Zootaxa 5566 (1): 119–144
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5566.1.5
http://zoobank.org/urn:lsid:zoobank.org:pub:440E683F-887D-4818-8832-7192B3217D92

A new genus and species of lappet moths (Lepidoptera: Lasiocampidae) from Central Asia with notes on the systematics of the family

EVGENIY A. BELJAEV[1] *, PAVEL YU. GORBUNOV[2] & STANISLAV K. KORB[3]
[1]*Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, 100-letiya Vladivostoka avenue, Vladivostok, 690022, Russia.*
[2]*Institute of plant and animal ecology, Ural Division of the Russian Academy of Sciences, 8th Marta Str. 202/3, Ekaterinburg, 620144 Russia.*
pg18@yandex.ru; https://orcid.org/0000-0003-1913-7894
[3]*Russian Entomological Society, Nizhny Novgorod Branch, P.O. Box 97, Nizhny Novgorod 603009, Russia.*
stanislavkorb@list.ru; https://orcid.org/0000-0002-1120-424X
**Corresponding author: beljaev@biosoil.ru; https://orcid.org/0000-0003-0194-8525*

Abstract

A new genus, *Zolotuhia* **gen. nov.**, with the type species *Zolotuhia paradoxa*, **sp. nov.**, from Kyrgyzstan, Talassky Mt. Range, is established in the lepidopteran family Lasiocampidae. The new genus is characterized by a surprising mix of features in the appearance, wing pattern, wing venation, male and female genitalia, shared with different groups of lappet moths. Based on the review of morphology in the Chondrosteginae/Poecilocampinae/Macromphaliinae lineage of Lasiocampidae, a tentative morphological phylogeny of the genera in the Chondrosteginae/Poecilocampidae group is proposed and two new synonyms: Chondrostegidae Tutt, 1902, = Poecilocampinae Tutt, 1902, **syn. nov.**, = Trichiurinae Tutt, 1902, **syn. nov.**, is established. The generic composition of Chondrosteginae *s.l.* is discussed. For *Chondrostegoides nobilorum* Zolotuhin, 2007 a new combination is established: *Trichiurana nobilorum* (Zolotuhin, 2007), **comb. nov.** For the dorsal dilation of the valve sacculus located lateral to juxta in Lasiocampidae, early inappropriately named as "valve saccular lobe", a new name "dorso-basal saccular lobe" is offered. Some problems in the morphology, phylogeny and systematics of Lasiocampidae are addressed.

Key words: bombycoid moths, Kyrgyzstan, morphology, new genus, new species, nomenclature, phylogeny, taxonomy

Introduction

Lappet moths (Lasiocampidae) is a diverse Lepidoptera family containing over 2000 species of the world fauna (Zolotuhin 2015). Despite the significant progress in the study of these moths in recent years, largely associated with the activities of Dr. Vadim Viktorovich Zolotuhin (15.06.1967, Ulyanovsk—03.06.2021, Ulyanovsk, Russia), the family Lasiocampidae cannot be considered well-investigated taxonomically and faunistically.

This publication was initiated by the discovery of an amazing lappet moth in Central Asia, which due to its unusual habitus and simple structure of the male genitalia, was first associated with some unknown "winter" geometrid moth from the subfamily Ennominae. However, a study of the wing venation helped to undoubtedly classify this curious lepidopteran as a lappet moth. Yet, elucidating the systematic position of the species in this family has encountered great difficulties.

The current paper is devoted to the description of this moth as a new species and a new genus of Lasiocampidae, and to a discussion of its systematic position based on the morphology of imago. Also, a number of problems in the taxonomy in the related groups of lappet moths have been addressed. As a result, a preliminary outline of the phylogeny in the Chondrosteginae / Poecilocampinae / Macromphaliinae lineadge of subfamilies is proposed based primarily on literary data. It serves primarily to search for probabale relationshps of the newly described genus and for demonstrate the current state of the problem, and does not constitute a proposal of a well-founded phylogeny.

Accepted by R. Zahiri: 29 Oct. 2024; published: 7 Jan. 2025

Materials and methods

Specimens belonging to a new species were collected by the second and third authors during the autumn (late September—mid-October) expeditions of 2022 and 2023. They were collected using UV-traps of three different constructions: tent-based and tripod-based equipped with high emission UV-sources (300W and 160W UV-lamps) and tripod-based equipped with low emission UV-sources (UV-bulbs of 8W and 27W).

The photos of moths, and the male (Fig. 12) and the female genitalia were captured using a Nikon D7100 DSLR camera with an AF Micro Nikkor 105 mm 1:2.8D and AF-S Micro Nikkor 60 mm 1:2.8G ED lenses by P. Gorbunov. The images of the external structures and the male genitalia (Fig. 13) were captured using an Olympus SZX16 stereomicroscope with a DP74 Olympus digital camera in the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Vladivostok, by E. Beljaev. The figures were processed using Adobe Photoshop CS4.

Wing venation nomenclature is based on Wootton's (1979) system, which was adopted for Lepidoptera by Kristensen (2003). The structures of the copulatory apparatus (genitalia) are named traditionally, according to the Klots (1970) dictionary with additions after Kuznetsov & Stekolnikov (2001), and Kristensen (2003).

The holotype and part of the paratypes of the new taxon are deposited in the Zoological Institute of the Russian Academy of Sciences (St.-Petersburg, Russia), some paratypes are in the authors' collections.

Phylogenetic analysis was performed on the basis of the classical ideas of cladistics by Willy Hennig (1966) by the manual logical analysis of the distribution of morphological characters between taxa.

Co-author contributions (using the CRediT roles). **Evgeniy Beljaev**: conceptualisation (lead); investigation (equal); visualisation (equal); writing—original draft preparation (lead); and writing—review & editing (lead). **Pavel Gorbunov**: investigation (lead), resources (lead), visualisation writing—original draft preparation (equal), writing—review & editing (supporting). **Stanislav Korb**: resources (equal); writing—review & editing (supporting).

Results

Descriptions

***Zolotuhia*, genus nova**

http://zoobank.org/urn:lsid:zoobank.org:act:2AF73C45-FD14-4771-8E19-E164ECD04E50

Type species: *Zolotuhia paradoxa*, species nova, by present designation.

Male. Forehead in lower part at the level of 1/3 of eye height with moderately high cylindrical projection (frontoclypeal process) bearing crown of small serrations along distal edge. Antennae bipectinate, rami extremely long, reaching 1/4 of flagellum length. Middle and hind tibia without spurs. Forewings grey with light L-shaped discal spot and with single distinct dark submarginal line. Forewing veins Rs3 and Rs4 stalked, hindwings with humeral Sc-Rs cell lacking, vein Sc+R1 short, reaching costal margin of wing at about 2/3 of its length. In male genitalia, gnathos with medial pair of long, strong, spine-like processes, fused basally. Valvae wide, with almost square apical part; sacculus with wide and short lobe-shaped distal process. Vesica of phallus with dense group of few small and short spiny cornuti.

Female. As for male, but antennal rami short, and colouration of forewings more uniform, without transverse lines and with distinct light discal spot only. In the female genitalia, bursa copulatrix with inflated ductus bursae and with oval corpus bursae forming two almost equal sections separated by narrow bridge.

Etymology. The genus *Zolotuhia* (feminine) is named after Dr. Vadim Zolotuhin, an outstanding specialist of the family Lasiocampidae, who untimely passed away in 2021. The last two letters from his surname—"in"—have been omitted in order to more harmoniously latinize the word.

***Zolotuhia paradoxa*, species nova**

http://zoobank.org/urn:lsid:zoobank.org:act:7CBBEA5D-518B-4E87-A703-EB547D90C1E1
(Figs 1–15)

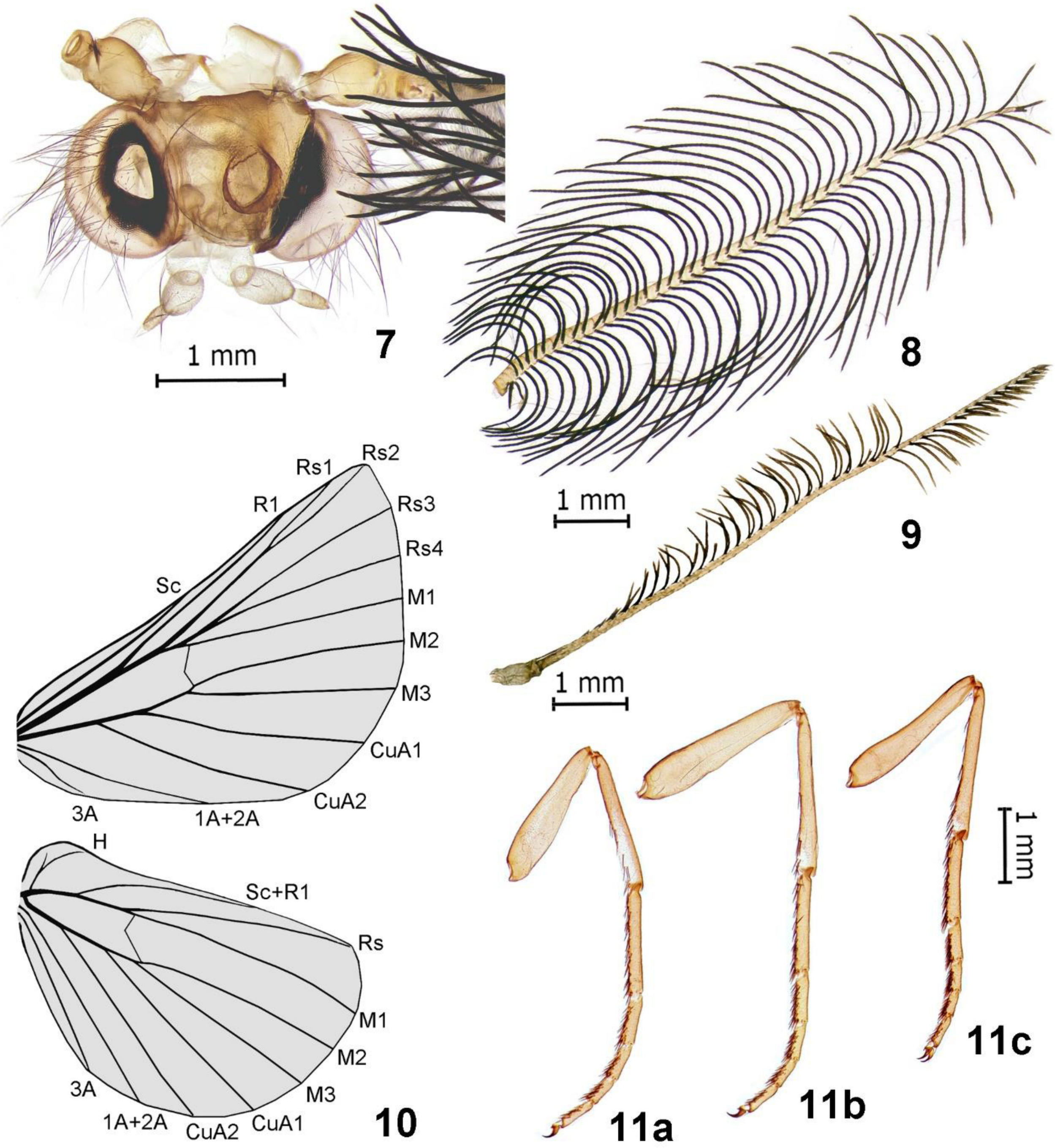
Material examined. ***Holotype*** ♂, 9.10.2023, Kyrgyzstan, Talassky Mt. Range, Chickan River basin at Itagar River mouth, 2020 m a.s.l., 42°09'47"N, 72°49'21"E, leg. P. Gorbunov & S. Korb. ***Paratypes***: 11 ♂♂, 2.10.2022, Kyrgyzstan, Moldo-Too Mt. Range, 15 km NW of Kazarman village, Naryn River valley, 1220 m a.s.l., 41°30'46" N, 73°55'38" E, leg. P. Gorbunov, S. Korb & V. Zurilina; 1 ♂, 4 ♀♀, 6–7.10.2023, Kyrgyzstan, Fergansky Mt. Range, 12 km NE of Tash-Komyr town, Sary-Bel' River valley, 892 m a.s.l., 41°25'16"N, 72°18'59"E, leg. P. Gorbunov & S. Korb; 241 ♂♂, 20 ♀♀, 9.10.2023, Kyrgyzstan, Talassky Mt. Range, Chickan river basin at Itagar River mouth, 2020 m a.s.l., 42°09'47"N, 72°49'21"E, leg. P. Gorbunov & S. Korb; 1 ♂, 10.10.2023, Kyrgyzstan, Dzhumgal-Too Mt. Range, 7 km E of Susamyr village, Western Karakol River valley, 2120 m, 42°11'25"N, 74°03'19"E, leg. P. Gorbunov & S. Korb.

Moth (Figs 1–6)**.** Forewing length in males 12.5–17.5 mm, in females 14.0–17.5 mm (females are not bigger than males, at least in the examined specimens). Head, thorax, and abdomen densely covered with very long hair-like dark grey and light yellow-grey scales, forming light and dark transverse stripes on abdomen. Abdomen posteriorly with long and forked brush of hair-like scales.

FIGURES 1–6. *Zolotuhia paradoxa* sp. nov., mots. 1—holotype, male; 2—paratype, male; 3—paratype, female; 4—male in nature, melanistic form; 5—male in nature, common form; 6—female in nature.

Head (Fig. 7). Palpi short, three-segmented, first segment wide, rounded, second one oval, third segment thin, elliptical, approximately 3 times shorter than second one, with small notch at apex (vom Rath's organ). Proboscis missing. Forehead in its lower part at the level of 1/3 of the eye height with wide cylindrical projection (frontoclypeal process) bearing crown of small serrations along distal rib. Vertex simple. Eyes oval, strongly convex, approximately equal in height to forehead maximum width, and covered with long thin cilia.

Antenna (Figs 8, 9) with 44–45 segmented flagellum, bipectinate, pair of rami arising from ventral side of flagellomeres; scapus strongly swollen. In males, flagellum dorsally covered with light scales, decreasing in width from 2.0 mm at the base to 0.6 mm at the apex of flagellum; rami black, extremely long, reaching 2.8 mm (almost 1/3 of flagellum length). In females, antenna with thinner flagellum and with short rami reaching 0.7 mm (no more than 1/10 of flagellum length), five basal flagelomeres without rami.



FIGURES 7–11. *Zolotuhia paradoxa* sp. nov., external structures. 7—head and patagia, anterio-lateral view; 8—male antenna, ventral view; 9—female antenna, latral view; 10—wing venation; 11—legs: 11a—fore legs, 11b—mid legs, 11c—hind legs.

Thorax. Patagia and tegulae densely covered with long hair-like scales, completely covering base of wings and thorax. Ventral arms of laterocervicalia free and very close to probasisternum.

Wings. Forewings triangular with slightly concave costal margin and strongly convex outer margin. Hindwings straight along anterior margin, rounded along outer margin, and with broadly rounded anal angle. Wings of females more elongated than those of males. The ratio of the wing length to its maximum width in males is 1.7 (in the fore wing) and 1.5 (in the hind wing), and in females it is 2.1 and 1.7, respectively.

