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A comparative overview of the neuropteran assemblage of the Lower Cretaceous Yixian Formation (China), with description of a new genus of Psychopsidae (Insecta: Neuroptera)

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ABSTRACT

Alloepipsychopsis lata gen. et sp. nov. (Psychopsidae) is described from the Barremian Yixian Formation. Mesithoninae is considered as a subfamily of Berothidae, stat. nov., *Baissoleon* as a member of Nymphidae, sit. nov., and *Chimerochrysopa* as Mesochrysopidae, sit. nov. The taxonomic composition of the neuropteran assemblage of this formation (including undescribed material) is summarized. It includes approximately 65 species belonging to 15 families. The assemblage is dominated by Chrysopidae and Ithonidae in terms of number of specimens, while other Lower Cretaceous impression localities are dominated by other families: Psychopsidae (English Purbeck and Wealden; East Siberian Baissa), Mesochrysopidae (Spanish Las Hoyas), and Myrmeleontoidea (Brazilian Crato Formation). The great diversity of Ithonidae and Kalligrammatidae in the Yixian Formation compared with other Cretaceous localities supports the hypothesis of an existence of a refugium of Jurassic terrestrial relicts in East Asia.
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1. Introduction

Fossils of the Yixian Formation belong to the famous Jehol biota that existed in East Asia during the Lower Cretaceous (Zhou et al., 2003; Chang, 2008; Zhang et al., 2010). This formation is distributed in the north-eastern provinces of China (mainly in western Liaoning, Inner Mongolia, and northern Hebei; Wan et al., 2007), but the majority of fossils come from Liaoning. These fossils are mostly beautifully preserved, and represent a wide variety of animal and plant taxa. The most well known of these are the feathered dinosaurs, primitive birds and angiosperms (Chang, 2008, and references therein; O'Connor et al., 2010). The insect fossils are also numerous and diverse (Ren et al., 2010b, and references therein). The geological setting, stratigraphic sections, age, palaeoenvironment, and biota of the Yixian Formation have been described and discussed in many publications (e.g., Ren et al., 1995; Swisher et al., 1999; Barrett, 2000; Ding et al., 2001; Chen et al., 2004, 2005; Fürsich et al., 2007; Jiang and Sha, 2007; Sha, 2007; Chang, 2008; Ren and Makarkin, 2009; Zhang et al., 2010).

The first Neuroptera were described from the Yixian Formation in 1995 (Ren et al., 1995). To date, 23 named neuropteran species (17 genera) belonging to eight families have been recorded: Aetheogrammatidae, Ascalochrysidae, Berothidae, Chrysopidae, Kalligrammatidae, Mesochrysopidae, Myrmeleontidae, and Psychopsidae (Ren and Guo, 1996; Ren and Yin, 2002; Ren, 2003; Nel et al., 2005; Ren and Engel, 2008a,b; Ren and Makarkin, 2009; Yang et al., 2009; Ren et al., 2010a; Peng et al., 2011). The family Osmylidae was recorded from this formation erroneously: the osmylid assignment of two genera turned out to be incorrect (Ren et al., 1995; Ren and Guo, 1996); one of them is considered here to belong to Ithonidae, the other is "familia incertae sedis" (Table 1). Undescribed material contains 144 neuropteran specimens (including a specimen described herein) belonging to fifteen families; among them are Ithonidae, Mantispidae, Osmylidae, Palaeoleontidae, and Nymphidae.

Herein we describe a new genus and species of Psychopsidae from the Yixian Formation, and summarize the available data on the taxonomic composition of the neuropteran assemblage from the formation (including undescribed material), and compare it with those of other Lower Cretaceous impression localities (especially, the English Purbeck and Wealden, the Spanish Las Hoyas, and the East Siberian Baissa).

2. Material and methods

The vast majority of the 167 neuropteran specimens come from the Huangbanjigou locality (Table 2); five undescribed specimens

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Table 1
List of the described taxa of Neuroptera from the Yixian Formation, northeast China. All species were collected from the Huangbanjigou locality except *Yanosmylus rarivenatus* which is from Gaositai.

	Family	Species	References
1	Berothidae	*Oloberotha sinica* Ren and Guo, 1996	Ren and Guo, 1996
2	Chrysopidae	*Mesypochrysa* cf. *chrysopoides* Ponomarenko, 1992	Nel et al., 2005
3		*Lembochrysa miniscula* Ren and Guo, 1996	Ren and Guo, 1996
4		*Lembochrysa polyneura* Ren and Guo, 1996	Ren and Guo, 1996
5		*Paralembochrysa splendida* Nel et al., 2005	Nel et al., 2005; Ren and Makarkin, 2009
6	Mesochrysopidae	*Tachinymphes delicatus* (Ren and Yin, 2002)	Ren and Yin, 2002; Nel et al., 2005
7		*Tachinymphes magnificus* Nel et al., 2005	Nel et al., 2005
8		*Mesascalaphus yangi* Ren in Ren et al., 1995	Ren et al., 1995
9		*Longicellochrysa yixiana* Ren et al., 2010	Ren et al., 2010a
10	Ascalochrysidae	*Ascalochrysa megaptera* Ren and Makarkin, 2009	Ren and Makarkin, 2009
11	Kalligrammatidae	*Sophogramma eucallum* Ren and Guo, 1996	Ren and Guo, 1996
12		*Sophogramma papilionaceum* Ren and Guo, 1996	Ren and Guo, 1996
13		*Sophogramma plecophlebium* Ren and Guo, 1996	Ren and Guo, 1996
14		*Sophogramma lii* Yang et al., 2009	Yang et al., 2009
15		*Kalligramma liaoningense* Ren and Guo, 1996	Ren and Guo, 1996
16		*Limnogramma mirum* Ren, 2003	Ren, 2003
17		*Oregramma gloriosum* Ren, 2003	Ren, 2003
18	Aetheogrammatidae	*Aetheogramma speciosum,* Ren and Engel, 2008	Ren and Engel, 2008a
19	Psychopsidae	*Undulopsychopsis alexi* Peng et al., 2011	Peng et al., 2011
20		*Alloepipsychopsis lata* gen. et sp. nov.	This paper
21	Myrmeleontidae	*Choromyrmeleon othneius* Ren and Guo, 1996	Ren and Guo, 1996
22		*Choromyrmeleon aspoeckorum* Ren and Engel, 2008	Ren and Engel, 2008b
23	Ithonidae	*Lasiosmylus newi* Ren and Guo, 1996	Ren and Guo, 1996
24	*Familia incertae sedis*	*Yanosmylus rarivenatus* Ren in Ren et al., 1995	Ren et al., 1995

are from the Dawangzhangzi and Dakangpu localities; all from Liaoning Province. Thirty-one undescribed specimens were collected near Liutiaogou Village (Ningcheng City) and Nanyingpan Village (Duolun County) in Inner Mongolia; one specimen is from the Gaositai locality in Hebei Province. All are deposited in Capital Normal University, Beijing, China (CNUB), except for one psychopsid specimen, which is housed in the Liaoning Chaoyang Bird Fossils National Geopark, China.

The majority of photographs were taken using a Nikon Digital Camera DXM1200C attached to a Leica MZ12.5 stereomicroscope. Other photographs were taken using a Nikon D100 Digital Camera. The line drawings were prepared with CoralDraw 12 graphics software with the aid of Adobe Photoshop CS2.

Table 2
The number of specimens of Neuroptera collected from different localities of the Yixian Formation, northeast China. BAI, Baitugou; DAK, Dakangpu; DAW, Dawangzhangzi; GAO, Gaositai; HUA, Huangbanjigou; LIU, Liutiaogou.

