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.

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

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 Tillyardemiidae (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 Tillyardemiidae G. Zalessky, 1938

Tillyardemiidae 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); synonymized 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 М or М 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, Bara, Kishert’ (Russia: Perm Region; Lower Permian, Kungurian Stage), and Zalazna (Russia: Kirov Region; Upper Permian, Vyatian 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
3(2) SC ends near wings mid length.
4(2) Preradial field narrow
5(7) Preradial field wide
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 М5
9(8) Base of M merged with CuA
10(7) Costal fan is lacking

**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.

NOTE. Family Heteroptilidae was erroneously synonymized 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 M₅, 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. A₁ simple, A₂ 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; synonymized 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* differ 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 *M₅*, 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, A₁ simple, A₂ with four branches. Transverse veins simple.

**MEASUREMENTS.** Forewing length 10 mm.

![Fig 3](image1.png)

![Fig 4](image2.png)

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; Rasnitsyn, 2002, 112; Béthoux & Nel, 2002: 25; Béthoux et al., 2003: 277; Rasnitsyn & Aristov, 2013: 686; 2015: 19.

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

DIAGNOSIS. Forewing with prominent ScA, reaching wing basal third, pre-costal 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 M₁, divided into branches at wings mid length, MA and RS with fissures, where they are connected by transverse vein. M₅ 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 M₅, 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, M₅ 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 O. 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 Lower Permian locality Chekarda in Russia (Kungurian Stage, Perm Region) but differs in narrow costal field, fewer number of RS branches and M₅, 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, M₅ 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 O. permiana is a result of preservation; perpendicular anterior branches at the SC base usually merge with SC and ScA.

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+M₅ with three or more branches, posterior branch of CuA simple. A₁ with three branches, A₂ simple or with two branches. Transverse veins simple.

MEASUREMENTS. Forewing length about 15 mm.
Figs 5, 6. *Opistocladius arquatus* Carpenter, 1976, forewing, holotype MCZ, № 5882.

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