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A new fossil species of snakeflies (Raphidioptera: Mesoraphidiidae) from the Late Cretaceous of Kazakhstan, with notes on Turonian Neuropterida

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ABSTRACT

Alloraphidia kyzylzharica sp. nov. is described from the Late Cretaceous (early Turonian) locality at Kyzylzhar, southern Kazakhstan. It is very similar to *A. dorfi*, but easily distinguished from it by wing shape and venation. We restrict the genus *Alloraphidia* to these two species. *Ascalapharia raphidiformis* is considered a member of Baissopteridae, sit. nov. Turonian Neuropterida are mainly characterized by a mixture of specialized genera of extinct families, and genera (sometimes modern) of highly advanced taxa, reflecting a sequence of global mid-Cretaceous crisis of non-marine biocoenoses.

1. Introduction

The order Raphidioptera (snakeflies) is today a relict group, the least diverse order of Holometabola, distributed only in the Northern Hemisphere (Grimaldi and Engel, 2005). Snakeflies were more diverse in the Mesozoic, when they occurred even in equatorial regions. They are especially numerous in Late Jurassic to Early Cretaceous Asiatic localities (see Jepson and Jarzembowski, 2008), but are only fragmentarily known in the fossil record from the Late Cretaceous. Hitherto, only two species of Mesoraphidiidae have been described from this period: *Nanoraphidia electroburmica* Engel, 2002a from earliest Cenomanian of Burmese amber (age after Shi et al., 2012) and *Grimaldiraphidia luzzii* (Grimaldi, 2000) from Turonian New Jersey amber, both belonging to the tribe Nanoraphidiini (Bechly and Wolf-Schwenninger, 2011). A few other undescribed snakeflies have been reported from three other Late Cretaceous localities: north-eastern Siberia (two from the Obeshchayushchiy locality and three from the Arkagala Formation) and Canadian amber (Ponomarenko, 2002; McKellar and Wolfe, 2010; pers. obs.). Here, we treat *Ascalapharia raphidiformis* Makarkin, 1990 from the early Turonian of Kyzylzhar, southern Kazakhstan, as a member of Baissopteridae, and describe a new species of Mesoraphidiidae (Alloraphidiinae), also from that locality.

In the Turonian, especially the early Turonian, snakeflies lived in a notably warm greenhouse climate (Zhou, 2012; Uramoto et al., 2013), contrary to extant raphidiopterans. In general, this was an important formative interval in the pre-history of the modern biota. We summarize and analyze all available data on the taxonomic composition of the Neuropterida assemblages from Turonian localities, and find that Turonian Neuropterida are mainly characterized by specialized genera of extinct families, and to a lesser extent genera of highly advanced taxa, some extant.

2. Material and methods

The single specimen described herein is from the Kyzylzhar (=Kzyl-Zhar, Kzyl-Dzhar) locality, and is deposited in the fossil insect collection of the Paleontological Institute (PIN) of the Russian Academy of Science in Moscow, Russia. The locality is situated in the north-western offshoots of the Karatau mountain range in southern Kazakhstan, Kyzyorda (or Qyzylorda) Oblys (=Kzyl-Orda Oblast'), Chiili district. Its age is considered early Turonian based on its flora (Shilin, 1986). The deposits of this locality were formerly considered as lagoonal (Zherikhin, 1978; Kalugina, 1980), but now as fluvial (Rasnitsyn and Zherikhin, 2002; Sinitshenkova, 2002). The locality has yielded a rather diverse assemblage of insects and

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plants (Zherikhin, 1978). The flora is dominated by Platanaceae (Samsonov, 1966, 1967; Shilin, 1986).

The specimens were examined using a Leica MZ 9.5 and a MPS-2 dissecting microscope. Line drawings were prepared using Adobe Photoshop CS3, and photographs were taken by Leica M165C stereomicroscopes.

We follow Bechly and Wolf-Schwenninger's (2011) systematics of fossil taxa at the family, subfamily and tribe levels. Wing venation terminology used here in general follows that applied to other Neoptera (e.g., Béthoux, 2005; Béthoux and Jarzembowski, 2010). Crossveins are designated after the longitudinal veins which they connect and are numbered in sequence from the wing base, e.g., 1ra-rp, first (proximal-most) crossvein connecting RA and RP; 2scp-r, second crossvein between ScP and RA; icu, crossvein between CuA and CuP. Terminology of wing spaces and details of venation (e.g., traces, veinlets) follows Oswald (1993).

Wing abbreviations used in the text and figures are as follows: AA1 to AA3, first to third branches of analis anterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; MA, media anterior; MP, media posterior; R, radius; RA, radius anterior; RP, radius posterior; RP1 (RP2, RP3), proximal-most branch (second, third) of radius posterior; ScA, subcosta anterior; ScP, subcosta posterior.

3. Systematic palaeontology

Order: Raphidioptera Navás, 1916
Family: Mesoraphidiidae Martynov, 1925
Subfamily: Alloraphidiinae Carpenter, 1968
Genus *Alloraphidia* Carpenter, 1968

Type species. Alloraphidia dorfi Carpenter, 1968, by original designation.

Diagnosis. Fore- and hind wings very narrow; ScP short, entering costal margin very far from pterostigma (length from termination of ScP to pterostigma much longer than pterostigma length); pterostigma relatively short, closed by 2scp-r proximally and second branch of RA distally, with one incorporated pterostigmal branch of RA; in forewing, origin of RP well distad fork of M; three discoidal cells; AA1 with one to two branches; in hind wing, CuP not fused with AA1.

