Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera)

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Abstract. The Mesozoic chrysopid-like Planipennia are revised and several new genera and species are described. The new superfamily Chrysopoidea is proposed for the extant and fossil Chrysopidae, and the fossil families Liassochrysidae n. fam., Allopteridae Zhang 1991 n. sensu, Mesochrysopidae Handlirsch, 1906 n. sensu, Tachinymphidae n. fam., and Limaiidae Martins-Neto and Vulcano 1989 n. sensu. A phylogenetic analysis of the Chrysopoidea is proposed, based on the wing venation characters. With at least the four families Allopteridae, Mesochrysopidae, Tachinymphidae, and Chrysopidae, showing different wing venation patterns, the systematic diversity and morphological disparity of the Chrysopoidea are maximal during the Late Jurassic and Early Cretaceous. The Mesozoic family Limaiidae was still present during the Paleocene/Eocene suggesting a minimal impact on the Chrysopoidea of the crisis of the diversity at the K-T boundary. Other Cenozoic Chrysopoidea can be attributed to the Chrysopidae *sensu stricto*.

Résumé. Planipennia mésozoïques de la lignée « chrysope » : une approche phylogénétique (Insecta, Neuroptera). Les Planipennia mésozoïques du type « chrysope » sont révisés. Plusieurs nouveaux genres et espèces sont décrits. La nouvelle superfamille Chrysopoidea est proposée pour les Chrysopidae Schneider 1851 actuels et fossiles, et les familles fossiles Liassochrysidae n. fam., Allopteridae Zhang 1991 n. sensu, Mesochrysopidae Handlirsch 1906 n. sensu, Tachinymphidae n. fam. et Limaiidae Martins-Neto & Vulcano 1989 n. sensu. Une analyse phylogénétique des Chrysopoidea est proposée, basée sur les caractères de nervation alaire. Avec au moins les quatre familles Allopteridae, Mesochrysopidae, Tachinymphidae et Chrysopidae qui montrent des schémas de nervation alaire différents, la diversité systématique et la disparité morphologique des Chrysopoidea sont maximales durant le Jurassique supérieur et le Crétacé inférieur. La famille mésozoïque Limaiidae était encore présente dans le Paléocène/Eocène, suggérant un impact minime sur les Chrysopoidea de la crise à la limite Crétacé/Cénozoïque. Les autres Chrysopoidea cénozoïques peuvent être attribués aux Chrysopidae sensu stricto.

F ossil Mesozoic "chrysopids" are now relatively well known after the discoveries of Panfilov (1980), Martins-Neto & Vulcano (1989a, b), Ansorge and Schluter (1990), Martins-Neto (1992, 2000), Makarkin (1992, 1994, 1997), Nel & Henrotay (1994), and others. Nevertheless, several new chrysopid-like insects have been recently discovered in the Early Cretaceous outcrop of Las Hoyas (Cuenca, Spain). Also, new material from the Late Jurassic and Early Cretaceous of China and Brazil is now available. A direct exam of the holotype of *Mesochrysopa zitteli* (Meunier 1898) gave new information concerning its fore and hind wing vena-

tions. These new data greatly increase our knowledge of the diversity of the Mesozoic chrysopids.

If nearly all the Cenozoic Chrysopidae can be attributed to the extant subfamilies Nothochrysinae and Chrysopinae, the numerous Mesozoic species that are currently attributed to this group have more uncertain positions. Furthermore, the Mesozoic family Allopteridae Zhang 1991 would be related to the enigmatic group "Mesochrysopinae" (Zhang 1991), but on the basis of unpolarized characters and without any phylogenetic analysis. Thus, there is a rather great confusion in the classification of the Mesozoic chrysopid-like Planipennia.

The phylogenetic relationships between the various neuropteran families also greatly varied through time. The different authors proposed very different patterns depending of the character sets they used, based on larvae,

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larvae and imagos, even adding egg structures (Withycombe 1925) in a non-phylogenetic classification. Since Withycombe (1925), Martynova (1952) proposed a phylogenetic tree for Neuroptera; Schluter (1986: fig. 3) compared Withycombe's (1925), and Martynova's (1952) classifications and phylogenetic trees and based his classification on extant and fossil families. Lastly, Aspöck (1995, 1996, 2002) and Aspöck *et al.* (2001) proposed new phylogenies of the extant families, mainly based on larval and adult body characters.

MacLeod (1964) divided all neuropteran larvae into "hemerobioid" type and "myrmeleontoid" type. Henry (1982) divided the Neuroptera in two suborders Hemerobiiformia and Myrmeleontiformia. Aspöck (1995, 1996) proposed a third suborder Nevrorthiformia, based on the sole extant family Nevrorthidae. This new suborder was first considered as the sister group of the Myrmeleontiformia, and later, as sister group of all other Neuroptera (Aspöck *et al.* 2001). The definitions of almost all families greatly varied with the authors, but the results of New (1990), widely congruent with those of Withycombe (1925), seem to be supported by the internal structure of the female genitalia (Sziraki 1996).

Sister group of the lineage [Hemerobiidae + Polystoechotidae] for Whitycombe (1925), the Chrysopidae are placed with the Hemerobiidae in the same lineage Hemerobioidea by Martynova (1952: 222). Schluter (1986: fig. 3) put them with the Hemerobiidae and Brucheiseridae. Lastly, the cladistic analysis of Aspöck *et al.* (2001) generated a consensus cladogram in which the position of the Chrysopidae is rather uncertain because of the inner polytomy of their clade of the "higher Hemerobiiformia". But Aspöck (2002) preferred a cladogram with the Chrysopidae and Osmylidae as sister groups, indicating that the Chrysopidae are also similar to Hemerobiidae.

The Chrysopidae are potentially sister group of the Hemerobiidae, or of the Osmylidae, or of the clade [Coniopterygidae + Sisyridae], or the clade [Dilaridae + Mantispidae + Rhachiberotidae + Berothidae]. Aspöck *et al.* (2001) did not give the set of the most parsimonious cladograms that generated their strict consensus tree. Also, after the analyses of the sole larval characters, Aspöck (1992) put the Chrysopidae as sister group of the [Osmylidae + Sisyridae + Hemerobiidae + Coniopterygidae + Dilaridae + Berothidae + Mantispidae], and Aspöck (1995, 1996) put them as sister group of the Osmylidae. In conclusion, the phylogenetic position of the Chrysopidae remains rather uncertain.

Also, the cladistic-based phylogenies of the Chrysopidae only concern the Recen taxa (Brooks &



Figure 1

Nomenclature of fore wing venation of extant Chrysopidae. C costal vein; ScP Subcosta Posterior; RA Radius Anterior; RP Radius Posterior; rx radial crossveins; MA Median Anterior; MP Median Posterior; Psm pseudo-median vein; CuA Cubitus Anterior; CuP Cubitus Posterior; Psc pseudo-cubital vein; m1 and m2 first and second median cells; c1, c2, and ddc cubital cells; im intra-median cell; AA Analis Anterior; AP Analis Posterior; bsx basal subcostal crossvein; i.g. inner gradate cross-veins; o.g. outer gradate cross-vein; st pterostigma.



Figure 2 Fork of MP into MP1 + 2 and MP3 + 4 in the fore wing of a Recent *Chrysopa* sp.

Barnard 1990; Brooks 1997) (Fig. 4). Even if they are cladistic, these works are not based on real outgroup comparisons, but on *a priori* character polarisations with a hypothetical ancestor. There is no attempt based on real outgroups. The fossil groups "Mesochrysopinae" and Allopteridae are currently attributed to the "chrysopid" lineage on the basis on non-cladistic arguments. Schluter (1982, 1984) and Martins-Neto & Vulcano (1989a) proposed two different, although similar phylogenies of the fossil and Recent "Chrysopidae". They are not based on a cladistic treatment of a matrix of taxa/characters, after the comparison with one or several outgroups. Nel & Henrotay (1994) made the first attempt at such an analysis, but it suffers of the lack of restudy of some important taxa, such as Mesochrysopa, and the absence of others, such as Allopteridae Zhang 1991. Thus, we propose here a new phylogenetic analysis of the chrysopoid lineage.

We use the nomenclature of wing venation of Kukalová-Peck & Lawrence (2004), rather than Adams (1967), completed by Brooks & Barnard (1990), Ansorge & Schluter (1990) and Adams (1996), with the following abbreviations for the vein names (Fig. 1): C: Costa, ScP: Subcosta Posterior, RA: Radius Anterior, RP: Radius Posterior, MA: Median Anterior, MP: Median Posterior, CuA: Cubitus Anterior, CuP: Cubitus Posterior, AA: Analis Anterior, AP: Analis Posterior.

In all Neuroptera, the fore wing veins R and MA are basally fused, after Kukalová-Peck and Lawrence (2004); RP + MA emerges from RA, and MA from RP. MP is divided into two branches MP1 + 2 and MP3 + 4. In Recent Chrysopidae, MP3 + 4 is divided in two distal branches of at least the same diameter, an anterior MP3 + 4a and a posterior MP3 + 4b that reaches CuA (Fig. 2). MP1 + 2, MA, and possibly some branches of RP are fused to constitute a pseudo-median vein noted Psm. The veins CuA, MP3 + 4a, and possibly MP1 + 2, MA and some branches of RP are fused to constitute a pseudo-cubital vein noted Psc. In Allopteridae, there is a supplementary longitudinal vein in the area between MP3 + 4b + CuA and MP3 + 4a, which is not a branch of MP3 + 4 as it is emerging as a secondary vein from it. We propose to call it MPspl. We call inner gradate (i.g.) and outer gradate (o.g.) series the series of gradate cross-veins that are more pronounced than the other gradate series of cross-veins.

Several cells have a great systematic and phylogenetic interest: (1) intra-median cell im between MP1 + 2 and MP3 + 4. It can be crossed by veins (Fig. 3); (2) cells m1 and m2 between MP/MP3 + 4 and Cu/CuA, at wing base, separated by a cross-vein 1m; (3) cells c1, c2, and dcc between CuA and CuP; in hind wing, the "banksian cell" b is limited by RP + MA, MA, MP1 + 2, and basally by the cross-vein sxv. This cell can be completely reduced, because of the fusion between MA with MP1 + 2.

The fossil insects from Las Hoyas (Spain) are sometimes deformed by diagenesis (Martínez-Delclòs *et al.* 2004). Therefore, the dimensions of the material from this outcrop are only indicative. We have chosen the undeformed and less deformed wings for our diagnoses and descriptions, other specimens are only indicative.

Superfamily CHRYSOPOIDEA n. taxon

Included families. Chrysopidae Schneider 1851 (extant and fossil) and the fossil families Liassochrysidae n. fam., Allopteridae Zhang 1991 n. sensu, Mesochrysopidae Handlirsch 1906 n. sensu, Tachinymphidae n. fam., and Limaiidae Martins-Neto and Vulcano 1989 n. sensu.

List of synapomorphies. Brooks & Barnard (1990) gave no diagnostic character of the Recent Chrysopidae. Ansorge & Schluter (1990) proposed the following diagnostic characters of Recent and fossil 'Chrysopidae': RA runs parallel with ScP for the whole of its length; RP (+ MA) arises from R near wing base and has many posterior branches; presence of the two series of gradate cross-veins. These characters alone are not sufficient to characterize even the Recent Chrysopidae because they are also present in many other neuropteran families, such as Polystoechotidae, and even some Osmylidae. After our new phylogenetic analysis, the Chrysopoidea

can be characterized by the following combination of wing venation characters: (1) presence of a well defined cell im in fore wing, different in size and shape from the more distal cells and distinctly limited by the branches of MP; (2) fore wing basal cross-vein between MP and Cu exactly opposite base of MP; (3) a common stem RP + MA; (4) presence of, at least, two series of gradate cross-veins in radial area; (5) hind wing CuA separated from MP, with only a distal fusion of branch (es) of MP3 + 4 in some taxa; (6) fork of Cu into CuA and CuP in a basal position, near wing base and more or less opposite base of MP; (7) fork of MP not distal, in basal third of wing, thus branches MP1 + 2 and MP3 + 4 rather long, although distally fused with MA or CuA in some taxa. The Mantispidae also have a cell im frequently very different from other cells and one or two rows of gradate cross-veins, but their hind wing CuA is partly fused with MP (New 1989).

Family LIASSOCHRYSIDAE n. fam.

Type genus. *Liassochrysa* Ansorge & Schluter 1990 (only one species *L. stigmatica* Ansorge & Schluter 1990, based on a single fore wing, Early Jurassic, Dobbertin, Germany) (Ansorge & Schluter 1990; Nel & Henrotay 1994).

Diagnosis. This taxon strongly differs from other families of Chrysopoidea in the following characters: (1) vein AA with two long branches apically forked; (2) vein AP with several branches; (3) area between CuA and CuP long, divided into 4-5 cells;

(4) presence of a subelliptic pterostigma; (5) ScP ending on C well basal of apex of RA; (6) apex of RA not at wing apex, distinctly more basal, apex of RP at wing apex; (7) only three cross-veins in area between RA and main branch of RP, the second being distinctly oblique. Characters (1)-(3) are plesiomorphies, characters (4) and (7) appear autapomorphic in the chrysopid lineage, and character (5) is a convergency with the Limaiidae, probably due to the presence of the particular pterostigmal structure. *Liassochrysa* falls at the very base of the Chrysopoidea after the present phylogenetic analysis (see below).

Family ALLOPTERIDAE Zhang 1991

Type genus. *Allopterus* Zhang 1991. Other genera: *Karenina* Martins-Neto 1997 (n. sit.), *Triangulochrysopa* n. gen., *Armando-chrysopa* n. gen.

Remark. *Mesascalaphus yangi* Ren *et al.* 1995 from the Late Jurassic-Early Cretaceous of China is probably not an Ascalaphidae but an Allopteridae. Although, it is not very well figured and photographied. It seems to have an elongate pronotum and the organisation of the radial, median and cubital areas of this family, especially the allopterid "X-crossing". It can be separated from other Allopteridae species in its very elongate wings. But, only a complete revision of the type specimen will allow to definite decision on its exact position. The list of fossil taxa attributed to the Allopteridae is given in Appendix 1.



Figure 3 Different types of fore wing cell im in extant Chrysopidae.





New diagnosis. Zhang (1991) proposed a diagnosis of this family based on the genus Allopterus. After the present addition of the three genera Karenina, Armandochrysopa n. gen., and Triangulochrysopa n. gen., it is necessary to emend it as follows: fore- and hind wing hyaline; distinct differences between fore and hind wing in shape, size and venation; fore wing distinctly longer and broader than hind wing; in fore wing, costal area narrow; cross-veins between C and ScP all simple; ScP and RA fused; ScP + RA ending at wing apex; RP + MA with a single stem arising from R near wing base; RP with numerous posterior branches; i.g. and o.g. cross-veins well defined (more pronounced than other gradate series) and more or less parallel; MA simple, not fused with MP or with any branches of RP; MP divided into two branches MP1 + 2 and MP3 + 4; MP1 + 2 and MP3 + 4 strongly diverging at their base, delimiting a broad area with at least three rows of cells and a well defined but more or less zigzagged secondary vein "MPspl" between them; MP3 + 4 strongly approximating CuA, meeting in one point or distally fused with it; a large "X-crossing" constituted by basal part of MP3 + 4, basal part of CuA, distal part of MP3 + 4 (+ CuA), and a strong secondary vein in area between MP1 + 2 and MP3 + 4a; MP1 + 2 and MP3 + 4a never fused with MA or CuA; CuA and CuP simple; organization of cubital and anal areas identical to those of Chrysopidae, i.e. presence of two cells c1 and c2, a strong angle in CuP close to its base, three simple anal veins; presence of a cell im well defined by MP1 + 2, MP3 + 4, and MP3 + 4a; hind wing triangular with a distinct tornus; hind wing venation more or less reduced, but similar to fore wing one; presence of a well-defined and elongate banksian cell b; prothorax elongate; fore legs raptorial, at least in Allopterus. The other body characters listed by Zhang (1991) in his diagnosis are not preserved in Spanish and Brazilian taxa. Thus, it is not possible to be accurate of their presence in Karenina and Triangulochrysopa n. gen.

The broad area between the branches of MP in the fore wings of the Allopteridae is not present in the Recent Chrysopidae, and in its two potential sister groups Osmylidae and Hemerobiidae (New 1983a, b, 1988, 1990). Thus this character is probably apomorphic for the Allopteridae, but it is also present in Tachinymphes. The presence of a well-defined vein MPspl is an apomorphy of Allopteridae (a distinctly more zigzagged and poorly defined vein is present in Tachinymphes). The presence of the 'X-crossing' of fore wing MP3 + 4 with CuA is a probable autapomorphy of the Allopteridae, although a similar structure exists in the hind wing of the Osmylidae. The elongate pronotum, present in all known Allopteridae is also autapomorphic. The raptorial fore legs is probably also an apomorphy but it is known with certainty only in Allopterus. Such spines are also present in the tachinymphid genus Tachinymphes that has not the other specialised allopterid characters (elongate pronotum, fore wing "X-crossing", vein MPspl). Allopterus mayorgai n. sp. has long antennae, unlike the short antennae of Tachinymphes (see below). More or less similar legs structures are convergently present in Mantispidae and Rachiberothidae.

Genus Allopterus Zhang 1991

Type species. *Allopterus luianus* Zhang 1991. Other species: *Allopterus mayorgai* n. sp.

New diagnosis. This genus can easily be separated from *Triangulochrysopa* n. gen., *Armandochrysopa* n. gen., and *Karenina* in its rounded and very short hind wing.

Allopterus luianus Zhang 1991

1991 Allopterus luianus Zhang 1106-1107, figs 1-2 (original description)

Material. Holotype specimen L88501-L88502, Shandong Provincial Museum, China.

Occurrence. Laiyang Formation, Late Jurassic. Laiyang, Shandong Province, China.

Allopterus mayorgai n. sp. (Figs 5.1, 5.2, 6.1, and 7.1)

1989 "Neuropteros planipenne" Martínez-Delclós, 72, fig. 13 2004 Neuroptera, Chysopidae Martínez-Delclòs *et al.*, 39, fig. 5D

Material. Holotype specimen LH-18570, paratype specimen LH-18571, both housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Etymology. After Mr. José Mayorga from Madrid, Spain.

Diagnosis. This new species differs from *Allopterus luianus* in the following characters: in fore wings, three to four rows of cells between RP and o.g. cross-veins, instead of six; five parallel gradate series of cross-veins instead of six-seven in *A. luianus;* RP with eleven to fourteen posterior branches, instead of sixteen; cell c1 distinctly broader and shorter; wings smaller than those of *A. luianus;* ratio hind wing length/fore wing length, 0.45 for *A. mayorgai* n. sp., 0.41 for *A. luianus.*

Description. The body of the holotype is badly preserved but the impressions of a fore- and a hind wing are clearly visible. The body and the fore wings of the paratype are better preserved but its hind wings are less visible.

Holotype (Figs. 5.1 and 7.1). Fore wing broad, rounded, 17.3 mm long, 6.9 mm wide; ratio length/width, 2.5; wing base poorly preserved; two anal veins AP and AA visible; AP nearly straight with a cross-vein between it and AA; AA slightly curved,



Figure 5

1, Allopterus mayorgai, LH-18570, habitus of the holotype. 2, A. mayorgai, LH-18571, paratype. 3, Triangulochrysopa sanzi, LH-8100, habitus of the holotype. 4, T. sanzi, LH-18572, paratype. 5, T. sanzi, 92/2/3, paratype. 6, Karenina breviptera, MNHN-DHT R.55200. 7, Armandochrysopa borschukewitzi, MNHN-DHT R.55201, habitus of the holotype. Scale bar: 10 mm.



1, *Allopterus mayorgai*, drawing of fore wing, paratype LH-18571. 2, *Triangulochrysopa sanzi*, drawing of fore wing, holotype LH-8100. Scale bars: 5 mm.

reaching posterior wing margin very obliquely and distally divided into two branches; AA and Cu well separated (minimal distance between Cu and AA, 0.4 mm), with two (or three) cross-veins between them; distance between AA and CuP somewhat smaller than the width of cell c1; Cu emerging from common stem R + M + Cu near wing base; Cu basally straight and a short distance from its base divided in two long parallel branches CuA and CuP, about 1.4 mm distal of its base; cross-vein 1m between Cu and MP clearly present, opposite base of MP; CuP basally at right angle with Cu and distally parallel to CuA; two cells c1 and c2; two dcc cells separated by a small vein; c1 four-sided, 1.9 mm long and 0.7 mm wide; c2 pentagonal, 2.3 mm long and 1.0 mm wide; CuA long and straight, distally fused with MP3 + 4, 2.4 mm distal of its base; two broad cells m1 and m2 separated by crossvein 1m; m1 1.0 mm long, 0.5 mm wide; m2 2.8 mm long, 0.6 mm wide; MP basally straight, separated from R + M 1.9 mm distal of wing base and divided into MP1 + 2 and MP3 + 4 2.1 mm distal of its base; proximal part of MP3 + 4 very short (0.8 mm long) and strongly diverging from MP1 + 2; a broad area between MP1 + 2 and MP3 + 4, with a zigzagged secondary vein MPspl between them; MP3 + 4b distally fused with CuA in their distal part; MP3 + 4 and MP3 + 4b (+ CuA) very strong, making a wide "X-crossing" over wing with basal part of CuA and MP3 + 4a in area between MP1 + 2 and MP3 + 4b (+ CuA), just above cell c2; MP3 + 4b (+ CuA) distally reaching posterior margin; cell im pentagonal, very long and broad, 2.1 mm long and 0.9 mm wide; cross-vein 3m separating im from more distal cells; distal area between MP1 + 2 and CuA very wide with three rows of cells; CuA never in contact with MP1 + 2 or MA; MP1 + 2 more or less parallel with MP3 + 4a and MP3 + 4b (+ CuA); vein Psc absent: no fusion between MP3 + 4 + CuA, MP1 + 2 and MA (see Adams 1967: fig. 44-45, 1996); MP1 + 2 slightly curved; general direction of the series of outer gradate cross-veins (o.g.) nearly perpendicular to MP1 + 2; MP1 + 2 not fused with MA, but more or less parallel, 0.3 mm apart; MA and RP basally fused, RP + MA emerging from R making an acute angle, 3.3 mm distal

of wing base; MA well-defined; no vein Psm as none of the branches of RP are fused with MA; RP with eleven parallel posterior branches directed towards posterior wing margin; main branch of RP slightly zigzagged; sixteen cross-veins present in area between RA and RP, all perpendicular to RA and RP; the two veins defined by the two series of the inner gradate cross-veins i.g. and outer gradate cross-veins (o.g.) well defined and slightly zigzagged; three rows of cells between posterior wing margin and o.g. cross-veins, two rows of cells between i.g. and o.g. cross-veins and two rows of cells between i.g. cross-veins and main branch of RP; i.g. and o.g. cross-veins distally convergent; RA and ScP parallel and 0.2 mm apart; RA and ScP apically fused, 2.6 mm basal of wing apex; in area between C and ScP, cross-veins opposite point of fusion of RA with ScP similar to those in more basal positions; no pterostigmal structure; about thirty straight cross-veins in costal area between ScP and C, perpendicular to ScP and C; costal area never widened, 0.5 mm wide; transverse basal subcostal vein bsx between R and ScP not preserved; no other distal cross-vein between RA and ScP; RA + ScP reaching wing apex; area between RA + ScP and C narrow, with simple and straight cross-veins; no visible tympanal organ; humeral vein simple, 1.9 mm distal of wing base; no tuft of long hairs at base of MP.

