnk* — винкулум.

was treated earlier as an apomorphy of Ennomini s.l. [Beljaev, 2008a].

3. Presence of an additional branch of the intravalvar muscle m_{7b} which derives from the juxta near the distal end of m_3 . In the Ennominae the intravalvar muscle often produces an additional branch which can be attached to the juxta. However in the related tribe Prosopolophini the intravalvar muscle does not touch the juxta (examined in *Colotois pennaria* (Linné, 1761) and *Descoreba simplex* Butler, 1878). So, this character can be considered as a synapomorphy of *Pero* and Ennomini s.l.

4. Species of *Pero* do not have ventral membrani- zation of the vinculum, which is an autapomorphy of the Ennomini s.l. So, they form sister group to the last tribe.

Previously the presence of a complete transtilla with weakly developed basal processes was considered to favour a basal phylogenetic position for the Azelinini in the ennomines [Beljaev, 1994, 2006a, b]. However recent investigations show that the presence of medially separate lobe-like costulae (gemitransillae sensu Kuznetsov, Stekolnikov [2001]) with a well-developed basal process and crossing of muscles m_2 and m_4 needs to be treated as a synapomorphy for all the geometrine lineage of subfamilies (Archiarinae + Ennominae + Desmobastrinae + Geometrinae) [Beljaev, 2008b]. Therefore the characteristic transtilla of *Pero* must be regarded as an autapomorphy, as well as the development of a narrow sclerotized cucullus separated from the valvula by a deep ventral fold, and the presence of a specific heavily sclerotized caulis flexibly articulated with the juxta.

Unusually for ennomines, in *P. occidentalis* the labides are ankylosed with the sides of the caulis. In addition, the labides are weakly sclerotized and demonstrate a tendency to reduction; nevertheless they form a defined fold on the anellus, as in Ennomini s.l. and do not raise doubts their homology. It is probable that only the species of *Pero* from «Group 6» [Poole, 1987: 62] possess labides such as those in the described species. In other groups of the genus labides have evidently coalesced with the caulis as part of the entire heavy sclerotized structure supporting the aedeagus ventrally. In some cases they remain on the caulis as short lateral sclerotized processes (as in *Pero haxairei* Lévêque, 2006 [Lévêque, 2006, Fig. 7]) or are secondarily separated in the form of elongate plates placed laterad of the caulis (as in *Pero janichoni* Lévêque, 2007 [Lévêque, 2007, Fig. 5]). This fusion of labides with caulis could possibly also be treated as an apomorphy of *Pero*.

The strongly developed subanal plate, usually presenting modification of the eighth sternite in the male cannot be treated as basal apomorphies of *Pero* because not all members of the genus possess these structures.

Genetic composition and taxonomical rank of Azelinini. As mentioned above, 3 genera are currently included in the tribe - *Pero*, *Nepitia* and *Stenaspila-*

todes. The male genitalia of the type species of *Nepitia*, *Nepitia detractaria* Walker, 1866, are superficially similar to those in *Pero* [Poole, 1970, Figs 3, 4; Pitkin, 2002, Fig. 264]. However, they have a different shape to the costulae, which are separated medially and possess a very thin median portion, which, probably, is an extremely long and slender tubular basal process. Also, the juxta has a much more dorsal position and further removed from the vinculum, which is not characteristic for *Pero*. The fine structure of the juxta also differs markedly: the median depression is lacking, the pair of dorsal extensions are more similar to proper processes from the juxta, than to modified labides. The structure of the juxta suggests a different shape of the muscle m_3 . The distal portion of the valva is very narrow, and the structure of sclerotization on the medial wall of the valva differs markedly from those in *Pero*. These characters argue against linking *Pero* and *Nepitia*. Generally, the male genital structure may indicate a relationship between *Nepitia* and the group «tribes Caberini/Baptini» (sensu Pitkin [2002]; H) supertribe Caberidii sensu Beljaev [2006a, b]). For the elaboration of the systematic position of the genus *Nepitia* the male genitalia musculature needs to be examined.

