

# A new assemblage of Early Cretaceous green lacewings (Chrysopidae: Neuroptera) from Transbaikalia

Alexander V. Khrarov

Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.  
Email: a-hramov@yandex.ru

**ABSTRACT:** One new genus and four new species of Chrysopidae are described from the Lower Cretaceous of Khasurty, Transbaikalia (Russia): *Mesypochrysa cannabina* sp. nov.; *M. naranica* sp. nov.; *Aberrantochrysa buryatica* gen. & sp. nov.; and *A. pulchella* gen. & sp. nov. The abundance of Chrysopidae in Mesozoic localities is discussed.

**KEY WORDS:** Aphids, Baissa, fossil insects, Khasurty, Yixian Formation.



Today, the family Chrysopidae (green lacewings) is the second largest family of Neuroptera after Myrmeleontidae, with 1200 Recent species in approximately 80 genera (Brooks & Barnard 1990). In terms of abundance, green lacewings occupy first place amongst Neuroptera in present-day forest ecosystems, at least in the temperate zone. For example, Chrysopidae accounted for 43 % of all Neuroptera which were collected from light traps in Virginia, USA during one season (Penny *et al.* 2007). The percentage of Chrysopidae was 82 % when Neuroptera were collected in the same way over eight years in southeast Norway (Greve & Kobro 1998).

The earliest known fossil record of Chrysopidae is from the Daohugou beds of China, which is Bathonian to Callovian, or Callovian to Oxfordian, in age (Khrarov *et al.* 2016). Almost since its appearance, this family became quite numerous. The proportion of green lacewings to all Neuroptera in the Upper Jurassic–Lower Cretaceous localities is similar to that seen nowadays (Fig. 1). Putting aside psychopoid lacewings, a heterogeneous group represented by a few different families (Peng *et al.* 2011; Khrarov & Makarkin 2015), it can be said that green lacewings often played the most prominent part in neuropteran assemblages of that time.

Apart from two rare genera of uncertain subfamily affiliation (*Paralembochrysa* Nel *et al.*, 2005 from the Yixian Formation of China and *Araripechrysa* Martins-Neto & Vulcano, 1989 from the Crato Formation of Brazil), all Mesozoic green lacewings known as imagoes belong to the extinct subfamily Limaiinae. In turn, about 90 % of specimens of Mesozoic Limaiinae are representatives of the genus *Mesypochrysa* Martynov, 1927. This genus, known from all over Eurasia and recorded also from the Crato Formation of Brazil (see list in Khrarov *et al.* 2016), seems to have had a widespread distribution during the Upper Jurassic–Lower Cretaceous (Fig. 1); similar to some Recent genera, such as *Chrysoperla* Steinmann, 1964. *Mesypochrysa*, without doubt, was the most abundant and widespread taxon amongst all Mesozoic lacewings.

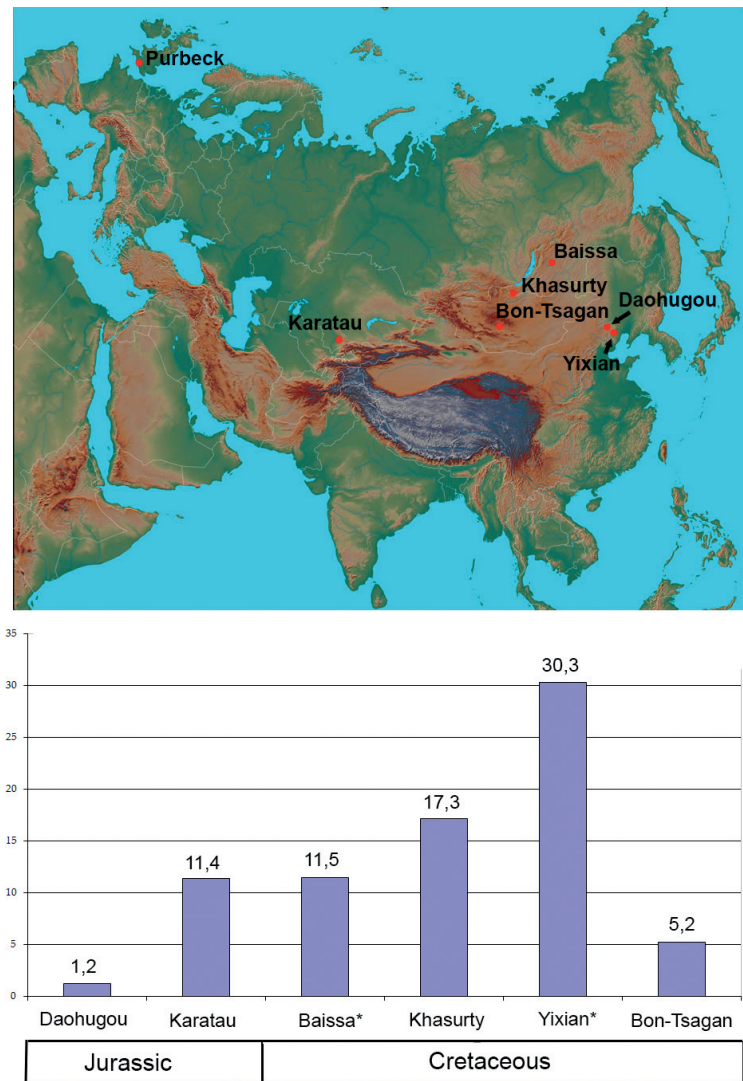
Besides *Mesypochrysa*, up to now, the only other well-established genus of Mesozoic Limaiinae was *Baisochrysa* Makarkin, 1997. This is known from at least three localities: Karatau, Upper Jurassic of Kazakhstan (Khrarov *et al.* 2016); Baissa, Lower Cretaceous of Transbaikalia (Makarkin 1997); and the Yixian Formation, Lower Cretaceous of China (V. N. Makarkin, pers. comm. 2015) However, *Baisochrysa* is

far less abundant than *Mesypochrysa*. Monotypic *Cretachrysa* Makarkin, 1994 from the Upper Cretaceous (Campanian) of the Obeshchayushchiy locality (Russia), the only known Upper Cretaceous green lacewing, was described based on a fragmentary forewing. This fact does not allow subfamily determination with certainty, but *Cretachrysa* cannot be excluded from Limaiinae (Makarkin 1994).