	Family	Localities						Total
		HUA	DAW	DAK	LIU	BAI	GAO	
1	Chrysopidae	33		–	5	9	–	47
2	Ithonidae	27		–	4		–	31
3	Psychopsidae	11	2		3		–	16
4	Kalligrammatidae	12		–	–	–	–	12
5	Mantispidae	11		–	–	–	–	11
6	Osmylidae	3	1		–	5	–	9
7	Mesochrysopidae	4		1	–	–	–	5
8	Nymphidae	2		–	3		–	5
9	Aetheogrammatidae	3	1		–	–	–	4
10	Myrmeleontidae	4		–	–	–	–	4
11	Ascalochrysidae	3		–	–	–	–	3
12	Berothidae	3		–	–	–	–	3
13	Palaeoleontidae	1		–	–	–	–	1
14	“Cratochrysidae”	–		–	–	1	–	1
15	“Familia nova A”	–		–	–	1	–	1
	Total	117	4	1	15	16	–	153
	Neuroptera fam. indet.	9		–	1	3	1	14
	Total	126	4	1	16	19	1	167

We follow the traditional (sensu Wootton, 2003) venational terminology of Comstock (1918) with the recent interpretation of Oswald (1993) and Archibald and Makarkin (2006). Wing vein abbreviations are as follows: C, costa; Sc, subcosta; R, radius; R1, first branch of R; Rs, radial sector; Rs1, most proximal branch of Rs; M, media; MA, media anterior; MP, media posterior; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; 1A–3A, first to third anal veins.

3. Localities

3.1. Huangbanjigou

This locality is situated approximately 21 km south of Beipiao in the western Liaoning Province (see map in Chen et al., 2005, fig. 1). It belongs to the Jianshangou Member (Bed) of the lower Yixian Formation (Wang and Zhou, 2008). The late Barremian age of this fossil-bearing stratum in the Sihetun area (including Huangbanjigou) is considered to be well supported by radiometric dating, from 126.1 ± 1.7 to 124.6 ± 0.1 Ma (Swisher et al., 1999, 2002; Wang et al., 2001b; Chen et al., 2004; Yang et al., 2007), although the uppermost beds of Huangbanjigou locality are early Aptian, 123.3 ± 0.5 – 122.8 ± 1.6 Ma (Wang et al., 2001a; Yang et al., 2007).

3.2. Dawangzhangzi

This locality is situated in Lingyuan County, approximately 180 km southwest of Beipiao in the western Liaoning Province (see map in Taylor et al., 1999, fig. 1). It belongs to the Dawangzhangzi Member (Bed) of the middle Yixian Formation, and is dated as early Aptian, 122.5 ± 0.3 – 122.2 ± 0.2 Ma (Wang and Zhou, 2008).

3.3. Dakangpu

This locality is in Liulongtai Township, Yixian County, Liaoning Province (see map in Shen et al., 1998, fig. 1). The Dakangpu Bed is considered to be equivalent to the Dawangzhangzi Member (Bed)

of the middle Yixian Formation and is dated as early Aptian (Wang and Zhou, 2008; Carpenter and Ishida, 2010).

3.4. Liutiaogou

This locality is close to Liutiaogou Village (Dashuangmiao Town, Ningcheng County, Chifeng City) in Inner Mongolia. Its age is not clear, because radiometric dating is not available. The horizon is thought to be equivalent to either the Jianshangou or Dawangzhangzi Bed (Evans and Wang, 2010).

3.5. Baitugou

The locality is situated near Nanyingpan Village (Sanbeigou Town, Duolun County) in Inner Mongolia. The precise age is unknown. The deposits of this locality "await to be extensively investigated in the future" (Jin et al., 2008, p. 2826).

3.6. Gaositai

The locality is not far from Gaositai Railway Station (Gaositai Town, Chengde City) in Hebei Province. The stratigraphic section of the Yixian Formation at the Gaoshitai locality has been described by Ren et al. (1995, fig. 2–1). The precise age is unknown.

4. Systematic palaeontology

Class: Insecta Linnaeus, 1758
Order: Neuroptera Linnaeus, 1758
Family: Psychopsidae Handlirsch, 1906
Genus *Alloepipsychopsis* gen. nov.

Type and only species. *Alloepipsychopsis lata* gen. et sp. nov.

Derivation of name. Allo- (from Greek *allos*, other), and *-epipsychopsis* (from *Epipsychopsis*, a psychopsid genus-group name), with reference to the similarity of the hind wing venation between the genera.

Diagnosis. May be distinguished from similar genera by larger size (*Pterinoblattina* Scudder, 1885 much smaller), very oblique branches of CuA and CuP, and widely spaced crossveins between Sc, R1, and Rs (these branches clearly at an angle with CuA, CuP, and the crossveins closely spaced in *Epipsychopsis* Makarkin, 2010), and the presence of costal crossveins (absent in *Kagapsychops* Fujiyama, 1978).

Remarks. The wing venation of *Alloepipsychopsis* gen. nov. is most similar to those of *Kagapsychops continentalis* Makarkin, 1994 from the Upper Cretaceous (Turonian) Kzyl-Zhar locality in Kazakhstan, and the two species of *Epipsychopsis* from the Lower Cretaceous Baissa locality in Siberian Transbaikalia (see Makarkin, 1994, fig. 1, and 2010, fig. 2A, B), but is distinguished from them as indicated in the diagnosis. The multi-branched Rs1 as found in this genus is characteristic of the forewing venation of some Cretaceous genera ascribed to Psychopsidae (e.g., *Kagapsychops*, *Embaneura* Zalessky, 1953, *Grammapsychops* Martynova, 1954), but this feature was hitherto unknown in the hind wing.

Alloepipsychopsis lata sp. nov.
Figs. 1, 2

Derivation of name. Latin *latus*, broad, with reference to wider hind wings compared with *Epipsychopsis*.

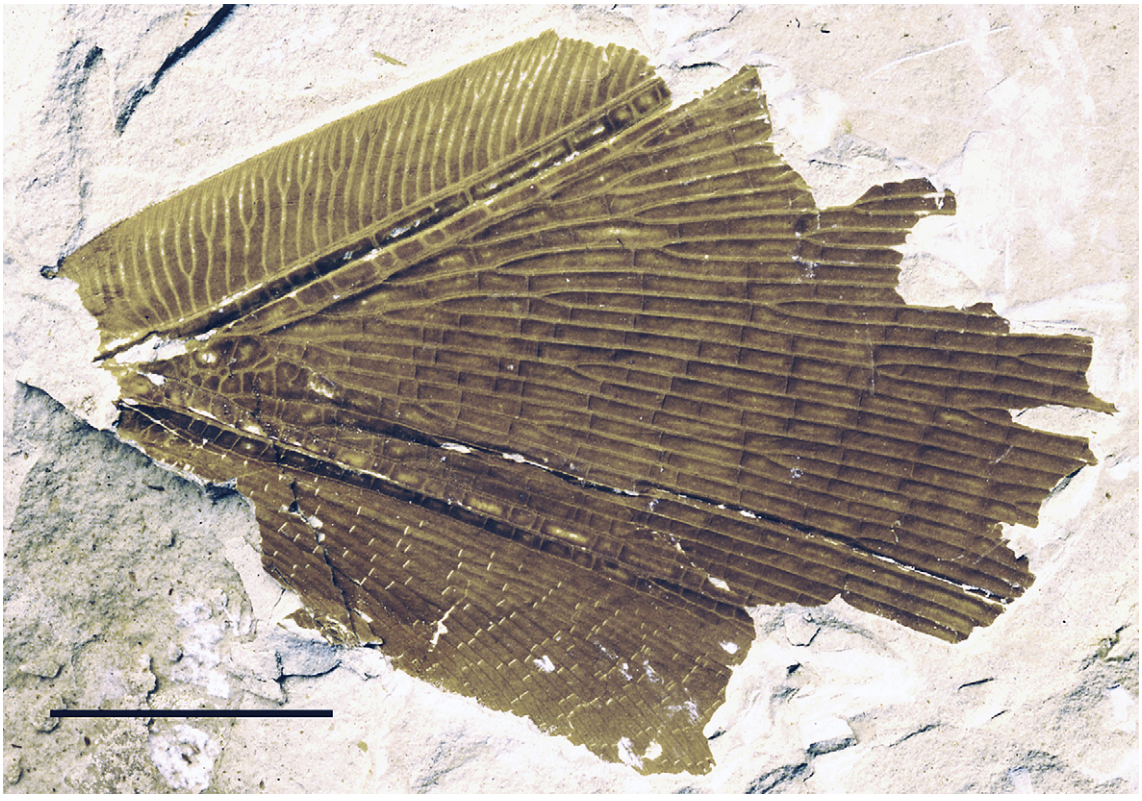

Fig. 1. *Alloepipsychopsis lata* gen. et sp. nov., photograph of the holotype CNU-NEU-LB2011007. Scale bar represents 10 mm.