In males, wing pattern formed by alternating dark grey and light grey scales. In fresh individuals scale covering of two layers: continuous lower one of small rounded light scales bearing 8–10 ray-like processes along outer semicircle; and with upper layer of raised, much larger, dark and light, mostly elongated (hair-like and broom-like) scales, which sparse on most of wing surface and dense in wing basal portion and along its costal margin. All scales are attached weakly and come easily off, exposing wing membrane. Forewing upper side wing pattern with distal spot, and usually with four transverse lines: antemedial, postmedial, submarginal and marginal. Antemedial line indistinct (often invisible), starting on wing costal margin slightly basal to discal spot, crossing discal cell with sharp fracture touching discal spot, and going obliquely to inner margin of wing base. Medial field between antemedial and postmedial lines not darkened. Discal spot distinct, roughly L-shaped, formed by raised broom-shaped white scales, sparsely framed by dark scales. Postmedial line moderately distinct with blackish thickening at intersections with veins, located close to middle part of wing at approximately equal distances from discal spot and from submarginal line, moderately smoothly curved outward almost parallel to outer margin of wing. Submarginal line dark, distinct, continuous, outlined with light scales along its inner side, located approximately at middle between postmedial line and wing outer margin, and nearly parallel to them, but with protrusion between the veins M3 and CuA1 and with sharp outward bend at inner margin of wing. Marginal line in form of small vague dark dots between veins on outer margin of wing plate. Wing fringe wide, 1.2–1.5 mm width, only slightly narrower than distance between submarginal line and wing plate margin, of grey colour with darkened outer margin. Fringe scales of two types: very long, 1.0–1.5 mm, broom-shaped with filiform base and expanded apical part about 0.2 mm long, bearing 3–6 filaments at apex of about 0.2 mm long); and short ones, 0.3–0.4 mm, of similar shape.

Hindwings with only faintly defined postmedial line and weak points of marginal line. Unlike forewings, distal half of hindwing slightly darkened in comparison with its basal part. Fringe same as on forewings.

Individual variability of the wing pattern in males consists of different degrees of forewing darkening. In more darkly coloured moths the transverse lines are less distinct. The antemedial line especially often disappears: it is more or less noticeable in only a quarter of the type specimens only. In rare cases the male forewings are completely dark grey (like those of the females), or even black. In this case, the wing pattern is represented only by a light discal spot, sometimes in combination with a lighter marginal field outward from the submarginal line (Fig. 4).

In females, forewing colouration is much more uniform, with light distal spot distinct only. The transverse lines are usually not present, sometimes with the exception of weakly defined postmedial and submarginal lines.

Wing venation (Fig. 10). Veins thick, slightly protruding on surface of wing, thinning towards the wing margin. Forewing with Sc short, ending on anterior wing margin at about middle of wing. Five radial veins: R1 from 2/3 of discal cell length; Rs1 and Rs2 very close together, from long common stem which approximately 2/3 of Rs2 length; Rs1 going to costal margin of wing and Rs2 going to the apex of wing; Rs3 and Rs4 on common stem which about ¼ of Rs3 length. M1 from anterior end of discal vein, M2 from posterior end of discal vein near base of M3. Bases of M3 and CuA1 not close together, CuA1 from discal cell at about ¾ of its posterior margin length, CuA2 from middle of discal cell and going to tornus of wing. 1A+2A relatively short, reaching 2/3 of the wing length along inner margin. 3A short, free, not connected to 1A+2A.

Hindwings with humeral Sc–Rs cell missing. Humeral (H) veins varying: H vein single, strong, long, curved, ending on costal wing margin at level of SC+R1 base, with thin branch directed towards to dorso-basal angle of wing; or H veins two closely located to each other, of them basal vein thin and short, and distal vein strong, as described above, but not branching. Vein Sc+R1 short, arising from middle of discal cell and ending on costal wing margin at about two-third of its length. Rs from discal cell slightly basal to discal vein, M2 and M3 from posterior corner of discal cell, CuA1 from discal cell slightly basal to M3, CuA2 from discal cell at about 1/3 of its length. Anal veins two, long, CuP fold missing.

The wing venation variability mainly consists of the structural diversity of humeral veins, which can differ even on the right and left wings of the same moth.

Legs (Fig. 11) of moderate length, relatively thin. Fore, middle and hind legs similar to each other, weakly differing only in length and ratio of parts. Middle legs slightly longer than front and hind legs, which almost of same length. Femora laterally with long hair-like scales. Fore tibia (Fig. 11a) slightly shortened, only little longer than first segment of tarsus, without epiphysis. Middle and hind tibia (Figs 11b, 11c) without spurs. Tarsi and tibiae of all legs with numerous moderately strong spines up to middle of their length along ventral side.

Abdomen. Segments 1–8 without modifications.

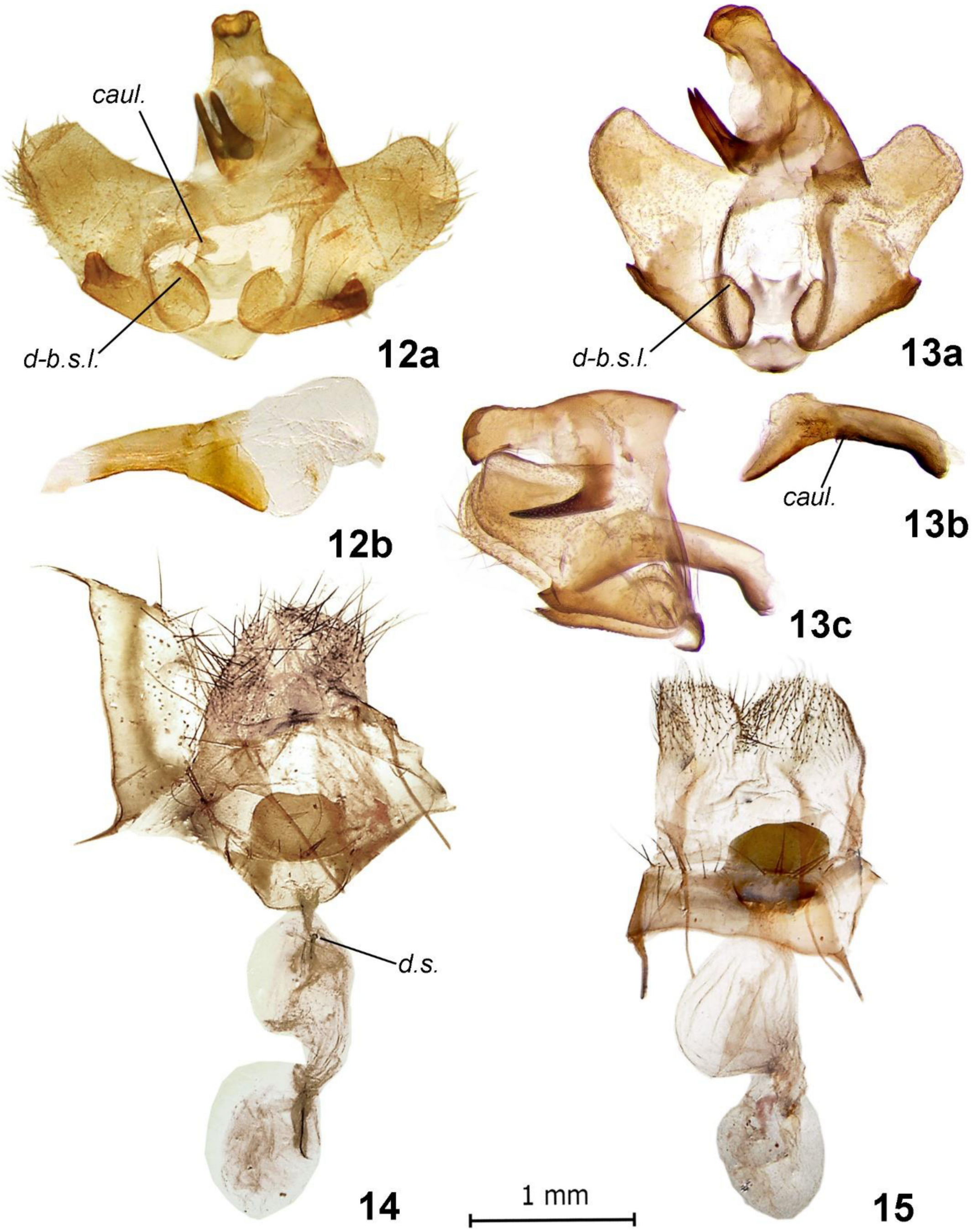
Male genitalia (Figs 12, 13). Tegumen small, oblong, vinculum narrow, with small wide rounded saccus. Uncus basally fused with tegumen, strong, bottle-shaped in frontal plane, laterally wide, with slightly bulbous apical portion bearing median dorso-posterior shallow groove and pair of small ventro-apical pointed projections. Gnathos in shape of a half ring, dorsally fused with tegumen, laterally wide, moderately sclerotised, ventrally with pair of long, strong spine-like processes, fused basally and directed posteriorly. Valvae symmetric, wide, solid, moderately sclerotised, with almost square cucullus (apical portion of valva distal to sacculus). Costal sclerotisation of valva weakly expressed, dorso-basal processes of valvae (hemitranstilla or basal process) missing. Sacculus moderately sclerotised, with weakly convex setose dosro-basal lobe (dorso-basal saccular lobe, see the Discussion), and with wide and short, oval, ladle-shaped distal process of sacculus (cuiller). Juxta wide and short, V-shaped, closely articulated with middle part of aedeagus. Caulis small, groove-like, tightly attached to aedeagus ventrally (Fig. 13b), but not coalesced (Fig. 12a). Phallus with short flattened-cylindrical aedeagus with short caecum bent ventrally and with apex in form of oblique dilated gutter, bent ventrally. Vesica membranous, with two moderate swellings bearing ventrally dense group of few short spiny cornuti and broad scobinate zone.

It should be noted that, although the shape of the vesica resembles that of the female bursa copulatrix (see below), its volume corresponds only to the volume of the swollen portion of the ductus bursae.

Female genitalia (Figs 14, 15). Papillae anales rounded (about 1 mm in diameter), semimembranous, with numerous strong setae. Ovipositor short, almost as long as papillae anales. Posterior apophyses about 1.5 mm long, approximately same length as eighth tergite, with wide triangular base and thin distal portion. Eighth tergite trapezoid, narrow, its width 2.8 times of its length, latero-posteriorly and posteriorly with sparse combs of strong setae (Fig. 14). Anterior apophyses three times shorter than posterior apophyses. Ventral area of eighth abdominal segment membranous, with large, rounded, lobe-like sclerotised postvaginal plate connected laterally with tergite by pair of long, narrow, triangular bars (Fig. 14). Ostium narrow, opening at the bottom of moderately large membranous cup-lake vaginal sinus. Ductus bursae membranous, inflated posteriorly, narrowed and longitudinally moderately wrinkled anteriorly, with ductus seminalis arising latero-ventrally from posterior portion of inflation of ductus bursae (Fig. 14). Corpus bursae membranous, oval, without sclerotisations, close to inflated portion of ductus bursae in size.

Distribution. Kyrgyzstan. The species is currently known from four locations in the lower part of the Naryn River basin (Fig. 16). Due to the extremely poor study of the autumn seasonal aspect of Lepidoptera in this region, it can be assumed that the range of this species is wider and covers a significant part of the mountainous Central Asia.

Ecology. The biotope of *Zolotuhia paradoxa* sp. nov. is stony and rocky mountain slopes abundantly covered with shrub vegetation, with an altitude range from 850 to 2100 m above sea level. The species had its maximum abundance, dominating among all other moths, in the lower part of the rocky slope of southern exposure, overgrown with dense thickets of the Turkestan (Pamir-Tienshan) shrubby cherry *Amygdalus ulmifolia* (also known with combinations as *Prunus* (*Louiseania*) *ulmifolia* or *Aflatunia ulmifolia*) (Figs 17, 18), and other shrubs such as *Zabelia corymbosa*, *Rosa maracandica*, *Lonicera stenantha*, *Spiraea hypericifolia* and *Cotoneaster* sp. Such a high abundance of *Zolotuhia paradoxa* sp. nov. in this place suggests that *A. ulmifolia* can be a host plant for the caterpillars of the described species. However, considering that monophagy is generally atypical for lappet moths, this shrub is unlikely to be the only host plant for *Z. paradoxa* sp. nov. Possibly, the dense and high thickets are capable of creating a local microclimate (more humid, with a smaller amplitude of temperature fluctuations under their canopy), favourable for the development of caterpillars and leading to a high population size.



FIGURES 12–15. *Zolotuhia paradoxa* sp. nov., male and female genitalia, paratypes. 12—male genitalia, Talassky Mt. Range, at Itagar River mouth: 12a—ventral view, aedeagus removed; 12b—aedeagus and vesica, lateral view from left, basal process of aedeagus lacking; 13—male genitalia, Moldo-Too Mt. Range, 15 km NW of Kazarman village: 13a—ventral view, aedeagus removed; 13b—aedeagus, lateral view from right; 13c—lateral from right. 14—female genitalia, ventral view, 8th abdominal tergum deflected, moth from Talassky Mt. Range, at Itagar River mouth; 15—female genitalia, ventral view, moth from the same locality. *caul.*—caulis, *d-b.s.l.*—dorso-basal saccular lobe, *d.s.*—base of ductus seminalis.

Adults are active at night. All the collected females flew to the light of the UV lamp only in the first hour after sunset, after that their flight ended. The flight of the males began after the completion of the female flight, and continued until dawn, when the air temperature dropped to 0ºC.

In all four locations known at present, despite the difference in altitudinal zones, moths were collected in the first ten days of October. Since adults do not feed (do not have a proboscis), it can be assumed that their life span and flight period are very short. In the mountain-steppe belt (900–1200 m) near Kazarman village and Tash-Kumyr village they flew together with noctuid species of the early autumn seasonal aspect, such as *Caradrina* spp., *Eugnorisma mikkolai* Varga, Ronkay, Ronkay & Gyulai, 2015, *Euxoa bogdanovi* (Erschoff, 1874), *Catasema vulpina* (Staudinger, 1888), *Metopodicha antherici* (Christoph, 1884), *Dryobotodes contermina* (Graeser, 1892), *Bryomixis lichenosa* Ronkay & Varga, 1990, *Polymixis colluta* (Draudt, 1934), *P. trisignata* (Ménétriès, 1849), *Dichagyris amoena* (Staudinger, 1892), and *D. singularis* (Staudinger, 1877). Whereas in the mountain-forest belt (2000–2200 m) of the Talas and Dzhumgal-Too ridges they were collected almost exclusively together with wintering species of the genus *Dasypolia* Guenée, 1852, and *Nekrasovia pliuschi* Ronkay & Varga, 1993 of the late autumn seasonal aspect.

Etymology. The species is named *paradoxa* (Latin, adjective, feminine: contrary to expectation) because it combines morphological characters in an unexpected way.

