

## IMPORTANT NEW INSECT FOSSILS FROM CARRIZO ARROYO AND THE PERMO-CARBONIFEROUS FAUNAL BOUNDARY

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**Abstract**—This study reports fossil insects collected at Carrizo Arroyo in central New Mexico (Red Tanks Member of the Bursum Formation, near the Carboniferous/Permian boundary), which are deposited in the New Mexico Museum of Natural History and the University of New Mexico. In total, 109 specimens are described in taxonomic detail, which represent at least 47 species (33 of which are described as new herein), 30 genera (12 new), 17 families and 13 orders. Other fossils discovered at Carrizo Arroyo, but not studied in detail in this report are those referred to the Blattida (roaches) and Panorpidia (scorpionflies). Among the most important findings of this study, however, includes discovery of scorpionflies in these deposits, which now represents the earliest appearance in the fossil record of this important group. Characteristics of this assemblage are (i) the abundance of taxa typical of Permian time and relative rarity of those typical of Carboniferous time, (ii) the absence or rarity of insects of aquatic association other than *Dasyleptus* spp. (Machilida: Dasyleptidae) and (iii) the predominately small and medium-sized fragmentary character of the majority of the insect fossils.

### INTRODUCTION

The transition from the Carboniferous to Permian was one of the most important events in the history of insects. As is shown by Rasnitsyn and Quicke (2002), few higher level insect taxa became extinct or suffered radical decline at that time. Among these were only a few orders, mainly of low diversity, such as Paoliida, Triplosobida and Eoblattida. On the other hand, diversification of ordinal-level taxa in the vicinity of the Carboniferous/Permian boundary was possibly the greatest in the history of the class. Indeed, five superorders, including the diverse and important book-louse-like insects (Psocidea), hemipteroids, beetles, neuropteroids (Myrmeleontidea) and mecopteroids (Papilionidea), and several important orders including true mayflies and stoneflies, enter the geological record at this time. Additionally, other orders radically increased their diversity during Permian time including Palaeomanteida (miomopterans), Hypoperlida, Grylloblattida and Orthoptera (nomenclature after Rasnitsyn and Quicke, 2002). Unfortunately, however, a detailed picture of the above processes is not yet available because insect fossil sites from the Carboniferous to Permian transition are uncommon and rarely well explored.

In these circumstances the recent collection of fossil insects from strata very near the Carboniferous/Permian (Virgilian-Wolfcampian) boundary at Carrizo Arroyo is of principal importance. Even though this fossil insect site was discovered almost 30 years ago and its potential importance recognized by various palaeoentomologists (see Rowland, 1997), little definitive work has been published until now. The present fossils were recovered from two levels in the Red Tanks Member of the Bursum Formation at Carrizo Arroyo, which is about 70 km southeast of Albuquerque in central New Mexico. Lucas and Krainer (2002) provide details on the location, stratigraphy and other fossils of Carrizo Arroyo, including ascertainment of the age of the insect-bearing strata by interbedded marine fossils. This study is based on fossils selected from several hundred specimens deposited in the New Mexico Museum of Natural History and University of New Mexico, herein abbreviated as NMMNH and UNM, respectively.

Courtesy of Dr. J. Mark Rowland in 1997, Dr. Spencer Lucas and Prof. Barry S. Kues in 2002, the senior author was privileged to study the collection of Carrizo Arroyo insects kept at NMMNH and at UNM.

Under the care, help and hospitality of the above persons as well as of other people at NMMNH, A.P. Rasnitsyn was able to prepare draft line drawings and color photos of the fossils. This material was used by the present team of authors to prepare the descriptions and inferences below. All fossils were examined except some roaches and a few others that were unavailable during APR's visit. The reasons for omission of roaches is the absence of the blattidan specialist in our group of authors. Another exception is Hanidae (Dictyoneurida) and Dasyleptidae (Machilida), which were studied by photographs made by Dr. Rowland, rather than directly by fossils. As a result, 87 specimens kept at NMMNH and 22 at UNM have been studied in taxonomic detail, and additionally, 89 roach specimens were examined for statistical purposes.

### SYSTEMATIC PALEONTOLOGY

**Subclass Lepismatona Latreille, 1804. The wingless insects**  
**Order Machilida Grassi, 1888 (= Archaeognatha Börner, 1904 =**  
**Microcoriphia Verhoeff, 1904, + Monura Sharov, 1957).**

**The bristletails**

**by A.P. Rasnitsyn**

**Family Dasyleptidae Sharov, 1957. The monurans**

For details concerning the order of bristletails, including the reason for subordinating Monura under Machilida, see Rasnitsyn and Quicke (2002). The only Paleozoic family of bristletails consisted of a single genus, *Dasyleptus* Brongniart, 1885, which has been recently revised (Rasnitsyn, 2000). Four monuran species have been previously described from the Upper Carboniferous (Stephanian) of Commeny in France (*D. lucasi* Brongniart, *D. noli* Rasnitsyn), Lower Permian (Leonardian) of Elmo in Kansas (*D. sharovi* (Durden)), and lower Upper Permian (Ufimian?) of Kaltan in SW Siberia (*D. brongniarti* Sharov). However, several more collections of undescribed material that are definitely or possibly referable to the monurans have been reviewed by Rowland (1997). The data available imply a (sub)aquatic way of life of monurans. The monuran identity of the trace fossil *Tonganoxichnus* Mangano et al. from the Upper Carboniferous of Kansas (Mangano et al., 1997) is not doubtless (Rasnitsyn, 2000).

From Carrizo Arroyo, at least two species of *Dasyleptus* are re-

corded herein: an aberrant species described as a new, and another, also probably new, was not formally described because of insufficient material. Additionally, eight poorly preserved specimens are questionably referred to as *Dasyleptidae*. For the purposes of calculation (see Discussion) the latter are arbitrarily counted as *Dasyleptidae*.

***Dasyleptus rowlandi* Rasnitsyn, sp. nov.**

**Figure 1**

*Dasyleptus* sp: Rowland, 1997, p. 3, figure 3; Rasnitsyn, 2000, p. 151.

**Holotype.** NMMNH P-26902, locality NMMNH L-3437, molting cast of a medium developmental instar with the thoracic part disarticulated and in part lost.

**Paratypes.** 10 specimens kept at NMMNH, probably all representing molting casts and thus all are incomplete; from localities NMMNH L-3434 and L-3437. NMMNH P-36988, 36989, 36994-36996, 37002, 37007, 37012-37014.

**Description.** Body size variable depending on instar, the largest available specimen (holotype) has abdomen with tail about 7 mm long (small compared to other species and thus probably immature). Integument moderately dark. Morphology of head, thorax and appendages other than tail insufficiently known. Antenna with pedicel about 2.5-3 times as long as wide, as wide as flagellum, basal flagellomeres about 1.3-1.7 times as long as wide. Last segment of maxillary palp, if correctly identified, about 4.5 times as long as wide, slightly wider than penultimate segment, with dorsal contour slightly convex and ventral slightly concave. Legs comparatively narrow, with tibia about twice as long as wide, about as wide as femur, wider than tarsus. Claw comparatively short (insufficiently preserved for precise measurements). Body segments as preserved not distinctive, except for abdominal tergum X about 1.5 times as long as tergum IX. In the holotype, tail shorter than abdomen, with ca. 18 segments, wider than long except for several apical ones which are somewhat longer than wide.

**Comparison.** As preserved, the present species is similar to *D. lucasi* and *D. brongniarti* and differs from *D. noli* in having abdominal tergum X long. The new species differs from *D. lucasi*, *D. brongniarti* and *D. sharovi* in basal flagellomeres slightly elongate (very elongate in *D. lucasi*, transverse in *D. brongniarti*, and quadrate in *D. sharovi*). Additionally, it differs from *D. noli* in narrow apical segment of maxillary palp and short claw. If correctly interpreted, the new species differs from all other species in having thoracic tergum 1 not much shorter than tergum 2, and from *D. sharovi* in the tergum 1 lacking a transverse suture at least dorsally.

**Remarks.** Incomplete preservation of all specimens studied consequently leaves the above description less than complete. Nevertheless, this new species is quite distinct from all the other species except *D. sharovi*, which lacks comparative information concerning the hind body part and not the fore one as in *D. rowlandi*.

The relative abundance of the species in the assemblage is understandable supposing *Dasyleptus* to be autochthonous in the Carrizo Arroyo lake, possibly the only autochthonous aquatic insect there. It is enigmatic that the species is represented only by molting casts of younger developmental instars: not a single complete body fossil was found, nor a molting cast of a supposedly mature specimen. The agent of such taphonomical selectivity is difficult to hypothesize.

**Etymology.** The species name is for entomologist Dr. J. Mark Rowland.

***Dasyleptus* sp.**

**Figure 2**

**Referred material.** NMMNH P-37000, locality NMMNH L-3433, incomplete molting cast of a medium developmental instar, with most appendages and abdominal apex lost, head damaged and thorax somewhat disarticulated.

**Description.** Body length up to abdominal segment IX about 6

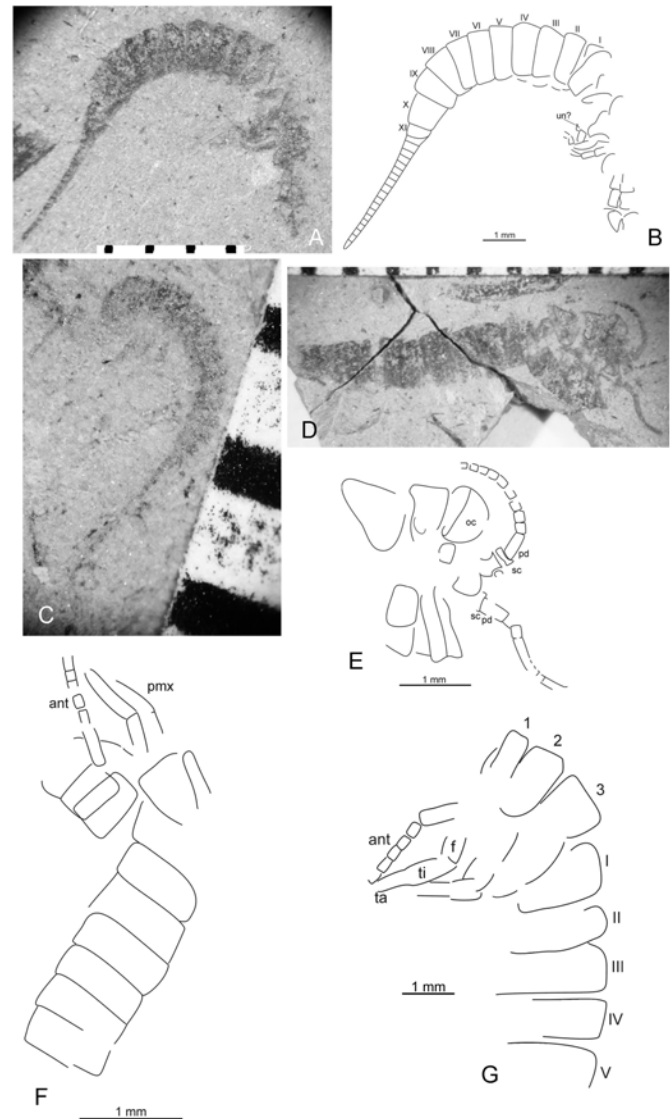


FIGURE 1. *Dasyleptus rowlandi* Rasnitsyn, sp. nov.: A, B – NMMNH P-26902, holotype; C – NMMNH P-36994; D, E – NMMNH P-37002; F – NMMNH P-36996; G – NMMNH P-36995. Symbols (in this and following figures): ant – antenna, f – femur, pmx – maxillary palp, ta – tarsus, ti – tibia, un – claw; thoracic segments are numbered in Arabic, abdominal ones – in Roman figures.

mm. Integument moderately pale. If correctly identified, maxillary palp with one of its segments wide (some 3.2-3.4 times as long as wide), and thoracic tergum 1 almost as long as tergum 2.

**Comparison.** The present specimen may differ from all congeners by its long thoracic tergum 1, although this length is known in *D. rowlandi* with still less certainty. Possibly differs from all *Dasyleptus* except *D. noli* by its wide maxillary palp segment. Additionally, it differs at least from *D. rowlandi* by its paler color.

**Remarks.** The sole specimen at hand most probably represents a distinct species. However its incomplete preservation state and resulting problems with its morphological interpretation make its formal description premature.

**Order uncertain**

**Genus *Microcarrizo* Rasnitsyn, gen. nov.**

**Type species.** *Microcarrizo paradoxicum* Rasnitsyn, sp. nov.

**Diagnosis.** Size small. General appearance reminiscent of younger *Dasyleptus* and late embryos and newly born Machilidae except for num-

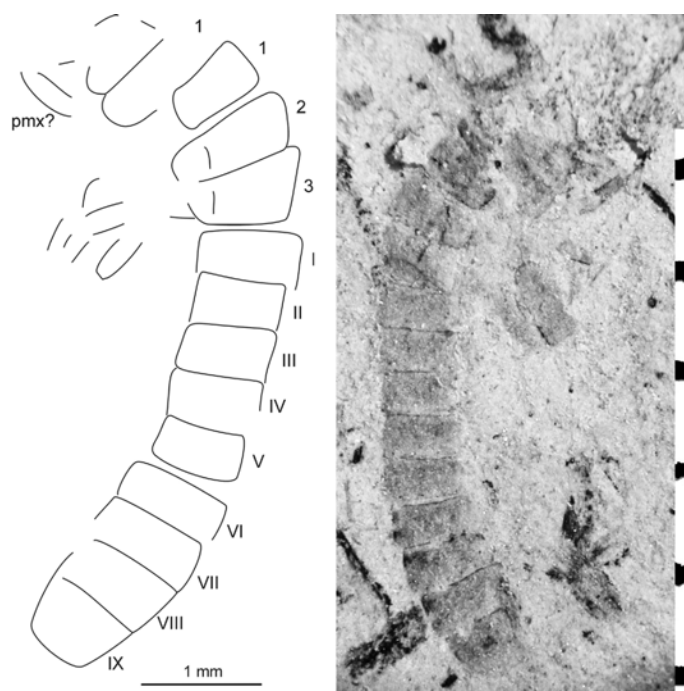


FIGURE 2. *Dasyleptus* sp., NMMNH P-37000.

ber of abdominal segments, possibly also in absence of enlarged, leg-like maxillary palps, and from *Dasyleptus* also in eye form. Head with eyes large, oval, separated. No signs of enlarged maxillary palp preserved. Thoracic segments as preserved similar to abdominal ones, pro- and mesothoracic ones looking shorter. Legs short, with tibiotarsal segment entire, with leg segments thick, short (less than twice as long as wide). Abdomen apparently nine-segmented, with VIII segment longest, subconical, IX small. Cerci absent, paracercus shorter than abdomen, less than 15-segmented, thick basally, almost streamlined with abdomen.

**Taxonomic position.** The fossils under discussion look like an ordinary juvenile *Dasyleptus* except for the two less abdominal segments, round eyes and possibly absence of the leg-like maxillary palps. This puzzling combination of characters prevents straightforward interpretation of its taxonomic position. Crucial is the number of abdominal segments. Machilida and Lepismatona in general never shows anamorphic development (with the segment number growing postembryonically). So, if the fossils are interpreted correctly, despite their similarity with *Dasyleptus* they belong neither to Machilida nor to Lepismatida. It cannot be ruled out definitely that *Microcarrizo* represent an immature winged insect, however no similar immatures are known thus far. This might even imply a new, undescribed insect order, although the material at hand is clearly insufficient to go in this direction beyond the above conclusion.

**Etymology.** The genus name refers to the small size (micron is the Greek for small) and locality. Gender neuter.

***Microcarrizo paradoxicum* Rasnitsyn, sp. nov.**

**Figure 3**

**Holotype.** NMMNH P-37011 (locality NMMNH L-3437), comparatively well preserved insect with most head appendages lost.

**Paratype.** NMMNH P-36992 (locality NMMNH L-3433), less well preserved fossil (possibly molting cast) with head ill-preserved and appendages lost.

**Description.** Holotype body length with paracercus, as preserved, 4.9 mm (without paracercus 3.3 mm), eye vertical diameter ca. 0.3 mm, three apical leg segments combined ca. 0.45 mm, paracercus length 1.6

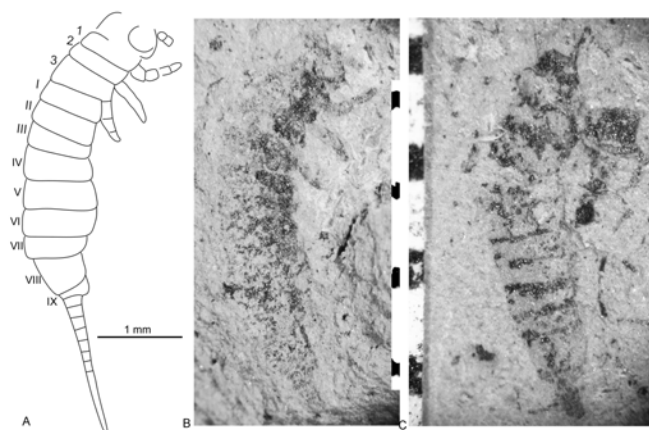


FIGURE 3. *Microcarrizo paradoxicum* Rasnitsyn sp. nov., A, B – holotype, C – paratype.

mm; paratype body length without paracercus 3.2 mm. Integument dark (better seen in paratype), when shed revealing fine longitudinal rugosity. Basalmost preserved antennal (flagellar?) segments subquadrate.

**Remarks.** As preserved, the paratype shows one less abdominal segment, which is due to the imperfect preservation state, for a gap sufficient for one segment is seen between the thorax and abdomen.

**Etymology.** The species name refers to its contradictory character set (*paradoxicum* is the Latin for paradoxical).

**Subclass Scarabaeona Laicharting, 1781.**

**The winged insects**

**Order Caloneurida Handlirsch, 1906**

**by A.P. Rasnitsyn**

The current system of the Order Caloneurida (= Caloneuroidea) is not satisfactory (Rasnitsyn, 2002); however, there is a rather clear cut taxon which can be informally called as caloneuridan proper (Caloneurida s.str.). It embraces the forms with the usual (more or less neutral) M followed with four (or more) straight and simple veins in a particular order (Fig. 1). The first of these vein is convex, the following two are concave, closed again with one or more convex veins. I interpret the first two, convex and concave, veins as the secondarily (reversally, atavistically) free  $M_5$  and CuA, the following veins being ordinary CuP and A. This group almost precisely corresponds to the Order Caloneuroidea by Rohdendorf (1962) and Carpenter (1992), except for *Synomaloptila longipennis* Martynov, 1938, which belongs rather to the Order Hypoperlida (Rasnitsyn, 1980, 2002a). However, in spite of being essentially uniform and showing no convincing suprageneric subgroups, the order is traditionally split into a number of families which are almost as many as the genera they include (13 genera in eight families excluding Synomaloptilidae and unplaced genera in Carpenter, 1992). For this reason I prefer to abandon the family structure of the proper caloneuridans and to lump all the genera under the family name Caloneuridae Handlirsch, 1906, until enough information accumulates to permit a more sound subdivision.

A separate family of caloneuridans is Herdinidae, which is known by the only brachypterous species *Herdina mirificum* Carpenter and Richardson, 1971 (see also Shear, Kukalová-Peck, 1990; Kukalová-Peck, 1991; Kukalová-Peck, Brauckmann, 1992) from the Pennsylvanian (Westphalian D) of Mazon Creek in Illinois. In spite of the striking difference in short and wide wings with coarse reticulation (which are expected features of brachyptery), the general venation scheme is typically caloneuridan, with two concave veins CuA and CuP between two convex ones ( $M_5$  and 1A). The basal connection between CuA and  $M_5$  does not contradict the caloneuridan affinity of *Herdina*, for the same is true also for *Boltonaloneura*. Kukalová-Peck (1991) gives a different inter-

pretation with a single concave vein between convex  $M_5$  (her CuA) and 1A: in her figures CuP is figured as a straight thick vein in contrast to what I consider CuA, which appear there as a thin, zigzag secondary vein separating two rows of cells. However, a good photograph by Carpenter and Richardson (1971, fig. 19) displays these two vein as having similar structure. Justifying better the family status of Herdinidae are body characters that are unlikely resulting from the brachypterous and probably, in part, the paedomorphic nature of *Herdina*. These are its robustness and particularly wide prothoracic and abdominal paranota that are recorded in no Caloneuridae.

There are more Paleozoic (Pennsylvanian) fossils showing considerable similarity to the Caloneuridae, except that they lack free  $M_5$ , so as their M is followed with usual components: the anteriormost convex vein ( $M_5$ +CuA), then the only concave vein (CuP), and one or more convex ones (A). Some of these fossils are otherwise typical caloneurids, in having their wing elongate, costal space narrow, all veins but RS and M being straight and simple, M with at most three branches, and usually also in having crossveins rather regular. These are, besides the three species described below as new, *Emphyloptera lecrivaini* Pruvost, 1919, *Geroneura wilsoni* Matthew, 1889, *Hapaloptera gracilis* Handlirsch, 1906, and possibly the incompletely preserved *Tshecalculus inaspectus* Novokshonov, 2000. Some other fossils are generally the same except that they show a few comparatively weak, slanting branches mounting CuA toward its apex (*Protocollaria ingens* Brongniart, 1885, *Endoiasmus reticulatus* Handlirsch, 1906), or forked CuP (*Aenigmatodes danielsi* Handlirsch, 1906; this species has been placed in Hypoperlida by Rasnitsyn, 1980, 2002, but simple CuA contradicts this attribution). All these fossils are considered herein as Caloneurida and tentatively included under the family name Hapalopteridae Handlirsch, 1906. As to a few other fossils considered as possible caloneuridans by Rasnitsyn (2002a), *Metropator pusillus* Handlirsch, 1906 and *Paoliola gurleyi* Melander, 1903 are deviant in being polyneurous and have different general appearance, so at present I would prefer to leave them as satellite genera of Caloneurida. The same concerns also *Cymenophlebia carpentieri* Pruvost, 1919 with its sinuate CuA, and *Kliveria incerta* (Kliver, 1886) with the deep CuA fork. As for *Sypharoptera pneuma* Handlirsch, 1911, its widely forked CuA has nothing to do with Caloneurida and rather is suggestive of Hypoperlida.

#### Family Caloneuridae Handlirsch, 1906

Caloneuridae: Handlirsch, 1906-08: 140.

Sthenaroceridae Handlirsch, 1906-08: 149 (**syn. nov.**)

Euthygrammatidae Martynov, 1928: 49 (**syn. nov.**)

Eohymenidae Martynov, 1937: 9 (**syn. nov.**)

Permobiellidae Tillyard, 1937: 101 (**syn. nov.**)

Anomalogrammatidae Carpenter, 1943: 74 (**syn. nov.**)

Paleuthygrammatidae Carpenter, 1943: 70 (**syn. nov.**)

Plesiogrammatidae Carpenter, 1943: 73 (**syn. nov.**)

Apsidoneuridae Carpenter, 1961: 151 (**syn. nov.**)

Amboneuridae Carpenter, 1980: 111 (**syn. nov.**)

**Diagnosis.** Wings elongate (length three or more times width), fore and hind pairs venationally alike, with costal space narrow, crossed with subvertical crossveins rather than oblique branches of SC and R. All veins but RS and M straight and simple, RS usually pectinate backward, rarely more than with four branches, M with at most three ordinary (not distinctly convex) branches followed with convex, free  $M_5$ , followed in turn with CuA and CuP, both concave and interconnected basally. Anal veins 1-4, convex. Body structure when (rarely) known stick-insect like except for wings sometimes roof-like (in *Caloneura*, *Sthenarocera*).

Genera included are treated in the key below. They are all found in Paleozoic of Euramerica and Angaraland ranging from mid-Carboniferous (Moscovian) to mid-Upper Permian (Lower Tatarian).

