

Article



https://doi.org/10.11646/zootaxa.5004.3.4 http://zoobank.org/urn:lsid:zoobank.org:pub:165EF9FB-D5CB-4C31-B439-9AA58D1B65EF

New genus of gelechiid moths (Lepidoptera: Gelechiidae) from Borneo, and its four new species

MARGARITA G. PONOMARENKO^{1,2}*, MICHAIL M. OMELKO^{1,3} & NATALIA V. OMELKO^{1,4}

¹Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 690022, Russia

- ² margp@biosoil.ru; https://orcid.org/0000-0003-4566-6837
- ³ nomelko@mail.ru; b https://orcid.org/0000-0003-0782-5411
- *Corresponding author. | margp@biosoil.ru

Abstract

Tawaya gen. n. and its four new species (*T. flaventia* sp. n., *T. rutila* sp. n., *T. luteola* sp. n. and *T. armeniaca* sp. n.) are described from Borneo. A key to the described species is provided. The taxonomic position of a new genus within the subfamily Dichomeridinae (Gelechiidae) is proposed based on a combination of molecular and morphological analyses.

Key words: *Tawaya*, Dichomeridinae, new genus, new species, Malaysia, taxonomy

Introduction

It has long been accepted that the tropical regions of the planet are arenas of intense endogenous evolution due to increased biotic competition, on one hand, and the weakening of pressure from abiotic factors due to the evenness of climate, on the other. These regions play a significant role in macrophylogenesis and the speciation processes, forming the basis for the hypothesis of the "equatorial pump" (Darlington 1957), which was subsequently developed and explored in detail on the basis of paleobotanical material in the Phytospreading concept (Meyen 1987). High rates of morphogenesis under the most favorable conditions of a warm and humid climate allow taxa to maintain specializations resulting from deep morphological transformations, which would most likely be eliminated by natural selection in higher latitudes with pronounced seasonality. The study of such specialized groups is always complicated by the problem of establishing relationships of new taxa and determine their taxonomic position in the system. These complications were also faced by the authors of this work.

This work is based entirely on material collected on Borneo, an island in southeast Asia's Malay Archipelago. Four new species were identified, all of which possess unique specializations in the genitalia allowing them to be assigned to a new genus. To establish relationships and the position of the new genus in the family system of Gelechiidae, an integrative approach was used, combining molecular and comparative morphological analyses. The extraction of genome DNA and morphological study of the specimens were performed by authors in the Federal Scientific Center of the East Asia Terrestrial Biodiversity (FSC of Biodiversity), Far Eastern Branch of Russian Academy of Sciences (Vladivostok). The polymerase chain reaction (PCR) of target fragments in samples and sequencing of amplicons were carried out by first author at the Laboratory of Ecology and Evolutionary Biology of the Aquatic Organisms at the Far Eastern Federal University (FEFU, Vladivostok). In the descriptions of the new taxa, terminology follows Klots (1970) with modifications after Ponomarenko (2005). The holotypes and paratypes of new species and vouchers of samples processed for molecular study are deposited in the Federal Scientific Center of the East Asia Terrestrial Biodiversity (FSC of Biodiversity), Far Eastern Branch of Russian Academy of Sciences (Vladivostok).

Material and methods

Material. Field work on the gelechiid biodiversity in Borneo, Malaysia was conducted by the second author. The specimens of the new species were collected in the state of Sabah. In 2018 moths were collected in the vicinity of Keningau at an altitude of 950 m a.s.l. In 2019 field work was conducted near Tawau in lowland dipterocarp forest. Gelechiid moth specimens for comparative molecular analysis were sampled in the southern Russian Far East, mainly in Primorskiy Kray, with several species collected in Sakhalin Is., Amurskaya Oblast', and the Jewish Autonomous Region. One specimen was sampled from the Republic of Khakassia and Ukraine. Moths were collected by net diurnally and attracted to light at night. The specimens for genetic research mainly were preserved in 96% ethanol, but DNA was also extracted from dry samples. Additional specimens were processed as dry material for morphological study. Specimens used in the DNA analyses are listed in Table 1, along with their collecting locality and the number of vouchers deposited FSC of Biodiversity.

In total, 40 species representing 26 genera and 3 subfamilies of Gelechiidae were included in phylogenetic analysis. The subfamily Anacampsinae is not represented because recently collected material was unavailable to us. A representative of the family Blastobasidae was included as an out-group. The molecular analysis was based on 84 sequences of two nuclear fragments, 28SD1 and 28SD2.

Morphological study. Male and female genitalia were prepared by standard lepidopterological techniques (e.g., Falkovitsh & Stekolnikov 1978) and included maceration of the soft tissue in 10–15% KOH. The membranous parts of the genitalia were stained using chlorazol black. Structures of the genitalia were studied using a Nikon SMZ-10 stereomicroscope. Following their examination, the genitalia of both sexes were slide-mounted using Euparal following the technique described by Robinson (1976). Genitalia slides are identified by the acronym MP (M.G. Ponomarenko), who prepared the slides. Images of adults were captured with a Nikon D300 camera equipped with a 50 mm macro lens; images of wing venation and genitalia were captured using an Olympus SZX16 microscope with a DP74 Nikon digital camera. Descriptions of the new species are accompanied by line drawings of male genitalia.

Molecular study. Genomic DNA from abdominal muscles was extracted following the protocol recommended in the Purification of Genomic DNA from insects appended to Qiagen DNeasy Blood & Tissue Kit (Qiagen GmbH, Hilden, Germany), with the following modifications. Since genitalia in micromoths have diagnostic significance, the abdomen of every sample was not grinded for lysis to save copulative apparatus for further slide-mounting with Euparal as voucher. One individual of each species was sampled for genomic DNA. The two nuclear fragments of 28S ribosomal RNA protein-coding gene were selected for molecular analysis—expansion segment D1 and expansion segment D2. Both fragments have been tested and shown to be valuable to be included into the molecular analysis of insects (Hymenoptera, Diptera, Lepidoptera) (e.g., Hancock *et al.* 1988; Schmitz & Moritz 1994; Abraham *et al.* 2001; Gillespie *et al.* 2006; Shirk *et al.* 2015). Of the two, fragment D1 is more conservative, whereas expansion segment D2 is more informative across family, genus, and species levels within orders and families of arthropods (Gillespie *et al.* 2006).

PCR-sequencing of the target fragments was made by the Sanger method. In PCR, the primer combinations 5'-GGGGAGAAAAGAAACTAAC-3' and 5'-CAACTTTCCCTTACGGTACT-3' were used for 28SD1, following Larsen (1992; cf. Abraham *et al.* 2001), and primer combinations 5'-AGAGAGAGTTCAAGAGTACGTG-3' and 5'-TTGGTCCGTGTTTCAAGACGGG-3 for 28SD2, following Belshaw & Quicke (1997). Each PCR amplification was performed in a total volume of 20 μl of PCR mixture consisting of 10 μl GoTaq® Green Master Mix, 1 μl 2.5 μΜ/μl of each forward and reverse primers, 0.5 μl 25 mM MgCl₂, 6.5 μl deionized water, and 1 μl of DNA for each sample. The temperature of annealing was 50°C. PCR products were cleaned using a Thermo Scientific FastAP Thermosensitive Alkaline Phosphatase (Thermo Fisher Scientific, USA), and then amplified using the protocol of BigDye Terminator v.3.1 Cycle Sequencing Kit. The cleaning of DNA sequencing reactions was made using a high-throughput purification method with a magnetic bead-based D-PureTM DyeTerminator Cleanup kit. PCR fragments were sequenced in Genetic Analyser 3130xl, (Applied Biosystems, USA). The visualization of sequences and exportation for editing and alignment were completed with Program Sequence Scanner v 1.0 (Applied Biosystems 2005). The amplified sequences of 28SD1 (313-337 bp) and 28SD2 (477-486 bp) were aligned and analyzed with the software packages FinchTV 1.4.0. (Patterson *et al.* 2004) and MEGA-7 (Kumar *et al.* 2016).