Discussion

We should preface this discussion with the following remarks.

1. Zolotuhin *et al.* (2012) subordinated the subfamily Macromphaliinae to the subfamily Poecilocampinae (as a tribe Macromphaliini), based on some similarities in the structure of the male genitalia, however, without taking into account their structure in the type species of the genus, *Macromphalia* C. Felder & R. Felder, 1874 (see below). In addition, they excluded American genus *Hypopacha* Neumoegen & Dyar, 1893 from Macromphaliini and transferred it to Poecilocampini, based on the external similarity of the moths and on the some similar strictures in the male genitalia. However, he disregarded the Franklemont's (1973) statement that *Hypopacha grisea* (Neumoegen, 1882) (the type species of the genus) has a clear morphological specialisation—the abdominal hood—in common with the rest of the Macromphaliinae. The subordination of Macromphaliini to Poecilocampinae was accepted partially. Thus, the databases BOLD (2024), BugGuide.Net (2024) and Lepiforum e.V. (2024) adopted this subordination, but Pohl *et al.* (2016), Ferge *et al.* (2018), Marquis *et al.* (2019) and Piovesan *et al.* (2023), as well as the data base Butterflies and Moths of North America (Lotts & Naberhaus 2024) preserved subfamily Macromphaliinae. We consider the decision by Zolotuhin *et al.* (2012) to be insufficiently justified, and in the Discussion we consider Poecilocampinae, Macromphaliinae and Chondrosteginae as taxa of equal rank. Some details of the probable relationships between these subfamilies will be discussed below.

2. The nominal taxon *Chondrostegoides nobilorum* Zolotuhin, 2007, in terms of the external characteristics of moths (in habitus, features of the wing pattern and their venation) is close to *Trichiurana meridionalis* Aurivillius, 1921. The photograph of the holotype genitalia of *Ch. nobilorum*, published by Zolotuhin (2007b, fig. 4) while describing the species, is identical to the photograph of the genitalia published later by this author (Zolotuhin 2015, ill. 7b) as "*Trichiurana*" without any comments on the *nobilorum* species. Apparently, the author discovered his mistake, but did not have time to establish a new combination or synonymy. The BOLD database contains two species in the genus *Trichiurana* Aurivillius, 1921, *T. meridionalis* Aurivillius, 1921 and "*Trichiurana nobilorum*", as nearest neighbours with p-distance of 4.97% (BOLD 2023a; BOLD 2023b). However, the nomenclatural act was not formalised, so here we propose a new combination *Trichiurana nobilorum* (Zolotuhin, 2007), **comb. nov.** Based on the external similarity of the moths, we consider the structure of the genitalia of *T. nobilorum* to be close to that of the type of the genus, *T. meridionalis*, the copulatory apparatus of which has not been described. On the Afromoths website (De Prins & De Prins 2011–2023), the moth's characteristics in the photographs of "*Chondrostegoides nobilorum*" match those of *T. meridionalis*, not *T. nobilorum*.

3. The genitalia of the type species of the genus *Chondrostegoides* Aurivillius, 1905, *Ch. capensis* Aurivillius, 1905, have not been described. For the purposes of this publication, we accept the concept of this genus according to Zolotuhin (2007b) and believe that the genitalia of the males of *Chondrostegoides magna* Zolotuhin, 2007 and *Chondrostegoides jamaka* Zolotuhin, 2007 depicted in the cited article correspond to those of *Ch. capensis* in the generic characters.

4. Due to an unclear systematic position of the genus *Phantosoma* Zolotuhin et Kostjuk, 2000, assigned by Zolotuhin (2015) to Poecilocampini, we do not include this genus in the relationship analysis of the new genus. The position of the monotypic genus *Phantosoma* within Poecilocampini and, in general, within the group of Chondrosteginae, Poecilocampinae, and Macromphaliinae, is questionable. As the authors themselves note, the type species of the genus, *Phantosoma witti* Zolotuhin et Kostjuk, 2000, the description of which is based on a single

female, morphologically is not close to any of the known genera of lappet moths. A distal position of the anastomosis of Sc and Rs on the hindwings in relation to the discal cell is noteworthy and is unknown in Lasiocampidae. Among lappet moths, a similar position of the contact between Sc and Rs, but without the formation of an anastomosis, is known only in *Chionopsyche* Aurivillius, 1909 (Chionopsychinae), which can be considered as a sister lineage to all other modern Lasiocampidae. An interpretation of the short vein connecting the discal cell with the anastomosis of Sc and Rs is contradictory. Zolotuhin & Kostjuk (2000: 142) first wrote that "Sc forming an anastomose with Rs", which would assume the short vein to be the base of Rs. However, below they clarify that "the common branch Sc+Rs connected with M by a short transversal vein" (*loc. cit.*: 142), which is usually considered as R1.

Indeed, determining the homology of the hind wing vein connected the discal cell with the stem Sc+R1+Rs in Lasiocampidae is difficult. The problem of the origin of this vein can be solved by suggesting that R1 merged with the base of Rs in the common ancestor of lappet moths, which resilted in the formation of an anastyomosis Sc+R1 with Rs. This hypothesis is supported by a strong shortening of the anterior vein of the discal cell characteristic for the family. Probably, significant enlargement of the humeral cell in Selenepherini and Gastropachini led to secondary restoration of the vein R1 between the base of Rs and Sc.

In this context, based on the wing venation, *Phantosoma* can be attributed to a separate (sub)basal branch of Lasiocampidae, which retains the ancestral position of the Sc and Rs anastomosis being distal to the discal cell. This does not allow the genus to be associated with either Poecilocampinae or any other described high taxon of Lasiocampidae.

Turning to the discussion of *Zolotuhia* gen. nov., the first thing to be noticed is that the genus has a unique set of characteristics. Habitually and by the wing venation (large discal cells, degenerative Sc–Rs cell on the hindwing, Rs vein arising of the from the discal cell), the characters of the new genus correspond to those of the subfamilies Chondrosteginae, Poecilocampinae, and Macromphaliinae. Based on the male genitalia with wide lobe-like valvae the specimens of the new genus are similar to the moths from the first two subfamilies. However, determination of the relationships within this group based on morphological characteristics faces difficulties.

The male antennae apparently have the longest rami (in relation to the length of the flagellum) in the entire family. The costal margin of the forewings is concave, as in *Chondrostega*, *Chondrostegoides*, *Mesocelis* Hübner, 1820 and *Trichiurana*. The combination of the wing pattern characters is unique. The presence of a light discal spot on the forewings is characteristic for many representatives of the subfamily Lasiocampinae (in the genera *Eriogaster* Germar, 1810, *Lasiocampa* Schrank, 1802, *Odonestis* Germar, 1812, *Dendrolimus* Germar, 1812, *Pyrosis* Oberthür, 1880, and others), but is unknown in Chondrosteginae, Poecilocampinae, and Macromphaliinae.

The presence of a distinct submarginal line on the forewings, which becomes the most noticeable element of the wing pattern, is generally not typical for lappet moths. At first glance the line looks like the postmedial line of other Lasiocampidae. Among the discussed subfamilies, a clear submarginal line in the form of a dark distinct stripe or a series of spots is present in the African genera *Trichiurana* and the golden-spotted lappet moths (*Haplopacha* Aurivillius, 1905, *Dasychirinula* Hering, 1926, *Auripluvia* Tujuba *et al.*, 2024, and *Eudoumbia* Tujuba *et al.*, 2024), in which it also is the most prominent element of the wing pattern. Also, the submarginal line is clearly expressed in the most of American Macromphaliinae. In general, the pattern of the forewings (except the discal spot) in the new genus most closely resembles that of *Hypopacha grisea* from Macromphaliinae, but the male genitalia do not share any common diagnostic characters.

The features of the wing venation in lappet moths serve as a source of many key characters for the identification and delimitation of taxa in this family. In *Zolotuhia* gen. nov., the combination of the wing venation characters is unique.

Firstly, the position of the veins Rs3 and Rs4 on the common stem, which occurs in Lasiocampidae rarely and scattered, is noteworthy. It is described in *Chionopsyche* (Chionopsychinae) (Zolotuhin 2015, figs. 4i and 5e), in *Trichiurana* (Aurivillius 1921: 236) (Chondrosteginae *sensu* Zolotuhin 2015), *Lechriolepis* Butler, 1880 and *Closterothrix* Mabille, 1879 (Lasiocampinae) (Aurivillius 1927). However, the position and number of the veins in the wing sector between Rs3 and M2 are variable. In the genus *Chondrostega*, the largest species, *Chondrostega vandalicia* Millière, 1865, has a full set of veins and the variable position of Rs4 found either on a common stem with M1 (Lemaire & Minet 1998, fig. 18.1.D, as "*Chondrostega tingitana* Powell, 1916", which was synonymized with *Ch. vandalicia* by Zolotuhin (2015)), or on a common stem with Rs1+Rs2 (Freina *et al.* 2015, fig. 7), or on a common stem with Rs4 (*loc. cit.*, fig. 12, neotype of *Ch. vandalicia*). In *Chondrostega pastrana* Lederer, 1858 and *Chondrostega hyrcana* Staudinger, 1871 (which were examined by the first author in ZISP) only two veins are present between the Rs2 and M2, and in different moths of either species the anterior vein being stalked with either stem Rs1+Rs2 or the posterior vein (as it is figured in "*Chondrostega* sp.": Zolotuhin 2015, ill. 43). In the genus *Chondrostegoides*, in *Ch. capensis* the vein Rs4 is present and placed on a common stem with M1 (Aurivillius 1905: 325, fig.), and in *Ch. ruficornis* (Aurivillius, 1921) there are only two veins between Rs2 and M2 (Swedish Museum 2005).

The homology of these two veins is unclear. It can be assumed that in *Chondrostega* and *Chondrostegoides* the reduction of one vein occurred as a result of a vanishing of Rs3, since this is variable in *Ch. vandalicia*. The lack of one vein between Rs2 and M2 is known for the Neotropical genus *Tytocha* Schaus, 1924 (Macromphaliinae) (Draudt 1927). In this genus, the vein number was decreased apparently due to the fusion of Rs4 and M1, which form a short fork in the related genera of Macromphaliinae.

Thus, the position of vein Rs3 is morphologically inconsistent. Due to the mosaic distribution of the venation characters in the Rs3–M1 group throughout the lappet moth family, the presence of the stalked Rs3 and Rs4 cannot be considered as a reliable synapomorphy of the taxa in the considered genus group.

Forewings of the males in *Zolotuhia* gen. nov. are similar in shape to those of *Chondrostega* and *Chondrostegoides*, in which the vein R1 is directed to the forewing apex. However, this position in the new genus is occupied by Rs2, similar to that in *Poecilocampa* Stephens, 1828, *Trichiura*, *Trichiurana*, *Giselea* Zolotuhin, 2007, *Haplopacha*, and *Bombycomorpha* C. Felder & R. Felder, 1874 from Chondrosteginae and Poecilocampinae, in most Macromphaliinae and in a number of Lasiocampinae (including Malacosomini).

In the new genus a short free vein 3A, directed to the inner margin of the forewing, is present behind the base on the vein 1A+2A. Among Lasiocampidae, a similar vein is depicted only for *Bombycomorpha pallida* Distant, 1897 (Joannou & Gurkovich 2009, plate 1, fig. 8), whereas in the other lappet moths 3A is not expressed or fused by the apex with the base of 1A+2A.

In the hindwing the new genus is characterized by the presence of a short SC+R1, directed to the anterior margin of the wing, similar to that in *Poecilocampa* and *Trichiura*. However, the place of origin of SC+R1 is different from the last two genera. In *Zolotuhia* gen. nov. SC+R1 arises from the discal cell from about mid-position between the base of the wing and Rs–M1 forking, whereas in *Poecilocampa* and *Trichiura* it arises in various position in relation to base of Rs.

It should be noted that the study of the wing venation in a large number of moths from the genera *Poecilocampa* (in *P. populi* (Linnaeus, 1758), *P. alpina* (Frey & Wullschlegel, 1874) and *P. tenera* O. Bang-Haas, 1927) and *Trichiura* (in *T. crataegi* (Linnaeus, 1858), *T. ilicis* (Rambur, 1858) and *T. kopetdaghi* Dubatolov & Zolotuhin, 1992) has shown that arising of SC+R1 just from the point of arising of Rs and arising of SC+R1 from the discal cell shortly before the Rs also often occur in addition to the typical position of SC+R1 shortly stalked with Rs.

As to hindwings humeral veins, *Poecilocampa*, *Trichiura*, *Bombycomorpha* and *Haplopacha* have one strong vein, while *Chondrostega* and *Chondrostegoides* (together with *Chionopsyche*) have two of those. *Zolotuhia* gen. nov. demonstrates an "intermediate" state with one strong vein and a second weak one, but in variable position, which may indicate that the origin of the single H vein was by the merging of two. Notably, the position of SC+R1 in *Zolotuhia* gen. nov. strongly resembles that of the second humeral vein in *Chondrostegoides capensis* (see Aurivillius 1905).

In general, the wing venation in *Zolotuhia* gen. nov., on the one hand, is unique, and on the other—it combines the characters of many genera of Chondrosteginae and Poecilocampinae, which makes it impossible to associate it with any of these subfamilies by such set of characters.

Most representatives of the discussed group of the subfamilies have a cephalic prominence (frontoclypeal process) of various shapes: cylindrical with a flat crown-shaped apex in *Zolotuhia* gen. nov.; in the shape of a truncated cone with an almost same "crown" at the apex in *Haplopacha* and *Eudoumbia*; in the form of a high and strongly toothed, chisel-like process in *Chondrostega*; in the shape of a truncated laterally pressed cone with a small serrulate apical ring in *Poecilocampa* and *Trichiura*; cone-shaped in *Dasychirinula*, *Bombycomorpha*, *Chondrostegoides*, *Trichiurana* and in Macromphaliinae; and in *Mesocelis*, *Giselea* and *Auripluvia* the frontoclypeal process is not present (Aurivillius 1905, 1921, 1927; Oberthür 1916; Franclemont 1973; Zolotuhin 2007a 2015; Joannou & Gurkovich 2009; Freina *et al.* 2015; Dupont *et al.* 2016; Tujuba *et al*. 2024). Thus, the features (and the presence) of the frontoclypeal process in the group of the lappet moths under consideration are mosaic and, like the features of wing venation, do not bear a clear intergeneric phylogenetic signal. Apparently, the specialisation of the frontoclypeal process in the discussed group occurred after the phylogenetic divergence of the main ancestral lines.

The male genitalia of *Zolotuhia* gen. nov. is in general similar to those of the Palearctic genera *Giselea* and *Trichiura* (especially *T. ilicis*), and the African *Bombycomorpha* and *Trichiurana*. However, the new genus is clearly distinguished by the bifurcated gnathos, by the presence of cornuti on the vesica and by the almost square-shaped cucullus. A bottle-shaped (in frontal projection) uncus is present in *Giselea* and *T. ilicis*, but in *Zolotuhia* gen. nov. the apex of the uncus is much more massive. With a bulbous apex of the uncus and a long, pointed gnathos, the new genus resembles the African *Bombycomorpha* and *Trichiurana*, but their distal process of sacculus is absent or very short. The bifurcated gnathos of the new genus appears to represent its unique autapomorphy among lappet moths. A tendency towards bifurcation of the dorso-posterior appendages of tegumen is observed in Macromphaliinae, but in this subfamily the uncus bifurcates, while the gnathos, when present, remains whole.