#### Key to the genera of Caloneuridae:

1. SC short, hardly reaching 0.6 wing length. M fork starting near wing midlength. 2  
- SC surpassing 0.6 wing length. 6
2. RS with two branches. Size small (near 10 mm). *Anomalogramma parva* Carpenter 1943 (P<sub>1</sub>, Elmo)  
- RS with more than two branches. Size larger.. 3
3.  $M_5$  & CuA far apart. Wing wide. Crossveins irregular. *Amboneura closei* Carpenter, 1980 (C<sub>2</sub>, Allegany Fm.)  
-  $M_5$  & CuA close aligned. 4
4. Venation rich (RS with four, M with three, A with four branches), M anastomosing with RS, crossveins mainly regular, wings narrow. *Boltonaloneura subtilis* (Bolton, 1925) (C<sub>3</sub>, Commeny)  
- Venation less rich (RS with three or four, M with two, A with two branches), M not anastomosing RS. 5
5. Wing wide, crossveins mainly regular. *Permobiella perspicua* Tillyard, 1937 (P<sub>1</sub>, Elmo)  
- Wing narrow, crossveins forming intercalaries between apical veins. *Pseudobiella fasciata* Carpenter, 1970 (Kinney Brick Quarry in New Mexico, Wild Cow Form., latest Carboniferous)
- 6 (1). CuA & CuP closely aligned. RS simple. Wing narrow. 7  
- CuA aligned to  $M_5$  as close as or, usually, much more close than to CuP. RS branching. 8
7. SC almost reaching wing apex. M fork about 0.3 wing length. Wing length about four times width. *Euthygramma parallelum* Martynov, 1928 (P<sub>2</sub>, Soyana)  
- SC hardly 0.7, M fork about 0.4 wing length. Wing length about 10 times width. *Gelastopteron gracile*. Carpenter, 1976 (P<sub>1</sub>, Elmo)
- 8 (6).  $M_1$  arching basally making M fork wide. 9  
- M fork narrow, or M simple. 10
9. RS with 4 branches. SC reaching 0.8 wing length. *Homaloptila* Meunier, 1911 (*similis* Meunier, 1911) (C<sub>3</sub>, Commeny)  
- Costal space narrow. RS with two branches. SC variable. *Apsidoneura* Carpenter, 1943 (*flexa* Carpenter, 1943, P<sub>1</sub>, Elmo; *sottii* Burnham, 1984, C<sub>3</sub>, Montseules-Mines)
- 10 (8). Precostal area and intercalary veins between R and RS, CuA and CuP present. 2A long, pectinate *Eohymen maculipennis* Martynov, 1937 (P<sub>2</sub>, Kargala)  
- No precostal area and intercalary veins between R and RS, CuA and CuP. 2A not long and pectinate. 11
11. SC reaching 0.8 wing length. M simple. 2A very short or lost. 12  
- SC shorter. 13
12. RS with four branches. Wing length about four times width. *Plesiogramma* Carpenter, 1943 (*medialis* Carpenter, 1943, P<sub>1</sub>, Elmo; *kemerovoensis* Martynova, 1948, P<sub>2</sub>, Kaltan; *maueri* Novokshonov, 1998, P<sub>1</sub>, Tsherkarda)  
- RS with three branches. Wing length about five times width. *Paleuthygrammella aberrans* (Martynov, 1938) (P<sub>2</sub>, Soyana)
- 13 (11). RS branching either once or irregularly and beyond 0.8 wing length. *Paleuthygramma* Martynov, 1930 (*tenuicornis* Martynov, 1930, P<sub>1</sub>, Tsherkarda; *acuta* Carpenter, 1943, P<sub>1</sub>, Elmo; *ventricosa* sp. nov.; possibly also '*Aspidoneura*' [sic!] *reducta* Zimmermann, 1962; P<sub>1</sub>, Oklahoma)  
- RS branching before 0.8 wing length, regularly and more than once. 14
14. RS with five or more branches. 15  
- RS with three (sometimes four?) branches. 16
15. Costal space widened subbasally. RS base at about

0.6 wing length. Wing length about 3.5 times width.  
*Caloneura dawsoni* Brongniart, 1885 (C<sub>3</sub>, Commentry)  
 - Costal space narrow. RS base at wing midlength.

Wing length about 5.5 times width. *Sthenarocera pachytyloides* Brongniart, 1885 (C<sub>3</sub>, Commentry)

**16.** M forked. Crossveins less dense. *Vilviopsis* Martynov, 1938 (*extensa* Martynov, 1938, P<sub>2</sub>, Soyana; *reducta* (Carpenter, 1943), P<sub>1</sub>, Elmo; *picta* sp. nov.; *Caloneurella carbonaria* Carpenter, 1934 from Alleghany Fm. also might go here)

- M simple.

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**17.** Crossveins very dense. M<sub>3</sub> and CuA closely aligned *Vilvia densinervosa* Zalesky, 1933 (P<sub>1</sub>, Tshkarda)

- Crossveins well spaced. M<sub>3</sub> and CuA about as distant as CuA and CuP. *Pruvostiella lecomtei* (Pruvost, 1919) (C<sub>2</sub>, Pas-de-Calais)

### *Vilviopsis picta* Rasnitsyn, sp. nov.

#### Figure 4

**Holotype.** UNM 13141 and 13142 (part and counterpart), locality NMMNH L-3433, wing lacking base and small part of apex.

**Paratypes.** UNM 6839, wing lacking near basal 0.3, locality NMMNH L-3433, and NMMNH P-26912, locality NMMNH L-3437, damaged apical half of wing.

**Description.** Wing 14.6 mm long as preserved (about 16 mm full length), 4.3 mm wide (width: length ratio ~1:3.7) in holotype, 4.7 mm wide and about 14.5 mm full length in paratype 6839 (width: length ratio ~1:3), with three deeply dark transverse bands in part interconnected along fore and hind wing margins. Basal dark band placed between M and RS origins, medial band started before M fork and finished at RS fork and M<sub>3</sub> apex, and apical band delimited by second RS fork and M<sub>2</sub> apex basally, and apices of R and M<sub>1</sub> distally. Costal space weakly and gradually narrowing toward apex except for slight apical pterostigma-like widening. SC running near R until wing midlength, then gradually approaching C (not traceable near wing apex). R gently curved along wing margin, approaching wing apex. R space conspicuously enlarged. RS three- or four-branched, started at about 0.33 wing length, forked at about 0.6 wing length. M started near basal 0.2 wing length, forking near wing midlength, with M<sub>1</sub> connected to RS subbasally by conspicuous crossvein, and usually clearly angular at junction. M<sub>3</sub>, CuA, CuP, 1A and 2A straight as preserved. Crossveins in part irregular, branching along wing margin, long and sinuate in R space, rare in costal space, otherwise rather regular and more or less uniformly spaced for about 0.7-1.5 their length.

**Comparison.** The new species differs markedly from the congeners in its bright color pattern and long, mostly sinuate crossveins in R space. Additionally, it differs from *V. extensus* Martynov in smaller size, wider wing and radial space, from *V. reducta* Carpenter in less arcuate hind margin and presence of two anal vein. Comparison with *Caloneurella carbonaria* Carpenter, which also might belong to *Vilviopsis*, is not easy because of some contradictions between the published photograph and line drawing (Carpenter, 1934, figs. 1, 2). Based on the former, *C. carbonaria* differs in distal origin of RS (not much before M fork), much more sinuate RS (including RS<sub>1</sub>), and particularly in M<sub>3</sub> and CuA, which run close to each other except widely diverge apically.

**Remarks.** Paratype UNM 6839 differs in having four RS branches instead of three, M<sub>1</sub> not angular subbasally, and wing more wide, so it might represent a distinct although similar species.

**Etymology.** Species name refers to the painted appearance of the fossil (*pictus* is the Greek for painted).

### *Paleuthygramma ventricosa* Rasnitsyn, sp. nov.

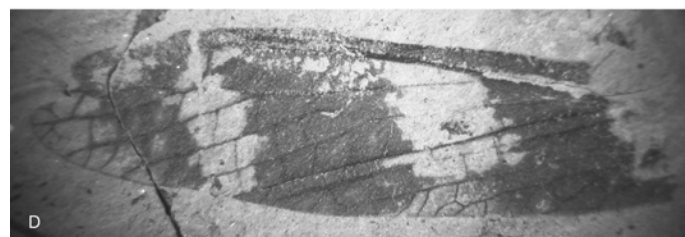
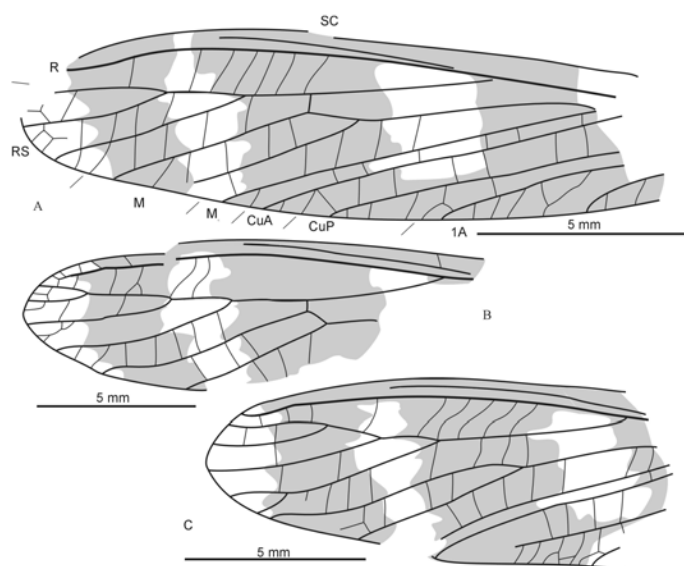


FIGURE 4. *Vilviopsis picta* Rasnitsyn sp. nov.: A, D – holotype, B – UNM 6839, C – NMMNH P-26912.

#### Figure 5

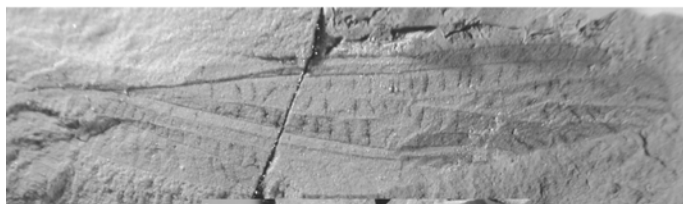
**Holotype.** NMMNH P-26918, locality NMMNH L-3433, almost complete but somewhat damaged wing.

**Description.** Wing 13.2 mm long, 2.8 mm wide (width: length ratio ~1:3.7) in holotype, 4.7 mm wide and about 14.5 mm full length in paratype 6839 (width: length ratio ~1:4.7), with straight fore margin and hind margin much extending backward in mid 0.3 of wing length, and with no color pattern preserved. Costal space of almost constant width except more wide basally. SC running close to R within mid 0.5 wing length (not preserved both before and beyond it). R straight except gently curved along wing margin apically, almost reaching wing apex. R space somewhat enlarged medially. RS 2-branched, started at about 0.35 wing length, forked at about 0.8 wing length. M started near basal 0.2 wing length, forking near wing midlength, with M<sub>1</sub> connected to RS subbasally by short crossvein, angular at junction. M<sub>3</sub>, CuA, and CuP close and parallel to each other except CuA and CuP more distant basally. M<sub>3</sub> sinuate subapically (CuA and CuP not preserved there). 1A diverging with CuP, apparently not reaching wing margin. 2A short or absent (not preserved). Hind wing margin before apical 0.3 wing length widely free of longitudinal veins. Crossveins rather regular and dense except well spaced in costal and subcostal space (more dense subapically in costal space). Wide posterior wing space with conspicuous long crossveins.

**Comparison.** The new species differs from all congeners by the characteristically extended wing hind margin with wide space behind longitudinal veins which is crossed by long, dense crossveins, and also by the absence of any long anal vein behind 1A.

**Etymology.** Species name refers to the curious wing form (*ventricosus* is the Latin for potbellied).

### Family Haplopteridae Handlirsch, 1906

FIGURE 5. *Paleuthygramma ventricosa* Rasnitsyn sp. nov., holotype.

Haplopteridae: Handlirsch, 1906-08: 304

Aenigmatodidae: Handlirsch, 1906: 683 (**syn. nov.**)Protokollariidae: Handlirsch, 1906-08: 137 (**syn. nov.**)Emphylopteridae: Handlirsch, 1922: 69 (**syn. nov.**)

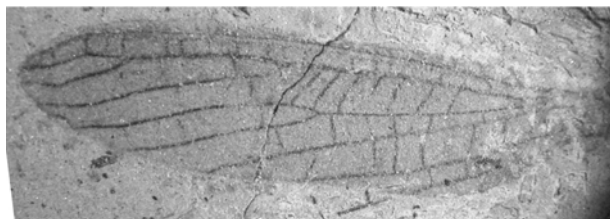
**Diagnosis.** Wings elongate (length three or more times width), with costal space not wide. SC meeting RS, its branchlets not abundantly branching. M lacking free  $M_5$  as straight, simple, convex vein followed with concave CuA and CuP.

Genera included are represented in the key below.

#### Key to the genera of Haplopteridae:

1. CuP forked. RS and M forming two faced three-branched combs. CuA simple. Wing closely reticulated. *Aenigmatodes danielsi* Handlirsch, 1906 ( $C_2$ , Mazon Creek)
  - CuP simple. 2
2. M simple. 3
  - M with two or more branches. 5
3. CuA with anterior branches. SC more than half wing length. *Protocollaria ingens* Brongniart, 1885 ( $C_3$ , Commentry)
  - CuA simple, SC short or absent. 4
4. SC present, not reaching wing midlength. CuA simple. *Arroyopteron indolatum* sp. nov.
  - SC lost. CuA with oblique, branchlet-like subapical crossveins (or crossvein-like branchlets). *Carrizopteron longum* gen. nov.
- 5 (2). M with five-branched backward comb. *Tshecalculus inaspectus* Novokshonov, 2000 ( $P_1$ , Tshekarda).
  - M with at most three branches. 6
6. M with hind (third) branch concave but otherwise  $M_5$ -like (straight, early starting, and running close to CuA), and with true  $M_5$ . SC reaching C near wing apex. *Haploptera gracilis* Handlirsch, 1906 ( $C_2$ , Mazon Creek)
  - No  $M_5$ -like concave vein. 7
7. RS and M with facing three-branched combs, RS branches long, in part forked subapically. SC short. *Geroneura wilsoni* Matthew, 1889 ( $C_2$ , New Brunswick)
  - M two-branched. SC more than half wing length. 8
8. CuA with short apical posterior branches. Costal space wide basally. Crossveins not quite regular, forming cell rows between RS and M. *Endoiasmus reticulatus* Handlirsch, 1906 ( $C_2$ , Mazon Creek)
  - CuA simple. Costal space narrow. Crossveins regular. *Emphyloptera lecrivaini* Pruvost, 1919 ( $C_2$ , Lens in N. France).

#### Genus *Carrizarroyo* Rasnitsyn, gen. nov.

FIGURE 6. *Carrizarroyo calopterus* Rasnitsyn sp. nov., holotype.

#### Type species *C. calopterus* sp. nov.

**Diagnosis.** Costal space very narrow, lacking SC and with few crossveins. RS starting near wing base, pectinate. M two-branched, almost straight before forking, free at least beyond basal 0.2 wing length. CuA, CuP and 1A all simple, straight.

**Species included.** Type species only.

**Etymology.** The generic name is from the locality (gender masculine).

#### *Carrizarroyo calopterus* Rasnitsyn, sp. nov.

##### Figure 6

**Holotype.** NMMNH P-26916, locality NMMNH L-3433, wing lacking extreme base.

**Description.** Wing 10.8 mm long as preserved (about 11.5-12 mm full length), 2.8 mm wide (width: length ratio ~1:4), with no distinct color pattern. Costal space of almost uniform width (slightly wider in basal 0.3). R almost reaching wing apex. RS three-branched, with first fork at about apical 0.45, second at apical 0.2 wing length. M fork near wing midlength. Crossveins rather regular, rare in costal space, uniformly spaced in R space, otherwise more numerous near wing midlength.

**Etymology.** Species name refers to nice looking appearance of the fossil (from Greek *calo-* meaning beautiful, and Greek *pteron* meaning wing).

#### Genus *Carrizopteron* Rasnitsyn, gen. nov.

**Type species.** *C. longum* sp. nov.

**Diagnosis.** Wing very narrow. Costal space very narrow, lacking SC and probably crossveins. RS pectinate, with more than three branches, starting probably not far from wing midlength. M simple, almost straight, free at least beyond basal 0.3 wing length. CuA almost straight, subapically with oblique, branchlet-like crossveins (or short, crossvein-like branchlets). CuP simple, straight. 1A short, simple, straight, slightly zig-zag at junctions with crossveins, leaving space for at most one more very short anal vein.

**Species included.** Type species.

**Etymology.** The generic name is from the locality and *pteron* which is the Greek for wing (gender neuter).

#### *Carrizopteron longum* Rasnitsyn, sp. nov.

##### Figure 7

**Holotype.** UNM 6860, locality NMMNH L-3433, almost complete but slightly damaged wing.

**Description.** Wing 11.8 mm long as preserved (about 12-12.5 mm full length), 2.4 mm wide (~1:5), with no distinct color pattern. Costal space of almost uniform width (slightly wider in basal 0.3). R almost reaching wing apex. RS sinuate, 6-branched, with apical branches small, somewhat irregular, and probably varying in number. First fork at

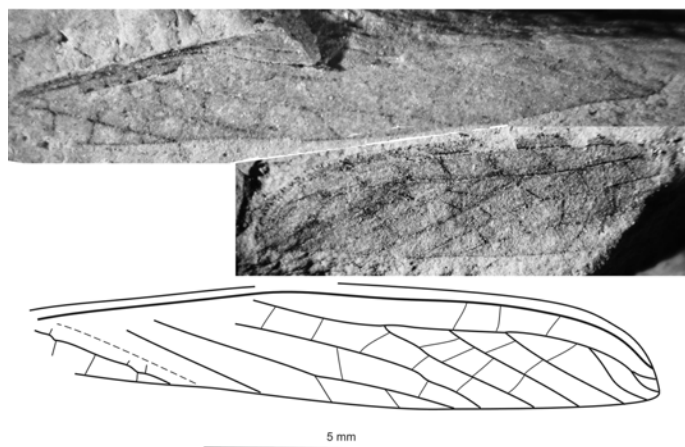


FIGURE 7. *Carrizopteron longum* Rasnitsyn sp. nov., holotype.

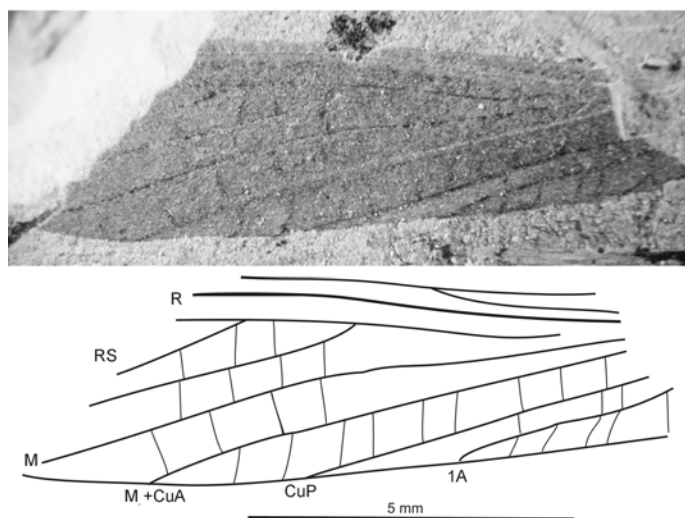


FIGURE 8. *Arroyopteron indolatum* Rasnitsyn sp. nov., holotype.

about apical 0.45, irregular branching starting at apical 0.1 wing length. CuA with two branchlet-like crossveins placed almost equidistant between CuA and CuP apices. Crossveins not particularly regular in respect of both spacing and inclination. 1A reaching 0.25 wing length.

**Etymology.** Species name refers to the proportions of the fossil.

#### Genus *Arroyopteron* Rasnitsyn, gen. nov.

**Type species.** *A. indolatum* sp. nov.

**Diagnosis.** Costal space narrow, with SC short (not reaching wing midlength), meeting C. RS pectinate, probably with more than three branches, starting rather near wing base. M simple, almost straight, free at least beyond near wing base. CuA and CuP straight, CuA without distinctly branchlet-like subapical crossveins. 1A slightly sinuate, running near wing hind margin and so leaving space for not more than one very short additional anal vein.

**Species included.** Type species.

**Etymology.** The generic name is from the locality and *pteron* which is the Greek for wing (gender neuter).

#### *Arroyopteron indolatum* Rasnitsyn, sp. nov.

##### Figure 8

**Holotype.** UNM 13145, locality NMMNH L-3433, wing fragment without base and apex.

**Description.** Wing fragment 10 mm long as preserved (about 13–14 mm full wing length), 3.2 mm wide (~1.4–4.5), with no distinct color

pattern. Costal space tapering toward apex at least until near 0.7 wing length, apparently lacking crossveins. SC hardly surpassing 1A apex, not reaching RS fork. R, RS, M and 1A gently sinuate, CuA and CuP straight. RS possibly started within basal 0.2 wing length, with two posterior branches preserved, probably 4–6-branched. M showing no indication of connection with CuA all over preserved fragment, apically far surpassing second RS fork. CuA surpassing second RS fork, CuP slightly surpassing first RS fork. Crossveins preserved only posterior of RS, regular, spaced mainly for 0.7–1.5 of their length, generally subvertical to longitudinal veins except more oblique and branchlet-like under 1A and, very slightly so, under CuA apex.

**Etymology.** Species name refers to the incomplete preservation state of the fossil (*indolatus* is the Latin for poor, portionless).

#### Order Hypoperlida Martynov, 1928

By A.P. Rasnitsyn

#### Family Anthracoptilidae Handlirsch, 1922

(= *Strephocladidae* Martynov, 1938)

#### Genus *Carrizocladus* Rasnitsyn, gen. nov.

**Type species.** *C. longus* sp. nov.

**Diagnosis.** Size large (fore wing some 4 cm in type species). Fore wing with SC branchlets long, slanting, sinuate, RS starting within basal 0.25 of wing length and then running very close to R, its branches numerous, strictly pectinate, parallel. M two-branched, with no evident connection to RS connection to CuA may be simply not preserved). CuA with four main branches forming backward comb from short horizontal basal section of CuA<sub>1</sub>, not abundantly branching. No network evident, regular spaced crossveins present at least in RS area.

**Remarks.** In spite of imperfect preservation state, the fossils can be attributed to the order Hypoperlida and family Anthracoptilidae because of long, slanting, abundantly branched SC branches, coupled with lack of individualized, poor in branching CuA<sub>2</sub> characteristic of Strephoneuridae. The fossils differs from Anthracoptilina (and from all Anthracoptilina with the above SC structure) in having CuA pectinate backward, and in RS starting within basal 0.25 of wing length and running very close to R. The latter character is indicative also for some Eoblattidae (order Eoblattida, see Rasnitsyn, 2002 for details) which differs in rather ordinary SC branching and also in RS and CuA not regularly pectinate.

**Species included.** Two species described herein, one of them being only tentatively included.

**Etymology.** The name is after the locality and the genus *Strephocladus*. Gender masculine.

#### *Carrizocladus arroyo* Rasnitsyn, sp. nov.

##### Figure 9

**Holotype.** UNM 6862, locality NMMNH L-3433, somewhat crumpled fore wing lacking base including all anal area and very apex, of fair preservation state.

**Description.** Wing 39 mm long as preserved (full length near 41–43 mm), with no color pattern preserved. Costal space moderately wide, generally wider than subcostal one, with subcostal branchlets rather spaced, not abundantly branched. R and RS sinuate, RS with seven weakly sinuate branches, CuA branches mainly gently curved or almost straight, not necessary more than four in number.

**Etymology.** The name is after the locality.

#### ?*Carrizocladus deter* Rasnitsyn, sp. nov.

##### Figure 10

**Holotype.** UNM 6856, locality NMMNH L-3433, fragment of large fore wing lacking anterobasal, short posterobasal, and much of posteroapical part, of mean preservation state.

**Description.** Wing fragment 21 mm long as preserved (full length probably some 30 mm), with no color pattern preserved. Costal space much wider than subcostal one, with subcostal branchlets not much

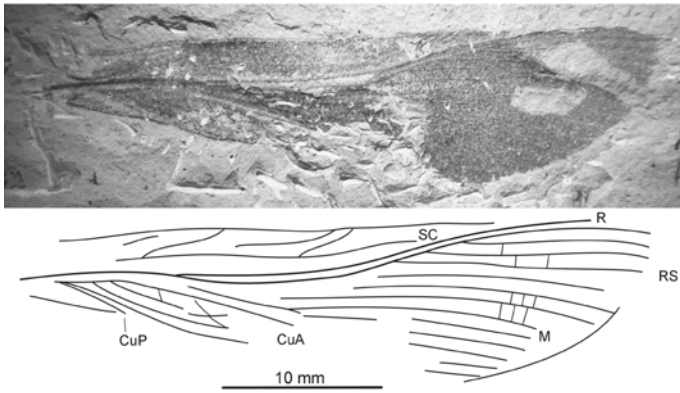


FIGURE 9. *Carrizocladus arroyo* Rasnitsyn sp. nov., holotype.

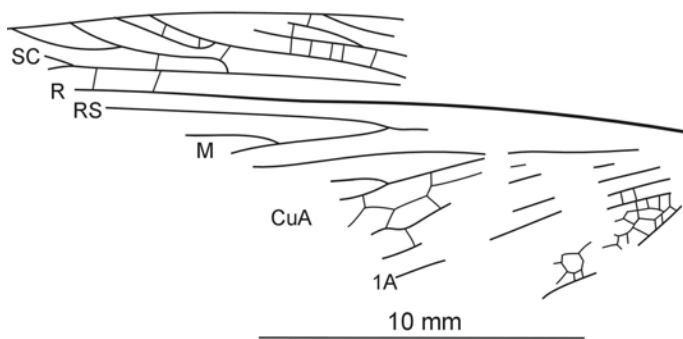


FIGURE 10. *?Carrizocladus deter* Rasnitsyn sp. nov., holotype.

spaced, well branched, with numerous crossveins between branchlets as well as between SC and R. As preserved, R, RS, M, and Cu, and their branches straight or very gently curved. RS starting not far from wing base (precise place of origin unknown), at least its part running close to R. M fused with RS for a distance (possibly also with CuA), forking shortly after leaving RS. CuA branching not well known, possibly pectinate backward, with posterior branches disorganized into rows of large cells except basally. Anal area with close network at least subbasally.