Species included. Alloraphidia dorfi from the Albian/Cenomanian of Redmond (Labrador, Canada); *A. kyzylzharica* sp. nov. from the early Turonian of Kyzylzhar (Kazakhstan).

Comments. Alloraphidia may be distinguished from the two other genera of Alloraphidiinae by its very narrow wings; the origin of RP is located well distad the fork of M (approximately at the level of M in *Archeraphidia* Ponomarenko, 1988 and *Pararaphidia* Willmann, 1994); and AA1 with one to two branches in the forewing (AA1 is usually simple in *Archeraphidia* and *Pararaphidia*).

Three other species from the Early Cretaceous of eastern Asia are currently considered as belonging to the genus *Alloraphidia*: *A. petrosa* Ponomarenko, 1988 (Mongolia: Bon-Tsagan), *A. asiatica* Ponomarenko, 1993 (Russia: Transbaikalia: Baissa), and *A. anomala* Ren, 1997 (China: Huangbanjigou, Yixian Formation) (Engel, 2002a; Jepson and Jarzembowski 2008). These species were probably attributed to *Alloraphidia* due to the similar structure of the pterostigma with that of *A. dorfi*, i.e., relatively short and closed by 2scp-r proximally and the second branch of RA distally, and with one incorporated pterostigmal branch of RA. However, *Alloraphidia petrosa* has two discoidal cells (three in the type species and *A. kyzylzharica* sp. nov.), and MP and CuA are fused for a rather long distance in the forewing (these veins are not fused in the type species and *A. kyzylzharica* sp. nov.). The forewings of *A. asiatica* and *A. anomala* are relatively broad, their ScP is long, and MP and CuA at least touch or are fused (these conditions are strongly different in the type species and *A. kyzylzharica* sp. nov.). Also, 3ra-rp is located distad the pterostigma in *A. asiatica* (located within the pterostigma in the type species and *A. kyzylzharica* sp. nov.). Therefore, these species cannot be assigned to *Alloraphidia*. Their taxonomic affinity within Alloraphidiinae will be clear when other species with similar venation are described.

Alloraphidia is the type genus of the family Alloraphidiidae (Carpenter, 1968). This taxon is now considered as a subfamily (Bechly and Wolf-Schwenninger, 2011) and thought to include three genera from the Cretaceous of Canada, Mongolia, China, Kazakhstan, and the Transbaikalian Russia: *Alloraphidia*, *Archeraphidia* and *Pararaphidia* (Engel, 2002a; Bechly and Wolf-Schwenninger, 2011).

Alloraphidia kyzylzharica sp. nov.
(Figs. 1–3)

Derivation of name. From Kyzylzhar, the type locality of the new species.

Type material. Holotype No. 2383/159 (part, counterpart), deposited in PIN. An incomplete specimen lacking head, prothorax, and abdomen.

Type locality and horizon. Southern Kazakhstan: Kyzylzhar. Late Cretaceous (Turonian).

Diagnosis. Most similar to *Alloraphidia dorfi* but easily differs by slightly wider wings, longer pterostigma, presence of rather long apparent fusion of R+M+CuA, presence of crossvein 3r-m in forewing.

Description. Meso- and metathorax preserved, but details not clear.

Forewing narrow, 7 mm long, 1.6 mm wide. Costal space relatively narrow. Presumed ScA long, rather clearly visible in distal part, almost indiscernible in proximal part. Subcostal veinlets widely spaced, five as preserved (probably six when complete). ScP very short, entering costal margin at wing mid-point or slightly proximad (termination of ScP not preserved). Subcostal space moderately broad, slightly narrowed near termination of ScP; two crossveins preserved: 1scp-r located much closer to M+CuA than to origin of RP; 2scp-r closing pterostigma proximally. Pterostigma elongate, closed by 2scp-r proximally, second branch of RA distally; colour not detected. RA long, not zigzagged distally, entering wing margin slightly before apex; with three branches: (1) incorporated pterostigmal branch; (2) smoothly curving branch closing pterostigma distally; (3) shorter branch distad pterostigma. Portion of RA distad pterostigma long. RP originating slightly proximad wing mid-point, strongly zigzagged, shallowly forked distally. Two crossveins between RA, RP: 2ra-rp short, located well distad origin of RP1, well proximad 2scp-r; 3ra-rp long, located distad origin of RP2, within pterostigma. Two branches of RP: RP1 deeply forked, each branch again rather deeply forked; RP2 simple. One crossvein between branches of RP, connecting stem of RP, anterior branch of RP1. Free portion of M before fusion with CuA not visible (probably closely adjoins R). MA deeply dichotomously forked. MP zigzagged,

