

A new genus of Mantispidae (Insecta: Neuroptera) from the Eocene of Germany, with a review of the fossil record and palaeobiogeography of the family

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A new mantispid genus and species *Symphrasites eocenicus* gen. sp. nov. is described from the Middle Eocene of the Messel Pit fossil site, Germany. It has been placed, with confidence, in the subfamily Symphrasinae, the fossils of which were previously unknown. A review of the known fossil species of Mantispidae is provided, and their systematic placements are discussed. *Liassochrysa stigmatica* Ansoerge & Schlüter, 1990 is assigned to Mantispidae, and therefore Liassochrysidae is a new synonym of Mantispidae; a second, more complete specimen of *Mesomantispia sibirica* Makarkin, 1997 is described from the Early Cretaceous Baissa locality, Russia; *Mantispidiptera* Grimaldi, 2000 is excluded from the family; *Vectispa* Lambkin, 1986 is referred to subfamily Mantispinae; and the assignment of *Whalfera* Engel, 2004 to Rhachiberothidae is validated. The origin and palaeobiogeography of the mantispids are briefly discussed: the concept of ousted relicts – which assumes that former widely distributed taxa were replaced with groups originating in the tropics – is assumed to best explain the present distribution of the family. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 701–716.

ADDITIONAL KEYWORDS: Messel Pit – Symphrasinae.

Mantispids, or mantidflies, represent one of the most specialized groups in the order Neuroptera, both morphologically (adults with long prothorax and raptorial forelegs) and biologically (larvae that develop in the egg sacs of spiders and in the nests of aculeate Hymenoptera). The taxon is comparatively speciose, with more than 400 extant species (Ohl, 2004; in collaboration with Oswald JD).

The family is generally accepted to be divided into four extant subfamilies: Symphrasinae, Drepanicinae, Mantispinae, and Calomantispinae (Lambkin, 1986a). In addition, the extinct subfamily Mesomantispinae was established for *Mesomantispia* Makarkin, 1997. The vast majority of extant species belongs to Mantispinae, a more advanced group with a worldwide distribution, whereas the subfamilies Symphrasinae and Drepanicinae, with more primitive characters, are not

as speciose and are today restricted to Australia and the Americas (Fig. 1).

Mantispid fossils are rather rare. Only six named species (plus two unnamed) have been previously assigned to the family with confidence, excluding *Mantispidiptera* Grimaldi, 2000 and *Whalfera* Engel, 2004, of which the mantispid affinity is doubtful (see below). In this study, we describe a new genus and species of the basal subfamily Symphrasinae from the Middle Eocene Messel Pit in Germany. Hitherto, no fossil record of this subfamily was known. It is one among more than 12 000 fossils in the Messel insect collection of the Forschungsinstitut Senckenberg (FIS), which is consistent with the rarity of Mantispidae in the fossil record. We provide a critical review of the taxa previously assigned to the family, and add *Liassochrysa* Ansoerge & Schlüter, 1990. The fossil record of this group now comprises ten species. We briefly discuss the origin and palaeobiogeography of the Mantispidae, and suggest a possible explanation of its distributional pattern.

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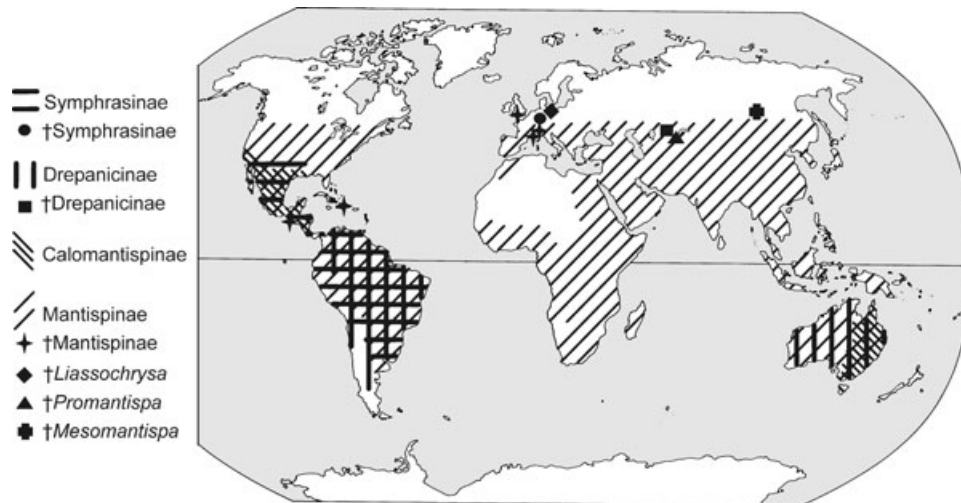


Figure 1. Distribution of extant and fossil Mantispidae.

LOCALITY AND STRATIGRAPHY

The Messel Pit fossil site is located on the eastern side of the Rhine rift valley in Germany, about 20 km south-east of Frankfurt am Main and 8 km north-east of Darmstadt. This site is presently a large pit: 1 km × 0.7 km in area, and some 60 m in depth. It is a Konservat-Lagerstätte that is famous for the extraordinary preservation of its fossils (e.g. Schaal & Ziegler, 1992; von Koenigswald & Storch, 1998). Ongoing excavations have yielded a multitude of insect fossils, which offer unique insights into the terrestrial and lacustrine palaeoecosystems of Messel (e.g. Lutz, 1986, 1990, 1991; Tröster, 1991, 1993a, b, c, 1994; Hörnschemeyer & Wedmann, 1994; Hörnschemeyer, 1994; Wedmann & Hörnschemeyer, 1994; Richter & Baszio, 2001a, b; Wappler & Engel, 2003; Wappler, 2003; Wappler & Andersen, 2004; Richter & Wedmann, 2005).

The fossils are embedded in darkly coloured, finely laminated claystone sediments rich in organic substances ('oil shale'), which were deposited in a meromictic lake (e.g. Goth, 1990). A drilling project conducted in 2001 showed that the former Lake Messel was a maar lake, which is a small deep lake that had its origin in an explosive volcanic eruption. The former lake basin had an original diameter of about 1.5 km, and a depth of about 300–400 m (Harms, 2002; Felder & Harms, 2004). Biostratigraphically, the sediments from Messel represent the European Mammal Reference Level MP 11 of the Geiselalian (Schmidt-Kittler, 1987; Franzen, 2005). According to recent research, the deposits have an age of about 47 Myr (Mertz *et al.*, 2004; Mertz & Renne, 2005). The uppermost strata of the Messel Formation can be subdivided by the marker horizons M, alpha, beta, and gamma (from top to bottom).

MATERIAL AND METHODS

The specimen described in this paper was collected at the Messel Pit in 1999, 0.75–0.77 m above marker horizon alpha. It is housed in the collection of the Messelforschung department of the FIS, specimen MeI 8384, and stored permanently in glycerin to prevent damage by desiccation. The specimen was examined with a Leica MZ 9.5 Stereomicroscope. Drawings were produced directly from the specimen with a camera lucida attachment on a Leica MZ 9.5 Stereomicroscope. Photographs were made with a Leica MZ 16 Stereomicroscope, and either JVC (model KY-F70B) or Nikon Coolpix 8700 digital cameras.

Palaeogeographical hypotheses are based on current plate tectonic models and palaeogeographical reconstructions, for example maps by Briggs (1995) and Scotese (2003). We mostly follow the traditional (*sensu* Wootton, 2003) venational terminology of Lambkin (1986a), except for the median vein (M), which we treat as in Comstock (1918): Lambkin's media anterior (MA) is treated here as the proximal branch of the radial sector (Rs). No clear evidence is found to support the hypothesis that in the forewing of Neuroptera this vein has been derived from M [see Oswald (1993) for a discussion of the problem in Hemerobiidae]. We treat the costal crossveins of Lambkin (1986a) as subcostal veinlets, as in Oswald (1993).

VENATION ABBREVIATIONS

Longitudinal veins are abbreviated in upper case, crossveins are abbreviated in lower case. 1A–3A, anal veins; C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; pt, pterostigma; R1, first branch of radius;

Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta. The principal crossveins are designated after the longitudinal veins that they connect, and are numbered in sequence from the wing base, e.g. the crossveins between M (or MP) and Cu (or CuA) are 1m-cu and 2m-cu.