The cornuti on a vesica are rarely present on the moths from the considered subfamilies. Among the genera of the Old World they are only known in the new genus and in the African golden-spotted lappet moths (in *Eudoumbia*, *Auripluvia* and *Dasychirinula*, except the *Haplopacha* with the vesica bearing the tubular field of minute cornuti medially not forming plate or process), yet they are different in structure (see Tujuba *et al*. 2024). Also, cornuti are present in some American Macromphaliinae.

The review of the adult morphology in the subfamilies Chondrosteginae, Poecilocampinae, and Macromphaliinae demonstrates a wide and scattered distribution of characters. It does not allow us to clarify the relationships of the new genus. According to the modern systematics paradigm, the correct determination of the systematic position of a given taxon should be made in a phylogenetic context. However, the phylogeny of Lasiocampidae is still poorly studied.

The phylogenetic position of the family Lasiocampidae within the monotypic superfamily Lasiocampoidea is relatively stabilized as a sister branch to the superfamily Bombycoidea *s.l.*, which consists of an extensive series of families including Anthelidae, Apatelodidae, Bombycidae, Brahmaeidae, Carthaeidae, Endromidae, Eupterotidae, Phiditiidae, Saturniidae, and Sphingidae, as it was adopted by Kitching *et al.* (2018). Earlier Minet (1991, 1994; Lemaire & Minet 1998) proposed Anthelidae to be a sister family to the lappet moths, but molecular phylogenetics placed this family as one of the terminal branches within Bombycoidea (Zwick 2008; Zwick *et al.* 2011; Regier *et al.* 2013).

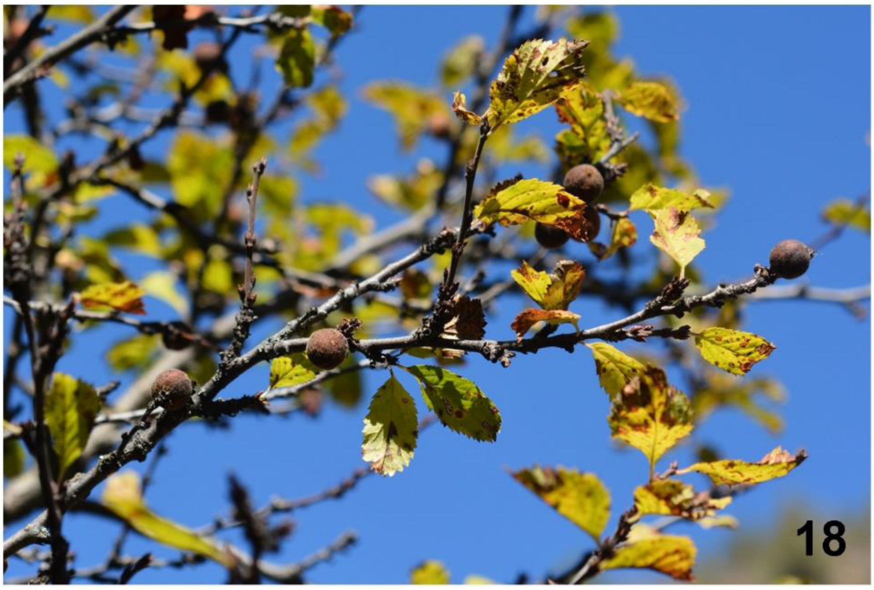
Within the family Lasiocampidae, the molecular phylogeny supports the basal position of Chionopsychinae (Regier *et al.* 2013), which is consistent with a proposal by Minet (1994) and Lemair & Minet (1998) based on the unique morphology of *Chionopsyche* moths. However, Zolotuhin (2015: 54) in his system of the family Lasocampidae placed Chionopsychinae between Poecilocampinae and Malacosominae, justifying this position by the deep specialisation of the male genitalia in *Chionopsyche*. He concluded the following: "These clearly expressed features of specialisation distinguish Chionopsychinae from the truly archaic [extant less derived, note by E. Beljaev] subfamilies Chondrosteginae and Poecilocampinae, that do not allow them to be considered as the most primitive group of the family" (*loc. cit.*: 53). This judgment is based on typological rather than phylogenetic logic and cannot be adopted in this study.

After the divergence of Chionopsychinae the family subdivides into the two large branches: one containing Lasicampinae (including Malacosomini) and the other—a group of subfamilies Chondrosteginae, Poecilocampinae, and Macromphaliinae. Of the genera representing the second branch, only *Tolype* Hübner, 1820 (*T. austella* Franclemont, 1973 and *T. notialis* Franclemont, 1973) and *Artace* Walker, 1855 (*A. cribaria* (Ljung, 1826)) from Macromphaliinae, *Poecilocampa* (*P. populi*) from Poecilocampinae, and *Chondrostega* (*Ch. vandalicia*) from Chondrosteginae were involved in the molecular phylogenetic studies in various combinations (Regier *et al.* 2000; Regier *et al.* 2008, Zwick 2008, Zwick *et al.* 2011, Regier *et al.* 2013). Although the type genus of Macromphaliinae, *Macromphalia* was not included in these studies, and the male genitalia in *Tolype* and *Artace* differ strongly from the type of the genus, the both genera can tentatively be accepted as correctly representing this subfamily.

In Regier *et al.* (2008) the cluster *Poecilocampa* + (*Tolype* + *Artace*) is reliably sister to the rest of the included Lasiocampidae (in the absence of *Chionopsyche*), and *Poecilocampa* is also reliably sister to the sister pair *Tolype* + *Artace*. However, in Zwick *et al.* (2011) genus *Poecilocampa* is contradictorily combined either with the cluster (*Tolype* + *Atrace*) or with the cluster Lasiocampinae (in the absence of *Chondrostega*). In both cases the support of the branches is low. In the most robust phylogeny by Regier *et al.* (2013), *Poecilocampa* is again separated from Lasiocampinae and forms a common terminal cluster with *Chondrostega*, while *Tolype* opposes them as a sister branch, but with moderate support for these nodes (with bootstrap values of 66–73%).

16

17



18

FIGURES 16–18. Collecting sites and biolopes of *Zolotuhia paradoxa* sp. nov. 16—collecting sites of the species in Kirgizstan. 17—thickets of *Amygdalus ulmifolia* in the type locality of *Zolotuhia paradoxa* sp. nov. in Talassky Mt. Range. 18—*A. ulmifolia*, branches with leaves and fruits.

Thus, based on the molecular data it can be accepted that Chondrosteginae, Poecilocampinae and Macromphaliinae are monophyletic group of taxa sister to Lasiocampinae (including Malacosomini), and that Chondrosteginae and Poecilocampinae form a terminal pair sister to Macromphaliinae. Although, the large genetic distances between all three taxa, and moderate support of the nodes, indicate significant genetic divergence of these lineages. Relying on these molecular-genetic data, we attempted to estimate the phylogenetic relationships between the genera associated by Zolotuhin (2015) with Chondrosteginae and Poecilocampinae on basis of morphological characters taken mostly from literature.

Morphological in-depth research of Lasiocampidae were published a few only. From the considered subfamilies, some information on the skeleton is available in Lemaire & Minet (1998), and on the skeleton-muscular apparatus of the male genitalia in Stekolnikov & Zolotuhin (1994), and Zwick (2009). According to Lemaire & Minet (1998), the ventral arms of the laterocervicalia in Chondrosteginae and Poecilocampinae are free and located very close to probasisternum, unlike in Macromphaliinae and Lasiocampinae, which have these arms more or less fused mesally and placed remotely from the basisternum. The aterocervicalia ventral arms in the new genus are as it is described for Chondrosteginae and Poecilocampinae. Considering the molecular phylogeny of lasiocampids, a very close position of laterocervicalia to probasisternum can be treated as synapomorphy of Chondrosteginae and Poecilocampinae, however, there are no data on the state of this character in the African genera.

The musculature of the male genitalia in the considered subfamilies is described and illustrated in detail only for *Poecilocampa pupuli* (Stekolnikov & Zolotuhin 1994; Zwick 2009). For *Chondrostega pastrana*, *Chondrostega* sp., and *Macromphalia* (two unidentified species) only descriptions (with no pictures published) are available (Stekolnikov & Zolotuhin 1994; Zwick 2009, supplementary data). This dataset shows that:

—In *Poecilocampa pupuli*, the genital sclerites and musculature are slightly modified in relation to their supposed ground plan for bombycoid Lepidoptera.

—In the genus *Chondrostega*, the muscles M3 and M7 are lost. It is combined with the structural simplification of the genitalia skeleton: very short juxta, degenerated quiller, and complete reduction of the hemitranstyllae correlating with the attachment of M4 to the membrane of diaphragma. This simplification can be explained by the tendency towards miniaturisation (pumilisation) of moths, accompanied by a specific set of morphological reductions (see Beljaev *et al.* 2014).

—In *Macromphalia* the male genitalia have a deeply specialized structure of sclerites, accompanied by the loss of the muscles M3 and M4, which obviously does not represent an ancestral type of the musculature for the subfamily Macromphaliinae. It is likely that the macromphaline genus *Hypopacha* may have a genital structure that is closest to the ancestral type for this subfamily, since it has the well-developed hemithrastylae and juxta, as well as a complete vinculum (unlike in *Macromphalia* with vinculum split ventrally), suggesting the presence of the M3 and M4 muscles.

Based on the research review on the skeleton-muscular male genital structure we can only assume that *Poecilocampa* probably retains close to an ancestral state, while *Chondrostega* and Macromphaliinae demonstrate a loss of some, but different, muscles. So, these data do not provide sufficient information to a well-grounded conclusion about the genus-level phylogenetic relationships in the analysed subfamilies. Therefore, we restricted ourselves to the characters of the head, wing venation, tibiae, and sclerites of the male genitalia. The morphological data were adopted from the below sources as follows (arranged by alphabetical order of taxa):

—on *Auripluvia*: from Tujuba *et al*. (2024);

—on *Bombycomorpha*: from Joannou & Gurkovich (2009);

—on *Chondrostega*: from Aurivillius (1894), Grünberg (1911), Oberthür (1916), Freina *et al.* (2015), Zolotuhin (2015), Seven & Akýn (2019), and original data on the wing venation and frontoclypeal process;

—on *Chondrostegoides*: from Aurivillius (1905, 1927), Swedish Museum (2005, "*Chondrostega ruficornis*"), Zolotuhin (2007b), and De Prins & De Prins (2011–2021)

—on *Dasychirinula*: from Hering (1926), Dupont *et al.* (2016), and Tujuba *et al*. (2024);

—on *Eudoumbia*: from Tujuba *et al*. (2024);

—on *Giselea*: from Zolotuhin (2007a, 2015);

—on *Haplopacha*: from Aurivilius (1905), Dupont *et al.* (2016), and Tujuba *et al*. (2024);

—on Macromphaliinae: from Draut (1927), Forbes (1942), Costa Lima (1950), Ureta (1957), Franclemont (1973), Rodriguez & Angulo (2007), Montero-Ramírez *et al.* (2011), Zolotuhin (2015), Heiner Ziegler (2007–2022), Cahurel (2022), and Cornell University Insect Collection (2023);

—on *Mesocelis*: from Aurivillius (1927), and Zolotuhin (2015);

—on *Poecilocampa*: from Aurivillius (1894), Grünberg (1911), Chistyakov & Zolotuhin (1994), Saldaitis & Pekarsky (2015), Zolotuhin (2015), Monasterio *et al.* (2021), and original data on the wing venation and frontoclypeal process;

—on *Sphinta* Schaus, 1904: from Schaus (1904), Franclemont (1973), BOLD (2023c), and Cornell University Insect Collection (2023);

—on *Trichiura*: from Aurivillius (1894), Grünberg (1911), Zolotuhin (2007a, 2015), and original data on the wing venation and frontoclypeal process;

—on *Trichiurana*: from Aurivillius (1921, 1927), Zolotuhin (2007b), and De Prins & De Prins (2011–2021);

—on *Zolotuhia*: original data.

Establishing the polarisation of morphological characters, which consists in assigning them relative plesiomorphic and apomorphic states, is classically based on the outgroup criterion. An outgroup taxon should be selected as phylogenetically sister to the analyzed in-group, and its characters should be considered ancestral (plesiomorphic) relative to the in-group. The choice of an outgroup taxon will determine the polarisation of the character states in the in-group.

For the analyzed group of subfamilies, the sampling of outgroup is problematic. The designation of the most basal subfamily Chionopsychinae as outgroup could be phylogenetically optimal, but its representatives are extremely specialized morphologically (especially in the genitalia).

As result of the search through the all other Lasiocampidae, the South American genus *Sphinta*, with an unclear taxonomic position within Lasiocampidae, was selected as outgroup for the analyzed subfamilies. Franclemont (1973: 29) writes: "*Sphinta* differs in so many ways that I am excluding it from the Macromphaliinae; I am inclined to place it in a subfamily by itself. The tergum of the eighth abdominal segment of the male is normal; it does not form a hood over the tegumen and the uncus. The male genitalia are almost diagrammatic in appearance. The venation of the hind wing resembles that of *Gloveria* [Lasiocampinae, note by E. Beljaev] … in the relationship of Sc+R1 to Rs. However, in the forewing R4 arises from the stalk of R5+M1 as in the Macromphaliinae". It should be added here that the character "R4 arises from the stalk of R5+M1" is common for most Lasiocampidae, and the differences between taxa consist only in the origin of the discal vein before or after the arising of R4. The relationship of Sc+R1 to Rs in form of their short stalking from small accessory cell (as in *Gloveria* Packard, 1872) is characteristic to the members of the tribes Lasiocampini and Trabaliini (*sensu* Zolotuhin *et al.* 2012; Zolotuhin 2015) (Lasiocampinae), and also similar to that in *Phantosoma* (but accessory cell larger), which is one of tentative basal lasiocampid genera. The male genitalia of *Sphinta* demonstrates the most generalized structure of the valva known for the family Lasiocampidae, having distinct cucullus without tend to membranisation (as it occurs in Poecilocampinae and Chondrosteginae) or other specialisation, and well sclerotized sacculus with firm and short distal process (see photo of the male genitalia of *Sphinta schausiana* Jones, 1912 in: Cornell University Insect Collection 2023). Only uncus and gnathos appear secondary modified, but in different way than in other Lasiocampidae.

Photos of the larva and pupa of S*phinta* (*cossoides*?) are posted by Marcelo (2022) on the Brazilian website Insetologia—Identificação de Insetos. The larva on facies can be classified as morphological "type 1" of the five types of lasiocampid larvae established by Zolotuhin (2015: 33): "The body is cylindrical in shape; the hairs are all the same size and are located, including on warts (*Chondrostega*)" [in Russian]. In addition to *Chondrostega*, the larvae of *Mesocelis* (Chondrosteginae), *Trichiura* (Pecilocampinae), and *Hypopacha* and *Euglyphis* (Macromphaliinae) can also be classified in this type.