Hind wing broad and small, 2.2 times shorter than fore wing, 7.8 mm long, 3.9 mm wide; ratio length/width 2; venation reduced; hind wing triangular in shape with a distinct tornus in posterior wing margin between MP1 + 2 and MP3 + 4; anal area and CuP not preserved and only distal part of CuA visible; MP emerging from R 1.2 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 1.6 mm distal of its base; MP3 + 4 basally short and straight and distally zigzagged; angle between MP1 + 2 and MP3 + 4 very open; MP1 + 2 never fused with RP or MA; base of RP + MA distally recessed midway between wing base and apex, 4.1 mm from wing base; a broad cell between MP1 + 2 and RP + MA basal of base of RP + MA; cross-vein sxv between RP + MA and MP1 + 2 0.5 mm long; banksian cell b long and broad (1.6 mm long and 0.8 mm wide), nearly in middle of wing; MA short; RP with two short posterior branches; radial area very reduced, with only three crossveins between RA and RP; ScP and RA distally fused, 0.9 mm basal of wing apex; thirteen cross-veins between ScP and costal margin, all straight and perpendicular to ScP and C; costal area not widened, 0.3 mm wide; five short curved cross-veins in area between ScP + RA and wing apex but no preserved cross-vein in area between ScP and RA, 0.15 mm wide.

Paratype LH-18571 (Figs 5.2, 6.1). Distinctly larger than holotype; left fore wing 23.6 mm long, 5.9 mm wide; ratio length/width, 4.0; right fore wing 20.0 mm long, 6.6 mm wide; ratio length/width, 3.0; left wing distinctly longer and narrower than right wing because of diagenetic deformation, the right wing being the less deformed one; anal and cubital areas poorly preserved; very few differences with holotype fore wing, some of them, like apparent division of cell im into two smaller cells, being uncertain and due to fossilisation artefacts. Main differences are: o.g. cross-veins not zigzagged; i.g. cross-veins less welldefined; three or four rows of cells between o.g. cross-veins and posterior wing margin; cross-veins in area between ScP + RA and wing apex more numerous and longer; fourteen branches of RP instead of eleven. Hind wings more poorly preserved than in holotype, about 7.2 mm long and 3.4 mm wide; ratio length/width, 2.1. Preserved parts are similar to the holotype.

Head transverse, 1.0 mm long, 2.4 mm wide; basal part of antennae preserved, with numerous undifferentiated segments; thorax elongate; prothorax very long and narrow, longer than wide, 3.0 mm long, 1.0 mm wide; mesothorax 2.3 mm long, 2.7 mm wide, rather broad and spherical; metathorax poorly preserved but looking transverse; legs poorly preserved, but fore leg very elongate, with femur bearing strong spines, probably raptorial, inserted in anterior quarter of prothorax; abdomen elongate, about 8.1 mm long and 2.3 mm wide.

Discussion. There are few differences between these two specimens and we considere all of them compatible with intraspecific variations or fossilisation artefacts. Thus, these specimens probably belong to the same species, well characterized by the relative dimensions and triangular shape of the very small hind wings. Allopterus mayorgai n. sp. is clearly related to the Chinese Late Jurassic Allopterus luianus Zhang 1991. There are very few visible differences between them in the fore wings, enumerate in the diagnoses. These differences only justify a specific separation. The elongate pronotum, transverse head with large eyes and fore legs elongate bearing strong spines on femur suggest that this insect was carnivorous (possibly insectivorous), with strong convergencies with Mantispidae and Mantodea in its head, thorax and fore leg structures.

Genus Triangulochrysopa n. gen.

Type species. Triangulochrysopa sanzi n. sp.

Etymology. After *Chrysopa* and triangle in reference of the appearance of the hind wing.

Diagnosis. Hind wing triangular falcate, with a distinct tornus, and distinctly smaller than fore wing; anal area narrow; CuA and MP3 + 4 distally strongly fused, making a "Y-shaped" structure; MP1 + 2 not aligned but MP3 + 4 aligned with basal part of MP; a long and narrow banksian cell b. In both fore- and hind wing: ScP and RA distally fused; o.g. cross-veins very well-defined; costal areas never widened; fore wing: anal area wider than that of hind wing, with AP1, AP2 and AA distinctly separated; areas between AA and CuP and between CuP and CuA very broad; MP3 + 4b distally fused with CuA; presence of allopterid "X-crossing"; cell im quadrangular, wide but longer than broad; area between MP3 + 4b (+ CuA) and MP1 + 2 very wide; no distal fusion between MP3 + 4b (+ CuA) and MP1 + 2; a strong basal cross-vein between MA and MP1 + 2; area of RP very wide in the fore wing; cross-veins between ScP + RA and C short, straight and simple. Although some of these characters are probable symplesiomorphies, others, like triangular falcate hind wings, Y-shaped structure of CuA and MP3 + 4 in hind wings and the MA perpendicular to RP at its base are autapomorphies of Triangulochrysopa n. gen.

Triangulochrysopa sanzi n. sp. (Figs 5.3-5.5, 6.2, and 7.2-7.5)

Material. Holotype specimen LH-8110a/b, paratypes: specimens 92/2/3 (coll. Museo de Cuenca), LH-18572, LH-18573, LH-18574a/b, coll. Armando Diaz-Romeral, deposited in the Museo de Cuenca, housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. After Prof. Jose Luis Sanz from Madrid, Spain.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Diagnosis. That of the genus.

Description. Holotype LH-8110 (Figs 5.3, 6.2): Impression of a body with the four wings connected to the thorax; right wings overlapped and abnormally elongate due to tectonic deformation; only left hind wing base preserved; left fore wing wellpreserved, broad, 33.3 mm long, 10 mm wide; ratio length/width, 3.3; right fore wing distinctly narrower than left wing, due to fossilisation artefact, 39.2 mm long, about 9.0 mm wide, ratio length/width, 4.3; left wing apparently less deformed than right wing, thus only left fore wing dimensions given below; jugal lobe not preserved, fore wing bases destroyed; AP2 almost straight; AP1 and AP2 clearly separated, 1.0 mm apart, with a long crossvein between them; AP1 slightly curved, 4.5 mm long, reaching posterior wing margin very obliquely; only one cross-vein between AP1 and AA; AA straight, distally divided into two branches reaching posterior wing margin nearly at right angle; AA and Cu clearly separated, 0.4 mm apart, three cross-veins between CuP and AA and one between Cu and AA; distance between AA and CuP only a little smaller than width of cell c1; Cu basally straight and distally divided in two long parallel branches CuA and CuP, 2.5 mm distal of its base; basal transverse vein 1cu between Cu and AA (sensu Adams 1967) long, 0.6 mm long, 1.2 mm distal of wing base, very close to Cu base; CuP making a right angle with Cu and distally parallel with CuA; two cells c1 and c2 (sensu Brooks and Barnard 1990) and two cells dcc separated by a small longitudinal vein; c1 2.5 mm long and 1.0 mm wide; c2 2.9 mm long and 1.2 mm wide; CuA long, straight and strongly approximates MP3 + 4 3.4 mm distal of its origin; two broad cells m1 and m2 (sensu Brooks and Barnard 1990), separated by vein 1m (sensu Adams 1967); m1 nearly triangular, 1.6 mm long, 1.7 mm wide; m2 3.0 mm long, 1.7 mm wide; 1m very long, 1.7 mm long, opposite base of MP; MP emerging from R 4.3 mm distal of wing base, straight and distally divided into MP1 + 2 and MP3 + 4, 2.6 mm distal of its base; a broad area between MP1 + 2 and MP3 + 4a, with a zigzagged secondary MPspl between them; basal part of MP3 + 4 very short, 1.1 mm long and strongly diverging from MP1 + 2; MP3 + 4b distally fused with CuA; MP3 + 4 and MP3 + 4b (+ CuA) very strong; presence of allopterid 'X-crossing', just above cell c2; distal portion of MP3 + 4a more or less parallel with MP1 + 2, zigzagged and distinctly weaker than its proximal part and CuA; two elongate cells between MP1 + 2 and MP3 + 4a, the more proximal of these cells being im, very long, 2.6 mm long and 1.1 mm wide; cross-vein 3m

(sensu Adams 1967) separating im and the more distal cell; area between MP1 + 2 and MP3 + 4b (+ CuA) very wide with three rows of cells; CuA never fused with MP1 + 2 or MA; MP1 + 2 parallel with MP3 + 4b (+ CuA); Psc absent; MP1 + 2 slightly curved, becoming parallel with wing margin and continuing into the outer gradate cross-veins; MP1 + 2 more or less distally fused with MA at base of o.g. cross-veins; MA and MP1 + 2 nearly parallel, basal of o.g. cross-veins, minimal distance between MA and MP1 + 2 being 0.3 mm; MA and RP basally fused; RP + MA emerging from R with an acute angle, 5.3 mm distal of wing base; MA nearly perpendicular to RP at base; no definite Psm as none of the branches of RP is fused with MA; RP divided into eighteen parallel branches directed towards posterior wing margin; main branch of RP distally slightly zigzagged and basally straight; twenty-six cross-veins between RA and RP, all perpendicular to RA and RP; i.g. cross-veins are less well-defined than o.g. crossveins (sensu Brooks and Barnard 1990) but both very numerous; four or five rows of cells between wing margin and o.g. crossveins, two to four rows of cells between i.g. and o.g. cross-veins and four rows of cells between i.g. cross-veins and main branch of RP; i.g. and o.g. cross-veins distally convergent; RA and ScP basally parallel, 0.2 mm apart and distally fused, 5.2 mm basal of wing apex; in left fore wing, costal cross-veins opposite point of fusion of RA and ScP similar to other cross-veins of costal area, with no definite pterostigmal structure; in right fore wing, area opposite fusion of RA and ScP reticulate, with many small cells between cross-veins; about forty straight cross-veins in costal area, perpendicular to ScP and to costal wing margin; transverse basal subcostal vein (vein bsx sensu Brooks and Barnard 1990) between R and ScP not preserved, if present; no other visible distal crossvein between RA and ScP; RA + Sc reaching wing apex; a wide area between RA + ScP and costal wing margin, with seven rows of irregular cells and six sigmoidal secondary veins; no visible tympanal organ; humeral vein simple, 1.2 mm distal of wing base; a tuft of long hairs (2.1 mm long) at base of MP.

Hind wing. Only basal portion of left hind wing and apical portion of right hind wing preserved; right hind wing wide, about 31.6 mm long, 5.7 mm wide; ratio length/width, 5.5; hind wing more or less triangular falcate; anal veins not preserved; CuP and CuA parallel but base of CuP not preserved; cell c1 + 2 between CuP and CuA long and narrow, 3.0 mm long and 0.6 mm wide and a short cell along posterior wing margin; cell m2 between CuA and MP long and narrow, 5.4 mm long and 0.5 mm wide; cell m1 not preserved; MP emerging from R 2.1 mm distal of wing base; MP divided in MP1 + 2 and MP3 + 4, 2.9 mm distally; MP3 + 4 strongly approximating CuA 2.5 mm distally but diverging again distally, with four rows of cells between them along posterior wing margin; MP1 + 2 long, basally straight and distally zigzagged; MPspl long curved, beginning 1.6 mm distal of MP3 + 4 base; two rows of cells between MP1 + 2 and MPspl and one row between MPspl and MP3 + 4; RP + MA separating from RA 4.6 mm distal of wing base; MA separating from RP 2.8 mm distally; a short, 0.6 mm long, cross-vein sxv between RP + MA and MP1 + 2, 1.3 mm distal of base of RP + MA; a banksian cell b, 3.2 mm long, 0.8 mm wide, closed by sxv and MA, between MP1 + 2 and RP + MA; MA long, not distally fused with MP1 + 2; MA and MP1 + 2 more or less parallel with branches of RP; main branch of RP nearly straight; many posterior branches of RP, five of them being visible in left wing and eleven in right wing, but probably fifteen to seventeen; numerous, about nine to ten, rows of cells in radial area between RP and posterior wing margin; area between RP and RA 1.1 mm wide, with about fifteen to twenty straight and short cross-veins; area between RA and ScP not well preserved, thus the presence of cross-veins is impossible to determine, width of this area 0.3 mm; veins RA and ScP distally fused, 2.8 mm basal of wing apex (in the right wing); RA + ScP reaching wing apex; area between ScP and C narrow, 0.5 mm wide (right wing), never widened, with more than twenty six crossveins basal of fusion between ScP and RA; area between RA + ScP and C not well preserved but with 5-7 sigmoidal transverse veins, 4.0 mm long (right wing), with many cross-veins between them.

Specimen 92/2/3 (Figs. 5.5 and 7.5-7.6). Impression of thorax and abdomen with four wings in connexion; apical part of fore wings missing but hind wings complete; right fore wing deformed, elongate by fossilisation; left fore wing normal but with its base difficult to interpret because of hind wing overlapping it; venation very similar to that of LH-8110; main differences as follows: length of preserved part of fore wing 23.8 mm, probable length 30-35 mm, width 8.8 mm, ratio length/width 3.4-3.9; wing wide; anal area similar to that of LH-8110; structures of areas between CuA, CuP and AA very confuse because of presence of overlapping hind wing; distal fusion of MP3 + 4b and CuA and areas between MP1 + 2, MP3 + 4 and CuA similar to those of LH-8110; cell im shorter than that of LH-8110, 1.9 mm long, 1 mm wide; MA not clearly fused with MP1 + 2 but MA beginning at right angle with RP + MA and cross-vein between MA and MP1 + 2 directly aligned with base of MA, as strong as base of MA, and distinctly stronger than distal portion of MA (Fig. 7.6); radial area similar to that of LH-8110, with 3-4 rows of cells between RP and i.g. cross-veins, 3-5 rows of cells between i.g. and o.g. cross-veins and five rows of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins distally convergent; apparently some small cross-veins between RA and ScP.

Hind wing distinctly triangular falcate, 19.8 mm long, 5.4 mm wide, ratio length/width, 3.6; structure of anal area very confuse because of presence of overlapped fore wing; a similar long and narrow cell m2 but apparently crossed by a short vein, perpendicular to MP and CuA; cell m1 visible at base of wing; a supplementary cross-vein between MA and MP1 + 2, near base of MA; vein sxv distinctly more oblique than in LH-18572, 1.0 mm long; banksian cell b 2.4 mm long, 0.9 mm wide; area distal of base of MA partly aberrant as branches of RP are very confuse and abnormal; MA and MP1 + 2 apparently basally separated and only confluent in o.g. cross-veins; o.g. cross-veins basally better defined than those of LH-8110a; three rows of cells between RP and o.g. cross-veins; RA and ScP fused 20.0 mm distal of wing base and 1.8 mm basal of apex, nearer to apex than for LH8110a; apical area also narrower, with shorter branches of RA + ScP, these branches being nearly straight, simple and without any cross-veins between them. The venation of specimen 92/2/3 is much more similar to that of LH-18572 than to that LH-8110a.

Specimen LH-18572 (Figs 5.5, 7.4). Impression of a nearly complete specimen with the four wings in connexion with the body but they are partly overlapping. The differences with the holotype specimen are as follows: fore wing distinctly narrower than that of LH-8110a; fore wing 39.2 mm long, 8.1 mm wide; ratio length/width 4.8; fore wing narrow; no visible jugal lobe at wing base; veins AP2, AP1 and AA clearly visible; two short cross-veins between AP2 and AP1; distance between AP2 and AP1 along wing margin 2 mm; AP1 nearly straight; one crossvein between CuP and AA and another one between Cu and AA; cell c1 2.9 mm long, 0.8 mm wide; cell c2 2.7 mm long, 1.1 mm wide; three cells dcc separated by a small longitudinal vein and a small cross-vein; CuA long and straight, fused with MP3 + 4b 6.6 mm distal of its origin; length of m1 2.1 mm, width 1.2 mm; length of m2 4.4 mm, width 1.0 mm; cross-vein 1m very long, 1.2 mm long; MP separating from R 3.5 mm distal of wing base, straight, divided into MP1 + 2 and MP3 + 4 3.3 mm distal of its base; cell im 3.1 mm long, 1.0 mm wide; RP + MA separating from R 5.1 mm distal of wing base; fore wing i.g. cross-veins of LH-18572 less distinct than those of LH-8110a; maximal width between RA and ScP 0.3 mm, but distally fused, 4.9 mm basal of wing apex; humeral vein 3.1 mm distal of wing base; costal area between ScP and C not broadened, 0.9 mm wide.

Hind wings distinctly shorter than fore wings, triangular falcate; probable length of right hind wing circa 21.6 mm, width 7.1 mm, ratio length/width 3.0; cell c2 2.1 mm long and 0.6 mm wide, c1 basally broken; also a short cell along posterior wing margin between CuP and CuA; a long and narrow cell m2 + m1 between CuA and MP, 4.6 mm long, 0.5 mm wide; cross-vein between m2 and m1 not preserved; MP separating from R 1.2 mm distal of wing base; MP divided in MP1 + 2 and MP3 + 4, 1.7 mm distally; MPspl beginning 2.6 mm distal of MP3 + 4 base; RP + MA separating from RA 4.0 mm distal of wing base; MA long, never fused with MP1 + 2; MA and MP1 + 2 being more or less parallel; main branch of RP basally nearly straight but distally zigzagged; RP with thirteen posterior branches; numerous, about six to eight, rows of cells in radial area between RP and posterior wing margin; hind wing RP area of LH-18572 narrower than that of LH-8110a; area between RA and ScP 0.3 mm wide, with no preserved cross-vein between ScP and RA; RA and ScP distally fused, 2.5 mm basal of wing apex, area between RA + ScP and C not well preserved but with 5-7 short transverse veins with no visible cross-veins between them. Pronotum elongate and narrow, 4.0 mm long, 1.5 mm wide.

Specimen LH-18573 (Figs 7.2-7.3). The fore wing venation is very similar to that of LH-8110. Fore wing length 29.2 mm, width 10.0 mm, ratio length/width, 2.9; this specimen has the main characters of the species, i.e. very strong CuA, basal part of MP and fusion between CuA and MP3 + 4b identical to those of other specimens; distal part of MP1 + 2 distinctly weaker than MP3 + 4b (+ CuA); also vein MA nearly perpendicular to RP at its base and its distal part distinctly weaker than first crossvein between MA and MP1 + 2.

Specimen LH-18574 alb. Impression of thorax and abdomen with wings in connexion; posterior part of fore wings deteriorated but the hind wings complete; venation very similar to that of LH-8110, with main differences listed below: fore wing length *circa* 27.5 mm, width *circa* 8.4 mm, ratio length/width 3.3; fore wing broad; anal area and area between CuA, CuP and AA not preserved; distal fusion between MP3 + 4 and CuA and areas between MP1 + 2, MP3 + 4 and CuA similar to those of LH-8110; cell im shorter than that of LH-8110, 2.3 mm long, 1.1 mm wide; MA similar, not fused with MP1 + 2 but MA beginning at right angle on RP + MA, and cross-vein between MA and MP1 + 2 directly aligned with base of MA, as strong as MA base, and distinctly stronger than distal portion of MA; radial area not well preserved but similar to that of LH-8110, with 3-4 rows of cells between RP and i.g. cross-veins, 3-5 rows of cells between i.g. and o.g. cross-veins and five rows of cells between RP and ScP but this is not certain.

Hind wing distinctly triangular falcate, 18.1 mm long, 6.9 mm wide, ratio length/width 2.6; structure of anal area confuse but very narrow, 0.7 mm wide between CuA and posterior wing margin; a similar long and narrow cell m2, 4.2 mm long, 0.6 mm wide, crossed by a short vein, perpendicular to MP and CuA; cell m1 visible at wing base; a supplementary cross-vein between RP + MA and MP, near base of MP; anterior branch MP1 + 2 of MP angular, with a supplementary crossvein between it and RP + MA; vein sxv oblique, 0.7 mm long; banksian cell b 2.9 mm long, 0.8 mm wide, area distal of base of MA well preserved: MA and MP1 + 2 well separated and only confluent in o.g. cross-veins; o.g. cross-veins basally better defined than those of LH8110a; four rows of cells between RP and o.g. cross-veins instead of six; RA and ScP fused 17.0 mm distal of wing base and 1.8 mm basal of wing apex, nearer to apex than in LH8110a; apical area also narrower, with shorter transverse veins between C and RA + ScP, nearly straight, very simple and without any cross-veins between them. The venation of specimen LH-18574a/b is very similar to that of specimen 92/2/3.

Discussion. All these specimens are clearly related and differ in few characters: possible fusion of MA with MP1 + 2 in hind wing; in hind wing, transverse veins in apical area between RA + ScP and C more or less long; i.g. cross-veins more or less well defined in fore wing; fore wings more or less broad; in hind wing, number of rows of cells in radial area between RP and o.g. cross-veins; vein sxv more or less oblique in hind wing. These differences are of minor importance compared to the numerous important shared characters, listed above in the diagnosis of the genus.

Genus *Karenina* Martins-Neto 1997 (in Allopteridae n. sit.)

Type species. Karenina breviptera Martins-Neto 1997.

