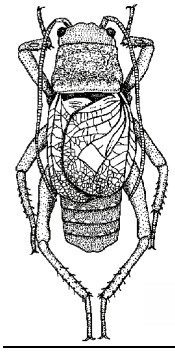

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REVISION OF THE GENERA *HETEROPTILON*, *NUGONIONEURA* AND *OPISTOCLADUS* FROM THE LOWER PERMIAN OF USA (INSECTA: CNEMIDOLESTIDA: TILLYARDEMBIIDAE, NUGONIONEURIDAE AND PARMAPTERIDAE)

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Summary. Holotypes of *Heteroptilon costale* Carpenter, 1976, *Nugonioneura problematica* Tillyard, 1937 and *Opistocladus arquatus* Carpenter, 1976 from Lower Permian Elmo locality in Kansas (USA) are redescribed. Family Heteroptilidae is synonymized with Tillyardembiidae; family Nugonioneuridae **nom. resurr.** is restored from synonyms of Tococladidae. Both families were attributed to the order Cnemidolestida. Monotypic genus *Opistocladus* Carpenter, 1976 is attributed to the family Parmapteridae (Cnemidolestida). Key to genera of Tillyardembiidae is provided also.

Key words: Insecta, Cnemidolestida, taxonomy, Permian, North America.

Д. С. Аристов. Ревизия родов *Heteroptilon*, *Nugonioneura* и *Opistocladus* из нижней перми США (Insecta: Cnemidolestida: Tillyardembiidae, Nugonioneuridae и Parmapteridae) // Дальневосточный энтомолог. 2020. N 401. С. 1-9.

Резюме. Переописаны голотипы *Heteroptilon costale* Carpenter, 1976, *Nugonioneura problematica* Tillyard, 1937 и *Opistocladus arquatus* Carpenter, 1976 из нижнепермского местонахождения Эльмо в Канзасе, США. Семейство Heteroptilidae сведено в синонимы к Tillyardembiidae, а семейство Nugonioneuridae восстановлено из синонимов семейства Tococladidae. Оба семейства отнесены к отряду Cnemidolestida. Род *Opistocladus* Carpenter, 1976 в составе типового вида отнесен к семейству Parmapteridae (Cnemidolestida). Дана определительная таблица родов семейства Tillyardembiidae.

INTRODUCTION

Monotypic families Heteroptilidae and Nugonioneuridae were described from Elmo locality (Leonardian Stage of Lower Permian, Kansas, USA) as representatives of the order Protorthoptera (Carpenter, 1976). Subsequently Heteroptilidae were retained within protorthopterans by the same author and Nugonioneuridae attributed to "Neoptera order uncertain" (Carpenter, 1992). Later, both families were synonymized with the family Tococladidae of the order Hypoperlida (Rasnitsyn, 2002). The type genera and species for both families (*Heteroptilon* Carpenter, 1976 and *Nugonioneura* Tillyard, 1937) are examined and redescribed below. Heteroptilidae is synonymized with Tillyardembiidae (Cnemidolestida). Nugonioneuridae is restored from synonymy and also transferred to the order Cnemidolestida. Genus *Opistocladus* Carpenter, 1976 originally was attributed to family Tococladidae of order Protorthoptera (Carpenter, 1976). Afterwards Tococladidae was considered as belonging to orders Protorthoptera (Carpenter, 1992), Hypoperlida (Rasnitsyn, 2002) or Archaeorthoptera (Béthoux & Nel, 2002). Herein the genus *Opistocladus* is transferred to the family Parmapteridae (Cnemidolestida).

TAXONOMY

Order Cnemidolestida Handlirsch, 1937

Suborder Cnemidolestina Handlirsch, 1937

Family Tillyardembiidae G. Zalessky, 1938

Tillyardembiidae G. Zalessky, 1938: 64 (type genus: *Tillyardembia* G. Zalessky, 1937); Sharov, 1962: 124; Rasnitsyn, 1980: 152; Carpenter, 1992: 123; Storozhenko, 1997: 8; 1998: 91; 2002: 279; Aristov & Rasnitsyn, 2009: 263; 2010: 17; 2012: 48; 2014: 411; Aristov, 2014: 20; Aristov, 2018: 1382.

Permocapniidae Martynov, 1940: 20 (type genus: *Permocapnia* Martynov, 1940); synonimized by G. Zalessky, 1950: 41–60.

Heteroptilidae Carpenter, 1976: 346 (type genus: *Heteroptilon* Carpenter, 1976); Carpenter, 1992: 126; **syn. n.**

Type genus: *Tillyardembia* G. Zalessky, 1937.