Molecular analysis. The molecular character tree with inferred relationships between gelechiid taxa including representatives of the new genus was constructed based on the two nuclear fragments 28SD1 and 28SD2 using the Maximum Likelihood statistical method, Kimura 2-parameter model with using software packages MEGA-7. The

.....continued on the next page

TABLE . List of taxa from the family Gelechiidae sampled for molecular study.
The geographic names having established English variants are indicated according to the latter. The other names transliterated directly from names used in the geographic maps.
The acronyms are used in the Table. Regions: Primorskiy Kray—PK, Jewish Autonomous Region—JAR, Amurskaya Oblast'—AO, Republic of Khakassia—RK; collectors:
M.M. Omelko

$T_{\mathcal{L}}$ $T_{\mathcal{L}}$ abfamily $A_{\mathbb{L}}$			
π ubfamily A	Tawaya flaventia sp. n .	E Malaysia, state of Sabah, 9 km NNW Keningau, 15.03.2018 (MO)	V-MP-621
ıbfamily A	Tawaya armeniaca sp. n.	E Malaysia, state of Sabah, 24 km N Tawau, 19.08.2019 (MO)	V-MP-623
	Subfamily Anomologinae		
M	Metzneria lappella (Linnaeus)	Sakhalin, Yasnomorskoe vill., 18.07-28.07.2019 (MP)	V-MP-479
W	Monochroa cytisella (Curtis)	PK, Shkotovskij distr., Anisimovka vill., 13.07-16.07.2017 (MP)	V-MP-508
E	Eulamprotes atrella ([Denis et Schiffermüller])	JAR, Leninskij distr., 4 km SE Leninskoe vill., Solonechnaya river outfall (MP)	V-MP-35
C	Caulastrocecis sp.	PK, Khankaiskij distr., 2.5 km NNE Dvoryanka vill., 2-4.07.2009 (MP)	V-MP-89
$P_{\rm c}$	Polyhymno celata (Omelko)	PK, 18 km SE Spassk-Dal'nii, "Kalinovka" recreation center, 9.07.2018 (MP)	V-MP-417
P_{ϵ}	Polyhymno pontifera (Meyrick)	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 02.08.2016 (MP)	V-MP-515
C	Cnaphostola biformis Omelko	PK, Khasanskij distr., 14 km SW Slavyanka settl., Ryazanovka vill., 13.08.2010 (MP)	V-MP-38
10 C	Cnaphostola venustalis Omelko	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.2016 (MP)	V-MP-513
11 A	Aristotelia mesotenebrella Park	PK, 22 km NE Nakhodka, Lozovyi Range, Peretinskaya Pad', 14-15.05.2009 (MP)	V-MP-36
Subfamily Gelechiinae	elechiinae		
12 G	<i>Gelechia anomorcta</i> Meyrick	AO, 35 km WWS Zavitinsk, Zavitaya riv., 15.08.2005	V-MP-42
13 G	<i>Gelechia atrofusca</i> Omelko	JAR, 8 km SE Leninskii, Vertoprashikha river outfall, 6.07.2005 (MP)	V-MP-43
14 Ai	Aroga velocella (Zeller)	PK, Chuguevskij distr., 39 km E Yasnoe vill., Snezhnaya mtn., "Zov Tigra" reserve, 5-9.07.2013 (MP)	V-MP-9
15 49	Agnippe albidorsella (Snellen)	PK, Shkotovskij distr., Anisimovka vill., 13.07-16.07.2017 (MP)	V-MP-506
16 E _l	Ephysteris subovata (Povolný)	PK, Oktyabrskii distr., 18 km W Pokrovka vill., middle course of Orlikha riv., 18-19.05.2004 (MP)	V-MP-47
17 G	Gnorimoschema epithymella (Staudinger)	AO, 6 km WWN Belogorsk, Tom' riv., 25.08.2006 (MP)	V-MP-48
18 C	Caryocolum cassella (Walker)	JAR, Obluchenskii distr., 4 km E Radde vill., Lagar riv., 16-19.07.2005 (MP)	V-MP-49
19 C	Chorivalva bisaccula Omelko	PK, Khasanskij distr., 36 km S Slavyanka settl., Telyakovskij Bay, 7-9.07.2016 (MP)	V-MP-509
$20 P_{\ell}$	Parastenolechia argobathra (Meyrick)	PK, Khasanskij distr., 36 km S Slavyanka settl., Telyakovskij Bay, 7-9.07.2016 (MP)	V-MP-510

TABLE	TABLE 1. (Continued)		
No	Name of species	Locality	Voucher Nos.
21	Helcystogramma compositaepictum (N. Omelko et M. Omelko)	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 02.08.2016 (MP)	V-MP-514
22	Dichomeris oceanis Meyrick	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 02.08.2016 (MP)	V-MP-365
23	Dichomeris rasilella (Herrich-Schäffer)	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.2016 (MP)	V-MP-372
24	Dichomeris harmonias Meyrick	PK, Shkotovskij distr., Anisimovka vill., 13.07-16.07.2017 (MP)	V-MP-378
25	Dichomeris cuspis Park	PK, Khasanskij distr., 14 km SW Slavyanka settl., Ryazanovka vill., 13.08.2010 (MP)	V-MP-384
26	Dichomeris bulawskii Ponomarenko et Park	PK, Khankaiskij distr., 2.5 km NNE Dvoryanka vill., 29.04.2012 (MP)	V-MP-385
27	Dichomeris derasella ([Denis et Schiffermüller])	PK, Chuguevskij distr., 31 km SE Chuguevka vill., Verkhneussuriiskii biological station, 20.07.2018 (MP)	V-MP-418
28	Dichomeris okadai (Moriuti)	PK, Shkotovskij distr., Anisimovka vill., 13.07-16.07.2017	V-MP-505
29	Acanthophila liui (Li et Zheng)	PK, Khasanskij distr., 14 km SW Slavyanka settl., Ryazanovka vill., 13.08.2010 (MP)	V-MP-382
30	<i>Neofaculta taigana</i> Ponomarenko	PK, Chuguevskij distr., "Zov Tigra" Nat. Park, 16 km SE Yasnoe vill., Pobedinskaya polyana, 7-10.06.13 (MP)	V-MP-84
31	Nothris lemniscella (Zeller)	RK, Shirinskii distr., Chemoe Ozero settl., 29.07.2019 (EA)	V-MP-556
32	Hypatima venefica Ponomarenko	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.2016 (MP)	V-MP-373
33	Hypatima excellentella Ponomarenko	PK, Khasanskij distr., 14 km SW Slavyanka settl., Ryazanovka vill., 13.08.2010 (MP)	V-MP-383
34	Encolapta tegulifera (Meyrick)	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.2016 (MP)	V-MP-374
35	Encolapta tegulifera (Meyrick)	PK, Shkotovskij distr., Anisimovka vill., 13.07-16.07.2017	V-MP-507
36	Faristenia omelkoi Ponomarenko	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 27.08.2016 (MP)	V-MP-371
37	Faristenia furtumella Ponomarenko	PK, Khasanskij distr., Furugelm Isl., 16.07-22.07.2015 (MP)	V-MP-388
38	Empalactis mediofasciana (Park)	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.2016 (MP)	V-MP-604
39	Ananarsia eleagnella (Kuznetzov)	Ukraine, Kherson, 20.06.2005 (MP)	V-MP-76
40	Ananarsia bipinnata (Meyrick)	Sakhalin, Yasnomorskoe vill., 18.07-28.07.2019 (MP)	V-MP-482
41	Anarsia bimaculata Ponomarenko	PK, Khasanskij distr., 14 km SW Slavyanka settl., Ryazanovka vill., 18.07.2008 (MP)	V-MP-75
Family	Family Blastobasidae		
42	Neoblastobasis biceratala Park	PK, Vladivostok, 5 km SEE Okeanskaya st., Bogataya Griva ridge, 05.08.16 (MP)	V-MP-605

resulting length of concatenated sequences after alignment was 765–776 bp in samples included in the molecular analysis. The divergence (evolutionary distance) between nucleotide sequences of the 28SD fragments in gelechiid species was estimated by the Pairwise Distance method, using the Kimura 2-parameter model (Kimura 1980).

Descriptions of new taxa

Tawaya Ponomarenko, M. Omelko, et N. Omelko gen. n.

Type species: Tawaya flaventia sp. n.

Diagnosis. The new genus is distinguished by the extremely small size of adults, which have a forewing length of 2.2–3.2 mm and a hindwing width of about 0.9 times its length. The intervals of wing indices (length to width at the middle ratio) in the new genus is 5.6–5.8 for forewings and 11.5–12.2 for hindwings, which is remarkably larger than any known representatives of any subfamily of Gelechiidae, with forewings 3.7–5.5, and hindwings 2.8–4.3. The new genus possesses a unique complex of characters in the male genitalia, the combination of which is found in no other gelechiid genera: short degenerative tegumen, rhomboidal or triangular in shape; uncus and gnathos absent; and well-developed parategminal sclerites present (Figs 10–21). The well-developed parategminal sclerites are typical in shape of Dichomeridinae, their joining with the valva and tegumen along with their shape provide evidence that the new genus belongs in this subfamily. This assignment is also supported by molecular analysis.

Adult (Figs 1–7). Head pale sandy, sandy, light grey and grey. Antennal scape whitish, pale sandy, black, or yellowish brown; flagellum whitish, pale sandy, or yellowish grey, alternating with blackish grey or black. Basal segment of labial palpi very short, brownish or blackish; second segment brownish or blackish on outer surface, white distally; third segment shorter than second, whitish with two black rings near base and beyond middle. Labial palpus of some species with third segment black at apex.

