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D. S. Aristov. NEW SUBORDER OF THE PALEOZOIC-MESOZOIC ORDER CNEMIDOLESTIDA (INSECTA: GRYLLONES). – Far Eastern Entomologist. 2016. N 311: 13-22.

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Summary. Families Parmapteridae Aristov et Rasnitsyn, 2015, Protembiidae Tillyard, 1937, Pinideliidae Storozhenko, 1997 from the Paleozoic of the North America and Eurasia, and Juraperlidae Huang et Nel, 2007 from the Mesozoic of the Asia are assigned to the new suborder Parmapterina **subord. n.** of the order Cnemidolestida. Origin of the superorder Orthopteroidea is discussed.

Key words: Insecta, Cnemidolestida, Parmapterina, taxonomy, Carboniferous, Permian, Triassic, Jurassic.

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Резюме. Семейства Parmapteridae Aristov et Rasnitsyn, 2015, Protembiidae Tillyard, 1937 и Pinideliidae Storozhenko, 1997 из палеозоя Северной Америки и Евразии и Juraperlidae Huang et Nel, 2007 из мезозоя Азии выделены в качестве подотряда Parmapterina **subord. n.** отряда Cnemidolestida. Обсуждается происхождение надотряда Orthopteroidea.

Gerarida is considered as the most primitive order of the orthopteroids (superorder Orthopteroidea) (Gorochov, 2004). Eoblattida *sensu* Rasnitsyn, 2002 were supposedly ancestral to this order; the branching *CuP* in the forewing was considered the principal apomorphy. In addition, gerarids, as well as the other orthopteroids, have the precostal area separated by the "*C*", *SC* ending on *C*, base of *RS* and first bifurcation of *M* shifted towards the middle of the wing, and *CuA* dividing into CuA_1+M_5 and CuA_2 (Gorochov, 2004). *R* and CuA_1+M_5 in Gerarida are convex, and *RS* and *M* are strongly concave. Most of the above-listed characters are typical of the Carboniferous Cheliphlebiidae (Aristov, 2014). This family is distinguished from gerarids only by the presence of posterior branches of *CuA* in the intercubital area and by the simple *CuP*. This similarity is so strong that it makes cheliphlebiids more similar to gerarids than to other primitive Orthopteroidea. Therefore, it is preferable to treat Cheliphlebiidae as Orthopteroidea incerti ordinis.

All the above-listed apomorphies of orthopteroids are separately found in several families of primitive Perlidea (Parmapteridae, Protembiidae, Pinideliidae and Juraperlidae), assigned in this study to the suborder Parmapterina of the order Cnemidolestida. The family Parmapteridae is characterized by the anastomosis M_5+CuA_1. The genus *Parmaptera* is also known to have the base of *RS* and first bifurcation of *M* shifted towards the middle of the wing (Figs. 1–3), and one of the species of *Heterologus* is known to have a short bifurcation on *CuP*. In *Heterologus R* and *M* are basal to M_5, M_5 itself and CuA_1 are strongly convex, *RS* and *M* are concave. Some Protembiidae have the anastomosis M_5+CuA_1 and the costal lobe (area at the base of the costal area separated by a fold, functional counterpart of the precostal

area; Fig. 4). All Juraperlidae have the typical false costa; *Ferganomadygenia* has M_5 joining CuA_1 and a short fork on *CuP* (Fig. 5); *Juraperla* has the base of *RS* shifted towards the middle of the wing. In *Juraperla* M_5 joins *CuA* just proximal to its bifurcation. The common feature of all above-listed families distinguishing them all from orthopteroids is *SC* that ends on *R* or ends in bifurcation on *R* and *C*. Paranota of the pronotum are absent in these families, as well as in gerarids. Thus, gerarids are probably descended from Carboniferous Parmapterina similar to Parmapteridae, in which the apex of *SC* shifted onto *C*, the precostal area evolved (the structure of the base of the costal area of Parmaridae is unknown), and the division of *CuP* became proximal.