INSTITUTIONAL ABBREVIATIONS

FIS, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; MB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia.

SYSTEMATIC PALAEONTOLOGY

INSECTA LINNAEUS, 1758

NEUROPTERA LINNAEUS, 1758

MANTISPIDAE LEACH, 1815

SYMPHRASINAE

NAVÁS, 1909

Diagnosis: [based mainly on Lambkin, 1986a; modified here; different diagnostic character states are designated by numerals, e.g. (10)]. Fore tarsus 4-segmented (1), with terminal segment enlarged, apically pointed (2); adjacent segment arising near its middle (3) in both male and female. Female with externally evident ovipositor (4). Trichosors (i.e. small setigerous thickenings of wing margin between tips of veins, veinlets) often well developed, around almost entire wing margin, except basally (5). Pterostigma situated between R1 and the costal margin (6). Sc entering wing margin within pterostigma, often poorly discernible (7). In forewing two subcostal crossveins, intermediate (2sc-r), distal (3sc-r); basal crossvein (1sc-r) lacking (8); crossvein 3sc-r single, long (9); only two r1-rs crossveins (10); CuP touching 1A proximally (11); M fused basally with R for considerable distance (12); crossvein a2-a3 absent (13). Hindwing with only one r1-rs crossvein (14); CuP present (15); basal crossvein r-m sinuate (16).

Included genera: *Symphrasites* gen. nov. from the Middle Eocene of Germany; *Plega* Navás, 1928, *Trichoscelia* Westwood, 1852; and *Anchieta* Navás, 1909; the latter three extant and distributed from South America to southern North America (Fig. 1).

Remarks: The species of the subfamily Symphrasinae are easily distinguished from others of the family, in particular by a short Sc that always terminates within the pterostigma, so that the pterostigma is located between R1 and the costal margin. In other mantispids (except *Mesomantispa*) the Sc approaches R1 and terminates distal to the pterostigma (the latter is always located anterior to Sc). The majority of extant

symphrasine species have been examined, with no exceptions found (K. M. Hoffman, pers. comm. 2004; V. N. Makarkin, pers. observ.). Some published drawings incorrectly imply that Sc is bent to R1 and then fused with R1 in the subfamily (e.g. Tjeder, 1959: fig. 244; Willmann, 1990: fig. 16; Hoffman, 2002: fig. 537). In symphrasine species the terminal portion of Sc, and generally the veins within the pterostigma, are inconspicuous. Sc seems to disappear distal to 3sc-r1, making it appear to terminate on R1. Although it is often poorly visible, in all species the Sc actually continues distal to 3sc-r1. This can be deduced from the observation that a number of veinlets terminate on C within the pterostigma (i.e. distal to 3sc-r1), but because they do not arise from R1, this probably indicates the presence of the Sc distal to 3sc-r1 in these species. In *Mesomantispa*, the Sc appears to also terminate at R1, but the true relationship is unclear (see below). The structure of the distal part of the Sc in the Symphrasinae is similar to that of some Rhachiberothidae and Berothidae, in that the Sc is far removed from R1 and often poorly discernible (it is sometimes atrophied) distal to 3sc-r (e.g. Aspöck & Mansell, 1994: fig. 43 for Rhachiberothidae; Archibald & Makarkin, 2004: fig. 3 for Berothidae).

The relationships of Rhachiberothidae and Symphrasinae remain unclear. They are obviously closely related (e.g. Tjeder, 1959; Willmann, 1990, 1994; Aspöck & Nemeschkal, 1998), and the question asked by Tjeder in 1959 remains relevant: 'is *Symphrasis* [*sic*, read as Symphrasinae] really as closely related to the other Mantispidae as to be included in that family?' (Tjeder, 1959: 275). This problem is, however, outside the scope of this paper (see also below under *Whalfera*).

The Symphrasinae are considered to be the sister group of [Drepanicinae + (Calomantispinae + Mantispinae)] and they are regarded to be the most plesiomorphic mantispids (Lambkin, 1986a). We believe that the latter concept requires some re-examination, however. Indeed, some character states of their venation and prothorax are plesiomorphic in the family [compare characters (5), (15), and (16) of the subfamily diagnosis – additionally, the humeral veinlet in the forewing is recurrent and the anterior part of the pronotum is not closed ventrally (i.e. not tubular) in some species]. Symphrasinae, however, possess more numerous and striking apomorphic character states in their venation and in the structure of their foreleg and abdomen [characters (1)–(4), (6)–(8), and (10)–(14) of the subfamily diagnosis]. Most of these states are plesiomorphic in the Drepanicinae. The exceptions are some apomorphies of this subfamily, e.g. CuP in the hindwing is absent; the basal crossvein r-m is either upright or at most inclined, but not sinuate; and the prothorax is entirely tubular (but all of these characters are shared by Mantispidae and Calomantispidae).

So, Drepanicinae might be considered at least as plesiomorphic as Symphrasinae.

GENUS *SYMPHRASITES* GEN. NOV.

Etymology: Symphras- (from *Symphrasis*, a mantispid genus-group name) + -ites (a traditional suffix of fossil genera), in reference to the symphrasine affinity of the genus. Gender masculine.

Type species: *Symphrasites eocenicus* sp. nov.

Included species: The type species only.

Diagnosis: In forewing MP deeply forked (17); trichosors present at most in apical portion of wing (18); R1 comparatively long (19); CuP deeply forked once (20); crossvein 2r-m present, connecting Rs1, MA proximal to gradate series of crossveins (21).

Remarks: We are confident of the placement of this genus in Symphrasinae, as it possesses important forewing diagnostic character states of this group (5)–(7), (9), and (10) (see diagnosis of the subfamily above). Some character states are not, however, available in the examined specimen [i.e. (8), (11), and (12)], as the basal portion of a wing is either lacking or strongly folded. In some other ways *Symphrasites* gen. nov. differs quite strongly from other known genera of the subfamily. Interestingly, a number of the character states of *Symphrasites* are derived with regard to the states of extant genera [characters (17), (18), and (20), see below].

Character state (17): MP is never deeply forked in any species of Mantispidae; this is undoubtedly an autapomorphy of the genus/species. Alternatively, this may be an anomaly of this specimen. Only other specimens will resolve this.

Character state (18): The trichosors are present in all examined extant species of Symphrasinae. They are, however, sometimes not distinct, and therefore may be difficult to detect in impression/compression fossils. In any case, the appearance of trichosors in *S. eocenicus* is clearly less distinct than in most of the extant species.

Character state (19): In all examined species of the extant Symphrasinae, R1 enters the wing margin well before the apex; in *S. eocenicus* it enters more distad, almost near the apex. The condition of R1 entering the wing margin near the apex may be considered plesiomorphic, as it also occurs in *Liassochrysa* and *Promantispa*.

Character state (20): The structure of CuP in *Symphrasites* most resembles that of some species of *Anchieta* and *Trichoscelia*, where CuP is deeply forked once. However, the closely spaced branches of CuP as found in *S. eocenicus* do not occur in either *Anchieta* or *Trichoscelia*. In the other extant Symphrasinae, one of the branches of CuP is forked again, or the fork of CuP is not so deep, and its branches are not clearly parallel.

Character state (21): Crossvein 2m-r is absent in other species of Symphrasinae (as well as in the vast majority of other mantispids), and its presence in *Symphrasites* may be considered either as a plesiomorphy or as an autapomorphy of the genus. 2m-r also occurs in the Jurassic *Liassochrysa*, *Promantispa* and the extant *Ditaxis*, but in these genera 2m-r is a part of the inner, more basally located, gradate series of crossveins continuing from Rs to CuP (in *Promantispa* this series is incomplete). So, it is reasonable to assume that the crossvein 2m-r in these genera and *Symphrasites* appeared independently.

SYMPHRASITES EOCENICUS SP. NOV.

(FIGS 2–4)

Etymology: From the Eocene, in reference to the age of the type specimen.

Holotype: Specimen MeI 8384, deposited in FIS. An incomplete, partly folded, well-preserved forewing.