Forewing length 2.2–3.2 mm; forewing pale sandy, sandy, yellowish brown, or greyish-brown, with pattern consisting of indistinct blackish strigulae on proximal half of wing, and two black spots in pale border with small blackish strigulae below them on distal part of wing; a row of black dots along costal and outer margins in distal 0.3 of wing. Venation with Sc to costa at about 0.3 of wing length; R₅ and M₁ short-stalked, R₅ to costa before apex, M₁ to dorsal margin beyond apex; M₂ greatly reduced or absent; M₃ separate, close to CuA₁ basally; CuA₁ and CuA₂ separate basally, to dorsal margin; 1A+2A forked at base. Hind wing grey or brownish with concolorous fringe. Hindwing venation with Sc to costa beyond middle; Rs to apex, connate with M₁ basally; M₁ to termen, M₂ greatly reduced or absent; CuA₁ and CuA₂ from Cu stem separately, 2A short, to dorsal margin at 0.2 wing length (Fig. 8). Legs pale sandy, sandy, or grey on outer surface with brownish, fuscous, or blackish, darkening, more intensive on fore- and midtibiae and tarsi of all legs; foreleg tibia with white spot on outer surface or one or two white oblique stripes at middle and white band distally on outer surface; mid-tibia with raised scales on lateral side in proximal 0.5, with rings of whitish and pale sandy scales in middle and distal parts; hind tibia with brush of hair-like brownish-yellow, pale sandy, grey, or dark-grey scales on anterior margin and in proximal part on posterior margin; segments of tarsi of all legs whitish distally, two basal tarsomeres of hind tarsi with collar of long-stemmed scales distally.

Second abdominal sternite with relatively deep rounded incision between long well-developed apodemes, distinct long sinuous venulae and drop-like opening at the 0.7 distally (Figs. 9, 23, 28).

Male genitalia (Figs 10-21). Uncus and gnathos absent. Tegumen extremelly short reduced, arched, nearly rhomboidal or triangular and hollowed posteriorly; joined to valvar basal processes (hemitranstilla) and parategminal sclerites (appendix appendicular sensu Hodges 1986). Cuculli with narrow distal part and more or less widened proximal part, often with dense patch of short, flattened scales along apex. Aedeagus almost straight, tubular, with ejaculatory ductus entering along longitudinal axis. Sacculi and juxta fused with vinculum into single large sclerite supporting and grasping aedeagus latero-ventrally. Two relatively long ventral processes, probably homologous to juxta, enveloping aedeagus laterally and joined to posterior margin of vinculum. Saccus well-developed.

Female genitalia (Figs 22, 24, 26). Papillae anales slightly sclerotized, ovipositor moderate or short. Gland sack present distally on 8th segment. Ostium near anterior margin or at level of middle part of 8th segment, narrow, more or less sclerotized laterally, goblet-like or cup-shaped. Ductus bursae membranous and tubular, rarely with colliculum containing sclerotization. Bursae copulatrix membranous, lacking signum, ductus seminalis arising in its posterior part.

Distribution. Malaysia (Sabah).

Etymology. The generic name is derived from the city Tawau, in the vicinity of which much of the material was collected.

Key to the species based on the male genitalia

Tawaya flaventia Ponomarenko, M. Omelko et N. Omelko sp. n.

Type material. Holotype: ♂, Borneo, E Malaysia, state of Sabah, 9 km NNW Keningau, 28.02.2018 (leg. M. Omelko).

Paratypes: $5 \circlearrowleft$, $2 \circlearrowleft$, same locality, 28.02-26.03.2018, GS 153 (\circlearrowleft), 156 (\circlearrowleft) MP; $4 \circlearrowleft$, $2 \hookrightarrow$, 24 km N Tawau, 17.08–05.09.2019 (leg. M. Omelko).

Diagnosis. The new species is similar to all congeners in forewing pattern, but it can be identified by the cucullus with a conspicuous ledge-like widening at the middle and the triangular shape of the tegumen in the male genitalia; and by goblet-like antrum with sclerotization elongated anteriorly in the female genitalia. In contrast, in the related species *T. luteola*, *T. rutila*, *T. armeniaca*, the cucullus is slightly widened in basal part in the male genitalia and the antrum is cup-like (*T. armeniaca*) or narrow and sclerotized laterally (*T. rutila*) in the female genitalia.

Adult (Figs 1, 2). Head grey or light grey interspersed with brownish or blackish-brown scales on vertex. Antennal scape whitish with dispersed brown scales; flagellum pale sandy alternating with black in proximal 0.5, and with 1–2 black segments alternated with 1–2 pale sandy segments in distal 0.5. Basal segment of the labial palpus brownish; second segment longer than apical segment, widened distally, mostly brownish, white-ringed distally; third segment white at base, middle, and apex, with two black rings near base and beyond middle.

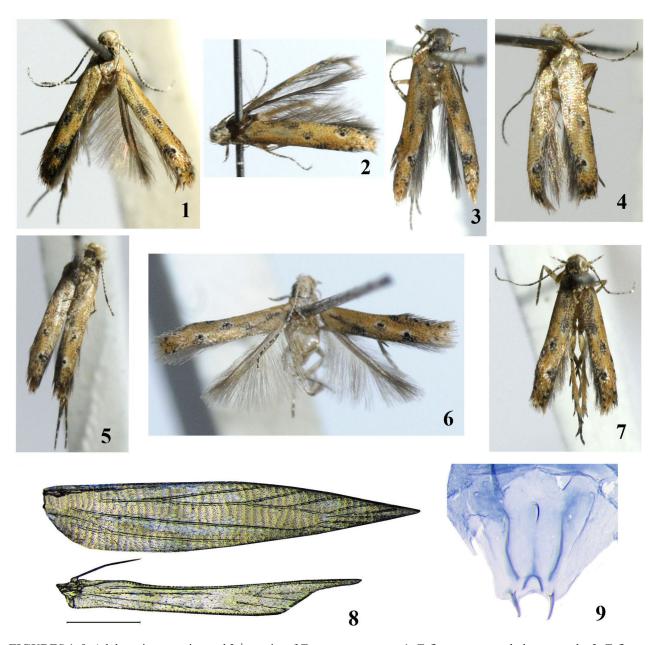
Forewing length 3.0–3.2 mm. Forewing brownish-yellow, with dispersed blackish scales and small black spots before middle and beyond 0.66 wing length, both bordering by white scales anteriorly and alternated by brown and white scales posteriorly. Several indistinct fuscous spots on anal vein in proximal 0.5, along costal margin in distal 0.5. Apical part of wing with a row of black dots along costal part and termen. Fringe yellowish-brown along wing apex and termen, grey along dorsal margin. Hindwing and fringe grey. Forelegs unicolorous, dark sandy, or tibia and tarsi brownish, tibia with white oblique stripe at middle. Femora in mid- and hind-leg grey with brownish darkening on outer surface along posterior margin. Mid-tibia brownish with raised elongate scales dorsally in proximal part and white rings in middle part and distally, tarsomeres brown. Hind tibia yellowish-brownish, fuscous laterally in proximal 0.5 or along entire tibia, with dark sandy or dark grey brush of hair-like scales on their dorsal margin and in proximal part of their ventral margin.

Male genitalia (Figs 10–12). Tegumen triangular and arched, deeply hollowed on posterior margin, joined with parategminal sclerites and valvar basal processes (hemitranstilla). Cucullus narrow digitate in distal 0.33, ledge-like widened at middle, and slightly narrowing to base, with crest of flattened chaetae densely distributed along apical margin and strong needle-like thorns along dorsal margin in middle part, with large, complex basal process with a protruding triangular plate. Aedeagus long, its length exceeding total length of genitalia, narrow, tube-like in distal 0.33, inflated at middle and with narrower obliquely incised basal part. Ejaculatory duct entering along longitudinal axis. Vinculum band-like, with slender saccus, 0.2 times length of aedeagus. Juxta fused with posterior margin of vinculum into single sclerite and covering aedeagus latero-ventrally, deeply split distally into two strongly sclero-tized lobes bearing short thick thorns laterally.

Female genitalia (Fig. 22). Ovipositor long, membrane between 8th and 9th segments 2 times as long as 8th segment, with membranous large probably gland sack (about 0.66 of ovipositor width) at middle of ovipositor on dorsal side. Papillae anales moderate in length, 0.22 times as long as ovipositor, slightly sclerotized. Apophyses posteriores 2.3 times as long as apophyses anteriores. Ostium at level of anterior margin of 8th segment. Antrum sclerotized latero-dorsally, membranous ventrally, goblet-shaped, narrowing between inflated distal and tubular anterior part, latter with elongated triangular sclerotization ventrally. Ductus bursae slightly sclerotized, narrow, tube-like, enlarged into gutter-shaped dorsal sclerotization anteriorly. Bursae copulatrix small, oval, membranous, as long as tubular part of ductus, signum absent; ductus seminalis arising in posterior part of bursae.

Distribution. Malaysia (Sabah).

Etymology. The species name is derived from Latin root "*flaveo-*" meaning yellow, which is corresponding to the dominant colour in the forewings.