**Remarks.** The present species differs much from the type species (in width of costal and subcostal space, SC branching, M fused temporarily with RS, disorganized CuA branches) and, if better known, would probably deserve placing into a genus of its own. Given the available information on the fossil, this does not seem justified.

**Etymology.** The name refers to the preservation state of this unique fossil (*deter* is the Latin for poor).

**Order Dictyoneurida Handlirsch, 1906 (= Palaeodictyoptera  
Goldenberg, 1854)  
by N.D. Sinitshenkova**

Dictyoneurida is one of the numerous Palaeozoic orders that attracts attentions by its large size (up to more than 50 cm wingspread), prothoracic paranota, two pairs of long and wide wings that are often brightly patterned, long cerci, and with a long sucking beak that is sometimes preserved. The dictyoneurids wings spread permanently to the side and don't fold over the abdomen at rest; they have rich venation and often various kinds of archdictyon.

The order contains two suborders (Dictyoneurina and Frankenholziina) and eight superfamilies (Sinitshenkova, 2002) which can be identified mainly by the venational characters, inasmuch as most families are known only by isolated wings. Most probably it is the dictyoneurid thermophily which defines their distributional pattern. They occurred mainly in the north hemisphere and were widespread only in Euramerica. A few records are known in Argentina, Tasmania, East Siberia, and Mongolia. The most ancient representative of the order, *Delitzschala bitterfeldensis* Brauckmann et Schneider, is described from the latest Early Carboniferous (Namurian A) of Germany. The group flourished in the Middle and particularly in the Late Carboniferous, and became rare in the Upper Permian. No dictyoneurids are known in the Triassic.

Dictyoneuridans were terrestrial insects that frequented the crowns of tree plants both as imago and nymph. At least some of them sucked out seeds of the cordaitalean gymnosperms. This insect group is of great importance for studying coevolutionary trends between the Paleozoic plants and insects. Reduction of fodder plants by the end of the Paleozoic most probably caused extinction of the order.

#### Suborder Dictyoneurina Handlirsch, 1906

#### Superfamily Dictyoneuroidea Handlirsch, 1906

#### Family Dictyoneuridae Handlirsch, 1906

The dictyoneurids represent a highly diverse family with more than 30 genera and about 70 species, and is widespread in Europe, Siberia and North America in the Middle and Late Carboniferous and Late Permian.

#### *Titanodictya* Handlirsch, 1906

#### *Titanodictya rowlandi* Sinitshenkova, sp. nov.

#### Figure 11

**Holotype.** UNM 6863, Carrizo Arroyo L-3433, Part and counterpart of well preserved adult wing apex no. (3433).

**Paratype.** NMMNH P-26907, part and counterpart of poorly preserved wing apex, Carrizo Arroyo L-3433.

**Description.** Adult wing fragment 15.5 mm long as preserved and 11.3 mm wide at level of posterior RS branch, total wing length about 46 mm. Wing apex widely rounded. Costal space narrowing toward wing apex. Sc short. RS with anterior branch twice dichotomously forked, with posterior branch forking near wing margin. Principle veins intercalated with distinct short and thin veins at wing margin. Costal and radial areas with numerous crossveins, areas between RS branches with two or three cell rows.

**Comparison.** Differs from the only other species in the genus, *T. jucunda* (Scudder, 1885) from the Upper Carboniferous Upper Transition Group, of Campbells Ledge near Pittston, Pa., USA, in widely rounded wing apex and in smaller size: *T. jucunda* with its 55-60 mm of wing length is one of the largest dictyoneuridans.

**Remarks.** Dictyoneuridans have almost homonomous wings which are similar venationally and differ mainly in wider basal third of the hind wing. With only the apical wing fragment at hand, it is impossible to identify which wing pair it represents.

Carpenter (1992) records *Titanodictya jucunda* as Palaeodictyoptera incertae sedis. On the contrary, Sinitshenkova (2002) referred to *T. jucunda* as belonging to superfamily Dictyoneuroidea based on short SC, dense archdictyon and narrow wing apex. Dictyoneuroidea contains three families: Dictyoneuridae, Peromapteridae and

needs thorough review of the described material. Indeed, based on the present evidence, I think it is more reasonable to consider *Titanodictya* as a member of the family Dictyoneuridae.

**Etymology.** The species is named for entomologist Dr. J. Mark Rowland.

#### Superfamily Calvertielloidea Martynov, 1932

#### Family Calvertiellidae Martynov, 1932

The calvertiellids represent an advanced family with five monotypic genera known from the Permian of Europe and North America.

#### *Carrizopteryx* Kukalová-Peck & Peck, 1976

#### *Carrizopteryx lucasi* Sinitshenkova, sp. nov.

#### Figure 12

**Holotype.** UNM 8174, locality NMMNH L-3433, part and counterpart of the well preserved forewing apex.

**Description.** Fore wing 15 mm long and 7.3 mm wide as preserved, full wing length about 30 mm. Wing apex rounded. Costal space distinctly widened near the apex. SC short, not reaching wing apex. R long, ending at the wing apex. RS five-branched, with anterior one twice forking, its first branch with short fork. MA simple, MP with 2 branches preserved. Archedictyon irregular, with small cells, covering all wing membrane including pterostigmal and radial areas. No crossveins present.

**Comparison.** Differs from *C. arroyo* Kukalova-Peck and Peck, the only other species in the genus, in costal and radial areas filled with archedictyon rather than with crossveins, and in smaller size of archedictyon cells.

**Remarks.** *C. arroyo* was described from well preserved adult hind wing from the same locality (Kukalova-Peck and Peck, 1976). The present wing is much narrower and so it is considered to be a fore wing.

**Etymology.** This species is named for paleontologist Dr. Spencer G. Lucas.

#### Family Spilapteridae Brongniart, 1893

The family combining almost 20 genera with more than 30 species distributes in Europe, Siberia and North America in the Carboniferous and Lower Permian. Characteristic of the family are oligomerized venation, absence of archedyction and presence of numerous cross veins.

#### Spilapteridae incertae sedis

#### Figure 13

Specimens UNM 8172, UNM 6853, and UNM 3156, all from locality NMMNH L-3433, are fragments of large wings insufficient for more close identification. The large size, irregularly anastomosed crossveins, and color pattern of the wing fragments are most similar to that of *Bojoptera colorata* Kukalová known from Westphalian C of Central Bohemian Coal Basins (Kukalová, 1958). However, the fragments at hand differ in having the crossveins less regular and more abundantly forking and interconnected than in *B. colorata*.

#### Suborder Frankenholtiina Guthörl, 1962

#### Family Hanidae Kukalová-Peck, 1975

by N.D. Sinitshenkova

The Hanidae represent a highly specialized family that was previously known by only two species of the single genus *Hana* Kukalova-Peck, 1975 from the Lower Permian of Moravia (Czech Republic) (Kukalova-Peck, 1975). The family is characterized by extremely narrow petiolate wings with a dense archedictyon and a deeply undulating posterior margin. Hanidae was described in the order Megasecoptera (=Mischoptera), a supposed descendant of Dictyoneurida, and recently has been transferred to the latter order (Sinitshenkova, 2002).

#### Genus *Forcynthia* Sinitshenkova, gen. nov.

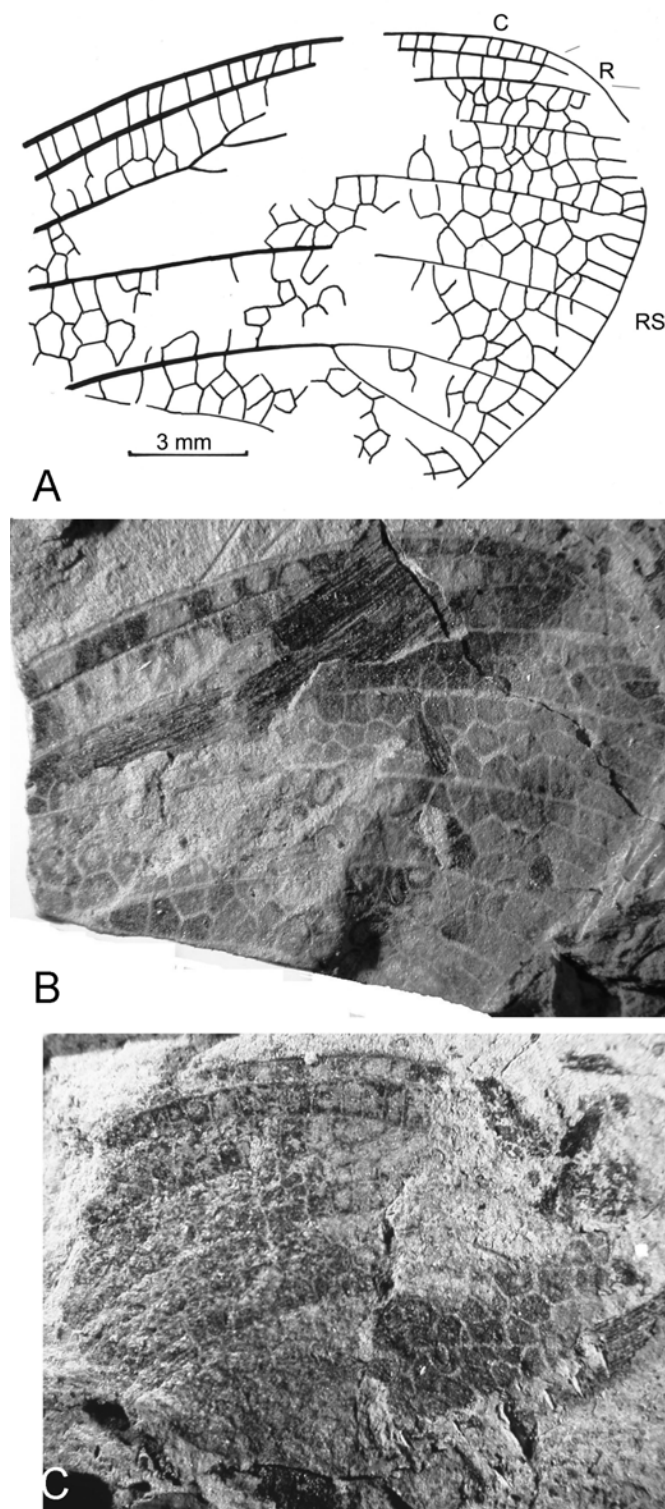


FIGURE 11. *Titanodictya rowlandi* Sinitshenkova sp. nov.: **A, B** – holotype, **C** – paratype, NMMNH P-26907.

Saarlandiidae, of which *Titanodictya* fits the former in having MP pectinated forward (backward so in Peromapteridae and Saarlandiidae). Within Dictyoneuridae *Titanodictya* is closely related to *Dictyoneura* Goldenberg from which it differs by the wing fore margin, which is of concave within the apical third, and by its large size. Many dictyoneurids are described on the basis of fragments of isolated wings, which creates problems in their identification. It is clear that the order

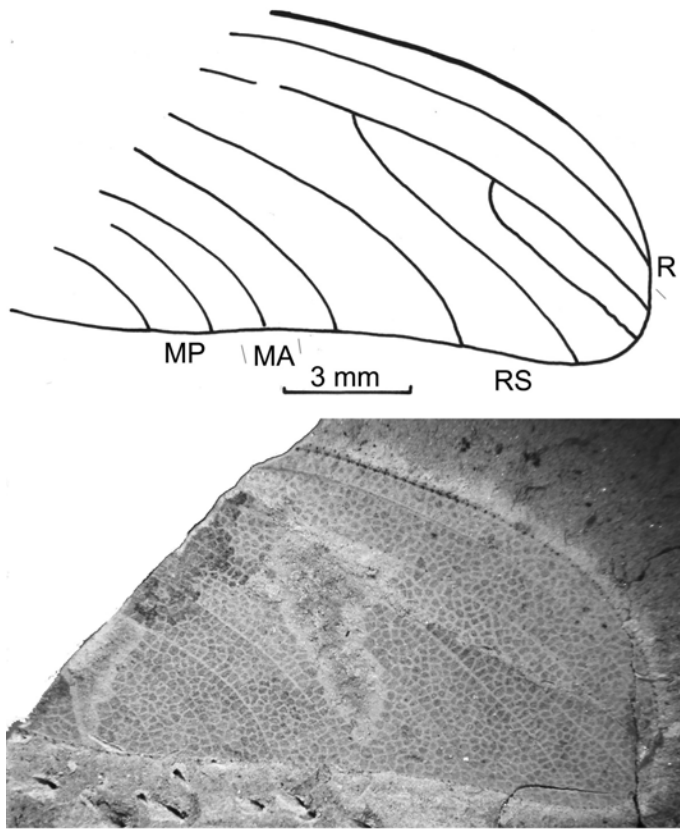


FIGURE 12. *Carrizopteryx lucasi* Sinitshenkova sp. n., holotype.

Hanidae genus indet.: Rowland, 1997: 4, Figure 5.

**Type species.** *F. cynthiae* sp. nov.

**Diagnosis.** Similar to *Hana* Kukalová-Peck, 1975, the only other genus in the family, except RS being probably disintegrated (with branches originating directly from R or perhaps also from MA), MP simple, short, the vein labeled by Kukalová-Peck (1975) as CuA lost, and posterior wing margin armed basally with two spines, and with distal flap short and high.

**Remarks.** The preservation state of the only known fossil is imperfect making difficult its morphological interpretation. In particular, the veins between R and MP are not clearly defined, especially their interconnections. Also the vein position in respect to the wing membrane (convex vs. concave) is not always apparent. This makes tentative our interpretation of RS and, to a less extent, MA.

The interpretation of the two posterior veins as CuA and CuP, and not as CuP and 1A, respectively, as in Kukalová-Peck (1975), is because these veins are, respectively, convex and concave, and not reverse.

The basal posterior spines are of great interest because they have no parallel in other insects, and their function is completely obscure. In particular, the first idea that might come to mind is that the spines help either interconnecting wings in flight or fixing them at rest, but this looks unlikely. Indeed, the proper function of long petiolate wings is to secure slow and highly maneuverable flight (best exemplified by damselflies) which is particularly advantageous in case of four-winged flight with two wing pairs operating at different (up to opposite) phase angles (e.g., Wootton and Kukalová-Peck, 2000). Wing interconnection in flight is generally unknown in the whole superorder Dictyopteroidea (= Palaeodictyopteroidea), and would seem particularly disadvantageous in case of these petiolate wings. As to the possible function of wing fixing in the rest position, it is characteristic of various insect groups that fold their wings over body at rest, but hardly possible when the



FIGURE 13. Spilapteridae incertae sedis, specimen UNM 6853.

wings are kept permanently outstretched, as in Dictyopteroidea.

**Species included.** Type species.

**Etymology.** This genus is named for Mrs. Cynthia Rowland.

***Forcynthia cynthiae* Sinitshenkova, sp. nov.**

**Figure 14**

**Holotype.** NMMNH P- 26908; locality NMMNH L- 3433, incomplete right wing.

**Description.** Wing fragment 57 mm long as preserved (about 65 mm full wing length), 9 mm wide at the level of subapical flap, dark except small marginal hyaline spots at and beyond medial flap. Anterior margin slightly concave in basal half, hind margin with two distinct flaps: more wide medial flap with slightly impressed top, and more short and high subapical flap. SC reaching beyond subapical flap, subcostal area almost twice as wide as costal one except in wing base where all C, SC, R and M close approaching to each other. RS as preserved with three branches originated directly from R distally of medial flap (bases of RS<sub>2</sub> and RS<sub>3</sub> indiscernible), and possibly with RS<sub>4</sub> fused with MA. MA base not apparent, M forking possibly before medial flap. CuA distant of MP, with three short apical branches within medial flap, CuA<sub>1+2</sub> stalk as long as CuA<sub>1</sub>. CuP simple, neither connected nor approaching to CuA basally, well spaced with it and slightly less so with wing hind margin, reaching it just before medial flap. No anal veins preserved. Archdictyon irregular, with cells moderately large (indiscernible in most wing surface). Two basal stout spines are about 0.2 mm length and spaced for 1.8 mm. This specimen was figured and discussed by Rowland (1997).

**Etymology.** This species is named for Mrs. Cynthia Rowland.

**Family incertae sedis**

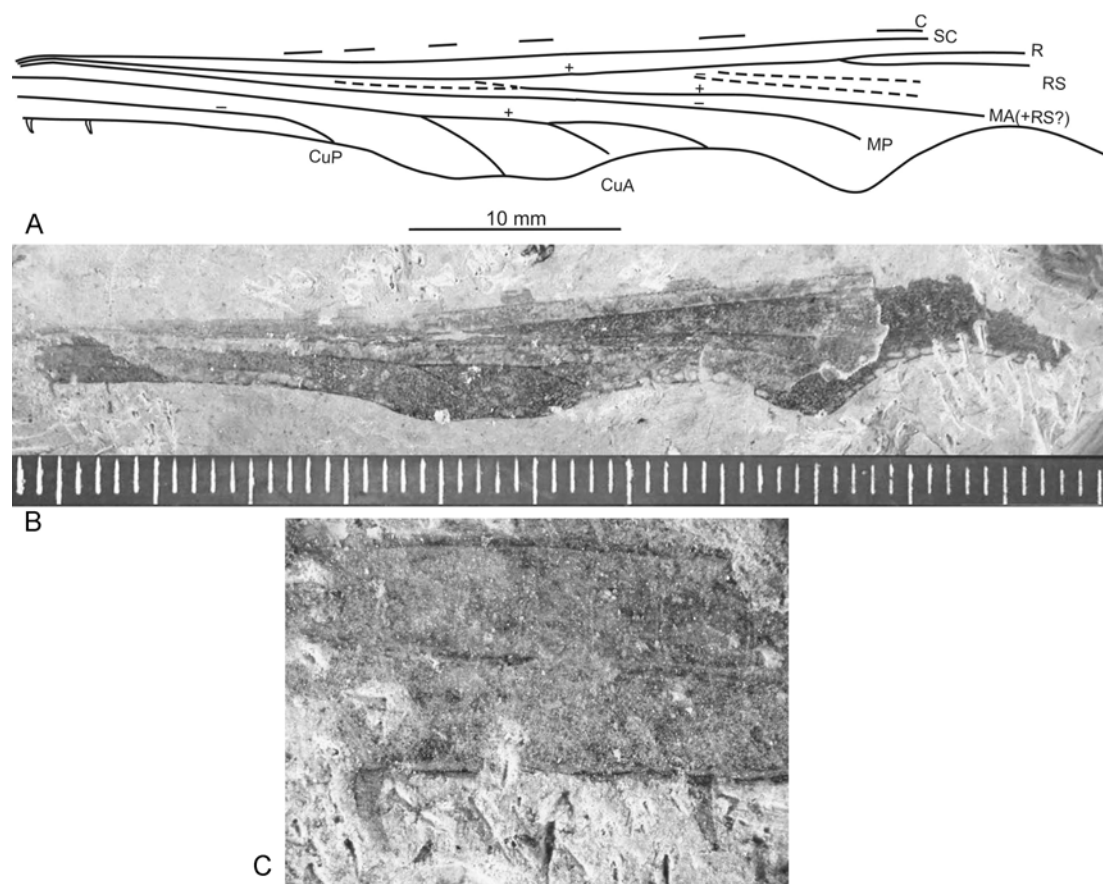


FIGURE 14. *Forcynthia cynthiae* Sinitshenkova holotype: A, B – general view, C – basal teeth.

by N.D. Sinitshenkova

#### Figure 15

Specimen NMMNH P-26903 from locality NMMNH L-3433 represents a part and counterpart the fore and hind wing pads with fragments of thorax. It might belong to the nymph of last stage of Dictyonaurida. This identification is based on long wing pads with rich venation. The nymph is rather large: with its wing pad 8.2 mm long, the body length should be approximately 30 mm. The nymphal size could correspond to the above described *C. lucasi*, but other characters available are incomparable, so association of these two fossils on this only base is not possible.

#### Order Diaphanopterida Handlirsch, 1906

(= *Diaphanopteroidea* Handlirsch, 1919)

by N.D. Sinitshenkova

Small order with about 50 species in 25 genera and eight families which differs from other dictyonaurideans in the roof-like wing folding at rest, small prothoracic paranota, and in fore and hind wings which are almost identical in form and venation pattern and lacking archidictyon. Ovipositor curved, probably used for inserting eggs into plant tissues, cerci very long. The mode of life is similar to that of Dictyonaurida.

The order is widespread in North Eurasia and North America from the earliest Middle Carboniferous (Namurian B) to the Early Permian.

#### Family Martynoviidae Tillyard, 1932

This family with five genera and eight species is restricted to the Lower Permian of North America.

*Phaneroneura* Carpenter, 1947

#### *Phaneroneura rineharti* Sinitshenkova, sp. nov.

#### Figure 16

**Holotype.** NMMNH P-26905, locality NMMNH L-3433, part and counterpart of isolated fore wing.

**Description.** Fore wing 7.6 mm long and 1.8 mm wide. Wing well costalized, almost four times as long as wide. SC not quite reaching wing midlength. RS two-branched. MA leaving RS stem almost at wing midlength. Wing membrane clear except darkened apical third, dark transverse band at wing midlength, narrow dark stripe along CuA stalk not reaching its base, costal and subcostal spaces basally, and less dark, wing very base.

**Comparison.** The new species resembles *Ph. martynovae* Carpenter, 1947 from the Lower Permian of Oklahoma (Carpenter, 1947) in wing shape, but differs in clearly smaller size and two-branched RS. In the latter two characters it is similar to another species from the Lower Permian of Oklahoma, *Ph. reducta* Carpenter, 1947, but differs from it in having long and narrow wing.

**Etymology.** The species is named after Mr. Larry Rinehart, who collected many insect fossils from Carrizo Arroyo kept at the New Mexico Museum of Natural History and Science.

#### Family Astenohymenidae Tillyard, 1924

This family with two genera and 16 species occurs in the Lower Permian of Urals and North America.

#### *Astenohymen* Tillyard, 1924

*Astenohymen micron* Sinitshenkova, sp. nov.

#### Figure 17

**Holotype.** NMMNH P-26901, locality NMMNH L-3433, part and counterpart of four overlapped wings



FIGURE 15. Unidentified nymph of Dictyoneurida (possibly *Carrizopteryx lucasi*), line drawing and aligned photos of the part and counterpart, specimen NMMNH P-26903.

**Description.** Fore wing about 3 mm long (holotype wing fragment 2 mm long), its width about 0.7 mm. Pterostigma is poorly developed. The stem MA+RS is comparatively long. The base of Rs when derived from MA+RS strongly curved MP strait. Cross vein r-rs is slightly basely than rs-m, ma-mp is in considerable distance from RS base.

**Comparison.** The new species differs from other congeners in its small size. Additionally it is similar to *A. gracilis* Tillyard, 1926 by curved base of RS deriving from MA+RS but differs by basal position of ma-mp. By the presence of the last feature *A. micron* resembles *A. affinis* Tillyard, 1926 and *A. kansasensis* Tillyard, 1926 differing from them by curved base of RS.

**Remarks.** The genus *Asthenohymen* is restricted to the Lower Permian: three of its species are described from the Kungurian of Urals (Zalessky, 1939; Novokshonov, Novokshonova, 1998) and 12 from the Leonardian Oklahoma and Kansas (Tillyard, 1924; 1926; Carpenter, 1947). Recently Carpenter (1992) synonymized *Karoohymen* Riek 1976 from the Upper Permian of Natal, South Africa (Riek, 1976) under *Asthenohymen*. This decision is considered disputable (Novokshonov, Novokshonova, 1998); unfortunately the present material provides not enough new information to resolve the problem.

**Etymology.** Species name refers to its small size (*micron* is the Greek for small).

*Asthenohymen zonatus* Sinitshenkova, sp. nov.

Figure 18

**Holotype.** NMMNH P-26906, locality NMMNH L-3433, part and counterpart of the overlapped fore wings with not complete venation.

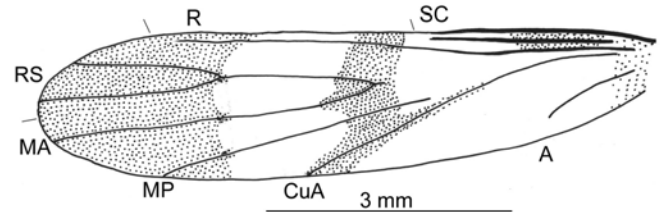
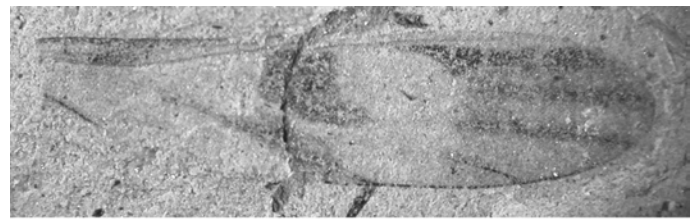


FIGURE 16. *Phaneroneura rineharti* Sinitshenkova sp. nov., holotype.