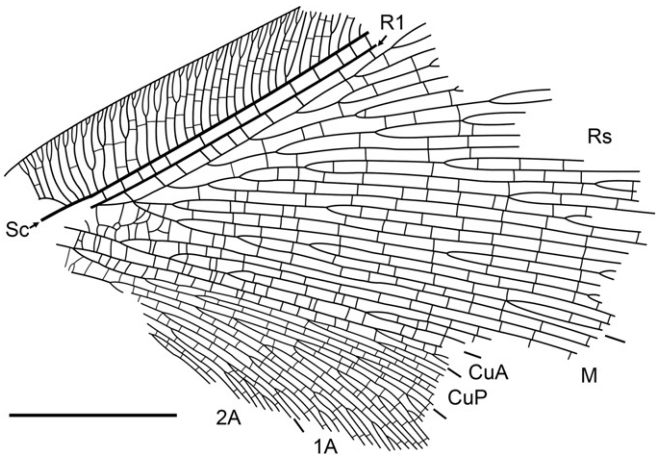

Fig. 2. *Alloepipsychopsis lata* gen. et sp. nov., holotype CNU-NEU-LB2011007, drawing of hind wing. Scale bar represents 10 mm.

Type material. Holotype CNU-NEU-LB2011007, deposited in CNUB. A well-preserved incomplete hind wing, Huangbanjigou locality, Beipiao City, Liaoning Province, China; Early Cretaceous Yixian Formation.

Description. Hind wing broad, probably sub-triangular in shape; preserved length 32 mm (along radius; estimated length about 50 mm); preserved width 27 mm (perpendicular to radius). Trichosors not present on costal margin (other margins not preserved). Costal space equally broad for entire preserved length. Subcostal veinlets closely spaced, all once or twice forked. Humeral veinlet well-developed, recurrent, branched, with at least three distal branches forked once. Costal crossveins connecting subcostal veinlets quite numerous, not forming distinct series; one to three crossveins between each two veinlets (absent between four basalmost veinlets). Subcostal space relatively narrow, with 13 widely, rather irregularly spaced crossveins preserved. Rs originating relatively far from wing base. R1 space (between R1 and Rs) relatively narrow, with 11 widely and irregularly spaced crossveins preserved. Rs with eight preserved branches, of which at least six proximal are dichotomously branched. Rs1 multi-branched, with proximalmost fork located near its origin. M with four anteriorly directed pectinate branches in basal half of wing, all parallel to each other. Basal region between R (then Rs, basal part of Rs1) and M broad, filling with crossveins forming reticulation. Crossveins in radial to medial spaces numerous, forming mainly irregular gradate series. Cu dividing into CuA and CuP relatively far from wing base. CuA distally branched (only basal part of proximalmost branch of CuA preserved). CuP with three preserved very oblique branches, running parallel to CuA and then proximalmost branch of CuA. 1A profusely branched, with anterior trace parallel to CuP, pectinate, with four deep, very oblique branches which fork 1–4 times. 2A well-developed (incompletely preserved). 3A not preserved. Crossveins between branches of CuP, 1A and 2A short, numerous, mostly forming gradate series. Wing colouration uniformly fuscous (appears bright brown), with several small pale patches with blurred outlines in subcostal, radial and medial spaces, especially between M and CuA. Colouration of longitudinal veins pale to brownish, except anal veins which appear darker; costal veinlets paler than longitudinal veins; crossveins pale brownish, except those between branches of CuP, 1A and 2A which appear white, and between subcostal veinlets which appear brownish.

Remarks. The wing is considered to be hind because of the clearly concave CuA; in the forewing this vein is convex (see Makarkin et al., 2009).

5. Taxonomic composition of the neuropteran assemblage of the Yixian Formation

5.1. Chrysopidae

Chrysopids are very common in this formation and clearly dominate the neuropteran assemblage (30.2% of all identified neuropterans). Three genera and four species have been described (Ren and Guo, 1996; Nel et al., 2005), and many specimens are found among undescribed material (Fig. 3C); the majority probably belong to the genera *Lembochrysa* Ren et Guo, 1996 and *Mesypochrysa* Martynov, 1927, but one belongs to *Paralembochrysa* Nel et al., 2005. The venation of the monotypic genus *Paralembochrysa* is peculiar; it was treated as "familia incertae sedis" by Nel et al. (2005), but included in Chrysopidae by Ren and Makarkin (2009). The genus *Mesypochrysa* is widely distributed in the Upper Jurassic–Lower Cretaceous of at least Eurasia; in particular, it is found in the Upper Jurassic Karatau locality in Kazakhstan, the English Purbeck, the Siberian Baissa, and the Mongolian Bon-Tsagaan, and possibly the Crato Formation.

5.2. Ithonidae

Ithonids are particularly diverse in the Yixian Formation, and dominate (together with Chrysopidae) the neuropteran assemblage (20.1% of all identified neuropterans). Four distinct groups of ithonids are represented: (1) the taxa that are very similar to typical Ithonidae characteristic now of the Australia fauna (Fig. 3D); three specimens are known, two from the Liutiaogou locality, and one from Huangbanjigou; (2) the taxa that were previously treated as the family Polystoechotidae, which are now a part of Ithonidae s.l. (Winterton and Makarkin, 2010); these superficially resemble those characteristic of the present-day New World ithonid fauna, especially *Polystoechotes* Burmeister (Fig. 3E); (3) the "rapismatid-like" taxa (Fig. 3F); there is a single forewing which most likely belongs to the genus *Principiala* Makarkin and Menon; previously recorded from the Brazilian Crato Formation and the English Wealden (Makarkin and Menon, 2007; Jepson et al., 2009); (4) a new group that is unknown from the extant fauna (Fig. 3G); these are the most abundant. *Lasiosmylus newi* Ren et Guo belongs to this last group. It was described within Osmylidae (Ren and Guo, 1996) but is here transferred to Ithonidae. This group possesses a rather simplified venation.

5.3. Psychopsidae (s.l.)

Sixteen specimens are found (10.4% of all identified neuropterans), one of which was described by Peng et al. (2011), and the new genus and species described above. The majority of specimens are rather atypical psychopsids, including the species described by Peng et al. (2011). They have a costal space that is strongly narrowed towards the wing apex and few crossveins (Fig. 4E); by these features, they are similar to some specimens from the English Purbeck and Wealden that were assigned to Psychopsidae (Jepson et al., 2009, in press), and to numerous specimens from Baissa. These specimens are tentatively assigned to this family pending more detailed examination.