Type locality and horizon: Messel pit near Darmstadt, Hesse, Germany; grid square E8/9. Messel Formation, lower Middle Eocene (lowermost Lutetian, MP 11), from +0.575 to +0.77 m above local marker horizon alpha.

Diagnosis: Same as for *Symphrasites* gen. nov.

Description: Forewing with rounded apex, c. 14–15 mm long (estimated, 12 mm preserved), c. 5.6–5.7 mm wide (estimated, 4.5 mm preserved). Trichosors present but indistinct, restricted mainly to apicalmost portion of wing margin (Fig. 4). Costal space narrowed towards wing apex. Subcostal veinlets simple, straight, oblique, and widely spaced. Sc stout, appears atrophied after distal subcostal crossvein (3sc-r), apparently entering wing margin within pterostigma. Pterostigma distinct, pale, strongly haired, situated between R1 and costal margin; incorporated veinlets almost invisible, rows of macrotrichia not distinct. Subcostal space rather narrow, not dilated towards apex; three crossveins detected: two intermediate (2sc-r), closely spaced, situated after origin of Rs, one distal (3sc-r). R1 entering margin slightly before wing apex, with at least eight veinlets distal to pterostigma, all forked. Space between R1 and costal margin distal to pterostigma comparatively broad. Origin of Rs far removed from wing base. R1 space rather narrow, with two rather short crossveins. Rs with 11 branches, all forked (mainly deeply). Single gradate series of crossveins continuing from most distal branch of Rs to CuP, with 14 crossveins. Crossvein 1r-m connects stem of Rs apparently with stem of M slightly proximal to primary fork; crossvein 2r-m present, connects Rs1 and MA. Origin of M not preserved; basalmost parts of MA and MP diverged at angle more than 45°, distal to

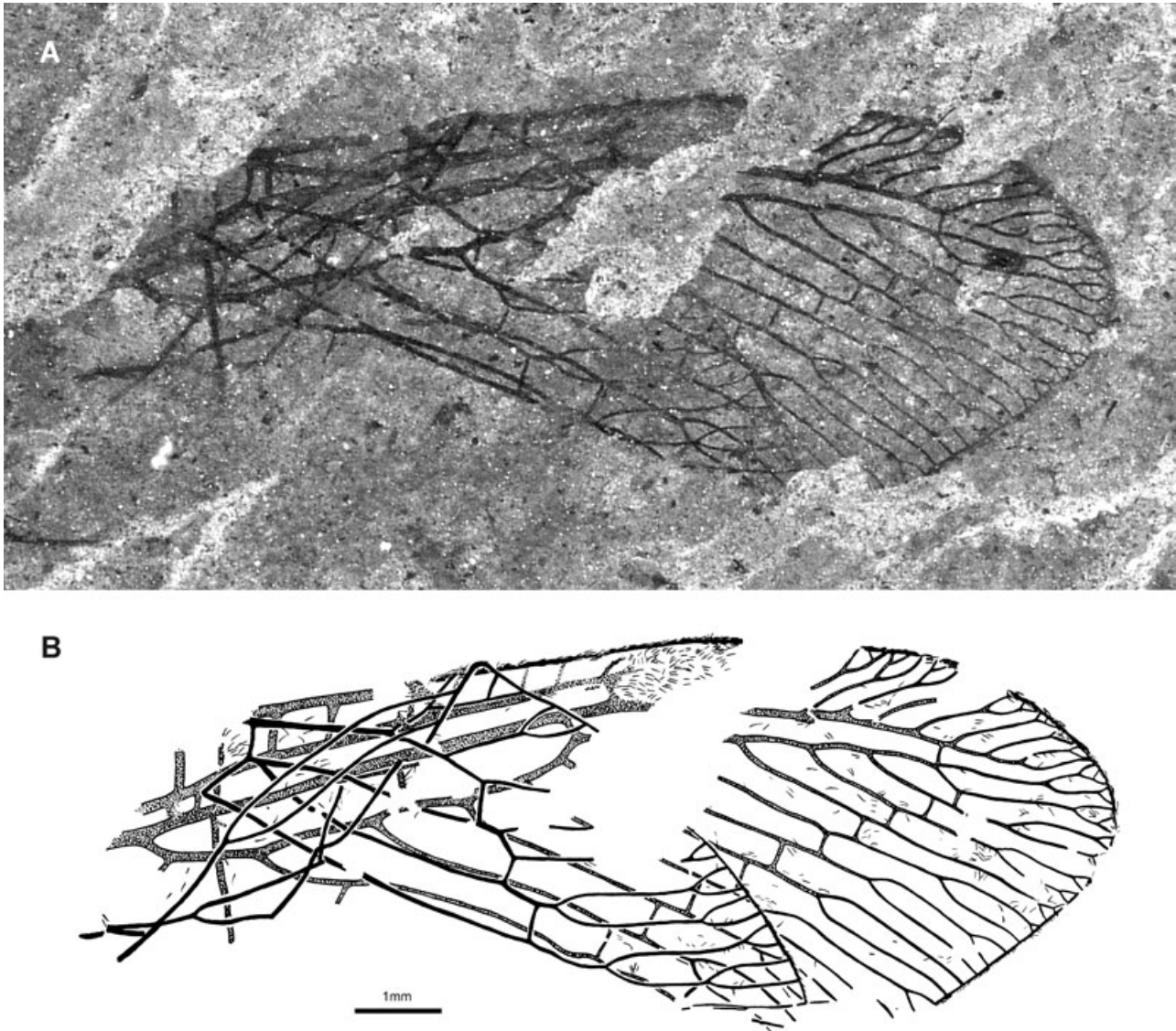


Figure 2. *Symphrasites eocenicus* gen. et sp. nov., holotype MeI 8384. A, photograph. B, drawing of the forewing. Scale bar = 1 mm.

origin of Rs; MA straight before gradate series, twice forked distally; MP deeply forks slightly distal to crossvein 2m-cu, so MP has two long branches, each of which forked twice distally. Origin, primary forking of Cu not preserved. CuA with comparatively few branches, apparently with three branches. CuP deeply forked once, its branches closely spaced, nearly parallel. Anal area very crumpled. Wing membrane without maculation.

Remarks: The two closely spaced intermediate crossveins in the subcostal space (both named here 2sc-r) may present an anomaly caused apparently by the duplication of this crossvein. Such duplications often occur, for example, in the Hemerobiidae (e.g. Makarkin,

1995), but apparently were not reported hitherto in the Mantispidae. On the other hand, this part of the wing is not well preserved, and it is very difficult to discern the more basal vein 2sc-r in the fossil (compare Fig. 3).

FOSSIL RECORD OF MANTISPIDAE

A total of ten fossil species of the mantispid clade are known from the Early Jurassic to the Miocene (see Fig. 7; two are not named, only illustrated). Six species are considered to belong to six monotypic extinct genera (*Liassochrysa*; *Promantispa* Panfilov, 1980; *Mesomantispa*; *Symphrasites* gen. nov.; *Vectispa* Lambkin, 1986a; *Prosagittalata* Nel, 1989), and two to the extant genera *Gerstaeckerella* Enderlein, 1910 and

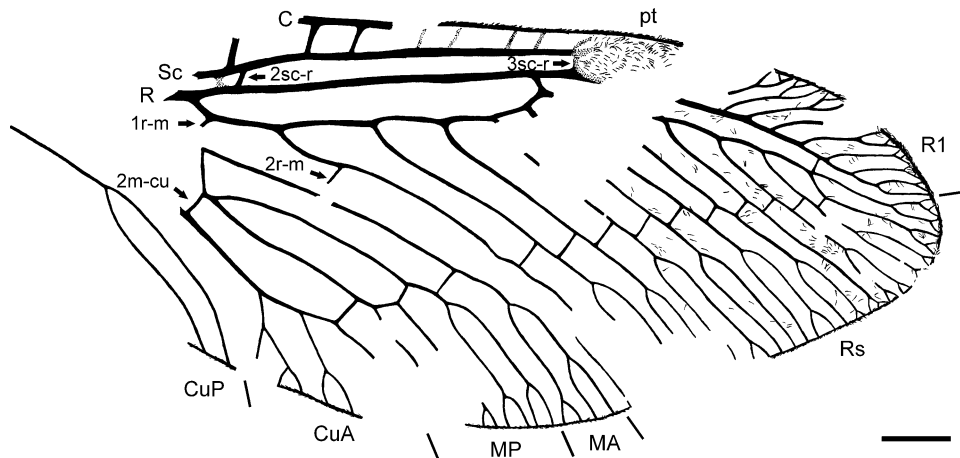


Figure 3. *Symphrasites eocenicus* gen. et sp. nov. Reconstruction of the forewing venation of the holotype FIS MeI 8384. All unassignable veins are omitted in the drawing. C, costa; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; pt, pterostigma; R, radius; R1, first branch of radius; Rs, radial sector; Sc, subcosta. Scale bar = 1 mm.