EMENDED DIAGNOSIS. Small and medium sized insects. SC ends in forking on C and RS. Starting in wings basal third, RS branching abundantly, with branches

occupy whole wing apex. M with prominent M_5 or M merged with CuA on a short section near the base. M with few branches, not split into MA and MP, start branching past base of RS. CuA start branching in its distal third, forms posterior branching comb. Posterior branches of CuA are lacking. Anal area small, with two or three anal veins.

COMPARISON. The family is most similar to Emphylopteridae from Carboniferous of France, but differs in branching CuA. Emphylopteridae have simple CuA (Aristov, 2014).

COMPOSITION. Five genera: *Tillyardembia* G. Zalessky, 1937 from Chekarda, Barda, Kishert' (Russia: Perm Region; Lower Permian, Kungurian Stage), and Zalazna (Russia: Kirov Region; Upper Permian, Vyatkian Stage), *Heteroptilon* Carpenter, 1976 (USA: Kansas; Lower Permian, Leonardian Stage), *Kungurembia* Aristov, 2004 from Chekarda and Soyana (Russia: Arkhangelsk Region; Middle Permian, Kazanian Stage), *Kamamica* Aristov et Rasnitsyn, 2014 from Tyul'kino (Russia: Perm Region; Lower Permian, Kungurian Stage), *Paralongzhua* Prokop, Szwedo, Lapeyrie, Garrouste et Nel, 2015 from Lodève (France: Languedoc Region; Middle Permian, Salagou Formation), and *Udembia* Aristov, 2018 from Kostovaty (Russia: Udmurtia; Middle Permian, Urzhumian Stage).

NOTE. The genus *Paralongzhua* was described within Archaeorthoptera *nec* Panorthoptera as family undetermined taxon (Prokop *et al*., 2015). Comparison with the rest of tillyardembiids shows attribution of *Paralongzhua* to this family (see key below).

Key to genera of the family Tillyardembiidae based on forewing characters

1(6) Costal field near base of RS is equal in width with subcostal one.
2(3) SC ends in wings distal third ..... ***Paralongzhua*** Prokop, Szwedo, Lapeyrie, Garrouste et Nel, 2015
3(2) SC ends near wings mid length.
4(2) Preradial field narrow ..... ***Udembia*** Aristov, 2018
5(7) Preradial field wide ..... ***Heteroptilon*** Carpenter, 1976
6(1) Costal field near base of RS wider that subcostal one.
7(10) Forewing with costal fan at the base of subcostal field.
8(9) Base of M not merged with CuA, M and CuA connected with short M_5 ..... ***Tillyardembia*** G. Zalessky, 1937
9(8) Base of M merged with CuA ..... ***Kamamica*** Aristov et Rasnitsyn, 2014
10(7) Costal fan is lacking ..... ***Kungurembia*** Aristov, 2004

Genus *Heteroptilon* Carpenter, 1976

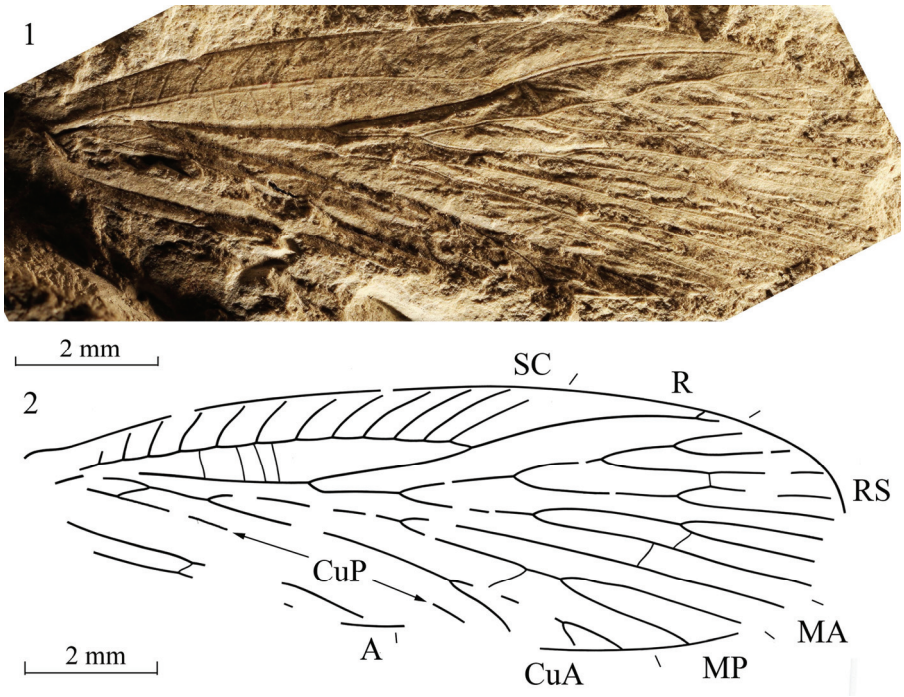
Heteroptilon Carpenter, 1976: 347; 1992: 126; Rasnitsyn, 2002: 112; Béthoux *et al*., 2003: 278.