5.4. Kalligrammatidae

Kalligrammatids are relatively abundant (7.8% of all identified neuropterans) and diverse. Four genera and seven species have

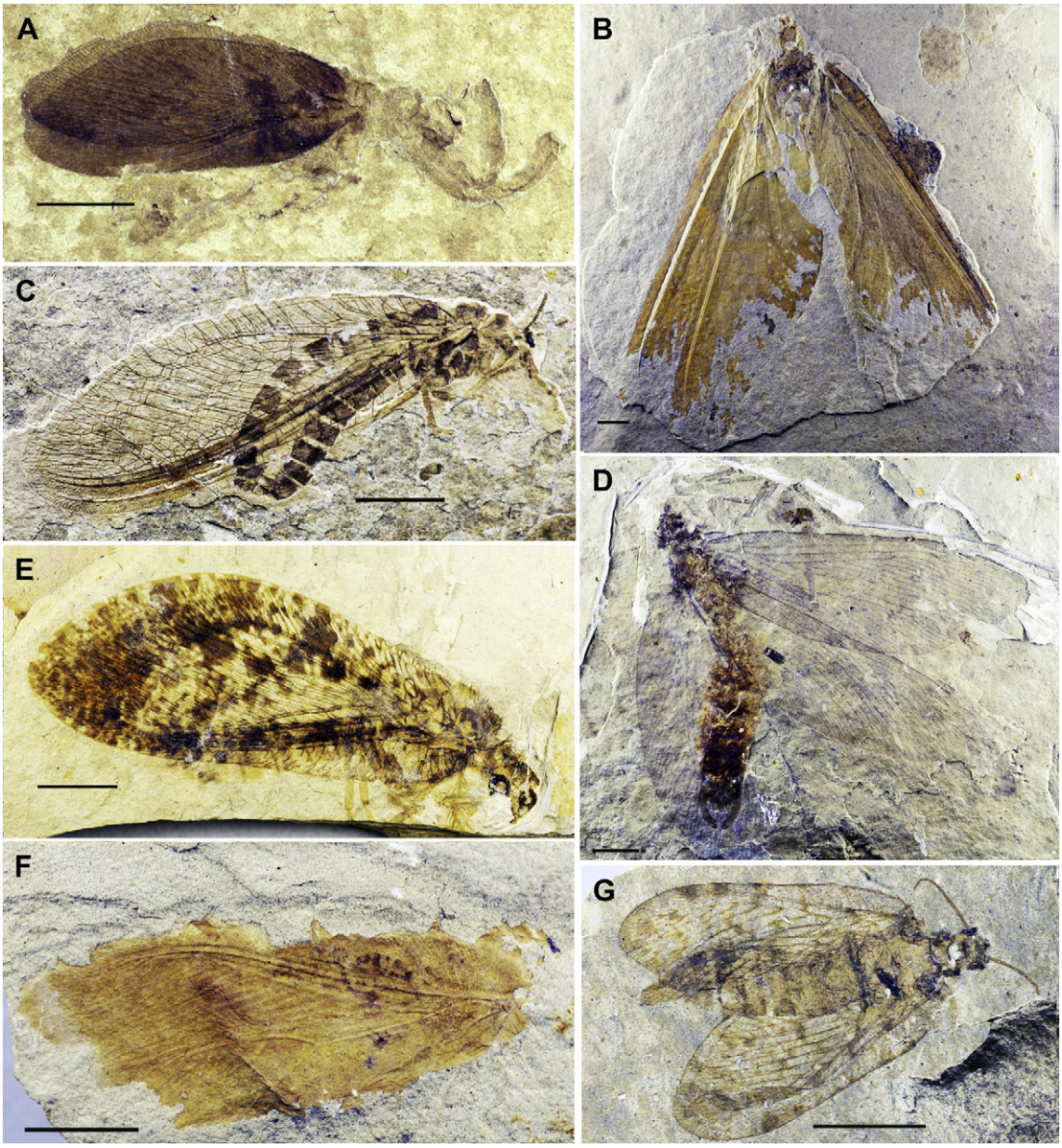

Fig. 3. Neuroptera (undescribed) from the Yixian Formation. A, Mantispidae. B, Ascalochrysidae. C, Chrysopidae. D–G, Ithonidae. Scale bar represents 5 mm.

been described from the Huangbanjigou locality in Liaoning Province (Ren and Guo, 1996; Ren, 2003; Yang et al., 2009). Undescribed material includes three specimens from this locality: two are poorly preserved and their affinities are difficult to determine, and three belong to *Sophogramma* Ren and Guo (one of these is probably *S. papilionaceum* Ren and Guo, 1996; Fig. 4A). The genus *Sophogramma* represented in the formation by four species is widely distributed over Eurasia; it is found also in the Siberian locality of Baissa and English Purbeck (Makarkin, 2010; Jepson et al., in press).

5.5. Mantispidae

Eleven specimens have been found (7.1% of all identified neuropterans), all with body parts preserved, which represent at least four genera (Fig. 3A). All of these taxa probably belong to the subfamily Mesomantispinae established for one species (two specimens) of the genus *Mesomantispa* Makarkin from the Baissa locality (Makarkin, 1997a). Mesomantispinae is the most "primitive" mantispid subfamily; it also occurs in the Middle Jurassic locality of Daohugou (unpublished data).

5.6. Osmylidae

Several undescribed specimens have been collected (5.8% of all identified neuropterans), mainly poorly preserved and incomplete. One undescribed new genus and species is represented by a female specimen (Fig. 4F). Its venation appears to be quite similar to that of Gumillinae, but if so, this genus is distantly related to other gumilline genera.

5.7. Mesochrysopidae

This family constitutes only 3.2% of identified neuropteran specimens, but is quite diverse. Three genera and four species have