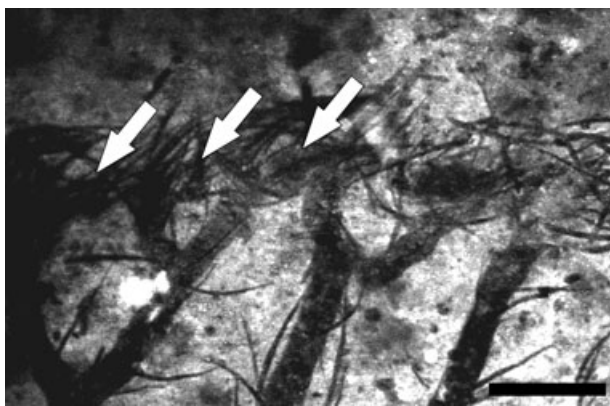


Figure 4. Apical portion of forewing margin of *Symphrasites eocenicus* showing trichosors (arrows). Scale bar = 100 μ m. Laser scanning photograph.

Climaciella Enderlein, 1910. Two additional genera (*Mantispidiptera* and *Whalfera*) most probably do not belong to the family. Mantispid (neither described nor illustrated) are also known from the Upper Jurassic of China (Dong Ren, pers. comm. 2003 to V. N. Makarkin). Below, the species are discussed following their geological age, beginning with the oldest taxon.

Hitherto, the oldest known mantispid species was the Late Jurassic *Promantispa similis* Panfilov, 1980 (Lambkin, 1986a; Grimaldi & Engel, 2005). Makarkin & Menon (2005) are of the opinion that the Early Jurassic (Late Liassic) *Liassochrysa stigmatica* Ansoerge & Schlüter, 1990 from Dobbertin (Germany) is more similar to this species than to any other fossil species. *L. stigmatica* was previously treated as belonging to either Mesochrysopidae (either as a subfamily of Chrysopidae or as a distinct family) (e.g.

Ansoerge & Schlüter, 1990; Adams & Penny, 1992; Carpenter, 1992; Ponomarenko, 2002; Makarkin & Archibald, 2003), or the monotypic family Liassochrysidae (Nel, Delclòs & Hutin, 2005a). We assume that this species is a member of the mantispid stem group. Unfortunately, no obvious venational autapomorphies of Mantispidae are known, although Aspöck & Mansell (1994) treated paired trichosors (not single as in other Neuroptera) as an autapomorphy of Mantispidae. However, this condition is found only in Symphrasinae and some Drepanicinae. Nevertheless, the combination of the characters of *Liassochrysa* clearly indicates a mantispid affinity, i.e. the structure of the pterostigmal region (see below), the venation (particularly the configuration of Rs, M, Cu, the anals, and the arrangement of the principal crossveins), the presence of a jugal lobe, and the absence of trichosors and nygmata (small sensory structures in the wing membrane).

Examination of photos of the holotype (taken by C. Neumann, at the MB) indicates that the original drawing of *L. stigmatica* is adequate (Ansoerge & Schlüter, 1990: fig. 3) except for the structure of the pterostigmal region, which is actually similar to that of drepanicinae: Sc forms the lower margin of the pterostigma, approaches R1 (to which it is connected by one very short crossvein), and terminates on the costal margin distal to the well-developed pterostigma. The incorporated subcostal veinlets in the pterostigma are faintly visible (Fig. 5A). The jugal lobe (not mentioned in the original description) is probably well-developed, and folded. *Liassochrysa* is particularly similar to the extant Australian genus *Ditaxis* McLachlan, 1867 (Drepanicinae) in the structure of the pterostigmal region and by the presence of two regularly gradated series of crossveins, a unique

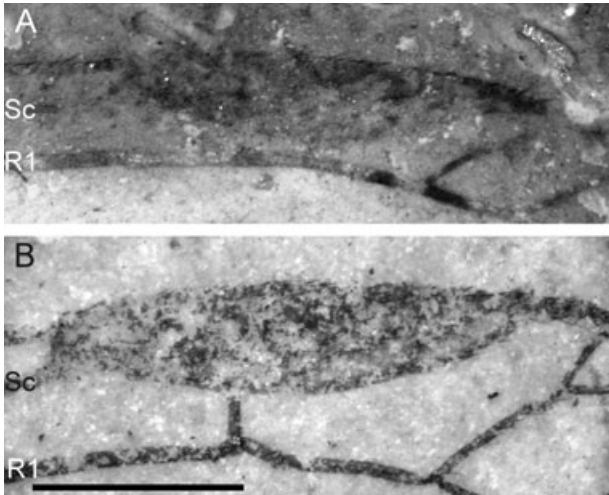


Figure 5. The forewing pterostigma of the Jurassic mantispids. A, *Liassochrysa stigmatica* Ansoerge & Schlüter 1990, holotype MB.I 5046 (No. LDA301, formerly from the Ansoerge collection, Dobbertin, Germany); (photograph converted to standard right dorsal view); photograph by C. Neumann, MB. B, *Promantispa similis*, holotype PIN 2784/1080 (Karatau, Kazakhstan; Karabastau Formation). R1, first branch of radius; Sc, subcosta. Scale bar = 1 mm for both parts.

character state in the extant Mantispidae (see Lambkin, 1986a: fig. 34, but note the different vein terminology). The main differences of *Liassochrysa* from *Ditaxis* (as well as from other Drepanicinae) are the presence of several additional basal crossveins in *Liassochrysa*, i.e. the marginal ma-mp, mp-cua, cua-cup, cup-1a, and 1a-2a, which are probably a continuation of the outer gradate series of crossveins, and the basalmost cua-cup (i.e. between CuA and CuP two additional crossveins are present). In the extant mantispids only one crossvein cua-cup is present, which is located more or less opposite 2m-cu, distal to the proximal additional crossvein of *Liassochrysa*. So, we may tentatively homologize this proximal crossvein as 1cua-cup, lost in other mantispids, and the single cua-cup of the extant species as 2cua-cup.

Promantispa similis was described from the Late Jurassic of Karatau, Kazakhstan (Panfilov, 1980). The holotype is an almost complete, well-preserved forewing. Examination of the type shows that the original drawing is mostly correct (Panfilov, 1980: fig. 96, reprinted in Lambkin, 1986b: fig. 693, and Willmann, 1994: fig. 17). We find, however, the following differences: the incorporated subcostal veinlets within the pterostigma are faintly visible and hairy (Fig. 5B); only one (distal) 2a-3a is present, the basal 'crossvein' 2a-3a is actually a part of the folded jugal lobe. Also, we treat a very short crossvein connecting M and R basally as a true crossvein (representing possibly an

anomalous variation) not 'the free basal piece of MA' (Lambkin, 1986a: 23).