The Mesozoic record of immature stages of Chrysopidae is scarce. Newly-hatched lacewing larva described from Campanian Canadian amber as Chrysopidae (Engel & Grimaldi 2008) belongs to Berothidae, according to Wedmann *et al.* (2013). Family assignment of the highly derived chrysopoid larva *Hallucinochrysa diogenesi* Pérez-de la Fuente *et al.*, 2012 from Lower Cretaceous amber of Spain is unclear (Pérez-de la Fuente *et al.* 2012). Recently, chrysopoid larvae were reported from Lower Cretaceous Lebanese and mid-Cretaceous Burmese amber (Wang *et al.* 2016). Interestingly, with the exception of 12 larvae, the majority of more than 100 chrysopoid specimens found in Burmese amber do not display morphology associated with debris-carrying behaviour typical for immature stages of modern green lacewings (Wang *et al.* 2016). It is possible that the absence of adaptations for debris-carrying camouflage is an ancestral condition, which could have been retained in Limaiinae (Khrarov *et al.* 2016), so some naked larvae from Burmese amber may belong to this subfamily. However, the taxonomic affiliation of the material discussed by Wang *et al.* 2016 needs further examination. For example, the specimen NIGP164055 from Burmese amber, which is labelled as “chrysopoid adult” in Wang *et al.* 2016 (fig. S1, C in Supplementary Materials) in fact belongs to Osmylidae (subfamily Gumillinae).

The subfamily Limaiinae crossed the Cretaceous–Paleogene boundary but, after their heyday in the Mesozoic era, this group, was soon superseded by extant subfamilies of Chrysopidae, perhaps under pressure from ant predation (Khrarov *et al.* 2016). The last member of Limaiinae was *Protochrysa* Willmann & Brooks, 1991, known from the Lower Eocene of Europe and North America (Makarkin & Archibald 2013).

This present paper describes and discusses a new assemblage of Chrysopidae (all Limaiinae) from the Lower Cretaceous of Khasurty in Transbaikalia. More than 3,000 fossil insects have been collected in this locality (Sinitshenkova 2011); amongst them are 52 specimens of Neuroptera. The fauna of Neuroptera



**Figure 1** (Above) Mesozoic localities of Eurasia where Chrysopidae have been found. (Below) percentage of specimens of Chrysopidae to all Neuroptera in Mesozoic localities of Eurasia (\*data from Makarkin *et al.* 2012; statistics for the Purbeck Limestone Group are not available).

is not very diverse and is dominated by lacewings with a ‘cellularised’ venation pattern somewhat similar to that of Mesochrysopidae or Gumillinae (Osmylidae). A few Berothidae and psychopsoid lacewings (perhaps Polystoechotidae) have also been found in Khasurty, each represented by 1–2 specimens. Chrysopidae, with nine specimens, make up 17.3 % of all Neuroptera. This is one of the highest percentages of green lacewings in Mesozoic localities (Fig. 1). Based on this material, *Aberrantochrysa* gen. nov. with two species, is erected herein, the third Mesozoic genus to be placed in Limaiinae with certainty. Besides that, two new species of *Mesypo-chrysa* are described from Khasurty, in addition to the 17 already known species of this genus (see list in Khramov *et al.* 2016). Thus, Khasurty is the seventh Eurasian locality where *Mesypo-chrysa* has been recorded.