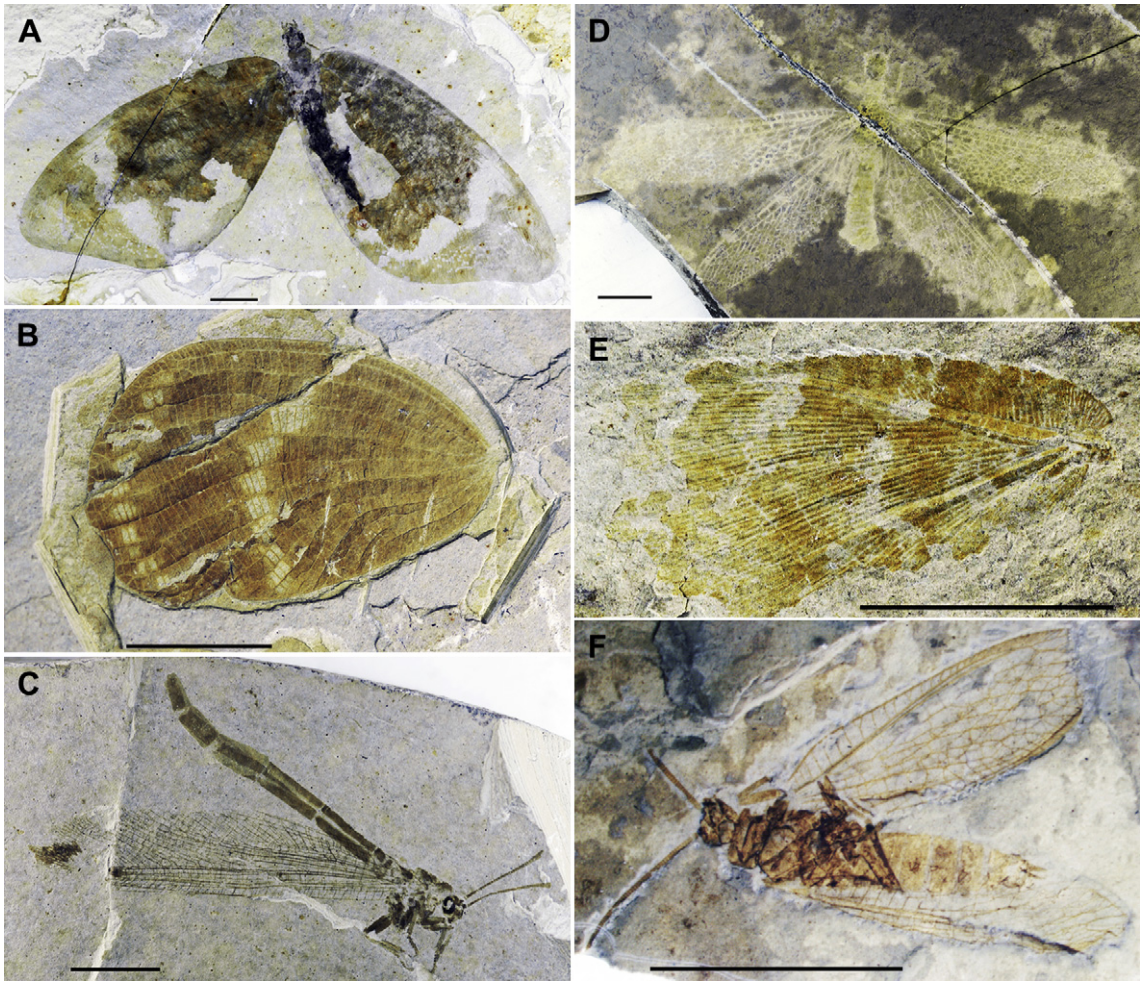

Fig. 4. Neuroptera (undescribed) from the Yixian Formation. A, Kalligrammatidae. B, Aetheogrammatidae. C, Palaeoleontidae. D, Mesochrysopidae. E, Psychopsidae. F, Osmylidae. Scale bar represents 10 mm.

been described from this formation (Ren and Yin, 2002; Nel et al., 2005; Ren et al., 1995, 2010a), one more genus and species is awaiting description. Of these, the genus *Tachinymphes* Ponomarenko, 1992 was widely distributed in Eurasia at that time; it is found in the Spanish Las Hoyas and Siberian Baissa localities (Nel et al., 2005). Similarly, an undescribed genus occurs in both the Dakangpu locality of the Yixian Formation and Las Hoyas (Fig. 4D). Two other genera are endemic to the formation.

5.8. Nymphidae

Five undescribed specimens (representing four species) have yet to be studied in detail. One specimen from Liutiaogou is a small forewing with a venation most similar to that of *Baissoleon* Makarkin, 1990b from the Baissa locality. Another species from Liutiaogou is a relatively large specimen that resembles the species of the Mesozoic genus *Mesonymphes* Carpenter, 1929, in particular *M. sibiricus* Ponomarenko, 1992a from the Baissa locality. The relationship of two other species (three specimens, one from Liutiaogou, two from Huangbanjigou) with other nymphid genera is unclear.

5.9. Myrmeleontidae

One ant-lion genus *Choromyrmeleon* Ren and Guo with two closely related species (two specimens) has been described from the Huangbanjigou locality (Ren and Guo, 1996; Ren and Engel, 2008b); undescribed material includes two additional specimens of this genus, probably *C. aspoeckorum* Ren and Engel, 2008b. The genus is assigned here to the subfamily Araripeneurinae based on the absence of pre-sectorial crossveins, 1A and CuP basally separated, and general similarity of the venation. The status of this taxon is still uncertain; sometimes it is treated as a separate family, Araripeneuridae (Martins-Neto, 2003; Martins-Neto et al., 2008). Hitherto, the subfamily was known only from the Crato Formation of Brazil where it is represented by numerous species (see list in Martill et al., 2008a) and perhaps the Mongolian Bon-Tsagaan locality (see below). *Choromyrmeleon* is most closely related to *Blittersdorffia* Martins-Neto and Vulcano, which is certainly the most "primitive" genus among Araripeneurinae found in the Crato Formation.

5.10. Aetheogrammatidae

This family is only known from the holotype, represented by an incomplete specimen (Ren and Engel, 2008a). Undescribed material comprises three specimens, two of which represent new taxa, one from Huangbanjigou (Fig. 4B), and another from Dawangzhangzi. The venation of Aetheogrammatidae is similar to that of Kalligrammatidae, and the former might be a specialized branch of the latter.

5.11. Ascalochrysidae

These large neuropterans are known only from two isolated hind wings (including the holotype) and an incomplete undescribed specimen (Fig. 3B). This family is related to Mesochrysopidae and endemic to this formation (Ren and Makarkin, 2009).

5.12. Berothidae

Three specimens have been found, of which two (undescribed) are poorly preserved. The well-preserved specimen was described as the monotypic genus *Oloberotha* Ren and Guo, 1996. Its forewing venation is very similar to that of *Mesithone* Panfilov, 1980, the type species of the family Mesithonidae, which is believed to be a "possible primitive Berothidae" (Grimaldi and Engel, 2005, pp. 349, 356). The berothid affinity of *Oloberotha* is evidenced from the hind wing venation, and rather long scapus of its antennae, characteristic of Berothidae. *Mesithone gracilis* Panfilov, 1980, the only species of the genus which possesses the body (although poorly preserved) and the hind wings, is also clearly berothid based on the hind wing venation and the long scapus. Therefore, we treat this taxon as the subfamily Mesithoninae, stat. nov., composed of the Upper Jurassic/Lower Cretaceous genera *Mesithone* and *Oloberotha*. It should be noted, however, that their venation is rather similar to those of the mantispid Mesomantispinae and the genus *Doratomantispa* Poinar and Buckley from the late Albian Burmese amber (Poinar and Buckley, 2011).

5.13. Palaeoleontidae

There is one undescribed well-preserved palaeoleontid specimen, which represents a new genus and species. It differs from other genera by having a slightly clavate antennae similar to those of Myrmeleontidae (Fig. 4C).

5.14. "Cratochrysidae"

One quite poorly preserved specimen from the Baitugou locality very much resembles *Cratochrysa willmanni* Martins-Neto, 1994 from the Brazilian Crato Formation; their wing colour, size, shape and the preserved venation are similar (compare Fig. 5A and Martins-Neto, 1994, pl. 1, fig. D). *Cratochrysa* Martins-Neto, 1994 is the type and only genus of the family Cratochrysidae, which was hitherto restricted to the Crato Formation (Martins-Neto, 2003; Martins-Neto and Rodrigues, 2009). However, this family name is unavailable (no description and no definition), although the taxon appears to be valid.

5.15. Familia nova A

The wings of one specimen from the Baitugou locality are very similar to those of the genus *Palaeogetes* Makarkin, 1990c from the Upper Cretaceous locality of Tyul'kili, Kazakhstan (Fig. 5B). These taxa represent an undescribed family occurring also in the Middle Jurassic locality of Daohugou (V. Makarkin, Q. Yang, D. Ren, under study).

5.16. Neuroptera familia indeterminata

Some incomplete and poorly preserved specimens are hard to determine. One relatively well-preserved specimen is similar to the enigmatic genus *Mantispidiptera* Grimaldi, 2000 whose family affinity is unclear (Wedmann and Makarkin, 2007). An incomplete hind wing from the Gaositai locality was described in Osmylidae (Ren and Guo, 1996). However, this hind wing is too small for Osmylidae (approximately 8 mm long; 10 mm is the smallest known osmylid species) with preserved venation not completely concordant with that of Osmylidae. Most probably, it belongs to Berothidae, although this is a preliminary determination.

5.17. Summary

There are approximately 65 species belonging to 15 families of Neuroptera currently known to occur in the Yixian Formation. The described taxa are listed in Table 1; six other families (Mantispidae, Osmylidae, Palaeoleontidae, Nymphidae, "Cratochrysidae", "Familia nova A") are present among undescribed material. Two families (Aetheogrammatidae and Ascalochrysidae) are endemic to the formation. Chrysopidae and Ithonidae dominate the neuropteran assemblage. Ithonidae are especially diverse. Four other families (Psychopsidae, Kalligrammatidae, Mantispidae, and Osmylidae) sub-dominate the assemblage; they were quite common and diverse. Other families are not common; of these Mesochrysopidae, Myrmeleontidae, Nymphidae, and Aetheogrammatidae are possibly not as rare as the others, which are represented by single specimens (1–3), i.e., Palaeoleontidae, Ascalochrysidae, Berothidae, "Cratochrysidae", and "Familia nova A". The relative rarity of Psychopsidae is especially noteworthy.