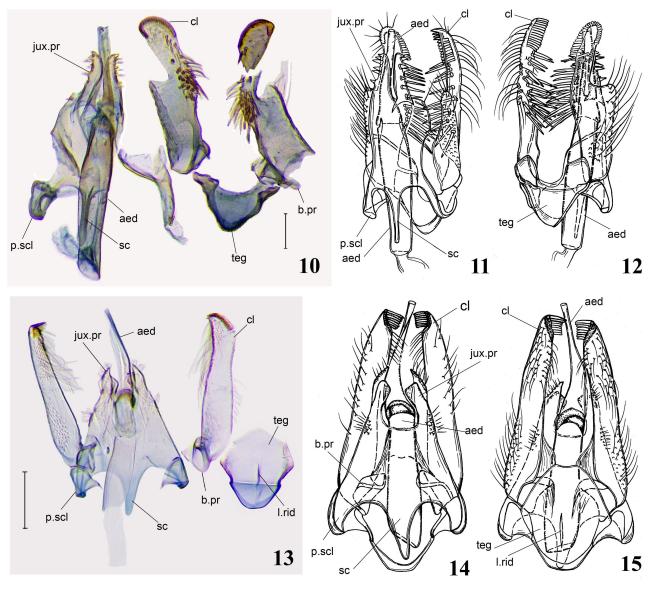
FIGURES 1–9. Adults, wing venation and 2nd sternite of *Tawaya* **gen. n.** spp. 1, *T. flaventia* **sp. n.**, holotype, male; 2, *T. flaventia*, paratype, female; 3, *T. rutila* **sp. n.**, holotype, male; 4, *T. rutila*, paratype, female; 5, *T. luteola* **sp. n.**, holotype, male; 6, *T. armeniaca* **sp. n.**, paratype, male; 7, *T. armeniaca*, paratype, female; 8, *T. flaventia*, venation, voucher V-MP-621; 9, *T. luteola* **sp. n.**, 2nd sternite of the female. Scale bar 0.5 mm.

Tawaya rutila M. Omelko, Ponomarenko et N. Omelko sp. n.

Type material. Holotype: \circlearrowleft , Borneo, E Malaysia, state of Sabah, 24 km N Tawau, 21.08.2019 (leg. M. Omelko). Paratypes: $1 \circlearrowleft$, $2 \circlearrowleft$, same locality, 18.08–03.09.2019 (leg. M. Omelko); GS 155 (\circlearrowleft) , 159 (\circlearrowleft) MP.

Diagnosis. The new species can be easily separated by the rhomboidal shape of the tegumen, the presence of medial triangular lobes in the distal part of the juxtal processes, and the aedeagus with an arched sclerotization beyond the middle in the male genitalia; and by the 8th segment with a transverse band-like sclerite ventrally, the narrow antrum with lateral sclerotized sides, and the culliculum with a twisted sclerotization in the female genitalia. In contrast, in *T. luteola* there are no lobes in the distal part of the processes of the juxta in the male genitalia; and a colliculum and transverse band-like sclerite ventrally in the 8th segment are lacking, and the antrum has a different shape in the female genitalia.

Adult (Figs 3, 4). Head pale sandy, yellowish-brown, or dark grey. Antennal scape whitish with black band at middle; flagellum with alternating white and black segments in proximal part, and with alternating one white and two black segments in distal part. Basal segment of labial palpus brownish or blackish; second segment brownish or blackish, white-ringed distally; third segment white, with two black rings at base and before apical third.



FIGURES 10–15. Male genitalia of *Tawaya* **gen. n.** spp. 10, *T. flaventia* **sp. n.**, voucher V-MP-621, GS 153 MP; 11, *T. flaventia*, ventral view; 12, *T. flaventia*, dorsal view; 13, *T. rutila* **sp. n.**, paratype, GS 155 MP; 14, *T. rutila*, ventral view; 15, *T. rutila*, dorsal view. *aed*—aedeagus, *b.pr*—basal process of valva, *cl*—cucullus, *jux.pr*—process of juxta, *l.rid*—longitudinal ridge of tegumen, *p.scl*—parategminal sclerite, *sc*—saccus, *teg*—tegumen.

Forewing length 2.2–2.7 mm. Forewing yellowish-brown, with two blackish indistinct spots in proximal part, distal part with two black spots at middle and in apical part near dorsal margin, both spots bordered by whitish scales and each with black strigula dorsad; apical part with a row of black dots along costal part and termen. Fringe yellowish-brown along wing apex and termen, dark grey along dorsal margin. Hindwing and fringe dark grey. Legs pale sandy or sandy laterally, with blackish or fuscous tibiae and tarsi. Foreleg tibia with oblique white stripe at middle and white-ringed distally. Mid-leg tibia with raised elongated scales dorsally in proximal part and collars of elongated scales in middle and distally. Hind leg tibia with brush of hair-like pale sandy scales on dorsal and ventral margins in proximal part.

Male genitalia (Figs 13–15). Tegumen rhomboidal, with sclerotized longitudinal ridge at middle of anterior part, lateral angles strongly sclerotized at junction with parategminal sclerites and basal processes of valvae. Cucullus slightly narrowed at 0.66 distally, and weakly inflated towards base, with dense crest of flattened chaetae along rounded apex, with large quadrangular basal process. Aedeagus longer than total length of genitalia, narrow, tubelike basally, with strong arched sclerotization beyond middle, curved to right at 0.66 distally, distal 0.33 with left side sclerotization. Ejaculatory duct entering along longitudinal axis. Vinculum, juxta, and probably sacculi fused into single ventral sclerite surrounding aedeagus latero-ventrally; distal processes of juxta pointed apically and with triangular lobes limiting mobility of aedeagus dorsally. Saccus triangular, its length slightly exceeding its width at base.

Female genitalia (Fig. 24). Ovipositor short, membrane between 8th and 9th segments 0.5 length of papillae anales, with large membranous sack (of uncertain function) arising from near posterior margin of 8th tergite. Papillae anales sclerotized, moderate in length, slightly shorter than apophyses posteriores. Apophyses posteriores almost of same length as apophyses anteriores. 8th segment with transverse band-like sclerite ventrally. Ostium at level of middle part of 8th segment. Antrum narrow, with sclerotized lateral sides. Ductus bursae membranous posteriorly, in anterior part with semi-sclerotized colliculum spirally left twisted and enclosing S-shaped, ribbon-like sclerotization. Bursae copulatrix membranous and elongated, as long as ductus bursae, signum absent; ductus seminalis arising from posterior part of bursae. Tergite of 7th segment with anteriorly diverging pockets containing strong subulate chaetae (Fig. 25).

Distribution. Malaysia (Sabah).

Etymology. The species name is derived from Latin "*rutilus*" meaning reddish-yellow, which refers to the colour and brightness of the forewings.

Tawaya luteola M. Omelko, Ponomarenko et N. Omelko sp. n.

Type material. Holotype: ♂, Borneo, E Malaysia, state of Sabah, 24 km N Tawau, 29.08.2019 (leg. M. Omelko); GS 157 (♂) MP.

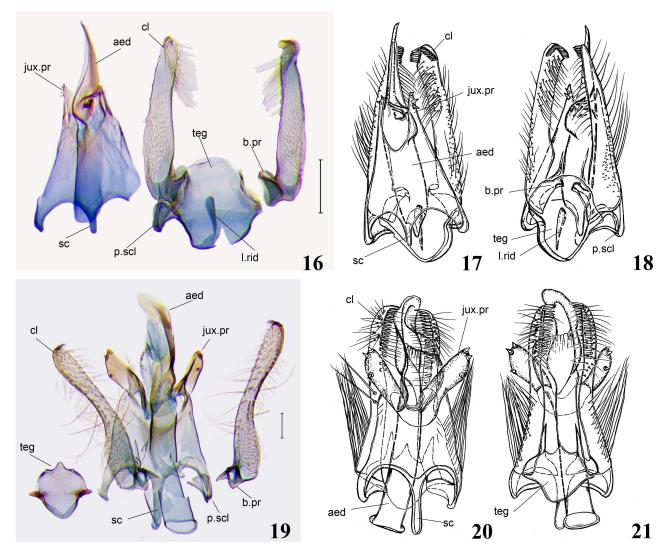
Diagnosis. The new species is distinguished by characters of the male genitalia: the tegumen with a well-developed longitudinal ridge in the anterior half with a rounded posterior margin; the processes of the juxta evenly tapering towards setaceous apices; and the aedeagus can-opener-shaped in the distal part, which is strongly sclerotized. In contrast, the related *T. rutila* has medial lobes in the distal part of the juxtal processes, the latter dilated before the apex, and the aedeagus is evenly narrowed apically.

Adult (Fig. 5). Head whitish. Antennal scape black, white-ringed distally; flagellum with white alternated with black. Labial palpus with basal segment black; second segment black, white distally; third segment white with black rings at base and before apex.