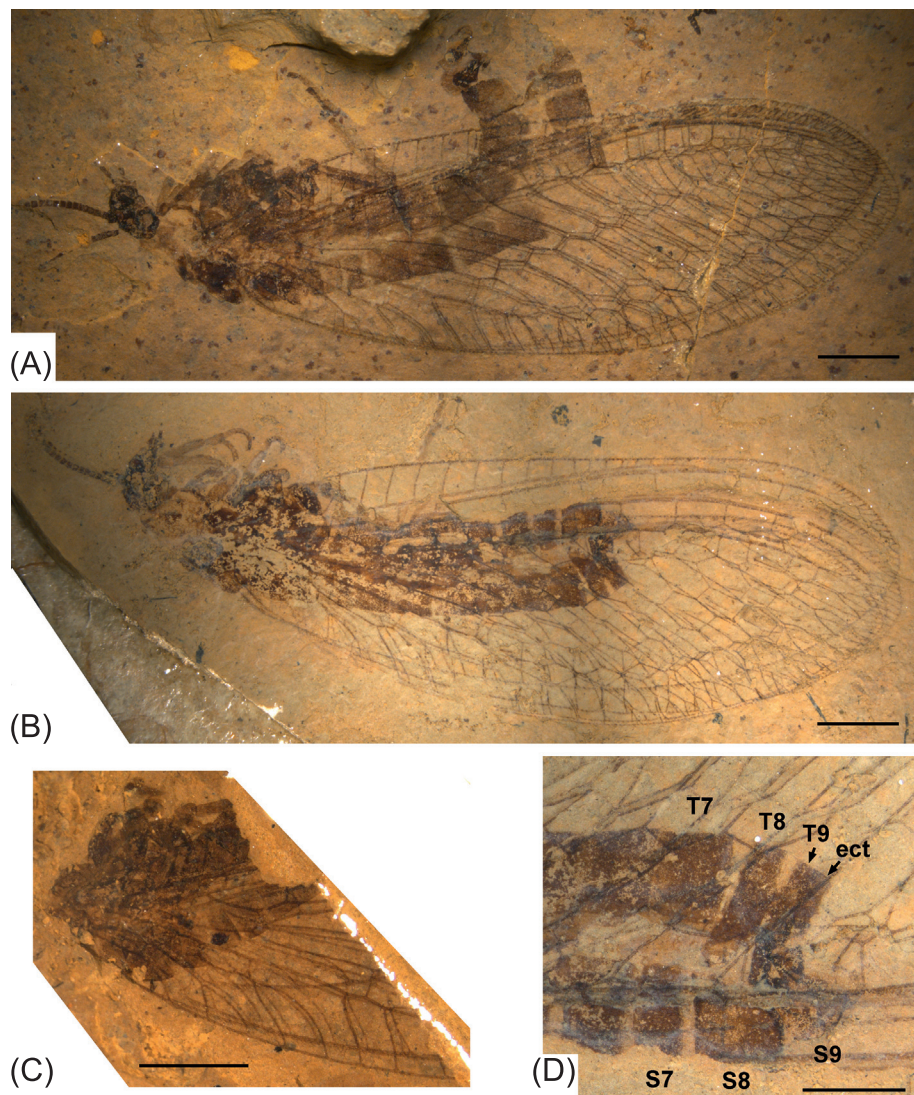
## 1. Material and methods

The Khasurty locality, the origin of the material, is situated in the Zakamenskii District of Buryat Republic, 25 km east of Zakamensk, close to the Mongolia–Russia border (50°20′59.98″N; 103°37′36.93″E). Insect-bearing deposits are

exposed along a hillside; the length of the outcrop is 15–20 m. Plant remains are rare in Khasurty; most of them are seeds and mosses (Ignatov & Shcherbakov 2011). Insects are overwhelmingly in the majority amongst all fossils from this locality. The age of the deposits was preliminary determined as the lowermost part of Lower Cretaceous, on the base of insect fauna composition (Sinitshenkova 2011; Kopylov 2012); but see discussion below.

Material was collected during three expeditions undertaken by the Laboratory of Arthropods of the Borissiak Palaeontological Institute. The expeditions were headed by D. E. Shcherbakov (in 2004) and D. S. Kopylov (in 2009 and 2014). The present author participated in the 2009 expedition. All specimens described below are housed at the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow.

The traditional nomenclature of wing venation is used following Adams (1967): C = costa; Sc = subcosta; R = radius; R1 = first branch of R; Rs = radial sector; Rsl = most basal branch of Rs; M = media; MA = media anterior; MP = media posterior; MP1 = anterior branch of MP; MP2 = posterior branch of MP; Cu = cubitus; CuA = cubitus anterior; CuP = cubitus posterior; A1–A3 = first to third anal



**Figure 2** *Mesypochrysa cannabina* sp. nov. (Chrysopidae): (A) holotype, PIN 5340/2005; (B) paratype, PIN 5026/1087, male; (C) paratype, PIN 5340/2009; (D) PIN 5026/1087, male terminalia. Abbreviations: ect = ectoproct; S = sternite; T = tergite. Scale bars = 2 mm (A–C); 1 mm (D).

veins; im = basal intramedian cell; 2m–cu = second cross-vein connecting MP and CuA; 2m–cu cell is wing area posterior to cross-vein 2m–cu and bounded by CuA and MP1; 1cua–cup and 2cua–cup = proximal and distal cross-veins connecting CuA and CuP.

## 2. Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Chrysopidae Schneider, 1851

Subfamily Limaiinae Martins-Neto & Vulcano, 1989

Genus *Mesypochrysa* Martynov, 1927

*Mesypochrysa cannabina* sp. nov.

(Figs 2, 3)

**Holotype.** PIN 5340/2005, complete insect. Lower Cretaceous, Khasurty locality, Zakamensk District, Buryatia, Russia.

**Paratypes.** PIN 5026/1087, complete insect, male; PIN 5340/2009, basal part of wings.

**Derivation of name.** After cannabis plantations grown by local people close to the fossil site.

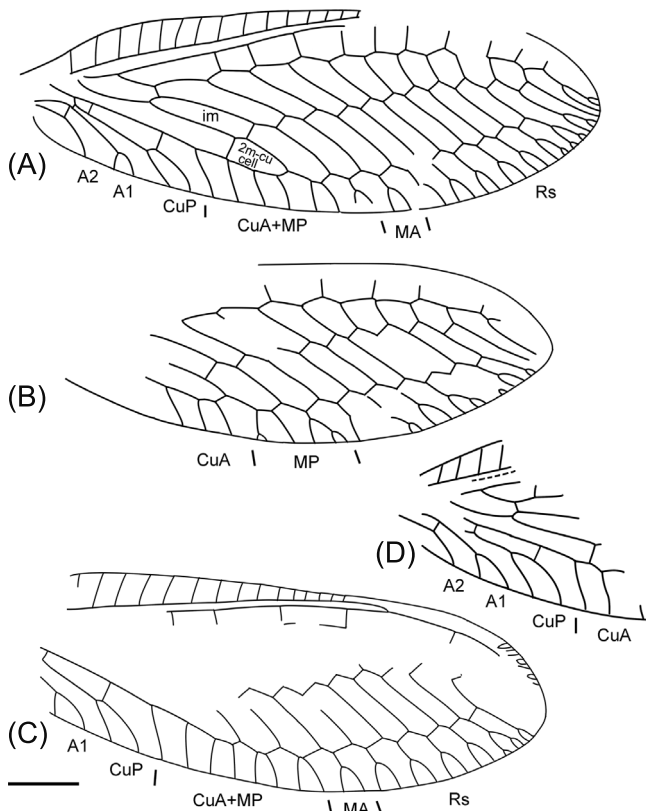
**Diagnosis.** Forewing: CuA and MP with six unforked branches, upper branch of CuP fork smooth, A1 with small or medium-sized terminal fork, A2 simple.

**Description. Forewing.** Wing length 16 mm, width 5.5 mm; Rs with ten branches, most of them with simple terminal fork; Rs cells of second row elongated (length-to-width ratio *c.*4.5:1); length ratio of 2m–cu cell to im cell is more than 1:2.