Type species: *Heteroptilon costale* Carpenter, 1976, by original designation.

DIAGNOSIS. Forewing with costal fan in the base of subcostal field. Preradial field near the base of RS is very wide. Costal field near the base of RS is equal in width to subcostal one. SC ends right past wings mid length. Apex of SC and base

of RS, which starts at the level of wings basal third, are drawn close. M merges with CuA near its base, M start branching at wings mid length. CuA branching at its apex, branching comb short.

SPECIES INCLUDED. Type species only.



Figs 1, 2. *Heteroptilon costale* Carpenter, 1976, forewing, holotype MCZ, № 5878.

NOTE. Family Heteroptilidae was erroneously synonimized under Tococladidae (Hypoperlida) by reason of similarity of the genera *Heteroptilon* and *Opistocladus* (Rasnitsyn, 2002). It was based mainly on RS drawn close to apex of SC, which ends in forking into C and R. This character is not unique for *Opistocladus* and is characteristic for many Cnemidolestidae (Cnemidolestida; see: Aristov, 2014). From Tococladidae *Heteroptilon* differs in anastomosis of M+CuA and lacking of posterior branches of CuA in intercubital field. In Tococladidae M and CuA are connected by M_5, CuA with posterior branches in intercubital field (Carpenter, 1976; Béthoux *et al*., 2003).

***Heteroptilon costale* Carpenter, 1976**

Figs 1, 2

Heteroptilon costale Carpenter, 1976: 347, fig. 8; 1992: 126, fig. 73, 7; Béthoux *et al*., 2003: 278.

MATERIAL. Holotype MCZ, № 5878, positive imprint of deformed forewing; United States, Kansas, Dickinson County, Banner Township, 5 km southeast of Elmo

town, Elmo locality; Lower Permian, Lower Leonardian, Sumner Group, Wellington Formation, Carlton Member; in MCZ.

REDESCRIPTION. Anterior margin of forewing is convex. Anterior branches of SC near wings mid length are numerous and long, strongly inclined anteriorly. RS branching early and abundantly, posteriorly subpectinate, with nine branches. Anterior branch of M simple, posterior with two apices. CuA with three branches. A_1 simple, A_2 bifurcated. Transverse veins simple, numerous in subcostal field.

MEASUREMENTS. Forewing length 15 mm.

Family Nugonioneuridae Carpenter, 1976, nom. resurr.

Nugonioneuridae Carpenter, 1976: 377 (type genus: *Nugonioneura* Tillyard, 1937); Rasnitsyn, 1980: 43; Carpenter, 1992: 500; synonimized under Tococladidae by Rasnitsyn (2002).

Type genus: *Nugonioneura* Tillyard, 1937.

DIAGNOSIS. Small insects. Forewings preradial field is moderately wide. SC ends in forking into C and R near wings mid length. RS starts at the wing's mid length, drawn near to SC apex, merged with MA, equal in size with CuA. Base of M at the short area merged with CuA, M starts branching at wings mid length. CuA without posterior branches, starts branching before its mid length. Apices of anal veins are not merging with each other.

COMPARISON. *Nugonioneura* is most similar to *Psoroptera* Carpenter, 1976 (Cnemidolestida: Psoropteridae) (Aristov, 2014) from the Permian locality Elmo in USA, it differs in SC, ends with forking into C and R, apex of SC drawn close to base of RS, which starts at wings mid length, lacking of anal loop. In Psoropteridae SC ends at C, apex of SC not drawn close with base of RS, which starts at wings basal quarter (Aristov, 2014).

GENERAE INCLUDED. Type genus.

NOTE. Like *Heteroptilon*, *Nugonioneura* was attributed to hypoperlids Tococladidae (Rasnitsyn, 2002). *Heteroptilon* differs from the most similar genus *Opistocladus* in late branching of M, anastomosis of M and CuA bases and lacking of posterior branches of CuA. In Tococladidae M branching in wings basal third, M and CuA are connected by M_5, CuA have posterior branches in intercubital field (Carpenter, 1976; Béthoux *et al*., 2003).