Forewing length 2.5 mm. Forewing greyish-yellow; proximal part without pattern, with dispersed brownish and black scales along costal margin; distal part with two black spots bordered by white—just beyond middle and at about 0.8 wing length, closer to dorsal margin. Fringe brownish along costa in apical part, brownish-yellow at apex, dark grey along termen and dorsal margin. Hindwing and fringe greyish-brown. Femora of forelegs pale sandy, with conspicuous darkening on outer surface, tibia sandy on medial side, blackish on outer surface, with white band at middle and white distally. Femora of mid-leg sandy, with brownish darkening on outer surface; tibia dark brown with whitish collar distally. Hind-leg pale sandy with darkening on femora, tibia, and tarsi; tibia with yellowish-brown brush of short hair-like scales dorsally.

Male genitalia (Figs 16–18). Tegumen rhomboidal, with sclerotized longitudinal ridge at middle of anterior

part, lateral angles strongly sclerotized at junction with basal processes of valva and parategminal sclerites. Cucullus evenly narrowing towards apex, with dense crest of flattened chaetae along rounded apex, with large quadrangular basal process. Aedeagus long, exceeding total length of genitalia, tubular, parallel-sided in proximal 0.5, distal strongly sclerotized part can-opener-shaped, tapering distally toward elongate, pointed apex. Ejaculatory duct entering along longitudinal axis. Vinculum, juxta, and probably sacculi fused into single ventral sclerite surrounding aedeagus latero-ventrally; distal processes of juxta pointed apically, with strong setae in apical part laterally. Saccus triangular, its length equal to its basal width.



FIGURES 16–21. Male genitalia of *Tawaya* **gen. n.** spp. 16, *T. luteola* **sp. n.**, holotype, GS 157 MP; 17, *T. luteola*, ventral view; 18, *T. luteola*, dorsal view; 19, *T. armeniaca* **sp. n.**, voucher V-MP-623, GS 154 MP; 20, *T. armeniaca*, ventral view; 21, *T. armeniaca*, dorsal view. Scale bar 0.1 mm.

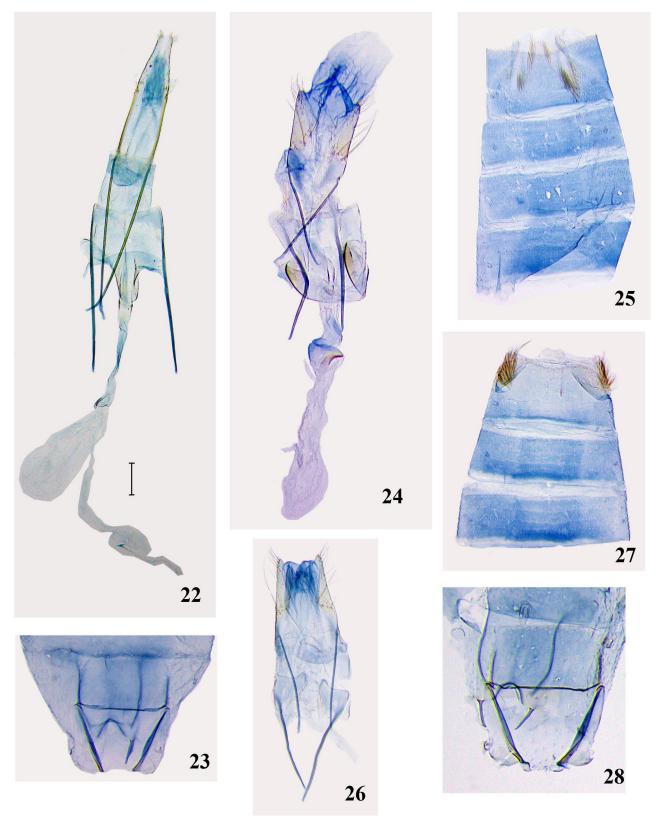
Female unknown.

Distribution. Malaysia (Sabah).

Etymology. The species name is derived from Latin "*luteolus*" meaning yellowish, referring to the colour of the forewings.

Tawaya armeniaca Ponomarenko, M. Omelko et N. Omelko sp. n.

Type material. Holotype: \circlearrowleft , Borneo, E Malaysia, state of Sabah, 24 km N Tawau, 18.08.2019 (leg. M. Omelko). Paratypes: $5 \circlearrowleft$, $5 \circlearrowleft$, same locality, 17.08–05.09.2019 (leg. M. Omelko); GS 154 (\circlearrowleft), 158 (\circlearrowleft) MP.



FIGURES 22–28. Female genitalia, 2nd sternite and 7th abdominal segments of *Tawaya* **gen. n.** spp. 22, *T. flaventia* **sp. n.**, paratype, GS 156 MP; 23, *T. flaventia*, 2nd sternite; 24, *T. rutila* **sp. n.**, paratype, GS 159 MP; 25, *T. rutila*, 7th abdominal segment, paratype; 26, *T. armeniaca*, paratype, GS 158 MP; 27, *T. armeniaca*, 7th abdominal segment, paratype; 28, ditto, 2nd sternite, paratype. Scale bar 0.2 mm.

Diagnosis. The new species is easily distinguished by characters of the male genitalia: the tegumen has a knob on the posterior margin; the processes of the juxta are dilated into wide trapezoidal plates, distally bearing strong thorns on the outer margin; and the aedeagus has ribbon-like sclerotization expanded into an oval plate apically on the left side. The female genitalia are distinguished by the sternal part of the 8th segment represented by triangular plates and the antrum cup-shaped. In contrast, in the closely species *T. luteola* and *T. rutila*, tegumen lacks a knob on the posterior margin; the juxta processes narrow distally or are slightly dilated before their apices and lack thorns; the aedeagus lacks a distal expansion; and the female has a transverse band-like sclerotization on the 8th segment and the antrum is narrow with sclerotized sides.

Adult (Figs 6, 7). Head pale sandy. Antennal scape pale sandy in proximal part and distally, in distal part with blackish or brownish band; flagellum with pale sandy or whitish segments alternating with segments having a black upper surface, distal part with 1–3 alternating pale sandy or whitish and 1–3 black segments. Labial palpus with basal segment brownish; second segment brown and white-ringed distally; third segment white, black-ringed near base, beyond middle and with black apex.

Forewing length 2.5–2.8 mm. Forewing ground colour yellowish-red; proximal part with two indistinct brownish strokes; at middle a black spot in whitish border and with indistinct brownish strigula under it; apical part with two black spots—costal and subdorsal, both in whitish border and with brownish indistinct strigula posteriorly; a row of black dots along costal margin and termen in apical part. Fringe yellowish-red along costa and termen in apical part of wing, dark-grey along dorsal margin. Hindwing and fringe dark-grey in male, dark sandy in female. Legs pale sandy or sandy, with darkening on fore- and mid-tibiae and tarsi of all legs. Forelegs tibia with white spot in middle and white-ringed distally; mid-leg tibia with raised elongate scales on outer surface in proximal part and pale sandy rings in middle part and distally; proximal part of hind tibia with a brush of pale sandy hair-like scales on lateral and medial sides.

Male genitalia (Figs 19–21). Tegumen sub-rhomboidal, with sclerotized lateral margins, oval anteriorly, with triangularly pointed lobe on posterior edge. Cucullus digitate, evenly narrowing at middle, slightly inflated basally, with dense crest of flattened chaetae along rounded apex, with large quadrangular basal process. Aedeagus long, exceeding total length of genitalia, tubular, with almost parallel sides in proximal 0.5; left side of distal part with ribbon-like sclerotization expanded into an oval plate apically. Ejaculatory duct entering along longitudinal axis. Vinculum, juxta, and probably sacculi fused into a single ventral sclerite surrounding aedeagus latero-ventrally; distal processes of juxta dilated into wide trapezoidal plates, each bearing three short strong thorns distally. Saccus relatively narrow and long, its width 0.2 times that of base.

Female genitalia (Fig. 26). Ovipositor short, membrane between 8th and 9th segments ca/ 0.5 length of papillae anales, with large, membranous sack (of uncertain function) arising from near posterior margin of 8th tergite. Papillae anales sclerotized, moderate in length, 0.75 length of apophyses posteriores. Apophyses anteriores and apophyses posteriores of equal length. 8th segment splitted ventrally, with narrow membranous insertion between sternal trapezoidal sclerites. Ostium at level of anterior margin of 8th segment. Antrum cup-shaped. Ductus bursae tube-like, membranous. Bursae copulatrix membranous, ovaoid, slightly shorter than ductus bursae, signum absent; ductus seminalis arising in posterior part of bursae. Tergite of 7th segment with lateral triangular pockets containing strong subulate chaetae (Fig. 27).

Distribution. Malaysia (Sabah).

Etymology. The species name is derived from the Latin "armeniaca," the species name of the apricot tree, which has orange-yellow fruits; the name refers to the bright reddish-yellow colour of the forewings.