Close relationship of the genus *Stenaspilatodes* to *Pero* is also questionable. Following the original description of the genus, the male genitalia of *Stenaspilatodes* [Franclemont, Poole, 1972, Figs 5, 6] do not show clear synapomorphic characters with *Pero*, excepting a probable uninterrupted transtilla. Other features are different: *Stenaspilatodes* has a different shape to the top of the gnathos, a different construction of the tegumen with a defined dorsal sagittal rib, well developed pointed basal processes on the transtilla, narrow and not separated from the costa cucullus, a different juxta with both median depression and separate caulis lacking. Labides are also absent, judging by the original figure in Franclemont and Poole. The general male genitalia structure clearly suggests that *Stenaspilatodes* belongs to the group supertribes Ennomidii + Epoinidii (sensu Beljaev [1994, 2006a, b]), and, possibly to Ennomidii proper. I am unable to indicate a more exact position for *Stenaspilatodes* based on published data.

Thus, I propose to retain in the tribe Azelinini only the nominotypical genus *Pero*. Despite this reduction of the generic composition, in my opinion the taxonomic rank of the Azelinini as a separate tribe is not doubtful. The set of their apomorphies is unique for the ennomines, and distinctly separates them from the Ennomini s.l. The functioning of the male genitalia also looks to be unique. The separation of the cucullus from the costa and its strong sclerotization in combination with the structure of the ventral portion of the valva (*ala valva* of Birket-Smith [1965, 1974]) suggest that at the contraction of the flexor of the valva the cucullus has to be strongly bent medially, which is uncommon in the Ennominae.

However, the extreme taxonomical disequilibrium between the Ennomini s.l. and the Azelinini is noteworthy. The former contains 148 genera [Beljaev,

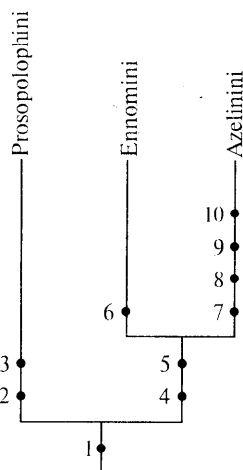


Fig. 3. Phylogenetic relationships of the tribes Azelinini, Ennomini and Prosoplophini. Black circles — apomorphies: 1 — labides shaped as narrow sclerotized bridges' between juxta and base of transtilla; 2 — male genitalia heavily sclerotized; 3 — gnathos lacking; 4 — in the male genitalia muscle m_1 paired and distally attached to median depression of juxta; 5 — in the male genitalia flexor of valva (m_2) divided into 2 branches and dorsal from them (m_2) derives from juxta dorsad of the end of m_1 ; 6 — vinculum ventrally divided by membranous region; 7 — transtilla entire, narrow bridge-like medially, lobe-like basally, with vestigial basal processes; 8 — cucullus narrow, sclerotized, separated from costa by membranous region and divided from valvula by ventral fold; 9 — caulis heavy sclerotized, flexibly articulated with juxta; 10 — labides ankylosed with lateral sides of caulis.

Рис. 3. Филогенетические связи триб Azelinini, Ennomini and Prosoplophini. Чёрные кружки — апоморфии: 1 — лабиды в виде узких склеротизированных «мостов» между юкстой и основанием косту; 2 — гениталии самцов сильно склеротизированы; 3 — гнатос отсутствует; 4 — в гениталиях самцов мускула m_1 парный и дистально прикреплен к медианной инвагинации юксты; 5 — в гениталиях самцов флексор вальвы (m_2) разделён на 2 ветви, дорсальная из которых (m_2) отходит от юксты дорсальнее конца m_1 ; 6 — винкулум вентрально разделён мембранозной; 7 — транстилла цельная, медиально в виде узкого моста, с рудиментарными базальными выростами; 8 — кукулус узкий, склеротизированный, отделён от косты мембранозной областью и обособлен от вальвулы вентральной складкой; 9 — каулис сильно склеротизирован, гибко сочленён с юкстой; 10 — лабиды спаяны с латеральными сторонами каулиса.

2008a] against a single one in the Azelinini. It should be noted that the morphological diversification of the genitalia in *Pero* is comparable with that in the Ennomini s.l. Probably, it would be reasonable to separate the whole genus *Pero* as it currently stands into a series of smaller genera, more or less equal to the groups of species proposed by Poole [1987].

Conclusion. Based on the skeleton-muscular characters of the male genitalia, the tribe Azelinini needs to be considered as sister to the tribe Ennomini s.l. (Fig. 3). The status of Azelinini as a separate tribe is confirmed. The supertribe Azelinidii [Beljaev, 1994, 2006a, b] is cancelled.

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