Thus, S*phinta* dies not demonstrate belonging to any known lineage of Lasiocampidae, and supposedly presents one of the most basal branches in the family. Therefore, we considered this genus as outgroup for the purposes of this study.

The polarisation of characters was carried out mainly on the basis of the outgroup criterion. In some cases, when the outgroup criterion could not be applied, we accepted the criterion of morphological simplicity. The involved characters are described in the List of the probable plesiomorphic and apomorphic states (Table 1), where plesiomorphies marked by zero after the number of the character. The distribution of the plesiomorphic and apomorphic states of characters among the genera is given in the Table 2, and allocation of the apomorphies on the tentative phylogenetic tree is illustrated on the synapomorphogram (Fig. 19).

TABLE 1. List of the probable plesiomorphic and apomorphic states of characters in the lappet moths from subfamilies Chondrosteginae, Poecilocampinae, Macromphaliinae and in the genus *Sphinta*.

	Characters	**States**
1	Hindwing venation in the humeral area	1.0—with humeral cell formed by connection of Sc to discal cell by means of transverse vein, and with short or lacking humeral veins; 1.1—with humeral cell formed by anastomosis of Sc with discal cell, and with long humeral vein(s) reaching or almost reaching costal margin of wing.
Note. The plesiomorphic state is supposed based on the wing venation in the *Phantosoma* and *Sphinta*.		
2	Tergum and sternum of male eighth abdominal segment	2.0—simple; 2.1—forms a bluntly pointed hood, and sternum of eighth segment is modified into a plate.
3	Forewing	3.0—without spots with iridescent golden scales; 3.1—with basal and discal spots with iridescent golden scales.
4	In the male genitalia, hemitanstilla of valva	4.0—ancestrally is present as short firm medial process; 4.1—lobe-like weakly sclerotised or lacking.
5	Middle and hind tibia with spurs	5.0—distinct, one pair each; 5.1—rudimentary or lacking.
6	In the male genitalia, cornuti on vesica of phallus	6.0—present; 6.1—lacking, but probably modified into series of spines or into horny processes around distal opening of aedeagus laterally; 6.2—lacking, distal opening of aedeagus without ornamentation.
7	In the male genitalia, juxta dorsally	7.0—closely articulated with aedeagus but not ankylosed with it; 7.1—ankylosed with aedeagus with gutter-like inclosing of basal portion of aedeagus ventrally.
8	In the male genitalia, cuiller on sacculus of valva	8.0—moderately long; 8.1—long, strong, horn-like; 8.2—short or lacking.
Note. The plesiomorphic state of cuiller as a “moderately long” is supposed based on its wide distribution in the Chondrosteginae/Poecilocampinae generic complex and its presence in *Sphinta*.		
9	In the male genitalia, dorso-basal saccular lobe	9.0—as moderately protuberant extension of dorso-basal angle of medial wall of sacculus near juxta; 9.1—as digital or bulbous process; 9.2—as plat-like dilation of dorso-basal angle of medial wall of sacculus.
10	Costal margin of forewing	10.0—slightly convex or almost straight; 10.1—clearly concave.
11	Hindwing with Sc+R1	11.0—arising from discal cell far from the Rs–M1 forking; 11.1—arising from Rs or from discal cell close to Rs—M1 forking.
Note. The plesiomorphic state is supposed based on most common structure of the veins in the Chondrosteginae/Poecilocampinae generic complex and in Macromphaliinae, and the apomorphic state is considered as partial return (recapitulation) to the plesiomorphic state 1.0.		

.....continued on the next page

TABLE 1. (Continued)

<table>
<tr><th></th><th>Characters</th><th>States</th></tr>
<tr><td>12</td><td>In forewing, veins in the sector between Rs2 and M1</td><td>12.0—with Rs4 and M1 stalked, Rs3 stalked with stem Rs4+M1 or arising from discal cell;
12.1—with Rs3 from common stalk Rs1+Rs2, and with Rs4 and M1 stalked;
12.2—with Rs3 and Rs4 stalked;
12.3—with Rs3 and Rs4 separately from common stalk Rs1+Rs2;
12.4—with Rs3 lacking.</td></tr>
<tr><td colspan="3">Note. The plesiomorphic state is supposed as most common in the discussed genera, and in Macromphaliinae and <i>Sphinta</i>. However, basal lasiocambid genus <i>Chionopsyche</i> and probably basal <i>Phantosoma</i> possess stalked veins Rs3 and Rs4.</td></tr>
<tr><td>13</td><td>In the male genitalia, gnathos with medial dilation</td><td>13.0—in form of long triangular process;
13.1—hardly sclerotized, semi-oval or semi-rounded;
13.2—in form of long bifurcated process;
13.3—bilobate;
13.4—narrow lobe-like and tends to be reduced).</td></tr>
<tr><td colspan="3">Note. The plesiomorphic state is supposed based on the most common structure in the discussed genera and in Macromphaliinae. For <i>Haplopacha</i> the state is given based on <i>H. lunata</i> as a single species of the genus with the developed gnathos.</td></tr>
<tr><td>14</td><td>Forewing with vein R1 and Rs1</td><td>14.0—R1 runs to costal margin and Rs1 runs to apex or to costal margin near apex;
14.1—R1 runs to apex and Rs1 runs to outer margin near apex.</td></tr>
<tr><td>15</td><td>In the male genitalia, dorsal lobe of valva</td><td>15.0—comparatively long, oblong;
15.1—rudimentary papillae-like;
15.2—short, rounded.</td></tr>
<tr><td>16</td><td>Head with frontoclypeal process</td><td>16.0—simple conic;
16.1—wide cone with flat crown-shaped top;
16.2—conic, serrated ventro-laterally;
16.3—in form truncated, laterally narrowed cone with serrulate apical ring;
16.4—in the form of a high, strongly toothed rim;
16.5—lacking.</td></tr>
<tr><td colspan="3">Note. The plesiomorphic state is supposed based on the criterion of simple structure. However, hypothetically, all types of frontoclypeal process can be derived from the type “corona on short cone” characteristic to <i>Haplopacha</i> and <i>Zolotuhia</i>, which kept many possible ancestral characters. Presence of simple conic frontoclypeal process in Macromphaliinae is given following Zolotuhin (2015); we did not find other literature data on this matter.</td></tr>
<tr><td>17</td><td>Fore tibia</td><td>17.0—simple, without apical spurs;
17.1—with apical spurs.</td></tr>
<tr><td>18</td><td>Females with wings</td><td>18.0—normally developed;
18.1—rudimentary.</td></tr>
</table>

TABLE 2. Distribution of the probable plesiomorphic and apomorphic states of characters in the lappet moths from subfamilies Chondrosteginae, Poecilocampinae, Macromphaliinae and in the genus *Sphinta*.

Number of a character (see Tab. 1)	*Sphinta*	Macromphaliinae	*Haplopacha*	*Eudoumbia*	*Auripluvia*	*Dasychirinula*	*Trichiura*	*Poecilocampa*	*Giselea*	*Zolotuhia*	*Bombycomorpha*	*Trichiurana*	*Mesocelis*	*Chondrostegoides*	*Chondrostega*
1	1.0	1.1	1.1	(1.1)	(1.1)	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1
2	2.0	2.1	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	n.d.	2.0	2.0
3	3.0	3.0	3.1	3.1	3.1	3.1	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
4	4.0	4.0	4.0	4.0	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	n.d.	4.1	4.1
5	n.d.	5.0	5.0	5.0	5.0	5.0	5.1	5.1	n.d.	5.1	5.1	n.d.	n.d.	5.1	5.1
6	6.2	6.0, 6.2	6.2	6.0	6.2	6.0	6.1	6.1	6.1	6.0	6.2	6.2	n.d.	6.2	6.2
7	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.0	7.1	7.1	n.d.	7.1	7.1
8	8.0	n.a.	8.1	8.1	8.1	8.1	8.0, 8.1, 8.2	8.1	8.0	8.0	8.2	8.2	n.d.	8.2	8.2
9	9.0	9.1	9.1	9.1	9.1	9.1	9.0	9.0	9.0	9.0	9.0	9.2	n.d.	9.2	9.2
10	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.1	10.0	10.1	10.1	10.1	10.1
11	11.0	11.0	11.0	(11.0)	(11.0)	11.0	11.1	11.1	11.0	11.0	11.0	11.1	11.0	11.0	11.0
12	12.0	12.0	12.1	(12.1)	(12.1)	12.1	12.0	12.0	12.0	12.2	12.3	12.2	12.0	12.0	12.0, 12.4
13	13.3	13.0	13.0	13.1	13.3	13.4	13.0, 13.3	13.0	13.0	13.2	13.0	13.0	n.d.	13.4	13.4
14	14.0	14.0	14.0	(14.0)	(14.0)	14.0	14.0	14.0	14.0	14.0	14.0	14.0	14.0	14.1	14.1
15	15.0	15.0	15.0	15.0	15.0	15.1	15.0	15.0	15.0	15.0	15.0	15.0	n.d.	15.2	15.2
16	n.d.	16.0	16.1	16.1	16.5	16.2	16.3	16.3	16.5	16.1	16.0	16.0	16.5	16.0	16.4
18	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.0	18.1	18.0, 18.1	18.1
17	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.0	17.1	17.0	17.1

Legend. n.a.—not applicable: a character that is not applicable to the taxon due to a deep modification of the morphological structure; n.d.—no data: lack of morphological information available to the authors of the article.

Note. The states of the wing venation characters (in brackets) in *Eudoumbia* and *Auripluvia* are taken to be the same as in *Haplopacha*, since original descriptions of the first two genera (Tujuba *et al*. 2024) contain nothing about the difference their wing venation from that of the last genus.

The monophyly of the group of the subfamilies Chondrosteginae, Poecilocampinae, and Macromphaliinae can be supported by a probably synapomorphic structure of humeral cell. It is formed by Sc anastomosis with discal cell, whereas in the other lappet moths with a small humeral cell the Sc vein is connected with discal cell by the transverse vein of unclear homology (possibly the result of a fusion of R1 with the base of Rs, see above). In the considered group of subfamilies the humeral cell is combined with the long humeral veins (one or two) reaching the costal margin of the wing. A similar structure of the humeral cell is also present in Malacosiomini, but their cell is combined with the short humeral veins. Taking other morphological and genetic features of the last tribe into account, we tentatively consider this similarity to be a homoplasy.

Generally, the humeral cell formed by Sc anastomosis with discal cell correlates with the vein Sc+R1 arising from discal cell, except *Poecilocampa* and *Trichiura* (and *Trichiurana* following the original description of this genus: Aurivillius 1921). Three latter genera demonstrate a tendency to have Sc+R1 and Rs connected, as it is the case in most Lasiocampidae including tentative basal genera *Phantosoma* and *Sphinta*. Possibly the stalked or connate Sc+R1 and Rs is one of the basal apomorphies of Lasiocampidae except *Chionopsyche*. However, in *Poecilocampa*, *Trichiura*, and *Trichiurana* it looks rather like an apomorphic partial recapitulation of the ancestral state.

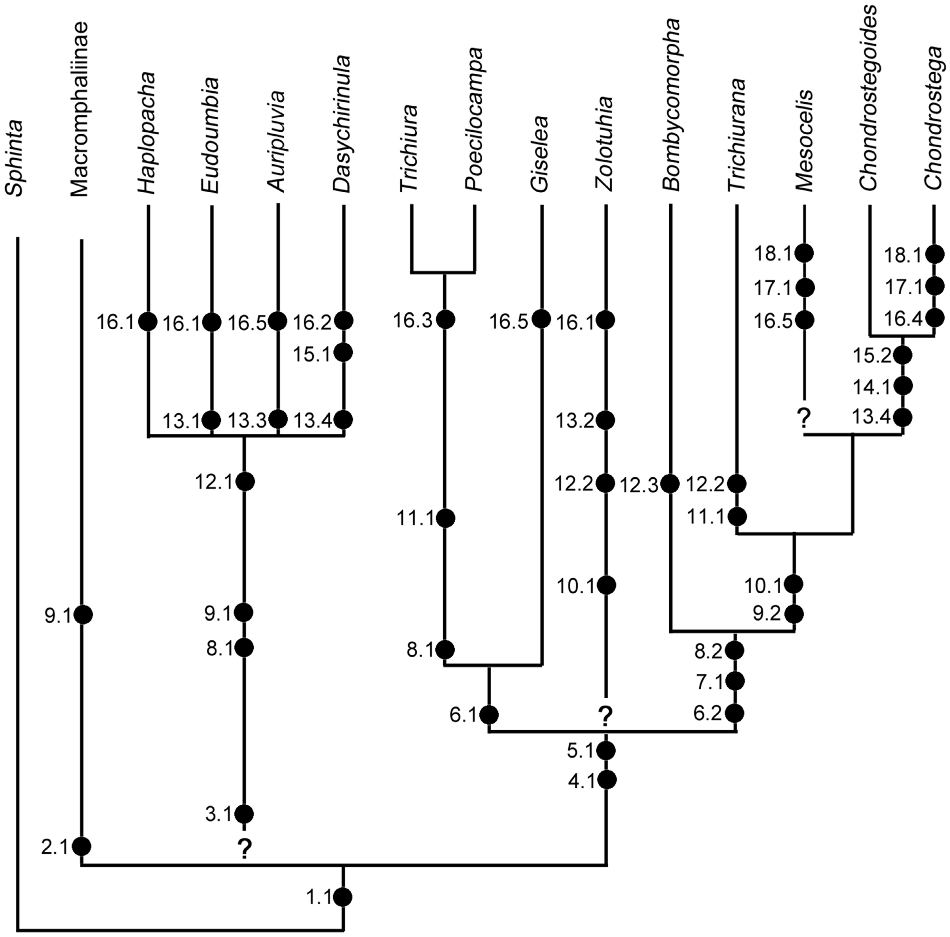


FIGURE 19. Tentative hypothesis on the phylogenetic relationships of the genera from Chondrosteginae, *s.l.* For the descriptions of apomorphies (black rings) see Table 1 and Table 2.

In the group of genera within the subfamilies Chondrosteginae and Poecilocampinae, the group of genera of the African golden-spotted lappet moths (*Haplopacha*, *Dasychirinula*, *Eudoumbia*, and *Auripluvia*) form a distinct monophyletic group, characterized by a unique probable synapomorphy: basal and discal spots with iridescent golden scales on the forewing. Additionally, this group exhibits a tendency to develop extremely long ductus bursae in female genitalia, which corresponds to the length of the vesica in the male phallus and may also represent a synapomorphy for the group.