Several groups of Carboniferous insects that demonstrate some similarity to Parmapterina and Gerarina are known to date. The family Cheliphlebiidae is compared to these groups above. *Herbstiala herbsti* Shmidt, 1953 of the family Herbstialidae (Protorthoptera: Carpenter, 1992; Paoliida: Prokop *et al*., 2013, Westphalian of Germany) is characterized by the precostal area present, *SC* ending on *R*, *M* dividing in the middle of the wing, and *CuP* dividing. *Herbstiala* is distinguished from Parmapterina and Gerarina in the absence of division of *CuA* into CuA_1 and CuA_2 and presence of the clavus (assigned to Gryllones incerti ordinis: Rasnitsyn & Aristov, 2016). *Merlebachia grimaldi* Waterlot, 1934 (incerti ordinis: Carpenter, 1992; Westphalian of France) has a combination of the precostal area, *RS* beginning distally, *M* dividing distally, and *CuP* dividing (Fig. 6). This species is distinguished from Parmapterina and Gerarina by the absence of the division of *CuA* into CuA_1 and CuA_2 and by the very long anal area (Waterlot, 1934). *Polyernus complanatus* Scudder 1885 (Eoblattida incertae familiae: Rasnitsyn, 2002, Westphalian of the United States) possibly also had the precostal area; the base of *RS* and first bifurcation of *M* are shifted in this species towards the middle of the wing, M_5 joins CuA_1, and *CuP* divides (Fig. 7). *P. complanatus* is especially similar to Gerarida and differs from Gerarida and Parmapterina in the presence of broad paranota. In addition, this species differs from Gerarida in *SC* ending on *R* (Rasnitsyn, 2002). *Stenoneura fayoli* Brongniart, 1885 (Stephanian of France; Eoblattida, Stenoneuritidae: Rasnitsyn, 2004) is similar in the absence of paranota, distal beginning of *RS* and first bifurcation of *M*, M_5 joining *CuA* distal to its first bifurcation, and dividing *CuP* to Parmapterina and Gerarina and differs from them in *SC* ending on *C* and *CuA* without division into CuA_1 and CuA_2 (Béthoux & Nel, 2002; Rasnitsyn *et al*., 2004). The absence of the division of *CuA* into CuA_1 and CuA_2 in *Herbstiala*, *Merlebachia*, and *Stenoneura* and the presence of paranota in *Polyernus* do not allow me to assign these genera to Parmapterina. Until additional material on primitive Carboniferous Gryllones becomes available, I suggest treating the above-listed genera as Cnemidolestida incertae sedis, close to Parmapterina.