New diagnosis. *Karenina* differs from *Allopterus* in its elongate hind wing. The differences between *Karenina* and *Triangulo-chrysopa* n. gen. are as follows: fore wing cell c1 and c2 nearly of the same length in *Triangulochrysopa* n. gen., instead of c1 distinctly shorter than c2 in *Karenina;* fore wing MA separating



Figure 7

Figure / 1, *Allopterus mayorgai*, LH-18570, fore and hind wings of the holotype. 2, *Triangulochysopa sanzi*, LH-18573, paratype fore wing. 3, *T. sanzi*, LH-18573, basal part of the fore wing, showing the relationship between RP, MA, and MP veins. 4, *T. sanzi*, LH-18572, paratype hind wing. 5, *T. sanzi*, 92/2/3, paratype hind wing. 6, *T. sanzi*, 92/2/3, basal part of the fore wing showing the relationship between the veins RA, RP, and MA. 7, *Karenina breviptera*, MNHN-DHT R.55200, left fore wing. 9, *K. breviptera*, MNHN-DHT R.55200, left fore wing. 9, *K. breviptera*, MNHN-DHT R.55201, holotype right fore wing. *11, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *13, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *13, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *14, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *13, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *14, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *14, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *13, A. borschukewitzi*, MNHN-DHT R.55201, holotype left fore wing. *14, MNHN-DHT* R.55201, holotype left for Scale bars: 1 mm.

from RP at level of cell im in *Triangulochrysopa* n. gen., instead of four cells distally in *Karenina;* fore wing cell im longer than broad in *Triangulochrysopa* n. gen., unlike in *Karenina;* fore wing MP3 + 4 strongly approximating CuA but not fused with it; hind wing MA separating from RP at level of cell im in *Triangulochrysopa* n. gen., instead of three cells distally in *Karenina;* hind wing less triangular in *Karenina* than in *Triangulochrysopa* n. gen.

Karenina breviptera Martins-Neto 1997 (Figs 5.6, and 7.7-7.9)

1997 Karenina breviptera Martins-Neto, 74, fig. 1B-C (original description)

Material. Holotype specimen AMNH-44411, American Museum of Natural History, New York, USA. Other new specimen: MNHN-DHT R.55200, deposited in the Laboratory of Palaeontology, Muséum National d'Histoire Naturelle, Paris, France.

Occurrence. Crato Formation, Aptian. Santana do Cariri, Araripe Basin, Brazil.

Redescription. The original description is based on the holotype specimen, which is clearly less complete than the new specimen R.55200 described below.

Fore wing wide but elongate, circa 26 mm long, against 25 mm in holotype, 7.8 mm wide, ratio length/width, 3.3; posterior part of wing base poorly preserved; anal veins not clearly visible; AA and Cu well separated; Cu separated from R + M + Cu near wing base; Cu basally straight and distally divided in two long parallel branches CuA and CuP, about 1.2 mm distal of its base; cross-vein 1m between Cu and MP clearly present, opposite base of MP; CuP basally at right angle with Cu and distally parallel to CuA; two cells c1 and c2; probably one dcc cell; c1 four-sided, 1.2 mm long, 0.5 mm wide; c2 pentagonal, 2.0 mm long, 0.8 mm wide; CuA long and straight, distally strongly approximating MP3 + 4 but not touching it in specimen R.55200, 3.1 mm distal of its base; two broad cells m1 and m2 separated by cross-vein 1m; cell m1 about 1 mm long, 0.8 mm wide; m2 3.0 mm long, 0.7 mm wide; MP basally straight, emerging from R about 2.5 mm distal of wing base and divided into MP1 + 2 and MP3 + 4 2.0 mm distal of its base; proximal part of MP3 + 4 very short, 1.0 mm long, and strongly diverging from MP1 + 2; MP3 + 4 distally straight; a short crossvein between MP3 + 4 and CuA; presence of allopterid "X-crossing" constituted by MP3 + 4, cross-vein between MP3 + 4 and CuA and secondary MPspl, MPspl zigzagged; MP3 + 4 distally reaching posterior margin; cell im four-sided, nearly as wide as long, 1.1 mm long, 1.0 mm wide; cross-vein 3m separating im from more distal cells; area between MP3 + 4 and CuA with one row of cells; area between MP3 + 4 and MP1 + 2 distally widened with three rows of cells; CuA never in contact with MP3 + 4, MP1 + 2 or MA; MP1 + 2 parallel with MP3 + 4 and CuA; vein Psc absent: no fusion between CuA, MP3 + 4, MP1 + 2 and MA; MP1 + 2 slightly curved; outer gradate cross-veins all nearly aligned and nearly perpendicular to MP1 + 2; MP1 + 2 not fused with MA, but more or less parallel, about 1.2 mm apart; MA

and RP basally fused, RP + MA emerging from R + M making an acute angle, circa 3.8 mm distal of wing base; MA emerging from RP + MA 5.0 mm distal of precedent point; MA welldefined; first cross-vein between MP1 + 2 and MA not very oblique, no vein Psm; all branches of RP not fused with MA; RP with eight parallel branches directed towards posterior wing margin; main branch of RP slightly zigzagged; twelve cross-veins present in area between RA and RP, all perpendicular to RA and RP; inner gradate cross-veins and outer gradate cross-veins welldefined and slightly zigzagged; four rows of cells between posterior wing margin and o.g. cross-veins, two rows of cells between i.g. and o.g. cross-veins and one row of cells between i.g. crossveins and main branch of RP; i.g. and o.g. cross-veins distally convergent; RA and ScP parallel and 0.37 mm apart; RA and ScP apically fused, 3.5 mm basal of wing apex; cross-veins opposite fusion of RA with ScP similar to those in costal area; no clear pterostigmal structure; about thirty straight cross-veins in costal area between ScP and C, perpendicular to ScP and C; costal area never widened, 1.1 mm wide; transverse basal subcostal vein bsx between R and ScP not preserved or absent; no other distal crossvein between RA and ScP; RA + ScP reaching wing apex; area between RA + ScP and C not widened, narrow, 0.8 mm wide, with simple and straight cross-veins; no visible tympanal organ; humeral vein simple, about 0.2 mm distal of wing base; no tuft of long hairs at base of MP.

Hind wing 1.6 times shorter than fore wing, about 16 mm long, about 4.8 mm wide, ratio length/width, 3.3; venation not reduced; hind wing triangular in shape; posterior wing margin not preserved but general shape of wing suggesting presence of a distinct tornus in posterior wing margin between MP1 + 2 and MP3 + 4; anal area and CuP not preserved and only a part of CuA visible, also unknown in holotype; MP emerging from R about 1 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 1 mm distal of its base; MP3 + 4 basally straight and distally zigzagged; angle between MP1 + 2 and MP3 + 4 not very open; MP1 + 2 never fused with RP or MA; base of RP + MA about 3.2 mm from wing base; a broad cell between MP1 + 2 and RP + MA basal of base of RP + MA; cross-vein sxv between RP + MA and MP1 + 2 0.5 mm long, perpendicular to both veins, no vein Psm; banksian cell b long and broad, 1.9 mm long and 0.6 mm wide, nearly in middle of wing; MA parallel at length with MP1 + 2; RP with six long posterior branches; radial area with i.g. and o.g. cross-veins parallel, with two rows of cells between them; o.g. cross-veins not aligned as in fore wing; about ten cross-veins between RA and RP; ScP and RA distally fused, 1.4 mm basal of wing apex; twenty three cross-veins between ScP and costal margin, all straight and perpendicular to ScP and C; costal area not widened, 0.5 mm wide; four short curved crossveins in area between ScP + RA and wing apex but no preserved cross-vein in area between ScP and RA, 0.2 mm wide.

Body rather poorly preserved. Length of body *circa* 23 mm, of abdomen *circa* 14 mm; pronotum elongate, about 3 mm long.

Discussion. Although the holotype is more poorly preserved than the specimen R.55200, there are very few differences between the common preserved parts of the two specimens. The wing dimensions are also similar, viz. holotype fore wing length, 25 mm and hind

wing length, 16 mm against 26 mm and 16 mm respectively for specimen R.55200. Thus, we propose to consider that the two specimens belong to the same species. Martins-Neto (1997, 2000) attributed Karenina to the Ascalaphidae subfamily uncertain. Martins-Neto inaccurately indicated that the general aspect of the wing venation of Karenina is close to that of the recent taxon Fillus paradoxus (Wheele 1908) because the homologies of several veins are not respected: among other structures, Fillus has a fore wing vein with a strong fork but it is not the division of MP into MP1 + 2 and MP3 + 4 as in Karenina, but the division of CuA into two secondary branches CuA1 and CuA2; the vein MP of Fillus is simple and long parallel with CuA; vein MP3 + 4 is a very short oblique vein in Fillus, as in Ascalaphidae, Nemopteridae, Myrmeleontidae and Nymphidae (Penny 1981; New 1989; Aspöck 1995; Adams 1996). The differences with Triangulochrysopa n. gen. are listed above in the new diagnosis of Karenina.

Genus Armandochrysopa n. gen.

Type species. Armandochrysopa borschukewitzi n. sp., other species: Armandochrysopa inexpecta n. sp.

Etymology. After Mr. Armando Diaz-Romeral from Cuenca (Spain), who kindly gave us several specimens for this study, and *Chrysopa*.

Diagnosis. Closely similar to *Karenina*, the main differences being as follows: fore wing MP3 + 4 meeting CuA in one point, instead of being simply connected by a short cross-vein as in *Karenina* (visible in both holotype and new specimen of *Karenina breviptera*); fore wing i.g. cross-veins less well aligned than in *Karenina;* in hind wing, first cross-vein between MP1 + 2 and MA more distinctly oblique instead of being perpendicular to both veins, thus MA is apparently branching on MP1 + 2; hind wing less triangular than in *Karenina*.

Armandochrysopa borschukewitzi n. sp. (Figs 5.7, and 7.10-7.13)

Material. Holotype specimen MNHN-DHT R.55201, coll. Borschukewitz, Paleontological Laboratory, Muséum National d'Histoire Naturelle, Paris, France.

Etymology. After Mr. Borschukewitz who kindly donated an important collection of fossil insects to the Museum National d'Histoire Naturelle, Paris.

Occurrence. Crato Formation, Aptian, Santana do Cariri, Araripe Basin, Brazil.

Diagnosis. This species is very similar to *A. inexpecta* sp. nov, the main differences being as follows: all wings distinctly shorter; vein Psm more poorly defined in fore wing; only ten cross-veins between RA and RP in fore wing, instead of thirteen in *A. inexpecta* n. sp.

Description. Body poorly preserved and useless; fore wing wide but elongate, circa 16.0 mm long, 5.3 mm wide, ratio length/width 3.0; posterior part of wing base poorly preserved; anal veins not clearly visible; AA and Cu probably well separated; Cu probably emerging from R + M near wing base; Cu distally divided in two long parallel branches CuA and CuP; cross vein 1m between Cu and MP not preserved; two cells c1 and c2; one dcc cell; c2 pentagonal; CuA long and straight, distally fused with MP3 + 4b, circa 3.7 mm distal of its base; cross-vein 1m not preserved; cell m2 2.5 mm long, 0.7 mm wide; MP basally straight, emerging from R + M circa 1.6 mm distal of wing base and divided into MP1 + 2 and MP3 + 4 1.7 mm distal of its base; part of MP3 + 4 proximal of its division into MP3 + 4a and MP3 + 4b rather short, 0.9 mm long, and strongly diverging from MP1 + 2; a zigzagged secondary vein between MP1 + 2 and MP3 + 4a; MP3 + 4a distally straight; MP3 + 4b distally meeting CuA in one point; presence of allopterid "Xcrossing", distal of cell c2; MP3 + 4b (+ CuA) distally reaching posterior margin; cell im broad quadrangular, 1.3 mm long, 1.0 mm wide; cross-vein 3m separating im from more distal cells; area between MP1 + 2 and MP3 + 4b (+ CuA) distally widened with three rows of cells; MP3 + 4b (+ CuA) never in contact with MP1 + 2 or MA; MP1 + 2 parallel with MP3 + 4a and MP3 + 4b (+ CuA); vein Psc absent: no fusion between MP3 + 4a and MP1 + 2; outer gradate cross-veins all nearly aligned and with general direction nearly perpendicular to MP1 + 2; MA and RP basally fused, RP + MA emerging from R making an acute angle, circa 3.8 mm distal of wing base; MA emerging from RP + MA 5.0 mm distal of precedent point; MA welldefined; MP1 + 2 not fused with MA, but more or less parallel, about 1.2 mm apart; second cross-vein between MP1 + 2 and MA distinctly oblique, thus a very rudimentary vein Psm; all branches of RP not fused with MA; RP divided into seven parallel branches directed towards posterior wing margin; RP slightly zigzagged; eleven cross-veins present in area between RA and RP, all perpendicular to RA and RP; series of inner gradate crossveins and outer gradate cross-veins well defined and slightly zigzagged; three rows of cells between posterior wing margin and o.g. cross-veins, two rows of cells between i.g. and o.g. crossveins and two rows of cells between i.g. cross-veins and main branch of RP; RA and ScP parallel and 0.4 mm apart; RA and ScP apically fused, 2.4 mm basal of wing apex; cross-veins in area between C and ScP + RA similar to those in costal area; no clear pterostigmal structure; 20-30 straight cross-veins in area between ScP and C, perpendicular to ScP and C; costal area never widened, 0.5 mm wide; transverse basal subcostal vein bsx between R and ScP not preserved or absent; no other distal crossvein between RA and ScP; RA + ScP reaching wing apex; area between RA + ScP and C not widened, narrow, 0.8 mm wide, with simple and straight cross-veins; no visible tympanal organ; humeral vein not preserved; no tuft of long hairs at base of MP.

Hind wing 1.2 times shorter than fore wing, *circa* 13.7 mm long, *circa* 3.2 mm wide, ratio length/width, 4.3; venation not reduced; hind wing elongate, apparently not triangular in shape; posterior wing margin not preserved but general shape of wing suggesting absence of a distinct tornus in posterior wing margin between MP1 + 2 and MP3 + 4; anal area completely reduced, with no anal vein; Cu basally straight and distally divided in two

long parallel branches CuA and CuP, about 0.5 mm distal of its base; cross-vein 1m between Cu and MP clearly present, opposite base of MP but slightly distal of base of CuP; CuP basally at right angle with Cu and distally parallel to CuA; two cells c1 and c2; one dcc cell; c1 four-sided, 1.3 mm long and 0.4 mm wide; c2 pentagonal, 0.8 mm long and 0.4 mm wide; CuA long and straight, never fused with MP3 + 4; MP emerging from R about 0.9 mm distal of wing base; MP divided into MP1 + 2 and MP3



Figure 8

I, Armandochrysopa inexpecta, LH-18575, habitus of the holotype. *2, Tachinymphes magnificus*, MNHN-DHT R.55225, holotype. *3, Tachinymphes paicheleri*, LH-18576, habitus of the holotype. *4, T. paicheleri*, LH-18577, paratype isolate wing. *5, Tachinymphes penalveri*, LH-18585, holotype. *6, T. penalveri*, LH-18586, paratype. Scale bars: 10 mm.

+ 4 2.0 mm distal of its base; MP3 + 4 zigzagged; angle between MP1 + 2 and MP3 + 4 not very open; MP1 + 2 never fused with RP or MA; base of RP + MA about 3.1 mm from wing base; a broad cell between MP1 + 2 and RP + MA basal of base of RP + MA; cross-vein sxv between RP + MA and MP1 + 2 0.3 mm long and distinctly oblique, thus presence of a rudimentary vein Psm; banksian cell b long and broad, 1.6 mm long and 0.4 mm wide, nearly in middle of wing; MA parallel at length with MP1 + 2; RP with six long posterior branches; radial area with i.g. and o.g. cross-veins parallel, with two rows of cells between them; eight cross-veins between RA and RP; ScP and RA distally fused, 1.6 mm basal of wing apex; 20 cross-veins between ScP and costal margin, all straight and perpendicular to ScP and C; costal area not widened, 0.3 mm wide; six short curved cross-veins in area between ScP + RA and wing apex but no preserved cross-vein in area between ScP and RA, 0.2 mm wide.

Body rather poorly preserved, *circa* 17.0 mm long, abdomen *circa* 9.0 mm long; pronotum elongate, about 3.0 mm long.

Armandochrysopa inexpecta n. sp. (Figs 8.1, and 9.1-9.2)

Material. Holotype specimen LH-18575, housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. *Inexpecta* in reference to presence of a representative of this Brazilian genus in the Spanish Early Cretaceous.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas, Cuenca Province, Spain.

Remark. The differences with *Armandochrysopa borschukewitzi* n. sp. are listed in the diagnosis of this last species.

Description. Impression of abdomen and thorax with four wings in connection; wings more or less overlapping; body not well preserved; right fore wing basally abnormal, deformed, but left fore wing normal; fore wing 23.0 mm long, 5.6 mm wide, ratio length/width 4.1; fore wing narrow and elongate; costal area between C and ScP not widened, maximal width 0.6 mm; 30 cross-veins of costal area basal of fusion between RA and ScP, all perpendicular to ScP and C; area between ScP and RA rather wide, 0.1 mm wide; ScP and RA distally fused, 1.5 mm basal of wing apex; no sclerotized pterostigmal structure; cross-veins between ScP and C simple, slightly undulate in area between RA + ScP and wing apex, with no cross-veins between them; RP + MA separating from R 3.5 mm distal of wing base; MA separating from RP 3.8 mm distally; free part of MA short, 0.6 mm long; first basal cross-vein between MA and MP1 + 2 distinctly oblique and aligned with distal part of MA, to constitute base of pseudo-vein Psm; Psm basally rather straight and aligned with RP; distally, i.g. cross-veins aligned with Psm; RP with fourteen branches; a supplementary series of gradate cross-veins between to RP and i.g.; MP separating from R + M 2.5 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 1.7 mm distal of its base; MP1 + 2 regularly curved; vein MPspl between

MP1 + 2 and MP3 + 4a well defined and rather weakly zigzagged; MP3 + 4 strongly diverging from MP1 + 2, MP3 + 4b connected with CuA in one point, 0.9 mm distal of MP3 + 4 base; allopterid 'X-crossing' structure present; MP3 + 4a distally weakly zigzagged; cell im long and quadrangular, 1.7 mm long and 0.7 mm wide on left wing, 2.2 mm long and 0.6 mm wide on right wing; no clear vein Psc; o.g. cross-veins well aligned; one or two supplementary rows of gradate veins between o.g. cross-veins and posterior fore wing margin; two (distally one) rows of cells between i.g. cross-veins and o.g. cross-veins; i.g. and o.g. cross-veins being distally convergent; base of CuA near wing base; cross-vein 1m between CuA and MP opposite base of MP; cell m1 not 1.1 mm long, cell m2 is elongate, 2.7 mm long and 0.5 mm wide; CuP separating from CuA near wing base; c1 1.2 mm long, 0.4 mm wide; length of c2, 1.6 mm; width, 0.6 mm; CuP with two simple branches reaching posterior wing margin; AA two-branched and well separated from CuP, with two cross-veins between them; AP is not well preserved.

Hind wing 1.1 times shorter than fore wing, 20.7 mm long, 4.8 mm wide, ratio length/width 4.3; hind wing shorter, broader than fore wing; costal area as narrow as that of fore wing, 0.5 mm wide, with about thirty cross-veins basal of fusion between ScP and RA; no defined sclerotized pterostigma; apical cross-veins between ScP + RA and C simple and less undulated than in fore wing; vein RP + MA separating from RA 2.1 mm distal of wing base; no cross-vein between RP + MA and MP basal of base of MA; vein sxv between MP and MA 0.3 mm long and very oblique; banksian cell b 1.9 mm long, 0.3 mm wide, narrow and pentagonal; MA and RP divided 2.5 mm distal of base of RP + MA; like in fore wing, a supplementary series of gradate crossveins between RP and i.g.; MP1 + 2 and MA not clearly fused together to constitute vein Psm, a very oblique and short crossvein between them; Psm and distally i.g. cross-veins very welldefined and well aligned; i.g. and supplementary series of gradate cross-veins well-parallel; MP separating from R + M 0.1 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4, 1.5 mm distally; MP1 + 2 basally straight and distally curved; MP3 + 4 strongly zigzagged; basal cross-vein between MP3 + 4 and CuA long, 0.5 mm long; base of CuP opposite that of MP; cell c1 1.2 mm long, 0.6 mm wide; cell c2 1.1 mm long, 0.5 mm wide; o.g. cross-veins well defined, distally aligned and nearly reaching wing apex; one supplementary incomplete zigzagged row of gradate veins parallel with Psm and o.g. cross-veins in middle part of wing; also 4-5 rows of cells between posterior wing margin and o.g. cross-veins; two (distally one) rows of cells between o.g. and he i.g. cross-veins, i.g. and o.g. cross-veins being distally convergent.

Pronotum elongate, 3.5 mm, 1.5 mm wide; head deformed, 3.6 mm long, 2.8 mm wide; eyes rounded, 0.8 mm wide, 1.2 mm apart; body strongly deformed, but *circa* 27.0 mm long; abdomen 12.0 mm long, 4.0 mm wide.

Family MESOCHRYSOPIDAE Handlirsch 1906

Type genus. *Mesochrysopa* Handlirsch 1906. Other genera: *Aristenymphes* Panfilov, 1980; *Macronymphes* Panfilov 1980, and *Protoaristenymphes* Nel & Henrotay 1994.

New diagnosis. The status of this group greatly varied in the literature (see summary in Nel and Henrotay 1994). Previous diagnoses were based on plesiomorphic characters. The Mesochrysopidae n. sensu is a monophyletic group characterized by combination of "presence of a very long hypostigmatic cell in the distal part of the area between RA and RP", together with 'numerous cross-veins in the basal part of this area'. This elongate cell is not preserved in the type specimen of Protoaristenymphes but this genus is very close to Aristenymphes. Liassochrysa has also such a long cell but it has very few crossveins in this area and its anal veins strongly differ from those of the Mesochrysopidae. The Mesochrysopidae, except maybe Mesochrysopa, share with the Limaiidae the very short fore wing cell c1. Other characters of the Mesochrysopidae are as follows: ScP and RA distally fused; numerous long veinlets in apical area between C and RA + ScP; RA + ScP ending at wing apex; long cell im in fore wing; basal cross-vein between im and CuA in a basal position; a fore wing vein Psc but no Psm. The hind wing structures of these taxa are still unknown, except partly in Mesochrysopa.

Remark. The list of the fossil taxa attributed to the Mesochrysopidae is given in Appendix 2.

Genus Mesochrysopa Handlirsch 1906

Type species. Mesochrysopa zitteli (Meunier 1898).