6. Comparison of the Yixian neuropteran assemblage with those from other Lower Cretaceous localities

6.1. Other Chinese Lower Cretaceous localities

There are numerous Lower Cretaceous insect localities in China (see e.g., Lin, 1994), but Neuroptera are described from only a few, i.e., from the Laiyang and Shahai formations (below). Two other Lower Cretaceous species have been described from Liaoning Province, from localities whose precise stratigraphic position are unclear: *Angaropsychops sinicus* Hong in W. Wang, 1980 (Chifeng City, Heishangou) and *Mesohemerobius jeholensis* Ping, 1928 ("Beipiao, Loc. 2101"). It is quite possible that these two localities belong to the Yixian Formation.

Angaropsychops sinicus, whose holotype is probably lost, is most similar to species of the genus *Epipsychopsis* from Baissa and *Alloepipsychopsis* gen. nov. from the Yixian Formation and, therefore, most probably belongs to Psychopsidae. *Mesohemerobius jeholensis* is known only from an inadequate drawing and description (the holotype is lost); it is now regarded as Neuroptera incertae sedis (Makarkin et al., 2003).

Liutaipsychops borealis, known only from a photograph (Lin, 1994, fig. 4A), is found in the Yincheng Formation of Liutai, Jilin Province. It is not formally described and the name is therefore unavailable; its holotype is probably lost (B.Q. Lin, pers. comm. to VM). Judging from the photograph, the specimen most probably belongs to Psychopsidae. The age of this formation is Aptian, according to Sha (2007).

6.1.1. The Laiyang Formation

The geological setting, stratigraphic section and entomofauna of the Laiyang Formation were described by Hong and Wang (1990) and Zhang (1992). Three neuropteran species of different families are described from the Third Member of this formation exposed near two adjacent villages, Nanligezhuang and Tuanwang, south of Laiyang City in Shandong Province (see Zhang, 1992, fig. 1): *Allopterus luianus* J. Zhang, 1991 (Mesochrysopidae: Allopterinae; Ren et al., 2010a); *Drakochrysa sinica* Yang and Hong 1990 (Chrysopidae), and *Hongosmylites longus* (Hong, 1996) (a psychopsoid family; Makarkin and Archibald, 2005). The age of this formation was considered Hauterivian–Barremian by Hong (1998), but now it has been correlated with either the Yixian Formation (Zhang, 2005) or the Jiufotang Formation (H. Zhang et al., 2010). The presence of closely related

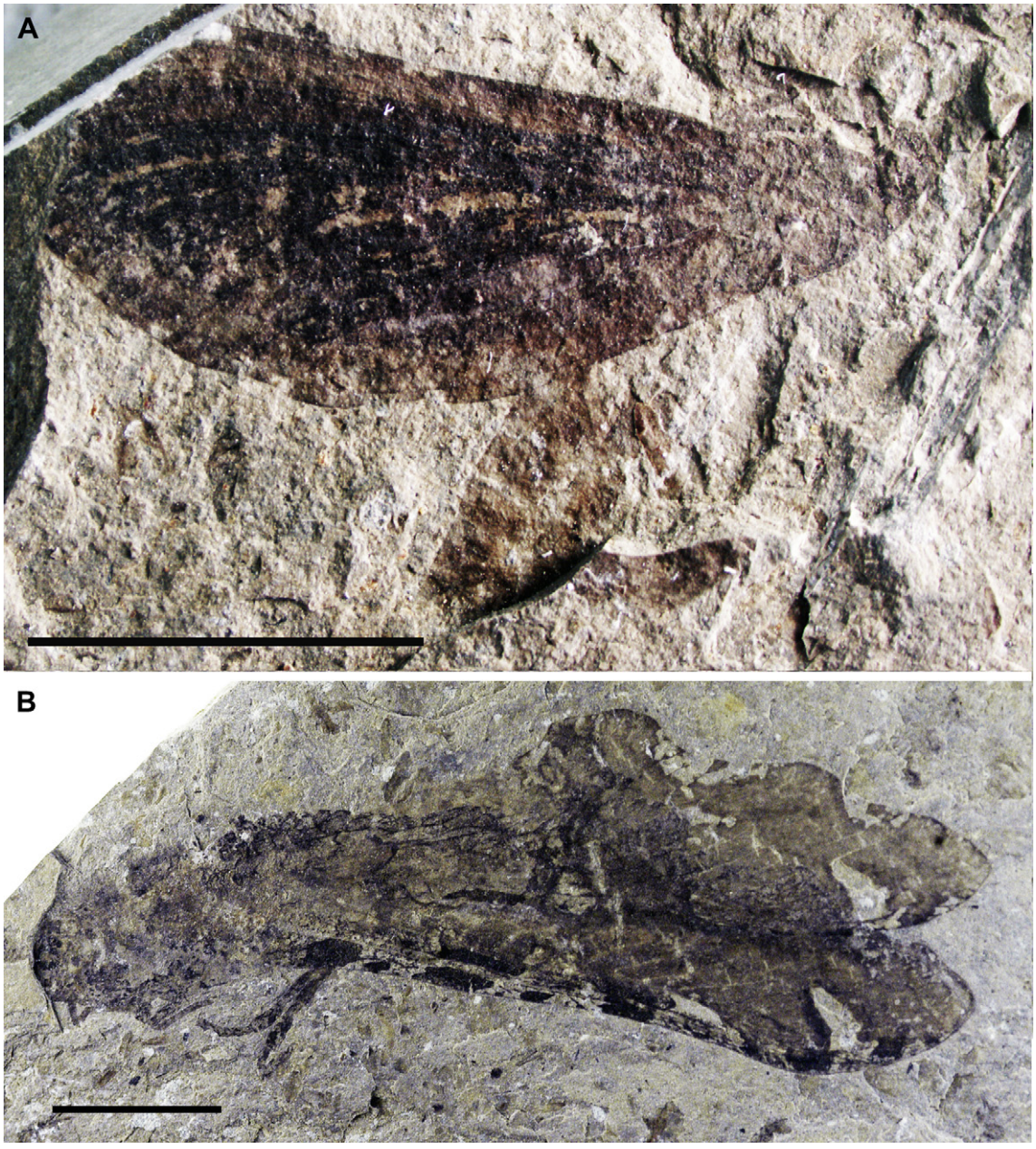

Fig. 5. Neuroptera (undescribed) from the Yixian Formation. A, "Cratochrysidae". B, "Familia nova A". Scale bar represents 10 mm.

species of the very specialized mesochrysopid genus *Allopterus* J. Zhang in both the Laiyang Formation and the Upper Barremian La Huérguina Formation implies that the age of the Laiyang Formation may be near to late Barremian. It supports the correlation of the Laiyang Formation with the Yixian Formation, which is dated as late Barremian.

6.1.2. The Jiufotang (=Shahai) Formation

One neuropteran species (*Liaoximyia sinica* Hong, 1988) was described from an exposure of this formation situated to the west of Xiwan Village near Meileyingzi in western Liaoning. Its age is Aptian according to Sha (2007). The taxonomic position of this species is quite unclear because the specimen is damaged and incomplete. It was originally assigned to Myrmeleontidae, but it does not belong to this family. It should probably be assigned to Mesochrysopidae (Makarkin and Menon, 2005).