The systematic position of *Promantispa* was analysed in detail by Lambkin (1986a) and Willmann (1994). Both authors drew a quite similar conclusion: 'its relationships must be considered as indeterminate' (Lambkin, 1986a: 23), and '*Promantispa* belongs to either the stem group of "higher" Mantispidae (= Symphrasinae on the one hand, and Drepanicinae + Calomantispinae + Mantispinae on the other hand), possibly even to the stem group of one of these two taxa' (Willmann, 1994: 201). Possibly *Promantispa* is most closely related to *Liassochrysa*: both have similar structure of M in that its stem is distinctly curved, whereas in other mantispids it is straight; the stem of M and MA run as a single (smooth) vein and MP appears to originate as its posterior branch; the structure of the pterostigmal region in both genera is similar (Fig. 5); the distal-most (marginal) crossvein cup-1a is present (absent in other mantispids, except for *Mesomantispa*). The following character states of *Promantispa* are interpreted to be derived with regard to *Liassochrysa*: the inner gradate series of crossveins is incomplete (complete in *Liassochrysa*), the marginal crossveins m-cu, cua-cup, and 1a-2a are absent (present in *Liassochrysa*), the marginal forks of 1A and 2A are absent (present in *Liassochrysa*). These genera possibly form one suprageneric taxon. This assumption is supported by the synapomorphy of the structure of M (see above). Unfortunately, this character state may be also treated as (sym)plesiomorphic, because it occurs only in these, the oldest known genera within the family.

The relationships of *Promantispa* with the genera of the remaining Mantispidae are more problematic. In general, its features are more similar to that of the genera of Drepanicinae than to those of other subfamilies. This resemblance may be, however, superficial. The most probable hypothesis is that *Promantispa* represents an extinct lineage that included *Liassochrysa*. The relationships of this lineage and other mantispid lineages are so far unclear.

Mesomantispa sibirica Makarkin, 1997 was described from the Early Cretaceous Baissa locality (Transbaikalia, Russia) on the basis of a basal 2/3 of a rather poorly preserved forewing (Makarkin, 1997). In 1997, a well-preserved apical 2/3 of a forewing (the specimen PIN 4210/5275) was collected at Baissa by a PIN expedition under the guidance of the late Dr Vladimir V. Zherikhin (1945–2001). Based on the identical maculation and similar venation, this wing is presumably associated with *M. sibirica* (the mention of colouration was omitted in the original description of the holotype, but re-examination of the type shows that maculation is partially present). Makarkin (1997) tentatively placed the genus *Mesomantispa* in the family Mantispidae (in the monotypic subfamily Mesoman-

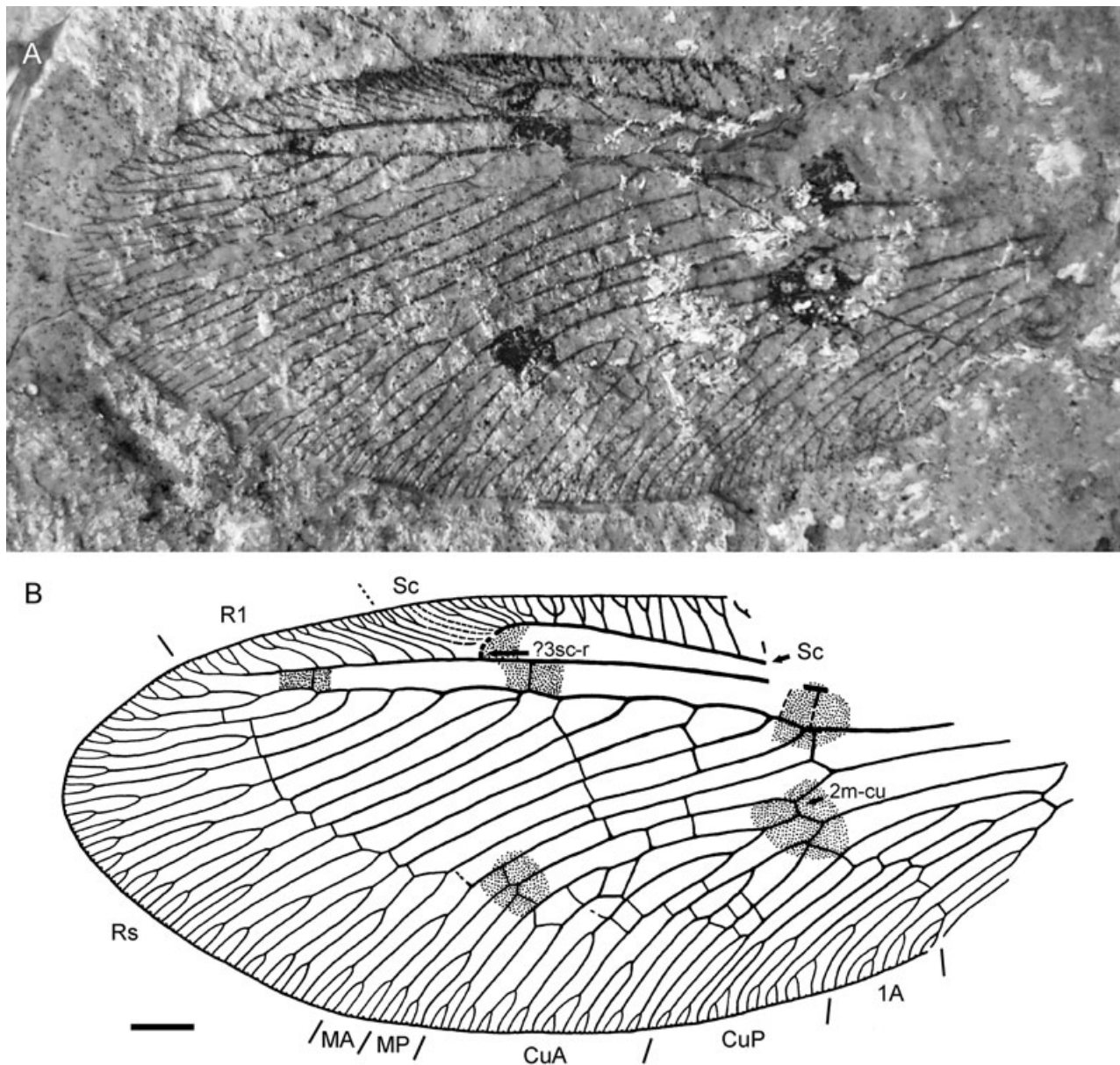


Figure 6. *Mesomantispa sibirica* Makarkin, 1997, specimen PIN 4210/5275. A, photograph of the forewing. B, drawing of the forewing. Dashed lines indicate poorly preserved veins. 1A, anal vein 1; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; R1, first branch of radius; Rs, radial sector; Sc, subcosta. Scale bar = 1 mm.

tispinae), whereas Ponomarenko (2002) did not exclude its membership in the Ithonidae. The new specimen provides evidence of the true mantispid affinity of *Mesomantispa*, and indicates that this species has perhaps the most generalized venation among known mantispids (Fig. 6). Study of this specimen shows that its significant features are as follows: trichosors are present around the entire margin of the wing, except basally; nearly all subcostal veinlets are forked and closely spaced; Sc is sharply bent to R1 apically, and

appears to terminate on it (but see below for discussion); the pterostigma is very inconspicuous; the subcostal space is clearly broadened distally; M is forked far distal to the origin of Rs; MA and MP are nearly parallel, not branched before the distal gradate series; CuA is multibranched, more or less pectinately forked, parallel to the hind margin of the wing for at least 3/4 of its length; CuP is multibranched, dichotomously forked; CuP is not touching 1A proximally; there are three gradate series of crossveins in the radial space;

between three and five crossveins r1-rs are arranged in three groups; and the crossveins between branches of Cu are numerous, including nearly complete series continuing from 2m-cu to the hind margin.

The pterostigmal region of *Mesomantispa* resembles that of Symphrasinae in that the terminal portion of Sc (distal to 3sc-r1) and the pterostigma are not evident. However, the overall structure of this region seems to be more similar to that of some *Drepanicus* Blanchard, 1851; in which the pterostigma is very inconspicuous, the subcostal veinlets distal to 3sc-r1 are indistinct, and Sc at 3sc-r1 is bent to R1 in a similar way. But in *Drepanicus*, the subcostal vein distal to 3sc-r1 is always easily identifiable (whereas in *Mesomantispa* it is not) and long, and indistinctly visible subcostal veinlets originate from it (whereas in *Mesomantispa* the putative Sc is shorter and veinlets do not originate from it). Otherwise, this genus most resembles those of Drepanicinae, although the venation of *Mesomantispa* is much richer and more complicated. Nevertheless, no obvious autapomorphies of this genus were detected (almost all character states distinguishing this genus from the others may be plesiomorphic). However, it is evident that the venational primitiveness and the 'symphrasine' structure of the pterostigmal region do not allow synonymizing the Mesomantispinae with other subfamilies. Therefore, the validity of this subfamily may be tentatively confirmed. Mesomantispinae seems, however, to be most closely allied to Drepanicinae.