The male genitalia of the African golden-spotted lappet moths strongly differ from those of the other representatives of Chondrosteginae and Poecilocampinae not only by the presence of cornuti, but also by the presence of prominent processes of the anellus between the juxta and sacculi, called "valve saccular lobes" (Dupont *et al.* 2016). In the topology these lobes correspond to the cristae of other moths, what is confirmed by the presence of characteristic setae on their top. This structure is also present in the other Chondrosteginae and Poecilocampinae in the form of a dorso-basal extension of the medial part of the sacculus, more or less convex (in *Poecilocampa*, *Trichiura*, *Giselea*, *Zolotuhia* gen. nov. and *Bombycomorpha*) or almost flat lamellar (in *Trichiurana*, *Chondrostegoides* and *Chondrostega*). However, this structure has never been specially described in the literature. Since the "saccular lobe" usually refers to the entire ventral part of the bifurcated valva, or (less commonly) to the distal process in the area of the sacculus, we adopted to this structure the name "dorso-basal saccular lobe" considering its topology (Figs 12a, 13a). The processes of similar localisation (probably homologous) are widely represented in the American

Macromphaliinae in different specific shape (see Ureta 1957; Franclemont 1973; Montero-Ramírez *et al.* 2011; also see photos of the genitalia of *Hypopacha grisea*, *Macromphalia dedecora* (Fiesthamel, 1839), *Tolype distincta* (French, 1890), *Artace colaria* Franclemont, 1973 and *Apotolype brevicrista* (Dyar, 1895) on the online database of the Cornell University Insect Collection (2023)). Some representatives of the subfamily Lasiocampinae also possess similar topologically homologous structure. For example, in the genus *Eucraera* Tams, 1930 (Trabaliini) it is described as an "additional projection" on sacculus: "Sacculus is trapezoid with an elongated spur-like process; additional projection is placed in the basal part, it is oval shaped and covered with short setae" (Prozorov 2016: 4).

The African golden-spotted lappet moths in their general appearance and the elements of the wing pattern, as well as in the deep division of the valvae into dorsal and ventral lobes and the presence of processes in the ventral part of the anellus, deviate from other Chondrosteginae/Poecilocampinae, and resemble representatives of Macromphaliinae (in appearance—especially *Norapidia* Draudt, 1927, *Hypopacha* and some *Euglyphis* Hübner, 1820).

Like some Macromphaliinae, the golden-spotted lappet moths retain spurs on the middle and hind tibiae, a sclerotized hemitranstilla (except for *Dasychirinula*, which has rudimentary cuculli), and cornuti on the vesica. These morphological features suggest a subbasal position for this group within the Lasiocampidae. However, no probable apomorphies were found to support a close relationship between the golden-spotted lappet moths and either the Chondrosteginae/Poecilocampinae or the Macromphaliinae. These similarities may be symplesiomorphies or homoplasies and in this context are phylogenetically uninformative. Typologically, they reduce the morphological "distance" between the old-world Chondrosteginae and Poecilocampinae on the one hand, and the American Macromphaliinae on the other, which makes their clear diagnosis difficult.

The relationships among the genera of African golden-spotted lappet moths fall outside the scope of this article. However, it is worth noting that, despite their similar external appearances, the male genitalia exhibit significant and multidirectional diversification. In *Eudoumbia* and *Auripluvia*, for instance, the gnathos is strongly developed while the uncus is reduced, whereas in *Dasychirinula*, the opposite occurs: the uncus is hypertrophied, and the gnathos is rudimentary. *Haplopacha* and *Eudoumbia* retain well-developed cuculli with hemitranstillae, whereas in *Auripluvia* they are noticeably weakened, and in *Dasychirinula* they are reduced to small papillary processes. The vesica armature also differs significantly between the genera. A possible synapomorphy shared by *Auripluvia* and *Dasychirinula* could be the bulbous base of the aedeagus and the presence of a needle-like cornutus on the vesica.

The remaining genera of the Chondrosteginae/Poecilocampinae group are contraposed to the African golden-spotted lappet moths by the reduced hemitranstillae and the absence of tibial spurs. However, both probable apomorphies cannot be considered completely reliable, since synapomorphic reductions are difficult to distinguish from homoplastic ones.

In the clade with Chondrosteginae/Poecilocampinae genera, three branches can be distinguished (Fig. 19). One of them includes the group *Giselea* + (*Poecilocampa* + *Trichiura*). It is supported by one possible synapomorphy—the presence of a series of spines or short horny processes around the distal opening of aedeagus, which can originate from cornuti on vesica similar to that in *Zolotuhia* gen. nov.

Another branch includes the large group of genera—*Bombycomorpha*, *Trichiurana*, *Mesocelis*, *Chondrostegoides* and *Chondrostega*, which can be characterized by a simple phallus without cornuti, by the juxta ankylosed with aedeagus, and by a short or vestigial cuiller on sacculus. In this group the monophyly of *Trichiurana* with the group *Chondrostega*—*Chondrostegoides*—*Mesocelis* is supported by the plate-like shape of the dorso-basal saccular lobe and the concave costal margin of the forewings. However, these characters conflict with the stalked Sc+R1 and Rs on the hindwings (similar to that in *Poecilocampa* and *Trichiura*) and the stalked Rs3 and Rs4 on the forewings (like in *Zolotuhia* gen. nov.).

Relationships within the group *Chondrostega*—*Chondrostegoides*—*Mesocelis* is controversial in result of conflict between the probable apomorphies. *Chondrostega* and *Chondrostegoides* share the unique apomorphy—forewing veins R1 runs to apex and Rs1 runs to outer margin, when in *Mesocelis* both are going to the costal margin. *Chondrostega* and *Mesocelis* share two apomorphies—fore tibia with apical spurs and females with rudimentary wings. However, the last character may by easily homoplastic, and apical spurs on fore tibia frequently occurs in different moths, whereas the forewing veins R1 runs to apex is unique apomorphy. Therefore, we take the last character as phylogenetically more reliable.

Zolotuhia gen. nov. is placed on the cladogram as a separate third branch with open connection since no probable synapomorphies of any pair of these three branches have been found. Typologically, *Zolotuhia* gen. nov.

is closest to *Giselea*, *Trichiurana* and *Bombycomorpha* in terms of the general similarity in the male genitalia. This resemblance is probably based on the symplesiomorphic states of characters though, which the new genus possesses in the greatest number among the genera of Chondrosteginae and Poecilocampinae with an exception of the African golden-spotted lappet moths. Thus, morphological phylogenetic research does not allow us to connect the genus *Zolotuhia* with either *Chondrostega* lineadge or *Poecilocampa* lineadge, and indicates its relationship with the complex of subfamilies Chondrosteginae/Poecilocampinae only.

In the literature, the delimitation of Chondrosteginae and Poecilocampinae is controversial. Franclemont (1973: 28) first who indicate the morphological similarity of Chondrosteginae and Poecilocampinae. He wrote: "I have assumed that the simple type of male genitalia found in the species of the genera *Chondrostega*, *Trichiura*, and *Poecilocampa* is the basic or unspecialized type for the family", but he did not associate *Poecilocampa* with any subfamily of Lasiocampidae. However, Regier *et al.* (2000: 179) erroneously attributed the association of Poecilocampinae with Chondrosteginae to Franclemont: "Franclemont (1973) revised this classification, moving *Poecilocampa* and *Trichiura* from Lasiocampinae to Chondrosteginae …".

Minet reestablished Poecilocampinae, including in the subfamily the genera *Poecilocampa* and *Trichiura* only. In the Key to subfamilies, he distinguished Poecilocampinae from Chondrosteginae by the hindwing with Sc+R partly fused with bath upper edge of discal cell and postdiscal section of vein Rs (in: Lemaire & Minet 1999: 329). Following this Key, all genera of Chondrosteginae/Poecilocampinae complex considered here have to be associated with Chondrosteginae, with the exception *Poecilocampa* and *Trichiura*. On the other hand, Minet noted that "the main autapomorpy of Poecilocampinae is the crown-shaped extremity of their frontal protuberance" (in Lemaire & Minet 1999: 329). But this type of frontal protuberance is present in *Zolotuhia* and in some African genera that have the venation of the hind wings of the Chondrosteginae type. Thus, the characters proposed by Minet for delimitation of Chondrosteginae and Poecilocampinae do not allow this to be realized taking into account the African and Asian lasiocampid genera.

Zolotuhin (2015) gave expanded diagnoses of Chondrosteginae and Poecilocampinae in the partial accordance with the characters proposed by Minet, but he attributed the crown-shaped frontal protuberance to Chondrosteginae, and distributed genera into the subfamilies in weak connection with his diagnoses. He included the genera *Chondrostega*, *Chondrostegoides*, *Trichiurana*, and *Mesocelis* into Chondrosteginae (*loc.cit.*: 99), and the genera *Bombycomorpha*, *Dasychirinula*, *Giselea*, *Haplopacha*, *Heteropacha* Harvey, 1874, *Phantosoma*, *Poecilocampa*, and *Trichiura* into Poecilocampini (*sensu* Zolotuhin) (*loc. cit.*: 109). The debatable systematic position of *Phantosoma* was discussed above. The genus *Heteropacha* is apparently included in Poecilocampinae erroneously, since the author in another part of his work correctly included *Heteropacha* in Lasiocampinae (in the tribe Gastropachini) (*loc. cit.*: 259). Obviously, the "*Heteropacha*" in Poecilocampini is a typo of the name of the North American genus *Hypopacha*, which Zolotuhin included in Poecilocampini based on the symplesiomorphic similarities in the male genitalia ("uncus developed, valvae of a generalized plan, wing pattern not modified": *loc. cit.*: 52). However, Zolotuhin does not take into account the specialisation of the eighth abdominal segment of the males of *Hypopacha*, an apomorpic character shared with other Macromphaliinae. He also omited the remark by Franclemont (1973: 31) on the similarity of the genitalia of this genus with the tropical American Macromphaliinae genera *Euglyphis*, *Nesara* Walker, 1855, and *Norapidia* Draudt, 1927, which Zolotuhin (*loc. cit.*: 142) preserved in this subfamily. Therefore, we cannot agree with the transfer *Hypopacha* in Poecilocampinae.

The system of Chondrosteginae and Poecilocampinae by Zolotuhin is built on a typological principle, as evidenced, for example, by his judgments about the taxonomic rank of Macromphaliinae and Chondrosteginae in terms of general similarity, generalized structure, and extreme specialisation (Zolotuhin 2015: 52–53) without indicating the probable synapomorphies. From a phylogenetic point of view, Chondrosteginae *sensu* Zolotuhin (2015) can potentially be recognized as a monophyletic group (with a reservation about the debatable position of *Trichiura*). However, Poecilocampini *sensu* Zolotuhin (2015), even in the remaining genera (without *Heteropacha* and *Phantosoma*), appear obviously paraphyletic in relation to Chondrosteginae. In fact, Poecilocampini *sensu* Zolotuhin is a taxon composed of morphologically less derived genera (stratum).

To avoid misunderstandings, it should be noted that the author incorrectly illustrated the genitalia of "*Macromphalia*" (Zolotuhin 2015, ill. 57b), which is actually a copy of the drawing of the genitalia of *Tolype velleda* (Stoll, 1791) from Franclemont (1973, fig. 7a). Also, Zolotuhin (2015: 47) stated, that "Franclemont proposed the following option for dividing the cocoon moths of the Nearctic fauna into subfamilies: Poecilocampinae, Macromphaliinae, Gastropachinae, Lasiocampinae (Lasiocampini and Malacosomatini) and Gonometinae

(Franclemont, 1973)” [in Russian]. However, Franclemont do not mentioned Poecilocampinae at all, and regarding the African subfamily Gonometinae, he noted only that “it may not prove to be a distinct subfamily from the Gastropachinae” (Franclemont 1973: 28).

Our analysis of the morphological characters of the genera associated with Chondrosteginae and Poecilocampinae, especially considering those of *Zolotuhia* gen. nov., shows their scattered distribution and the lack of possibility for a clear diagnostic of Chondrosteginae and Poecilocampinae as separate taxa, either phylogenetically or typologically. For this reason, we propose to consider all genera in one subfamily Chondrosteginae, as a senior name, without their association with tribes:

Chondrosteginae *sensu lato*
Chondrostegidae Tutt, 1902: 225.
= Poecilocampinae Tutt, 1902: 226, **syn. nov.**
= Trichiurinae Tutt, 1902: 226, **syn. nov.**
Haplopacha Aurivillius, 1905
Eudoumbia Tujuba *et al*., 2024
Auripluvia Tujuba *et al*., 2024
Dasychirinula Hering, 1926
Trichiura Stephens, 1828
Poecilocampa Stephens, 1828
Giselea Zolotuhin, 2007
Zolotuhia, **gen. nov.**
Bombycomorpha C. Felder & R. Felder, in C. & R. Felder & Rogenhofer, 1874.
Trichiurana Aurivillius, 1921
Mesocelis Hübner, 1820
Chondrostegoides Aurivillius, 1905
Chondrostega Lederer, 1858

The Chondrosteginae *s.l.* morphologically can be distinguished from other Lasiocampidae by a combination of the two characters: in the hind wing by a small humeral cell formed by Sc anastomosis with discal cell and bearing one or two long humeral veins reaching or almost reaching the costal margin of the wing, and in the abdomen by an unmodified eighth tergum and sternum of males. The former character is considered here as a probable synapomorphy of Chodrosteginae and Macromphaliinae, and the latter one—as a symplesiomorphy of Chondrosteginae with the other Lasiocampidae, except for Macromphaliinae. The structure of the humeral cell of Malacosiomini (Lasiocampinae) is similar to that of Macromphaliinae and Chondrosteginae *s.l.*, but the humeral veins are short and do not reach far to the costal margin of the wing.

Conclusion

A new enigmatic moth from the family Lasiocampidae was discovered in a poorly studied area of Central Asia, described here as *Zolotuhia paradoxa*, **genus & species nova**. In order to establish the relationships of the new genus, an attempt of morphological phylogenetic analysis of the genera in the subfamilies Chondrosteginae and Poecilocampinae was performed. This analysis revealed a scattered distribution of the characters across the genera and an impossibility of clear diagnosis of the subfamilies. As a consequence, a synonymy of subfamilies has been proposed: Chondrosteginae Tutt, 1902 (=Poecilocampinae Tutt, 1902, **syn. nov.**, =Trichiurinae Tutt, 1902, **syn. nov.**). The subfamily Chondrosteginae *s.l.* is proposed in the following generic composition: *Haplopacha* Aurivillius, 1905, *Eudoumbia* Tujuba *et al*., 2024, *Auripluvia* Tujuba *et al*., 2024, *Dasychirinula* Hering, 1926, *Trichiura* Stephens, 1828, *Poecilocampa* Stephens, 1828, *Giselea* Zolotuhin, 2007, *Zolotuhia* **gen. nov.**, *Bombycomorpha* C. Felder & R. Felder, 1874, *Trichiurana* Aurivillius, 1921, *Mesocelis* Hübner, 1820, *Chondrostegoides* Aurivillius, 1905, and *Chondrostega* Lederer, 1858. Of the genera were previously included in Poecilocampinae, the genus *Phantosoma* Zolotuhin et Kostjuk, 2000 we placed outside the subfamilies as one of the most basal taxa of Lasiocampidae, and the genus *Hypopacha* Neumoegen & Dyar, 1893 we retained the in the subfamily Macromphaliinae.