TAXONOMY

CLASS INSECTA LINNÉ, 1758

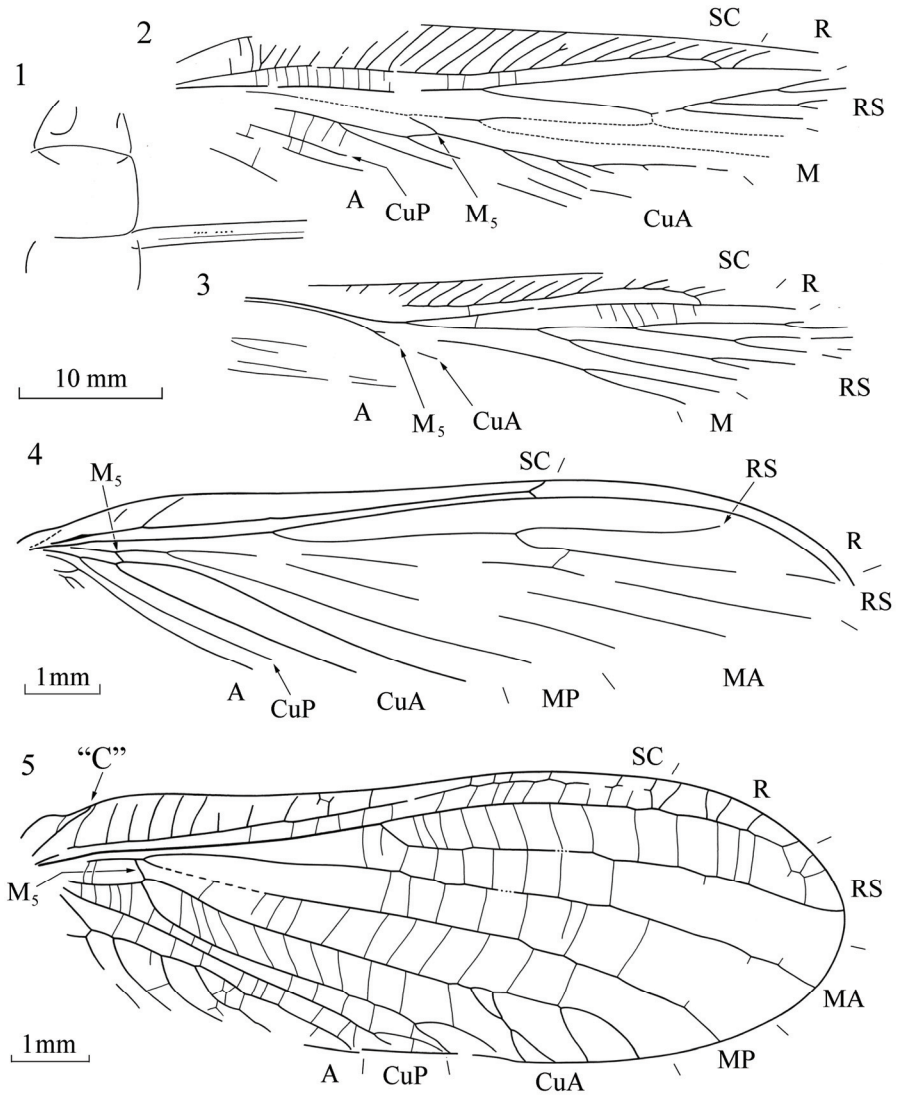
INFRACLASS GRYLLONES LAICHARTING, 1781

Superorder Perlidea Latreille, 1802

Order Cnemidolestida Handlirsch, 1937

Cnemidolestodea: Handlirsch, 1937: 63.
Cnemidolestida: Aristov, 2014: 5.

DIAGNOSIS. Pronotum without paranota; hindlegs not saltatorial. Wings folded flatly; right and left pairs of wings incompletely overlapping at rest. Forewing not elytrized, often



Figs. 1–5. Suborder Parmapterina, families Parmapteridae, Protembiidae and Juraperlidae. 1–3 – *Parmaptera p–ermiana* Aristov et Rasnitsyn, 2015, holotype PIN, No 1700/4935: 1 – part of body; 2, 3 – fore and hindwings, Chekarda, Lower Permian of Russia (after Aristov, Rasnitsyn, 2015, with changes); 4 – *Tshekardembia sharovi* Novokshonov, 1995, fragment of holotype PIN, No 4987/103, forewing (after Aristov, 2015a); 5 – *Ferganomadygenia plicata* Storozhenko et Vrsansky, 1995, holotype PIN, No 2555/717, Madygen, Middle Triassic of Kyrgyzstan (original).

with oligomerized venation. *RS* without sharp at joining crossveins; strong *r-rs* and *rs-m* absent. Base of *M* free, often with developed M_5 or fused with *CuA*. *M* starting branching in basal one-third of wing at some distance distal to M_5 (except in some Cnemidolestina). *CuA* usually without posterior branches in intercubital area (except in some Cnemidolestina), dividing rather distally, usually pectinate posteriad or (in Parmapterina) divided into CuA_1 and CuA_2 in its basal quarter; *CuP* simple (in some Parmapterina with short fork). Clavus usually absent. Hindwing at rest not tucking down transversely, with anal lobe tucking down, distinguished from forewing mainly by more proximal *RS* and more distally dividing *M* and *CuA*. Male genitalia symmetrical; ovipositor present; cerci articulate.

COMPOSITION. Two suborders from the late Paleozoic and early Mesozoic.