Discussion

The molecular analysis of the family Gelechiidae, including the new genus *Tawaya*, is based on two nuclear fragments, 28SD1 and 28SD2 (Fig. 29). The relative positions of subfamilies on the tree corresponds primarily to the reconstruction of relationships based on comparative and functional morphological analysis by Ponomarenko (2005). Since one of the goals of the present paper was to determine the taxonomic position of *Tawaya* within Gelechiidae, this discussion is focused on rooting this genus and its neighboring taxa. Two new species (*Tawaya armeniaca* **sp. n.** and *T. flaventia* **sp. n.**) were included in the molecular analysis, and they are sister taxa in the dendrogram. The representatives of *Tawaya* are rooted within the subfamily Dichomeridinae, in the tribe Chelariini, and form a monophyletic clade with the genera *Neofaculta* Gozmány and *Nothris* Hübner. The last two mentioned genera are

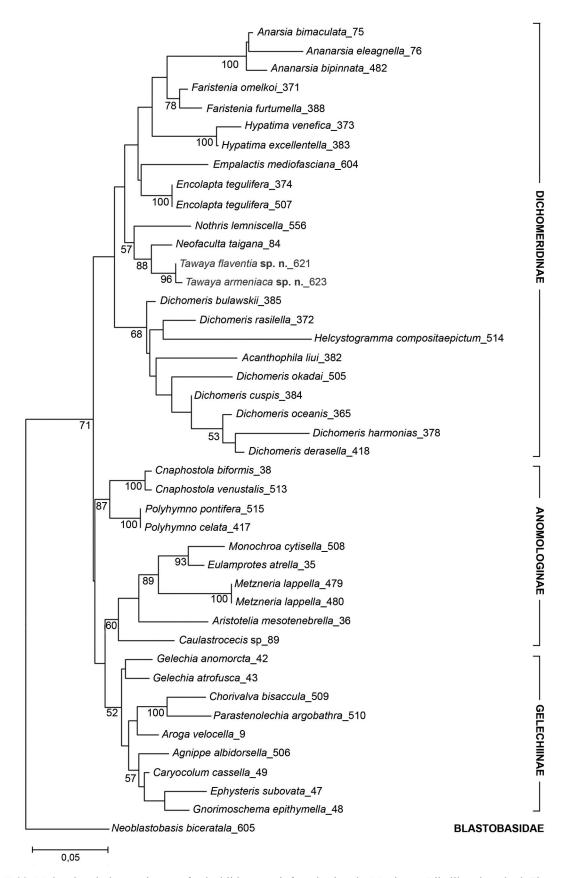


FIGURE 29. Molecular phylogenetic tree of gelechiid genera inferred using the Maximum Likelihood method. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) is given for those greater than 50%.