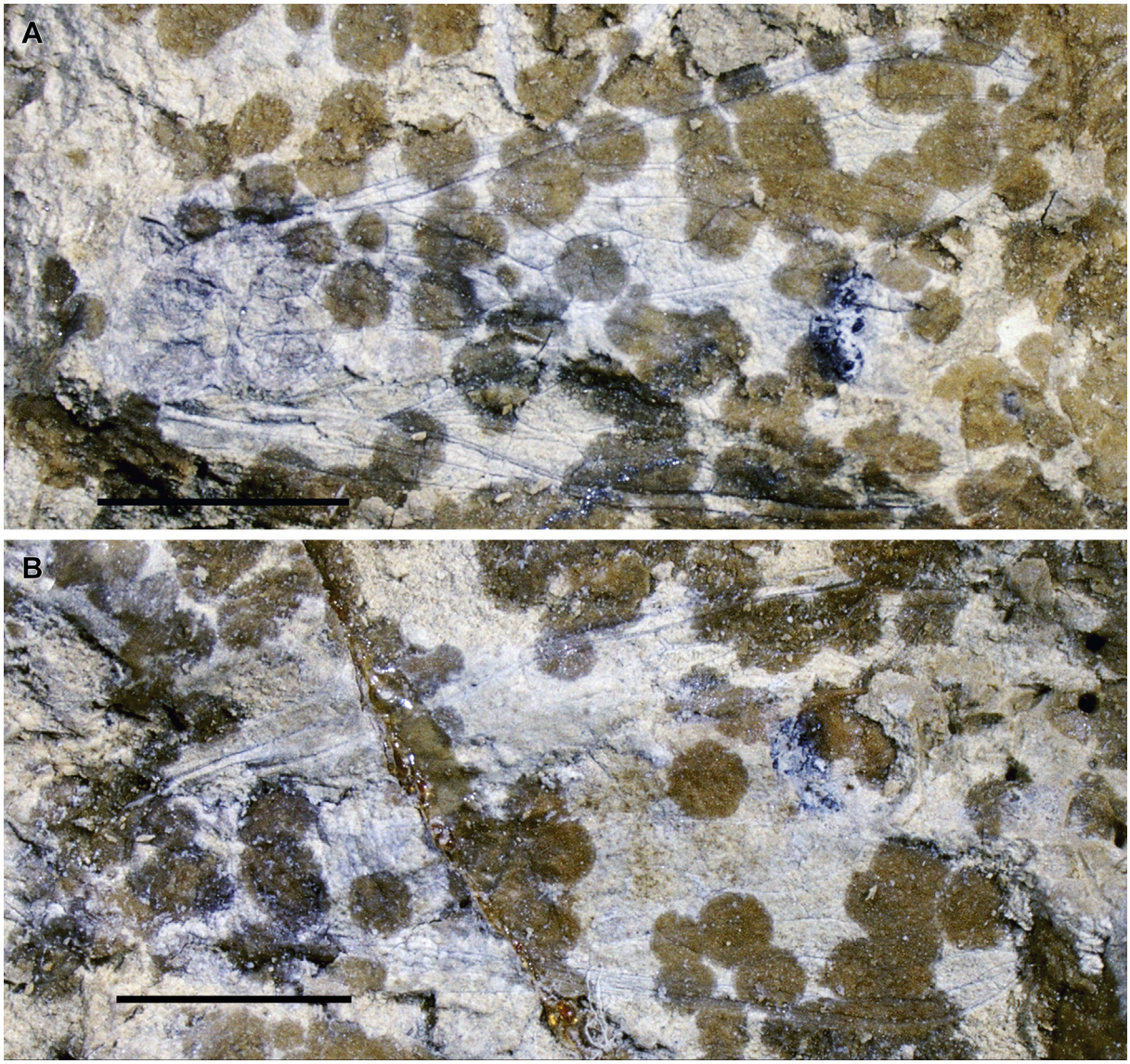

Fig. 1. *Alloraphidia kyzylzharica* sp. nov. Holotype PIN 2383/159. A, part. B, counterpart. Scale bar represents 2 mm.

anterior trace simple; with one long simple branch. Two long crossveins between MA, MP. Two crossveins between M, Cu connecting MP, CuA. CuA basally fused with M before point where M+CuA separates from apparent fusion with R forming rather long apparent fusion R+M+CuA; free M+CuA rather long. CuA distally zigzagged, with two short branches (proximal one simple, distal one incompletely preserved). CuP probably simple (incompletely preserved). AA1 pectinate, with two branches. AA2+3 with one distal branch preserved (basal portion not preserved). Crossvein iaa long.

Hind wing narrow, ca. 6.6 mm long, ca. 1.5 mm wide. Costal space rather narrow; subcostal veinlets widely spaced (three preserved). ScP incompletely preserved. Subcostal space narrow; crossveins not preserved. Pterostigma probably closed by branch of RA distally; its colour not detected. RA long, not zigzagged distally, entering wing margin slightly before apex; with two branches. RP originating nearly at proximal one-third of wing length, probably strongly zigzagged, shallowly forked distally. Three crossveins between RA, RP: 1ra-rp located proximad origin of RP1; 2ra-rp shorter than 1ra-rp; 3ra-rp located distad origin of RP2, within pterostigma. Two branches of RP, configured as in forewing. Crossvein between branches of RP not preserved. One crossvein between R/RP, M/MA preserved: 1r-m long, convergent proximally with R (basal-most portion not preserved). Basal portion of M not preserved; M dividing into MA, MP distad origin of RP. MA probably configured as in forewing. MP pectinate, with three poorly preserved branches (alternatively, MP deeply forked distally with two pectinate branches). Two long crossveins between MA, MP. One crossvein between M, Cu preserved; 2m-cu connects MP and anterior branch of distal fork of CuA. CuA distally rather deeply forked. CuP simple. AA1 fragmentarily preserved. AA2 with one distal branch preserved (basal portion not preserved). Crossvein iaa long.

Remarks. The pterostigma is light yellow in *Alloraphidia dorfi*, and not detectable in *A. kyzylzharica* sp. nov. due to motley coloration of the stone.

This specimen was formerly identified as a member of Inocelliidae (Zherikhin, 1978).