In the proposed generic composition, Chondrostegidae s.*l.* can actually be distinguished from Macromphaliinae by the plesiomorphic states of characters only. Furthermore, the morphological features of the African golden-spotted lappet moths (*Haplopacha*, *Dasychirinula*, *Eudoumbia* and *Auripluvia*) “build a bridge” between the Chondrostegidae *s.l.* and the American Macromphaliinae. Future research may reveal the advisability of uniting of Chondrosteginae and Macromphaliinae into one subfamily. In fact, Zolotuhin has already taken a step in this direction by proposing to downgrade the subfamily Macromphaliinae to the tribe Macromphaliini of the subfamily Poecilocampinae (Zolotuhin *et al.* 2012). However, at present, keeping the rank of Macromphaliinae as a subfamily seems more pragmatic.

In the phylogenetic study of Lasiocampidae, special attention should be paid to the South American genus *Sphinta*. Franclemont (1973) did not associate it with any subfamily, but tended to place in a subfamily by itself. The genus *Sphinta* has forewing venation characteristic for Macromphaliinae (but not unique to this subfamily), but the hindwings with the distinctly stalked Sc+R1 and Rs (as in many Lasiocampinae), and it has the more generalized male genitalia than those of *Poecilocampa* and *Zolotuhia* gen. nov. The genus *Sphinta* might be one of the key taxa to clarify the basal phylogeny in the family Lasiocampidae.

In the course of the work, the need for nomenclature formalization of the new combination became clear: *Trichiurana nobilorum* (Zolotuhin, 2007), **comb. n**ov., for *Chondrostegoides nobilorum* Zolotuhin, 2007. Also, a new name “dorso-basal saccular lobe” is proposed for the dorsal dilation of the valve sacculus located lateral to juxta, early inappropriately named as “valve saccular lobe” (Dupont *et al.* 2016). Possible origin of the vein connected common branch Sc+Rs with the stalk M on the hind wing in Lasiocampidae is hypothesised as a result of merging of R1 with the base of Rs in the common ancestor of the family.

Acknowledgments

The authors are deeply thankful to Mrs. Valentina O. Zurilina (Chelyabinsk, Russia) for her invaluable help during the field trip of 2022. Also, we express our sincere gratitude to Mr. Anton Skrobotov (Moscow, Russia) for his help in the search of some literature sources, as well as to Mr. Georgy Lazkov (Bishkek, Kyrgyzstan) and Mr. Vladimir Kolbintsev (Taraz, Kazakhstan) for identification of the plants from the biotopes where the moths of *Zolotuhia paradoxa* were collected, and to Mr. R. Haverinen (Vantaa, Finland) who supplied us with the UV-traps of different types. We also thank Dr. Alexey Matov (ZISP, Sankt-Petersburg, Russia) for valuable advice, as well as for the help in identification of the species from the family Noctuidae collected together with the considered lappet moth, and for the assistance during the work with the Lasiocampidae collection in ZISP.

The research was carried out within the state assignment of Ministry of Science and Higher Education of the Russian Federation (theme No. 124012400285-7).

References

Aurivillius, C. (1894) Die palaearktischen Gattungen der Lasiocampiden, Striphnopterygiden und Megalopygiden. *Deutsche entomolgische Zeitschrift*, *Lepidopterologisches Heft*, 7, 121–192.

Aurivillius, C. (1905) New African Lasiocampidae in the British Museum. *Transactions of the entomological Society of London*, 1905 (3), 313–326.

Aurivillius, C. (1909) Diagnosen neuer Lepidopteren aus Afrika. *Arkiv für Zoologie*, 5, 1–29.

Aurivillius, C. (1921) Descriptions of some South African Heterocera (Lepidoptera). *Annals of the South African Museum*, 18 (2), 235–244.
https://doi.org/10.5962/bhl.part.8025

Aurivillius, C. (1927–1930) Family: Lasiocampidae. *In*: Seitz, A. (Ed.), *The Macrolepidoptera of the World. The African Bombyces and Sphinges*. *Vol 14.* Alfred Kernen, Stuttgart, pp. 205–281 [1927], pls. 29–40 [1930].

Bang-Haas, O. (1927) *Horae Macrolepidopterologiae regionis palaearcticae*. *Vol. 1*. Kuppky und Dietze, Dresden, 128 pp.

Beljaev, E.A., Krivokhatskii, V.A. & Falkovich, M.I. (2014) Ecological and morphological adaptations of the winter moths *Cheimoptena pennigera* Danilevsky and *Desertobia nocturna* Viidalepp (Lepidoptera, Geometridae) to the environment of subboreal sandy desert. *Euroasian Entomological Journal*, 13 (6), 545–559.

BOLD (2023a) *Trichiurana meridionalis*. BOLD:AAJ8703. *In*: *Barcode of Life Data System*. Available from: http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:AAJ8703 (accessed 21 October 2023)

BOLD (2023b) *Trichiurana nobilorum*. BOLD:ABV4395. *In*: *Barcode of Life Data System*. Available from: http://www.boldsystems.org/index.php/Public_BarcodeCluster?clusteruri=BOLD:ABV4395 (accessed 21 October 2023)

BOLD (2023c) *Sphinta cossoides*. BOLD:ADF9994. *In*: *Barcode of Life Data System*. Available from: http://v3.boldsystems.

org/index.php/Public_RecordView?processid=LNAUV1789-17 (accessed 21 October 2023)

BOLD (2024) Subfamily: Poecilocampinae. *In*: *Barcode of Life Data System*. Available from: https://www.boldsystems.org/index.php/TaxBrowser_Taxonpage?taxid=86650 (accessed 22 April 2024)

BugGuide.Net (2024) Poecilocampinae. *In*: *Identification, Images, & Information for Insects, Spiders & Their Kin for the United States & Canada*. Iowa State University Department of Plant Pathology, Entomology and Microbiology, 2003-2024, Iowa. Available from: https://bugguide.net/node/view/34351/bgpage (accessed 21 October 2023)

Butler, A. (1880) On a collection of Lepidoptera from Madagascar, with descriptions of new genera and species. *The Annals and magazine of natural history; zoology, botany, and geology,* Series 5, (28), 333–344, (29), 384–395. https://doi.org/10.1080/00222938009459430

Cahurel, A. (2022) Cahurel-entomologie. Available from: https://cahurel-entomologie.com/gs/cahurel-entomologie.com (accessed 21 October, 2023)

Chistyakov, Yu.A. & Zolotuhin, V. V. (1994) Lasiocampids of the genus *Poecilocampa* Stephens, 1828 (Lepidoptera, Lasiocampidae) of Russia and neighbouring territories. *Entomologicheskoe Obozrenie*, 73 (2), 321–330. [in Russian]

Christoph, H. (1884) Lepidoptera aus dem Achal-Tekke-Gebiete. *Mémoires sur les Lépidoptères*, 1, 93–138.

Cornell University Insect Collection (2023) Available from: https://cuic.entomology.cornell.edu/ (accessed 21 October 2023)

Costa Lima, A.D. (1950) *Insectos do Brasil. 6 Tomo. Lepidopteros. 2e Parte.* Escola nacional de Agronomia, Rio de Janeiro, 420 pp.

De Prins, J. & De Prins, W. (2011–2021) *Chondrostegoides nobilorum* Zolotuhin, 2007. *In*: *Afromoths, online database of Afrotropical moth species (Lepidoptera)*. Available from: https://www.afromoths.net/species_by_code/CHONNOBI (accessed 15 November 2023)

Distant, W.L. (1897) On a collection of Heterocera made in the Transvaal. *The annales and magazine of natural history*, Series 6, 20 (116), 197–213. https://doi.org/10.1080/00222939708680612

Draudt, M. (1927–1928) Familie: Lasiocampidae. *In*: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde. 6. Die amerikanischen Spinner und Schwärmer*. A. Kernen, Stuttgart, pp. 565–624 [1927] + 625–628, pls. 75–86 [1928].

Draudt, M. (1934–1938). Phalaenae, die eulenartigen Nachtfalter. *In*: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde. Eine Systematische Bearbeitung der bis jetzt bekannte Gross-Schmetterlinge. Die Palaearktischen Eulenartigen Nachtfalter. 3 (Supplement).* Alfred Kernen Verlag, Stuttgart, pp. 1–22 + 96–332, pls. 1–26.

Dubatolov, V.V. & Zolotuhin, V.V. (1992) A list of the Lasiocampidae from the territory of the former USSR (Insecta, Lepidoptera). *Atalanta*, 23 (3/4), 531–548.

Dupont, S., Simonsen, T.J. & Zilli, A. (2016) *Haplopacha* (Lepidoptera: Lasiocampidae) reviewed: four new species, first descriptions of the genitalia of both sexes, and unique alar scale organs. *Zootaxa,* 4109 (4), 445–457. https://doi.org/10.11646/zootaxa.4109.4.3

Dyar, H.G. (1895) Notes on some southern Lepidoptera. *Canadian Entomologist*, 27, 242–247. https://doi.org/10.4039/ent27242-9

Ershov, N.G. (1874) Cheshuekrylyia (Lepidoptera). *In*: Fedtchenko, A.P. (Ed.), *Puteshestvie v Turkestan. Iss. II, vol. 2. Zoogeograficheskiye issledovaniya. Pt. 5, sect. 3. Izvestiia Imperatorskago obshchestva liubitelei estestvoznaniia, antropologii i etnografii, t. 11, iss. 2.* Devrien, St.-Petersburg & Moscow, pp. I–VI, 1–128, pl. 1–6. [in Russian] https://doi.org/10.5962/bhl.title.66063

Feisthamel, J.F. (1839) Supplement a la zoologie du voyage de la Favorite comprenant la description de Lepidopteres nouveaux. *Magazin Zoologique*, 9, 17–26.

Felder, C., Felder, R. & Rogenhofer, A.F. (1865–1875) *Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zoologischer Theil. Bd. 2. Abt. 2. Atlas.* Kaiserlich-Königliche Hof- und Staatsdruckerei, Wien, 548 pp., 140 pls.

Ferge, L.A., Balogh, G.J. & Johnson, K.E. (2018) Checklist of Wisconsin moths (superfamilies Mimallonoidea, Drepanoidea, Lasiocampoidea, Bombycoidea, Geometroidea, and Noctuoidea). *Wisconsin Entomological Society Special Publication*, 6, 1–45.

Forbes, W.T.M. (1942) The Lepidoptera of Barro Colorado Island, Panama. No. 2. *Bulletin of the Museum of Comparative Zoology at Harvard College,* 90, 265–406.

Franclemont, J.G. (1973) Mimallonoidea and Bombycoidea, Fascicle 20.1. *In*: Hodges, R.W. (Ed.), *Check List of the Lepidoptera of America North of Mexico including Greenland*. E.W. Classey, London, pp. 25–86.

Freina, J.J. de, León, Y.M., Antonietty, C.A. & Vila, R. (2015) Notes on the biology, distribution and taxonomy of *Chondrostega* Lederer, 1857 in the Iberian Peninsula with a description of the southern Spanish *Chondrostega escobesae* sp. nov. (Lepidoptera: Lasiocampidae). *Entomologische Zeitschrift mit Insekten-Börse*, 125 (4), 195–207.

French, G.H. (1890) Some new Colorado moths. Canadian Entomologist, 22 (3), 44–47. https://doi.org/10.4039/ent2244-3

Frey, H. & Wullschlegel, J. (1874) Die Sphingiden und Bombyciden der Schweiz. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 4 (5), 201–278.

Germar, E.F. (1810–1812) *Dissertatio sistens Bombycum species secundum oris partum diversitatem in nova genera distributes. Vol. 1 & 2.* In Officina Schimmelpfennigiana, Halis, 28 pp. & 51 pp. [1810 & 1812] https://doi.org/10.5962/bhl.title.65384

Graeser, L. (1892) Neue Lepidopteren aus Central-Asien. *Berliner entomologische Zeitschrift*, 37, 313–315. https://doi.org/10.1002/mmnd.18920370304

Grünberg, K. (1911–1912) [Lasiocampidae]. *In*: Seitz, A. (Ed.), *Macrolepidoptera of the World. Vol. 2. The Palaearctic Bombyces & Sphinges*. Verlag des Seitz'schen Werkes (Alfred Kernen), Stuttgart, pp. 148–180 [1911], pls. 24–29. [1912]

Guenée, A.M. (1852) Noctuélites 2. *In*: Boisduval, C. & Guenée, A.M. (Eds.). *Histoire naturelle des insectes. Species général des lépidoptères*. *Tome II. Vol. 6.* Roret, Paris, pp. 1–444.

Harvey, L. (1874) New Phalaenoid moths. *Bulletin of the Buffalo Society of Natural Sciences*, 1, 262–265.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana, 263 pp.

Hering, E.M. (1926–1930) Lymantriidae. *In*: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde. Eine Systematische Bearbeitung der bis jetzt bekannte Gross-Schmetterlinge. Die Afrikanischen Spinner und Schwärmer*. *Vol. 14.* Alfred Kernen Verlag, Stuttgart, pp. 129–204 [1926–1927], pls. 20–28. [1930]

Hübner, J. (1816–1826). *Verzeichniß bekannter Schmettlinge.* J. Hübner, Augsburg, 431 pp. https://doi.org/10.5962/bhl.title.48607

Joannou, J.G. & Gurkovich, A.V. (2009) A review of the genus *Bombycomorpha* C. Felder & R. Felder, 1874 with descriptions of a new species and a new subspecies (Lepidoptera, Lasiocampidae). *Neue Entomologische Nachrichten*, 63, 103–117.