No Species	4	42 4	41	40	39 38	8 37	36	35	8	33	32	31	30	59	28	27	26	25	24	23	
1 Tawaya_flaventia_621		0,084	34 0,08	0,084 0,086	6 0,08	0,082 0,081 0,082	0,082	0,071 0,071	0,071	0,084	0,089	0,084 0,089 0,082 0,076 0,086 0,087 0,086	9,076	980'0),087 (0,086	0,077	0,074	0,089 0,	920'0	42
2 Tawaya_armeniaca_623	0,003	l,	0,01	2 0,02	5 0,05	0,012 0,025 0,053 0,046	0,046	0,046 0,060 0,060 0,056 0,064 0,060 0,057	090'0	0,056	0,064	090'0	0,057	0,076 0,073 0,079	0,073	0,079	0,061 0,064	,064 0	0,087 0,	690'0	41
3 Metzneria_lappella_479	0,081 0,084	4		0,031	1 0,05	0,058 0,050	0,052	0,052 0,068 0,068	0,068	0,061 0,071	0,071	0,069 0,063 0,084 0,082	0,063	0,084 (3,082 (0,086	0,071 0	0,073	0,092 0,	0,077	40
4 Monochroa_cytisella_508	0,071 0,074	4 0,049	19		0,069	090'0 6	090'0	0,060 0,073	0,073	0,066	0,077	0,073 0,066 0,077 0,076 0,068	3,068	0,086	0,082 (0,087 ر	0,073 0	0,076	0,101 0,	6/0'0	39
5 Eulamprotes_atrella_35	0,061 0,064	4 0,050	50 0,022	2	1	0,042	0,042	0,042 0,042	0,042	0,052	090'0	0,042 0,052 0,060 0,058 0,058 0,077	0,058),077 (0,069 0,073	0,073	0,053 0,056 0,068	0990,	068 0,	090'0	38
6 Caulastrocecis_sp_89	0,060 0,060	0 0,066	56 0,063	3 0,052	2	ı	0,015	0.015 0,038 0,038 0,045 0,052 0,044 0,041 0,069 0,068 0,063	0,038	0,045	0,052	0,044	0,041	0,069),068	0,063	0,050 0,053 0,069	,053	0690	0,057	37
7 Polyhymno_cellata_417	0,055 0,058	8 0,07	0,071 0,064	4 0,056	6 0,050			0,035	0,035	0,041	0,050	0,035 0,035 0,041 0,050 0,045 0,044 0,066 0,068 0,066	0,044	990'C	0,068		0,044 0,060 0,073	090,	073 0,	0,053	36
8 Polyhymno_pontifera_515	0,055 0,058	8 0,07	71 0,06	4 0,05	0,071 0,064 0,056 0,050	000'0		1	0,000	0,049	0,049	0,000 0,049 0,049 0,042 0,039 0,065 0,063 0,052	0,039	0,065 (0,063	0,052	0,039 0,050 0,057	,050 0	057 0,	0,047	35
9 Cnaphostola_biformis_38	0,061 0,064	4 0,077	77 0,06	90'0 9	0,066 0,060 0,061	1 0,030	0,030			0,049	0,049	0,049 0,049 0,042 0,039 0,065 0,063 0,052	0,039	0,065	0,063 (0,039 0,050 0,057	,050 0		0,047	34
10 Cnaphostola_venustalis_513	0,063 0,066	6 0,07	77 0,06	90'0 9	1 0,05	0,077 0,066 0,061 0,058 0,032	0,032	0,006			0,012	0,012 0,058 0,058 0,077 0,081 0,079 0,049 0,069 0,079	0,058),077 (0,081),079 C	0,049 0	0 690	,0 670	0,064	33
11 Aristotelia_mesotenebrella_36	0,066 0,063	3 0,05	58 0,06	90'0 9	7 0,04	0,058 0,066 0,057 0,049 0,065	0,065	0,065 0,073	0,073			0,061	1,00,0	0,061 0,061 0,079 0,081 0,082 0,056 0,074 0,087	0,081),082 C	0 950'0	,074	,087 0,	0,071	32
12 Gelechia_anomorcta_42	0,049 0,052	2 0,06	34 0,06	4 0,05	6 0,04	0,064 0,064 0,056 0,045 0,050	0,050	0,050 0,055	0,055	0,055			0,036	0,036 0,079 0,063 0,061	0,063	0,061	0,045 0,052	,052 0	0,073 0,	0,050	31
13 Gelechia_atrofusca_43	0,047 0,050	0,06	34 0,05	8 0,04	9 0,04	0,064 0,058 0,049 0,044 0,046	0,046	0,046 0,047 0,047		0,060 0,024	0,024		Ť	0,064 0,053 0,047 0,036 0,039 0,061 0,042	0,053	0,047	036 0	039 0	,061 0,	042	30
14 Aroga_velocella_9			38 0,06	6 0,05	8 0,04	0,068 0,066 0,058 0,042 0,042	0,042	0,042 0,050 0,047 0,058 0,030	0,047	0,058	0,030	0,027		Ť	0,055 0,053 0,041 0,045 0,052	0,053	0,041	,045 0	.052 0,	0,049	59
15 Agnippe_albidorsella_506	0,050 0,050		38 0,06	6 0,05	8 0,04	0,068 0,066 0,058 0,041 0,049		0,049 0,060	0,057	0,049	0,049 0,032	0,035	0,028		ا	0,050 0,041	,041 0	0,035 0,058	,058 0,	0,052	28
16 Ephysteris_subovata_47	0,060 0,063		71 0,07	1 0,06	3 0,05	0,071 0,071 0,063 0,055 0,058 0,058 0,066 0,063 0,052 0,042 0,044 0,042	0,058	0,066	0,063	0,052	0,042	0,044	0,042	0,024		0	0,035 0,022 0,032	,022 0,	032 0,	0,032	27
17 Gnorimoschema_epithymella_48	0,053 0,057		77 0,07	7 0,06	9 0,05	0,077 0,077 0,069 0,054 0,055 0,055 0,060 0,057 0,057 0,035 0,038 0,039	0,055	0,060	0,057	0,057	0,035	0,038	0,039	0,036	0,028		0	0,025 0,036 0,025	036 0,	025	26
18 Caryocolum_cassella_49	0,047 0,050	0,06	36 0,06	4 0,05	5 0,03	0,066 0,064 0,055 0,039 0,046	0,046	0,046 0,053	0,050	0,049	0,019	0,050 0,049 0,019 0,019 0,022	0,022	0,018	0,028	0,021	ı	0	0,039 0,	0,032	25
19 Chorivalva_bisaccula_509	0,063 0,066	6 0,07	79 0,07	7 0,06	90'0 8	0,079 0,077 0,068 0,061 0,050 0,050 0,055 0,055 0,079 0,047 0,042 0,038 0,047 0,055 0,055	0,050	0,055	0,055	0,079	0,047	0,042	3,038	0,047 (),055 () 959 (0,039		0,	0,039	24
20 Parastenolechia_argobathra_510	0,064 0,068	8 0,08	36 0,07	7 0,07	2 0,06	0,086 0,077 0,072 0,066 0,055	0,055	0,055 0,066 0,063 0,084 0,049 0,039 0,041	0,063	0,084	0,049	0,039	0,041	0,052 0,063 0,060	0,063	090'0	0,039	0,036	l		
21 Helcystogramma_compositaepictum_	514	1 0,10	71 0,10	90,09	4 0,09	0,101 0,106 0,094 0,092 0,087	0,087	0,087 0,086 0,086 0,104 0,087 0,081 0,089 0,096 0,106 0,096	0,086	0,104	0,087	0,081	0,089	960'0	0,106 (960'0	0,086	0,094 0	0,094		
22 Dichomeris_oceanis_365	0,050 0,050	0,00	79 0,07	4 0,06	4 0,05	0,079 0,074 0,064 0,053 0,056 0,056 0,060 0,061 0,063 0,053 0,055 0,052 0,053 0,057 0,053 0,047 0,060 0,071	0,056	0,060	0,061	0,063	0,053	0,055	0,052 (0,053 (0,057 (0,053	,047	090	071 0,	0,081	
23 Dichomeris_rasilella_372	0,042 0,045	5 0,07	76 0,07	1 0,06	4 0,05	0,076 0,071 0,064 0,058 0,060 0,060 0,068 0,071 0,071 0,053 0,055 0,060 0,064 0,071 0,066 0,056 0,068 0,076	090'0	0,068	0,071	0,071	0,053	0,055	090,0	0,064 (0,071	990'(0950,	0890	076 0,	0,069 0,	0,030
24 Dichomeris_harmonias_378	0,065 0,066	90,0	32 0,08	1 0,08	1 0,06	0,082 0,091 0,081 0,069 0,066	990'0	0,066 0,074 0,079 0,086 0,073 0,073 0,071 0,078 0,083 0,079 0,069 0,082	0,079	0,086	0,073	0,073	0,071	0,078 (0,083 (0,079	0690'(,082	0,087 0,	0,079 0,	0,035
25 Dichomer_cuspis_384	0,041 0,044	4 0,07	77 0,07	3 0,06	3 0,05	0,077 0,073 0,063 0,055 0,052	0,052	0,052 0,064 0,063 0,068 0,050 0,052 0,047 0,047 0,055 0,055 0,039 0,057 0,058	0,063	0,068	0,050	0,052	0,047	0,047	0,055 (0,055 (0 660'(,057	058 0,	0,068 0,	0,018
26 Dichomeris_bulawskii_385	0,036 0,039	9 0,07	72 0,06	90,09	6 0,04	0.072 0.066 0.056 0.047 0.047 0.045 0.045 0.052 0.053 0.066 0.050 0.044 0.049 0.057 0.066 0.058 0.049 0.056 0.055	0,045	0,052	0,053	0,066	0,050	0,044	0,049	0,057),066 (0,058	0,049	,056 0	055 0,	0,063 0,	0,033
27 Dichomeris_derasella_418	0,050 0,050	0,00	34 0,08	1 0,07	1 0,06	0,084 0,081 0,071 0,060 0,064 0,064 0,071 0,076 0,069 0,058 0,060 0,061 0,061 0,068 0,055 0,071	0,064	0,071	0,076	0,069	0,058	0,060	0,061	0,061	3,068),068 c	0 250'(,071 0	0,079 0,	0,079 0,	0,013
28 Dichomeris_okadai_505	0,055 0,055		77 0,07	4 0,06	90'0	0,077 0,074 0,069 0,068 0,065	0,065	0,065 0,079 0,077 0,079 0,064 0,066 0,064 0,066 0,074 0,071 0,060 0,065 0,068	0,077	0,079	0,064	0,066	0,064 (990'C	0,074 (0,071	090'(,065 0	068 0,		0,049
29 Acanthophila_liui_382	0,069 0,069		30'0 98	11 0,07	7 0,06	0,086 0,091 0,077 0,063 0,071 0,071 0,081 0,081 0,082 0,069 0,069 0,064 0,069 0,083 0,079 0,063 0,076 0,076 0,076	0,071	0,081	0,081	0,082	690'0	0,069	0,064 (0,069	0,083 (0,079 (0 690'0	0 920	076 0,	081 0,	0,052
30 Neofaculta_taigana_84	0,019 0,018		79 0,06	90,06	3 0,06	0,079 0,069 0,063 0,060 0,055	0,055	0,055 0,061 0,063 0,066 0,047 0,045 0,052	0,063	990'0	0,047	0,045	0,052 (0,045 0,061 0,061 0,045 0,061	0,061	0,061	,045	,061	0,061 0,	0,077 0,	0,049
31 Nothris_lemniscella_556			36 0,07	4 0,07	4 0,06	0,086 0,074 0,074 0,068 0,069	690'0	0,069 0,071 0,069 0,081 0,058 0,053 0,058 0,065 0,074 0,068	0,069	0,081	0,058	0,053	0,058	0,065 (0,074 (0,068	0,058 0,068 0,069	0890,	0690	0,084 0	0,060
32 Hypatima_venefica_373	0,060 0,060	0,0	32 0,08	4 0,07	7 0,06	0,082 0,084 0,077 0,068 0,068	0,068	0,068 0,066 0,068 0,086 0,063 0,052 0,061 0,068 0,081 0,073 0,063 0,076 0,074	0,068	0,086	0,063	0,052	0,061	990'0	0,081	0,073	0,063	0 920,	074 0,	0,099	0,074
33 Hypatima_excellentella_383	055	8 0,07	79 0,07	70,07	4 0,06	0,079 0,077 0,074 0,063 0,063	0,063	0,063 0,060 0,063 0,086 0,058 0,047 0,056 0,063 0,076 0,068 0,058 0,071	0,063	0,086	0,058	0,047	0,056 (0,063	0,076	3,068	0,058	,071	0,069 0,	0,094 0	0,071
34 Encolapta_tegulifera_374	4	1 0,07	71 0,06	90'0	3 0,05	0,071 0,066 0,063 0,058 0,052		0,052 0,055 0,057	0,057	0,068	0,052	0,068 0,052 0,050 0,055 0,060 0,070 0,063 0,054	0,055 (0,060	0,070	0,063	,054 0	0,065 0	0,066 0,	0,087	0,050
35 Encolapta_tegulifera_507	0,041 0,041	1 0,07	71 0,06	90'0 9	3 0,05	0,071 0,066 0,063 0,058 0,052		0,052 0,055 0,057 0,068 0,052 0,050 0,055 0,060 0,070 0,063 0,054 0,065 0,066	0,057	0,068	0,052	0,050	0,055 (090'0	0,070	0,063	,054 0	,065	000	0,087	0,050
36 Faristenia_omelkoi_371	0,047 0,050	0,00	77 0,07	71 0,06	0,077 0,071 0,069 0,061	1 0,057	0,057	0,057 0,055 0,058 0,079 0,052 0,044 0,052	0,058	0,079	0,052	0,044	0,052 (0,058 0,076 0,066 0,053 0,063	0,076	990'0	,053 0	063 0		0,089	0,061
37 Faristenia_furtumella_388	0,046 0,049		71 0,07	1 0,06	90,06	0,071 0,071 0,069 0,063 0,058	0,058	0,058 0,055 0,058 0,078 0,049 0,041 0,050 0,052 0,069 0,063 0,047 0,058 0,060	0,058	0,078	0,049	0,041	0,050 (0,052 (0,069	0,063	,047	0 850,	0000	0,087	0,058
38 Empalactis_mediofasciana_604	0,053 0,057		32 0,07	79 0,07	9 0,07.	0,082 0,079 0,079 0,072 0,066	0,066	0,066 0,068 0,068 0,094 0,069 0,063 0,061 0,071 0,077 0,074 0,064 0,074	0,068	0,094	0,069	0,063	0,061	0,071),077 (0,074	,064 0	,074	0,074 0,	0,104 0	0,061
39 Ananarsia_eleagnella_76	0,069 0,073		0,094 0,081 0,082	1 0,08	2 0,082	2 0,081	0,081	0,081 0,081 0,087 0,084 0,094 0,073 0,061 0,068 0,069 0,081 0,082 0,060 0,076	0,084	0,094	0,073	0,061	0,068	0,069	0,081	0,082	090'0	0 920'	0,069 0,	0,098	0,082
40 Ananarsia_bipinnata_482	0,071 0,074	4 0,08	39 0,07	71 0,07	0,089 0,071 0,076 0,077	7 0,076	0,076	0,076 0,082 0,082 0,091 0,069 0,060 0,066 0,068 0,077 0,079 0,056 0,074	0,082	0,091	0,069	0,060	990'0	0,068),077 (0,079	0 990'0	,074	0,066 0,	0,092 0,	0,079
41 Anarsia_bimaculata_75	0,061 0,065	5 0,08	0,084 0,068 0,071	10,03	1 0,073	3 0,068	0,068	0,068 0,077	0,074	0,081	0,061	0,074 0,081 0,061 0,055 0,058	0,058 (0,060 0,069 0,071 0,052 0,069	0,069	0,071	,052 0	0 690'	0,063 0,	0,089	0,074
42 Neoblastobasis_biceratala_605	0,077 0,079	960'0 6	30'0 96	0,090 0,089	9 0,077	7 0,071	0,071	0,071 0,081	0,082	0,089	0,076	0,073	0,063	0,074	0,087	0,082	0,066 0	0,076	0,076 0,	0,101 0,	0,076
	_	7	3	4	2	6 7	8	6	9	7	12	13	4	12	16	11	18	19	70	72	22