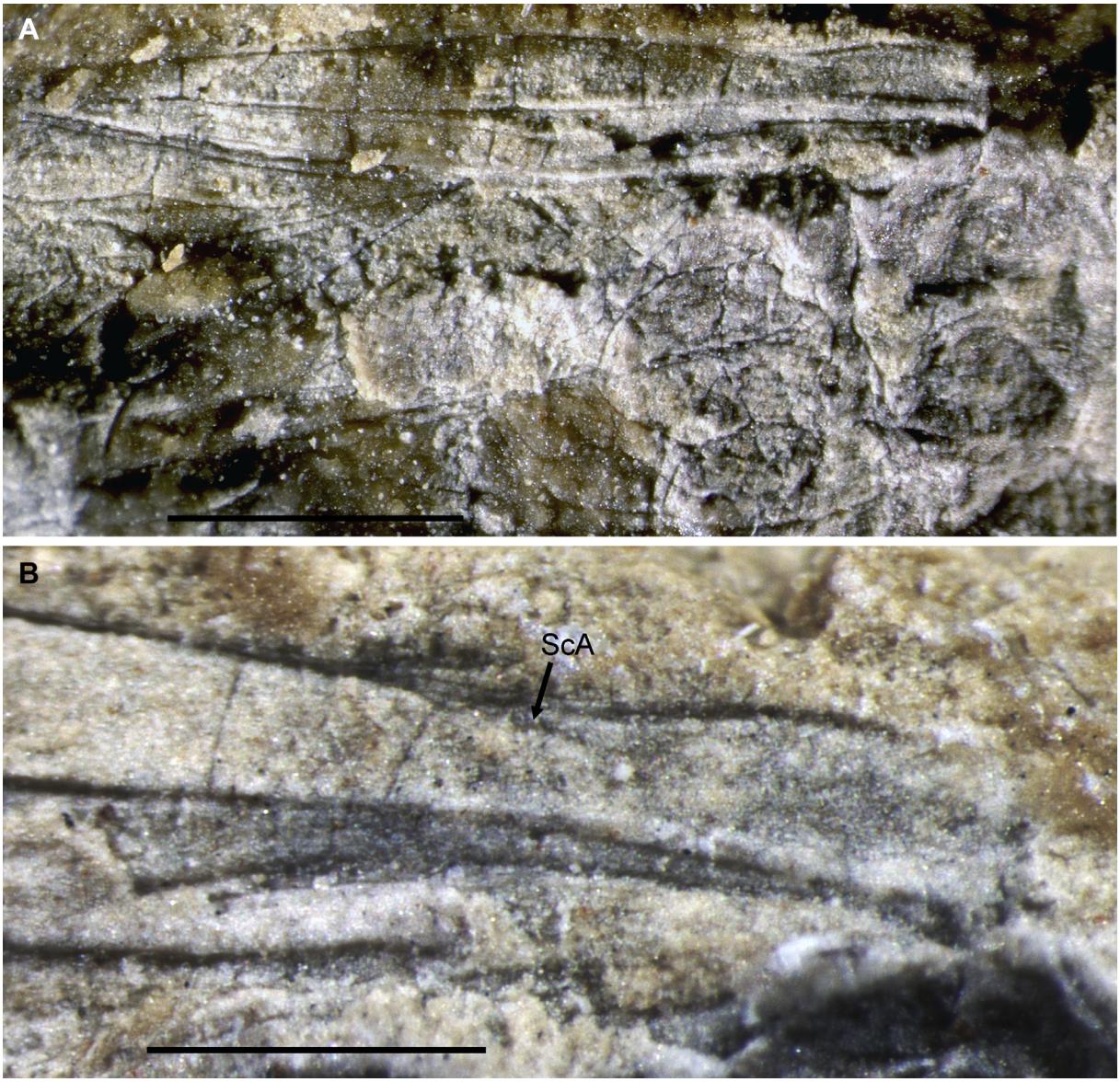

Fig. 2. *Alloraphidia kyzylzharica* sp. nov. Holotype PIN 2383/159. A, proximal part of the left wings. B, basal portion of the left wing costal space showing the presumed ScA. Scale bars represent 1 mm (A) and 0.5 mm (B).

4. Turonian Neuropterida assemblages

4.1. Kyzylzhar

Four species of Neuropterida are now known from the Kyzylzhar locality, two species of Neuroptera (*Gerstaeckerella asiatica* Makarkin, 1990 and '*Kagapsychops*' *continentalis* Makarkin, 1994), and two species of Raphidioptera (*Ascalapharia raphidiformis* Makarkin, 1990 and *Alloraphidia kyzylzharica* sp. nov.).

'*Kagapsychops*' *continentalis* is represented by a large incomplete forewing (see photograph of this specimen in Ponomarenko, 2002, fig. 259). Its family affinity is rather unclear. The type and only other species of this genus (*K. aranea* Fujiyama, 1978) is described from the Valanginian/Barremian Kuwajima Formation, western Honshu, Japan (age after Matsukawa et al., 2006) based on a less completely preserved forewing. The wing venation of both species is similar in general aspects, but distinct in details; e.g., '*K.*' *continentalis* has numerous crossveins in the subcostal space, whereas *K. aranea* does not (cf. Makarkin, 1990, fig. 1; Fujiyama, 1978, fig. 6). These species probably belong to different genera, and possibly even to other families, Psychopsidae and Osmylopsychopidae, respectively. The venation of '*K.*' *continentalis* is most similar to that of *Undulopsychopsis* Peng et al., 2011 from the Barremian of the Yixian Formation, in particular by the multi-branched RP1 and the presence of subcostal crossveins. *Undulopsychopsis* was reasonably assigned to Psychopsidae. The venation of the genus *Kagapsychops* excluding '*K.*' *continentalis* is most similar to that of the monotypic genus *Grammapsychops* Martynova, 1954 from the Cenomanian Kem' locality in Krasnoyarsk Krai, Siberia (lower horizons of the Simonovo Formation; the age after Golovneva, 2008). The systematic position of these genera was discussed by Jepson et al. (2009) as belonging to the Mesozoic family Osmylopsychopidae, which is characterized in particular by the following forewing conditions: RA and ScP are smoothly fused, the subcostal crossveins are absent, and the proximal branch of RP are profusely branched. Unfortunately, most of these and similar genera are represented by incomplete