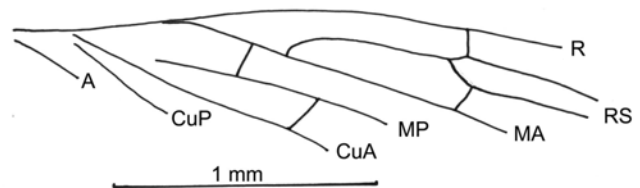
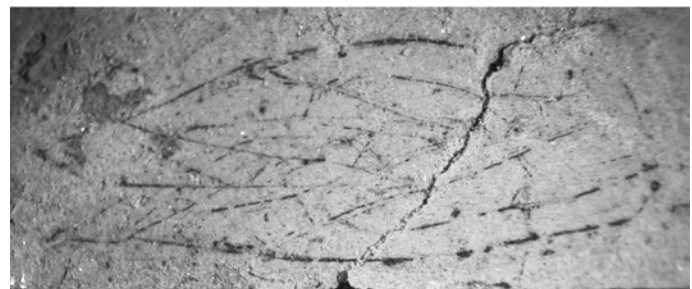


FIGURE 17. *Asthenohymen micron* Sinitshenkova sp. nov., holotype.

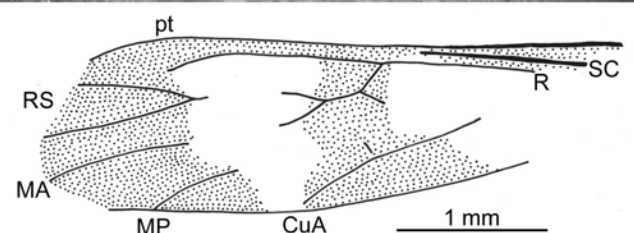


FIGURE 18. *Asthenohymen zonatus* Sinitshenkova sp. nov., holotype.

**Description.** Fore wing about 5.2-5.4 mm long (holotype wing fragment 3.8 mm long as preserved), 1.15 mm wide. Pterostigma well developed, RS fork wide. Stem MA+RS comparatively long, slightly concave; MA and RS with slightly curved bases when they diverge.

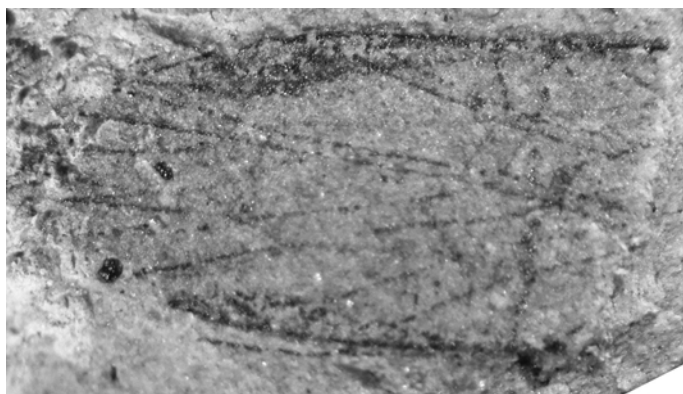


FIGURE 19. ?Asthenohymenidae indet., specimen NMMNH P-36622.

Cross vein ma-mp enters to the stem MA+RS almost at its middle. Wing membrane clear with dark base and apex and transverse dark tripe through RS+M.

**Comparison.** New species closely related to *A. affinis* because of well developed pterostigma, slightly concave stem of MA+RS and basal position of ma-mp a. It differs from *A. affinis* in slightly curved bases of MA and RS, in MA-MP meeting the MA+RS stem almost at its midlength, and in small size (wing of *A. affinis* is 7.3 mm long).

**Material.** Known only by the holotype.

**Etymology.** Species name refers to the wing color pattern (*zonatus* is Latin for banded).

#### ?Asthenohymenidae indet.

##### Figure 19

Specimen NMMNH P-36622, locality NMMNH L-3433, represents apical part of four wings folded flat (2.9 mm long, ca. 0.5 of full wing length), apparently similar to asthenohymenid wings, but with venation difficult to decipher. That is why it is left unnamed. At any case this fossil is not conspecific with the above species, because it shares large pterostigma with *A. zonatus* and clear wing membrane with *A. micron*. Additionally, it shows four wing as perfectly overlapped each other and so apparently folded flat rather than roof-like at rest. This character is unknown in entire order Diaphanopterida, making questionable even the ordinal position of the fossil.

#### Order Psocida (= Psocoptera)

By A.P. Rasnitsyn

#### Family Psocidiidae Tillyard, 1926 (= Dichentomidae Carpenter, 1932)

##### Genus *Dichentomum* Tillyard, 1926

##### ?*Dichentomum arroyo* Rasnitsyn, sp. nov.

##### Figure 20

**Holotype.** NMMNH P-26917, locality NMMNH L-3433, imperfectly preserved fore wing with base missing.

**Description.** Fore wing 3.2 mm long as preserved, some 3.7-3.9 mm full length, 1.3 mm wide, possibly slightly infuscated along outer and hind margin. SC not preserved. Pterostigma moderately large, meeting r-rs at its maximum width, with all lower margin convex, r-rs subvertical, almost 1.5 times as long as pterostigma wide and about as long as its distance from RS fork. RS forking at same level as  $M_{1+2}$ ,  $RS_1$  bending apically,  $RS_2$  following direction of RS stalk. Stalks of RS;  $M_{1+2}$  and  $M_{3+4}$  subparallel basad up to at least midlength of  $CuA_1$ , so M forking not distad  $CuA$  forking.  $M_{3+4}$  forking near apex of  $CuA$  fork.  $M_1$ ,  $M_3$  and  $CuA_1$  of near same length, arching ( $M_1$  less so).  $CuA$  fork 3.2 times as long as high.

**Remarks.** The fossil is tentatively attributed to *Dichentomum*

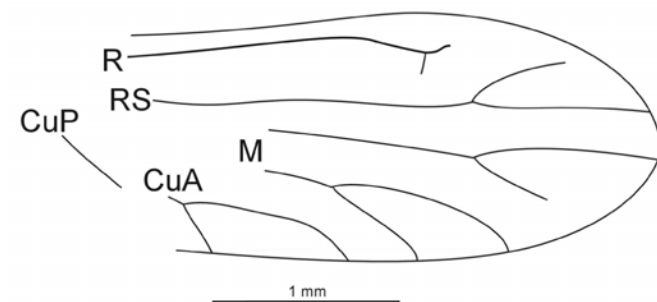
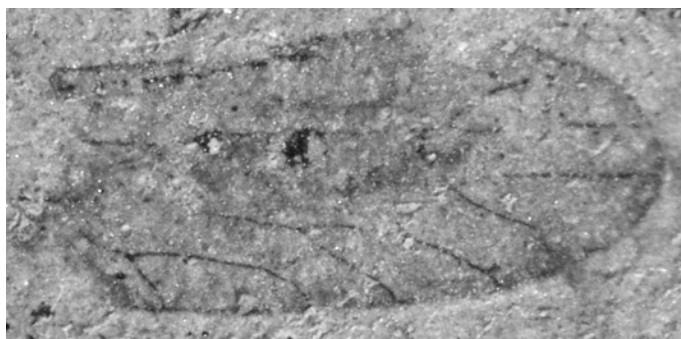


FIGURE 20. ?*Dichentomum arroyo* A. Rasnitsyn sp. nov., holotype.

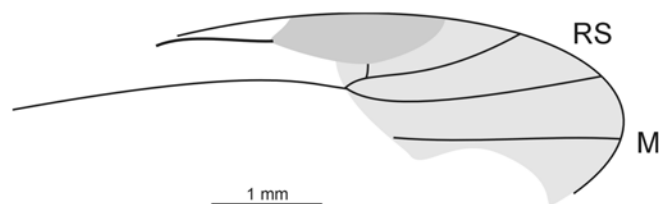


FIGURE 21. ?*Dichentomum* sp., specimen UNM 6840.

because, like this genus as well as *Parapsocidium* Zalesky, 1937, and *Eopsylla* Vishniakova, 1976, it has bulging pterostigma, but unlike the latter two genera it has all lower pterostigmal margin convex (not concave before r-rs) and r-rs subvertical (not oblique backward). The new species differs from all described Psocidiidae in having  $M_{1+2}$  and  $M_{3+4}$  stalks subparallel, indicating far basal position of M fork. This would imply a generic level distinction of the species but the sole specimen is badly incomplete.

**Etymology.** The name is after the Carrizo Arroyo fossil site.

##### ?*Dichentomum* sp.

##### Figure 21

**Referred material.** UNM 6840, locality NMMNH L-3433, incomplete fore wing with base, posterior half and much of fore margin missing.

**Description.** Fore wing 5.7 mm long as preserved, some 8-9 mm full length, 1.3 mm wide, with apex somewhat infuscated. Pterostigma as in previous species except possibly higher. Crossvein r-rs subvertical,

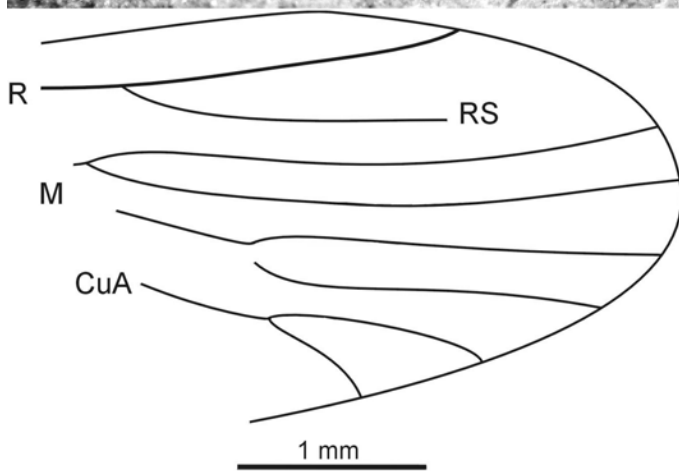
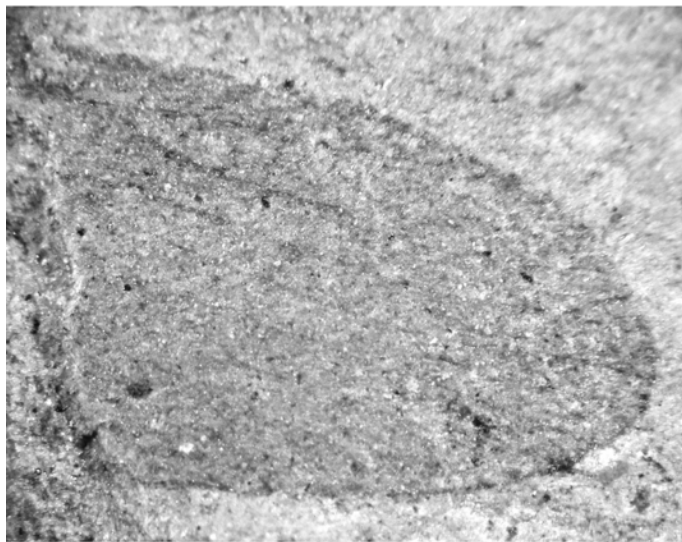


FIGURE 22. *Arroyoscyta novaemexicana* Rasnitsyn sp. nov., holotype.

very short, meeting  $RS_1$  beyond RS fork for more than r-rs length. RS fork very long, same probably true for  $M_{1+2}$  fork.

**Remarks.** Like in the previous species, the form of pterostigma is indicative of *Dichentomum*. However incomplete, the present fossil differs from all other known Psocidiidae as well, this time in the unusually long fork of RS (and possibly also of  $M_{1+2}$ ). Again, very incomplete preservation state prevents formal description of the fossil.

#### Order ?Hemiptera Linné, 1758

By A.P. Rasnitsyn

#### Family ?Archescytinidae Tillyard, 1926

Genus *Arroyoscyta* Rasnitsyn, gen. nov.

Type species. *A. novaemexicana* sp. nov.

**Diagnosis.** Fore(?) wing of medium size with costal margin probably more or less straight, costal space moderately narrow, SC short or absent (not entering distal wing half), pterostigma indistinct, R near straight in distal wing half, lacking fore branch delimiting pterostigmal cell, RS short (starting probably near wing midlength), simple, near straight except basally, M twice dichotomous,  $M_{1+2}$  forking before and  $M_{3+4}$  far beyond RS base, CuA two-branched, forking after  $M_{3+4}$ . Basal wing half and body unknown.

**Taxonomic position.** The wing fragment at hand similar to no insects other than Archescytinidae in general appearance and gross venational features. However, some details are discordant with this attribution, particularly when considering the age of fossil, which is older than all indisputable hemipterans. These characters are absence of SC or

its rudiment running along R, open pterostigmal cell, dichotomously four-branched M with unusually long fore fork, and CuA fork which is very short and distal thus inferring very long clavus. This makes possible only tentative attribution of the unique fossil to Archescytinidae and to Hemiptera in general.

**Species included.** Type only.

**Etymology.** The name is after the Carrizo Arroyo fossil site and *Archescytina*.

#### *Arroyoscyta novaemexicana* Rasnitsyn, sp. nov.

#### Figure 22

**Holotype.** NMMNH P-36624, locality NMMNH L-3433, apical half of (fore?) wing.

**Description.** Wing fragment 3.1 mm long and 2.2 mm long as preserved, full wing 5-6 mm long, subacute apically. Costal space somewhat darkened.  $M_{1+2}$  forking before RS base for about width of costal space,  $M_1$  and  $M_2$  arching backward,  $M_2$  meeting wing apex.  $M_{3+4}$  forking at about 0.2 CuA at about 0.3 of  $M_{1+2}$  fork length. CuA<sub>1</sub> and CuA<sub>2</sub> both slightly arching forward, spaced for CuA<sub>2</sub> length.

**Etymology.** Species name is after the source area (*novaemexicana* is the Latin attribute for New Mexico).

#### Order Palaeomanteida Handlirsch, 1906

(= *Miomoptera* Martynov, 1927)

by A.P. Rasnitsyn

#### Family Palaeomanteidae Handlirsch, 1906

The family Palaeomanteidae was defined by Rasnitsyn, 2002b to embrace miomopterans with M+CuA stalk which is usually long (or, if short, with CuA base better developed than M base) and with SC meeting C rather than R. The family covers more than 50 valid species in addition to 12 described herein. Palaeomanteidae is a rather clear cut family which is difficult to classify because of the uniform wing venation. Fore wing of the vast majority of species can be described as follows: SC meeting C within central 0.3 of wing length, with or, usually, without fore branchlets (which are often weak and indistinct); RS with three, rarely two or four pectinate branches; M and CuA with long common stalk and each with two branches; CuP simple, weak (often indistinct); only two (rarely three) anals; crossveins not numerous, weak, often not distinct. Hind wings are known in a minority of species and render little help in taxonomy of the family.

As a result, few characters are available for generic distinction. Further, some of the characters used were later found unstable or misinterpreted because of the postmortem deformation of fossils. This resulted in different but similarly oversynonymized systems by Carpenter (1992) and Rasnitsyn (2002b) with only five and three valid genera, respectively. However, the approach of these two authors was exceedingly skeptical. The present revision makes it possible to define more genera, although a few of them are not very distinct or possibly polyphyletic, being based on characters prone to independent origin. This particularly concerns the apparent shift of the fore M branch to RS which occurs independently in *Permonia*, *Miomatoneura*, *Miomatoneurella* and in *Permonikia aestiva*, as well as, possibly, within some of these genera. Additional problems arise with identification if this apparent shift takes place or not. The shift occurs because the usual r-m crossvein connected RS stalk with the base of  $M_1$  becomes aligned with  $M_1$  as much as, or more than,  $M_1$  does with its true base: the process is gradual, so as transitional states are not uncommon. Nevertheless I employ conservative approach in using this character until the type revision of all palaeomanteids is possible. Otherwise many described species would become unclassifiable. The present revision of the family system in large part relies on published descriptions and illustrations instead of the type material, and so it should be considered as strictly provisional, aimed mainly to make possible description of the rich material from Carrizo Arroyo.

Besides the fossils not formally described, four other taxa are not

included in the following key. *Archisialis praecox* Martynov, 1933 from the Upper Permian of Soyana in North Russia differs from all Palaeomanteidae but *Epimastax* and *Permonia* in large size (10.2 mm). It belongs to advanced palaeomanteids with long M+CuA but cannot be placed there with certainty because of incomplete preservation (SC not preserved and anal area missing). *?Delopterus pantherinum* sp. nov. differs from all known palaeomanteids by having spotted wings. Unfortunately it is preserved so incompletely that its attribution to *Delopterus* is mainly arbitrary: the only reason is that the alternative genera agreeing with preserved characters, viz. *Palaeomantis* and *Delopsocus*, are rare in Carrizo Arroyo. Two more fossils from Carrizo Arroyo most probably represent unique species but are not described herein and are not included in the key; one because of very incomplete preservation, another because it is a hind wing of unknown generic position (see below). *Palaeomantis tshekardensis* Novokshonov, 2000 (= *Epimastax tshekardensis* (Novokshonov, 2000), comb. nov.) and *Delopterus anale* (Martynov, 1928, described as *Leptoneurula analis*) are known from hind wings only and cannot be correctly compared to other congeners. *E. tshekardensis* is similar to the hind wing of *E. sojanensis* (Rasnitsyn, 1977) except for a four-branched RS. The combination and form *D. anale* is used because *Leptoneurula*, type species *L. analis*, has been synonymized with *Delopterus* (Carpenter, 1992).

Two genera synonymized under *Palaeomantis* by Carpenter (1992) are excluded from consideration. *Miomantisca clara* G. Zalesky, 1956, as well as *Miomoptilon pusillus* G. Zalesky, 1956 and *Paralioma palida* G. Zalesky, 1956, missed by Carpenter (1992), all are junior synonyms of *Sellardsiopsis conspicua* G. Zalesky 1939 (Palaeomantiscidae) (syn. nov.). Their types are now kept at the Paleontological Institute RAS, Moscow. The type of *Delopteriella gratiosa* G. Zalesky, 1956 has not been found yet, but the original drawing also recalls *Sellardsiopsis* G. Zalesky. However, given a considerable age difference (*D. gratiosa* is Ufimian and not Kungurian) their synonymization would not be justified on the above basis only.

As to *Miomatoneurites sylvensis* G. Zalesky, 1956, also synonymized under *Palaeomantis* by Carpenter (1992), its type is also available for study at the Paleontological Institute. It is a hind wing of fair preservation state which recalls *Permonikia aestiva* (Novokshonov, 2000). Their synonymization would result in extensive name changes, for *Miomatoneurites* has a priority over *Permonikia*. That is why I prefer to consider *M. sylvensis* as unplaced within Palaeomanteidae until its newly found type is better studied.

Unless stated otherwise, 'wing' means fore wing. Diagnoses of individual species are omitted, being explicit in the key provided below.

#### Key to the genera and species of Palaeomanteidae:

1. M+CuA short, more than three anal veins (hind wing M free). Wing 10 mm long or more. *Epimastax* Martynov. 2
  - M+CuA long, two, rarely three anal veins 4
2. M fork well basad of RS and CuA forks: *E. parvulus* Martynov (Tikhie Gory) 4
  - RS, M and CuA forking at about same level. 3
3. SC close to R. Anal crossveins sparse, simple: *E. sojanensis* (Rasnitsyn) (Soyana) 3
  - SC closer to C. Anal crossveins abundant, branching. *E. celer* Kukalová 4
4. Wing length about two time width, small (5 mm). RS three-branched: *Saeromioptera jordani* Guthörl (Saar) 5
  - Wing more elongate (except sometimes due to postsedimental deformation). 5
5. RS four-branched. SC with many fore branchlets. *Permonikia* Kukalová. 6
  - RS with two or three branches (unless M<sub>1</sub> shifted to RS imitating fourth branch: then M looking simple). 7
6. Fore wing 6.5 mm. M<sub>1</sub> not shifted to RS: *P. permoniki* Kukalová (Obora) 7
  - Fore wing more than 10 mm long. M<sub>1</sub> with double base (from M and RS): *P. aestiva* (Novokshonov)(Tshekarda)

- 7 (5). RS with two true branches, even if seemingly with three RS but with M simple (M<sub>1</sub> shifted to RS). CuA fork long, usually low. SC without preapical fore branches. 8
  - Wing 4-7 mm long. 8
    - RS with three true branches (sometimes seemingly with 4 RS and with M simple due to M<sub>1</sub> shifted to RS). 13
8. RS seemingly with three RS but with M simple (M<sub>1</sub> shifted to RS). *Miomatoneurella* O. Martynova. 9
  - M<sub>1</sub> not seemingly shifted to RS. *Delopterus* gen. nov. 12
9. Wing 7.2 mm long. True M<sub>1</sub> base present, vertical: *M. ostertali* Guthörl (Saar) 10
  - Wing 4-5 mm long. True M<sub>1</sub> base oblique or lacking. 10
10. RS fork distant from base of (shifted) M<sub>1</sub>. True M<sub>1</sub> base present, oblique: *M. boskovicensis* (Kukalová) (Obora) 11
  - RS fork close to base of (shifted) M<sub>1</sub>. True M<sub>1</sub> base absent. 11
11. RS base far distal of M base. Wing 4 mm long: *M. reducta* O. Martynova (Suriyokovo) 12
  - RS base far proximal of M base. Wing longer: *M. americana* sp. nov. (Carrizo Arroyo)
- 12 (8). Wing with three vertical dark bands. RS base far distal of M base: *D. zebra* sp. nov. (Carrizo Arroyo) 13
  - Wing dark in apical half. RS base far proximal of M base. *D. bicolor* sp. nov. (Carrizo Arroyo)
- 13 (7). M<sub>2</sub> fused with CuA<sub>1</sub> except basally. SC 0.4 times as long as wing. 2A with five branches: *Permodelopterus obscurum* (Kukalová) (Obora) 14
  - M<sub>2</sub> and CuA<sub>1</sub> not fused. 14
14. M<sub>2</sub> fused with RS<sub>3</sub> except basally and distally: *Neodelopterus anomalum* gen. sp. nov. (Carrizo Arroyo) 15
  - M<sub>1</sub> free (although can be seemingly shifted to RS). 15
15. Hind wing with striking pterostigma. Fore wing unknown: *Stigmodelopterus pterostigmalis* gen. sp. nov. (Carrizo Arroyo) 16
  - Neither for nor hind wing with striking pterostigma. 16
16. Hind wing CuA with two short, spaced preapical branches (alternatively possible to be described as simple with two short, spaced posterior crossveins). Color pattern in form of indistinct darkening along or between main veins. Fore wing unknown: *Tridelopterus variegatum* sp. nov. (Carrizo Arroyo) 17
  - Hind wing when known with CuA two-branched or, if described three-branched, with branches crowded and not crossvein-like. 17
17. M<sub>1</sub> seemingly shifted to RS: (with rs-m crossvein forming false M<sub>1</sub> base on RS, and sometimes with true M base lost). SC usually reaching forewing midlength. 18
  - M<sub>1</sub> not shifted to RS. 27
18. SC with preapical fore branches: *Permonia* Kukalová. 19
  - SC without preapical fore branches: *Miomatoneura* Martynov 20
19. Wing large (10 mm long being moderately procrusted lengthwise): *P. permoni* Kukalová (Obora) 21
  - Wing small (below 6 mm being much procrusted lengthwise): *P. arta* Kukalová, *P. insolida* Kukalová (Obora) (no good difference found)
- 20 (18). False base of M<sub>1</sub> close to base of RS. 21
  - False base of M<sub>1</sub> closer to junction with real base of M<sub>1</sub> than to base of RS. 22
21. False base of M<sub>1</sub> longer than RS before it: *M. palaeozoica* Kukalová (Obora) 23
  - False base of M<sub>1</sub> shorter than RS before it: *M. permica* Kukalová (Obora)
- 22 (20). RS between false base of M<sub>1</sub> and next RS fork longer than half RS length between two forks. 23
  - RS between false base of M<sub>1</sub> and next RS fork shorter than half RS length between two forks. 24
23. RS<sub>2</sub> about as long as stalk RS 1+2: *M. angusta* Kukalová