New diagnosis. This genus is characterized by the following features: CuA, MP3 + 4, MP1 + 2 and MA not fused in all wings; fore and hind wing costal areas not widened; ScP and RA distally fused; cross-veins between ScP + RA and C short, straight and simple, except those of apical part of wing, more or less undulate; o.g. cross-veins; fore wing cell im more or less quadrangular, long and broad; hind wing MP3 + 4 with three long posterior branches; veins MP3 + 4 and CuA not approximate, in all wing; no vein MPspl in all wings; fore wing area between MP1 + 2 and MP3 + 4 narrow, with one row of cells; a broad area between MP3 + 4 and CuA with two secondary longitudinal veins in fore wing.

Mesochrysopa zitteli (Meunier 1898) (Figs 9.3-9.5)

1898 *Hageniotermes zitteli* Meunier, 34, pl. 2, fig. 2. 1908 *Mesochrysopa zitteli*, Handlirsch, 612.

Material. Holotype specimen AS I 1031, Paläontologisches Museum München, Germany.

Diagnosis. That of the genus.

Occurrence. Solnhofen Formation, Solnhofen Plattenkalk (Malm Zeta 2b), Early Tithonian, Eichstatt-Solhnofen, Bavaria, Germany.

Redescription. Although well preserved, the hind wing venation has never been corrected figured and described. Impression of abdomen, part of head and thorax with four wings; fore wing, 32.2 mm long, 8.9 mm wide, ratio length/width 3.6; fore wing rather narrow and elongate; costal area between C and ScP not widened, maximal width 0.8 mm; about 26 cross-veins in costal area, perpendicular to ScP and C, basal of fusion between RA and ScP; ScP and RA strongly approximate and distally fused, 4.7 mm basal of wing apex; presence of six long and strongly approximate cross-veins in costal area, just opposite fusion between ScP and RA; cross-veins of area between RA + ScP and wing apex rather long and undulate with small cross-veins between them; RP + MA separating from R 4.5 mm distal of wing base; MA separating from RP obliquely, 4.6 mm distally; MA not fused with MP1 + 2 to constitute a Psm vein; MA reaching posterior wing margin and parallel to MP1 + 2; RP with 14 branches, not fused with MA; a long cell in distal part of area between main branch of RP and RA; a zigzagged supplementary series of gradate cross-veins between main branch of RP and i.g. cross-veins; i.g. cross-veins not directly connected with MA or MP1 + 2 but crossing obliquely basal branches of RP; MP separating from R + M 3.2 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 3.7 mm distally; MP1 + 2 very smoothly curved, directly aligned with proximal portion of MP; no vein MPspl; no 'X-crossing' between MP3 + 4 and CuA; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and short, 0.8 mm long; MP3 + 4 more or less parallel with MP1 + 2; a broad area between MP3 + 4 and CuA with two secondary longitudinal veins in fore wing; five cells between MP1 + 2 and MP3 + 4; quadrangular cell im very long and narrow, 5.7 mm long, 1.0 mm wide; no defined vein Psc; o.g. cross-veins distally nearly perpendicular to MA; o.g. cross-veins well aligned and straight; 1-2 supplementary rows of gradate veins between i.g. and o.g. cross-veins and three rows of gradate veins between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins distally convergent; base of CuA close to wing base; cross-vein 1m between CuA and MP a little distal of base of MP; cell m1 1.9 mm long, 1.1 mm wide; cell m2 longer, 4.8 mm long, 1.4 mm wide; Cu divided into CuP and CuA nearly opposite cross-vein 1m; cell c1 2.1 mm long, 0.8 mm wide; cell c2 2.9 mm long, 1.1 mm wide; c1 shorter than c2; CuP with three simple and short posterior branches; AA two-branched and well separated from CuP, with two cross-veins between them; AP1 simple; area between AA and posterior wing margin not very narrow, 1.5 mm wide.

Hind wing *circa* 28.7 mm long, 7.1 mm wide, ratio length/width 4.0; hind wing slightly shorter than fore wing, but hind wing narrower; costal area narrow, 0.6 mm wide, with about 17 cross-veins basal of fusion between ScP and RA; presence of 5-6 long and strongly approximate cross-veins in costal area, just opposite fusion between ScP and RA; apical cross-veins between ScP + RA and C similar to those of fore wing; RP + MA emerging from R *circa* 3.8 mm distal of wing base; no visible crossvein between RP + MA and MP basal of base of MA; vein sxv that would proximally close banksian cell b not visible but probably present; structure and dimensions of cell b cannot be determined; MA and RP separated 3.4 mm distal of base of RP + MA; a long cell in distal part of area between main branch of RP and RA; a supplementary series of gradate cross-veins between RP and i.g. cross-veins; cross-veins between MP1 + 2 and MA not very oblique, thus no well-defined vein Psm; i.g. cross-veins very well-defined, and weakly zigzagged; MP emerging from R + M 1.2 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 2.7 mm distally; MP1 + 2 nearly straight; MP3 + 4 never approximating CuA; MP3 + 4 with three posterior branches nearly parallel to CuA and MP1 + 2; three rows of cells between CuA and MP1 + 2; o.g. cross-veins well-defined, proximally irregular but distally aligned; a short supplementary row of gradate veins parallel with i.g. and o.g. cross-veins in middle part of wing; i.g. and o.g. cross-veins distally convergent; three rows of cells between posterior wing margin and o.g. cross-veins; cubito-anal area poorly preserved; posterior parts of cells c1 and c2 not preserved; AA and AP not preserved or absent.

Family TACHINYMPHIDAE n. fam.

Type genus. *Tachinymphes* Ponomarenko 1992 sit. nov. (Ponomarenko 1992a).

Other genus. Nanochrysopa n. gen.

Diagnosis. This monophyletic group is well characterized by the cells c1 and c2 posteriorly opened and anal veins atrophied in hind wings. Other characters are: fore wing area between ScP and C not basally broadened; ScP and RA distally fused; apex of ScP + RA very near or at wing apex; presence of long setae along some veins, especially the fore wing CuA (but character unknown in some *Tachinymphes* species); short antenna (but character unknown in *Nanochrysopa* n. gen.) (see phylogenetic analysis below).

Remark. The list of the taxa attributed to the Tachinymphidae n. fam. is given in Appendix 3.

Genus *Tachinymphes* Ponomarenko 1992 n. sit. (= genus *Siniphes* Ren & Yin, 2002 n. syn.)

Type species. *Tachinymphes ascalaphoides* Ponomarenko 1992. Other species: *Tachinymphes delicatus* (Ren & Yin 2002) (previously in genus *Siniphes*), *Tachinymphes paicheleri* n. sp., *Tachinymphes magnificus* n. sp., *Tachinymphes magnificus* n. sp.

Remarks. Ponomarenko (1992a) described the genus *Tachinymphes*. Ren & Yin (2002) separated the two genera *Tachinymphes* and *Siniphes* after the fork of MP well basal of base of RP + MA in hind wing of latter, instead of being opposite base of RP + MA in the former. In *T. paicheleri* and *T. penalveri*, the fork of MP is in an intermediate position between the two situations, thus, we propose to synonymize the two genera.

Diagnosis. Ren & Yin (2002) described in detail *Siniphes delicatus* and gave a generic diagnosis. We complete it after the study of the new species. Hind wing anal area very reduced, with AP and AA absent or rudimentary and very short; hind wing CuP very short, reduced to a cross-vein between CuA and posterior wing margin. Another interpretation of this pattern could be that CuP is lost and that there is a simple cross-vein between CuA and AA, but this 'cross-vein' is exactly in the position of a genuine CuP of the other chrysopoids. Therefore, we prefer to consider that CuP is still present but reduced to a very short vein between CuA and AA; hind wing cells c1 and c2 posteriorly open; fore wing MA strongly approximating MP1 + 2 at its base but not fused with it; CuA, MP3 + 4, MP1 + 2, and MA not distally fused in all wings; fore and hind wing costal areas not widened; ScP and RA distally fused; cross-veins between ScP + RA and C short, straight, and simple; o.g. cross-veins more or less aligned in all wing, better defined than i.g. cross-veins; fore wing cell im more or less quadrangular, long and broad; hind wing MP3 + 4 simple with no long posterior branches; hind wing MP3 + 4 and CuA very briefly fused or strongly approximate and diverging again distally; antennae very short.

Remarks. (1) Some specimens of *T. paicheleri* n. sp. and T. penalveri n. sp. have long hairs in radial area between i.g. and o.g. cross-veins, along vein R + MA, proximal of base of RP + MA; and along RP + MA, just proximal of base of RP + MA and along base of Cu. It is a unique character in the Chrysopoidea. Such hairs are not visible in other specimens and in the type specimen of T. magnificus n. sp. (absence or problem of preservation?). (2) Some specimens of T. paicheleri n. sp. and the type specimen of T. magnificus n. sp. have strong, sharp, and regularly disposed spines on the inner margin of their fore legs. The legs of the other specimens of T. paicheleri n. sp. and T. penalveri n. sp. are too poorly preserved to show these spines, but they were probably present. Ren & Yin (2002) indicated nothing on this point in the type specimen of *T. delicatus*.

Tachinymphes ascalaphoides Ponomarenko 1992

1992a *Tachinymphes ascalaphoides* Ponomarenko, 48-49, fig. 4b, c (original description)

Material. Holotype specimen PIN 3064/2420, Palaeontomological Laboratory [Paleontological Institute], Academy of Science of Russia, Moscow.

Occurrence. Zaza Fomation, Neocomian to Barremian-Aptian. Baissa, Vitim River, Transbaikalia, Russia.

Remarks. This species differs from *T. delicatus* and *T. magnificus* n. sp. in the relative positions of MP1 + 2 and RP + MA in hind wing and in the greater number of branches of RP and rows of cells in radial areas. It differs from *T. paicheleri* n. sp. in its o.g. cross-veins distinctly zigzagged instead of being well aligned, and from *T. penalveri* n. sp. in the relative positions of MP1 + 2 and RP + MA in hind wing.

Tachinymphes delicatus (Ren & Yin 2002) n. comb.

2002 Siniphes delicatus Ren & Yin, 269-272, figs. 1-4 (original description)

Material. Holotype specimen LB20001-LB20002, Department of Biology, Capital Normal University, Beijing, China.

Occurrence. Tithonian – Valanginian, *Coptoclava* – *"Ephemeropsis"* Fauna (Lin 1983: 393, 1994: 308-309; Ren & Yin 2002). Huangbanjiegou valley, Beipiao City, Liaoning Province, NE China.

Tachinymphes magnificus n. sp. (Figs 8.2, and 9.6-9.7)

Material. Holotype specimen MNHN-DHT R.55225, coll. Nel, Paleontological laboratory, National Museum of natural History, Paris, France.

Etymology. After the wonderful state of preservation of the holotype.

Diagnosis. This species is very close to *T. delicatus*, differing only in the following character: pterostigma of four wings distinctly shorter, only 0.8-0.9 mm long, instead of being 2.1 mm long as in *T. delicatus*, and free of cross-veins. It differs from *T. paicheleri* n. sp. as follows: less cross-veins in fore wing costal area but more than in hind wing; only six posterior branches of RP in fore and hind wing; o.g. cross-veins less well aligned, more zigzagged; distal part of fore wing vein CuA weakly zigzagged, with only one row of cells between it and posterior wing margin.

Occurrence. Tithonian – Valanginian, *Coptoclava* – "*Ephemeropsis*" Fauna (Lin 1983: 393, 1994: 308-309; Ren & Yin 2002). Huangbanjiegou valley, Beipiao City, Liaoning Province, NE China.

Description. Impression of abdomen, part of head and thorax with overlapped four wings; fore wing 23.4 mm long, 5.8 mm wide, ratio length/width, 4.0; fore wing narrow and elongate; costal area between C and ScP not widened, maximal width, 0.6 mm; 19 cross-veins in costal area, perpendicular to ScP and C, basal of fusion between RA and ScP; area between ScP and RA very narrow, 0.2 mm wide, these veins being basally separated but apparently fused, with no space between them between level of base of Cu to 2.1 mm distal of base of RP + MA; ScP and RA distally fused, 4.2 mm basal of wing apex; a very short dark (sclerotized?) pterostigmal structure, without any cross-veins, just basal of fusion between ScP and RA; cross-veins in area between RA + ScP and wing apex short, simple and straight; RP + MA separating from R 6.1 mm distal of wing base; MA separating from RP at nearly right angle, 2.9 mm distally; MA not fused with MP1 + 2 into a Psm vein; MA reaching posterior wing margin and remaining parallel with MP1 + 2; six branches of RP, not fused with MA; no zigzagged supplementary series of gradate cross-veins between main branch of RP and i.g. crossveins; i.g. cross-veins not directly connected to MA or MP1 + 2 but nearly making a right angle with more basal branch of RP; MP separating from R + M 2.9 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 2.9 mm distally; MP1 + 2 very smoothly curved; MP3 + 4 simple, not distally divided into two branches, no vein MPspl, and MP3 + 4 not strongly angular; no 'X-crossing' between MP3 + 4 and CuA; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and very short, 0.2 mm long; MP3 + 4 more or less parallel with CuA and MP1 + 2; four long cells between MP3 + 4 and CuA and six long cells between MP1 + 2 and MP3 + 4; cell im quadrangular, very long, narrow, 2.3 mm long, 0.7 mm wide; no defined vein Psc; o.g. cross-veins nearly perpendicular to vein MA; o.g. cross-veins rather well aligned; 1-2 supplementary rows of gradate veins between i.g. and o.g. cross-veins and also between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins distally convergent; base of CuA close to wing base; cross-vein 1m between CuA and MP exactly opposite base of MP; cell m1 1.2 mm long, 0.5 mm wide; cell m2 longer, 3.3 mm long, 0.7 mm wide; Cu divided into CuP and CuA a little basal of cross-vein 1m; cell c1 1.1 mm long, 0.4 mm wide; cell c2, 2.9 mm long, 0.7 mm wide; c1 distinctly shorter than c2; CuP with two simple branches reaching posterior wing margin; AA twobranched and well separated from CuP, with two cross-veins between them; AP very weak, 1.8 mm long with two very small posterior branches; area between AA and posterior wing margin very narrow, 0.3 mm wide; AP2 reduced or absent.

Hind wing 19.5 mm long, 4.3 mm wide, ratio length/ width 4.5; hind wing of nearly same length as fore wing, but narrower and more acute; costal area narrow, 0.4 mm wide, with 18 cross-veins basal of distal fusion between ScP and RA; ScP and RA similar to those of fore wing, viz. basally separated, then apparently fused, with no space between them, between level of base of MP and 1.7 mm distal of base of RP + MA, divided again distally, and apically fused again; a darker pterostigma crossed by three veins; apical cross-veins between ScP + RA and C straight, like in fore wing; RP + MA emerging from R 5.0 mm distal of wing base; no cross-vein between RP + MA and MP basal of base of MA and vein sxv that proximally closes banksian cell b; vein sxv short, perpendicular to MP and MA, 0.4 mm long; cell b long and narrow, 2.0 mm long, 0.6 mm wide, fivesided; MA and RP divided 2.9 mm distal of base of RP + MA; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; an oblique cross-vein between MP1 + 2 and MA, thus MA and MP1 + 2 apparently more or less fused together but no well-defined vein Psm; i.g. cross-veins very well defined, nearly perpendicular to MA; MP emerging from R + M 1.3 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 2.1 mm distally; MP1 + 2 nearly straight; MP3 + 4 meeting CuA in one point, 1.7 mm distal of MP3 + 4 base but diverging again distally; distal portion of CuA rather short, 2.1 mm long; distal portion of MP3 + 4 longitudinal, nearly parallel with CuA and MP1 + 2; two rows of cells between CuA and MP1 + 2; o.g. cross-veins well-defined but zigzagged; a short supplementary row of gradate veins parallel with i.g. and o.g. cross-veins in middle part of wing; i.g. and o.g. cross-veins distally convergent; two rows of cells between posterior wing margin and o.g. crossveins; cubito-anal area very reduced, cells c1 and c2 posteriorly opened on wing margin and vein CuP very short, looking like a simple cross-vein perpendicular to CuA and posterior wing



Figure 9

I, Armandochrysopa inexpecta, LH-18575, holotype fore wing. *2, A. inexpecta,* LH-18575, holotype hind wing. *3, Mesochrysopa zitteli,* AS I 1031, fore wing, after an original figure of R. Willmann. *4, Mesochrysopa zitteli,* AS I 1031, hind wing, after an original figure of R. Willmann. *5, Mesochrysopa zitteli,* AS I 1031, fore wing base. *6, Tachinymphes magnificus,* MNHN-DHT R.55225, holotype fore wing. *7, T. magnificus,* MNHN-DHT R.55225, holotype hind wing. *8, Tachinymphes paicheleri,* LH-18576, holotype right fore wing. *9, T. paicheleri,* LH-18576, holotype right hind wing. *10, T. paicheleri,* LH-18576, holotype left hind wing. *12, T. paicheleri,* LH-18577, paratype fore wing. *13, T. paicheleri,* LH-13175, paratype fore wing. Scale bar: 1 mm; 3-4 scale bars: 0.5 mm.

margin, 0.2 mm long; AA very short with two very short posterior branches reaching posterior margin; AP absent.

Discussion. This Chinese species shares with the two other *Tachinymphes* species several synapomorphies: hind wing cubito-anal reduced; hind wing cells c1 and c2 posteriorly open; hind wing anal veins reduced or absent; hind wing contact of veins CuA and MP3 + 4, giving a characteristic "X-shape" to these veins; shape and relative dimensions of hind wing; hind wing apex distinctly acute. Differences with *T. paicheleri* n. sp. are few and listed in the diagnosis of *T. magnificus* n. sp.

The exact age of this Liaoning Formation is controversial and could be Early Cretaceous (Barremian). The present discovery is congruent with this hypothesis.

Tachinymphes paicheleri n. sp. (Figs 8.3-8.4, and 9.8-9.13)

Material. Holotype specimen LH-18576; paratype specimens LH-18577 (Fig. 8.5), LH-18578, LH-8040a/b, and LH-13175a/b (Fig. 9.13), other possible specimens LH-18579, LH-18580, LH-18581, LH-18582, LH-18583, and LH-18584 (coll. Armando Diaz-Romeral), deposited in the Museo de Cuenca, Spain. Housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. In honour to our friend and colleague Dr. J.-C. Paicheler from Reims, France.

Diagnosis. This species differs from *Tachinymphes penalveri* n. sp. in the following characters: hind wing nearly as long as fore wing; fore wing radial area narrower with only three rows of cells between RP and o.g. cross-veins, instead of four rows. It differs from *T. magnificus* n. sp. and *T. delicatus* in its more numerous branches of RP, its i.g. cross-veins not zigzagged but very well aligned, and hind wing nearly as long as fore wing.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Description. Holotype LH-18576 (Figs 8.3, and 9.8-9.11): Impression of abdomen, part of head and thorax with overlapped four wings; fore wing 16.0 mm long, 4.2 mm wide, ratio length/width 3.8; fore wing narrow and elongate; costal area between C and ScP not widened, maximal width 0.4 mm; twenty five cross-veins in costal area, perpendicular to ScP and C, basal of fusion between RA and ScP; area between ScP and RA rather wide, 0.2 mm wide; ScP and RA distally fused, 2.6 mm basal of wing apex; a dark (sclerotized?) pterostigmal area, with six crossveins, just proximal of fusion between ScP and RA; cross-veins of area between RA + ScP and wing apex short, simple and straight; RP + MA separating from R 3.2 mm distal of wing base; MA separating from RP with a nearly right angle, 2.8 mm distally; MA strongly approximating MP1 + 2 at its base, but not clearly fused with MP1 + 2 to constitute base of a Psm vein; MA reaching posterior wing margin and parallel with MP1 + 2; RP with nine branches, separated from MA; no zigzagged supplementary series of gradate cross-veins between main branch of RP and i.g. cross-veins; i.g. cross-veins not directly connected with MA or MP1 + 2 but making a nearly right angle with more basal branch of RP; MP separating from R + M 1.8 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 1.8 mm distally; MP1 + 2 very smoothly curved; MP3 + 4 simple, not strongly angular; no vein MPspl; no 'X-crossing' structure; crossvein 2m nearly perpendicular to MP3 + 4 and CuA and very short, 0.2 mm long; MP3 + 4 more or less parallel with CuA and MP1 + 2; four long cells between MP3 + 4 and CuA and between MP1 + 2 and MP3 + 4; quadrangular cell im very long and narrow, 3.1 mm long, 0.4 mm wide; no defined vein Psc; o.g. cross-veins nearly perpendicular to MA; o.g. cross-veins well aligned and straight; 1-2 supplementary rows of gradate veins between i.g. and o.g. cross-veins and between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins distally convergent; base of CuA close to wing base; cross-vein 1m between CuA and MP exactly opposite base of MP; cell m1 0.9 mm long, 0.3 mm wide; cell m2 longer, 2.5 mm long, 0.5 mm wide; Cu divided into CuP and CuA opposite crossvein 1m; cell c1 1.1 mm long, 0.3 mm wide; cell c2, 1.7 mm long, 0.5 mm wide; c1 shorter than c2; CuP with two simple branches reaching posterior wing margin; AA two-branched and well separated from CuP, with two cross-veins between them; AP not visible (preservation or absence?); area between AA and posterior wing margin very narrow, 0.3 mm wide, thus AP1 and AP2 possibly reduced or absent.

Hind wing 14.9 mm long, 2.8 mm wide, ratio length/width 5.3; hind wing of nearly same length as fore wing, but narrower and more acute; costal area narrow, 0.3 mm wide, with fifteen cross-veins basal of fusion between ScP and RA; a defined sclerotized pterostigma crossed by three cross-veins; apical cross-veins between ScP + RA and C straight, like in fore wing; RP + MA emerging from R 3.7 mm distal of wing base; no cross-vein between RP + MA and MP basal of base of MA and vein sxv that proximally closes banksian cell b; vein sxv short, perpendicular to MP and MA, 0.2 mm long; cell b long and narrow, 2.0 mm long and 0.4 mm wide, five-sided; MA and RP separated 2.7 mm distal of base of RP + MA; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; an oblique cross-vein between MP1 + 2 and MA, thus MA and MP1 + 2 apparently fused together but no well-defined vein Psm; i.g. cross-veins very well-defined, nearly perpendicular to MA; MP emerging from R + M 0.7 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 2.0 mm distally; MP1 + 2 nearly straight; MP3 + 4 meeting CuA in one point, 1.0 mm distal of MP3 + 4 base but diverging again distally; distal portion of CuA rather short, 3.5 mm long and reaching posterior wing margin; distal portion of MP3 + 4 longitudinal, nearly parallel with CuA and MP1 + 2; two rows of cells between CuA and MP1 + 2; o.g. cross-veins well-defined, proximally irregular but distally aligned; a short supplementary row of gradate veins parallel with i.g. and o.g. cross-veins in middle part of wing; i.g. and o.g. cross-veins distally convergent; two rows of cells between posterior wing margin and o.g. cross-veins; cubito-anal area very reduced, cells c1 and c2 being posteriorly opened on wing margin and vein CuP very short, looking like a simple perpendicular cross-vein between

CuA and posterior wing margin, 0.5 mm long; c1, 0.8 mm long, 0.4 mm wide; c2, 0.7 mm long, 0.4 mm wide; AA very short with two very short posterior branches reaching posterior wing margin; AP completely fused with posterior wing margin.