Gerstaeckerella asiatica Makarkin, 1990 was described from the Late Cretaceous (Turonian) of Kzyl-Zhar (or Kzyl-Dzhar), Kazakhstan. It is represented by a well-preserved but crumpled hindwing. The drepanicine taxonomical affinity of *G. asiatica* is unquestionable. Its assignment to this extant genus (today restricted to South America) is based on hindwing venation, which is not distinguishable from that of the extant representatives of *Gerstaeckerella*, including the fine structure of the pterostigma. The possibility remains, however, that this similarity is convergent.

The genus *Mantispidiptera* Grimaldi, 2000 was created for two species (*Mantispidiptera enigmatica* Grimaldi, 2000 and *Mantispidiptera henryi* Grimaldi, 2000) from the Late Cretaceous (Turonian) amber of New Jersey, USA. These insects are remarkable for their minute sizes (body length 3–3.7 mm) and the reduction of their hindwings to 'halters' resembling those of Diptera (Grimaldi, 2000). The mantispid affinity of *Mantispidiptera* was inferred probably from raptorial forelegs (Grimaldi, 2000; Grimaldi & Engel, 2005), although the resemblance of the latter with those of Mantispidae is very remote (there are two rows of very short 'denticles' in *Mantispidiptera*, whereas all Mantispidae have well-developed cuticular spines). In this connection it should be noted that

raptorial forelegs are present among Neuroptera also in Rhachiberothidae, some Mesochrysopidae (*Allopterus* Zhang, 1991; Nel *et al.*, 2005a), and an undescribed 'myrmeleontid-like' neuropteran species (Nel *et al.*, 2005b). Otherwise, both species have nothing in common with Mantispidae: the prothorax is short, transverse, probably not tubular in *M. henryi*, and extremely short in *M. enigmatica*; the venation differs very strongly from that of mantispids, even considering a possible reduction of the venation in *Mantispidiptera*. Therefore, the systematic position of this enigmatic genus remains unclear, but it most probably does not belong to Mantispidae.

The holotype of *Vectispa relictta* (Cockerell, 1921) is a small fragment of a wing from the Late Eocene Bembridge Marls, Isle of Wight, UK. Later, Jarzembowski (1980) referred an almost complete forewing (which is folded along its longitudinal line) from the same locality to this species, and established a new genus for it within Mantispinae. It is not clear, however, if these two specimens really belong to the same species. Lambkin (1986a) analysed in detail the relationships of this genus within the family [based on the Jarzembowski (1980) specimen], and tentatively placed it in Drepanicinae, based on four (plesiomorphic) characters: (a) the structure of pterostigmal region ('pterostigma apparently quite distinct from R1 and connected with it by only short crossvein'); (b) three r-rs present; (c) M (= MP) 'apparently not fused with R for a considerable distance'; (d) intramedian (= iMP) cell simple, with MA (= MP1 + 2) and MP (= MP3 + 4) long and approximately parallel' (Lambkin, 1986a: 24; Lambkin's designations of the veins are given in brackets). However, the mantispine subfamily affinity is most likely because: (a) a similar structure of the pterostigma is found in extant species of *Climaciella* (Mantispinae) (e.g. *Climaciella amapaensis* Penny, 1982b: fig. 46); (b) three r-rs occur in most Mantispinae; (c) although the basal part of the forewing of *V. relictta* is poorly preserved, it is obvious that M is fused with R for a quite considerable distance; (d) such a long intramedian cell occurs in some Mantispinae [e.g. *Climaciella brunnea* (Say, 1824): Hoffman (2002): fig. 545]. The venation of *Vectispa* appears to be the most plesiomorphic in the Mantispinae.

The Middle Eocene species *Symphrasites eocenicus* gen. et sp. nov. is described and discussed above.

The systematic position of *Whalfera venatrix* (Whalley, 1983) is not clear. It was described from Middle Eocene British amber (Norfolk, UK), which is considered contemporary with Baltic amber (Jarzembowski, 1999). The holotype is incomplete; the head, thorax, legs and basal parts of the fore and hind wings are preserved. Whalley (1983) originally referred it to Platymantispinae: Platymantispini (= Symphrasinae); Grimaldi (2000) also considered it to be closely related

to the symphrasines. Willmann (1994) re-described this species/genus, and analysed its phylogenetic position; he considered it as the sister group of Mantispidae. Nel *et al.* (2005b) follow this view. Aspöck & Mansell (1994), Engel (2004), and Grimaldi & Engel (2005) tentatively transferred *W. venatrix* to Rhachiberothidae. Indeed, the features of *Whalferia* indicate its intermediate position between Rhachiberothidae and Mantispidae. On the one hand, in this species the basal subcostal crossvein is present, M is not fused basally with R, a recurrent vein is not developed, and the Sc of the hindwing is long. All these states are found in Rhachiberothidae, and not in Symphrasinae. On the other hand, the presence of either two or three (although indistinct) trichosors between the tips of each subcostal veinlet are not characteristic of Rhachiberothidae; this is considered an autapomorphy of Mantispidae (Aspöck & Mansell, 1994), although it is only found in Symphrasinae and Drepanicinae. The principal autapomorphy of Mantispidae (the pronotum posterior to the forelegs is prolonged), which occurs in all species of this family, is not detected with certainty in *Whalferia* because of poor preservation. Willmann (1994) assumes, nevertheless, that the pronotum posterior to the forelegs is slightly prolonged. But this point might be contested, as the published photos show rather clearly that the pronotum anterior to the forelegs is much longer than posterior (Whalley, 1983: figs 1, 2; Willmann, 1994: fig. 2). Thus, although there is a theoretical possibility of assigning this genus to a stem group of Mantispidae, the probability is greater that it belongs to Rhachiberothidae.

Prosagittalata oligocenica Nel, 1989 is described from the Late Oligocene of Céreste, France. The holotype is represented by a very small (forewing 5.45 mm long), relatively complete specimen lacking only the abdomen. In general, the wing venation of this species is rather typical for that of many small Mantispinae from the extant genera *Mantispa* Illiger, 1798; *Cercomantispa* Handschin, 1959; *Rectinerva* Handschin, 1959; *Sagittalata* Handschin, 1959 (see for example Poivre, 1981a, b, c, 1985). The genus *Sagittalata* is considered to be most closely related to *Prosagittalata*, from which the latter may be distinguished by its wider costal space, according to Nel (1989). This feature, however, is variable within mantispines and is too weak to be of significant generic meaning. The touching of Rs and MA (i.e. the crossvein 1r-m is lost and MA appears to arise from the cell 1R1) seems to be the only clear character state distinguishing this taxon from the others with similar venation. However, such a short fusion of Rs and MA occurs in at least some species of the extant New World genus *Climaciella* (e.g. *C. amapaensis* Penny, 1982b: fig. 46; *Climaciella porosa* Hoffman, 2002: fig. 547). The size and venation of *Climaciella* and *Prosagittalata* are very different; we

may reasonably assume therefore that this is a result of convergence. In any case, the validity of the extinct genus *Prosagittalata* needs further confirmation.

Climaciella (?) *henrotayi* Nel, 1989 is a large species (estimated forewing length 19.2–20 mm) described from the Late Oligocene of Dauphin, France. The holotype is represented by four incomplete overlapping wings and a very poorly preserved body. Nel (1989) provisionally assigned this species to the genus *Climaciella*. Actually, no species of this genus is similar to *C. henrotayi*, particularly in that the latter has a broader costal space (in *Climaciella* it is much narrower) and a different structure of the pterostigmal region (Sc and R1 are widely separated distally in *Climaciella*, whereas these veins closely approach one another in *C. henrotayi*, as in most other Mantispinae). Thus, the generic placement of this mantispine species remains unknown.