6.2. The Purbeck succession of southern England

The Purbeck Limestone Group of southern England is subdivided into the Lulworth and Durlston formations (Clements, 1993), the ages of which are generally accepted to be Early Berriasian and Late Berriasian respectively (Rasnitsyn et al., 1998; Jepson et al., in press), although radioactive dating is unavailable. Seventeen species (two of which are unnamed) of nine families have been recorded from the Purbeck, mostly originating from the Durlston Formation of Durlston Bay (Jepson et al., in press). Undescribed material includes more than 30 fragmentary and/or poorly preserved specimens (J. Jepson and E. Jarzembowski, pers. comm.). The assemblage is dominated by Psychopsidae (five species, mainly *Pterinoblattina* Scudder, and many undescribed poorly preserved incomplete specimens), and sub-dominated by Osmylidae (five species of four genera, including *Osmylopsis* Handlirsch). Kalligrammatidae

(including *Sophogramma*) and Prohemerobiidae are represented by two species each. Other families are represented by one species each: Chrysopidae (*Mesypochrysa*), Berothidae, Nymphidae (*Sialium* Westwood), possible Hemerobiidae, and one genus of uncertain family affinity.

Although this assemblage and that of the Yixian Formation have a quite different taxonomic structure (different family dominance and composition), they are some genera in common (*Sophogramma*, *Mesypochrysa*). However, these genera are among the most widely distributed in Eurasia.

6.3. The Wealden, southern England

The Wealden Supergroup of southern England consists of the Hastings and Weald Clay groups in the Weald Sub-basin and the Wealden Group in the Wessex Sub-basin (Allen and Wimbledon, 1991). One species of Kalligrammatidae has been described from the Valanginian Wadhurst Clay (Hastings Group) (Jarzembowski, 2001), other Neuroptera are from the Lower and Upper Weald Clay formations (Jepson et al., 2009). The age of the former is considered to be Hauterivian and the latter Barremian (Rasnitsyn et al., 1998). Ten genera (15–16 species) of the following five families were recorded from four localities (Clockhouse, Auclaye, Rudgwick, and Smokejacks): Ithonidae (one genus), Osmylidae (two genera), Kalligrammatidae (one unnamed genus), Psychopsidae, and two genera of Neuroptera "familia incertae sedis" (Jepson et al., 2009). The neuropteran fauna is distinctly dominated by Psychopsidae (four genera, 9–10 species). Ithonidae are represented by the genus *Principiala*, which also occurs in the Yixian Formation and the Brazilian Crato Formation (the only genus shared by this assemblage and that of the Yixian Formation). In general, the assemblage is rather similar to that of the Purbeck Limestone Group, but less diverse.

6.4. The Turga and Zaza formations, Transbaikalia

The Lower Cretaceous deposits of the Siberian Transbaikalia are rich in fossil insects (see Zherikhin, 1978). Neuroptera are found in four localities of two formations. The Turga and Semyon localities in eastern Transbaikalia (i.e., Zabaikalskii Krai, formerly Chita Oblast) belong to the Turga Formation, and the Baissa and Romanovka localities of western Transbaikalia (i.e., the Buryat Republic) belong to the Zaza Formation (see Zherikhin et al., 1999 for a comprehensive survey of the Zaza Formation).

Radioactive dating indicates a Hauterivian age for the lower subdivisions of the Turga Formation (131–134 Ma; Rasnitsyn and Zherikhin, 2002). There are no radiometric dates for deposits of the Zaza Formation, but it is thought to be younger than the Turga Formation (Ponomarenko et al., 2009). On the other hand, it is correlated with the Berriasian Purbeck succession (Rasnitsyn et al., 1998), and is considered to be pre-Barremian (Zherikhin et al., 1999) and Berriasian/Valanginian (Vršanský, 2003).

Two specimens are known from Turga: one is described as the psychopsid species *Angaropsychops turgensis* Martynova, 1949; the other is an undescribed species possibly belonging to the berothid Mesithoninae (Ponomarenko, 1990). There are several undescribed specimens from the Semyon locality, and two specimens are known from Romanovka. The vast majority of the Lower Cretaceous Transbaikalian Neuroptera come from the Baissa locality, which has yielded 139 specimens belonging to at least 11 families. This assemblage is distinctly dominated by Psychopsidae (s. l.), which constitute 53.2% of all neuropteran specimens, of which only a few taxa (two genera, three species) are described (Makarkin, 1997c, 2010). Most undescribed specimens are quite atypical psychopsids in which crossveins are almost entirely lacking and the costal space is relatively narrow. The absence of crossveins and general forewing venation of these taxa are rather similar to those of *Glottopteryx* Makarkin and Archibald, 2005 from the Lower Jurassic of Germany, the type genus of the psychopsoid family Glottidiidae. Therefore, it is possible that the majority of specimens from Baissa (and a few similar specimens from the Yixian Formation and Purbeck Limestone Group) actually belong to this family. However, until a revision of the psychopsoid families is carried out, these atypical specimens are here assigned to Psychopsidae (s. l.). Other psychopsoids are represented by the large Brongniartiellidae (one genus, two species) and Kalligrammatidae (one species) (Makarkin, 2010). Chrysopidae and Myrmeleontoids sub-dominate the assemblage. The former family (11.5% of all neuropterans) is known from two genera and seven species (Makarkin, 1997b). Myrmeleontoids (9.4% of all neuropteran specimens) are diverse, represented by three families: Nymphidae (three genera, including *Baissoleon*, sit. nov.; four species), Palaeoleontidae and Babinskaiidae (one species each) (Makarkin, 1990b; Ponomarenko, 1992a). Berothidae (Mesithoninae) are rather abundant (12 specimens), represented by two genera and four species, and some undescribed taxa (Makarkin, 1999). Ithonidae are represented by four undescribed "polystoechotid-like" specimens (Archibald and Makarkin, 2006; pers. obs.). Mantispidae (Mesomantispinae), Osmylidae, and Mesochrysopidae are rare, each represented by one genus and 1–2 species and specimens (Makarkin, 1990a, 1997a; Ponomarenko, 1992a; pers. obs.). Undescribed material includes 12 specimens (mainly poorly preserved or fragmentary) whose taxonomic affinity is currently unclear. Among them, a large forewing might belong to Ascalochrysidae, but this wing is too poorly preserved for a confident determination.

The composition of the neuropteran assemblages of the Zaza and Yixian formations differ greatly: the former is dominated by Psychopsidae, the latter by Chrysopidae and Ithonidae; in the former, Mesochrysopidae and Kalligrammatidae are represented by a single specimen of widely distributed Eurasian genera (i.e., *Tachinymphes* Nel et al., 2005 and *Sophogramma* respectively); in the latter, these families are common and diverse; in the former, the families Aetheogrammatidae and possibly Ascalochrysidae are absent, and Mantispidae occur rarely. It is unclear if these differences are a result of different environmental conditions or if they indicate deposits of different ages. Tentatively, we agree with authors who consider the age of the Zaza Formation to be pre-Barremian (Hauterivian) or early Barremian, i.e., slightly older than the Yixian Formation. Zhang and Rasnitsyn (2006) believed that the lacustrine sediments of the Yixian and Zaza formations are likely to be contemporaneous based on the hymenopteran assemblage.

6.5. Bon-Tsagaan (=Bon-Tsagan), Mongolia

This Mongolian insect locality is probably the richest in the Lower Cretaceous of Laurasia (Rasnitsyn and Zherikhin, 2002). The age of the Bon-Tsagaan deposits is not clear because radiometric data are unavailable. It is supposed to be Hauterivian/Barremian (Rasnitsyn et al., 1998; Vršanský, 2003) or Barremian/Aptian (Rasnitsyn and Zherikhin, 2002).