FIGURE 30. Pairwise distances of 28S (fragments D1 and D2) sequences of gelechiid taxa.

included in Chelariini on the basis of functional morphological investigations of the male genitalia by Ponomarenko (1993). Analyses of the genetic divergence (i.e., pairwise distance) of the new genus to other genera of the subfamily Dichomeridinae show a minimal distance of 0.018–0.019 (1.8–1.9%) between *Tawaya* and *Neofaculta*. The genetic divergence between the new genus and other genera of the tribe Chelariini are 0.041–0.058 (i.e., 4.1–5.8% in *Nothris*

Hübner, *Encolapta* Meyrick, *Faristenia* Ponomarenko, *Hypatima* Hübner). The pairwise distance of *Tawaya* to the tribe Anarsiini is 0.06–0.073 (6.0–7.3% in *Anarsia* Zeller and *Ananarsia* Amsel), and to the tribe Dichomeridini the distance is from 0.035–0.038 (3.5–3.8% in *Dichomeris*) to 0.07–0.076 (7.0–7.6% *Acanthophila* Heinemann and *Helcystogramma* Zeller) (Fig. 30). The degree of genetic divergence of a *Tawaya* to genera of the tribe Dichomeridini is the largest and overlaps with the distances between *Tawaya* and genera from the tribe Chelariini.

On the basis comparative morphological analysis, the Dichomeridinae consists of three tribes: Chelariini, Anarsiini and Dichomeridini. The monophyly of the subfamily is supported by two reliable synapomorphies: presence of parategminal sclerites, which are apodemes for muscles m_{ν} distinct ventral wall in tegumen; and intrategminal position of muscles m_2 (abductors of valvae). Of these two features, Tawaya possesses well-developed parategminal sclerites, the shape and position which exactly correspond to those in representatives of Chelariini. Since the parategminal sclerites are apodemes of the muscle m_s (adductors of valvae) and serve in valvar functioning, it seems reasonable to assume that in Tawaya these muscles would have the same position. The functional morphology of the male genitalia in Tawaya was not studied since the material was not fixed in ethanol. But the absence of the uncus and gnathos, reduction of the tegumen to a small, slightly arched plate provide evidence that there are deep morphological transformations of reduction character in the genitalia. Thus, muscle m_i (depressor of uncus, elevator of gnathos) is certainly absent since both sclerites, uncus, and gnathos, are absent; the ventral wall of the tegumen (one of the synapomorphy of the subfamily Dichomeridinae) is absent; and the intrategminal (within cylindric tegumen, that is typical for Dichomeridins) position of the muscle m_1 (flexor of valva) is lost. Therefore, considering these synapomorphies (i.e., presence of well-developed parategminal sclerites, and functioning of the latter as apodemes for muscle m_i), Tawaya should be assigned to the subfamily Dichomeridinae. The remaining morphological transformations accompanying the loss of structures and muscles could be considered evidence of the early divergence of the new genus from the general evolutionary stem of the group of genera within the subfamily Dichomeridinae and the subsequent independent development for a long time. Thus, the new genus is added to the generic list of Dichomeridinae with temporary taxonomic position—subfamily Dichomeridinae: genus *Tawaya* insertae sedis.

Acknowledgments

We express our cordial appreciation to Dr. John Brown (Washington, U.S.A.) for correcting of the grammar errors in our manuscript. Also, we grateful to K.A. Vinnikov and A.A. Semenchenko (Laboratory of Ecology and Evolutionary Biology of the Aquatic Organisms, FEFU, Vladivostok, Russia) for the opportunity to conduct the molecular part of this investigation using the equipment of the Laboratory and their helpful consultations on the Sanger sequencing method.

References

- Abraham, D., Ryrholm, N., Wittzell, H., Holloway, J.D., Scoble, M.J. & Löfstedt, C. (2001) Molecular Phylogeny of the Subfamilies in Geometridae (Geometroidea: Lepidoptera). *Molecular Phylogenetics and Evolution*, 20 (1), 65–77. https://doi.org/10.1006/mpev.2001.0949
- Applied Biosystems (2005) Sequence Scanner. Version 1.0. Applied Biosystems: Product Bulletin 106PB13-01. Available from: https://sequence-scanner.informer.com/1.0/ (accessed 6 July 2021)
- Belshaw, R. & Quicke, D.L.J. (1997) A molecular phylogeny of the Aphidiinae (Hymenoptera: Braconidae). *Molecular Phylogenetics and Evolution*, 7, 281–293.

https://doi.org/10.1006/mpev.1996.0400

- Darlington, P.J. (1957) Zoogeography: the geographical distribution of animals. John Wiley & Sons, Inc., New York, 675 pp. Falkovitsh, M.I. & Stekolnikov, A.A. (1978) Introduction. *In:* Medvedev, G.S. (Ed.), *Key to the insects of European part of Russia. Vol. 4. Lepidoptera. Part 1.* Nauka, Leningrad, pp. 5–27. [in Russian]
- Gillespie, J.J., Johnston, J.S, Cannone, J.J. & Gutell, R.R. (2006) Characteristics of the nuclear (18S, 5.8S, 28S and 5S) and mitochondrial (12S and 16S) rRNA genes of *Apis mellifera* (Insecta: Hymenoptera): structure, organization, and retrotransposable elements. *Insect Molecular Biology*, 15 (5), 657–686. https://doi.org/10.1111/j.1365-2583.2006.00689.x
- Klots, A.B. (1970) Lepidoptera. *In:* Tuxen, S.L. (Ed.) *Taxonomist's glossary of genitalia in insects*. Munksgaard, Copenhagen, pp. 115–130.
- Hancock, J.M., Tautz, D. & Dover, G.A. (1988) Evolution of the Secondary Structures and Compensatory Mutations of the

- Ribosomal RNAs of Drosophila melanogaster. Molecular Biology and Evolution, 5 (4), 393-414.
- Hodges, R.W. (1986) Gelechioidea: Gelechiidae (in part). Fasc. 7.1 Dichomeridinae. *In: Moths of America North of Mexico*. The Wedge Entomiological Research Foundation, Washington, pp. vii–xiii + 1–195.
- Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16 (2), 111–120. https://doi.org/10.1007/BF01731581
- Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33 (7), 1870–1874. https://doi.org/10.1093/molbev/msw054
- Larsen, N. (1992) Higher order interactions in 23S rRNA. *Proceeding of the National Academy of Sciences of the United States of America*, 89, 5044–5048. https://doi.org/10.1073/pnas.89.11.5044
- Meyen, S.V. (1987) Geography of macroevolution in higher plants. *Journal of General Biology*, 48 (3), 291–309.
- Patterson, J., Chamberlain, B. & Thayer, D. (2004) Finch TV. Version 1.4. 0. Publ. by Authors. [program]
- Ponomarenko, M.G. (1993) Functional morphological analysis of male genitalia of the gelechiid moths of the subfamily Dichomeridinae sensu novo (Lepidoptera, Gelechiidae). *Entomilogical Review*, 72 (2), 26–45.
- Ponomarenko, M.G. (2005) Gelechiid moths (Lepidoptera, Gelechiidae) of the Palaearctica: functional morphology of the male genitalia, phylogeny and taxonomy. *Meetings in memory of N.A. Cholodkovsky, St.-Petersburg*, 58 (1), 1–139. [in Russian]
- Robinson, G.S. (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist's Gazette*, 27, 127–132.
- Schmitz, J. & Moritz, R.F.A. (1994) Sequence analysis of the D1 and D2 regions of 28S rDNA in the hornet (*Vespa crabro*) (Hymenoptera, Vespinae). *Insect Molecular Biology*, 3 (4), 273–277. https://doi.org/10.1111/j.1365-2583.1994.tb00177.x
- Shirk, P.D., Perera, O.P., Shelby, K.S., Furlong, R.B., LoVullo, E.D. & Popham, H.J.R. (2015) Unique synteny and alternate splicing of the chitin synthases in closely related heliothine moths. *Gene*, 574, 121–139. https://doi.org/10.1016/j.gene.2015.08.001