A mantispid species (yet unnamed), certainly belonging to Mantispinae, is known from the amber of Chiapas, Mexico (Grimaldi & Engel, 2005: fig. 9.35: 354). Recent reinvestigations indicate that Mexican and Dominican amber are coeval, and that both are of early to middle Miocene age (J. Rust, pers. comm. 2006 to S. Wedmann). The specimen is almost complete: 10.4 mm in length, with forewing not more than 7 mm long (estimated). The venation of this species is most similar to that of *P. oligocenica* from Europe (see above); in particular, they share MA fused for a short distance with the stem of Rs, and a relatively small size. It is possible that this species belongs to the genus *Prosagittalata*.

Another unnamed mantispine species is known from Miocene Dominican amber (Grimaldi, 1996: unnumbered fig.: 93; Poinar & Poinar, 1999: fig. 129). The specimen is complete, rather large (length of specimen 0.9 inches = c. 22.5 mm; forewing c. 15 mm). Judging by the published photo and the drawing, it may be referred to a number of the genera distributed at present in this region, i.e. *Buyda* Navás, 1926; *Mantispa*, *Dicromantispa* Hoffman, 2002, *Leptomantispa* Hoffman, 2002, and *Zeugomantispa* Hoffman, 2002 (e.g. see Hoffman, 2002: figs 586–591). Most of these genera previously constituted the genus *Mantispa* s.l. Unfortunately, the diagnostic characters of the new genera established by Hoffman (2002) are not clear. So, it is at present very hard to determine the true generic placement of this fossil species. However, the name *Mantispa* s.l. appears most appropriate.

PALAEOBIOGEOGRAPHY OF MANTISPIDAE

Extant Mantispidae show a characteristic distribution pattern (Fig. 1). The advanced Mantispinae are distributed nearly worldwide, with fossil records from the Palaeogene of Europe and the Neogene of Central

America and the Caribbean (Chiapas and Dominican amber). The three other extant subfamilies are more restricted in distribution. Symphrasinae occur in the Neotropical and southernmost Nearctic regions (Penny, 1982a, b; Ohl, 2004). The Eocene *S. eocenicus* from Germany shows that Symphrasinae formerly had a wider distribution. A rather similar situation is found in Drepanicinae. Today they occur only in the Neotropical and Australian regions (Ohl, 2004). The single fossil drepanicine species, *G. asiatica* from Kazakhstan, is considered to belong to an extant genus that is currently widely distributed in the Neotropical region. Calomantispinae at present occur only in Central America to the southern Nearctic region and Australia. No fossil record of this group is known.

ORIGIN AND DIVERSIFICATION OF MANTIDFLIES

The Mantispidae might have originated sometime in the late Triassic to earliest Jurassic. One taxon of the paraphyletic extinct family 'Prohemerobiidae' (Ansorge, 1996) might be a possible candidate for ancestral mantispids. The 'Prohemerobiidae' are not yet revised, and it is perhaps reasonable that this family is not present in the cladogram showing the phylogenetic relationships of families of the Neuropterida (Grimaldi & Engel, 2005: fig. 9.4). However, the wings of *Prohemerobius dilaroides* Handlirsch, 1906 (the type for the family) and some undescribed species from the Late Lias of Germany are rather similar to those of the oldest mantispids in most of their characters, although the latter are clearly more derived (J. Ansorge & V. N. Makarkin, unpubl. data). Recently, *Permantispa emelyanovi* Ponomarenko & Shcherbakov, 2004 was described from either the terminal Permian or the basal Triassic of Siberia, based on an incomplete wing, and was preliminarily assigned to the Permian Permithonidae, but was principally compared with the Mantispidae. These authors assumed 'that the mantispid lineage originated from Permithonidae' (Ponomarenko & Shcherbakov, 2004: S201). In any case, the mantispid lineage might go back to the Triassic.

Most of the ancient history of Mantispidae is quite obscure. Only few Mesozoic mantispids are known; they mainly represent taxa from extinct lineages of the family (Fig. 7). The oldest fossil records are *L. stigmatica* from the Early Jurassic deposit of Dobbertin in Germany, and the Late Jurassic *P. similis* from Karatau, Kazakhstan. *Liassochrysa* and *Promantispa* appear to be rather closely related to each other, but their phylogenetic relationships within the family are unclear (see above). These fossils indicate that mantispids had evolved by the Early Jurassic in Eurasia. The occurrence of the generalized, early Cretaceous *M. sibirica* in Asia, which belongs to a different extinct lineage than that of *Liassochrysa* and *Proman-*

tispa, supports a probable great diversity of Mesozoic mantidflies in Asia and Europe. Therefore, the origin of Mantispidae may have been in the either European or Asian regions, and their initial diversification might have taken place during the Early–Middle Jurassic. But one must take into consideration that the lack of fossil finds of Mesozoic mantispids in regions other than Asia and Europe may well be the result of a lack of prolific fossil deposits (see Eskov, 2002: fig. 500). During the Jurassic, all present continents formed the supercontinent Pangaea. Therefore, there were no principal barriers for the wide dispersal of predacious insects. However, there may have been climatic restrictions. The Early Jurassic global climate ranged from temperate to tropical, the interior of Pangaea was dry and hot, and there were no ice caps at the poles. But during the Jurassic the climate became cooler, and by the Late Jurassic seasonal ice covered the polar regions as a result of the breakup of Pangaea (Scotese, 2003).

Since the Late Cretaceous, mantispid fossils can be assigned to extant subfamilies. The present occurrence of six species of *Gerstaeckerella* in South America (Ohl, 2004), and the fossil record of *G. asiatica* in Asia, suggest that this drepanicine genus was very widespread during Cretaceous times, and that its present distribution is relictual. A dispersal of drepanicine taxa may have occurred in Mesozoic times when Gondwanan continents were still situated close to one another, and were still in connection with the northern Laurasian continents north of the Tethys. The record of an extant genus of the Drepanicinae from the Late Cretaceous implies a minimum age for the existence of its sister taxon (Calomantispinae + Mantispinae). It should be noted that the genera of the extinct lineages (*Liassochrysa*, *Promantispa*, and *Mesomantispa*) are more similar to those of Drepanicinae than of any other extant subfamilies. Therefore, a presumable age of Drepanicinae might theoretically be much older than the Late Cretaceous. The more basal Symphrasinae (the sister group of the remaining extant Mantispidae, according to Lambkin, 1986a) must have existed at that time as well. The fossil record of a symphrasine species from Europe suggests that during the Eocene the Symphrasinae were distributed across Europe and North America (connected at that time by land bridges) at least, and only later became extinct in most of North America. But strictly speaking we do not know anything about their distribution at that time, except for their record at Messel: their dispersal to South America may well have occurred later; alternatively, their current distribution in this continent may be relict, persisting from their ancient Pangean area (if Symphrasinae are equally ancient). Phylogenetic analysis of the extant symphrasines might provide a further clue, but unfortunately they are in need of a generic revision.