Suborder Cnemidolestina Handlirsch, 1937

DIAGNOSIS. "*C*" absent (except in Ctenoptilidae and some Cnemidolestidae), costal lobe absent (except in Prygidae and some Spanioderidae and Sylvabestiidae). *SC* ending in distal third of wing in bifurcation on *SC* and *R* (except in Gerapompidae, Cymenophlebiidae, and Sylvabestiidae). *RS* beginning in basal third of wing (except in Prygidae and some Sylvabestiidae). *RS* and *M* convex or neutral. If first bifurcation not reduced (in some Cnemidolestidae), *M* dividing in basal one-third of wing (in Tillyardembiidae and Cymenophlebiidae near wing middle; in Prygidae M simple or with short fork). M_5 and first bifurcation of *M* not closely set. M_5 joining *CuA* at some distance proximal to its division into branches. *CuA* not divided into CuA_1 and CuA_2, pectinate posteriad, densely branching distal to its basal one-third. Posterior branches of *CuA* absent (except in Ctenoptilidae); *CuP* simple. Clavus absent (except in Cymenophlebiidae and some Cnemidolestidae).

COMPOSITION. 11 families from the Carboniferous and Permian of North and South America, Eurasia, Madagascar and from the Triassic of Europe: Cnemidolestidae Handlirsch, 1906, Spanioderidae Handlirsch, 1906, Gerapompidae Handlirsch, 1906, Cymenophlebiidae Pruvost, 1919, Emphylopteridae Handlirsch, 1922, Tillyardembiidae G.Zalessky, 1938; Psoropteridae Carpenter, 1976; Sylvabestiidae Aristov, 2000, Prygidae Aristov et Rasnitsyn, 2014, Neraphidiidae Aristov, 2014, and Ctenoptilidae Aristov, 2014.

Suborder Parmapterina Aristov, subord. n.

DIAGNOSIS. Base of costal area with costal lobe or with false *C*. *SC* ending in distal one-third of wing on *R* or in bifurcation (in some Protembiidae *SC* possibly ending on *C*). *RS* beginning near wing middle (in Protembiidae in basal one-third of wing). *M* dividing in basal quarter of wing (in Parmapteridae near middle or more distally). M_5 and first bifurcation of *M* closely set. M_5 joining *CuA* distal to its division into branches or immediately proximal to this bifurcation (in most Protembiidae base of *M* fused with *CuA* and also in most Protembiidae CuA_1 and CuA_2 diverging from this anastomosis as separate stems). In *Heterologus R* and *M* basal to M_5, M_5 itself and CuA_1 strongly convex, *RS* and *M* concave. In other genera *RS* and *M* weakly convex or neutral. *CuA* divided into CuA_1 and CuA_2 in its basal quarter, posterior branches of *CuA* absent, *CuP* simple (in *Heterologus duyiwuer* and *Ferganomadygenia* with short forks), clavus absent.

COMPARISON. The new suborder is distinguished from the suborder Cnemidolestina in the proximal division of *CuA* into CuA_1 and CuA_2, so that M_5 joins CuA_1, rather than the stem *CuA*. In Cnemidolestina M_5 joins *CuA* proximal to its division into branches, and *CuA* is not divided into CuA_1 and CuA_2.

COMPOSITION. Four families: Parmapteridae Aristov et Rasnitsyn, 2015 from the Carboniferous of USA and China and from the Permian of Russia; Protembiidae Tillyard, 1937 from the Permian of USA, Czech, Russia, Kazakhstan and Mongolia, Pinideliidae Storozhenko, 1997 from the Permian of Russia and Juraperlidae Huang et Nel, 2007 from the Triassic of Kyrdyzstan and the Jurassic of China.

NOTE. Juraperlidae are similar in wing venation to the Upper Permian Tunguskapteridae (Storozhenko & Vršanský, 1995), represented by a single genus, *Tunguskaptera* (the second genus of this family, *Ferganomadygenia*, is transferred below into Juraperlidae). This family is distinguished from Juraperlidae in the paranota of the pronotum, *SC* ending on *C*, and M_5 joining *CuA* basal to its first bifurcation. The family Tunguskapteridae (which includes only the type genus) should be assigned to the order Reculida (*sensu* Aristov, 2015b).