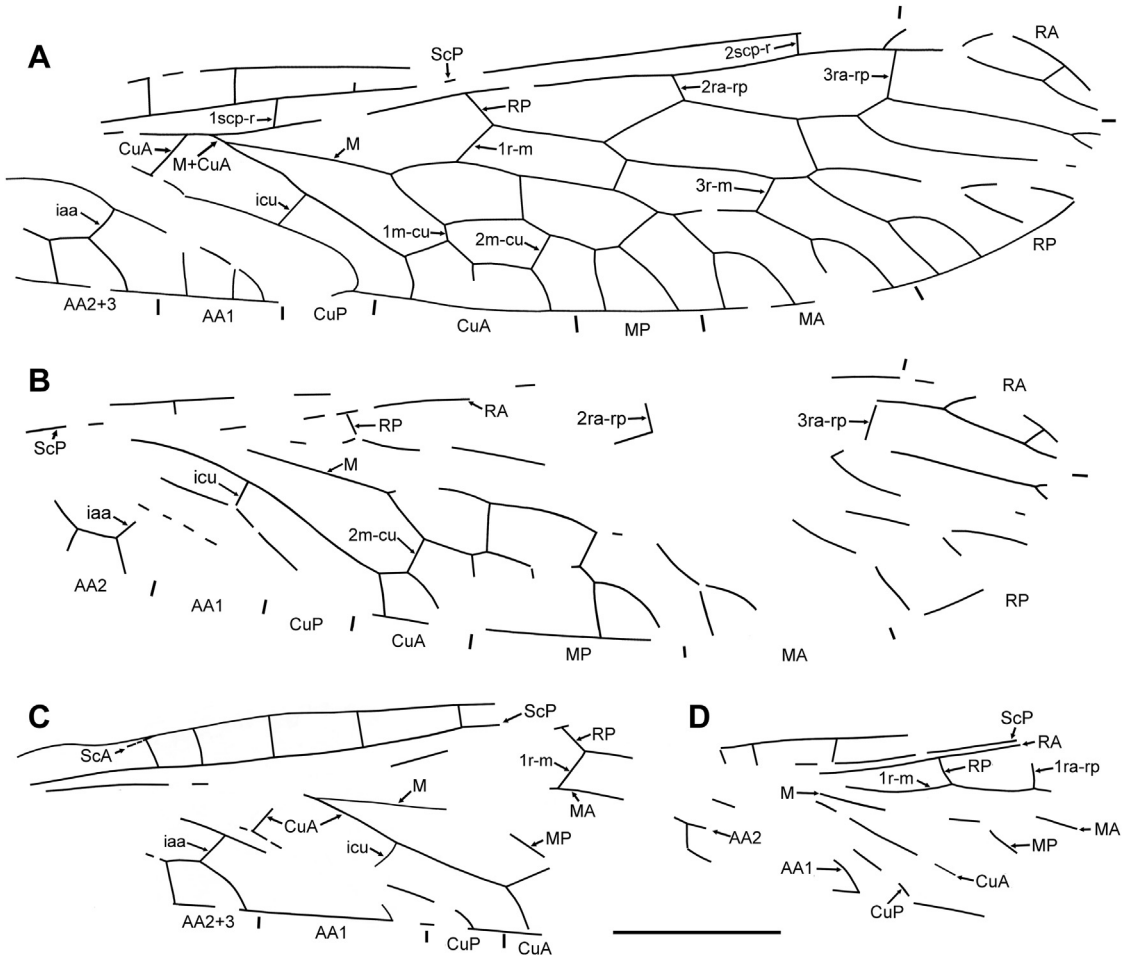

Fig. 3. *Alloraphidia kyzylzharica* sp. nov. Preserved wing venation of the holotype PIN 2383/159. A, right forewing (broken between CuP and AA1). B, right hind wing. C, left forewing. D, left hind wing. Scale bar represent 1 mm.

forewings with hind wings not preserved (or their venation is indiscernible), which makes determination of family affinity problematic.

Gerstaeckerella asiatica is represented by a nearly complete but crumpled hind wing (Fig. 4C). It was assigned to the extant genus currently distributed in South America (Mantispidae: Drepanicinae). In general, this assignment appears to be correct, at least no character states contradict this attribution.

Although *Ascalapharia raphidiformis* (Fig. 4A, B) was originally described as a Neuroptera incertae sedis taxon, it is now clear that this species belong to Raphidioptera with certainty, most probably to Baissopteridae due to the presence of numerous crossveins, and the structure of its pterostigma. *A. raphidiformis* differs from other species of Baissopteridae in having of a wing spot and denser radial crossveins. Such an apical fuscous spot is unknown in other fossil snakeflies, but all wings of the extant Chinese species *Inocellia elegans* Liu et al., 2009 have brown distal portions. *A. raphidiformis* may be treated as a most specialised taxon of Baissopteridae.

4.2. Gerofit

The Gerofit locality is located in southern Negev, Israel. It belongs to the Upper Shale Member of the Ora Formation, and is dated middle Turonian based on ammonites from underlying and overlying horizons. The locality represents both coastal wetlands by mangroves, marsh plants, back-mangrove freshwater macrophytes; and inland broadleaved lowland forests (Krassilov et al., 2005; Krassilov and Rasnitsyn, 2008).