Specimen LH-18578: Four wings connected with thorax. Similar to the holotype with the same venation and wings shape, this specimen confirms some of the particular characters of the species: (1) cubito-anal area of hind wing as reduced as in holotype, with no defined anal vein, open cells c1 and c2 and a reduced vein CuP; fore wing cell im very long; hind wing veins MP3 + 4 and CuA meeting in one point and strongly diverging distally; no fusion between MA and MP1 + 2 into Psm, in four wings. Fore wing 24.6 mm long, 6.0 mm wide, ratio length/width 4.1; hind wing, circa 22.0 mm long, 3.7 mm wide, ratio length/width 5.9. The main differences with the holotype are as follows: three rows of cells between i.g. and o.g. cross-veins instead of two, in fore wing; six cells plus cell im between MP1 + 2 and MP3 + 4 instead of four plus cell im, in fore wing; o.g. crossveins of hind wing all very well aligned; wings longer. This specimen has strong, long and sharp spines regularly disposed along the inner side of its fore femora (grasping legs).

Specimen LH-18577 (Figs. 8.4 and 9.12): A fore wing very similar to that of holotype, 18.3 mm long, 4.4 mm wide, ratio length/width, 4.1; anal area better preserved than that of holotype because vein AP1 visible, as a short vein with a cross-vein between AA and AP1; AP2 not visible and probably fused with posterior wing margin; cubito anal area narrow. The main difference with the holotype fore wing is the presence of 3-4 rows of cells between o.g. cross-veins and posterior wing margin.

Specimen LH-8040 a/b: A fore wing very similar to that of holotype, *circa* 21.0 mm long, 5.5 mm wide, ratio length/width, 3.8. Nevertheless, it differs from all other specimens of the *Tachinymphes* species in the presence of long hairs in the radial area between the i.g. cross-veins and the o.g. cross-veins (possible problem of preservation in other specimens).

Specimen LH-13175 a/b (Fig. 9.13): A body with wings, the left fore wing being very well preserved. Fore wing 15.9 mm long, 3.8 mm wide ratio length/width 4.2. The main difference with the holotype is also the presence of 3-4 rows of cells between o.g. cross-veins and posterior fore wing margin.

Specimen LH-18581: This specimen, although with a wing venation more poorly preserved than others, has also strong spines on the inner margin of fore femur. It also has very short antennae, as in *Tachinymphes delicatus*.

Discussion — All these specimens share numerous characters and are clearly related. The main differences being as follows: number of rows of cells between o.g. crossveins and posterior fore wing margin; number of branches of RP, i.e. seven branches in LH-18577, nine in LH-18576 (holotype) and in LH-13175, 8-9 in LH-18578, twelve in LH-8040a/b. All these differences are probably caused by diagenetic deformation and cannot justify a specific separation.

Tachinymphes penalveri n. sp. (Figs 8.5-8.6, 10.1, and 11.1-11.4)

Material. Holotype specimen LH-18585; paratypes specimens LH-18586, LH-18587, coll. Armando Diaz-Romeral, deposited in the Museo de Cuenca; LH-8033, and LH-8094, deposited in the collection of the Univesidad Autonoma de Madrid, Spain. housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. In honour to our friend and colleague Dr. Enrique Peñalver from Valencia, Spain.

Diagnosis. This species differs from *Tachinymphes paicheleri* n. sp. in the following characters: hind wing distinctly shorter than fore wing; fore wing radial area broader with four rows of cells between RP and o.g. cross-veins, instead of three. It differs from *T. delicatus* and *T. magnificus* n. sp. in its fore wing radial area broader with four rows of cells between RP and o.g. cross-veins, instead of three, and greater number of branches of RP.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Description. Holotype LH-18585 (Figs. 8.5 and 11.1): Fore wing 20.0 mm long, 5.1 mm wide, ratio length/width 3.9; fore wing elongate and less narrow than for Tachinymphes paicheleri n. sp.; costal area between C and ScP not widened, maximal width 0.4 mm; about twenty short cross-veins in costal area, more or less perpendicular to ScP and C, basal of fusion between RA and ScP; area between ScP and RA rather narrow, 0.1 mm wide; ScP and RA distally fused, 3.1 mm basal of wing apex; no visible dark (sclerotized?) pterostigmal structure; cross-veins in area between RA + ScP and wing apex short, simple and straight; RP + MA separating from R 3.7 mm distal of wing base; MA separating from RP at right angle, 3.2 mm distally; MA reaching posterior wing margin and parallel with MP1 + 2; RP with thirteen branches, not fused with MA; no supplementary series of gradate cross-veins between main branch of RP and i.g. crossveins; i.g. cross-veins not directly connected with MA or MP1 + 2 but beginning on first branch of RP at nearly right angle; MP separating from R + M 2.1 mm distal of wing base; MP divided into MP1 + 2 and MP3 + 4 1.6 mm distally; MP1 + 2 strongly curved and distally not fused with MA, but only connected with it by a very oblique cross-vein, no well defined base of a Psm; MP1 + 2 not directly aligned with proximal portion of MP; MP3 + 4 simple, not distally divided into two branches; no vein MPspl; MP3 + 4 strongly angular; no 'X-crossing' structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and short, 0.3 mm long; distally, MP3 + 4 more or less parallel to CuA and MP1 + 2; four long cells between MP3 + 4 and CuA and between MP1 + 2 and MP3 + 4; quadrangular cell im very long and narrow, 2.6 mm long, 0.7 mm wide; no defined vein Psc; o.g. cross-veins nearly perpendicular to vein MA, well aligned and straight; 1-2 supplementary rows of gradate veins between i.g. and o.g. cross-veins and 4-5 rows of cells between o.g. crossveins and posterior wing margin; i.g. and o.g. cross-veins distally convergent; base of CuA near wing base but distally more strongly zigzagged than that of Tachinymphes paicheleri n. sp.; cross-vein

1m between CuA and MP exactly opposite base of MP; cell m1 1.3 mm long, 0.4 mm wide; cell m2 longer, 2.1 mm long, 0.7 mm wide; Cu divided into CuP and CuA opposite crossvein 1m; c1, 1.7 mm long, 0.5 mm wide; c2, 1.7 mm long, 0.8 mm wide; c1 shorter than c2 but c2 very wide, nearly two times broader than c1; CuP with two simple branches reaching posterior wing margin; AA not well preserved but distinctly separated from CuP, with two cross-veins between them; area between



Figure 10

1, Tachinymphes penalveri, LH-18586, basal part of the fore and hind wings. 2, Nanochrysopa pumilio, LH-13217, habitus of the holotype. 3, PIN 2904/743, Mesypochrysa sp.. 4, Mesypochysa makarkini, PIN 2997/805, paratype fore wing. 5, M. makarkini, PIN 2997/2774, holotype fore wing; – 6, Mesypochrysa cf. chrysopoides, MNHN-DHT R. 63845. 7, Paralembochrysa splendida, MNHN-DHT R. 55224, habitus of the holotype. 8, Chimerochrysopa incerta, LH-18588, holotype, hind wing. Scale bars: 10 mm. AA and posterior wing margin narrow, 0.5 mm wide, AP present but very short.

Hind wing 14.7 mm long, 3.6 mm wide, ratio length/width 4.1; hind wingc distinctly shorter and narrower than fore wing and its apex less rounded; costal area narrow, 0.3 mm wide, with about fifteen cross-veins basal of fusion between ScP and RA; no defined sclerotized pterostigma; apical cross-veins between ScP + RA and C straight; RP + MA emerging from R 2.3 mm distal of wing base; probably no cross-vein between RP + MA and MP basal of base of MA and vein sxv closing proximally banksian cell b; sxv and cell b not preserved; base of MA not preserved; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; MA and MP1 + 2 probably not fused together, no visible vein Psm; i.g. cross-veins very well-defined, nearly perpendicular to MA; MP emerging from R + M 1.3 mm distal of wing base; division of MP into MP1 + 2 and MP3 + 4 not preserved; MP1 + 2 nearly straight; possible contact between MP3 + 4 and CuA not preserved; distal portion of CuA rather short, about 2 mm long and reaching posterior wing margin; two rows of cells between CuA and MP1 + 2; o.g. cross-veins well-defined, proximaly irregular but distally aligned; no short supplementary row of gradate veins parallel with i.g. and o.g. cross-veins in middle part of wing; i.g. and o.g. cross-veins distally convergent; probably two rows of cells between posterior wing margin and o.g. cross-veins; cubito-anal area reduced but not well preserved, structure of cells c1 and c2 and anal veins not visible.

Specimen LH-18586 (Figs. 8.6, 10.1, and 11.4). Fore and hind wings overlapping but venation very distinct; fore wings very similar to those of LH-18585 but with a very special character, i.e. presence of very long and numerous hairs, 2.2 mm long along R, just proximal of base of RP + MA and along base of Cu; base of hind wing well preserved, showing several characters not visible in holotype, viz. MP emerging from R 1.2 mm distal of wing base; MP forked into MP1 + 2 and MP3 + 4 1.8 mm distally; MP1 + 2 smoothly curved; MP3 + 4 meeting CuA in one point, 1.0 mm distal of base of MP3 + 4; distal portion of CuA short; cubito-anal area very reduced, cells c1 and c2 posteriorly opened along posterior hind wing margin and CuP very short, looking like a simple perpendicular cross-vein between CuA and posterior wing margin; c1, 0.7 mm long, 0.5 mm wide; c2, 0.7 mm long, 0.4 mm wide; AA very short and AP absent, probably fused with posterior wing margin; fore wing 22.9 mm long, 6.8 mm wide, ratio length/width 3.3; hind wing, 19.1 mm long, 4.1 mm wide, ratio length/width 4.6. This specimen has strong, long and sharp spines regularly disposed along the inner side of its fore femora (grasping legs).

We attribute the specimen LH-18587 (Fig. 11.3) to the same species. It is a nearly complete fore wing and has very few differences with the holotype, except in the wing shape and length (15.2 mm long, 4.7 mm wide, ratio length/width 3.2) but these differences could be related to fossilisation artefact or intraspecific variation.

LH-8033 (Fig. 11.2) is a basally broken hind wing with veins CuA, CuP, AA not clearly preserved. The structure of MP1 + 2, MP3 + 4 and distal part of CuA are identical to those of LH-18586. This specimen is of great interest because it has long hairs along vein R + MA, proximal of base of RP + MA. It demonstrates the presence of hairs in fore- and hind wings for

T. penalveri n. sp.; wing about 15.7 mm long, 4.2 mm wide, ratio length/width 3.7.

Specimen LH-8094a/b: Nearly complete specimen; attribution to Tachinymphes penalveri n. sp. based on fore and hind wing shapes and relative proportions, and venation very similar to that of holotype; fore wing 19.6 mm long, 6.1 mm wide, ratio length/width 3.2; hind wing 16.5 mm long, 3.7 mm wide, ratio length/width 4.4; main differences with holotype as follows: fore wing main branch of RP apparently much more zigzagged; fore wing cell im apparently divided in two smaller cells by a crossvein; in fore wing, a dark region maybe corresponding to a pterostigma between C and ScP, opposite point of fusion between ScP and RA. These differences are possibly related to problems of preservation.

Remark. The differences listed in the diagnoses of the new species *T. paicheleri* and *T. penalveri* justify a specific separation but these two taxa are clearly related within the same genus because they share several synapomorphic characters, like the great reduction of the anal and cubito-anal areas in the hind wing, while the fore wing anal and cubito-anal areas are not especially reduced.

Genus Nanochrysopa n. gen.

Type species. Nanochrysopa pumilio n. sp.

Diagnosis. This genus is well characterized as follows: in fore wing, presence of long hairs along CuA; no fusion between CuA, MP3 + 4, MP1 + 2 and MA, no veins Psm or Psc; in hind wing, MA very short and fused with MP1 + 2 into a vein Psm, MP3 + 4 very short and fused with CuA into a vein Psc; fore and hind wing radial areas very narrow with only three branches of RP; ScP and RA distally fused; cross-veins between ScP + RA and C short, straight, and simple; fore and hind wing costal areas never widened; fore wing cell im very broad and quadrangular; fore wing anal and cubito-anal areas broader than those of hind wing, hind wing AP absent, AA very short, and CuP reduced to a crossvein between CuA and posterior wing margin, hind wing cells c1 and c2 fused and posteriorly open; a supplementary crossvein between RP + MA and MP1 + 2 in hind wing, basal of vein sxv; hind wing banksian cell b pentagonal, short but wide; hind wing Psm straight and Psc zigzagged.

Etymology. After *Chrysopa* and latin *nanus* in reference to the very reduced dimensions of the type species.

Nanochrysopa pumilio n. sp. (Figs 10.2, and 11.5)

Material. Holotype specimen LH-13217a/b, housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. After the very reduced dimensions of the holotype.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Diagnosis. That of the genus.

Description. Four wings are connected to thorax, body poorly preserved; fore wing 9.6 mm long, 3.2 mm wide, ratio length/width 3.0; fore wing rather narrow, elongate and rounded; costal area between C and ScP not widened; maximal width 0.3 mm; minimal width 0.2 mm; about twenty four cross-veins in costal area, perpendicular to ScP and C, basal of fusion of RA and ScP; ScP and RA distally fused, 2.0 mm basal of wing apex; no dark (sclerotized?) pterostigmal structure; cross-veins in area between RA + ScP and wing apex short, simple and straight; RP + MA separating from R in a very distal position, 3.4 mm distal of wing base; MA separating from RP 0.8 mm distally; MA not fused with MP1 + 2 to constitute base of a Psm, but reaching posterior wing margin and parallel with MP1 + 2; only three branches of RP; no supplementary series of gradate crossveins between RP and i.g. cross-veins; i.g. cross-veins very few, zigzagged, and not directly connected with MA or MP1 + 2 but nearly at right angle with first branch of RP; MP separating from R + M 1.2 mm distal of wing base and 2.2 mm basal of RP + MA; MP divided into MP1 + 2 and MP3 + 4 1.0 mm distally; MP1 + 2 very smoothly curved and distally not fused with MA but only connected with it by a very oblique cross-vein; MP1 + 2 not aligned with proximal portion of MP; no vein MPspl, MP3 + 4 angular but no 'X-crossing' structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and very short, 0.1 mm long; MP3 + 4 zigzagged distally, and more or less parallel with CuA and MP1 + 2; three long cells between MP3 + 4 and CuA and also five long cells between MP1 + 2 and MP3 + 4; cell im quadrangular, very long and wide, 1.4 mm long, 0.7 mm wide; no defined vein Psc; distally, o.g. cross-veins nearly perpendicular to MA; o.g. cross-veins zigzagged; no supplementary row of gradate veins between i.g. and o.g. cross-veins and only one row of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins parallel; CuA beginning near wing base, distally less zigzagged than MP3 + 4; cross-vein 1m between CuA and MP basal of base of MP; cell m1 0.8 mm long, 0.2 mm wide; cell m2 longer, 1.8 mm long, 0.4 mm wide; CuP separated from CuA opposite cross-vein 1m; c1, 0.9 mm long, 0.3 mm wide; c2, 1.1 mm long, 0.3 mm wide; c1 shorter than c2 but c2 not distinctly broader than c1; CuP with three simple branches reaching posterior wing margin; AA not well preserved but distinctly separated from CuP, with one visible cross-vein between them; area between AA and posterior wing margin narrow, 0.3 mm wide; AP present and very short; a row of long hairs, 1.0 mm long, along CuA, distal of base of CuP; presence of long hairs along CuA.

Hind wing 8.9 mm long, 2.2 mm wide, ratio length/width 4.0; hind wing distinctly shorter and narrower than fore wing; wing apex acute; costal area narrow, 0.2 mm wide, with about twenty two cross-veins basal of fusion between ScP and RA; no defined sclerotized pterostigma; ScP and RA fused 1.9 mm basal of wing apex; apical cross-veins between ScP + RA and C straight; RP + MA emerging from R 3.4 mm distal of wing base; a cross-vein between RP + MA and MP proximal of base of MA and vein sxv; vein sxv perpendicular to MP and RP + MA, 0.4 mm long; banksian cell b short, 0.7 mm long, 0.5 mm wide; free part of MA between RP + MA and MP1 + 2 distinctly oblique,

0.4 mm long, distally fused with MP1 + 2; a very clear pseudovein Psm formed by fusion of MP1 + 2 and MA, reaching posterior wing margin near wing apex, at 84% of wing length; i.g. cross-veins absent; MP emerging from R + M 0.2 mm distal of wing base; division of MP into MP1 + 2 and MP3 + 4 1.4 mm distally; MP1 + 2 nearly straight; MP3 + 4 short and oblique, 0.5 mm long, distally fused with CuA into a very clear but zigzagged pseudo-vein Psc reaching posterior wing margin at 79% of wing length and more or less parallel with Psm; only one row of cells between Psc and MP1 + 2 (or Psm); o.g. crossveins very few, well-defined but zigzagged; radial area very narrow, with only two rows of cells between main branch of RP and posterior wing margin; only one row of cells between posterior wing margin and o.g. cross-veins; cubito-anal area very reduced; cell c1 + c2 posteriorly open, 0.7 mm long, 0.2 mm wide; CuP very short between Cu and posterior wing margin; AA very short and two-branched; AP not visible, probably fused with posterior wing margin.

Discussion. The presence of long hairs along the fore wing CuA strongly supports affinities with the genus *Tachinymphes*, as *T. paicheleri* n. sp. has similar hairs. Nevertheless, the fusion of MP3 + 4 with CuA into a vein Psc and that of MA with MP1 + 2 into a vein Psm, present in the hind wing of *Nanochrysopa* n. gen., is a derived character only present in Recent Chrysopidae. But this character could have been convergently acquired by *Nanochrysopa* and be related to its very narrow hind wing, distinctly narrower than the hind wings of Recent Chrysopidae. Also, Psm and Psc are absent in the fore wing of *Nanochrysopa*. Thus, we attribute *Nanochrysopa* to the Tachinymphidae, close to genus *Tachinymphes*.

Family **LIMAIIDAE** Martins-Neto & Vulcano 1989 n. sensu (formerly Chrysopidae: "Limaiinae" Martins-Neto & Vulcano 1989)

Type genus. Limaia Martins-Neto & Vulcano 1989. Other genera: Lembochrysa Ren & Guo 1996 sit. nov., Mesypochrysa Martynov 1927, Drakochrysa Yang & Hong 1990 sit. nov., Protochrysa Willmann & Brooks 1991 sit. nov., Araripechrysa Martins-Neto & Vulcano 1989a.

Remarks. Makarkin (1994) tentatively attributed *Cretachrysa* Makarkin 1994 (one species *C. martynovi* Makarkin 1994, Cenomanian, Russia) to the "Limaiinae". The distal halves of its wings are unknown thus the main diagnostic characters of this group are not preserved. As it falls with the Limaiidae in the present analysis (see below), we tentatively maintain it in this group. Makarkin (1997) indicated that the genus *Baisochrysa* (one species *B. multinervis* Makarkin 1997, Early Cretaceous of Baissa) is "apparently" a "Limaiinae", although he attributed it to a subfamily undeterminated. Unfortunately, it lacks the structures of the distal parts



Figure 11 1, Tachinymphes penalveri, LH-18585, holotype fore and hind wings. 2, T. penalveri, LH-8033, paratype hind wing. 3, T. penalveri, LH-18587, paratype fore wing. 4, T. penalveri, LH-18586, basal part of the fore and hind wings showing long hairs. 5, Nanochrysopa pumilio, LH-13217, holotype fore wing and hind wing; 6, Mesypochrysa intermedia, PIN 2066/1139, holotype. 7, Mesypochrysa sp., PIN 2904/743, fore wing. 8, Mesypochrysa sp., PIN 2066/1177, fore wing. 9, Mesypochrysa makarkini, PIN 2997/2774, holotype, fore wing. 10, M. makarkini, PIN 2997/805, paratype, fore wing. Scale bars: 1 mm.

of vein ScP and RA. Nevertheless, it falls with this group in the present phylogenetic analysis. The list of taxa attributed to the Limaiidae is given in Appendix 4.

The type genus *Limaia* is based on two poorly known species that would clearly need a redescription (Makarkin 1997). In particular, the organization of the veins CuP and AA are unknown in the type species *L. conspicua*, and looks very strange in *L. adicotomica*, as AA and AP seem to be basally fused with CuP, unlike in all other known Chrysopoidea. Also, the type species of *Mesypochrysa*, *M. latipennis* Martynov 1927, from the Late Jurassic of Karatau, is based on a rather poorly preserved specimen, with the veins CuP, AA and AP badly known (Martynov 1927).

Diagnosis. Martins-Neto and Vulcano (1989a: 191) proposed the following diagnosis: (1) "MP1 + 2 few angulated in the intersections with the outer and inner gradated cross-veins, not interrupted by a Psm or Psc". This is clearly a plesiomorphic condition, not sufficient to characterize a monophyletic group; (2) "well-defined intramedial cell". The cell im is present in all chrysopoids; (3) "basal subcostal cross-veins and timpanic organ absent". It is extremely difficult to establish the presence or absence of these structures in fossil chrysopoids; (4) "little jugal lobe of anterior wing". This structure is extremely difficult to observe in fossils specimens and obviously not preserved in the type specimen and in other specimens of the type species *Limaia conspicua* (after the figures in Martins-Neto and Vulcano 1989a, b; Martins-Neto 2000). This diagnosis is clearly not sufficient to characterize a monophyletic group.