**Hindwing.** Wing length *c.*14 mm, width 5 mm; Rs with nine branches, some of them terminally twice forked; Rs cells of second row elongated (length-to-width ratio *c.*4:1).

**Male terminalia.** Sternite 8 twice as wide as sternite 7; tergite 8 narrow, ectoproct almost not separated from tergite 9; tergite 7 as wide as sternite 8.

**Remarks.** *M. cannabina* closely resembles *M. cf. chrysopoides* from the Lower Cretaceous Yixian Formation (*sensu* Nel *et al.*, 2005) in venation. The only characters which distinguish *M. cannabina* from this species are the unforked A2 in the forewing and the smaller size (forewing length of *M. cf. chrysopoides* is 24.5 mm) and more elongated cells of Rs of the second row in both fore- and hindwing. In having six unforked branches of CuA and MP in the forewing, *M. cannabina* differs from all other species for which this character is known, except *M. magna*



**Figure 3** *Mesypochrysa cannabina* sp. nov. (Chrysopidae): (A) holotype, PIN 5340/2005, forewing; (B) holotype, PIN 5340/2005, hindwing; (C) paratype, PIN 5026/1087, forewing; (D) paratype, PIN 5340/2009, forewing. Scale bar = 2 mm.

Makarkin, 1997, *M. intermedia* Panfilov, 1980 and *M. miniscula* (Ren & Guo, 1996). *M. cannabina* can be distinguished from these three species by its forked A1 in the forewing. In addition, *M. cannabina* differs from *M. magna* in the greater length ratio of the 2m–cu cell to the im cell in its forewing; and from *M. miniscula* in its more numerous Rs branches and greater size.

From the rest of the species, *M. cannabina* differs in the following characters: from *M. polyclada* Panfilov, 1980 in the less terminally branched forewing branches of Rs; from *M. minuta* Jepson *et al.*, 2012 and *M. reducta* Panfilov, 1980 in the more numerous branches of Rs in its hindwing; from *M. falcata* Makarkin, 1997 in the less numerous branches of Rs in its hindwing; and from *M. minima* Makarkin, 1997 in the narrower and more elongated cells of Rs in its hindwing. *M. cannabina* is only the third known Mesozoic green lacewing with male Terminalia; previously they have been reported only for *Mesypochrysa* sp. from Karatau and for *Mesypochrysa cf. intermedia* from Daohugou (Khramov *et al.* 2016). Compared to them, *M. cannabina* possesses a much broader sternite 8 and a less discernible boundary between tergite 9 and the ectoproct.

*Mesypochrysa naranica* sp. nov.  
(Fig. 4)

**Holotype.** PIN 5340/2013, nearly complete insect, Lower Cretaceous, Khasurty locality, Zakamensk District, Buryatia, Russia.

**Derivation of name.** After Naran, the god of the Sun in Buryat mythology.

**Diagnosis.** Forewing: CuA and MP with seven unforked branches; cross-vein 1cua–cup situated close to fork of CuP; upper branch of CuP with sharp bend; A1 terminally forked.

**Description.** Forewing. Wing length 16.5 mm, width 5.5 mm; Rs with nine branches, half of them terminally twice-forked; length ratio of 2m–cu cell to im cell is about 1:2.

**Remarks.** At a first glance, *M. naranica* looks similar to *M. cannabina* from the same locality. However, they should be treated as two different species, for three reasons at least. First, *M. naranica* has cross-vein 1cua–cup situated very distally in the forewing, close to the fork of CuP, whilst in *M. cannabina*, as well all other species, the cross-vein 1cua–cup is situated more proximally, close to the point of connection of CuA and CuP.

Secondly, *M. naranica* possesses seven unforked branches of CuA and MP in its forewing, in contrast to the six in the forewing of *M. cannabina*.

Thirdly, the upper branch of the CuP fork in the forewing of *M. naranica* forms an angle at the point of conjunction with cross-vein 2cua–cup, whereas this vein is smooth in *M. cannabina*.

*M. naranica* differs from the rest of the species in the distal position of the 1cua–cup cross-vein, and in having seven unforked branches of CuA and MP. It shares the latter character only with *M. curvimedia* and *M. angustialata*, but they appear not to have forked A1 in the forewing. Because of insufficiently preserved hindwing venation, it is difficult to compare *M. naranica* with species known only from hindwings.

Genus *Aberrantochrysa* gen. nov.

**Type species.** *Aberrantochrysa buryatica* sp. nov.

**Derivation of name.** From the genus name *Chrysopa* and ‘aberrant’, which indicates untypical, with respect to the venation pattern.

**Diagnosis.** Medium-sized insects (forewing length *c.* 17–20 mm).

**Forewing.** Two gradate series of cross-veins present in RS area; inner gradate series irregular, with some cross-veins violating stair-step order; outer gradate series well-arranged; Rs branches smooth, anal veins branched terminally, if A1 forked once; CuP with three branches.