The insect assemblage of Gerofit consists of less than twenty specimens (Anisyutkin et al., 2008), which includes one described species of Neuroptera, *Samsonileon fragmentatus* Ponomarenko in Dobruskina et al., 1997. This monotypic genus belongs to the myrmeleontoid family Palaeoleontidae, known only from the Cretaceous. It is most closely related to another monotypic genus, *Metahemerobius* Makarkin, 1990 from the Coniacian of the Sym Formation at the Antibes locality, Kemerovo Oblast' in Siberia (age after Shchepetov et al., 2009). The venation of both genera appears to be the most specialized in the family by the proximal branch of MP+CuA and CuP running parallel and very close for a considerable distance, and AA1 long and pectinately branched. These are the youngest known record of Palaeoleontidae.

4.3. New Jersey amber

Amber from central New Jersey (U.S.A.) lying in the South Amboy Fire Clay belongs to the Raritan Formation. It contains an exceptional diversity of inclusions, i.e., the remains of plants, fungi, and animals. It is assigned to the Turonian based on pollen (Grimaldi et al., 2000; Grimaldi and Nascimbene, 2010).

The Neuroptera assemblage includes five species of Coniopterygidae, eight (three unnamed) of Berothidae, two of Dipteromantispidae, and an adult and larva (both unnamed) of

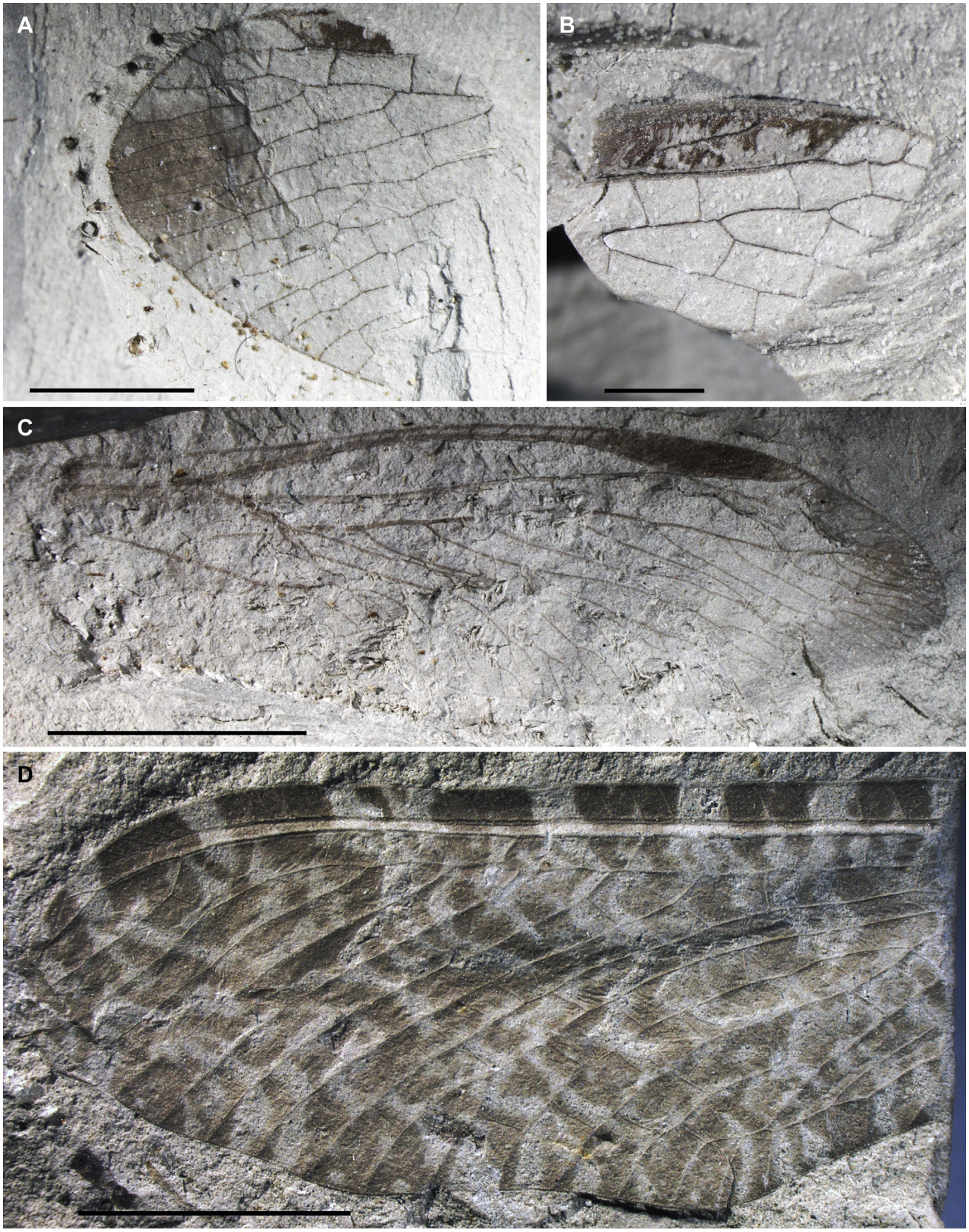

Fig. 4. Turonian Neuropterida from Kazakhstan. A, *Ascalapharia raphidiformis* Makarkin, 1990, holotype PIN 3289/15, part (Kyzylzhar). B, same, counterpart. C, *Gerstaeckerella asiatica* Makarkin, 1990, holotype PIN 2783/188 (Kyzylzhar). D, *Palaeogetes ponomarenkoi* Makarkin, 1990, holotype PIN 3314/1 (Kangazgan). Scale bars represent 2 mm (A), 1 mm (B), and 5 mm (C, D).