- (Obora)  
- RS2 much shorter than stalk RS 1+2: *M. candida* Kukalová (Obora)
- 24** (22). Wing longer than 7mm. 2A simple when known. 25  
- Wing shorter than 6.5 mm. 26
- 25.** Wing pale more or less. CuA fork moderately narrow: *M. frigida* Martynov (Soyana)  
- Wing dark except pale base and large pale spot near midlength. CuA fork very narrow and long: *M. rotundata* Martynov (Soyana)
- 26** (24). Wing 6.2 mm. long: *M. intermedia* Martynov, 1928 (Soyana)  
- Wing 5 mm long: *M. parvula* Martynov, 1930 (Tikhie Gory)
- 27** (19). SC length 0.3-0.35 (rarely 0.4) times fore wing length, with one or no preapical fore branches. 2A with one or two branches. *Delopterus* Sellards. 28  
- SC length 0.45-0.55 times fore wing length. 38
- 28.** Wing ca. 3.5 mm long: *D. radtshenkoi* O. Martynova (Kaltan)  
- Wing 4 mm or longer. 29
- 29.** Wing 4-4.5 mm long. 30  
- Wing longer than 5 mm. 31
- 30.** Wing with dark apex and preapical vertical dark band: *D. zonatum* sp.nov. (Carrizo Arroyo)  
- No vertical dark bands: *D. minutum* Sellards (Elmo)
- 31** (29). SC with preapical fore branch. CuA fork very long and low. Wing 6.3 mm: *D. hangardi* Guthörl (Saar)  
- SC without preapical branch. CuA fork shorter and higher. 32
- 32.** Wing longer than 7 mm. SC longer (almost reaching level of M fork). 33  
- Wing shorter than 7 mm. SC usually ending well before M fork 34
- 33.** RS<sub>1</sub> half as long as RS<sub>1+2</sub> stalk: *D. kaltanicum* O. Martynova (Kaltan)  
- RS<sub>1</sub> ca. 0.7 times as long as RS<sub>1+2</sub> stalk: *D. insigne* (Martynov) (Tikhie Gory)
- 34** (32). 2A deep sinuate and with 2 branches: *D. latum* Sellards (Elmo)  
- 2A less sinuate, usually simple. 35
- 35.** Wing longer than 6.5 mm, with subapical dark band continuing posterobasally: *D. fasciatus* Tillyard (Elmo)  
- Wing 5-6 mm long. Color pattern different, if any. 36
- 36.** Pterostigmal arching of R distinct and long (longer than RS<sub>1+2</sub> fork). No distinct color pattern: *D. incertum* Martynov (Tikhie Gory)  
- Pterostigmal arching of R shorter or indistinct. Wing dark in distal half. 37
- 37.** Dark area extending basad at wing midwidth. M stalk weak, not well seen: *D. rasnitsyni* Novokshonov (Tshekarda)  
- Inner border of wing darkening near straight, subvertical. M stalk normal: *D. commune* sp. nov. (Carrizo Arroyo)
- 38** (27). 2A with three or more branches, or anal crossveins forming network. SC without preapical fore branches. *Perunopterum* Kukalová 39  
- 2A with one or two branches. 45
- 39.** Anal crossveins forming network: *P. corium* Kukalová (Obora)  
- No anal network. 2A with three or more branches. 40
- 40.** Wing length 6.5-8 mm. 41  
- Wing length 4.5-5.5 mm. 42
- 41.** Anal veins almost or completely fused at place of anal crossvein to form lancet-like cell: *P. sylvaensis* Martynov, 1940 (Tshekarda; attribution is based on detached forewing PIN 1700/1293, holotype venation being largely obscured).  
- Anal veins separated with usual long crossvein: *P. lepidum* (Kukalová), *P. mirum* Kukalová (Obora)
- 42** (40). 1A forked: *P. lumbiforme* Kukalová (Obora) (two paratypes of *peruni* also run here: they differ from the rest of that species also in unusually long RS stalk and can form distinct species)  
- 1A simple. 43
- 43.** SC length 0.45 times wing length: *P. peruni* Kukalová (Obora)  
- SC length 0.55-0.6 times wing length. 44
- 44.** 2A branches less spaced, probably four in number: *P. macrum* Kukalová (Obora)  
- 2A branches well spaced, three in number: *P. truncatum* Kukalová (Obora)
- 45** (38). SC with fore preapical branchlets: *Palaeomantis* Handlirsch, 1904 46  
- SC without fore preapical branchlets: *Delopsocus* Tillyard, 1928 47
- 46.** Wing dark in apical half. Penultimate SC branchlet long, oblique, distant of apical one: *?P. apicalis* sp.nov. (Carrizo Arroyo)  
- Wing not darkened in apical half. Penultimate SC branchlet shorter, less oblique and less distant: *P. schmidtii* Handlirsch, 1904 (= *P. aequalis* Martynov, 1928, syn. nov.; synonymy is because *aequalis*, with its RS and M forking at one level, represents only an extremity of the variability spectrum of *schmidtii*) (Tikhie Gory)
- 47** (45). 2A simple. 48  
- 2A forked. 51
- 48.** Fore wing 5.5-6 mm long. 49  
- Fore wing 4.2-4.7 mm long. 50
- 49.** SC ending at wing midlength. CuA forking distally of M. Wing pale: *D. elongatus* Sellards, 1909 (Elmo)  
- SC ending distinctly before wing midlength. CuA forking basally of M. Wing dark except base and, possibly, large vertical spot at midlength: *D. stenopterus* sp. nov. (Carrizo Arroyo)
- 50** (48). CuA<sub>1</sub> smoothly following CuA stalk: *D. lepidus* Kukalová (Obora)  
- CuA<sub>2</sub> smoothly following CuA stalk: *D. sinuosus* Kukalová (Obora)
- 51** (47). CuA fork narrow. Wing 6 mm long: *D. kansanum* Carpenter, 1933  
- CuA fork wide. 52
- 52.** RS and M forking at one and the same level. Wing 4.6 mm long: *D. kamensis* Carpenter, 1933  
- RS forking distad of M. Wing 5.7 mm long: *D. furcatulus* Martynov, 1930

### Genus *Palaeomantis* Handlirsch, 1904

#### *?Palaeomantis apicalis* Rasnitsyn, sp. nov.

#### Figure 23

**Holotype.** NMMNH P-36612, locality NMMNH L-3433, fore wing with base missing except toward hind margin.

**Description.** Fore wing 5.8 mm long, ca. 1.8 mm wide (~1:31), with apical half infuscated. SC reaching wing midlength, with at least one long, slanting, well spaced preapical branchlet. R weakly sinuate toward apex, with pterostigma indicated. RS<sub>1</sub>: RS<sub>1+2</sub>(stalk): RS(stalk) ratio ~ 1:1.4:1.5. M fork and CuA fork at similar levels proximal of that of RS fork. CuA fork not narrow, with both branches angled with stalk. 1A and 2A simple, 2A angled at place of interanal crossvein.

**Remark.** No other palaeomanteids are known with the above structure of SC apex, for those with SC pectinate have branchlets more erected and less spaced. Of these, *Palaeomantis* is most similar in other characters (narrow wing well under 10 mm long, SC reaching wing midlength RS three-branched, M<sub>1</sub> free).

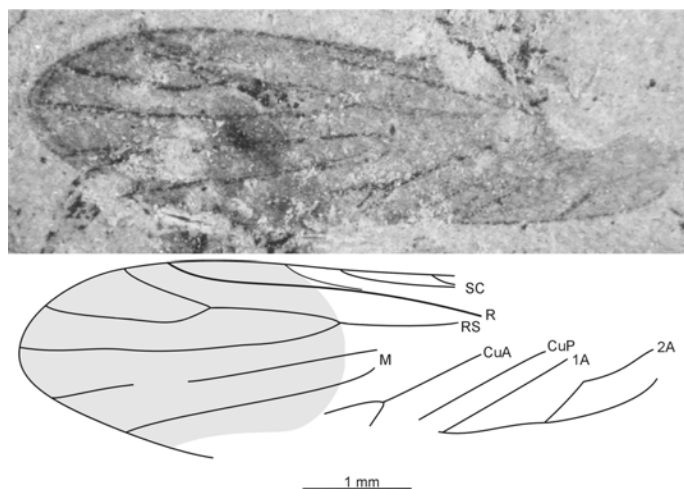


FIGURE 23. ?*Palaeomantis apicalis* Rasnitsyn sp. nov., holotype.

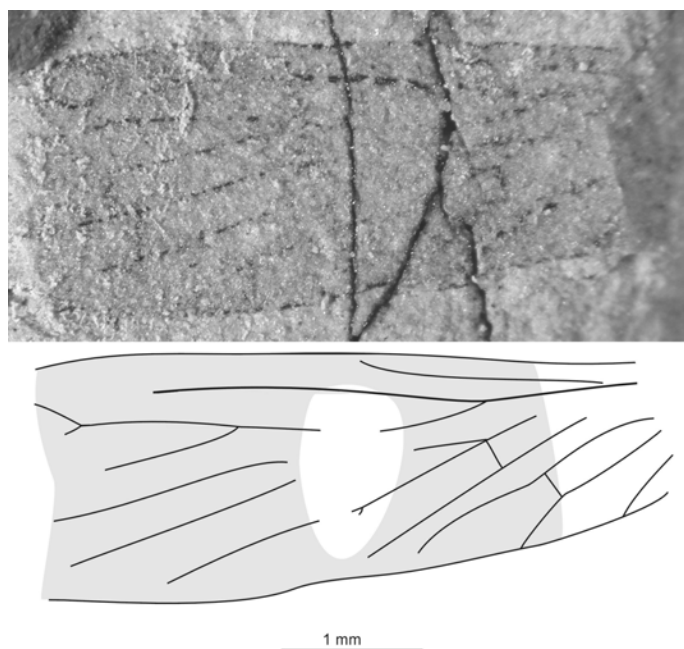


FIGURE 24. *Delopsocus stenopterus* Rasnitsyn sp. nov., holotype.

**Etymology.** The name is after the dark wing apex.

**Genus *Delopsocus* Tillyard, 1928**

***Delopsocus stenopterus* Rasnitsyn, sp. nov.**

**Figure 24**

**Holotype.** NMMNH P-36611, locality NMMNH L-3433, imperfectly preserved fore wing with apex missing.

**Description.** Fore wing 4.6 mm long as preserved, ca. 5.5 mm full length, 1.8 mm wide (~1:31), infusate except base and, possibly, vertically oval pale spot at midlength, although this looking rather as damage. SC reaching 0.55 wing length. Pterostigmal area not preserved.  $RS_{1+2}$  stalk 0.7 times as long as RS stalk. RS, M and CuA forks near aligned, with RS fork most distal.  $CuA_1$  almost twice as long as CuA stalk, almost aligned to it. 1A and 2A simple, 2A slightly angled at  $a_1$ - $a_2$ , 3A present.

**Etymology.** The name is after the narrow wing.

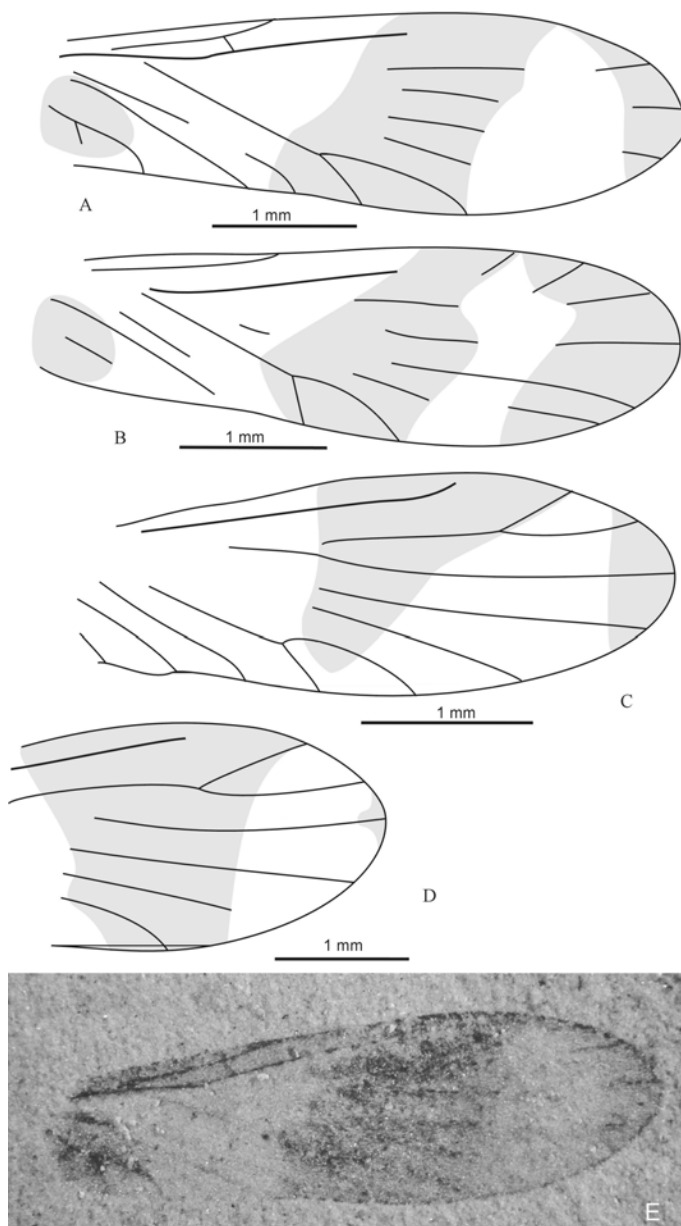


FIGURE 25. *Delopterum zonatum* Rasnitsyn sp. nov.: A, E - holotype, B-D - paratypes NMMNH P-36598, 36600, and 36607, respectively.

**Genus *Delopterum* Sellards, 1909**

***Delopterum zonatum* Rasnitsyn, sp. nov.**

**Figure 25**

**Holotype.** NMMNH P-36599, locality NMMNH L-3433, near complete fore wing of imperfect preservation state. Paratypes NMMNH P-36598, 36600, 36601, 36607, same locality, near complete wings (36598, 36600) and apical wing fragments (36601, 36607).

**Description.** Fore wing 4.0-4.4 mm long, 1.3-1.4 mm wide (~1:31), with darkened apex, preapical vertical belt (more or less through  $RS_{1+2}$  and  $CuA_1$ ) and, often, elongate spot in anal area. SC reaching 0.35 wing length. R near straight before apex, with no pterostigma indicated.  $RS_{1+2}$  stalk more than twice as long as  $RS_1$ . CuA fork moderately high, with both branches angled with stalk, with  $CuA_1$  convex. 1A simple, 2A forked, near straight before apex.

**Remarks.** Color pattern varies so as apical darkening may be near lost or, contrary, may connect to preapical band at fore margin.

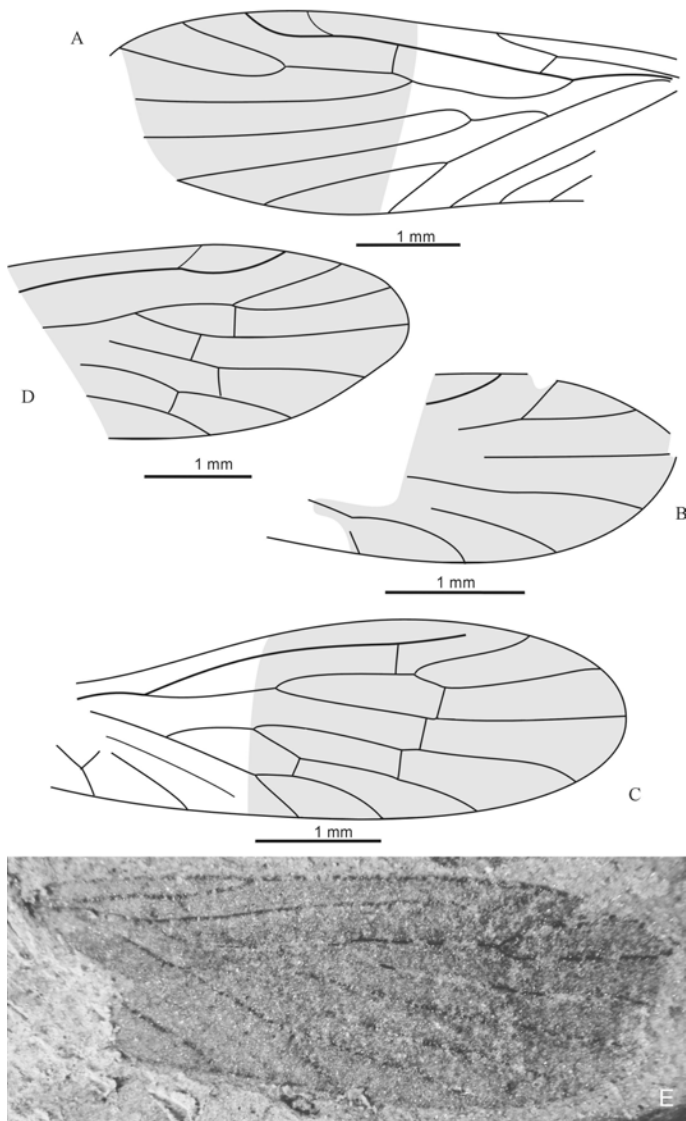


FIGURE 26. *Delopterum commune* Rasnitsyn sp. nov.: A, E –holotype, B–D – paratypes NMMNH P-36602, 36609, and 36617, respectively.

Also basal spot may be lost.

**Etymology.** The name is after the dark preapical band (*zona* is the Greek for belt).

***Delopterum commune* Rasnitsyn, sp. nov.**

**Figure 26**

**Holotype.** NMMNH P-36615, locality NMMNH L-3433, near complete fore wing with the very base and apex missing, of good preservation state. Paratypes NMMNH P-36602, 36613, 36614, 36617, same locality, and 36609, locality NMMNH L-3437, near complete fore wing (36609) and partial wings or apical wing fragments (36602, 36613, 36614, 36617).

**Description.** Fore wing 5–6 mm long, 2 mm wide (~1:2.7–3.1), with dark apical half. SC reaching 0.3 wing length (0.35 in damaged paratype 36614). R usually more or less sinuate before apex and with pterostigma indicated but short.  $RS_1:RS_{1+2}:RS$  varying from 1:1.2:1.5 in holotype to 1:1.1:1 in 36609. M fork somewhat basad of both RS and CuA forks. CuA fork moderately high, with both branches angled with stalk, with  $CuA_1$  convex or straight. 1A simple, 2A almost straight near apex.

**Remarks.** Of two near complete wings, 36609 differs from holo-

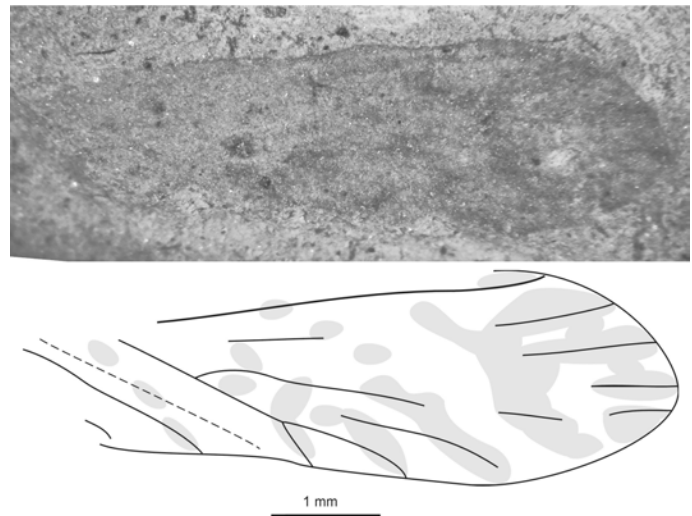


FIGURE 27. *Delopterum pantherinum* Rasnitsyn sp. nov., holotype.

type in smaller size, less distinct pterostigma and shorter CuA fork with convex  $CuA_1$ . Paratypes 36602 and 36613 share at least some of these characters in contrast to 36614, 36617 who share characters with the holotype. So two distinct species might be lumped here; more material is necessary to prove or disprove this suspicion.

**Etymology.** The name refers to abundance of the species.

***Delopterum pantherinum* Rasnitsyn, sp. nov.**

**Figure 27**

**Holotype.** NMMNH P-36605, locality NMMNH L-3433, fore wing lacking base and fore margin, of poor preservation state except for color pattern.

**Description.** Fore wing 6.2 mm long, with abundant small dark spots often fusing into longitudinal and oblique lines, particularly so along veins in apical wing part. CuA fork moderately short and low,  $CuA_1$  slightly angled with CuA stalk, weakly convex. 1A simple, near straight.

**Remarks.** As preserved, the fossil can be equally ascribed to *Palaeomantis*, *Delopterum* and *Delopsocus*. The present attribution is based solely on the fact that of those three genera only representatives of *Delopterum* are common in Carrizo Arroyo.

**Etymology.** The name refers to the unusual color pattern (*panthera* is the Latin for panther).

***Delopterum* sp.**

**Figure 28**

**Material.** NMMNH P-36608, locality NMMNH L-3437, fore wing lacking base and hind margin of poor preservation state except for color pattern.

**Description.** Fore wing 4.3 mm long as preserved (full length 4.7–5 mm), dark with transversal pale band through base of RS fork (possibly also with pale base). RS probably three-branched, with  $RS_1$  ca. 0.7 times as long as  $RS_{1+2}$  stalk.

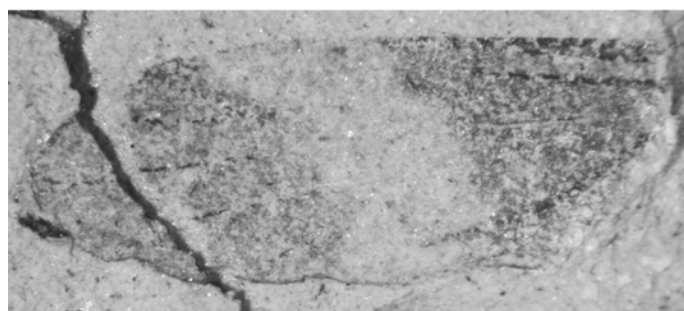
**Remarks.** Attribution to *Delopterum* is based entirely on the same reasoning as the previous species. The present one differs from others having similar color pattern in basal position of the pale band. However, it is too imperfectly preserved to be named.

**Genus *Miomatoneurella* O. Martynova, 1958**

***Miomatoneurella americana* Rasnitsyn, sp. nov.**

**Figure 29**

**Holotype.** NMMNH P-36618, locality NMMNH L-3433, fore

FIGURE 28. ?*Delopterium* sp., specimen NMMNH P-36608.

wing lacking apex, otherwise of fair preservation state.

**Description.** Fore wing 3.8 mm long as preserved (full length near 5 mm), dark except basally (unknown for apex). SC almost reaching  $RS_2$  base, possibly reaching 0.5 wing length. RS starting well proximally of M,  $RS_2$  base close to apparent base of M (“ $RS_3$ ”). True M base lost.  $1A$  and possibly  $2A$  simple,  $2A$  angled at  $a_1$ - $a_2$ .

**Etymology.** The name refers to the first New World occurrence of this genus.

#### Genus *Delopterinus* Rasnitsyn, gen. nov.

##### Type species *D. zebra* sp. nov.

**Diagnosis.** SC lacking preapical branchlets, reaching at most 0.4 wing length. RS 2-branched. M+CuA stalk long.  $M_1$  and  $M_2$  free. CuA fork ordinary.  $2A$  not multibranched.

**Included species.** Two species described herein.

**Etymology.** The name is modified from *Delopterium*. Gender masculine.

#### *Delopterinus zebra* Rasnitsyn, sp. nov.

##### Figure 30

**Holotype.** NMMNH P-36610, locality NMMNH L-3433, fore wing lacking anal area and very apex, otherwise of good preservation state.

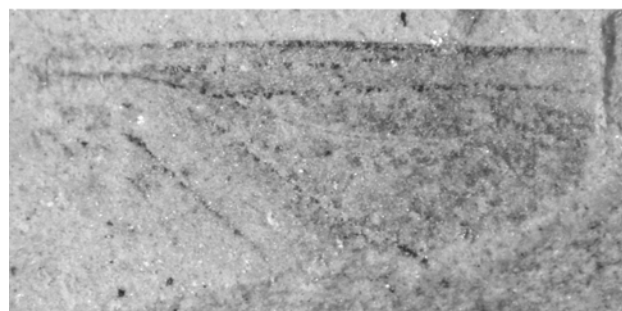
**Description.** Wing 5.1 mm long as preserved (full length near 5.5 mm), pale with dark apex and two transversal bands, one through base of RS fork, another through bases of M and CuA forks. SC reaching 0.3 wing length. R sinuate toward apex delimiting narrow pterostigma. RS fork distal of CuA fork and still more so of M fork.  $RS_1$  almost four times as long as RS stalk. CuA fork low, long, angled with both branches,  $CuA_1$  weakly concave in middle 0.3.

**Etymology.** The name refers to the banded color pattern.

#### *Delopterinus bicolor* Rasnitsyn, sp. nov.

##### Figure 31

**Holotype.** UNM 13144, locality NMMNH L-3433, fore wing lacking apex, part of fore margin, and small part of base, otherwise of good preservation state. Paratypes NMMNH P-26904, 36616, locality NMMNH L-3433, fore wing lacking base and subapical wing fragment, respectively.

FIGURE 29. *Miomatoneurella americana* Rasnitsyn, sp. nov., holotype.

**Description.** Wing about 6.5 mm, pale with dark apical half. SC reaching 0.4 wing length. R sinuate toward apex delimiting narrow pterostigma. RS fork distal of M and CuA forks taking similar position.  $RS_1$  about 1.7 times as long as RS stalk. CuA fork moderately low and long, angled with both branches,  $CuA_1$  weakly convex.

**Etymology.** The name refers to the pale-and-dark color pattern (bicolor is the Latin for two-colored).

#### Genus *Neodelopterium* Rasnitsyn, gen. nov.

##### Type species. *N. anomalum* sp. nov.

**Diagnosis.** RS three-branched.  $RS_3$  and  $M_1$  fused except short bases and long apices,  $M_2$  free. CuA fork ordinary. Wing base including SC and anal area unknown.

**Included species.** Type species only.

**Etymology.** The name is modified *Delopterium*. Gender neuter.

#### *Neodelopterium anomalum* Rasnitsyn, sp. nov.

##### Figure 32

**Holotype.** NMMNH P-36625, locality NMMNH L-3437, fore wing apical half of good preservation state.

**Description.** Wing fragment 4.6 mm long as preserved (full wing length near 6 mm), dark as preserved. R slightly sinuate toward apex delimiting narrow pterostigma. RS, M and CuA forks at near the same level.  $RS_1$  almost as long as  $RS_{1+2}$  stalk.  $M_1$  base present although apparently incomplete.  $RS_3$ + $M_1$  forking at about level of  $RS_{1+2}$  fork. CuA fork long, rather narrow,  $CuA_1$  almost following CuA stalk direction, very slightly convex.