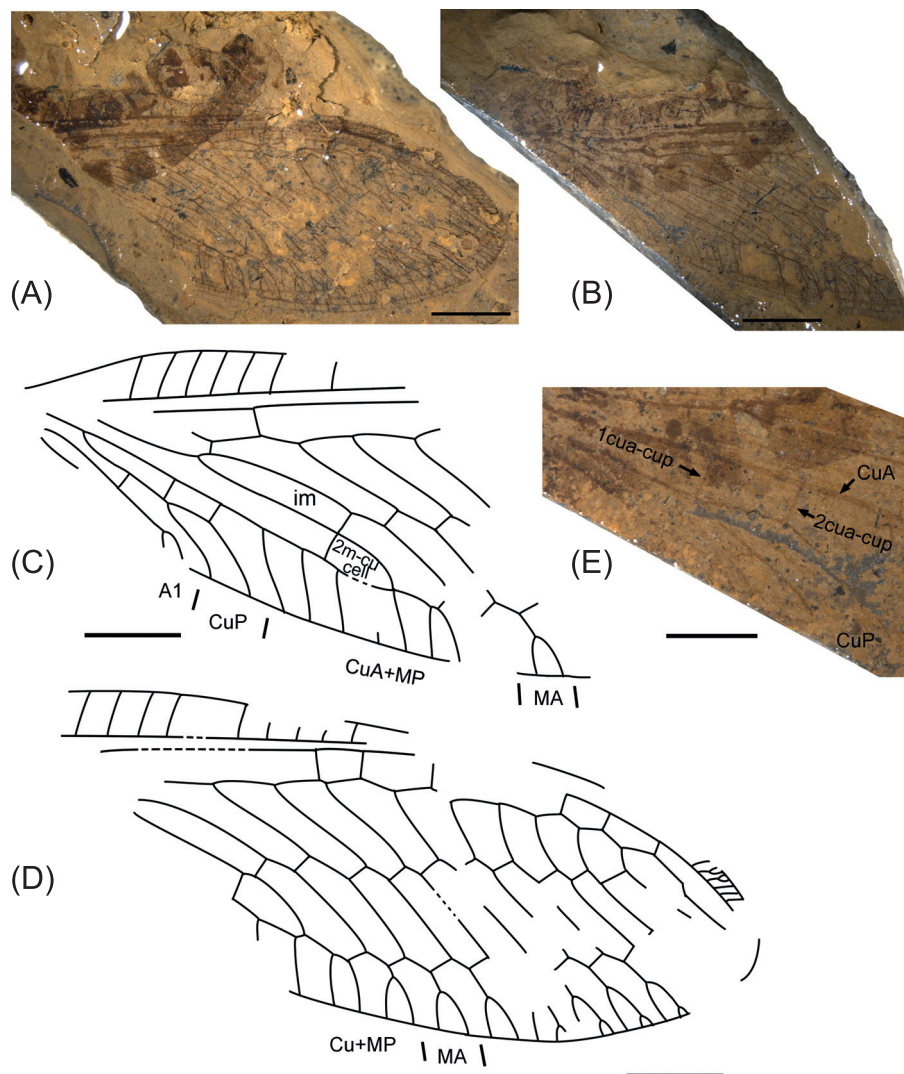
**Hindwing.** Two gradate series of cross-veins present in RS area, inner gradate series more arranged than one in forewing; Rs branches more zigzagged than in forewing; CuP with poorly developed terminal fork.

**Composition.** *Aberrantochrysa buryatica* sp. n. and *Aberrantochrysa pulchella* sp. n.

**Remarks.** *Aberrantochrysa* should be placed to Limaiinae with certainty, because its medial, cubital and anal veins demonstrate all the characteristics typical for this subfamily.

Cross-vein 2m–cu in the forewing of *Aberrantochrysa* runs into the distal part of the im cell, which is an apomorphy of Limaiinae (Makarkin & Archibald 2013). Whilst *Mesypochrysa* and *Baisochrysa* invariably have two branches of CuP in the forewing, *Aberrantochrysa* is special in having a third additional branch of CuP, except for the right forewing of *A. buryatica*. In contrast to the left forewing of the same individual (Fig. 5H), CuP in the right forewing of this species forms a two-branched fork (Fig. 5G), typical for *Mesypochrysa*. It is possible that in that case, the first of the branches of CuP detached from CuP and joined A1, thus making A1 twice-forked. However, if CuP has three branches, A1 is forked only once (Figs 5H, 6B).

The Rs branching pattern of *Aberrantochrysa* seems to be highly plesiomorphic. Rs branches in other fossil and Recent green lacewings are strongly zigzagged, because they run through two or three stair-step gradate series of cross-veins. In the case of *Aberrantochrysa*, only the outer gradate series of cross-veins is well-arranged, whilst the inner gradate series is in a chaotic condition, especially in the forewing. As a result, the Rs branches of *Aberrantochrysa* are almost smooth.



**Figure 4** *Mesypochrysa naranica* sp. nov. (Chrysopidae), holotype, PIN 5430/2013: (A, B) photographs of part and counterpart, the former is reversed; (C) drawing of left forewing; (D) drawing of right forewing; (E) costal area of left forewing. Scale bars = 2 mm (A–D); 1 mm (E).

In conclusion, judging by its venation, *Aberrantochrysa* could be regarded as the most basal member of the family. The high variability in venation between the right and left wings may also indicate the primitiveness of this genus.

*Aberrantochrysa buryatica* sp. nov.  
(Fig. 5)

**Holotype.** PIN 5340/2004, complete insect. Lower Cretaceous, Khasurty locality, Zakamensk District, Buryatia, Russia.

**Derivation of name.** After the Buryatia Republic.

**Diagnosis.** There are two cross-veins between CuP and CuA in the forewing.

**Description. Forewing.** Wing length 18.5 mm, width 6.8 mm; Rs with *c.*9 branches, most of them with simple terminal forks; some cross-veins in Rs area doubled, MP1 can fork before outer gradate series of cross-veins; CuA and MP with eight branches, simple or forked; CuP with two or three terminal branches; length ratio of 2m–cu cell to im cell is 1:2 or more.

**Hindwing.** Wing length *c.*16.5 mm, width 6 mm; Rs with 7–8 branches, some cross-veins in Rs area doubled; CuA with four branches, forked or simple; CuA and MP connected by 1–2 cross-veins, A1 forked.

**Remarks.** The venation of the species strongly varies between the wings of the same individual. In addition to the variation in CuP branching discussed above, MP1 is also variable. In the right wing, MP1 is forked before the outer gradate series of cross-veins (Fig. 5D, G), which is untypical for green lacewings, whilst in the left wing, MP1 runs as usual (Fig. 5H). The number of branches of CuA and MP is the same in the opposite fore- and hindwings, but in one wing they may be simple; in another, terminally forked. One wing may have doubled cross-veins in Rs area, whilst the opposite one may not.