Key to families of the suborder Parmapterina

1 (2) *SC* ending on *R*. *M* dividing into branches near wing middle or distal to it .... **Parmapteridae** Aristov et Rasnitsyn, 2015
2 (1) *SC* ending on *C* or ending in bifurcation on *C* and *R*. *M* dividing into branches in basal quarter of wing.
3 (6) Base of costal area with costal lobe.
4 (5) CuA_2 simple ..... **Protembiidae** Tillyard, 1937
5 (4) CuA_2 dividing ..... **Pinideliidae** Storozhenko, 1997
6 (3) Wing with precostal area ..... **Juraperlidae** Huang et Nel, 2007

Family Parmapteridae Aristov et Rasnitsyn, 2015

Parmapteridae: Aristov & Rasnitsyn, 2015: 19.

Type genus: *Parmaptera* Aristov et Rasnitsyn, 2015.

DIAGNOSIS. Large insects with small head, rather small pronotum, and long, possibly raptorial, forelegs. Forewing with costal area wide, *SC* ending on *R* in distal one-third of wing, *RS* beginning near wing middle (except in *Heterologus*), *M* starting branching near wing middle (in some *Heterologus* slightly more distally). M_5 joining CuA_1 proximal to its first bifurcation, M_5 and first bifurcation of *M* not closely set (except in *Parmaptera*). *CuP* simple (in some *Heterologus* with short bifurcations).

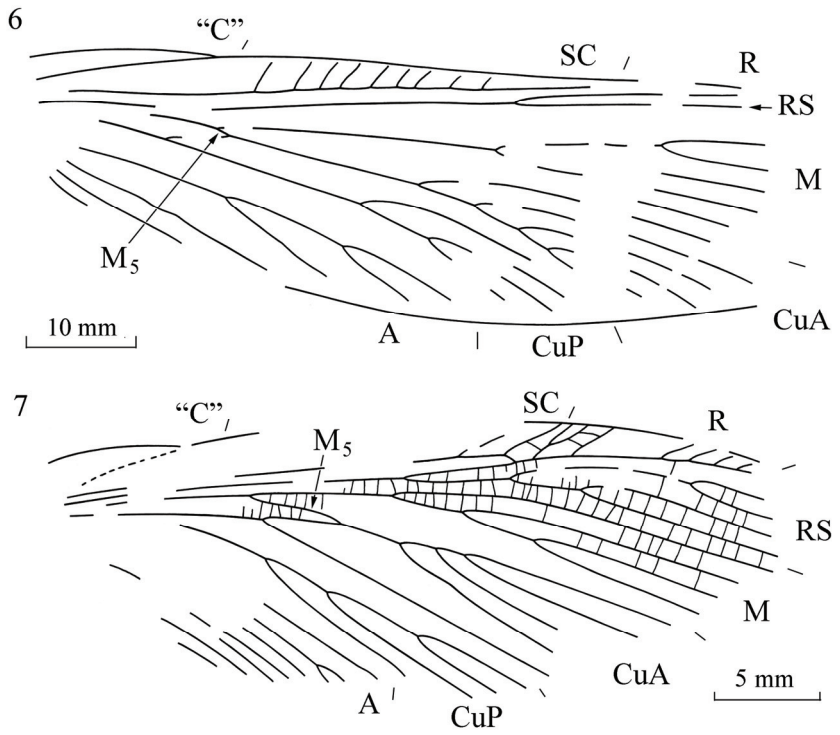
COMPOSITION. Two genera: *Parmaptera* Aristov et Rasnitsyn, 2015 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage) (Figs. 1–3) and *Heterologus* Carpenter, 1944 from Mazon Creek (USA, Illinois; Upper Carboniferous, Westphalian Stage) and Xiaheyan (China, Ningxia; Upper Carboniferous, Namurian Stage).