Psychopsidae (Grimaldi, 2000; Engel, 2002b; Engel and Grimaldi, 2008). Also, there is an undescribed, unusual hemerobiid (T. Weiterschan, pers. comm.). Raphidioptera are represented by one species of Mesoraphidiidae and one larva (Grimaldi, 2000).

All species of Coniopterygidae (belonging to *Apoglaesoconis* Grimaldi, 2000 and *Glaesoconis* Meinander, 1975) are assigned the tribe Fontenelleini of the subfamily Aleuropteryginae. This tribe is the most speciose in the coniopterygid fossil record, and is known from the Early Cretaceous to Recent.

Of the three genera of Berothidae (*Jersiberotha* Grimaldi, 2000, *Rhachibermissa* Grimaldi, 2000, *Nascimberotha* Grimaldi, 2000), two are endemic to the New Jersey amber fauna; one species of *Jersiberotha* occurs also in earliest Cenomanian Burmese amber. *Rhachibermissa* belongs to the subfamily Paraberothinae, which is restricted to the Cretaceous and includes ten genera (Makarkin and Kupryjanowicz, 2010). The subfamily affinities of the two other genera are unknown, but the morphology of *Jersiberotha* is quite typical of early to middle Cretaceous berothids.

The family Dipteromantispidae includes only two Cretaceous genera: *Dipteromantispa* Makarkin et al., 2013 from the Barremian Yixian Formation and *Mantispidiptera* Grimaldi, 2000 from New Jersey amber. This family is remarkable by its hind wings extremely modified as small structures resembling the halteres of Diptera (Makarkin et al., 2013). Both species of *Mantispidiptera* are minute insects (forewings are ca. 3 mm long), with raptorial forelegs.

One adult neuropteran species (unnamed) and one larva were assigned to Psychopsidae (Grimaldi, 2000). Indeed, the adult specimen appears to be psychopsoid, but its venation is so specialized (especially that of the hind wing: Grimaldi, 2000, fig. 4) that it is currently impossible to determine its family affinity with any certainty. The larva is small (2.5 mm long), probably a first instar. We strongly suspect that it belongs to psychopisoids by its general morphology, but its overall poor preservation precludes a definite family assignment.

The family Hemerobiidae is represented by an isolated forewing (ca. 7 mm long) deposited in the private collection of Thomas Weiterschan. Its venation is rather unusual, especially the configuration of M and Cu. The relationships between this species and other hemerobiids are entirely unclear.

The Raphidiopteran *Grimaldiraphidia luzzii* belongs to the tribe Nanoraphidiini (Mesoraphidiidae: Mesoraphidiinae), which includes four early to middle Cretaceous monotypic genera: *Lebanoraphidia* Bechly et Wolf-Schwenninger, 2011 from late Neocomian (Barremian?) Lebanese amber; *Cantabroraphidia* Pérez-de la Fuente et al., 2010 from Albian El Soplao amber (Spain); *Nanoraphidia* Engel, 2002 from earliest Cenomanian Burmese amber; and *Grimaldiraphidia* Bechly et Wolf-Schwenninger, 2011 (Bechly and Wolf-Schwenninger, 2011) from New Jersey amber. All of these species are very small. *G. luzzii* represents the youngest known record of the tribe.

4.4. Kangazgan

The Kangazgan locality, also known as Tyul'kili (Kordikova et al., 2001; Averianov, 2007a, b; Makarkin et al., 2012) and Gulkili (Zherikhin, 1978), is situated in southern Kazakhstan (Kzyl-Orda Oblast'). It belongs to the Zhirkindek Formation which is dated late Turonian to Coniacian based on foraminifers, vertebrates and plants (Kordikova et al., 2001). The plant-bearing horizon at the Kangazgan locality, where a neuropteran was found, is considered late Turonian based on the flora (Shilin, 1986). The formation has yielded a diverse assemblage of animals including gastropods, bivalves, brachiopods, crustaceans, selachians, osteichthyans, amphibians, lizards, trionychid turtles, crocodiles, and ornithomimid, tyrannosaurid, and dromaeosaurid dinosaurs (Nessov, 1995, 1997; Kordikova et al., 2001; Averianov, 2007a, b). The flora is dominated by angiosperms, mainly Magnoliaceae, Lauraceae, Platanaceae (Shilin, 1986, 1998, 2000), indicating "a low-lying coastal or coastal-marine environment" (Kordikova et al., 2001, p. 391).

The neuropteran *Palaeogetes ponomarenkoi* Makarkin, 1990 represents a single fossil insect known from the locality (Fig. 4D). Originally, it was provisionally assigned to Prohemerobiidae (Makarkin, 1990); however, it was subsequently considered to belong to an undescribed new family also occurring in the Middle Jurassic to Early Cretaceous of China (Makarkin et al., 2012). The phylogenetic position of this family is entirely unclear. *P. ponomarenkoi* is the youngest record of the family.

4.5. Arkagala Formation

The Arkagala Formation is situated in north-eastern Asia, in the Arkagala river basin (Russia: Magadan Oblast': upper reaches of the Kolyma river basin). Neuropterida fossils have been reported from two localities within the Upper Arkagala Coalfield of the Arkagala Coal Basin: (1) the right bank of Tal-Yuryakh stream (point 5a), which is the right tributary of the Arkagala river, and (2) the Gryaznyi stream, which is the left tributary of the Arkagala river (see map in Samylina, 1988, fig. 1). The deposits of the Arkagala Formation were probably deposited throughout the entire Turonian, from the Cenomanian/early Turonian to the Santonian (Markevich, 1989, 1995). The age of the Tal-Yuryakh locality is late Turonian/Santonian or late Turonian, based on pollen collected from insect-bearing layers by V. V. Zherikhin (Markevich, 1989, 1995). The precise age of the Gryaznyi locality is unclear, as its exact position in the section is unknown, but it is very likely Turonian. The deposits of the Arkagala Coal Basin represent swamp fossil assemblages (oryctocoenoses) (Zherikhin, 2002).