Genus *Nugonioneura* Tillyard, 1937

Nugonioneura Tillyard, 1937: 92; Carpenter, 1976: 337; 1992: 337; Béthoux *et al*., 2003: 278.

Type species: *Nugonioneura problematica* Tillyard, 1937, by original designation.

DIAGNOSIS. As for family because of monotypy.

SPECIES INCLUDED. Type species only.

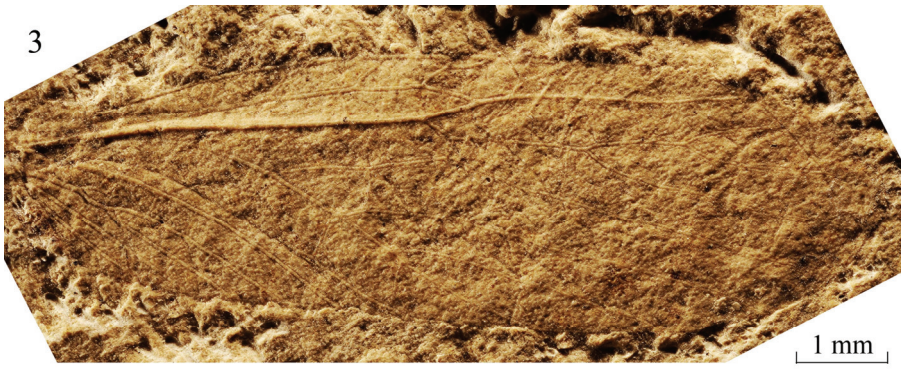
***Nugonioneura problematica* Tillyard, 1937**
Figs 3, 4

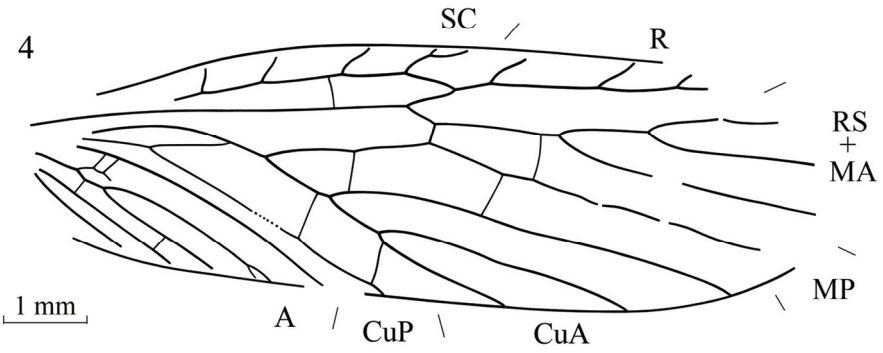
Nugonioneura problematica Tillyard, 1937: 94, fig. 4; Carpenter, 1976: 337, figs 1-3; 1992: 500; Béthoux *et al*., 2003: 278.

MATERIAL. Holotype MCZ, № 5895, positive imprint of forewing; United States, Kansas, Dickinson County, Banner Township, 5 km southeast of Elmo town, Elmo locality; Lower Permian, Lower Leonardian, Sumner Group, Wellington Formation, Carlton Member; in MCZ.

REDESCRIPTION. Small insects. Anterior margin of forewing is convex. Costal field in wings basal third equal to subcostal one in width. SC curved parallel to wings anterior margin. SC and R with sparse simple or Y-shaped anterior branches. RS+MA with three branches, MP simple. CuA anteriorly pectinate with three long branches. Intercubital field wide, A_1 simple, A_2 with four branches. Transverse veins simple.

MEASUREMENTS. Forewing length 10 mm.





Figs 3, 4. *Nugonioneura problematica* Tillyard, 1937, forewing, holotype MCZ, № 5895.

Family Parmapteridae Aristov et Rasnitsyn, 2015

Genus *Opistocladus* Carpenter, 1976

Opistocladus Carpenter, 1976: 342; 1992: 126; Rasnisyn, 2002, 112; Béthoux & Nel, 2002: 25; Béthoux *et al*., 2003: 277; Rasnisyn & Aristov, 2013: 686; 2015: 19.

Type species: *Opistocladus arquatus* Carpenter, 1976, by original designation.

DIAGNOSIS. Forewing with prominent ScA, reaching wing basal third, precostal field narrow. ScP ends at R. Costal field at base of RS equal in width to subcostal one. RS with few branches, starts at wings mid length, its base lies close to apex of ScP. M with prominent M_5, divided into branches at wings mid length, MA and RS with fissures, where they are connected by transverse vein. M_5 goes into CuA after its first divide into branches. Posterior branch of CuA with fissures where transverse veins merges with it. Anal area modified into clavus.