Kitching, I., Rougerie, R., Zwick, A., Hamilton, C., St Laurent, R., Naumann, S., Ballesteros Mejia, L. & Kawahara, A. (2018) A global checklist of the Bombycoidea (Insecta: Lepidoptera). *Biodiversity Data Journal*, 6, e22236. https://doi.org/10.3897/BDJ.6.e22236

Klots, A.B. (1970) Lepidoptera. *In*: Tuxen, S.L. (Ed.), *Taxonomist's Glossary of genitalia in Insects*. *2nd Edition*. Munksgaard, Copenhagen, pp. 115–130. https://doi.org/10.1163/9789004631663

Kristensen, N.P. (2003) Skeleton and muscles: adults. *In*: Kristensen, N.P. (Ed.), *Lepidoptera: Moths and Butterflies 2. Morphology, Physiology, and Development. Handbuch der Zoologie/Handbook of Zoology IV/36.* Walter de Gruyter, Berlin & New York, pp. 39–131. https://doi.org/10.1515/9783110893724.39

Kuznetsov, V.I. & Stekolnikov, A.A. (2001) *New approaches to the system of Lepidoptera of the world fauna (based on the functional morphology of abdomen)*. Nauka, St.-Petersburg, 462 pp. [in Russian]

Lederer, J. (1858) Noch einige syrische Schmetterlinge. *Wiener entomologische Monatsschrift,* 2 (5), 135–152. https://doi.org/10.1002/mmnd.47918580209

Lemair, C. & Minet, J. (1998) The Bombycoidea and their relatives. *In*: Fischer, M. (Ed.), *Handbook of Zoology 4. Arthropoda Insecta*. *Vol. 4.* Walter de Gruyter, Berlin & New York, pp. 353. https://doi.org/10.1515/9783110804744.321

Lepiforum e.V. (2024) Subfamilia Poecilocampinae Tutt, 1902. *In*: *Lepiforum e. V. Identification of butterflies and their preimaginal stages*. Available from: https://lepiforum.org/wiki/taxonomy/Lasiocampoidea/Lasiocampidae/Poecilocampinae/Macromphaliini?view=1&sort=a&regions (accessed 21 October 2023)

Linnaeus, C. (1758) *Systema Naturae per Regna Tria Naturae, Secundum Clases, Ordines, Genera, Species, cum Characteribus, Differentiis, Symonymis, Locis. Tomis I. Edition 10*. Laurentii Salvii, Holmiae, 824 pp. https://doi.org/10.5962/bhl.title.542

Lotts, K. & Naberhaus, Th. (coordinators). (2024) Family Lasiocampidae (Lasiocampid Moths). *In*: *Butterflies and Moths of North America*. Available from: https://www.butterfliesandmoths.org/taxonomy/Lasiocampidae (accessed 21 October 2023)

Ljung, S.I. (1826) Nya Insecter, utur egen samling, beskrifne. *Kongl Vetenskaps-Academiens Handlingar*, Norstedt & Söner, Stockholm, 344–349.

Mabille, P. (1879) Lepidoptera africana. *Bulletin et des Mémoires de la Societe Zoologique de France*, 3, 81–95.

Marcelo B. (2022) Ciclo de Mariposa Sphinta em Minas Gerais. *In*: Crash, C. (Ed.), *Insetologia - Identificação de Insetos*. Available from: https://www.insetologia.com.br/2022/10/ciclo-de-mariposa-sphinta-em-minas.html (accessed 21 October 2023)

Marquis, R.J., Passoa, S.C., Lill, J.T., Whitfield, J.B., Le Corff, J., Forkner, Re.E. & Passoa, V A. (2019). *Illustrated guide to the immature Lepidoptera on oaks in Missouri*. *FHAAST-2018-05.* U.S. Department of Agriculture, Forest Service, Forest Health Assessment and Applied Sciences Team, Morgantown, 369 pp.

Ménétriès, E. (1849) Catalogue des insectes recueillis par feu M. Lehmann avec les descriptions des nouvelles espèces. (Seconde et dernière partie.). *Mémoires de l'Académie impériale des sciences de Saint-Pétersbourg*, 6, 217–308.

Millière, P. (1865) *Iconographie et description de chenilles et lépidoptères inédits. Tome 2 ("1846").* E. Deyrolle fils, Paris, 506 pp. https://doi.org/10.3406/linly.1866.3944

Minet, J. (1991) Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Entomologica Scandinavica*, 22, 69–95. https://doi.org/10.1163/187631291x00327

Minet, J. (1994) The Bombycoidea: phylogeny and higher classification (Lepidoptera: Glossata). *Entomologica Scandinavica*, 25, 1–558. https://doi.org/10.1163/187631294x00045

Monasterio Y., de Freina, J.J., Escobés R. Hinojosa, J. C., Corbella, C., Farino, T., Huemer, P. & Vila, R. (2021) Reassessment of *Poecilocampa navalagamellae* Expósito, 2004 stat. nov. and its distribution in the Iberian Peninsula (Lepidoptera: Lasiocampidae, Poecilocampinae). *Entomologische Zeitschrift*, 131 (4), 223–238.

Montero-Ramírez, J.J., Janzen, D.H. & Hallwachs, W. (2011) A distinctive new species of *Euglyphis* Hübner (Lepidoptera: Lasiocampidae) from Costa Rica, with a checklist of the *Euglyphis* known from Costa Rica. *Zootaxa*, 3020 (1), 49–59. https://doi.org/10.11646/zootaxa.3020.1.2

Neumoegen B. (1882) Some new beauties from various parts of Arizona. *Papilio*, 1, 133–135.

Oberthür, Ch. (1916) Faune des Lepidopteres de Barbarie (Partie II). *Etudes de Lepidopterologie comparee*, 12, 179–371.

Oberthür, Ch. (1880) Faune des Lépidoptères de l'Île Askold. *Etudes d'Entomologie*, 5, 11–88.

Piovesan, M., Santos, F., Orlandin, E., Specht, A., Mielke, O. & Casagrande, M. (2023) Natural history and morphology of immature stages of *Tolype medialis* (Jones, 1912) (Lepidoptera: Lasiocampidae: Macromphaliinae). *Neotropical entomology*, 52 (5), 15. https://doi.org/10.1007/s13744-023-01059-9

Pohl, G.R., Patterson, B. & Pelham, J.P. (2016) *Annotated taxonomic checklist of the Lepidoptera of North America, North of Mexico*. Working paper published online by the authors at ResearchGate.net, 766 pp. https://doi.org/10.13140/RG.2.1.2186.3287

Powell, H. (1916) *Chondrostega Tingitana*, Powell. *In*: Oberthür, Ch. (Ed.), Faune des Lépidoptères de Barbarie (Partie II). *Etudes de Lepidopterologie comparee*, 12, pp. 298. https://doi.org/10.5962/bhl.title.8792

Prozorov, A.M. (2016) A review of the genus *Eucraera* Tams, 1930 (Lepidoptera: Lasiocampidae). *Entomofauna. Zeitschrift für Entomologie*, 37 (1), 1–32.

Rambur, P. (1858) *Catalogue systématique des lépidoptères de l'Andalousie*. Ballière, Paris, 412 pp. https://doi.org/10.5962/t.173069

Regier, J.C., Christopher, P., Mitter, C. & Hussey, A. (2008) A phylogenetic study of the "bombycoid complex" (Lepidoptera) using five protein-coding nuclear genes, with comments on the problem of macrolepidopteran phylogeny. *Systematic Entomology*, 33, 175–189. https://doi.org/10.1111/j.1365-3113.2007.00409.x

Regier, J.C., Mitter, C., Peigler, R.S. & Friedlander, T.P. (2000) Phylogenetic relationships in Lasiocampidae (Lepidoptera): Initial evidence from elongation factor-1α sequences. *Insect Systematics and Evolution*, 31, 179–186. https://doi.org/10.1163/187631200x00372

Regier, J.C., Mitter, C., Zwick, A., Bazinet, A.L., Cummings, M.P., Kawahara, A.Y., Sohn, J.-C., Zwickl, D.J., Cho, S., Davis, D.R., Baixeras, J.L., Brown, J., Parr, C., Weller, S., Lees, D.C. & Mitter, K.T. (2013) A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). *PLoS ONE*, 8, e58568. https://doi.org/10.1371/journal.pone.0058568

Rodriguez, M.A. & Angulo, A.O. (2007) *Macromphalia ancilla*: estados imaduros, morfologia y biologia en Chile (Lepidoptera: Lasiocampidae). *Tropical Lepidoptera,* 17 (1–2), 27–33.

Ronkay, L. & Varga, Z. (1990) Taxonomic and zoogeographical studies on the subfamily Cuculliinae (Lepidoptera, Noctuidae). Part II. *Esperiana*, 1, 471–497.

Ronkay, L. & Varga, Z. (1993) Taxonomic studies of the genera *Pseudohadena* Alphéraky, 1889 and *Auchmis* Hübner, [1821] (Lepidoptera, Noctuidae), Part IV. *Acta Zoologica Academiae Scientiarum Hungaricae*, 39 (1–2), 211–252.

Saldaitis, A. & Pekarsky, O. (2015) A new species, *Poecilocampa deqina* (Lepidoptera: Lasiocampidae), from China. *Zootaxa*, 3925 (4), 597–599. https://doi.org/10.11646/zootaxa.3925.4.9

Schaus, W. (1904) New species of American Heterocera. *Transactions of the American Entomological Society*, 30, 135–178.

Schaus, W. (1924) New species of moths in the United States National Museum. *Proceedings of the U.S. Natural History Museum*, 65, 1–74. https://doi.org/10.5479/si.00963801.2520

Schrank, F. (1802) *Fauna Boica. Durchgedachte Geschichte der in Baiern einheimischen und zahmen Thiere*. *Vol. 2.* Stein'schen Buchhandlung, Nürnberg, 412 pp.

Seven, E. & Akýn, K. (2019) Contributions list to the knowledge of Macro-Heterocera (Lepidoptera) fauna of Mutki District (Bitlis Province). *Sakarya University Journal of Science,* 23 (3), 435–445. https://doi.org/10.16984/saufenbilder.402727

Staudinger, O. (1871) *Catalog der Lepidopteren des europaeischen Faunegebiets (Edn. 2)*. Staudinger & Burdach, Dresden, 421 pp. https://doi.org/10.5962/bhl.title.9475

Staudinger, O. (1877) Neue Lepidopteren des europäischen Faunengebiets aus meiner Sammlung. *Entomologische Zeitung Stettin*, 38, 175–208.

Staudinger, O. (1888) Centralasiatische Lepidopteren. *Entomologische Zeitung Stettin*, 49, 1–65.

Staudinger, O. (1892) Neue Arten und Varietäten von Lepidopteren des paläarktischen Faunengebiets. *Deutsche entomologische Zeitschrift Iris,* 4 (2), 224–339.

Stekolnikov, A.A. & Zolotuhin, V.V. (1994) Phylogenetic position of the subfamilies of the Palearctic Lasiocampidae

(Lepidoptera) based on skeleton and muscles of male genitalia. *Vestnik Sankt-Peterburgskogo universiteta*, 3 (1) (3), 26–32. [in Russian]

Stephens, J.F. (1828) *Illustrations of British entomology; or, a synopsis of indigenous Insects, containing their generic and specific distinctions, with an account of their metamorphoses, times of appearance, localities, food and economy. Haustellata. Vol. 2 ("1892").* Baldwin and Cradock, London, 203 pp. https://doi.org/10.5962/bhl.title.8133

Stoll, S. (1791) *Aanhangsel van het werk, De uitlandsche kapellen: voorkomende in de drie waereld-deelen Asia, Africa en America. Supplement.* Barthelmy Wild, Amsterdam, 384 pp., 42 pls. https://doi.org/10.5962/bhl.title.65748

Swedish Museum (2005) *Chondrostega ruficornis* Aurivillius, 1921. Swedish Museum of Natural History. A checklist of the Lepidoptera in the Swedish Museum of Natural History Latest update: 29 September 2005. Available from: http://www2.nrm.se/en/lep_nrm/r/chondrostega_ruficornis.html (accessed 21 October 2023)

Tams, W.H.T. (1930) New Rhodesian Lepidoptera Heterocera. *Annals and Magazine of Natural History*, (10) 6 (32), 161–176. https://doi.org/10.1080/00222933.1930.11070793

Tujuba, T.F., Yakovlev, R.V., Saldaitis, A., Sulak, H., Aarvik, L., Murphy, R.J., Volkova, J.S., Traore, M.M., Revay, E.E., Müller, G.C., Prozorova, T.A. & Prozorov, A.M. (2024) Review of the African golden-spotted genera Haplopacha and Dasychirinula (Lepidoptera, Lasiocampidae, Poecilocampinae). *Acta Biologica Sibirica*, 10, 693–730. https://doi.org/10.5281/zenodo.12787215

Tutt, J.W. (1902) *A natural history of the British Lepidoptera: a text-book for students and collectors. Vol. 3*. S. Sonnenschein, London, 581 pp.

Ureta, E. (1957) Revisión de la familia Lasiocampidae en Chile. *Revista chilena de entomología*, 5, 123–142.

Varga, Z., Ronkay, G., Ronkay, L. & Giulay, P. (2015) *The Witt Catalogue. A taxonomic atlas of the Eurasian and North African Noctuoidea. Noctuinae II.* Heterocera Press, Budapest, 362 pp.

Walker, F. (1855) Part V.—Lepidoptera Heterocera. *In*: Walker, F. (Ed.), *List of the Specimens of Lepidopterous Insects in the Collection of the British Museum.* Printed by order of the Trustees, London, pp. 977–1257. https://doi.org/10.5962/bhl.title.58221

Wootton, R.J. (1979) Function, homology and terminology in insect wings. *Systematic Entomology*, 4 (1), 81–93. https://doi.org/10.1111/j.1365-3113.1979.tb00614.x

Ziegler, H. (2007–2022) Wildlife / Butterflies & Moths of Costa Rica. Available from: https://www.tropicleps.ch (accessed 21 October, 2023)

Zolotuhin, V.V. (2007a) An annotated distributional check-list of the genus *Trichiura* Stephens, 1828 with description of six new taxa, especially from Asia Minor (Lepidoptera: Lasiocampidae). *Nachrichten des entomologischen Vereins Apollo*, Suppl. 19, 37–48.

Zolotuhin, V.V. (2007b) Lasiocampidae (Lepidoptera: Lasiocampoidea). *In*: Mey, W. (Ed.), The Lepidoptera of the Brandberg Massif in Namibia. Part 2. *Esperiana Memoir,* 4, pp. 205–214.

Zolotuhin, V.V. (2010) A review of the genus *Chionopsyche* Aurivillius, 1909 with the description of a new species (Lepidoptera, Lasiocampidae: Chionopsychinae). *Atalanta*, 41 (3/4), 361–366.

Zolotuhin, V.V. (2015) *Lappet Moths (Lepidoptera: Lasiocampidae) of Russia and Adjacent Territories*. Ulyanovsk, Korporaciya Technologiy Prodvizheniya, 384 pp. [in Russian]

Zolotuhin, V.V., Efimov, R.V., Anikin, V.V., Demin, A.G. & Knushevitskaya, M.V. (2012) Changes in the suprageneric classification of Lasiocampidae (Lepidoptera) based on the nucleotide sequence of gene EF-1α. *Entomological Review,* 92 (5), 531–547. https://doi.org/10.1134/S0013873812050065

Zolotuhin, V.V. & Kostjuk, I.Yu. (2000) *Phantosoma witti* gen. et sp. nov., a new autumn lasiocampid moth from Turkmenistan (Lasiocampidae). *Nota lepidopterologica*, 23 (2), 141–146.

Zwick, A. (2008) Molecular phylogeny of Anthelidae and other bombycoid taxa (Lepidoptera: Bombycoidea). *Systematic Entomology*, 33, 190–209. https://doi.org/10.1111/j.1365-3113.2007.00410.x

Zwick, A. (2009) The principal structure of male genital sclerites and muscles of bombycoid moths, with special reference to Anthelidae (Lepidoptera: Bombycoidea). *Arthropod Structure & Development,* 38, 147–161. https://doi.org/10.1016/j.asd.2008.07.006

Zwick, A., Regier, J.C., Mitter, C. & Cummings, M.P. (2011) Increased gene sampling yields robust support for higher-level clades within Bombycoidea (Lepidoptera). *Systematic Entomology*, 36, 31–43. https://doi.org/10.1111/j.1365-3113.2010.00543.x