**Etymology.** The name refers to anomalous (for the order) partial fusion of  $RS_3$  and  $M_1$ .

#### Genus *Stigmodelopterium* Rasnitsyn, gen. nov.

##### Type species. *S. pterostigmalis* sp. nov.

**Diagnosis.** Hind wing with R deep sinuate before apex delimiting wide, moderately sclerotized pterostigma. RS three-branched. M+CuA stalk present, probably long.  $M_1$  free. SC and anal area unknown. Fore wing unknown.

**Remarks.** New genus displays a striking pterostigma which has no parallel in other miomopters. Characteristic of miomopters is similar development of pterostigma in both wing pairs, so it is unlikely that the new genus, even based on a hind wing, is a synonym of any known

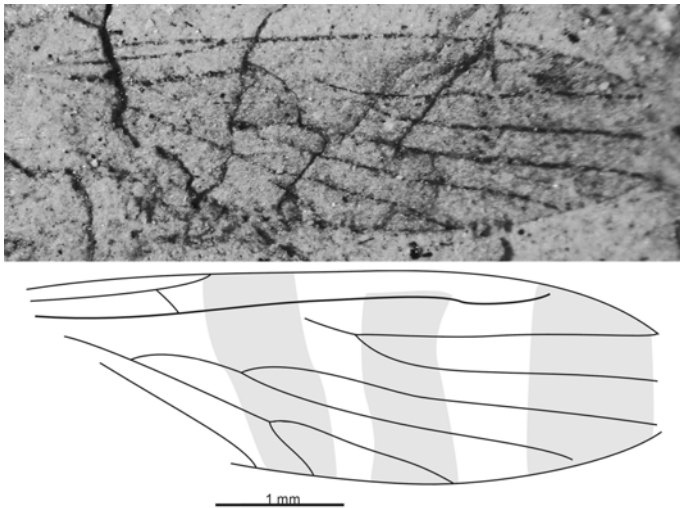


FIGURE 30. *Delopterus zebra* Rasnitsyn sp. nov., holotype.

taxon based on fore wings.

**Included species.** Type only.

**Etymology.** The name is after the striking pterostigma. Gender neuter.

***Stigmodelopterus pterostigmalis* Rasnitsyn, sp. nov.**

**Figure 33**

**Holotype.** NMMNH P-36606, locality NMMNH L-3433, hind wing lacking base, otherwise of good preservation state.

**Description.** Hind wing 5.8 mm long as preserved (full length near 7 mm), dark (possibly except basally). Pterostigma twice as wide as r-rs crossvein long. RS fork distal of CuA fork and still more so of M fork.  $RS_1$  0.9 times as long as  $RS_{1+2}$  stalk. CuA fork low, long,  $CuA_1$  weakly convex, angled with CuA stalk,  $CuA_2$  almost following direction of CuA stalk.

**Etymology.** The name is after striking pterostigma.

**Genus *Trideloapterum* Rasnitsyn, gen. nov.**

**Type species *T. variegatum* sp. nov.**

**Diagnosis.** Hind wing with no distinct pterostigma, with RS three-branched, M+CuA stalk long,  $M_1$  and  $M_2$  free, CuA straight or weakly sinuate till wing margin, with two well spaced hind branchlets or even crossveins rather than distinct apical fork.  $M_1$  free. SC and anal area unknown. Fore wing unknown.

**Remarks.** CuA fork is often slightly shorter in palaeomanteid hind wings than in their fore wings, but they never approach to the state found in the present genus. Three-branched CuA is sometimes described in fore wings of some Palaeomanteidae (e.g., *Miomatoneura angusta* Kukalová, *M. candida* Kukalová, *M. permica* Kukalová), but these cases CuA branches are shown long and crowded. This makes unlikely that any of described fore wings is a congener of the two following species and so justifies their attribution to a genus of their own.

**Included species.** Type only.

**Etymology.** The name refers to three CuA branchlets. Gender neuter.

***Trideloapterum variegatum* Rasnitsyn, sp. nov.**

**Figure 34**

**Holotype.** NMMNH P-36604, locality NMMNH L-3433, part and counterpart, hind wing lacking base and apex, of fair preservation state.

**Description.** Hind wing 5.3 mm long as preserved (full length near 5.5 mm), slightly infusate along or between veins and so looking

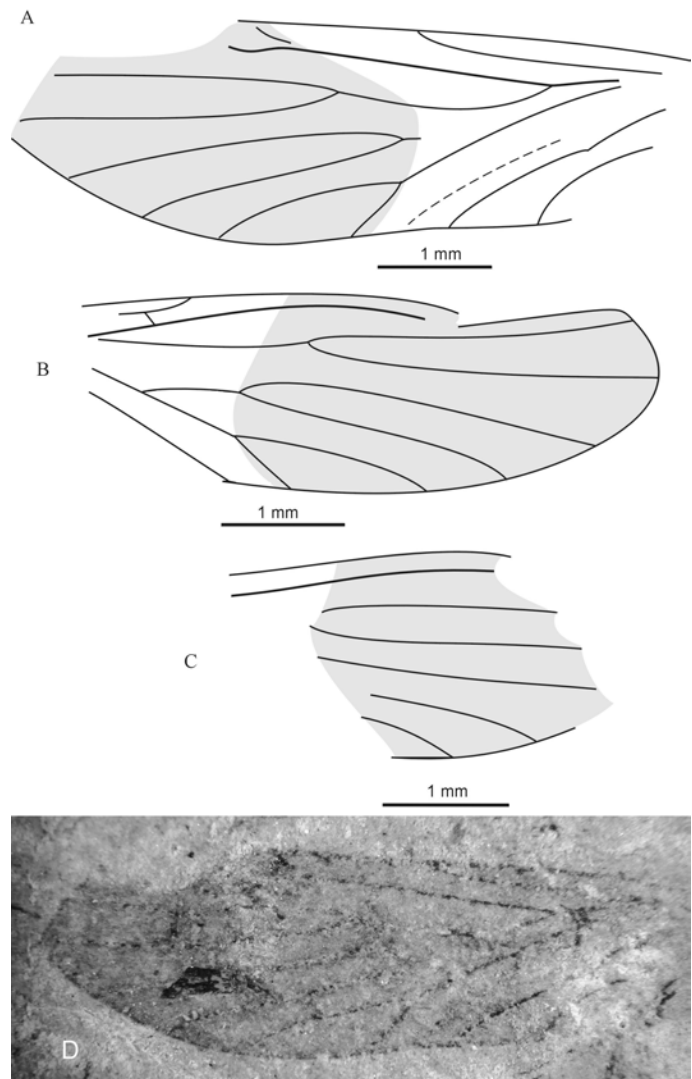


FIGURE 31. *Delopterus bicolor* Rasnitsyn sp. nov.: A, D – holotype, B, C – paratypes NMMNH P-26904 and 36616, respectively.

light variegated. R straight, with no pterostigma. RS fork far distal of M fork.  $RS_1$  0.8 times as long as  $RS_{1+2}$  stalk. CuA weakly sinuate,  $CuA_1$  weakly convex,  $CuA_2$  oblique,  $CuA_3$  almost vertical,  $CuA_2$  and  $CuA_3$  spaced for almost double  $CuA_3$  length. 1A long, straight, simple. SC and 2A not preserved.

**Etymology.** The name is after the color pattern.

**Palaeomanteidae indet.**

**Figure 35**

**Material.** UNM Cz 27, locality NMMNH L-3433, hind wing without basal fore margin and anal area of fair preservation state

**Description.** Hind wing 8.3 mm long as preserved (full wing hardly much longer) with dark apical half. R weakly sinuate, pterostigma hardly indicated. RS, M and CuA forking at about the same level. RS 3-branched,  $RS_1$  about as long as  $RS_{1+2}$  stalk. M branches free. CuA fork moderately low and long,  $CuA_1$  moderately convex, aligned with CuA stalk,  $CuA_2$  short, oblique.

**Remarks.** The fossil described is a rather ordinary palaeomanteid hind wing. However, the respective fore wing should be about 9 mm long: nothing similar has previously been found in Carrizo Arroyo thus indicating at least species rank distinction of the specimen. Formal description of a new species is not given here because the characters available do not permit its generic identity.

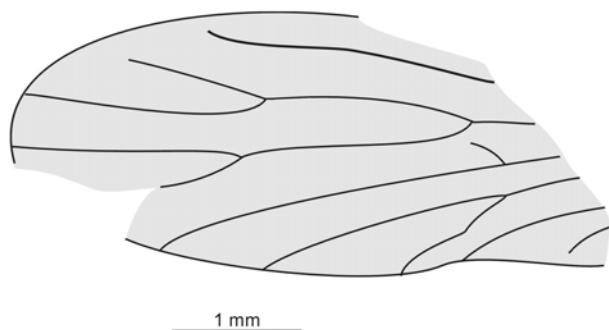


FIGURE 32. *Neodelopterus anomalum* Rasnitsyn sp. nov., holotype.

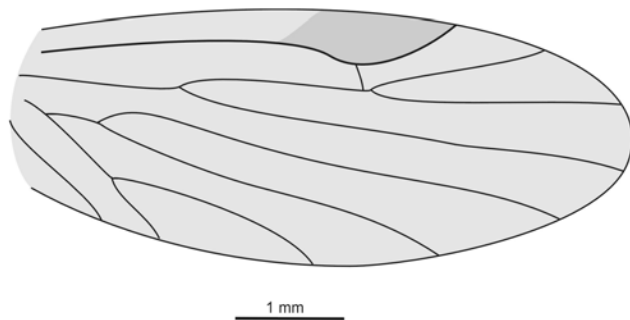
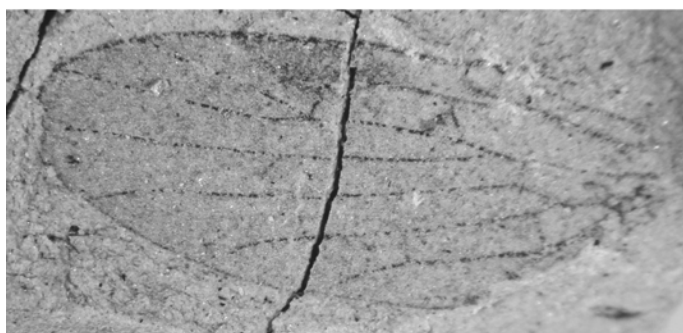


FIGURE 33. *Stigmodelopterus pterostigmalis* Rasnitsyn sp. nov., holotype.

**Order Panorpida Latreille, 1802**  
**By A.P. Rasnitsyn**  
**Figures 36-40**

One of the key orders of the holometabolous insects, scorpionflies were generally very common and diverse in the Permian and Mesozoic. The Early Permian, and particularly its first half, was an exception, with only three families and five genera recorded in the Artinskian stage of Elmo in Kansas and Obora in the Czech Republic (Novokshonov, 2002). It is thus of outstanding phylogenetic interest that five fossils of scorpionflies were discovered in the Carrizo Arroyo deposits, which thus

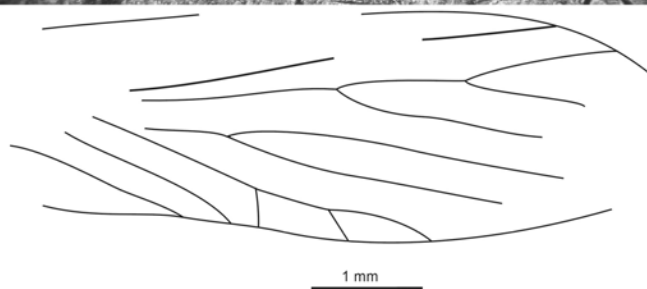
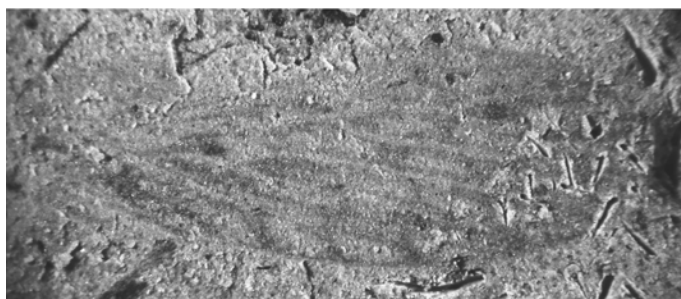


FIGURE 34. *Tridelopterus variegatum* Rasnitsyn sp. nov., holotype.

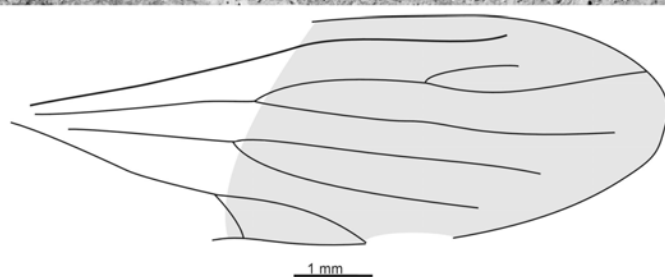


FIGURE 35. *Palaeomanteidae* gen. sp., specimen UNM Cz 27.

now represents the earliest appearance of this important group in the fossil record. Unfortunately, we were not able to prepare the taxonomic description of the material, so only a preliminary review is presented herein.

Three oldest known (Artinskian) families of Panorpida are Kaltanidae, Permopanorpidae, and Permochoristidae, of which the former family, generally the most plesiomorphic scorpionfly family, is represented there with an aberrant genus *Moravochorista* Kukalová-Peck and Willmann, 1989, whose association within Kaltanidae is not undoubted (Novokshonov, 1998, 2002). The Carrizo Arroyo fossils differ from these taxa as well as from all other scorpionflies rather radically and might represent one or two families of their own.

Of the fossils discovered, one (Fig. 36) is an apical wing fragment similar to other specimen but hardly conspecific with any of them because of its six-branched MP; otherwise it is difficult to classify. The remaining fossils, as represented by a hind wing (Fig. 37) and three fore wings (or superimposed wings of which only the fore wing characters are discernible; Figures 38-40 agree with other Permian Panorpida and

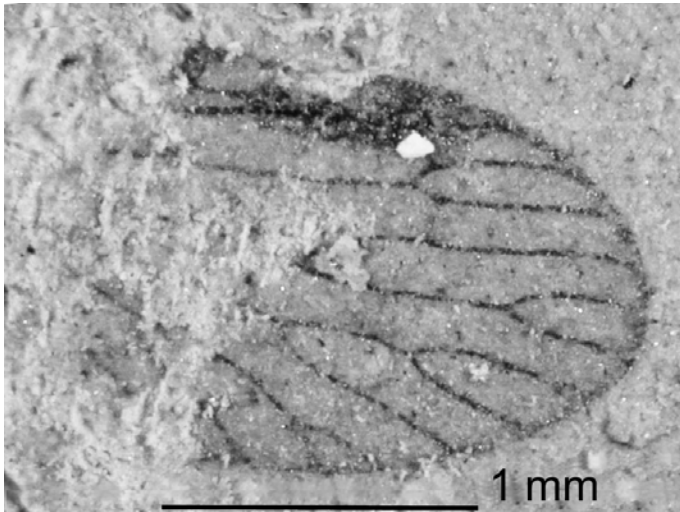


FIGURE 36. *Panorpida* indet., specimen NMMNH P-26920, apical wing

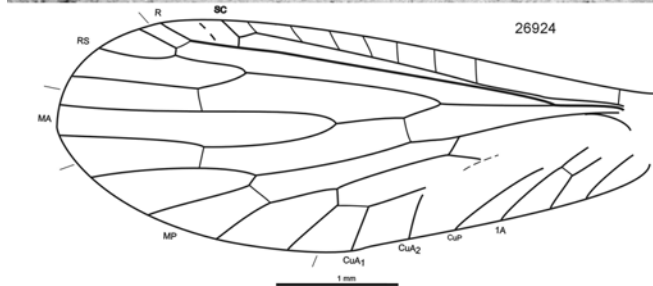
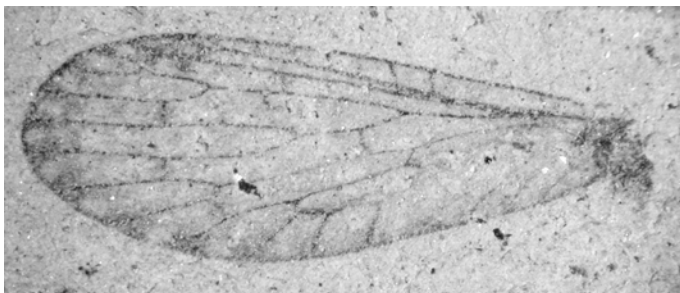


FIGURE 37. *Panorpida* indet., specimen NMMNH P-26924, hind wing.

are distinct from the archaic (Permian) neuropteroids, as defined by Novokshonov (1998, 2002), in having SC meeting C rather than R, SC branches simple, R fore branches not crowded distal to SC apex, pterostigma present (in two fore wings of three), MA more than two-branched, and CuA only two-branched. They clearly differ from another otherwise similar Permian order, the caddisflies, in having free anals which do not form an anal loop in the fore wing.

Within *Panorpida*, the fossils at hand possess the most distinctive character of *Kaltanidae*, the two-branched CuA. However, they hardly belong to *Kaltanidae*, or at least they are not typical *Kaltanidae*. All fore wings (Figs. 38-40) show a lower number of SC branchlets compared to *kaltanids*, viz. three or four not counting the humeral vein and SC apex. The hind wing (Fig. 37) is unusual in having numerous (seven) SC branchlets combined with impoverished RS and M system (nine total branches). More thorough study is necessary to decide if the fossils under discussion can be nevertheless included into *Kaltanidae*, or deserve creation of a new family, or perhaps two (one for specimens with weak

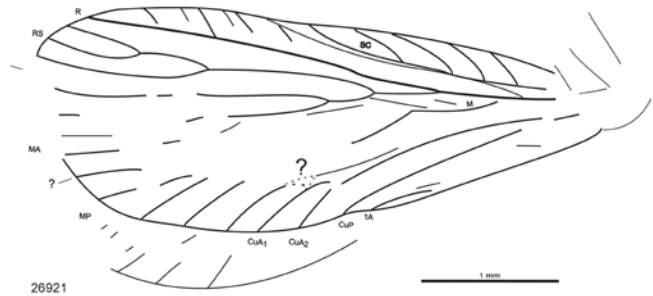


FIGURE 38. *Panorpida* indet., specimen NMMNH P-26921, fore wing.

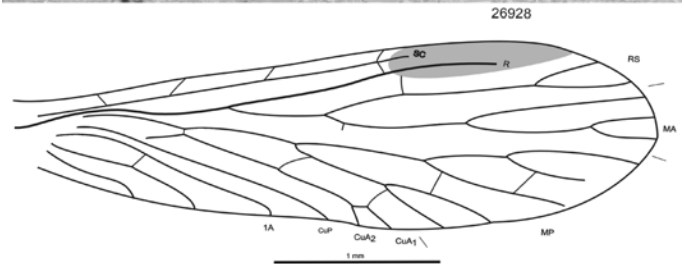
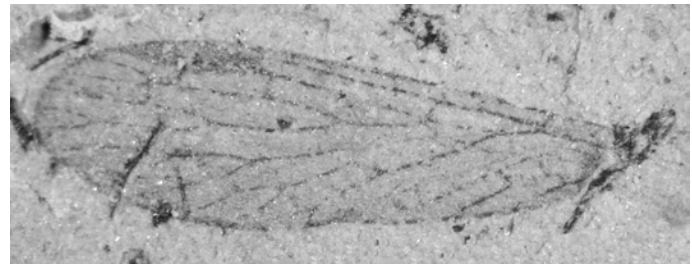


FIGURE 39. *Panorpida* indet., specimen NMMNH P-26928, fore wing.

SC branchlets, another for the one with a short SC).

All the scorpionfly wings collected look different at least at the species level: one of them has an extra MP branch (Fig. 36), another (Fig. 37) has numerous SC branchlets, the third (Fig. 38) has a short SC with long, curved branchlets. The remaining two wings (Figs. 38-40) differ from each other in the length of the MA and CuA forks.

#### Order ?*Eoblattida* Handlirsch, 1906 By A.P. Rasnitsyn

*Eoblattida* as defined by Rasnitsyn (2002c) is a paraphyletic group of Carboniferous insects supposedly ancestral to the entire Infraclass *Gryllones* (= *Polyneoptera*, = *Ortopteroidea* in the widest sense) that embraces the infraclasses *Blattidea*, *Perlidea* and *Gryllidea*, roach-like, stonefly-like and cricket-like insects, respectively. A core of the order forms the *eoblattid-spanioderid* assemblage which includes the families

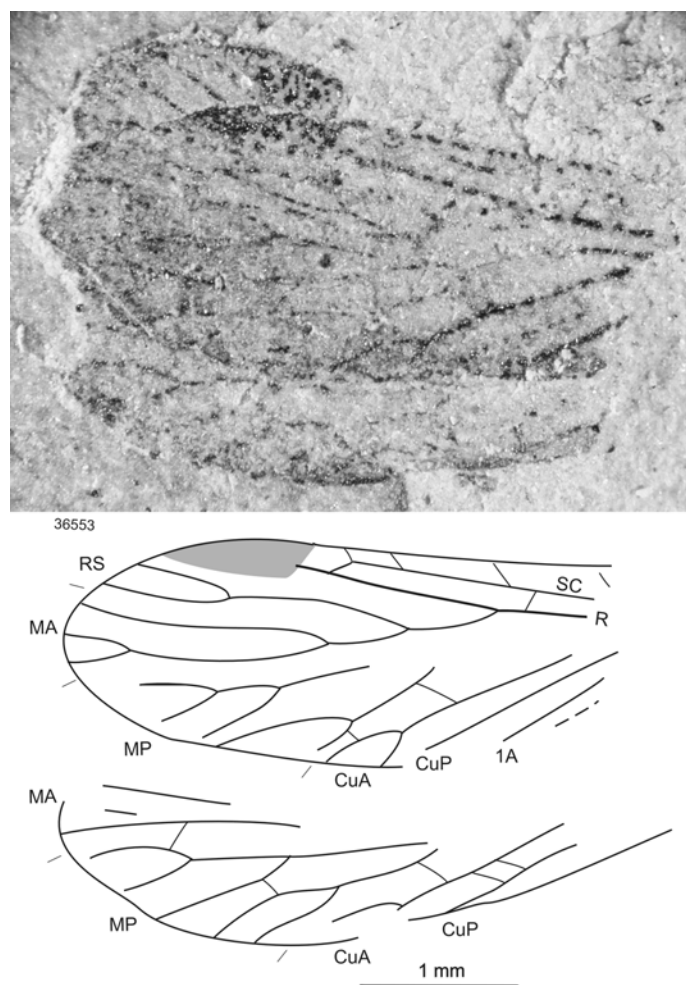


FIGURE 40. *Panorpida* indet., specimen NMMNH P-36553, fore wing and hind part of hind one.

Eoblattidae, Stenoneuridae, Ischnoneuridae (= Aetophlebiidae = Narkeminidae), Protophasmatidae, Spanioideridae, Geraridae, famous for their long and spiny pronotum, and their close relatives Homalophlebiidae. Other possible eoblattidans are Cacurgidae, Coseliidae, Pachytyloipseidae, Thoronysidae, Prototettigidae and Eucaenidae.

If attribution of the fossil below is correct, it is the first known Permian eoblattidan.

**Family ?Stenoneuridae Handlirsch, 1906**

**?Stenoneuridae incertae sedis**

**Figure 41**

**Material.** Specimen NMMNH P-36597, locality NMMNH L-3433, small fragment of large fore wing.

**Description.** Costal space very wide, crossed with dense, gently curved, simple or forked SC branches. Subcostal space much narrower, only slightly wider than radial space before RS base. RS starting subbasally but distal of  $M_3$  base, M forking still more distal (if at all).  $M_5$  short, oblique, CuA with double basal dichotomy, meeting  $M_5$  distal of 2<sup>nd</sup> fork. No crossvein preserved. Wing fragment 7 mm long along fore margin, full wing length possibly 40-60 mm.

**Taxonomic position.** The wing fragment displays a limited array of characters, and yet these are unusual and rather distinctive, viz., a combination of large size, wide costal space, and CuA which dichotomises twice near the very wing base and meets  $M_5$  beyond forking. I am aware



FIGURE 41. ?Stenoneuridae incertae sedis, specimen NMMNH P-36597.

of only one other insect with this character, *Stenoneura fayoli* Brongniart, 1893, which differs in much more basal origin of RS (Fig. 42); as to more striking absence of the archdictyon, this could well be due to the relatively poor state of preservation. Although evidently distinct from *Stenoneura* Brongniart, 1893 at least at the generic level, the fossil is too incomplete to warrant formal description.

**Remark.** The fossil represents a distinct Carboniferous element in the Carrizo Arroyo insect assemblage and possibly the first Permian member of Eoblattida.