Makarkin (1997: 108) proposed a "description" of the "Limaiinae", as follows: (1) Fore wing RA entering margin at or just beyond wing apex. Numerous, but not all, extant chrysopid genera have this character. Thus it cannot be considered as uniquely present in the Limaiidae; (2) RA with apical branches simple and very densely spaced. This character is present as branches of ScP + RA in Osmylidae, potential chrysopoid sister group, thus it is probably plesiomorphic; (3) branches of RP not coalescend with MA. Thus, there is no clear vein Psm. This character is plesiomorphic; (4) cell im long, at least four times as long as wide. This character is also plesiomorphic, as the corresponding cell between branches of MP is long in both Osmylidae and Hemerobiidae; (5) cross-vein between cell im and CuA shift far distal. The polarity of this character is difficult to establish as this cross-vein is not well defined in the Osmylidae. Willmann and Brooks (1991) considered that it is a plesiomorphy. Furthermore, this cross-vein is also shifted far distal in the allopterid genus Karenina; (6) two regular series of gradate cross-veins. This character is present in the majority of extant Chrysopidae, thus it is not sufficient to characterize the Limaiidae; (7) anal veins simple. The organization of the anal veins of Mesypochrysa magna Makarkin, 1997 is very similar to that of an extant Chrysopidae. Also, this area is very poorly preserved and badly known in the genus Limaia; (8) in hind wing, "M forked nearly opposite the arising of Rs" (or under the present wing venation terminology, fork of MP into MP1 + 2 and MP3 + 4 strongly approximate base of RP + MA) or "with the anterior branch

arising from the stem of Rs and the posterior branch straight" (MP unforked). This "character" is of composite nature as it concerns the presence versus absence of a fork of MP into MP1 + 2 and MP3 + 4 and the position of the fork of MP. Also, Mesochrysopa and the Recent genus Hypochrysa Hagen, 1866 have a fork of MP close to the base of RP + MA (Adams 1967). Thus, the first state of this character is not uniquely present in Limaiidae. The exact structure of the hind wing MP is very badly known in the two Limaia species (Martins-Neto 2000). It is not possible to establish that it is as described by Makarkin. The hind wing unforked MP of some Mesypochrysa species (M. criptovenata, M. magna, M. chrysopa, M. curvimedia, and M. minima) is a highly specialized feature, not shared by any other member of the chrysopid lineage. But it is unknown in many other species (M. intermedia, M. latipennis). It could well be an autapomorphy of the genus Mesypochrysa.

In conclusion, there is no clear autapomorphy that would characterize the Limaiidae in the previous studies. Nevertheless, they share with the extant Chrysopidae the presence of a vein Psc in the both wings (synapomorphy), even if they have no clearly defined vein Psm (plesiomorphy). They also share with Recent chrysopids a costal area rather broad basally.

The exact structure of the distal area between C, ScP and RA is rather enigmatic in the genera Lembochrysa, Mesypochrysa, Drakochrysa, Protochrysa, and Limaia. In Mesypochrysa intermedia, ScP is not fused with RA, but ending on C in a net of very small veinlets well basal of wing apex; RA is not fused with C but reaching wing apex; there is a net of very small and numerous veinlets between RA and C (+ ScP) (see Fig. 10.6 M. intermedia 2066/1139). The same structure is also present in other chrysopids from Karatau, such as specimens PIN 2904/743 (Figs. 10.3, and 11.7), PIN 2066/1177 (Fig. 11.8), PIN 2997/2774 (Fig. 11.9), and MNHN-DHT R. 63845 from China (Figs. 13.1-13.2, Mesypochrysa). Martynov (1927: fig. 12) figured the same structure for the type species Mesypochrysa latipennis. This structure of costo-radial area strongly differs from the rather basal fusion of ScP and RA with C of Paralembochrysa n. gen., in which there is no cross-veins between RA and C distal of fusion of ScP with C.

Unfortunately, Panfilov (1980) incorrectly figured this complex structure as a dark pterostigmal zone in which vein ScP would vanish. Martins-Neto (2000 and previous papers), Yang & Hong (1990), Willmann & Brooks (1991), Ren & Guo (1996), and Makarkin (1997) figured this area similarly to Panfilov in the taxa they described. It will be necessary to revise all the type specimens of these described species to determine their exact structure of the apical parts of veins ScP and RA, but it is highly probably that they are identical to what occurs in Mesypochrysa intermedia because these authors figured numerous veinlets at least in apical part of area between RA and C for these limaiid taxa. The organization of the apical ends of ScP and RA is very diverse in Recent Chrysopidae, i.e. distal fusion of ScP with RA in Nacaura Navas, 1913, ScP and RA completely separated and both veins ending on C near wing apex in the majority of taxa, even rather basal fusion of ScP with C with distal re-emergence of ScP in Kimochrysa Tjeder 1966 (Brooks & Barnard 1990). But no extant Chrysopidae has such a fusion of ScP with C far basal of wing apex and a broad distal area



Figure 12 Cratochrysa martinsnetoi, MNHN-DHT R. 63844, habitus of the holotype. Scale bar: 10 mm.

between RA and C (+ ScP) with numerous long and forked veinlets, as in Mesypochrysa intermedia. The exact phylogenetic value of this structure is difficult to establish, because it is apparently very homoplastic within the Hemerobiiformia. If the Osmylidae have a ScP distally fused with RA, ScP is ending directly on C in several Hemerobiidae. Also in the Polystoechotidae and Ithonidae, two most basal groups of Hemerobiiformia (Aspöck 2001), the situation greatly varies, i.e. in the ithonid genus Oliarces, ScP is not fused with RA, unlike in the another ithonid genus Ithone and in the genus Polysthoechotes (New 1990: fig. 23). Nevertheless, if we polarize it after the comparison with the Osmylidae, most probable chrysopoid sister group, the ScP completely separated from RA can be considered as an apomorphic character state, shared by the Limaiidae and Recent Chrysopidae. The ScP ending on C well basal of wing apex can be considered as an apomorphic character state, proper to the Limaiidae. The presence of numerous long, more or less forked veinlets in apical area between RA and C can be considered plesiomorphic.

In consequence, we propose the following new diagnosis of the Limaiidae: (1) veins ScP ending in C well basal of wing apex [to verify in several species of *Mesypochrysa*]; (2) presence of numerous veinlets in area between C and RA; (3) RA ending at or near wing apex; (4) only the two rows of i.g. and o.g. crossveins in radial area; (5) no Psm vein; (6) a better defined Psc vein than in Mesochrysopidae; (7) fore wing cell im elongate and narrow; (8) fore wing cross-vein between cell im and CuA in a very distal position.

The character (1) is also present in the very basal chrysopoid *Liassochrysa* and in *Paralembochrysa* n. gen. (in the strict chrysopid lineage). The former differs from Limaiidae in the structure of its cubito-anal veins and areas. The latter has a vein Psm in its hind wing, typical of the Chrysopidae *sensu stricto*.

Generic differences. It is very difficult to compare with some accuracy the limaiid genera because of the incom-

plete knowledge of *M. latipennis*, type species of Mesypochrysa. Even, the exact nature of its figured wing (see Martynov 1927: fig. 10) is not established with accuracy, as Adams (1967) proposed it could be a hind wing, but it has a forked MP, like in the fore wings of several other Mesypochrysa species There are important differences between the various species attributed to this last genus: the part of RP + MA of M. latipennis basal of the first basal cross-vein between it and MP1 + 2 is apparently long, as in Mesypochrysa intermedia Panfilov 1980, M. angustialata Makarkin 1997, M. curvimedia Makarkin 1997, the two Limaia species, and the two Lembochrysa species, but unlike in Mesypochrysa criptovenata Martins-Neto & Vulcano 1988, M. magna Makarkin 1997, or M. chrysopa Makarkin, 1997 (Martynov 1927; Ren & Guo 1996; Makarkin 1997; Martins-Neto 2000). Also, the cells in radial area between main branches of RP, i.g. and o.g. cross-veins are broad and short in M. latipennis and the two Lembochrysa species, unlike the narrow elongate cells of the other Mesypochrysa species and Limaia species Drakochrysa sinica Yang & Hong 1990 shares with the Limaiidae the main apomorphic character concerning the ScP and RA, proposed above. It shares with *M. magna* the presence of a simple hind wing vein MP (Yang & Hong 1990). The differences between the two genera are very few. Yang & Hong (1990) transferred M. intermedia Panfilov 1980 into the genus Drakochrysa, but Nel & Henrotay (1994) put in doubt this attribution and restored it in the genus Mesypochrysa. Lembochrysa shares with the Limaiidae all the diagnostic characters, and especially the main apomorphic character concerning veins ScP and RA, as proposed above (Ren & Guo 1996). It mainly differs from Mesypochrysa in the presence of hind wing forked MP. Protochrysa aphrodite and maybe another Protochrysa species recently described by Rust (in litteris 1999) (see below in the list of taxa) have an organisation of the areas between C, ScP and RA identical to that of Mesypochrysa, with ScP ending well basal of wing apex, presence of several veinlets between RA and C, and RA ending at wing apex (Willmann & Brooks 1991; Rust in litteris 1999). The other parts of the wing venation of *P. aphrodite* are very similar to those of Lembochrysa or Limaia, especially in its elongate cell im, very rudimentary vein Psm but welldefined vein Psc. Protochrysa differs from Mesypochrysa in its hind wing MP forked. There are few differences between Lembochrysa and Protochrysa, mainly in the narrower and longer cells of the radial area in the latter.

Mesypochrysa cf. chrysopoides Ponomarenko 1992 (Figs 10.6, and 13.1-13.2)

Material. Specimen MNHN-DHT R 63845, Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris.

Occurrence. Tithonian – Valanginian, stratigraphic level *"Coptoclava – Ephemeropsis"* Fauna. Huangbanjiegou valley, Beipiao City, Liaoning Province, NE China.

Description. Body visible in lateral view with the four wings ovelapping; head 2.1 mm long, 2.3 mm wide; eye rounded, 1.1 mm in diameter; both antennae apparently short or with distal parts not preserved; pronotum short, 1.5 mm long; abdomen 11.0 mm long, 5.0 mm wide; legs not raptorial; fore wing

24.5 mm long, 8.0 mm wide, ratio length/width 3.0; fore wing apically rounded; costal area between C and ScP distinctly widened basally, maximal width 1.2 mm; about ten cross-veins in costal area, perpendicular to ScP and C, basal of fusion between C and ScP; area between ScP and RA basally rather wide; C and ScP distally joined, 10.5 mm basal of wing apex; a long dark sclerotized pterostigmal structure, 15.0 mm distal of wing base, RA ending at wing apex; several short cross-veins between RA and C at least in distal part of pterostigmal area; RP + MA separating from R obliquely and in a basal position, 4.1 mm distal of wing base; MA separating from RP 4.3 mm distally; MA not fused with MP1 + 2 to constitute base of a Psm; MA reaching posterior wing margin and parallel with MP1 + 2; RP with ten branches; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; i.g. cross-veins zigzagged, not directly



Figure 13

1, Mesypochrysa cf. chrysopoides, MNHN-DHT R 63845, fore wing. 2, M. cf. chrysopoides, MNHN-DHT R 63845, hind wing. 3, Paralembochrysa splendida, MNHNDHT R. 55224, holotype fore wing. 4, P. splendida, MNHN-DHT R. 55224, holotype hind wing. 5, Cratochrysa martinsnetoi, MNHN-DHT R. 63844, holotype right fore wing. 6, C. martinsnetoi, MNHN-DHT R. 63844, holotype right hind wing. 7, C. martinsnetoi, MNHN-DHT R. 63844, holotype left hind wing. 8, Chimerochrysopa incerta, LH-18588, holotype, hind wing. Scale bars: 1 mm.

connected with MA or MP1 + 2 but at nearly right angle with first branch of RP; MP separating from R + M 2.5 mm distal of wing base and 1.4 mm basal of RP + MA, very near to it; MP separating into MP1 + 2 and MP3 + 4 3.1 mm distally; MP1 + 2 very smoothly curved, nearly aligned with proximal portion of MP, and not fused with MA; MP3 + 4 simple, not distally divided into two branches; no vein MPspl; no "X-crossing" structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and rather long, 0.8 mm long; distally, MP3 + 4 more or less parallel with CuA and MP1 + 2; quadrangular cell im very long and wide, 4.2 mm long, 0.8 mm wide; a well defined vein Psc aligned with CuA; o.g. series of cross-veins zigzagged; no supplementary row of gradate veins between i.g. and o.g. cross-veins and one row of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins parallel; base of CuA close to wing base; CuA distally less zigzagged than MP3 + 4; cross-vein 1m between CuA and MP at base of MP; cell m1 1.0 mm long, 0.4 mm wide; cell m2 very long, 6.7 mm long, 1.0 mm wide; CuP separated from CuA opposite cross-vein 1m; cell c1 1.2 mm long, 0.5 mm wide; c2 3.2 mm long, 1.0 mm wide; c1 distinctly shorter and narrower than c2; CuP with two branches reaching posterior wing margin; AA strongly approximating CuP, with a cross-vein between them; area between AA and posterior wing margin rather broad, 1.6 mm wide; AP well developed.

Hind wing 21.4 mm long, 6.8 mm wide, ratio length/width 3.1; hind wing relatively shorter than fore wing; apex acute; costal area narrow, 0.5 mm wide; ScP ending on C 15.4 mm from wing base and 6.5 mm from wing apex; a long dark pterostigmal area; RA ending at wing apex; numerous apical crossveins between C and RA; RP + MA emerging from R 2.7 mm distal of wing base; no cross-vein between RP + MA and MP proximal of base of MA; MP emerging from R + M 1.7 mm distal of wing base; simple, straight, and more or less parallel with CuA; pseudo-vein Psc less well defined than in fore wing; o.g. cross-veins well-defined but zigzagged; radial area rather wide, with three rows of long cells between main branch of RP and posterior wing margin; only one row of cells between posterior wing margin and o.g. cross-veins; cubito-anal area not reduced, cells c1 and c2 well distinct and closed; CuP divided into two short posterior branches; AA and AP not preserved.

Discussion. This fossil can be attributed to the genus *Mesypochrysa* because of the following characters: ScP ending on C well basal of wing apex, dark pterostigmal area between C and RA with numerous veinlets; long cells im; absence of defined Psm and well defined Psc, hind wing MP simple. It shares long wings with *M. magna*, *M. falcata*, and *M. chrysopoides* (fore wing 26.0 mm long). It differs from *M. magna* and *M. falcata* in its fore wing base of RP + MA elongate and emerging obliquely from R, as in *M. chrysopoides*. The wing length of *Mesypochrysa polyclada* is unknown but its ScP is fused with RA and its branches of RP are divided into numerous veinlets near posterior wing margin, unlike this specimen. The discovery of this representative of

the genus *Mesypochrysa* extends its distribution to the Chinese Lower Cretaceous.

Mesypochrysa makarkini n. sp. (Figs 10.4-10.5, and 11.9-11.10)

Material. Holotype specimen PIN 2997/2774, paratype specimen PIN 2997/805, Palaeontomological Laboratory, Paleontological Institute, Academy of Science of Russia, Moscow.

Etymology. After Dr Vladimir N. Makarkin from Vladivostok, Russia, specialist in fossil Neuroptera.

Occurrence. Late Jurassic, Callovian-Kimmeridgian or Oxfordian-Kimmeridgian. Karatau, Chimkent region, Southern Kazakhstan.

Diagnosis. Fore wing of moderate length, 16.3-16.8 mm long, rather broad; RP with 9-11 branches, RP + MA emerging obliquely from R; MP1 + 2 and MP3 + 4 distally rather zigzagged.

Description. Two isolated fore wings, respectively 16.8 mm long, 5.8 mm wide, ratio length/width 2.9 (PIN 2997/805, Figs. 10.4 and 11.10), and 16.3 mm long, 5.7 mm wide, ratio length/width 2.8 (PIN 2997/2774, Figs. 10.5 and 11.9); fore wing apex rounded; costal area between C and ScP distinctly widened basally, maximal width 0.8 mm; about 12 cross-veins in costal area, perpendicular to ScP and C, basal of fusion between C and ScP; area between ScP and RA basally rather wide; C and ScP distally joined about 5.0 mm basal of wing apex; a long dark sclerotized pterostigmal structure; RA ending at wing apex; several short cross veins between RA and C in pterostigmal area; RP + MA separating from R obliquely and in a basal position, 3.1 mm distal of wing base; MA separating from RP 1.5 mm distally; MA not fused with MP1 + 2 to constitute base of a Psm; MA reaching posterior wing margin and parallel with MP1 + 2; RP with 9-11 branches; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; i.g. cross-veins zigzagged, not directly connected with MA or MP1 + 2 but at nearly right angle with first branch of RP; MP separating from R + M 1.8 mm distal of wing base; MP separating into MP1 + 2 and MP3 + 4 2.6 mm distally, well distal of base of RP + MA; MP1 + 2 very smoothly curved, not fused with MA; MP1 + 2 nearly aligned with proximal portion of MP; MP3 + 4 simple, not distally divided into two branches; no vein MPspl; no 'X-crossing' structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and rather long, 0.6 mm long; distally, MP3 + 4 more or less parallel with CuA and MP1 + 2; quadrangular cell im very long, 2.8 mm long, 0.7 mm wide; a well defined but zigzagged vein Psc aligned with CuA; o.g. cross-veins zigzagged; no supplementary row of gradate veins between i.g. and o.g. cross-veins and one row of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. crossveins parallel; base of CuA close to wing base; CuA distally less zigzagged than MP3 + 4; cross-vein 1m between CuA and MP at base of MP; cell m1 0.9 mm long, 0.4 mm wide; cell m2 very long, 5.2 mm long, 0.8 mm wide; CuP separated from CuA opposite cross-vein 1m; cell c1 1.0 mm long, 0.4 mm wide; c2

2.4 mm long, 0.7 mm wide; c1 distinctly shorter and narrower than c2; CuP with two branches reaching posterior wing margin; AA strongly approximating CuP; area between AA and posterior wing margin rather broad, 1.2 mm wide; AP well developed.

Discussion. This fossil can be attributed to the Limaiidae on the basis of the particular "pterostigmal" area, relative positions of ScP, RA and C, shape of cell im, absence of Psm but presence of Psc. Even if it probably belongs to the genus Mesypochrysa, the lack of information on its hind wing structure (MP forked or not) forbids any definite attribution to this genus. It differs from *Lembochrysa* in its more numerous branches of RP, from Drakochrysa in its fore wing banksian cell distinctly longer. The comparison with Limaia is nearly impossible to do, as this last genus is badly known. Mesypochrysa makarkini differs from M. latipennis in its cells of radial area elongate. Because of its fore wing length, it differs from all other *Mesypochrysa* species, except M. criptovenata, M. chrysopa, M. curvimedia, and M. angustialata. It differs from M. criptovenata in the more numerous branches of RP (9-11 instead of 7-8). It differs from *M. chrysopa* in its base of RP + MA emerging obliquely from R, instead of at right angle. It differs from M. curvimedia in its MP1 + 2 and MP3 + 4 not smoothly curved but distally rather zigzagged. It differs from M. angustialata in its less numerous branches of RP (eleven instead of thirteen), and broader wings.

Mesypochrysa species undetermined (Fig. 11.8)

Material. Specimen PIN 2066/1177, Palaeontomological Laboratory, Paleontological Institute, Academy of Science of Russia, Moscow.

Occurrence. Late Jurassic, Callovian – Kimmeridgian or Oxfordian Kimmeridgian. Karatau, Chimkent region, Southern Kazakhstan.

Description. A single fore wing 11.6 mm long, 4.1 mm wide, ratio length/width 2.8; fore wing apex not preserved; costal area between C and ScP distinctly widened basally, maximal width, 0.6 mm; about 13 cross-veins in costal area, perpendicular to ScP and C, basal of fusion between C and ScP; area between ScP and RA basally rather wide; C and ScP distally joined, 2.8 mm basal of wing apex; a dark sclerotized pterostigmal structure, 9.5 mm distal of wing base, RA probably ending close to wing apex; several short cross-veins between RA and C in pterostigmal area; RP + MA separating from R obliquely and in a basal position, 2.3 mm distal of wing base; MA separating from RP 1.2 mm distally; MA not fused with MP1 + 2 to constitute base of a Psm; MA reaching posterior wing margin and parallel with MP1 + 2; RP with seven branches; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; i.g.

cross-veins zigzagged, not directly connected with MA or MP1 + 2 but at nearly right angle with first branch of RP; MP separating from R + M 1.2 mm distal of wing base; MP separating into MP1 + 2 and MP3 + 4 2.3 mm distally, well distal of base of RP + MA; MP1 + 2 very smoothly curved, not fused with MA; MP1 + 2 nearly aligned with proximal portion of MP; MP3 + 4 simple, not distally divided into two branches; no vein MPspl; no "X-crossing" structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and rather long, 0.4 mm long; distally, MP3 + 4 more or less parallel with CuA and MP1 + 2; quadrangular cell im very long and wide, 1.9 mm long, 0.6 mm wide; a well defined but zigzagged vein Psc aligned with CuA; o.g. cross-veins zigzagged; no supplementary row of gradate veins between i.g. and o.g. cross-veins and one row of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins parallel; base of CuA close to wing base; CuA distally less zigzagged than MP3 + 4; cross-vein 1m between CuA and MP at base of MP; cell m1 0.4 mm long, 0.2 mm wide; cell m2 very long, 3.9 mm long, 0.4 mm wide; CuP separated from CuA opposite cross-vein 1m; cell c1 0.8 mm long, 0.2 mm wide; c2 1.7 mm long, 0.5 mm wide; c1 distinctly shorter and narrower than c2; CuP with two bifurcate branches reaching posterior wing margin; AA strongly approximating CuP; area between AA and posterior wing margin rather broad, 0.7 mm wide; AP well developed.

Discussion. This fossil can be attributed to the Limaiidae on the basis of the particular "pterostigmal" area, relative positions of ScP, RA and C, shape of cell im, absence of Psm but presence of Psc. Even if it probably belongs to the genus Mesypochrysa, the lack of information on its hind wing structure (MP forked or not) forbids its definitive attribution to this genus. Its small size (wing 11.6 mm long) separates this fossil from all other Mesypochrysa species, except M. confusa, M. minima, and M. reducta. It differs from M. latipennis in cells of radial area between the i.g. and o.g. crossveins elongate instead of being very short. It is not possible to compare it to *M. confusa* because it is a very badly known species. *M. minima* is a poorly known species based on the distal three fourth of a hind wing. Makarkin (1997) separated it from other species on the basis of its small size, but its wing length is comparable to that of M. reducta (wing 11.5 mm instead of 12.1 mm in M. reducta). As M. reducta is based on a fore wing and *M. minima* on a fragmentary hind wing, this argument is not sufficient to correctly separate these two species. Our fossil differs from *M. reducta* from the same outcrop of Karatau in its fork of MP into MP1 + 2 and MP3 + 4 well distal of base of RP + MA, instead of being opposite in *M. reducta* (see Panfilov 1980: fig. 113). Unfortunately, it is not possible to accurately compare this new fossil to the type hind wing of *M. minima*. Therefore, we prefer to maintain it in open nomenclature, as a *Mesypochrysa* species.