Family Protembiidae Tillyard, 1937

Protembiidae: Tillyard, 1937: 243; Carpenter, 1950: 207; Sharov, 1962: 124; Rasnitsyn, 1980: 152; Carpenter, 1992: 115; Storozhenko, 1997: 7; 1998: 91; 2002: 279; Aristov & Rasnitsyn, 2011: 120.

Sylvardembiidae: Novokshonov, 2000: 44; Storozhenko, 2002: 297; Aristov, 2004: 85; synonymised by Aristov & Rasnitsyn, 2011: 120.

Type genus: *Protembia* Tillyard, 1937.



Figs. 6–7. Gryllones incertae sedis, forewings: 6 – *Merlebachia grimaldi* Waterlot, 1934, fragment of holotype, Merlebach, Upper Carboniferous of France (original drawing based on photograph of holotype MhUL, after Waterlot, 1934: Pt. XVIII, Fig. 1); 7 – *Polyernus complanatus* Scudder 1885, fragment of holotype USNM, No 38144, forewing; Mazon Creek, Upper Carboniferous of USA (original drawing based on photograph by A.P. Rasnitsyn).

DIAGNOSIS. Medium-sized insects. Head large or medium-sized; pronotum medium-sized, comparable in size to or markedly smaller than head. Legs medium-sized or shortened (sometimes strongly). Forewing with costal area usually somewhat wider than subcostal area, with pronounced costal lobe. *SC* ending in bifurcation on *C* and *R* or on *C* (in some *Aibolitus* on *R*) in distal half of wing (in *Soyanocadaver* and *Parbarmaleus* in basal quarter of wing). *RS* beginning in basal one-third of wing, often fused with *M*. Base of *M* usually fused with *CuA; CuA_1* and *CuA_2* diverging from anastomosis as separate stems (except in *Soyanocadaver* and some *Tshekardomina*). In *Tshekardembia* base of *M* free, *M_5* joining *CuA_1* and set closely to first bifurcation of *M*. *M* dividing in basal one-third of wing (in *Sigmophlebia* near wing middle). *CuP* simple. Ovipositor short (except in *Sojanoraphidia* and *Aibolitus*).

COMPOSITION. 15 genera: *Protembia* Tillyard, 1937 from Elmo (United States, Kansas; Lower Permian, Leonardian (Artinskian) Stage), *Sojanoraphidia* O. Martynova, 1952 from Chekarda (Russia, Perm Region; Lower Permian, Kungurian Stage) and Soyana (Russia, Arkhangelsk Region; Middle Permian, Kazanian Stage); *Ventopterum* Kukalová, 1964 from

Obora (Czech Republic, Moravia; Lower Permian, Sakmarian Stage); *Aibolitus* Novokshonov et Storozhenko, 1996 from Elmo and Chekarda; *Tshekardembia* Novokshonov, 1995 (Fig. 4); *Sylvardembia* Novokshonov, 1997; *Barmaleus* Novokshonov, 1997; *Paratillyardembia* Aristov, 2000 from Chekarda; *Parbarmaleus* Novokshonov, 1997 from Soyana; *Tshekardomina* Novokshonov et Aristov, 2002 from Chekarda, Soyana, and Bor-Tologoi (Mongolia, East Gobi Province; Middle Permian, Urzhumian Stage); *Sigmophlebia* Béthoux et Beckmeyer, 2007 from Midco (United States, Oklahoma; Lower Permian, Leonardian (Artinskian) Stage), Chepanikha (Russia, Udmurtia; Middle Permian, Urzhumian Stage), and Karaungir (Kazakhstan, East Kazakhstan Province; Middle Permian, Urzhumian Stage); *Repka* Aristov et Rasnitsyn, 2011 from Soyana; *Kuplya* Aristov, 2013 from Novo-Aleksandrovka (Russia, Orenburg Region; Upper Permian, Severodvinian Stage); *Soyanocadaver* Aristov, 2015 from Soyana; and *Kirovopteron* Aristov, 2015 from Kityak (Russia, Kirov Region; Middle Permian, Kazanian Stage).