Two described species of Neuroptera and three undescribed specimens of Raphidioptera are known from the Arkagala Formation.

The holotype of *Dactylomyius septentrionalis* Makarkin, 1990 (Gryaznyi locality) is interpreted as a hind wing of Myiodactylinae (Nymphidae), the only fossil species of this extant subfamily, which is today distributed mainly in Australia and New Guinea (with one species in Philippines). The venation is remarkable by its distal branches of MP being fan-shaped (strongly curved anteriorly) (Makarkin, 1990, fig. 2).

Arctopsychops zherikhini Makarkin, 1994 (Tal-Yuryakh; point 5a) is known from a poorly-preserved incomplete forewing, originally preliminary assigned to Psychopsidae. Its family affinity is actually unclear because of the fragmentary nature of the specimen.

Three undescribed raphidiopteran specimens from Tal-Yuryakh (point 5a) are poorly preserved and fragmentary. At least one of these belongs to Baissopteridae; the family affinities of others are unclear (pers. obs.).

4.6. Summary and conclusions

Thus, the Turonian Neuropterida include the following groups: of Neuroptera, large psychopsoids (Psychopsidae and/or Osmylopsychopidae) (three species); remarkable minute Dipteromantispidae (two species); specialized genera of Palaeoleontidae, Nymphidae and Familia nova A (one species each); unusual Hemerobiidae (one species); small Coniopterygidae (five species) and Berothidae (eight species); advanced Mantispidae (one species); of Raphidioptera, Baissopteridae (at least two species) and Mesoraphidiidae (Mesoraphidiinae: Nanoraphidiini and Alloraphidiinae, one species each).

Although the Turonian assemblage of Neuropterida is not speciose, its taxonomic composition is noteworthy. The impression

assemblages contain mainly morphologically unusual (specialized) genera of their families. Some of these are the youngest known representatives of extinct families, e.g., *Palaeogetes* Makarkin, 1990 (Familia nova A). Another peculiarity of the Turonian Neuropterida is the presence of highly advanced taxa. This is exemplified by the genera *Gerstaeckerella* Enderlein, 1910 and *Dactylomyius* Makarkin, 1990, the oldest known records of the modern subfamily Drepanicinae (Mantispidae) and Myiodactylinae (Nymphidae), respectively. Raphidioptera also include mainly specialized genera (Baissopteridae) and the youngest record of some extinct taxa (e.g., Alloraphidiinae).

The New Jersey amber assemblage shows rather close relationships with older amber assemblages, especially with that of earliest Cenomanian Burmese amber. These assemblages include mainly small neuropterans of the families Coniopterygidae and Berothidae, which were not especially diverse during the early to mid Cretaceous. Although the impression and amber assemblages cannot be compared due to taphonomic reasons, the New Jersey amber assemblage has some similar peculiarities as impression ones: the presence of morphologically unusual (specialized) genera of its families (e.g., undescribed genus of Hemerobiidae), and the youngest known representatives of extinct taxa (e.g., *Mantispidiptera* Grimaldi, 2000 from Dipteromantispidae; *Grimaldiraphidia* from Nanoraphidiini).

This unusual taxonomic composition of Turonian insect assemblages has been mentioned earlier (e.g., Anisyutkin et al., 2008; Golub and Popov, 2012). This is usually explained by a sequence of the global crisis of non-marine biocoenoses in the mid-Cretaceous hypothesized by Zherikhin (1978, 1980) and developed by Rasnitsyn (1988). This represents the great replacement of the 'Mesophytic' flora by the 'Cainophytic' with a dominance of angiosperms in the Albian/Cenomanian that was associated with its warmest climate: temperatures reached its maximum during the late Cenomanian/early Turonian, when tropical sea surface temperatures might have been as high as 35 °C and high latitude sea surface temperatures 20 °C or higher (a super-greenhouse word) (Huber et al., 1995; Bice and Norris, 2002; Wilson et al., 2002; Rückheim, 2005; Sokolova, 2009; Uramoto et al., 2013). Mass extinction of marine taxa across the Cenomanian/Turonian boundary is well known (e.g., Kauffman, 1995). The greatest change of terrestrial tetrapods is mentioned at this boundary in Asia (Nessov, 1995). Many insects groups also became extinct during the Cenomanian/Turonian or slightly later (e.g., orthopteran Locustopseidae; Sharov, 1968). On the other hand, a number of insect groups have appeared in this period. For example, the oldest fossil records of extant families or subfamilies appeared in the Turonian, e.g., dragonflies of the family Libellulidae (Fleck et al., 1999); ants of different subfamilies (Dlussky et al., 2004; Dlussky and Rasnitsyn, 2007); beetles of the subfamily Phloeocharinae (Staphylinidae) (Chatzimanolis et al., 2013). Moreover, some of these groups are represented in the Turonian by extant genera, e.g., *Paratropes* Serville (Blattodea: Ectobiidae); *Ergaula* Walker (Blattodea: Corydiidae); *Echinocnemus* Schönherr (Coleoptera: Curculionidae); *Phloeocharis* Mannerheim (Coleoptera: Staphylinidae) (Anisyutkin et al., 2008; Chatzimanolis et al., 2013).

Therefore, peculiarities of the taxonomic composition of the Turonian Neuropterida well agree with those found in other insect groups.

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