The neuropteran assemblage includes 170 specimens, of which only a few are described: five genera (five species) of Chrysopidae (*Mesypochrysa*), Hemerobiidae (*Cretomerobius* Ponomarenko), Myrmeleontoidea (*Paracroce* Ponomarenko, *Cretoleon* Ponomarenko), and Neuroptera "familia incertae sedis" (*Tachymerobius* Ponomarenko) (Ponomarenko, 1992b). The venation of the genus *Paracroce* is similar to that of Myrmeleontidae (Araripeneurinae) from the late Aptian Crato Formation, but the wing possesses trichosors not characteristic of the family (if these are not an artefact). *Cretoleon* Ponomarenko is believed to belong to Palaeoleontidae (Millet and Nel, 2010), but if so, this is very distantly related to other

genera of this family. The genera *Cretomerobius* and *Tachymerobius* have no close relatives in the Lower Cretaceous (but the latter has a quite distant relative in the Purbeck: Jepson et al., in press). Therefore, the neuropteran assemblage known to date is rather peculiar, and the only common genus occurring in both this and the Yixian Formation is the widespread *Mesypochrysa*.

6.6. Las Hoyas, Spain

The Spanish locality of Las Hoyas belongs to the La Huérguina Formation and dated as late Barremian. The characteristics of the geological setting, palaeoenvironment and biota are described by Sanz et al. (1988), Fregenal-Martínez et al. (2007), Fregenal-Martínez and Buscalioni (2009) and Buscalioni and Fregenal-Martínez (2010). The composition of the neuropteran assemblage of this formation is very unusual. It contains mainly Mesochrysopidae (20 specimens; six genera; Nel et al., 2005), and one undescribed specimen of Kalligrammatidae (Martínez-Delclòs and Nel, 1995). The forewing venation of the genus *Chimerochrysopa* Nel et al., 2005 appears to be quite aberrant but clearly a mesochrysopid type, and is here transferred to Mesochrysopidae (uncertain subfamily). The Las Hoyas mesochrysopid fauna shows clear intercontinental connections: two genera are in common with the Chinese Yixian (*Tachinymphes*) and the Laiyang formations (*Allopterus*), and one genus with the Brazilian Crato Formation (*Triangulochrysopa* Nel et al., 2005; Menon and Makarkin, 2008).

6.7. The Crato Formation, Brazil

This famous Lagerstätte is located in the Araripe basin (many localities) of north-eastern Brazil, and dated as late Aptian (Martill et al., 2008b). The formation is known to contain a rich neuropteran fauna, with more than 70 described species belonging to at least 13 families, including "Cratochrysidae" (Martins-Neto, 2003; Martins-Neto et al., 2008; Martins-Neto and Rodrigues, 2009, 2010; Millet and Nel, 2010). Many other specimens in various museums are awaiting examination. The neuropteran assemblage is distinctly dominated by Myrmeleontoidea: Myrmeleontidae (including Araripeneuridae), Babinskaiidae, Palaeoleontidae, Nymphidae, and possibly Ascalaphidae (the latter needs confirmation). Chrysopidae and Mesochrysopidae (six species each) are also quite diverse. Other families recorded from the Crato Formation occur rarely: "Psychopsidae" (probably Osmylopsychopidae), Kalligrammatidae (including Makarkiniidae), Ithonidae, perhaps Sisyridae (needs confirmation), Berothidae, "Cratochrysidae", and Osmylidae.

It is possible that the family "Cratochrysidae" and the genus *Principiala* recorded from the Crato Formation are represented in the Yixian Formation, and *Mesypochrysa* may be found in the former (needs confirmation), but in general the composition of these neuropteran assemblages differ strongly.

7. Conclusions

Fossils of all East Asiatic formations containing Neuroptera (Yixian, Jiufotang, Laiyang, Turga and Zaza formations) are usually considered to belong to a single Jehol biota, widely distributed in the Lower Cretaceous of East Asia, from Gansu, Mongolia and Russian Transbaikalia in the west to western Japan and Korea in the east (Wang, 1991, fig. 5; Chang, 2008, fig. 6; Huang and Ren, 2008, fig. 5). This region is thought to form a single biogeographic province (Wang, 1991). The evolution of the Jehol biota was recently analysed by Zhang et al. (2010). The Yixian Formation is situated in the central part of this large area.

Comparison of the neuropteran assemblages of the Yixian Formation with those of other Lower Cretaceous speciose Eurasian localities shows that they differ greatly. Deposits of these localities, however, also differ in their genesis: lagoonal (the Crato Formation; Martill et al., 2008b), predominantly lagoonal (the English Purbeck; Allen, 1998), lacustrine-lagoonal (the English Wealden; Allen and Wimbledon, 1991), and lacustrine (others analysed; Zherikhin et al., 1999; Fregenal-Martínez et al., 2007; Chang, 2008). These depositional differences can somewhat influence the taxonomic composition of the neuropteran assemblages, but this influence is probably minimal at family level. Thus, in three localities with deposits of different genesis (i.e., Purbeck, Wealden, and the Zaza Formation) the neuropteran assemblages are clearly dominated by psychopsoids. But the former two localities are much or slightly older than the Yixian Formation. There is enough difference in the structure of the neuropteran assemblages between the two formations of the Jehol biota, the Yixian (central) and Zaza (marginal) (see above), to be explained by both possible different local environments and different ages. The assemblage of the contemporaneous Las Hoyas locality is dominated by Mesochrysopidae, but this may be because insufficient material has been examined. The neuropteran assemblage of the younger Crato Formation is clearly dominated by myrmeleontoids, mainly Myrmeleontidae (Araripeneurinae). Therefore, the dominance of Chrysopidae and Ithonidae is an unusual feature of the neuropteran assemblage of the Yixian Formation. The family Ithonidae is known from single specimens in other Lower Cretaceous localities (the Wealden, the Crato Formation) or not known at all (the Purbeck, Las Hoyas). Ithonids are represented by more than one species (four specimens) only in the East Siberian Baissa; all of them correspond to group 2 of the Yixian assemblage. At present, this family is relict, restricted to some regions of the Americas, Australia and south-eastern Asia (Winterton and Makarkin, 2010), but in the Middle/Upper Jurassic of some Asian localities (e.g., Daohugou, Karatau) it was more diverse (unpublished data).

The abundance and great diversity of Kalligrammatidae in the Yixian Formation is also noteworthy. In other Eurasian localities this family occurs rarely, represented by single specimens. In general, it was most diverse in the Jurassic and it existed until the late Aptian (Crato Formation). The survival of this family in the stable continental environment of the Barremian Yixian Formation, as well as Ithonidae, whose ancestors flourished in the Jurassic, are in agreement with the data on the vertebrate taxa (Matsukawa et al., 2006). The presence of two families endemic to the Jehol Biota (Aetheogrammatidae and Ascalochrysidae) is characteristic. Both may be considered (provisionally) as relicts of the Jurassic period as well: a genus very similar to Aetheogrammatidae is known from the Upper Jurassic of Karatau (Ren and Engel, 2008a). Ascalochrysidae is probably an ancient family although unknown in older strata, because it possesses a set of plesiomorphic states (see Ren and Makarkin, 2009). These data support the hypothesis of an existence of a refugium of Jurassic terrestrial relicts in East Asia (Luo, 1999).

The family Mesochrysopidae is most characteristic of the Lower Cretaceous among Neuroptera. In the Jurassic, this family occurred rarely and was represented by another (more generalised) subfamilial taxon (Ren et al., 2010a); it is unknown in younger (Late Cretaceous) strata. Therefore, the rather great diversity of Mesochrysopidae in the Yixian Formation (and in general in the Jehol biota) is normal for that time.

The relative scarcity of Myrmeleontidae in the Yixian Formation is quite understandable: this was the time of origin of the family. In the Lower Cretaceous European localities this family is not known at all; however, their larvae were reported to occur in the late Albian Charentes amber in France (Perrichot et al., 2007, table 2).

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