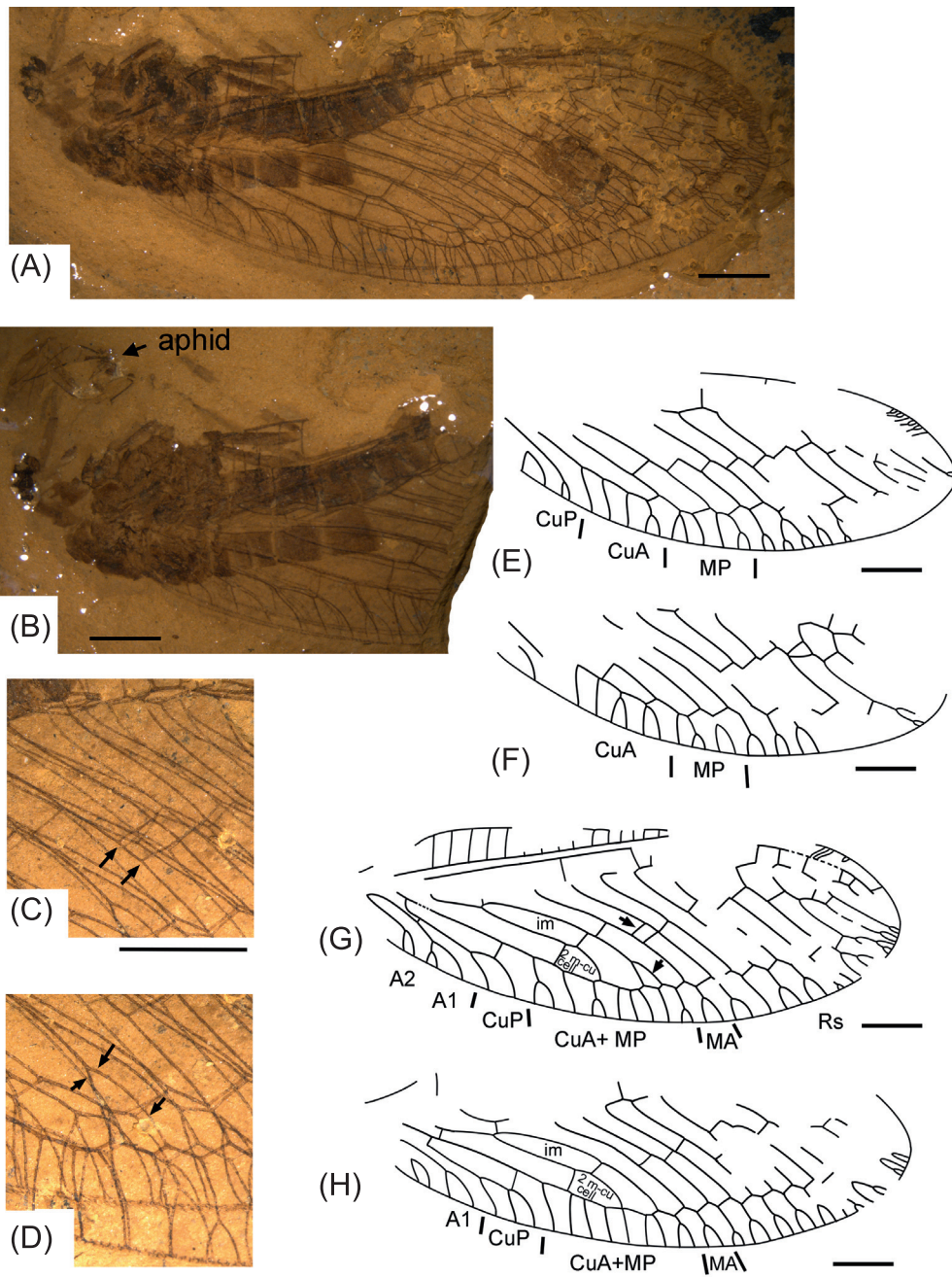
*Aberrantochrysa pulchella* sp. nov.  
(Fig. 6A, B, C)

**Holotype.** PIN 5026/815, complete insect. Lower Cretaceous, Khasurty locality, Zakamensk District, Buryatia, Russia.

**Derivation of name.** From ‘pulchellus’, Latin for beautiful.

**Diagnosis.** There are three cross-veins between CuP and CuA in the forewing.

**Description. Forewing.** Length as preserved 14 mm. One of the basal flagella is cone-shaped (flagella are cylindrical in antenna of *Mesypochrysa*, Fig. 6D); pronotum with U-like white pattern; mesothorax with X-like white pattern; meta-thorax uniformly dark; CuA and MP with more than six



**Figure 5** *Aberrantochrysa buryatica* gen. nov. et sp. nov. (Chrysopidae), holotype, PIN 5340/2004: (A, B) photographs of part and counterpart, the latter is reversed; (C) enlarged area of wings, double cross-veins marked by arrows; (D) enlarged area of wings, fork of MP1 marked by arrows; (E) drawing of right hindwing; (F) drawing of left hindwing; (G) drawing of right forewing; (H) drawing of left forewing. Scale bars = 2 mm (A–C, E–H); 1 mm (D).

branches; an additional cross-vein cua–cup present; second and third branches of CuP originates from common stem.