**?Eoblattida incertae sedis**

**Figure 43**

Specimen NMMNH P-36584, locality NMMNH L-3433, is a small fragment of fore wing, venationally similar to the one above (except for less wide costal space and absent, possibly not preserved,  $M_5$ ),

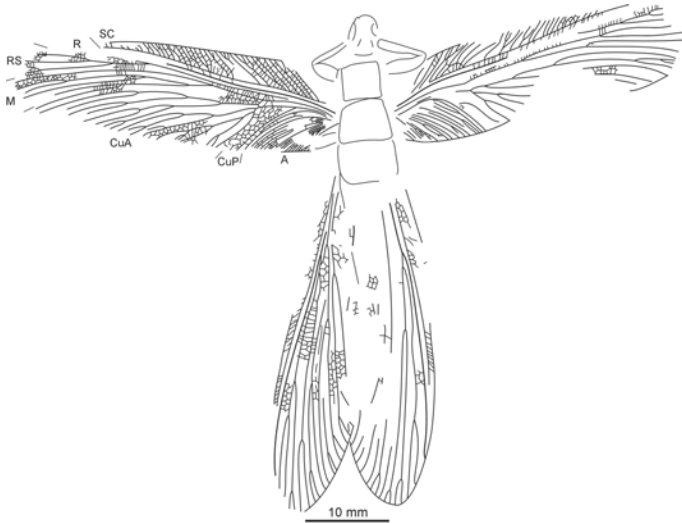


FIGURE 42. *Stenoneura fayoli* Brongniart, 1893, holotype, Stephanian of Commentary in France.

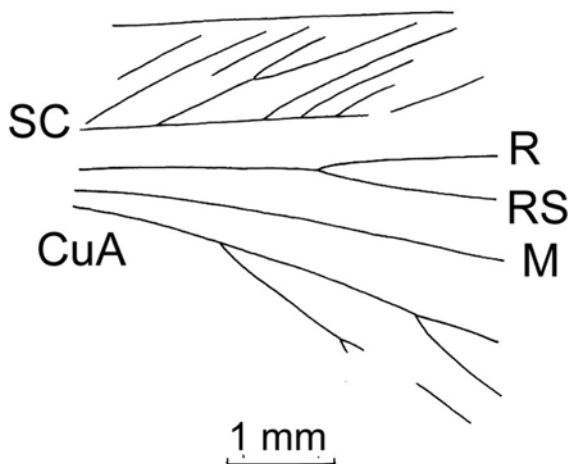
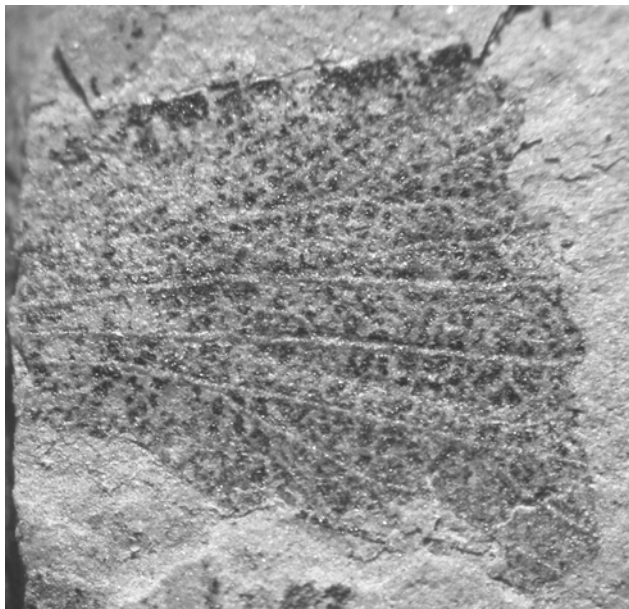


FIGURE 43. Eoblattida indet., specimen NMMNH P-36584.

but of several times smaller size. While this makes its relation to Eoblattida much less probable, but I mention it provisionally in the absence of any better alternative.

#### Order Grylloblattida Walker, 1914 by D.S. Aristov

This order is represented in the Late Carboniferous (Stephanian) by two families of low diversity, Protoperlidae (suborder Protoperlinae) and Daldubidae (suborder Lemmatophorinae), but which are unknown in the Permian (Storozhenko, 2002). The earliest Permian (Asselian) Niedermoschel assemblage in Germany is composed mainly or entirely of two species of *Artinska* (Lemmatophoridae) (Hörschemeyer, 1999). The next oldest (Artinskian) assemblage of Obora in the Czech Republic also has nothing in common with the Carboniferous and is dominated by the suborder Grylloblattinae and particularly by the family Liomopteridae. Toward the middle of the Permian (Kunurian and Kazanian Stages) grylloblattid insects became widespread and very abundant. After this the order declined, with the last winged grylloblattids becoming extinct in Lower Cretaceous. Now the order is represented by a single wingless family.

The Carrizo Arroyo grylloblattid assemblage, even if the oldest in the Permian, lacks any Carboniferous taxa. Both families and all the genera recorded are known also in the Artinskian of Euramerica, one of them (*Liomopterites*, Liomopteridae) persisting even in the earlier Late Permian (Kuznetsk Formation of Kaltan in Kuznetsk Basin, S. Siberia). The dominant family is Liomopteridae with 15 specimens and four described species, while Probnidae are rare (two specimens of a single species). Carrizo Arroyo is similar to Obora in liomopterid abundance and by the presence of *Depressopterum*, and to Elmo (Artinskian of Kansas) by the presence of *Probnis* and *Tapopterum*.

#### Suborder Grylloblattina Walker, 1914

##### Family Probnidae Sellards, 1909

##### Genus *Probnis* Sellards, 1909

##### *Probnis fossor* Aristov, sp. nov.

#### Figure 44

**Holotype.** NMMNH P-36578, locality NMMNH L-3433, fore wing without apex and the very base.

**Paratype.** UNM 3162, locality NMMNH L-3433, fragment of fore wing hind half.

**Description.** Small insect. Anterior margin of fore wing convex, SC terminated after wing midlength. Costal area as wide as subcostal. RS arising in proximal third of the wing, radial area as wide as medial. RS and MA branched not until distal quarter of wing length, MP with two branches. CuA branching into CuA<sub>1</sub> and CuA<sub>2</sub>, CuA<sub>1</sub> with 7-9 branches along posterior wing margin, CuA<sub>2</sub> simple, CuP simple, straight. Cross-veins simple or forming double row of cells in radial and medial areas and between distal branches CuA<sub>1</sub>. Length of fore wing about 10 mm.

**Comparison.** Differs from type species *P. speciosa* Sellards, 1909 (Lower Permian of Elmo in Kansas) in wide radial area and in double rows of cells both in radial and medial areas.

**Etymology.** Species name *fossor* is Latin for navy.

##### Family Liomopteridae Sellards, 1909

##### Genus *Tapopterum* Carpenter, 1950

##### *Tapopterum populus* Aristov, sp. nov.

#### Figure 45

**Holotype.** UNM 6851, locality NMMNH L-3433, almost complete fore wing without extreme apex.

**Paratypes.** UNM 6841?, 6866, NMMNH P-36579, locality NMMNH L-3433.

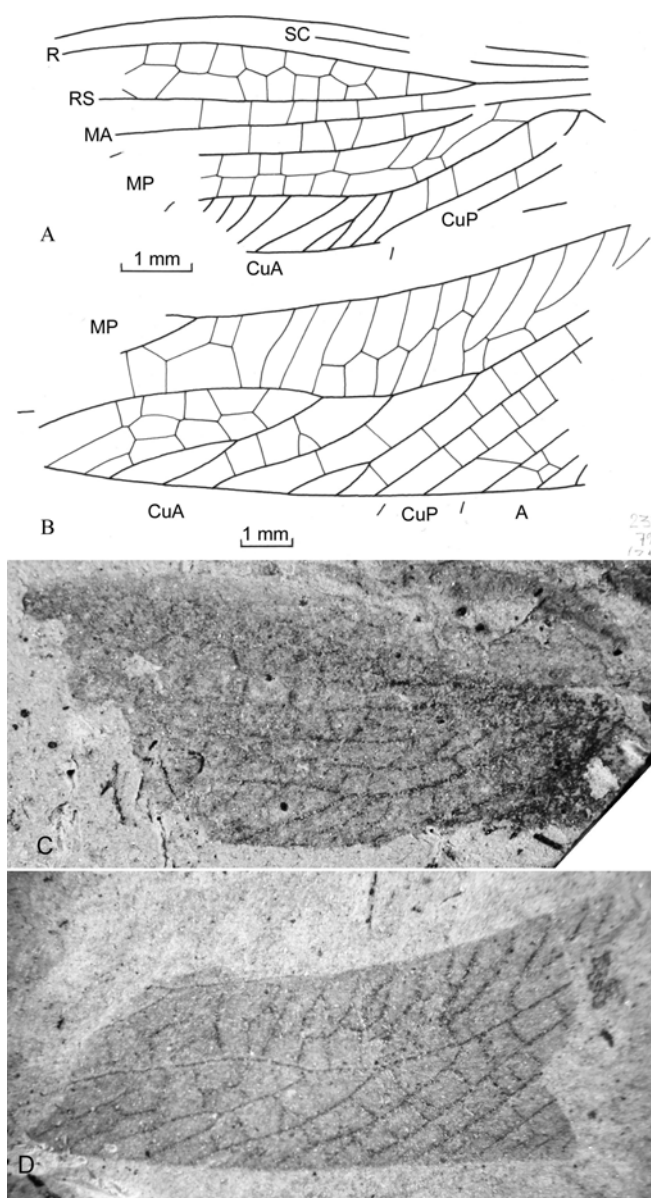


FIGURE 44. *Probnis fossor* Aristov sp. nov.: A, C – holotype, B, D – paratype.

**Description.** Anterior margin of fore wing nearly straight, costal area as wide as subcostal. SC with simple fore branches, terminating near wing apex. RS arising in proximal third of wing, with two or three branches, MA simple, MP with two branches.  $CuA_1$  with two branches,  $CuA_2$  simple, CuP straight. Cross-veins simple or forming double row of cells in medial area. Fore wing length 8–9 mm.

**Comparison.** Differs from type species *T. celsum* Carpenter, 1950 from Lower Permian of Elmo in Kansas in RS bearing two or three branches, in simple MA and also in small size.

**Etymology.** Species is named after its abundance (*populus* is the Latin for people).

#### Genus *Depressopterum* Kukalová, 1964

##### *Depressopterum generator* Aristov, sp. nov.

#### Figure 46

**Holotype.** NMMNH P-36586, locality NMMNH L-3433, fore wing fragment lacking anal area, base, apex and much of fore margin.

**Description.** Basal part of wing anterior margin straight, costal

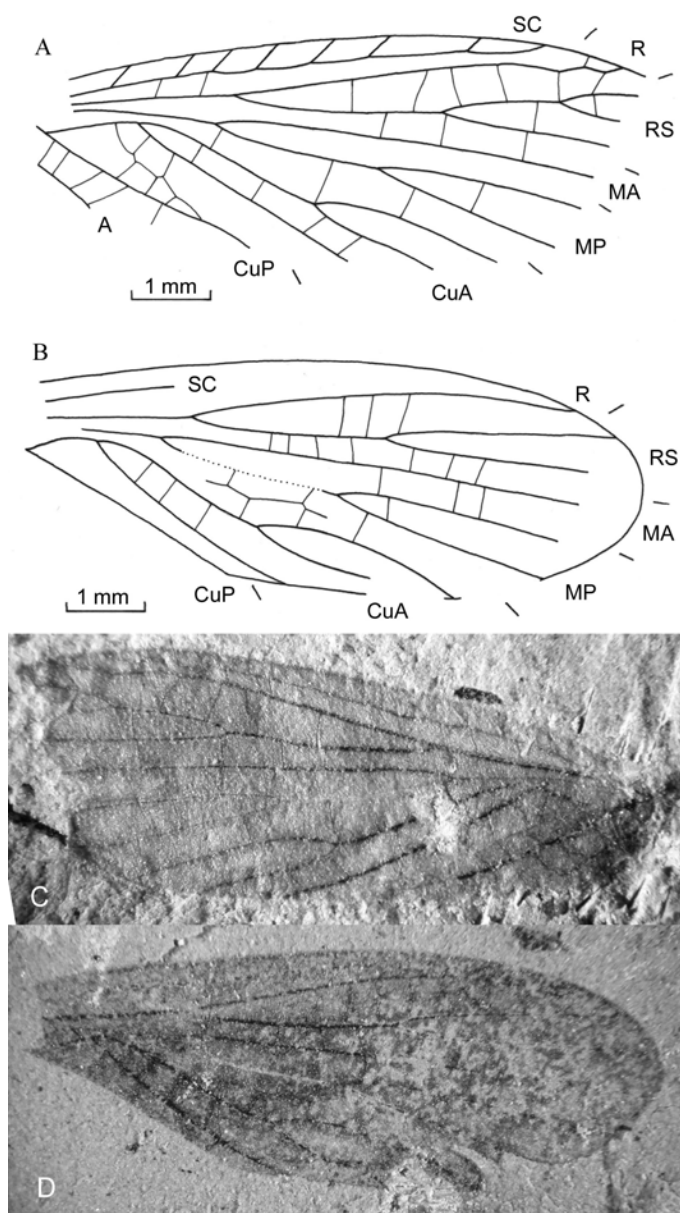


FIGURE 45. *Tapopterum populus* Aristov sp. nov.: A, C – holotype, B, D – paratype UNM 6866.

area as wide as subcostal, SC with simple fore branches. RS arising beyond proximal third of wing. Basal part of  $CuA$  S-shaped,  $CuA_1$  with three or more branches. Cross-veins simple. Length of wing fragment 4.5, full wing length about 10 mm.

**Comparison.** This species is similar to *D. senior* Kukalová, 1964 in shape of  $CuA$ , and to *D. mancum* Kukalová, 1964 (both from Lower Permian of Obora in the Czech Republic) in distal origin of RS (beyond proximal third of the wing length), but differs from both in small size.

**Etymology.** Species name *generator* is the Latin for ancestor.

#### Genus *Liomopterites* Sharov, 1961

##### *Liomopterites annosus* Aristov, sp. nov.

#### Figure 47

**Holotype.** UNM 6859, locality NMMNH L-3433, fore wing without anal area and with damaged apex and, in small part, fore margin.

**Description.** Anterior margin of fore wing convex, costal area as wide as subcostal. SC with simple fore branches, terminating near wing

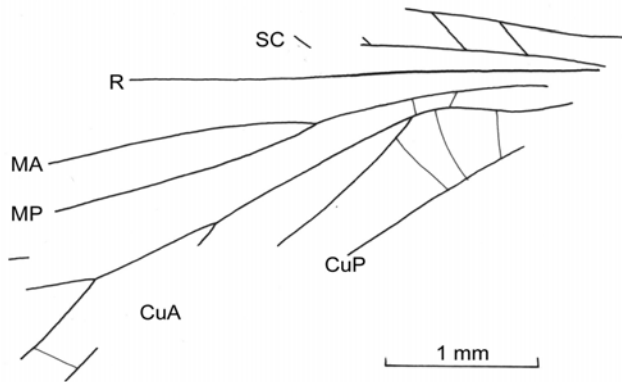


FIGURE 46. *Depressopterum generator* Aristov sp. nov., holotype.

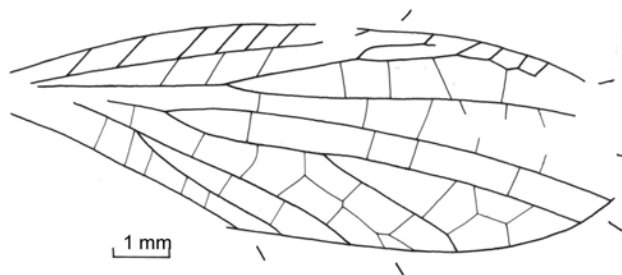
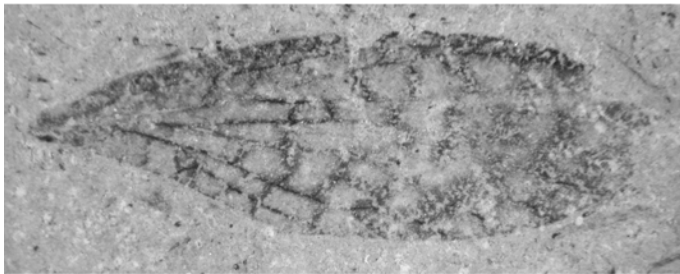


FIGURE 47. *Liomopterites annosus* Aristov sp. nov., holotype.

midlength. RS arising in the proximal third of wing, simple. MA simple, MP with two branches. CuA<sub>1</sub> nearly straight, simple, CuP straight. Cross-veins simple or forming double rows of cells in medial area and between branches of MP. Fore wing length 11.3 mm.

**Comparison.** Similar to *L. proximus* Sharov, 1961 and *L. accolis* Sharov, 1961 (from the Upper Permian of, respectively, Suriyokova I and Kaltan in Kuznetsk Basin, S. Siberia) in having simple CuA<sub>1</sub> and short SC, but differs in distal origin of RS and in simple RS and MA.

**Etymology.** Species name *annosus* is the Latin for ancient.

#### **Liomopteridae incertae sedis**

Specimens NMMNH P-36593, locality NMMNH L-3433 and

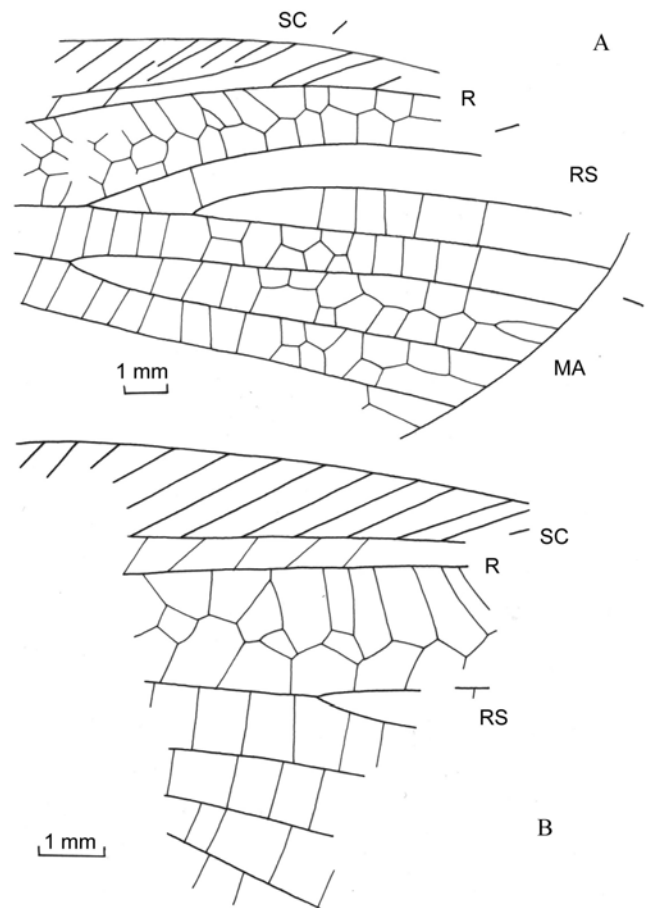


FIGURE 48. *Liomopteridae incertae sedis*: A, C - specimens NMMNH P- 36593, B - specimen NMMNH P-36555.

NMMNH P-36555, locality NMMNH L-3437 (Fig. 48), belong to one species which differs from other liomopterids in Carrizo Arroyo in large size and wide costal area.

Specimens NMMNH P-36580 (Figure 49), 36587, 36591, 36592 and UNM 6852, locality NMMNH L-3433 all represent liomopterid hind wings which cannot be further classified at present.

Specimen NMMNH P-36590, 36585 (part and counterpart), locality NMMNH L-3433, is a wing fragment in all probability belonging to Liomopteridae.

#### **?Grylloblattida incertae sedis**

Specimen NMMNH P-36589, 36596 (part and counterpart), lo-

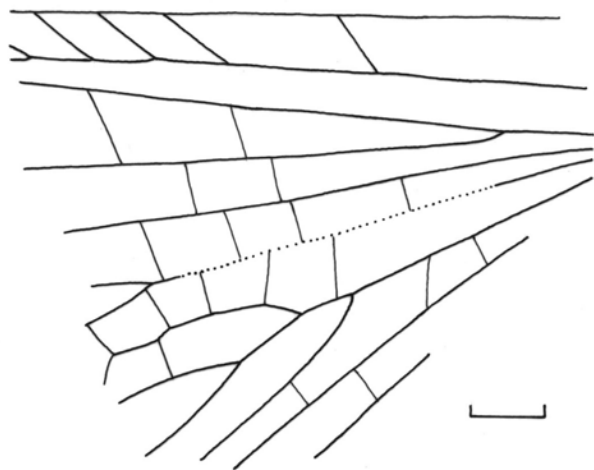


FIGURE 49. Liomopteridae incertae sedis, specimen NMMNH P- 36580. Scale bar = 1 mm.

cality NMMNH L-3433 (Fig. 50), belongs to a species which differs from all known grylloblattids in fused base of M and CuA combined with wide costal area.

### Order Orthoptera

by A.V. Gorochov

#### Family Thuringoedischidae Zessin, 1997

The family Thuringoedischidae was originally included in the suborder Ensifera without more exact determination of its systematic position (Zessin, 1997). Recently, this family was hypothetically put in the superfamily Permioraphidioidea (Gorochov & Rasnitsyn, 2002), which is one of two superfamilies of the infraorder Elcanidea (one of four infraorders of Ensifera) (Gorochov, 1995). Probably, Thuringoedischidae is the most primitive family of Permioraphidioidea, as their wings have not any anastomosis of MA with proximal parts of MP and MP+CuA1 (Fig. 51) characteristic for two other families of this superfamily: Permioraphidiidae Tillyard 1932 and Pseudelcanidae Gorochov 1987 (nomenclature of wing veins is given under Sharov, 1968, but with some corrections by Gorochov, 1995). Moreover, Thuringoedischidae may claim to be ancestral for both these families and all other Elcanidea, as their venation does not contradict it. On the other hand, the representatives of this family and all other Elcanidea are rather small insects with the both pairs of wings well adapted to flight unlike in other primitive Ensifera (infraorder Oedischidae), which usually preserve the larger size and the tegmen-like fore wings. A new genus, considered below, is a third genus of very primitive Ensifera, which may be included in Thuringoedischidae together with two other Early Permian genera: *Permoedischia* Kukalová 1955 (Czechia) and *Thuringoedischia* Zessin 1997 (Germany).

#### Genus *Hymenelcana* Gorochov, gen. nov.

Type species: *H. initialis* sp. nov.

**Diagnosis.** Fore wing with closed area between Sc and RA as in *Thuringoedischia*, but Sc much longer, its apex situated not far from apex of RA, and area between RA and costal edge of wing less narrow (distinctly wider than nearest part of area between RA and RS). From *Permoedischia*, this new genus distinguished by significant difference in width of some areas in fore wings: Sc-RA area much narrower than RA-RS area.

**Species included.** Type only.

*Hymenelcana initialis* Gorochov, sp. nov.

Figure 51

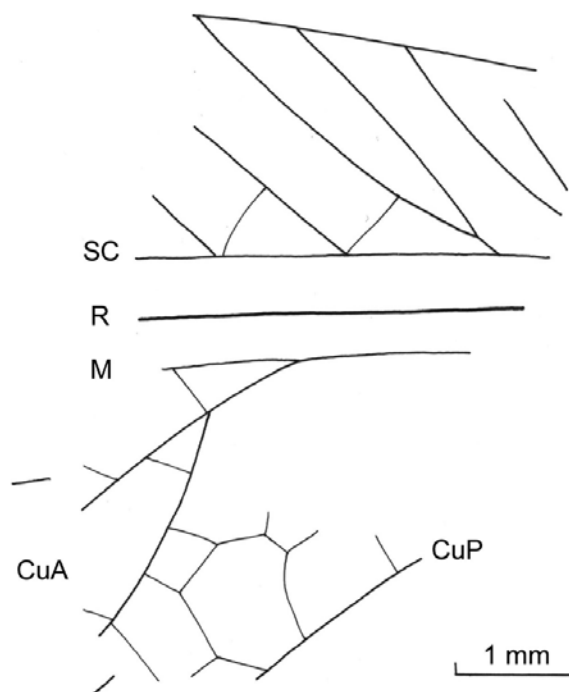
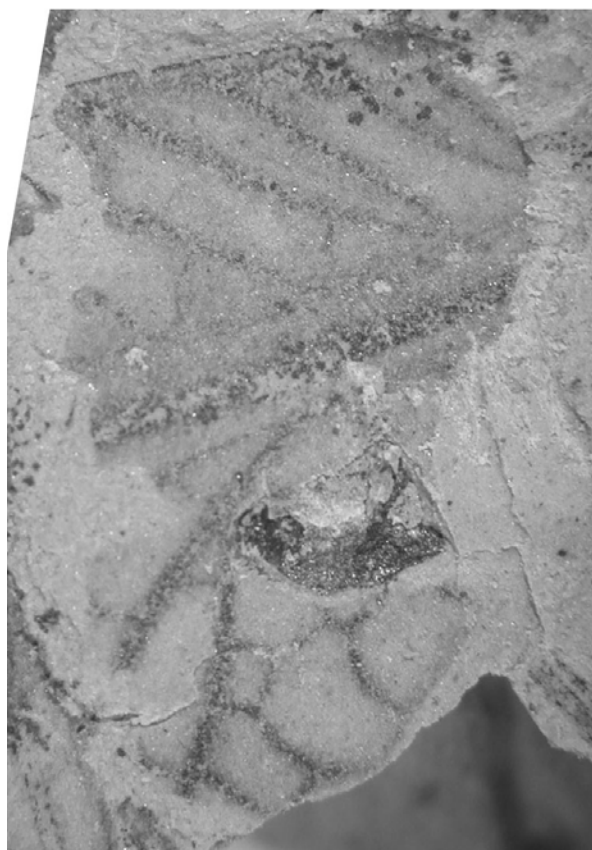


FIGURE 50. ?Grylloblattida incertae sedis, specimen NMMNH P- 36596.