CHRYSOPOIDEA FAMILIA INCERTAE SEDIS (maybe Chrysopidae Schneider 1851)

Genus Paralembochrysa n. gen.

Type species. Paralembochrysa splendida n. sp.

Etymology. After its superficial similarities with *Lembochrysa*.

Diagnosis. This genus is characterized by the following features: fore wing costal area basally widened and short; fore and hind wing ScP, RA and C distally fused, no apical area between these veins, but C + ScP + RA reaching wing apex; no cross-veins in the broad composite vein C + ScP + RA; RP + MA, MP and Cu basally strongly approximate, especially in fore wing; MA and MP1 + 2 not fused in fore wing; MA and MP1 + 2 distinctly fused and distally separated again in hind wing; no hind wing banksian cell b; MP3 + 4 and CuA not fused in fore and hind wing; fore wing CuA zigzagged; no clear vein Psc; only three basal i.g. cross-veins in fore and hind wing; o.g. cross-veins welldefined and zigzagged in fore and hind wing; distally, only two rows of long cells between RP and posterior wing margin; hind wing anal area narrower than that of fore wing; fore wing cell im quadrangular and long. The main diagnostic character and unique autapomorphy of Paralembochrysa is the fusion of ScP and RA with C in a broad vein reaching wing apex.

Paralembochrysa splendida n. sp. (Figs 10.7, and 13.3 – 13.4)

Material. Holotype specimen MNHN-DHT R. 55224, coll. Nel, Laboratory of Palaeontology, National Museum of Natural History, Paris.

Etymology. After the wonderful state of preservation of the holotype.

Occurrence. Tithonian – Valanginian, stratigraphic level *Coptoclava* – "*Ephemeropsis*" Fauna (Lin 1983: 393, 1994: 308-309). Huangbanjiegou valley, Beipiao City, Liaoning Province, NE China.

Description. Impression of a nearly complete insect with four wings nearly overlapping; venation nearly complete; fore wing 14.0 mm long, 4.6 mm wide, ratio length/width 3.0; fore wing rather narrow, rounded and not very elongate; costal area between C and ScP distinctly widened basally, maximal width, 0.6 mm, but very short; about ten cross-veins in costal area, perpendicular to ScP and C, basal of fusion between C and ScP; area between ScP and RA basally rather wide; C, ScP and RA distally joined, 6.8 mm basal of wing apex, these veins becoming indistinguishable; no cross-veins between RA, ScP and C in pterostigmal area to wing apex; RP + MA separating from R in a very basal position, 2.9 mm distal of wing base; MA separating from RP 3.3 mm distally; MA not fused with MP1 + 2 to constitute base of a Psm; MA reaching posterior wing margin and parallel with MP1 + 2; RP with seven branches; no supplementary series of gradate cross-veins between RP and i.g. cross-veins; i.g. crossveins very few and zigzagged, not directly connected with MA or MP1 + 2 but at nearly right angle with first branch of RP; MP separating from R + M 1.9 mm distal of wing base and 1.0 mm basal of RP + MA, very near to it; MP separating into MP1 + 2 and MP3 + 4 1.5 mm distally; MP1 + 2 very smoothly curved, not fused with MA; MP1 + 2 nearly aligned with proximal portion of MP; MP3 + 4 simple, not distally divided into two branches; no vein MPspl; MP3 + 4 only smoothly zigzagged; no 'Xcrossing' structure; cross-vein 2m nearly perpendicular to MP3 + 4 and CuA and rather long, 0.5 mm long; distally, MP3 + 4 more or less parallel with CuA and MP1 + 2; four long cells between MP3 + 4 and CuA and between MP1 + 2 and MP3 + 4; quadrangular cell im very long and wide, 1.8 mm long, 0.6 mm wide; no defined vein Psc; distally, o.g. cross-veins nearly perpendicular to MA; o.g. cross-veins zigzagged; no supplementary row of gradate veins between i.g. and o.g. cross-veins and one row of cells between o.g. cross-veins and posterior wing margin; i.g. and o.g. cross-veins parallel; base of CuA close to wing base; CuA distally less zigzagged than MP3 + 4; cross-vein 1m between CuA and MP distal of base of MP; cell m1 0.8 mm long, 0.3 mm wide; cell m2 longer, 1.6 mm long, 0.5 mm wide; CuP separated from CuA opposite cross-vein 1m; c1 1.6 mm long, 0.5 mm wide; c2, 1.6 mm long, 0.6 mm wide; c1 as long as c2 and c2 not distinctly broader than c1; CuP with two bifurcate branches reaching posterior wing margin; AA not well preserved but strongly approximating CuP, without any visible crossvein between them; area between AA and posterior wing margin rather broad, 0.7 mm wide; AP not visible.

Hind wing 11.4 mm long, 4.6 mm wide, ratio length/width 2.5; hind wing relatively broader and shorter than fore wing; apex rounded; costal area narrow, 0.4 mm wide, with about ten visible cross-veins basal of fusion between C, ScP and RA about 6.5 mm distal of wing base; no apical cross-veins between C, ScP and RA; RP + MA emerging from R 1.6 mm distal of wing base; no crossvein between RP + MA and MP proximal of base of MA; sxv and banksian cell b absent because of fusion between MA and MP1 + 2; MA distinctly oblique, 0.8 mm long, distally fused with MP1 + 2 for 1.1 mm; MA and MP1 + 2 clearly separating distally and reaching posterior wing margin independently; only two i.g. cross-veins; MP emerging from R + M 0.6 mm distal of wing base; division of MP into MP1 + 2 and MP3 + 4 2.3 mm distally; MP1 + 2 curved, 0.8 mm long basal of its fusion with MA; MP3 + 4 long, zigzagged, more or less parallel with CuA, and not fused with it; no pseudo-vein Psc; only one row of cells between CuA and MP3 + 4 and between MP3 + 4 and MP1 + 2; very few o.g. cross-veins, well-defined but zigzagged; radial area rather wide, with two rows of long cells between main branch of RP and posterior wing margin; only one row of cells between posterior wing margin and o.g. cross-veins; cubito-anal area not reduced, cells c1 and c2 well distinct; c1 closed, 1.4 mm long, 0.5 mm wide; c2 posteriorly open, 1.5 mm long, 0.5 mm wide; CuP divided into two short posterior branches; AA long and simple; width of anal area, 0.3 mm; AP not visible, probably fused with posterior wing margin.

Discussion. *Paralembochrysa* n. gen. is similar to the genera *Lembochrysa*, *Mesypochrysa*, and *Limaia* in the following characters: fusion of Sc with C well basal of

wing apex; cell im long; presence of only the two rows of i.g. and o.g. cross-veins; no Psm; anal veins simple, although this last character is not certain in Limaia. Paralembochrysa n. gen. differs from Mesypochrysa spp., Lembochrysa spp., and Limaia adicotomica in the fore wing fusion of RA with C and ScP in a broad costoapical vein without any small cross-veins in the apical part of costal area at wing apex, CuA distally zigzagged and not fused with MP3 + 4 into a Psc, i.g. cross-veins missing in apical part of fore wing, partial fusion of MA with MP1 + 2 in hind wing. Furthermore, it differs from Limaia in the fore wing veins RP + MA and MP strongly approximating at their bases (Ren and Guo 1996; Makarkin 1997; Martins-Neto 2000). Its vein ScP fused with C in a basal position could be a synapomorphy with the Limaiidae, but the organization of its veins RA and C completely differs from that of Limaiidae. Also, its fusion of MP1 + 2 with MA in hind wing is a derived state, only present in some recent Chrysopidae (Nothochrysa McLachlan, 1868, Pimachrysa Adams, 1956), suggesting that it is more closely related to extant Chrysopidae than to Limaiidae.

Remarks. The list of the fossil taxa currently attributed to the Chrysopidae is given in Appendix 5. The subfamilial attributions of these taxa proposed in literature should be confirmed after cladistic analyses of the Chrysopidae that would include the fossil taxa. The taxa are listed below after their respective age and outcrops.

NEUROPTERA familia Incertae sedis Genus Chimerochrysopa n. gen.

Type species. Chimerochrysopa incerta n. sp.

Etymology. After *Chrysopa* and chimera for the strangeness of the wing venation.

Diagnosis. This genus is well characterized by the following features of the (hind?) wing: area between ScP and RA nearly as broad as costal area in distal part; MA + RP very long basal of its separation into MA and RP; bases of MA + RP, MP and CuA strongly approximating very near to wing base; a rudimentary Psm as result of fusion of MA with MP1 + 2, thus no banksian cell; a rudimentary Psc as result of fusion of MP3 + 4 with CuA; area between CuA and CuP very wide; anal area, below CuP, very broad, with four long parallel veins, i.e. two branches of AA1, AP1 and AP2, all widely separated.

Chimerochrysopa incerta n. sp. (Figs 10.8 and 13.8)

Material. Holotype specimen LH-18588, housed in the Museo de las Ciencias de Castilla – La Mancha, in Cuenca, Spain.

Etymology. After the very uncertain relationships of this species.

Occurrence. La Huerguina Formation, Barremian. Las Hoyas outcrop, Cuenca Province, Spain.

Description. Impression of a complete (hind-?) wing; venation nearly complete and convexity of veins clearly visible; wing 14.0 mm long, 4.0 mm wide, ratio length/width 3.5; apex of wing rounded but wing narrow and elongate; costal area not widened, 0.4 mm wide, with about twenty five simple and straight cross-veins between C and ScP, between base and fusion of ScP with RA; area between ScP and RA rather wide, 0.3 mm wide, without any visible cross-veins; RA and ScP distinctly fused, 11.9 mm distal of wing base and 2.3 mm basal of wing apex; ScP + RA with a distinct apical curvature and parallel to costo-apical wing margin; apical area between C and ScP + RA 0.7 mm wide, with nearly twelve simple and undulate crossveins; concave vein RP + MA originating from R 1.7 mm distal of wing base, in a very basal position; common stem RP + MA very long, MA originating from RP 3.3 mm distal of base of RP + MA; RP with eight posterior branches; RP distinctly zigzagged, with about sixteen cross-veins between RA and RP (+ MA); MA clearly fused with the concave MP1 + 2, as the vein MA (+ MP1 + 2) is concave in its distal part, unlike the convex basal part of MA, MA not fused with the branches of RP; only a rudimentary vein Psm, formed by fusion of MA with MP1 + 2; no banksian cell; six rows of cells between RP and posterior wing margin; i.g. cross-veins making a well defined zigzagged vein; o.g. cross-veins not well defined; MP emerging from R + MA 1.0 mm distal of wing base, very near to it; MP long and straight basal its division into MP1 + 2 and MP3 + 4, 4.0 mm distal of its base; basal part of MP1 + 2 short, 0.2 mm long, basal part of MA short, 0.3 mm long, basal of Psm; angle between MP1 + 2 and MP3 + 4 very open; basal part of MP3 + 4 very short, 0.2 mm long, basal of its fusion with CuA; MP3 + 4 + CuA long and zigzagged, nearly parallel with Psm, with only one row of cells between them, thus vein Psc (or MP3 + 4 + CuA) rudimentary but never fused with Psm; Psm concave; Psc convex, their respective convexity showing that they are not simply the veins MA (for Psm) and MP3 + 4 (for Psc), because, in the contrary case, they would have inversed convexities; Cu beginning at wing base, divided into CuA and CuP 0.6 mm distal of its base, CuP making a nearly right angle with CuA; area between CuA and MP apparently crossed by four supplementary cross-veins (+ vein 1m), thus cell m1 crossed one time and cell m2 crossed three times, m1, 0.7 mm long; m2, 3.7 mm long; CuA convex, strongly zigzagged, 4.5 mm long basal of its fusion with MP3 + 4; CuA and concave CuP delimitating three long and narrow quadrangular cells c1, c2, and a supplementary c3; c1 1.0 mm long; c2 0.8 mm long; c3 0.9 mm long; CuP with three long and simple posterior branches; area between CuP, CuA, Psc and posterior wing margin very broad, with four secondary veins and four rows of cells between CuA and posterior wing margin; anal area very wide, 0.9 mm wide; AA1 with two distinct simple branches and 2.7 mm long; AP1 simple and 1.7 mm long; AP2 also simple and 1.1 mm long.

Discussion. The very wide anal area with four long anal veins strongly suggests that this specimen LH-18588 could be a hind wing, although there is no definite evidence of this hypothesis. Although it has some characters present in the Chrysopoidea (long common stem of RP + MA, presence of series of gradate cross-veins), we do not know if Chimerochrysopa n. gen. has the main synapomorphic characters of the Chrysopoidea sensu stricto, i.e. presence of a well defined cell im in fore wing and fore wing basal cross-vein between MP and Cu exactly opposite base of MP, these structures being absent in the known wing. It also differs from the advanced Chrysopoidea minus Liassochrysidae in its fork of MP in a very distal position, long area between CuA and CuP, with numerous cells, numerous anal veins. This taxon can only be considered as a Neuroptera of uncertain familial affinities, with some similarities with the Chrysopoidea.

Genus Cratochrysa Martins-Neto 1994

Type species. Cratochrysa willmanni Martins-Neto, 1994, other species: Cratochrysa sublapsa Martins-Neto 1997, Cratochrysa martinsnetoi n. sp., all from the Early Cretaceous, Araripe Formation, Brazil, Martins-Neto 1994, 1997, 2000) was originally included in the Chrysopidae. It is a Neuroptera of uncertain familial position, probably not related to the Chrysopidea (see below). Both *C. willmanni* and *C. sublapsa* are based on rather poorly preserved specimens. We describe a new specimen we can attribute to this genus but to a new species.

Cratochrysa martinsnetoi n. sp. (Figs 12 and 13.5-13.7)

Material. Holotype specimen MNHN-DHT R. 63844, coll. Borschukewitz, Paleontological laboratory, Museum National d'Histoire Naturelle, Paris, France.

Etymology. After Dr. Rafael Gioia Martins-Neto, specialist of fossil insects from Brazil.

Occurrence. Crato Formation, Albian. Santana do Cariri, Araripe Basin, Brazil.

Diagnosis. This species differs from the two other *Cratochrysa* species in its distinctly longer wings (fore wing 15.5 mm long, instead of 13.4 mm in *C. willmanni*, and 9.0 mm in *C. sublapsa*). Its veins RP, MA, MP, CuA, CuP and AA have distal forks near posterior margins, unlike the two other *Cratochrysa* species. This fossil corresponds to no other Neuroptera described from the Crato Formation *Caririberotha martinsi* Martins-Neto and Vulcano, 1990 and *Araripeberotha fairchildi* Martins-Neto and Vulcano, 1990 could superficially resemble this new fossil but they differ in the absence of i.g. cross-veins and the presence of forked veinlets in area between C and ScP (Martins-Neto 2000).

Description. Body circa 13.0 mm long; head 2.0 mm long, 2.0 mm wide; antenna 3.5 mm long, with circa 40 segments, all simple and short; thorax 5.0 mm long, pronotum not elongate; abdomen 6.0 mm long; fore wing 15.5 mm long, 5.3 mm wide; ScP not distally fused with RA but ending on anterior wing margin close to wing apex; RA ending at wing apex; 22 simple cross-veins in area between C and ScP; RA with four short apical branches; M separating from R 1.6 mm after wing base, a short vein emerging from M at its base, 0.2 mm long, and distally fused again with R, maybe corresponding to true vein MA; RP + MA separating from RA 2.9 mm from wing base; MA separating from RP 3.6 mm distally; MA with three short apical branches; RP with three main posterior branches, all forked at apex; at least 3-4 cross-veins between RA and RP (+ MA), more or less oblique; part of MP basal of its fork long, 2.8 mm long; no well defined cell im having a shape different of other cells of the same area; MP1 + 2 and MP3 + 4 parallel, with 4-5 long cells between them; both MP1 + 2 and MP3 + 4 with three small apical branches; basal cross-vein between M and Cu distinctly distal of base of M and that of CuP; CuP at right angle with CuA at its base; CuA and CuP very long, parallel, with eight cells between them; both CuA and CuP with three short apical branches; CuP and AA well separated and parallel; AA with two main branches, both distally forked; AP with numerous branches; a series of four o.g. cross-veins and a series of 4-5 i.g. cross-veins; No Psm; no Psc.

Hind wing 14.3 mm long, 4.5 mm wide; hind wing similar to fore wing; the main differences being as follows: free part of MA between M and RP longer, 0.9 mm long and ending on RP, not on R; M (/ MP) and CuA strongly approximate; cubito-anal areas not very well preserved.

Discussion. Except for its longer wings with more numerous short apical branches of main veins, this fossil is very similar to the other Cratochrysa species. It is better preserved than the type specimens of these species. After the present phylogenetic analysis, Cratochrysa falls in a very basal position, and shares with the 'true' Chrysopoidea the presence of the series of the i.g. crossveins. But this character alone cannot constitute a synapomorphy of the Chrysopoidea, as it is also present in numerous other neuropteran lineages (Polystoechotidae, Nevrorthidae, some Dilaridae, Mantispidae, Berothidae). It differs from the Chrysopoidea in its area between CuA and CuP very elongate, with four aligned cells or more and the absence of well individualized cell im in fore wing. Cratochrysa has some similarities with the Dilaridae: Nallachiinae from which it only differs in the presence of more numerous cells in the cubital area and the lack of long setae along wing veins (Adams 1970). Because of the absence of phylogenetic analysis of the Neuroptera that would include the wing venation characters, it is still not possible to accurately define the relationships of *Cratochrysa*. Thus we prefer to maintain it in open nomenclature as a Neuroptera familia incertae sedis stat. nov.

PHYLOGENETIC ANALYSIS OF THE CHRYSOPOIDEA

The present phylogenetic analysis is based on 34 wing characters and one body character, for 26 genera (table 1). We exclude *Drakochrysa* and *Lembochrysa* from the analysis because of their incomplete information and close similarity with *Mesypochrysa*. The chosen potential outgroups are *Nymphes* (Nymphidae), *Notiobellia* (Hemerobiidae), and *Porismus* (Osmylidae). The Osmylidae and Hemerobiidae are potential sister groups of the Chrysopidae, after Aspöck *et al.* (2001) and Aspöck (2002). We also added one Nymphidae because of their great similarity in the wing venation with some taxa currently attributed to the Chrysopidae (*Nymphoides*).

The characters were considered unordered and equally weighted. 31 characters are informative (see Appendix 6, and Table 1). The analyses were made using the computer software Paup* 4.0b10 for PC and MacClade 3.08a for Macintosh to visualize the distribution of the character states in the most parsimonious trees. Branch and bound searches were made with all the possible combinations of outgroups (one per one, by couples or by triplets). These choices did not affect the topology of the inner group in the resulting strict consensus cladogram. They gave 6328 equally most parsimonious trees, with a strict consensus cladogram given figure 14. These equally most parsimonious trees have the following main characteristics: length 64 steps, consistency index CI 0.5469, CI excluding uninformative characters 0.5246, retention index RI 0.7661, and RC 0.4190.

The genus *Nymphoides* Panfilov 1980 (based on two badly known taxa *Nymphoides latus* Panfilov 1980 from the Late Jurassic of Karatau, and *Nymphoides udensis* Ponomarenko 1984 from the Middle to Late Jurassic, Uda Formation, Buryatia) was first included in the Mesochrysopidae (Panfilov 1980; Ponomarenko 1984). Nel and Henrotay (1994) put in doubt its attribution to the chrysopid lineage. In the present analysis, it falls out of the Chrysopoidea. Thus, we prefer to exclude these two species from this group and consider them as Neuroptera of uncertain affinities. Ponomarenko (2003) included the genus *Osmylites* Haase 1890 (Upper Jurassic, Germany) in the Mesochrysopidae because its wing vena-





Table 1. Character matrix.

1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Nymphes	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0
Notiobellia	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Porismus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Allopterus	1	0	0	0	0	0	1	1	1	1	1	0	1	2	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	0
Triangulochrysopa	1	0	0	0	0	0	1	1	1	1	1	0	1	2	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	0	0	0
Karenina	1	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0
Armandochrysopa	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0
Mesochrysopa	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	?	0	?	0	0	1
Tachinymphes	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	0	0	0
Nannochrysopa	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	0	0
Limaia	0	0	0	1	1	2	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	?	0
Mesypochrysa	0	0	0	1	1	0	1	1	0	1	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	1	0
Drakochrysa	0	0	0	1	1	?	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	?	0
Lembochrysa	0	0	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0	0	1	0
Protochrysa	0	0	0	1	1	?	1	0	0	0	1	1	0	0	1	1	0	0	1	1	1	?	1	1	1	0	1	1	0	0	0	0	1	0
Paralembochrysa	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
Baisochrysa	0	0	0	?	?	2	1	0	0	0	1	1	0	0	?	2	0	0	1	1	1	?	1	1	1	0	1	2	0	0	0	0	0	0
Araripechrysa	0	0	0	1	1	?	1	0	0	0	1	0	0	0	0	?	0	?	1	1	1	?	1	1	1	0	1	1	0	0	0	0	0	0
Cratochrysa	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?	0	0	0	0	0	0	0	0	0	1	0	?
Protoaristenymphes	1	0	0	?	?	?	1	0	0	0	1	0	0	0	1	?	0	?	1	1	1	1	1	1	1	0	1	?	0	?	?	0	1	?
Aristenymphes	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	?	0	?	1	1	1	1	1	1	1	0	1	1	0	?	?	0	1	1
Macronympha	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	?	0	?	1	1	1	1	1	1	1	0	1	1	0	?	?	0	1	1
Liassochrysa	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	?	0	?	1	1	0	1	0	0	0	0	1	0	0	?	?	0	0	1
Nymphoides	0	?	0	0	0	0	1	0	0	0	0	2	0	0	0	?	0	?	1	0	0	?	0	0	?	0	1	1	0	?	0	0	?	?
Mesotermes	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	?	0	?	1	1	1	?	1	1	1	0	1	1	0	?	?	0	0	0
Cretachrysa	0	0	0	?	?	?	1	?	0	?	1	1	0	0	?	?	0	?	?	?	1	?	?	1	1	0	1	?	0	?	?	0	0	?
Nothochrysa	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Chrysopa	0	0	0	1	0	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0

tion is close to that of *Nymphoides*. The reconstruction of the wing venation of *Osmylites*, as proposed by Ponomarenko, strongly differs from that of *Mesochrysopa*, especially in the number of cells between the branches of median vein. Therefore, we consider that *Osmylites* has to be excluded from the Mesochrysopidae and the Chrysopoid lineage. The family Osmylitidae Martynova 1949 is restored and not a junior synonym of Mesochrysopidae, contra Ponomarenko (2003).