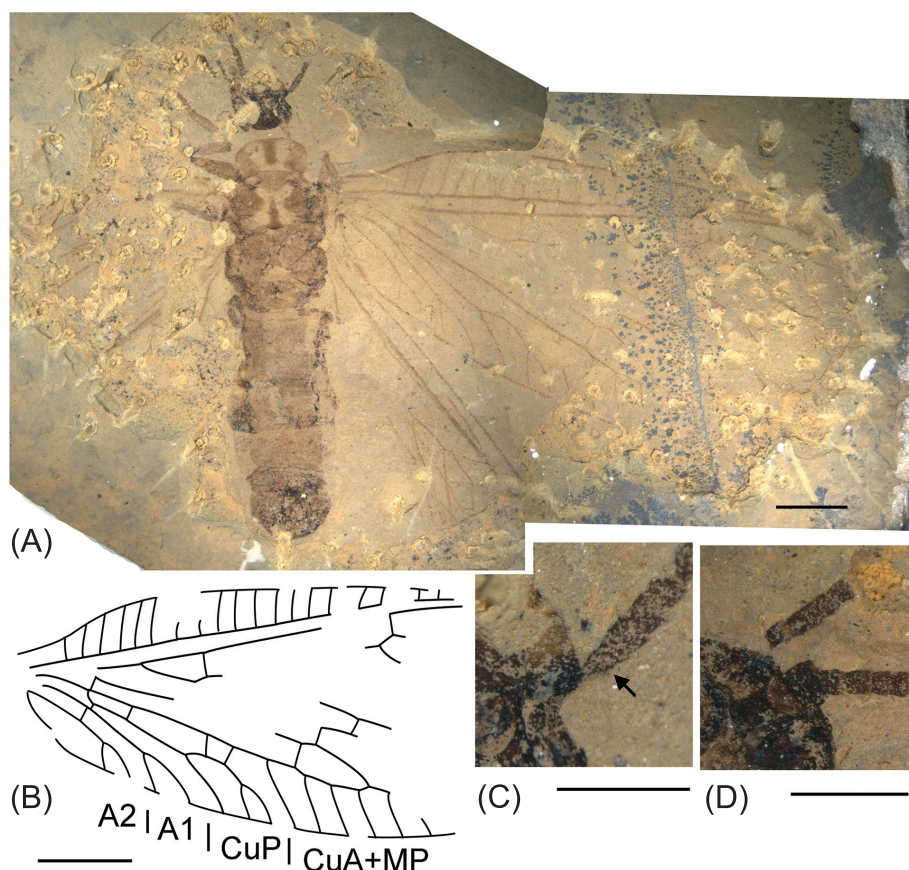
**Remarks.** *A. pulchella* can be distinguished from *A. buryatica* by the presence of an additional cross-vein between CuP and CuA.

### 3. Discussion

All green lacewings from Khasurty belonging to *Mesypochrysa* are characterised by possessing a terminally-forked A1. Such a condition is rather rare in this genus, most species of which possess a simple, unforked A1. There are only three members of *Mesypochrysa* with a forked A1: *M. chrysopoides* Pono-

marengo, 1992 from the Bon-Tsagan locality (Mongolia); and *M. cf. chrysopoides sensu Nel et al.*, 2005 and *M. polyneura*, both from the Yixian Formation. The age of the insect-bearing deposits of Bon-Tsagan is considered to be Barremian–Aptian (Rasnitsyn & Zherikhin 2002), which is nearly equal to the age accepted for the Yixian Formation (Makarkin *et al.* 2012). The presence of species of *Mesypochrysa* with a forked A1 may indicate that Khasurty is of the same age.

As mentioned above, *M. cannabina* is particularly similar to *M. cf. chrysopoides sensu Nel et al.*, 2005 from the Yixian Formation. This contradicts previous conclusions, according to which deposits at Khasurty were considered to be lowermost Cretaceous (Kopylov 2012). Recently, it has also been shown, on the base of ichneumonid wasps, that the Khasurty



**Figure 6** (A–C) *Aberrantochrysa pulchella* gen. nov. et sp. nov. (Chrysopidae), holotype, PIN 5026/815: (A) photo of complete specimen; (B) drawing of right forewing; (C) antenna, cone-shaped flagellum marked by arrow. (D) *Mesypochrysa cannabina* sp. nov., holotype, PIN 5340/2005, antenna. Scale bars = 2 mm (A, B); 1 mm (C, D).

deposits may not be as old as previously thought (Kopylov & Zhang 2015). It is worth noting that the species of *Mesypochrysa* from Khasurty do not resemble those from another Transbaikalian locality, Baissa, despite the geographical proximity. None of the species of *Mesypochrysa* from Baissa demonstrate terminally-forked veins in the forewings, but at least two of them possess a small 2m–cu cell compared to the im cell (Makarkin 1997), which is not the case for species from Khasurty. Perhaps the dissimilarity of the green lacewing assemblages from these two Transbaikalian localities can be explained by the difference in age: the Khasurty deposits appear to be younger than the Valanginian–Hauterivian Zaza Formation (Zherikhin *et al.* 1999), from which the insects were found at Baissa.

In relation to the percentage of Chrysopidae to all Neuroptera, the Khasurty locality stands in second place after the Yixian Formation (Fig. 1). This can perhaps be explained by a high number of aphids, which are the primary food source for green lacewing larvae. Aphids are the most common fossil insects in Khasurty, and they are even present on the rock slabs with green lacewing specimens (see Fig. 5B).

#### 4. Acknowledgements

The research was supported by RFFI grant No. 16-04-01498 and PalSIRP Sepkoski Grant-2015.

#### 5. References

Adams, P. A. 1967. A review of the Mesochrysinæ and Nothochrysinæ (Neuroptera: Chrysopidae). *Bulletin of the Museum of Comparative Zoology* **135**, 215–38.