**Referred material:** holotype NMMNH P-36564, locality NMMNH L-3433, distal half of a fore wing; paratype NMMNH P-36553, locality NMMNH L-3433, distal half of a fore wing. Non-type material: 3 fragments possibly belonging to the same species: NMMNH P-36572, distal part of a possible hind wing; NMMNH P-36570, distal half of a

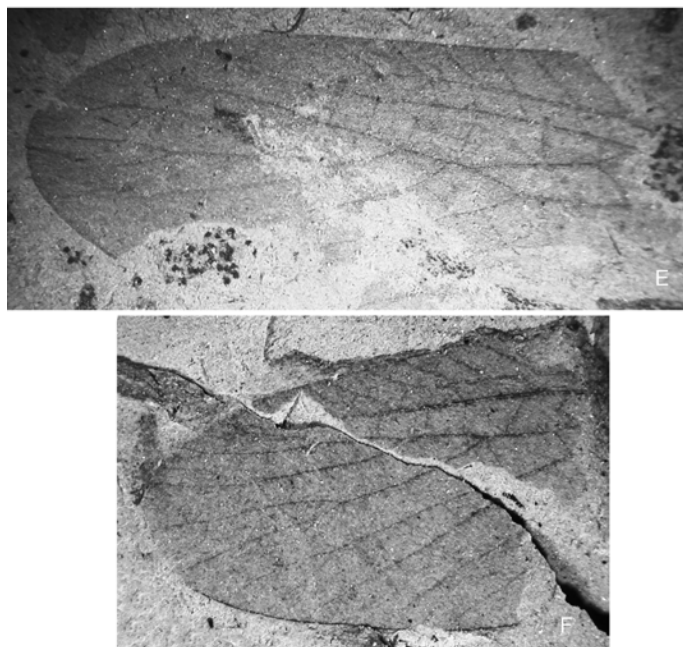
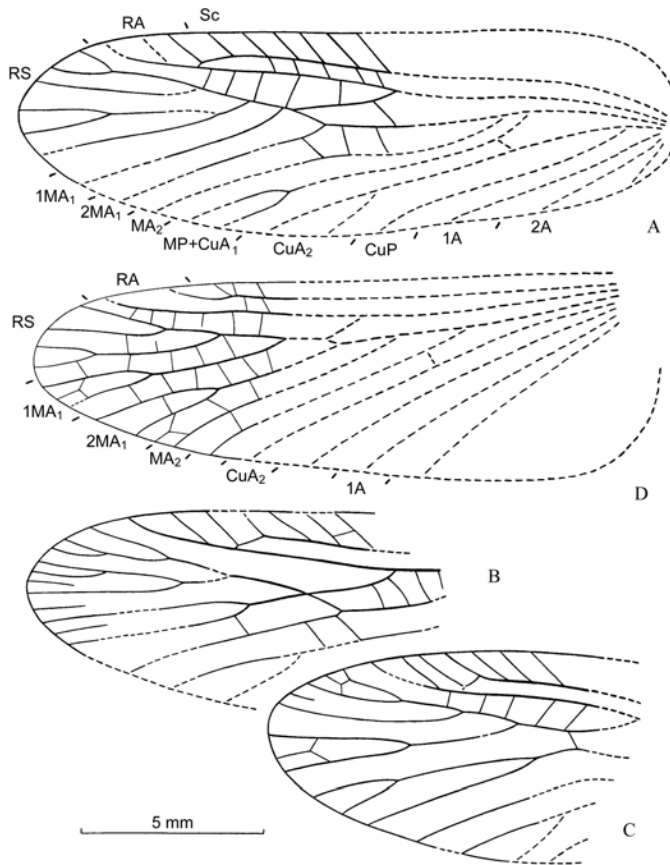


FIGURE 51. *Hymenelcana initialis* Gorochov, sp. n.: **A, B, C, E** –fore wing, holotype (**A, E**, restored), paratype (**B**, NMMNH P-36553), and aberrant specimen (**C**, NMMNH P-36570), **D, F** – supposed hind wing, NMMNH P-36572 (restored).

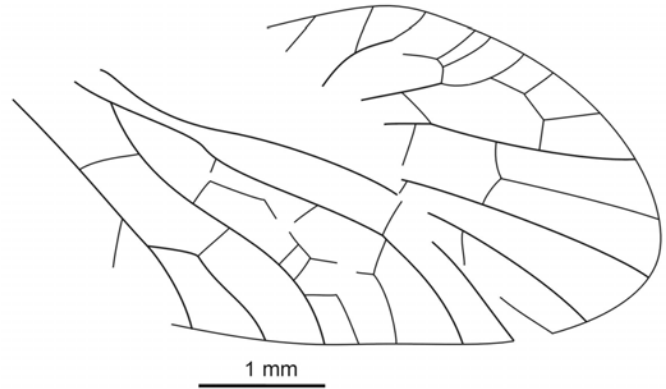
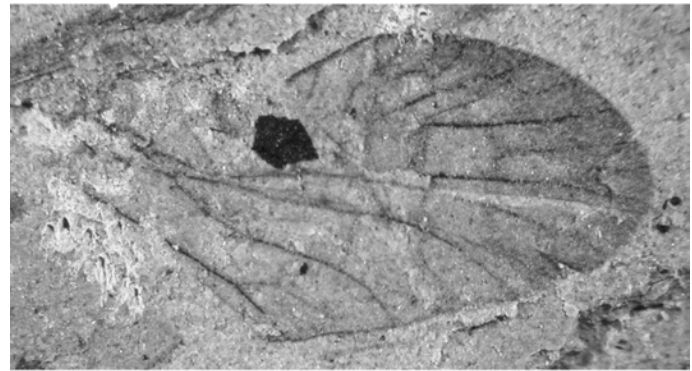


FIGURE 52. Insecta incertae sedis, specimen NMMNH P- 36557.

fore wing with probably aberrant venation; NMMNH P-36623, small part of a fore or hind wing; all from locality NMMNH L-3433.

**Description.** Fore wing (holotype). Thickened crossvein between apical branch of Sc and proximal branch of RA more or less longitudinal; proximal part of RS (before anastomosis with 1MA1) rather long; proximal part of 1MA1 (before anastomosis with RS) almost longitudinal; distal parts of 1MA1 and 2MA1 alone or with short (apical) branches only (Fig. 51A). Length of fragment 11 mm; hypothetical length of wing 18–20 mm.

**Variations.** Paratype distinguished from holotype almost only by distal part of 1MA1 with two long branches (Fig. 51B). Other (aberrant?) fragment differs from holotype and paratype in more transverse thickened crossvein between apical branch of c and proximal branch of RA, in almost transverse proximal part of RS, and in presence of two long branches of distal part of 2MA1 (Fig. 51C).

**Hind wing.** Distal fragment of one of wings has proximal parts of costal and subcostal areas almost equal (unlike in tegmina); it may belong to hind wing of this species (Fig. 51D).

#### ?Thuringoedischidae indet.

Wing fragments NMMNH P-36576 and P-36623, both from locality NMMNH L-3433, might belong to Thuringoedischidae but too incomplete to permit more precise identification.

#### Orthoptera incertae sedis

Fore wing base fragments with the well developed precostal space NMMNH P-36571, locality NMMNH L-3433, cannot be further identified.

#### Insecta incertae sedis

Specimen NMMNH P-36557, locality NMMNH L-3433 (Fig. 52), is a crumpled wing, 5.4 mm long, lacking its base and much of the fore margin, with a general appearance somewhat resembling an archaic beetle hind wing, but lacking any certain beetle characters. Similarly, no special similarity to neuropteroids can be indicated, although related-

TABLE 1. Overview of described fossils

| Taxon                                                | Position                          | specimens |     |       | Source                        |
|------------------------------------------------------|-----------------------------------|-----------|-----|-------|-------------------------------|
|                                                      |                                   | NMM       | UNM | Other |                               |
| <i>Dasyleptus rowlandi</i> Rasnitsyn                 | Machilida: Dasyleptidae           | 22        | ?   | ?     | Rowland, 1997, and this study |
| <i>Dasyleptus</i> sp.                                | Machilida: Dasyleptidae           | 1         |     |       | This study                    |
| <i>Microcarrizo paradoxicum</i> Rasnitsyn            | Lepismatona order uncertain       |           | 2   |       | This study                    |
| <i>Vilviopsis picta</i> Rasnitsyn                    | Caloneurida: Caloneuridae         |           | 1   | 2     | This study                    |
| <i>Paleuthygramma ventricosa</i> Rasnitsyn           | Caloneurida: Caloneuridae         |           | 1   |       | This study                    |
| <i>Carrizarroyo calopterus</i> Rasnitsyn             | Caloneurida: Haplopteridae        |           | 1   |       | This study                    |
| <i>Carrizopteron longum</i> Rasnitsyn                | Caloneurida: Haplopteridae        |           |     | 1     | This study                    |
| <i>Arroyopteron indolatum</i> Rasnitsyn              | Caloneurida: Haplopteridae        |           |     | 1     | This study                    |
| <i>Carrizocladus arroyo</i> Rasnitsyn                | Hypoperlida: Anthracoptilidae     |           |     | 1     | This study                    |
| ? <i>Carrizocladus deter</i> Rasnitsyn               | Hypoperlida: Anthracoptilidae     |           | 1   |       | This study                    |
| <i>Carrizopteryx arroyo</i> Kukalová-Peck, Peck 1976 | Dictyoneurida: Calvertiellidae    |           |     | 1     | Kukalová-Peck & Peck, 1976    |
| <i>C. lucasi</i> Sinitshenkova                       | Dictyoneurida: Calvertiellidae    |           |     | 1     | This study                    |
| <i>Titanodictya rowlandi</i> Sinitshenkova           | Dictyoneurida: Dictyoneuridae     |           | 1   | 1     | This study                    |
| Spilapteridae indet.                                 | Dictyoneurida: Spilapteridae      |           |     | 3     | This study                    |
| <i>Forcynthia cynthiae</i> Sinitshenkova             | Dictyoneurida: Hanidae            |           | 1   |       | Rowland, 1997 and this study  |
| Dictyoneurida indet. (nymph)                         | Dictyoneurida                     |           | 1   |       | This study                    |
| <i>Phaneroneura rineharti</i> Sinitshenkova          | Diaphanopterida: Martynoviidae    |           | 1   |       | This study                    |
| <i>Asthenohymen micron</i> Sinitshenkova             | Diaphanopterida: Asthenohymenidae |           | 1   |       | This study                    |
| <i>Asthenohymen zonatus</i> Sinitshenkova            | Diaphanopterida: Asthenohymenidae |           | 1   |       | This study                    |
| ? <i>Asthenohymenidae</i> indet.                     | Diaphanopterida                   |           | 1   |       | This study                    |
| ? <i>Dichentomum arroyo</i> A. Rasnitsyn             | Psocida: Psocidiidae              |           | 1   |       | This study                    |
| ? <i>Dichentomum</i> sp.                             | Psocida: Psocidiidae              |           |     | 1     | This study                    |
| <i>Arroyoscyta novaemexicana</i> Rasnitsyn           | ?Hemiptera: ?Archescytinidae      |           | 1   |       | This study                    |
| ? <i>Palaeomantis apicalis</i> Rasnitsyn             | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Delopsocus stenopterus</i> Rasnitsyn              | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Delopterum zonatum</i> Rasnitsyn                  | Palaeomanteida: Palaeomanteidae   |           |     | 5     | This study                    |
| <i>D. commune</i> Rasnitsyn                          | Palaeomanteida: Palaeomanteidae   |           |     | 10    | This study                    |
| ? <i>Delopterum pantherinum</i> Rasnitsyn            | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| ? <i>D.</i> sp.                                      | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Miomatoneurella americana</i> Rasnitsyn           | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Delopterinus zebra</i> Rasnitsyn                  | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>D. bicolor</i> Rasnitsyn                          | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Neodelopterum anomalum</i> Rasnitsyn              | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Stigmodelopterum pterostigmatis</i> Rasnitsyn     | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| <i>Tridelopterum variegatum</i> Rasnitsyn            | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| Palaeomanteidae gen. sp.                             | Palaeomanteida: Palaeomanteidae   |           |     | 1     | This study                    |
| Insecta indet.                                       | Coleoptera?? Myrmeleontidea??     |           | 1   |       | This study                    |
| Panorpida indet. sp. 1                               | Panorpida: cf. Kaltanidae         |           | 1   |       | This study                    |
| Panorpida indet. sp. 2                               | Panorpida: cf. Kaltanidae         |           | 1   |       | This study                    |
| Panorpida indet. sp. 3                               | Panorpida: cf. Kaltanidae         |           | 1   |       | This study                    |
| Panorpida indet. sp. 4                               | Panorpida: cf. Kaltanidae         |           | 1   |       | This study                    |
| Panorpida indet. sp. 5                               | Panorpida: cf. Kaltanidae         |           | 1   |       | This study                    |
| ? <i>Stenoneuridae</i> indet.                        | ?Eoblattida 1                     |           |     |       | This study                    |
| ? <i>Eoblattida</i> indet.                           | ?Eoblattida 1                     |           |     |       | This study                    |
| <i>Probnis fossor</i> Aristov                        | Grylloblattida: Probnidae         |           |     | 1 1   | This study                    |
| <i>Tapopterum populus</i> Aristov                    | Grylloblattida: Liomopteridae     |           | 1   | 3     | This study                    |
| <i>Depressopterum generator</i> Aristov              | Grylloblattida: Liomopteridae     |           | 1   |       | This study                    |
| <i>Liomopterites annosus</i> Aristov                 | Grylloblattida: Liomopteridae     |           |     | 1     | This study                    |
| Liomopteridae indet.                                 | Grylloblattida: Liomopteridae     |           | 8   | 1     | This study                    |
| ? <i>Grylloblattida</i> indet.                       | ?Grylloblattida                   |           |     |       | This study                    |
| <i>Hymenecana initialis</i> Gorochoy                 | Orthoptera: Thuringoedischidae    |           |     | 24+73 | This study                    |

ness cannot be ruled out. Two insect nymphs, one largely incomplete, with well developed wing pads (NMMNH P-36619, locality NMMNH L-3433; Fig. 53), another small and poorly preserved, possibly of the first instar (NMMNH P-36620, locality NMMNH L-3433; Fig. 54), although unidentifiable to the ordinal level, are important because they represent the only possible aquatic insects other than *Dasyleptus*. The former nymph might be

a stonefly but lacks any conclusive characters.

## DISCUSSION

This report is based on taxonomic study of only 109 insect fossils from Carrizo Arroyo. While a sample of this size may limit certain inferences concerning the faunal assemblage that it represents, some features of this sample are quite distinctive and merit specific discussion

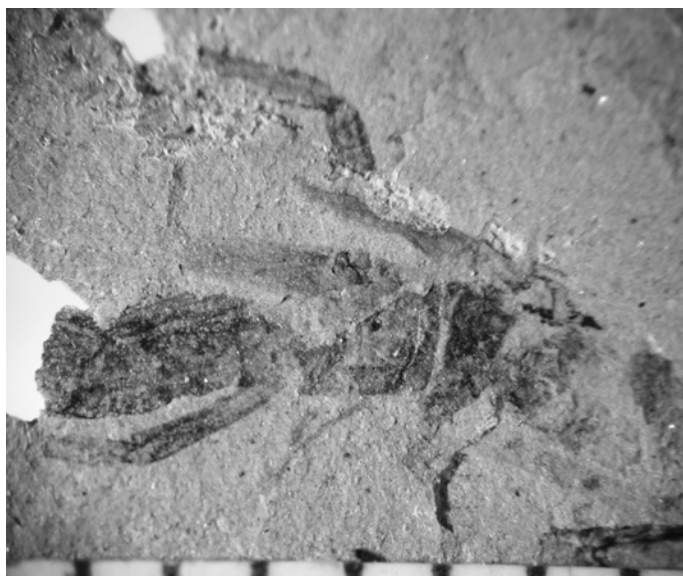


FIGURE 53. Insect nymph of obscure taxonomic position (possibly Perlida), specimen NMMNH P-36619.

below.

The fossils treated in taxonomic detail herein (Table 1) represent only a fraction of the material from Carrizo Arroyo upon which there is published data (see Rowland, 1997, and references therein). Additionally, the composition of the complete NMMNH insect collection from Carrizo Arroyo was examined by the senior author and Table 2 shows the order level composition.

#### Taphonomic features

The NMMNH insect collection from Carrizo Arroyo is highly dominated by small to medium sized (2-10 mm long) wings and wing fragments, unlike the UNM collection which also has few complete insect fossils, but which is composed of fragments of generally much larger insects. This is probably because the former collection was made by Dr. Spencer Lucas, Dr. J. Mark Rowland and Mr. Larry Rinehart, who were specifically intent upon recovering insect fossils so their collections probably better reflect the original composition of the oryctocenosis. Larger wings are much more commonly fragmented than are smaller ones, indicating that the selection in favor of small fossils was operating after insect death and before burial of their corpses, that is, at the stage of tanatocenosis. The relatively tough and durable cockroach fore wings are only moderately abundant in these deposits, thus sorting was not likely due to long distance transport by running waters. More likely, the principal factors were wave action and/or possibly predatory and scavenging activity of aquatic fish and invertebrates, albeit very little evidence of fish has been found in these deposits. Scant representation and diversity of aquatic insects does not imply unusual conditions in the water body yielding the insectiferous deposits. The most likely representatives of aquatic insects in Carrizo Arroyo are the moderately numerous *Dasyleptus* fossils and possibly a few, poorly preserved insect nymphs (Figs. 53, 54). Even if aquatic, these nymphs are possibly allochthonous (brought by water currents to the lake) thus making *Dasyleptus* (possibly also *Microcarrizo*) the only probable autochthonous element in the assemblage. *Dasyleptus* is generally the only reliably known aquatic insect of the Carboniferous, and even in the Lower Permian other aquatic insects were sufficiently uncommon to explain their rarity in or absence from the Carrizo Arroyo assemblage. Nevertheless, the case of *Dasyleptus* in Carrizo Arroyo is a taphonomical puzzle, for all its fossils are probably molting casts of younger developmental stages.

#### Chronostratigraphy



FIGURE 54. Unidentified, poorly preserved nymph, possibly of the first instar, specimen NMMNH P-36620.

Since the stratigraphic position of the insectiferous deposits of Carrizo Arroyo has been reliably established to be in the close vicinity of the Carboniferous/Permian boundary (Lucas and Krainer, 2002; and see Introduction), the following paragraphs can be aimed at clarifying certain events in the evolution of insect that occurred near that boundary, rather than to examine the local stratigraphy. Unless stated otherwise, considerations below on the temporal distribution of Palaeozoic insects are based on information compiled by Rasnitsyn and Quicke (2002).

Of the 13 insect orders recorded, a large majority are known to cross the above boundary. However, the extinct order Eoblattida, supposedly ancestral to the rest of the Infraclass Gryllones (formerly Polyneoptera, or orthopteroid insects in the widest sense), has been previously recorded only in the Carboniferous (Pennsylvanian), while booklice (Psocida), hemipterans and scorpionflies (Panorpida) enter the fossil record in the Lower Permian. Three more orders, Diaphanopterida, Grylloblattida, and Orthoptera, even though transitional, dramatically increased in diversity in the Lower Permian compared to the Carboniferous, where only two families each of diaphanopteridans and grylloblattidans, and one family of orthopterans are recorded, as opposed to eight, 24, and seven families, respectively, in the Lower Permian. Palaeodictyopterans (order Dictyonaurida) display a reverse diversification pattern, albeit much less strikingly, with eight Lower Permian families as opposed to 20 Stephanian families.

At lower taxonomic levels, the pattern is equally definite: three families are transitional (*Dasyleptidae*, *Caloneuridae*, *Anthracoilidae*),

TABLE 2. Order composition of the insect from Carrizo Arroyo in the NMMNH collection (unplaced taxa excluded).

| Order           | n   | %     |
|-----------------|-----|-------|
| Machilida       | 22  | 12.7  |
| Caloneurida     | 3   | 1.7   |
| Hypoperlida     | 1   | 0.6   |
| Dictyoneurida   | 3   | 1.7   |
| Diaphanopterida | 4   | 2.3   |
| Psocida         | 1   | 0.6   |
| ?Hemiptera      | 1   | 0.6   |
| Palaeomanteida  | 24  | 13.9  |
| Panorpida       | 5   | 2.9   |
| ?Eoblattida     | 2   | 1.2   |
| Blattida        | 91  | 52.6  |
| Grylloblattida  | 11  | 6.4   |
| Orthoptera      | 5   | 2.9   |
| Total           | 173 | 100.1 |

four are mainly or entirely Carboniferous (Hapalopteridae, Dictyoneuridae, Spilapteridae, Stenoneuridae) and 10 are mainly or entirely post-Carboniferous (Calvertiellidae, Hanidae, Martynoviidae, Asthenohymenidae, Psocidiidae, Archescytinidae, Palaeomanteidae, Probnidae, Liomopteridae, Thuringoedischidae). Of the 28 genera identified, besides the three transitional ones (*Dasyleptus*, *Miomatoneurella*, and *Delopterus*), and 13 endemic ones, there are 11 genera otherwise known only from the Permian, and only a single otherwise Carboniferous genus (*Titanodictya*). This implies that the Carrizo Arroyo insect assemblage demonstrates an essentially Permian composition. Moreover, the present evidence suggests that the main world-wide transition and taxonomic reorganization of the Carboniferous to Permian insect faunas probably took place during the short interval between Commeny times and Carrizo Arroyo times.

This is not to say that the Carrizo Arroyo assemblage is typical of the Lower Permian. The assemblage displays distinctive transitional features beyond the fact that there are several taxa present that are more characteristic of the Carboniferous. More indicative of the transitional nature is the ordinal composition of the assemblage and, particularly, the high representation of certain orders that are usually far subordinate. Like in the Upper Carboniferous of Montceau-Les-Mines in Central Massif, France (Burnham 1981), here in Carrizo Arroyo it is the order Palaeomanteida that is abundant and diverse, while, in contrast, in the basal Permian Niedermoschel assemblage in Germany it is the order Blattinopseida which is exceptionally abundant (Hörschemeier 1999).

The insect fossils come from two different stratigraphic levels within the Red Tanks Member, viz. localities NMMNH L-3433 and L-3437 (for details see Lucas and Krainer, 2002). No striking differences have been detected between the insect assemblages of these sites, but that might be due to insufficient material. Indeed, of 178 specimens identified, 148 come from L-3433 and 30 from L-3437, the ratio being about 5:1. In roaches, the ratio is essentially the same (91:20 ~ 4.5:1), and the same holds true for *Dasyleptus* (18:4 = 4.5:1). The remaining insects show somewhat different ratio (35:5 = 7) which is not indicative because the figures are small. For the present, there is no reason to consider the insects collected in the two localities separately, so they are treated here as a single assemblage.

#### Environmental Inferences

Unfortunately, the Carboniferous insects are only modest environmental indicators, because their profound taxonomic differences from

extant insects hinders using taxonomic analogy for environment reconstruction. General taxonomic diversity of the assemblage, and diversity of palaeodictyopterans in particular, indicates warm climate, at least distinctly warmer than that of the Upper Carboniferous Chunya locality in Central Siberia, which is dominated by a single species of Tchirkovaeidae. Phytophagous and particularly pollen and seed eaters are probably abundantly represented in all the insect orders recorded here, which is not unexpected for Paleozoic assemblages (see Rasnitsyn and Quicke, 2002 for details). Absence of undoubted predators is also not particularly indicative, because lack of dragonflies is most probably a result of the size-related burial selectivity, and other Paleozoic predators are not especially distinctive either morphologically or taxonomically. Lack of insects with apparent aquatic adaptations also bears little environmental implication because insects with such adaptations are generally uncommon in the Paleozoic assemblages. As exemplified by *Dasyleptus* (see Rasnitsyn and Quicke, 2002), aquatic habits of Paleozoic insects are usually identified by the abundance and distribution of their fossils rather than by their morphology. Thus from the ecological point of view the Carrizo Arroyo insect assemblage seems ordinary for the Paleozoic.

#### CONCLUSION

The Red Tanks Member of Carrizo Arroyo has yielded several hundred insect fossils of which 109 are studied here. The present sample includes at least 47 species (14 previously described, 33 described herein as new) which belong at minimum to 30 genera (28 formerly described, 12 new), 17 families and 13 orders. Also discovered at Carrizo Arroyo were several fossils of scorpionflies, which represents the earliest appearance in the fossil record of this important group. Even though dated as transitional between the Carboniferous and Permian, the Carrizo Arroyo insect assemblage is composed mostly of typically Permian taxa with few Carboniferous elements. However, it is not an ordinary Permian assemblage because of the absence or rarity of some characteristically Permian taxa like hemipterans and holometabolans other than miomopterans and scorpion flies; and because of the abundance of miomopterans which usually constitute a far less dominant position in most other assemblages. No significant environmental inference can be drawn at present from the insect fossils.

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