The genus *Cratochrysa* falls in the most basal position of the ingroup, but we prefer to exclude it from the Chrysopoidea *sensu stricto* (see above).

The clade Chrysopoidea n. sensu (see above) is supported by two synapomorphies i.e. characters "11, state 1", i.e. presence of a well defined cell im in fore wing, delimited by branches of MP and a distal constriction in area between MP1 + 2 and MP3 + 4 (a), and "22, state 1", i.e. fore wing basal cross-vein between MP and Cu exactly opposite base of MP. The clade Chrysopoidea minus Liassochrysidae n. fam. is supported by five synapomorphies, i.e. characters "21, state 1" (area between CuA and CuP short, with less than four aligned cells, but also present in *Notiobellia*), "23, state 1" (apex of vein CuA basal of level of half wing), "24, state 1" (AA with two simple branches or less, but also present in Nymphes), "25, state 1" (AP with only one or two branches, but also present in Nymphes), and "27, state 1" (fore wing fork of MP in a basal position, but also present in *Nymphoides*).

The clade Chrysopidae *sensu stricto* (represented by *Chrysopa* and *Notochrysa*) is supported by one synapomorphy (character "17, state 1", presence of a vein Psm in fore wing). The character "18, state 1", (presence of

a vein Psm in hind wing) is also present in the new genera Paralembochrysa and Nanochrysopa (close to Tachinymphes because of its hind wing cells c1 and c2 posteriorly opened, reduction of anal veins, and presence of long setae along vein CuA). The presence of Psm in Nanochrysopa n. gen. is probably due to the strong reduction of its hind wing, together with the reduction of its cubito-anal areas, but its long setae on wings is a more accurate synapomorphy, at least with the genus *Tachinymphes*. The same argument cannot be advocated for the presence of a Psm in Paralembochrysa n. gen. because its hind wings are of normal shape and dimensions. Thus, it could well be a potential synapomorphy of *Paralembochrysa* n. gen. with the Recent Chrysopidae but Paralembochrysa n. gen. strongly differs from this last group in its highly specialized structure of distal parts of veins C, ScP and RA.

The clade Limaiidae is supported by the characters "5, state 1" (apex of ScP in a distinctly more basal position than that of RA, strict synapomorphy), and "16, state 1" (presence of a hind wing Psc vein, convergently acquired by extant Chrysopidae). The clade [*Mesotermes* & Mesochrysopidae & Tachinymphidae & Allopteridae] is supported by the characters "1, state 1" (fore wing area between C and ScP not broadened), and "4, state 0" (ScP and RA distally fused). If these characters are strictly present in this clade among the Chrysopoidea, they are also present in numerous other neuropteran lineages.

Furthermore, the lack of information concerning the hind wing structures of numerous taxa of this clade and the presence of some characters shared by this group and the Limaiidae put some doubt on the reality of this clade. The position of the genus *Mesotermes* Haase 1890 (based on *Mesotermes heros* (Hagen 1862), Upper Jurassic, Solnhofen, Germany) (Hagen 1862; Haase 1890; Carpenter 1932; Nel & Henrotay 1994) is also rather uncertain, because of our poor knowledge concerning this taxon.

The three clades Tachinymphidae, Mesochrysopidae and Allopteridae are well supported by clear apomorphies, already listed in their respective diagnoses (see above).

In conclusion, the present phylogenetic analysis is only a first attempt. It will be necessary to test it after the discovery and study of better-preserved specimens, especially in the two groups Limaiidae and Mesochrysopidae.

The geological history of the Chrysopoidea is very complicate. The clade was already diverse during the Liassic, with at least the most basal known lineage Liassochrysidae n. fam. but also representatives of the more advanced groups Mesochrysopidae, suggesting an older age for the chrysopoid lineage. The Late Jurassic and Early Cretaceous Chrysopoidea were very diverse, with at least the four families Allopteridae, Mesochrysopidae, Tachinymphidae n. fam., Limaiidae, and Chrysopidae. The distribution of the Allopteridae in China, Spain and Brazil, of Mesochrysopidae in Germany, Spain, and China suggest that these families were probably widespread during the Late Jurassic and Early Cretaceous. The exact ages of extinction of these

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groups remain unknown, due to the lack of information on Late Cretaceous Neuroptera. The morphological disparity is also maximal during this period, with the highly specialized allopterid and tachinymphid wings and body structures. Interestingly, if the oldest known taxon (*Paralembochrysa* n. gen.) that could be related to the Recent Chrysopidae is Late Jurassic/Early Cretaceous, the Mesozoic family Limaiidae was still present during the Paleocene/Eocene. Other Cenozoic Chrysopoidea can be attributed to the Chrysopidae *sensu stricto*, with already an important diversity during the Paleocene. This suggests that the diversification of the Chrysopidae began during the Cretaceous. There is no evidence of an impact on the Chrysopoidea of the crisis of the diversity at the K-T boundary.

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Appendix

Appendix 1

- List of fossil taxa attributed to the Allopteridae
 - Allopterus Zhang 1991 Allopterus luianus Zhang 1991 (Late Jurassic, Shandong Province, China) (Zhang 1991).
 - Allopterus mayorgai n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).
 - Triangulochrysopa n. gen.
 - *Triangulochrysopa sanzi* n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).

Kerarina Martins-Neto 1997

- *Kerarina breviptera* Martins-Neto 1997 (Aptian/Albian, Crato Formation, Santana do Cariri, Brazil).
- Armandochrysopa n. gen.
- Armandochrysopa borschukewitzi n. sp. (Aptian/Albian, Crato Formation, Santana do Cariri, Brazil).
- Armandochrysopa inexpecta n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).

Appendix 2

List of fossil taxa attributed to the Mesochrysopinae

Mesochrysopa Handlirsch 1906

Mesochrysopa zitteli (Meunier 1898) (Tithonian, Sohnofen-Eichstatt, Germany).

Protoaristenymphes Nel & Henrotay 1994

Protoaristenymphes bascharagensis Nel & Henrotay 1994 (Toarcian, Bascharage, Luxembourg) (Nel & Henrotay 1994).

Aristenymphes Panfilov 1980

Aristenymphes perfectus Panfilov 1980 (Late Jurassic, Karatau, Kazakhstan) (Panfilov 1980; Nel & Henrotay 1994).

- Macronympha Panfilov 1980
- Macronympha elegans Panfilov 1980 (Late Jurassic, Karatau, Kazakhstan) (Panfilov 1980; Nel & Henrotay 1994).

Appendix 3

List of fossil taxa attributed to the Tachinymphidae n. fam.

- Tachinymphes Ponomarenko 1992 sit. nov.
 - Tachinymphes ascalaphoides Ponomarenko 1992 (Neocomian or Barremian-Aptian, Baissa, Transbaikalia).
 - Tachinymphes delicatus (Ren & Yin 2002) (Late Jurassic, Liaoning Province, China).
 - Tachinymphes magnificus n. sp. (Late Jurassic, Liaoning Province, China).

- Tachinymphes paicheleri n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).
- *Tachinymphes penalveri* n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).

Nanochrysopa n. gen.

Nanochrysopa pumilio n. sp. (Barremian, Huerguina Formation, Las Hoyas, Spain).

Appendix 4

- List of fossil taxa attributed to the Limaiidae
 - Limaia Martins-Neto & Vulcano 1989
 - *Limaia conspicua* Martins-Neto & Vulcano 1989 (Albian, Crato Formation, Santana do Cariri, Brazil) (Martins-Neto & Vulcano 1988 (1989), 1989; Martins-Neto 2000).
 - *Limaia adicotomica* Martins-Neto 1997 (Albian, Crato Formation, Santana do Cariri, Brazil)
 - Mesypochrysa Martynov 1927
 - *Mesypochrysa latipennis* Martynov 1927 (Late Jurassic, Karatau, Kazakhstan) (Martynov 1927).
 - Mesypochrysa intermedia Panfilov, 1980 stat. rest., (Late Jurassic, Karatau, Kazakhstan). Transferred in Drakochrysa by Yang & Hong (1990), but Nel & Henrotay (1994) put in doubt the last attribution. Makarkin (1997), in its revision of Mesypochrysa, did not formally restored it in this genus. Therefore, it is necessary to do so. We propose a new drawing of its fore wing venation, showing its structure of subcosta, radius anterior and costa (Fig. 11.6).
 - Mesypochrysa polyclada Panfilov 1980 (Late Jurassic, Karatau, Kazakhstan) (Panfilov 1980; Nel & Henrotay 1994). Panfilov (1980: 112) figured its ScP is fused with RA, which would be sufficient to exclude this fragmentary (only wing apex is known) and enigmatic species from the genus Mesypochrysa.
 - Mesypochrysa reducta Panfilov 1980 (Late Jurassic, Karatau, Kazakhstan) (Panfilov 1980; Nel & Henrotay 1994).
 - Mesypochrysa makarkini n. sp. (Late Jurassic, Karatau, Kazakhstan).
 - *Mesypochrysa criptovenata* (Martins-Neto & Vulcano 1989) (Aptian/Albian, Crato Formation, Santana do Cariri, Brazil) (Martins-Neto & Vulcano 1988 (1989), 1989; Martins-Neto 1992, 1997, 2000).
 - Mesypochrysa confusa (Martins-Neto & Vulcano 1989) (Aptian/Albian, Crato Formation, Santana do Cariri, Brazil) (Martins-Neto & Vulcano 1988 (1989), 1989; Martins-Neto 1992, 1997, 2000). It is a very badly known taxon, based on a poorly preserved fossil.

- Mesypochrysa chrysopoides Ponomarenko 1992 (Early Cretaceous, Bon-Tsagan, Mongolia) (Ponomarenko 1992b; Makarkin 1997).
- Mesypochrysa species cf. chrysopoides (Tithonian Valanginian, Liaoning Province, NE China).
- Mesypochrysa magna Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Mesypochrysa falcata Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Mesypochrysa chrysopa Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Mesypochrysa curvimedia Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Mesypochrysa angustialata Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- *Mesypochrysa minima* Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Drakochrysa Yang & Hong 1990
- Drakochrysa sinica Yang & Hong 1990 (Early Cretaceous, Laiyang Basin, Shandong Province, China) (Yang & Hong 1990).
- Lembochrysa Ren & Guo 1996
- *Lembochrysa miniscula* Ren & Guo 1996 (Late Jurassic, Liaoning Province, China) (Ren & Guo 1996).
- Lembochrysa polyneura Ren & Guo 1996 (Late Jurassic, Liaoning Province, China) (Ren & Guo 1996).
- Protochrysa Willmann & Brooks 1991
- Protochrysa aphrodite Willmann & Brooks 1991 (Paleocene/Eocene, Mo-Clay, Danmark) (Willmann & Brooks 1991; Rust in litteris 1999).
- Protochrysa species (Paleocene/Eocene, Mo-Clay, Danmark) (Rust in letteris 1999).

Araripechrysa Martins-Neto & Vulcano 1989

Araripechrysa magnifica Martins-Neto & Vulcano 1989 (Aptian/Albian, Crato Formation, Santana do Cariri, Brazil) (Martins-Neto & Vulcano 1988 (1989), 1989).

Baisochrysa Makarkin, 1997

- Baisochrysa multinervis Makarkin 1997 (Neocomian or Barremian-Aptian, Baissa, East Siberia) (Makarkin 1997).
- Cretachrysa Makarkin 1994
- *Cretachrysa martynovi* Makarkin 1994 (Cenomanian, northeastern Siberia, Russia) (Makarkin 1994).

Appendix 5

List of fossil taxa attributed to the Chrysopidae sensu stricto

Danochrysa Willmann 1993

Danochrysa madseni Willmann 1993 (Paleocene/Eocene, Mo-Clay, Danmark) (Willmann 1993; Rust in litteris 1999).

Stephenbrooksia Willmann 1993

- Stephenbrooksia multifurcata Willmann 1993 (Paleocene/Eocene, Mo-Clay, Danmark) (Willmann 1993; Rust in litteris 1999). Cimbrochrysa Schluter 1982
- Cimbrochrysa moleriensis Schluter 1982 (Paleocene/Eocene, Mo-Clay, Danmark) (Schluter 1982).
- Hypochrysa Schluter 1982
- Hypochrysa hercyniensis Schluter 1982 (Paleocene/Eocene, Mo-Clay, Danmark) (Schluter 1982).
- Paleochrysopa Semeria & Nel 1988
- Paleochrysopa monteilsensis Semeria & Nel 1988 (Late Eocene, Monteils, Gard, France) (Semeria & Nel 1988).
- Genus and species undetermined
- Chrysopidae "species A" (Late Eocene, Bembridge Marls, Isle of Wight, England) (Jarzembowski 1980).
- Archaeochrysa Adams 1967
- Archaeochrysa creedei (Carpenter 1935) (Eocene, Creede Formation, Colorado, USA) (Carpenter 1935, 1938; Adams 1967).
- Archaeochrysa paranervis Adams, 1967 (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Adams 1967).
- Archaeochrysa fracta (Cockerell, 1914) (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Cockerell 1914; Adams 1967).

Palaeochrysa Scudder 1890

- Palaeochrysa stricta Scudder 1890 (Eocene, Creede Formation, Colorado, USA) (Scudder 1890; Carpenter 1938; Adams 1967).
- Palaeochrysa concinnula Cockerell 1909 (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Cockerell 1909; Carpenter 1935; Adams 1967).
- Palaeochrysa wickhami Cockerell 1914 (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Cockerell 1914; Carpenter 1935; Adams 1967).
- Dyspetochrysa Adams 1967
- *Dyspetochrysa vetuscula* (Scudder 1890) (Late Eocene/Early Oligocene, Florrisant, Colorado, USA) (formerly in *Tribochrysa* Scudder 1890 and *Paleochrysa* Scudder 1890) (Scudder 1890; Cockerell 1908; Adams 1967).
- Tribochrysa Scudder 1885
- Tribochrysa inequalis Scudder 1885 (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Scudder 1885 1890; Adams 1967).
- *Tribochrysa firmata* Scudder, 1890 (Late Eocene/Early Oligocene, Florissant, Colorado, USA) (Scudder 1890; Adams 1967).

Nothochrysa McLachlan 1868

- Nothochrysa praeclara Statz 1936 (Oligocene, Rott, Germany) (Statz 1936).
- Nothochrysa stampieni Nel & Semeria 1986 (Late Oligocene, Aix-en-Provence, France) (Nel & Semeria 1986).
- Pronothochrysa Penalver et al. 1995
- Pronothochrysa vivesi Penalver et al. 1995 (Early Miocene, Ribesalbes, Spain) (Penalver et al. 1995).
- Chrysopa Leach 1815
- *Chrysopa sarmatica* Handschin 1937 (Miocene, Magyar Saros, Siebenburgen, Hungary) (Pongracz 1923; Handschin 1937).
- *Chrysopa martynovae* Makarkin 1991 (Middle Miocene, Stavropol region, Caucasus, Russia) (Makarkin 1991).
- *Chrysopa stavropolitana* Makarkin 1991 (Middle Miocene, Stavropol region, Caucasus, Russia) (Makarkin 1991).
- *Chrysopa miocenea* Makarkin 1991 (Middle Miocene, Stavropol region, Caucasus, Russia) (Makarkin 1991).

Appendix 6

List of characters. The characters that only concern the fore or the hind wing are indicated.

- 1. Fore wing area between C and ScP basally broadened (0) or not basally broadened (1). (Note: in Recent Chrysopidae, this area is distinctly broadened near its base, as in Recent Osmylidae and Hemerobiidae, potential sister groups of Chrysopidae.)
- Humeral vein at wing base between C and ScP simple (0) or ramified (1). (Note: in Chrysopidae, this vein is short and simple, as in Osmylidae, but it is ramified in nearly all Hemerobiidae.)
- Cross-veins in area between C and ScP all or nearly all simple (0) or forked (1). (Note: these veins are simple in Osmylidae, but forked in nearly all Hemerobiidae.)
- ScP and RA distally fused (0) or distally separated (1). (Note: these veins are fused in Osmylidae, but separated in Hemerobiidae and in the great majority of extant Chrysopidae.)
- Apex of ScP nearly at the same level as that of RA (0) or in a distinctly more basal position than that of RA (1).
- 6. Cross-veins of apical area between RA (+ ScP) and C long, numerous, and sometimes forked (0) or short and few (1).
- 7. RP and MA basally separated (0) or basally fused in a common vein RP + MA emerging from R (1).
- 8. MP (more precisely branches MP1 + 2 and/or MP3 + 4 of MP) ending on posterior wing margin distal of mid length of wing (0) or ending on posterior wing margin well basal of mid length of wing (1). Note: this character concerns the true vein MP, not the chrysopid pseudo-vein Psm.
- 9. Fore wing area between branches of MP narrow, with one row of cells (0) or broad, with a secondary vein MPspl (1).
- 10. Fore wing area between branches of MP very long (0) or short (1).
- 11. In fore wing, cell im between branches of MP not individualized, similar to other cells in more distal position (0) or well different in size or shape from more distal cells (1).

- 12. In fore wing, first basal cross-vein between cell im and CuA in a basal position (0) or in a very distal position (1).
- 13. In fore wing, MP3 + 4 and CuA make no 'X-crossing' (0) or make an 'X-crossing' (1).
- 14. In fore wing, MP3 + 4b and CuA never meeting (0), meeting in one point (1), or distally fused in a vein that end directly on posterior wing margin (2).
- 15. In fore wing, MP3 + 4 and CuA not fused in a Psc vein (0) or fused in a Psc vein (1).
- 16. In hind wing, MP3 + 4 and CuA not fused in a Psc vein (0) or fused in a Psc vein (1).
- 17. In fore wing, MP1 + 2, MA, and possibly branches of RP not fused in a Psm vein (0) or fused in a Psm vein (1).
- In hind wing, MP1 + 2, MA, and possibly branches of RP not fused in a Psm vein (0) or fused in a Psm vein (1).
- 19. Outer gradate cross-veins absent (0) or present (1).
- 20. Inner gradate cross-veins absent (0) or present (1).
- 21. Area between CuA and CuP very elongate, with four aligned cells or more (0) or shorter, with less than four aligned cells (1).
- 22. Fore wing first basal cross-vein of area between MP and Cu not opposite base of MP (0) or exactly opposite base of MP (1).
- 23. Apex of vein CuA at least at level of half wing (0) or basal of level of half wing (1).

- 24. AA with four branches or more (0) or with two simple branches or less (1).
- 25. AP with more than two branches (0) or with one or two branches (1).
- 26. Fore wing cell im- elongate, distinctly more than two times longer than wide (0) or shorter (1).
- 27. Fore wing fork of MP in a very distal position (0) or in a basal position (1).
- 28. Apex of RA distinctly basal of wing apex (0) or very near or at wing apex (1).
- 29. Long setae along fore wing vein CuA absent (0) or present (1).
- 30. Pronotum short (0) or elongate (1).
- Hind wing cells c1 and c2 between CuA and CuP posteriorly closed (0) or posteriorly opened (1).
- 32. Fore wing CuP with two branches or less (0) or with four branches or more (1).
- 33. Fore wing cell c1 not very short (0) or very short, more than three times shorter than cell c2 (1).
- 34. A very long cell in distal part of area between RP and RA absent (0) or present (1). (Note: If *Porismus* has not this long cell, some Osmylidae (*Eidoporismus*) have it. Such a cell is also present in Myrmeleontidae. Thus this character is apparently very homoplastic).

ANALYSE D'OUVRAGE

S. INGRISCH & F. WILLEMSE 2004. Bibliographia systematica Orthopterorum saltatoriorum. Systematic bibliography of saltatorial Orthoptera from Linnean times to the end of the 20th century (about 1750 to 2000). Pensoft, Sofia, 536 p., + 1 CD-Rom. Price: £94.00 | approx. \$173/€141. ISBN 954-642-206-1

Ingrisch and Willemse's *Bibliographia systematica Orthopterorum Saltatoriorum* gathers in 536 pages more than 14 000 references published on extant Orthoptera from about 1750 to 2000. The authors select the references in order to focus mostly on taxonomy, phylogeny, nomenclature, synonymy and classification. They omit most of the numerous short faunistical notes, but include wide-range faunistical surveys. Similarly, they consider selectively the very large literature on orthopteran morphology, behaviour, communication, bioacoustics, biochemistry, ecology and population dynamics, physiology, molecular analysis, etc. They discard however papers dealing with pest management and conservation, rearing techniques, predators, diseases, toxicology, abiotic factors, art and culture.

References are organized by alphabetical order, the letters being indicated on a black index on each page margin. Each reference is fully documented, i.e. author, date, complete title, abbreviated title of the journal, volume and pages. For multiauthored papers, a complete list of the authors is given. Book references also include the editor's name and place.

A CD-Rom is added to the printed version, with all the references gathered in a database which consists in a stand-

alone FileMaker Runtime software called BiblioSalta; it runs under Windows and Macintosh computers. In the database, the key information of each reference is located in six fields, i.e. author, year, title, source, volume and pages; other fields describe the abbreviated source, city and publisher, English translation or original title, abstract, keywords, language, personal notes, full author's name and date of publication. While the key information is given for nearly all the references, the other fields are often incomplete. In particular, few keywords are included, and not for all references. Selective search can be however performed on diverse criteria, including character chain, and selected references exported.

The database has been designed as an evolutive tool: it can be implemented with additional references, entered directly or from an existing file or website. It can also be documented by personal keywords, according to one's centres of interest.

As shown by the size of the *Bibliographia* book, by the way hardcovered and well-edited, Ingrisch and Willemse performed a huge work, gathering and bringing up to date the bibliography of late Cornelis Willemse, which should be associated to this book review. Notwithstanding this tremendous effort, one would always wish more facilities, especially to exploit this enormous database, as it is now available. A short keywork or code could have helped separating the references into some major fields of interest, thus making preliminary searches easier. Anyone interested in Orthoptera should anyhow be grateful to S. Ingrisch and F. Willemse for their most useful contribution, and hope that it will be actualized and completed regularly in the future!

Laure Desutter-Grandcolas