- Brooks, S. J. & Barnard, P. C. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). *Bulletin of the British Museum of Natural History, Entomology* **59**, 117–286.
- Engel, M. S. & Grimaldi, D. A. 2008. Diverse Neuroptera in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). *Nova Supplementa Entomologica* **20**, 1–86.
- Greve, L. & Kobro, S. 1998. Preliminary data on abundance of phototactic Neuroptera and Raphidioptera in SE Norway as indicated by light-trap catches. *Acta Zoologica Fennica* **209**, 119–20.
- Ignatov, M. S. & Shcherbakov, D. E. 2011. Lower Cretaceous mosses from Khasurty (Baikal Area of South Siberia). *Arctoa* **20**, 19–42.
- Jepson, J. E., Makarkin, V. N. & Coram, R. A. 2012. Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group of southern England. *Cretaceous Research* **34**, 31–47.
- Khranov, A. V., Liu, Q., Zhang, H. & Jarzembowski, E. A. 2016. Early green lacewings (Insecta: Neuroptera: Chrysopidae) from the Jurassic of China and Kazakhstan. *Papers in Palaeontology* **2**, 25–39.
- Khranov, A. V. & Makarkin, V. N. 2015. New fossil Osmolyptochrysoptera (Neuroptera) from the Early/Middle Jurassic of Kyrgyzstan, Central Asia. *Zootaxa* **4059**, 115–32.
- Kopylov, D. S. 2012. New Species of Praeichneumonidae (Hymenoptera, Ichneumonidae) from the Lower Cretaceous of Transbaikalia. *Paleontological Journal* **46**, 66–72.
- Kopylov, D. S. & Zhang, H. 2015. New ichneumonids (Insecta: Hymenoptera: Ichneumonidae) from the Lower Cretaceous of north China. *Cretaceous Research* **52**, 591–604.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, Vol. 1, 10th edn. Holmiae: Laurentii Salvii. 824 pp.
- Makarkin, V. N. 1994. Upper Cretaceous Neuroptera from Russia and Kazakhstan. *Annales de la Société entomologique de France* **30**, 283–92.
- Makarkin, V. N. 1997. Fossil Neuroptera of the Lower Cretaceous of Baissa, East Siberia. Part 3. Chrysopidae. *Spixiana* **20**, 107–18.
- Makarkin, V. N., Yang, Q. Peng, Y.-y. & Ren, D. 2012. A comparative overview of the neuropteran assemblage of the Lower Cretaceous Yixian Formation (China), with description of a

- new genus of Psychopsidae (Insecta: Neuroptera). *Cretaceous Research* **35**, 57–68.
- Makarkin, V. N. & Archibald, S. B. 2013. A diverse new assemblage of green lacewings (Insecta, Neuroptera, Chrysopidae) from the Early Eocene Okanagan Highlands, western North America. *Journal of Paleontology*, **87**, 123–46.
- Martins-Neto, R. G. & Vulcano, M. A. 1989. Neuropteros (Insecta, Planipennia) da Formação Santana (Cretáceo Inferior), Bacia do Araripe, Nordeste do Brasil. 1. Família Chrysopidae. *Anais Academia Brasileira de Ciencia* **60**, 189–201.
- Martynov, A. V. 1927. Jurassic fossil insects from Turkestan. Order Neuroptera. *Izvestia Akademii Nauk SSSR* **21**, 764–68.
- Nel, A., Delclós, X. & Hutin, A. 2005. Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Bulletin de la Société Entomologique de France* **41**, 29–69.
- Panfilov, D. V. 1980. [New representatives of lacewings (Neuroptera) from the Jurassic of Karatau.] In Topachevskiy, V. A. (ed.) *Mesozoic fossil insects*, 82–111. Kiev: Nauka Dumka. [In Russian.]
- Peng, Y.-y., Makarkin, V. N., Wang, X.-d. & Ren, D. 2011. A new fossil silky lacewing genus (Neuroptera: Psychopsidae) from the Early Cretaceous Yixian Formation of China. *ZooKeys* **130**, 217–28.
- Penny, N. D., Arias, J. R. & Armistead J. S. 2007. Seasonal Emergence of Neuroptera in Fairfax County, Virginia. *Proceedings of the California Academy of Sciences* **58**, 7–19.
- Pérez-de la Fuente, R., Delclós, X., Peñalver, E., Speranza, M., Wierzbos, J., Ascaso, C. & Engel, M. S. 2012. Early evolution and ecology of camouflage in insects. *Proceedings of the National Academy of Sciences* **109**, 21414–19.
- Ponomarenko, A. G. 1992. New lacewings (Insecta, Neuroptera) from the Mesozoic of Mongolia. *Transactions of the Joint Soviet–Mongolian Paleontological Expedition* **41**, 101–10.
- Rasnitsyn, A. P. & Zherikhin, V. V. 2002. Impression fossils. In Rasnitsyn, A. P. & Quicke, D. (eds) *History of Insects*, 437–44. Dordrecht: Kluwer Academic Publishers. xii + 517 pp.
- Ren, D. & Guo, Z.-g. 1996. On the new fossil genera and species of Neuroptera (Insecta) from the Late Jurassic of northeast China. *Acta Zootaxonomica Sinica* **21**, 461–79.
- Schneider, W. G. 1851. *Symbolae ad Monographiam Generis Chrysopae, Leach. Vratislaviae*: Hirt. 178 pp.
- Sinitshenkova, N. D. 2011. New Stoneflies (Insecta: Perlida = Plecoptera) from the Late Mesozoic Locality Khasurty, Transbaikalia. *Paleontological Journal* **45**, 552–58.
- Steinmann, H. 1964. The *Chrysopa* species (Neuroptera) of Hungary. *Annales Historico-Naturales Musei Nationalis Hungarici* **56**, 257–66.
- Wang, B., Xia, F., Engel, M. S., Perrichot, V., Shi, G., Zhang, H., Chen, J., Jarzembowski, E. A., Wappler, T. & Rust, J. 2016. Debris-carrying camouflage among diverse lineages of Cretaceous insects. *Science Advances* **2**, e1501918.
- Wedmann, S., Makarkin, V. N., Weiserschan, T. & Hörschemeyer, T. 2013. First fossil larvae of Berothidae (Neuroptera) from Baltic amber, with notes on the biology and termitophily of the family. *Zootaxa* **3716**, 236–58.
- Willmann, R. & Brooks, S. J. 1991. Insekten aus der Fur-Formation von Dänemark (Moler, ob. Paleozän/unt. Eozän). 6. Chrysopidae (Neuroptera). *Meyniana* **43**, 125–35.
- Zherikhin, V. V., Mostovski, M. B., Vršanský, P., Blagoderov, V. A. & Lukashevich, E. D. 1999. The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and West Transbaikalia. In Vršanský, P. (ed.) *Proceedings of the First International Palaeontological Conference, Moscow 1998*, 185–91. Bratislava: AMBA projects International.

---

MS received 29 May 2016. Accepted for publication 18 November 2016.