Family Pinideliidae Storozhenko, 1997

Pinideliidae: Storozhenko, 1997: 11; 1998: 116; Aristov, 2004: 91; 2015: 1324.

Type genus: *Pinidelia* Storozhenko, 1997.

DIAGNOSIS. Medium-sized and large insects. In forewing costal area with precostal lobe, costal area at base of *RS* narrower than or as wide as subcostal area. *SC* ending on *C* in distal half of wing. *RS* beginning in basal one-third of wing, free. Base of *M* free (in *Pinidelia* fused with CuA_1 over short distance), M_5 joining CuA_1, M_5 and first bifurcation of *M* closely set. *M* starting branching in basal quarter of wing, *MP* in *Kishertia* Aristov, 2004 desclerotized in wing middle. CuA_1 and CuA_2 branching; *CuP* simple.

COMPOSITION. Three genera: *Pinidelia* Storozhenko, 1997 from Tyulkino (Russia, Perm Region; Lower Permian, Ufimian Stage); *Kishertia* Aristov, 2004 from Kischert (Russia, Perm Region; Lower Permian, Kungurian Stage); *Idelopterum* Aristov, 2015 from Soyana (Russia, Archangelsk Region; Middle Permian, Kazanian Stage).

Family Juraperlidae Huang et Nel, 2007

Juraperlidae Huang, Nel, 2007: 837; Cui *et al*., 2010: 710.

Type genus: *Juraperla* Huang et Nel, 2007.

DIAGNOSIS. Medium-sized insects. Head and pronotum medium-sized, legs rather long. Forewing with costal area in basal half of wing wider than subcostal area. In *Ferganomadygenia* "*C*" short; in *Juraperla* "*C*" reaching wing middle. *SC* ending in bifurcation on *C* and *R*. *RS* beginning near wing middle (in *Ferganomadygenia* in basal third of wing). *RS*, *MA*, and *MP* simple. M_5 joining CuA_1 or joining *CuA* immediately proximal to its bifurcation. *M* starting branching in basal quarter of wing; M_5 and first bifurcation of *M* closely set. *CuP* simple or (in *Ferganomadygenia*) with short fork.

COMPOSITION. Two genera: *Juraperla* Huang et Nel, 2007 from Daohugou (China, Inner Mongolia; Middle Jurassic, Jiulongshan Formation) and *Ferganomadygenia* Storozhenko et Vrsansky, 1995 from Madygen (Kyrgyzstan, Osh Region; Middle Triassic, Ladinian Stage).

NOTE. *Ferganomadygenia* from Madygen was mentioned in the publication of the original description of Juraperlidae but was not included in this family (Huang & Nel, 2007).

Re-examination of the type has shown that in *F. plicata* Storozhenko et Vršanský, 1995 (Fig. 5) a short false costa runs at the base of the costal area, separating a small precostal area. This character and the general venation pattern (oligomerized *RS*, *MA*, and *MP* and M_5 joining CuA_1) make it possible to assign this genus to Juraperlidae. *Ferganomadygenia* differs from *Juraperla* in the short "*C*" and two-branched *CuA*. In *Juraperla* "*C*" reaches the wing middle, and *CuA* has four or five branches (Huang & Nel, 2007; Cui *et al*., 2010).

CONCLUSION

Therefore, the order Cnemidolestida is divided into two suborders, Cnemidolestina and Parmapterina. The former includes 11 families and 22 genera from the Paleozoic and Early Mesozoic of North and South America, Madagascar, and Eurasia. The latter includes four families and 22 genera from the Paleozoic and Mesozoic of North America and Eurasia. The order Cnemidolestida is assigned to Perlidea (Gryllones). Representatives of Cnemidolestida were ancestral to superorder Perlidea (stoneflies and earwigs) and to superorder Orthopteroidea (orthopterans, phasmids, and titanopterans). Titanopterans were ancestral to the other Orthopteroidea and most probably had evolved from Carboniferous representatives of Parmapterina.

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