COMPARISON. *Opistocladus* is most similar to genus *Parmaptera* Aristov et Rasnitsyn, 2015 from Lower Permian locality Chekarda in Russia (Kungurian Stage, Perm Region) but differs in narrow costal field, fewer number of RS branches and M_5, merges into CuA after its first branching. In *Parmaptera* costal field at base of RS four times wider than subcostal one, RS subpectinate, with five or more branches, M_5 merges into CuA after its second branching. CuP curved at its base. Anal area not modified into clavus (Aristov & Rasnitsyn, 2015). Lacking of precostal field on holotype of *P. permiana* is a result of preservation; perpendicular anterior branches at the SC base usually merge with SC and ScA.

SPECIES INCLUDED. Type species only.

NOTE. The taxonomic position of *Opistocladus strictus* Carpenter, 1976 from Elmo (Carpenter, 1976) and *O. kargalensis* Rasnitsyn et Aristov, 2013 from Kargala locality (Russia: Orenburg Region, Middle Permian, Urzhumian Stage (Carpenter, 1976; Rasnitsyn & Aristov, 2013) are not certain because of these taxa considerably differs from *O. arquatus* and probably belong to the family Tococladidae.

Opistocladus arquatus Carpenter, 1976

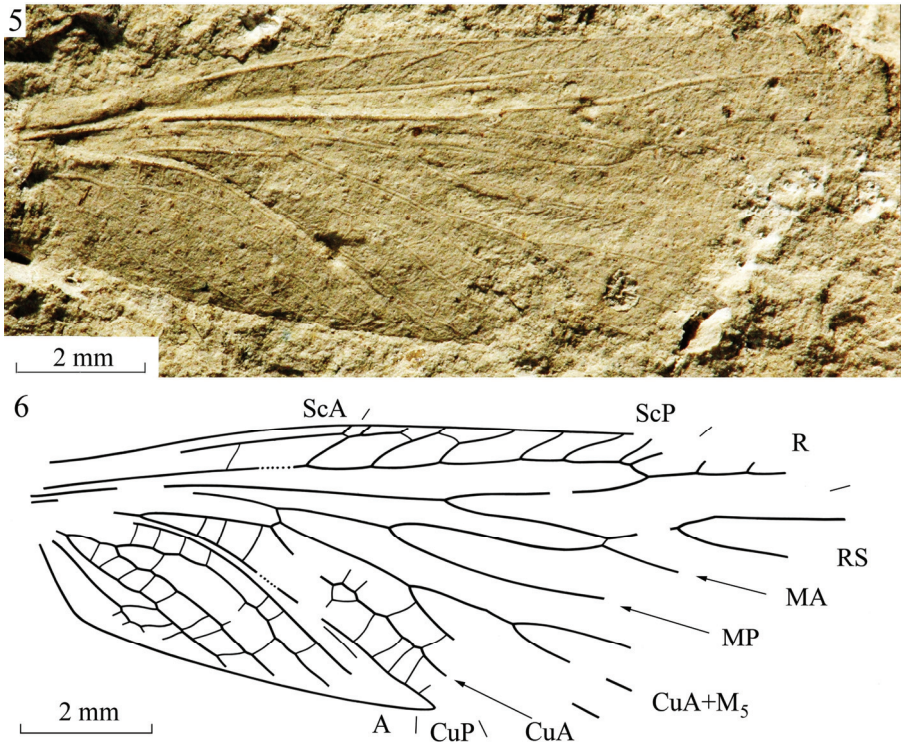
Figs 5, 6

Opistocladus arquatus Carpenter, 1976: 342, fig. 4; 1992: 126; Béthoux & Nel, 2002: 25; Béthoux *et al*., 2003: 278.

MATERIAL. Holotype MCZ, № 5882, positive and negative imprints of forewing; United States, Kansas, Dickinson County, Banner Township, 5 km southeast of Elmo town, Elmo locality; Lower Permian, Lower Leonardian, Sumner Group, Wellington Formation, Carlton Member; in MCZ.

REDESCRIPTION. Anterior branches of ScA sparse. RS with 2-3 branches. MA and MP are simple prior to wings distal third. CuA+M_5 with three or more branches, posterior branch of CuA simple. A_1 with three branches, A_2 simple or with two branches. Transverse veins simple.

MEASUREMENTS. Forewing length about 15 mm.



Figs 5, 6. *Opistocladus arquatus* Carpenter, 1976, forewing, holotype MCZ, № 5882.

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