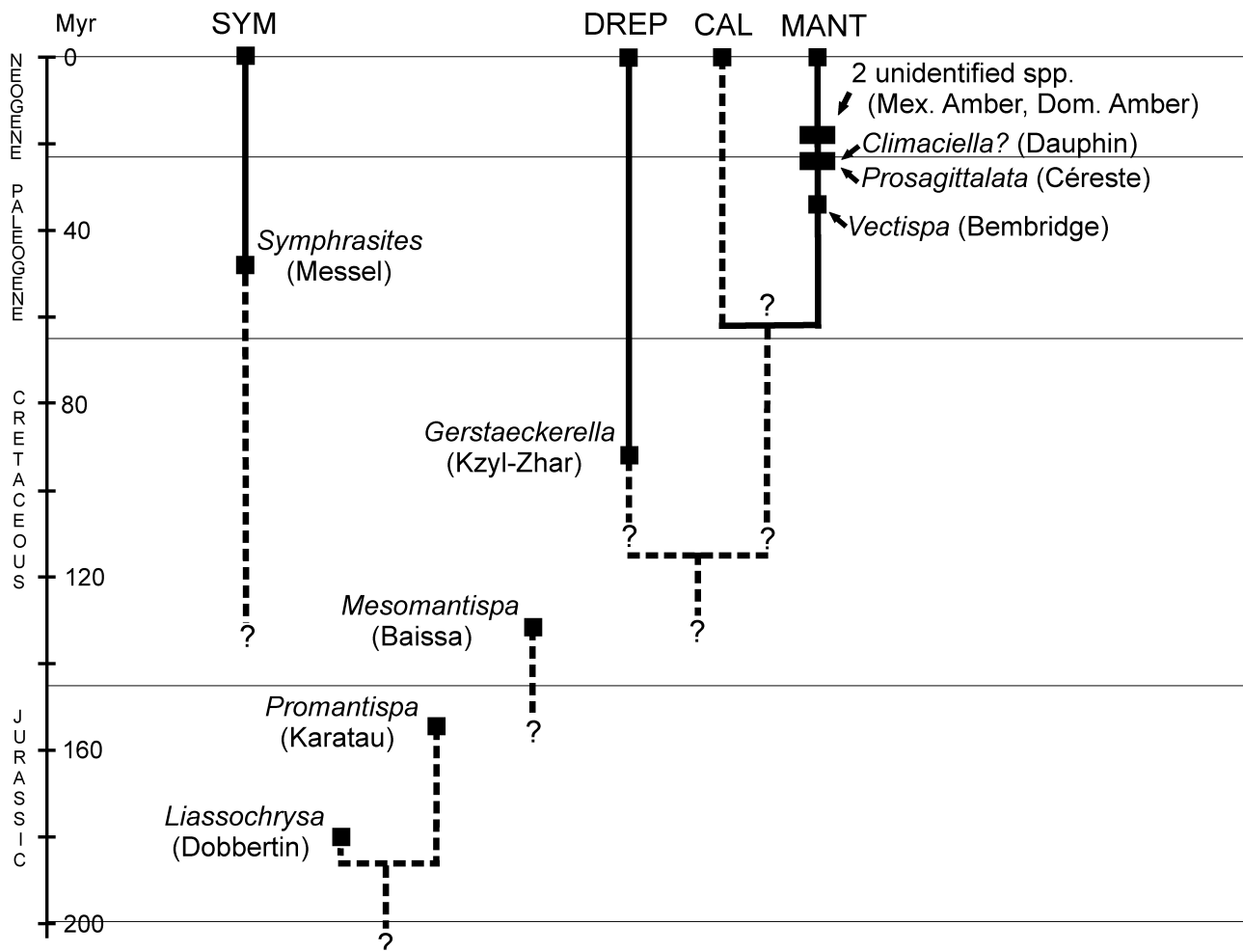


Figure 7. Fossil record and inferred time ranges of subgroups of Mantispidae, superimposed upon a preliminary phylogenetic tree, based mainly on Lambkin (1986a), modified here. CAL, Calomantispinae; DREP, Drepanicinae; MANT, Mantispinae; SYM, Symphrasinae. Dashed lines and '?' indicate uncertainty in relationships and time ranges.

Calomantispinae have at present a very disjunct distribution, which might be explained by an early evolution of their ancestors during the Jurassic, who then became widely distributed as a result of the breakup of Pangaea. As there is no fossil evidence to indicate that this clade is really this old, alternatively it can be assumed that crown-group members of Calomantispinae did not evolve until the Late Cretaceous or even later, dispersed widely, similar to the scenario assumed for marsupial mammals by Osborne & Tarling (1995), and then became extinct in the larger part of their former area. The discovery of fossil representatives of this group could help to solve these questions. Both scenarios outlined for the Calomantispinae can be transferred to the presently worldwide distributed Mantispinae. An early origin and following vicariance events could easily explain the cosmopolitan nature of Mantispinae (Lambkin, 1986a). However, Grimaldi & Engel (2005) assumed that the radiation

of Mantispinae to its present diversity might have occurred during the Tertiary. This hypothesis may be the case, as the oldest known fossil mantispine genus (the late Eocene *Vectispa*) appears to be the most plesiomorphic of the subfamily. A detailed analysis of the phylogenetic relationships among extant mantispines (which has yet to be carried out) probably would allow further conclusions concerning both the phylogenetic positions of the fossil taxa, particularly, the position of *Vectispa*, and confirmation of the validity and the position of *Prosagittalata* (see above), and the dispersal of this group.

POSSIBLE EXPLANATION OF THE DISTRIBUTION PATTERN OF MANTISPIDAE

Present 'hot spots' of diversity of taxa are often assumed to be the centres of their origin (e.g. Cox & Moore, 2005). Based on the extant distribution of the

Mantispidae, without considering their fossil record, one could easily assume that early mantispids (or their stem-group representatives) might have evolved in Gondwana. Indeed, this family shows a mostly Gondwanan range; the major diversity of extant species of the basal groups lies mainly in the Southern continents; only members of the most advanced subfamily Mantispinae are found also in the Ethiopian, Oriental, Palaearctic, and Nearctic regions (Ohl, 2004). Consideration of fossils, however, shows that the evolutionary history of the group was different than what their current distribution alone suggests.

Eskov (1987, 1992, 2002), Briggs (1995) and Grimaldi & Engel (2005) pointed out that austral disjunctions are generally much more widespread among groups of extant insects than are disjunct distributions in the Northern Hemisphere. There are competing hypotheses explaining extant Gondwanan ranges: vicariance biogeography (Platnick & Nelson, 1978, 1981; Grimaldi & Engel, 2005) and mobilistic biogeography (a short overview and criticism is presented in Eskov & Golovatch, 1986; Eskov, 1987) on the one hand, and dispersal scenarios such as the relict theory (Briggs, 1987, 1995) and the concept of ousted relicts (Eskov & Golovatch, 1986; Eskov, 1987) on the other. Mobilistic and vicariance biogeography indicate the Gondwanan pattern of extant groups of organisms to have originated during the Mesozoic on the former continent of Gondwana. The fragmentation of Gondwana to the present-day continents and their subsequent drift transformed their range into today's disjunct distribution. The relict theory and the theory of ousted relicts assume that these 'Gondwanan' groups were at one time widely distributed, and later either became extinct for most of their former areas or were 'ousted' by other (often more advanced) groups, apparently originating in the equatorial zone (e.g. Darlington, 1957; Briggs, 1995; Shcherbakov, 2000). Many of these groups survive in extratropical regions and exhibit either an antitropical or an amphitropical distribution. The latter hypothesis can be regarded to best explain the current and past distribution of many taxa, especially insects (e.g. Eskov, 1987, 1992; Briggs, 1995; Shcherbakov, 2000). The fossil occurrences of many groups in the Northern Hemisphere indicate that Northern extratropical relicts become extinct more easily than their Southern counterparts, which often survive until today (e.g. Eskov, 1987; Briggs, 1995; Poinar, 1996). Possible reasons for this may lie in former more extreme climatic conditions (e.g. glaciations) in the Northern Hemisphere (Grimaldi & Engel, 2005). The beginning of the Cenozoic was one of the warmest periods in the history of the Earth, but the Earth's climatic belts changed dramatically during the Cenozoic (e.g. Scotese, 2003). This Cenozoic climatic change was perhaps more pronounced on the

larger Northern land masses, which could have been conducive to these extinctions. Another possible explanation could be related to a more intense interspecific competition on the larger Northern landmasses (Briggs, 1995). The fossil record of mantispids is more or less concordant with the hypotheses of ousted relicts and the relict theory. Indeed, it shows that the more primitive Symphrasinae and Drepanicinae were once widespread, but that now their distribution is relict and restricted to the Gondwanan continents. The seven extant species of Calomantispinae at present show a disjunct distribution that can be interpreted as a relict distribution. The advanced Mantispinae seem to have 'ousted' the other groups as they are presently distributed worldwide. Eskov (1987) and Briggs (1995) emphasized the fact that groups with extant amphitropic (that is, circum-Antarctic) distribution often represent the most primitive taxa within their respective larger groups. The more primitive groups seem to retreat geographically from more specialized members of the group. This scenario may also be applied to mantidflies.

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NOTE ADDED IN PROOF

Since this paper was submitted, the species *Feroseta prisca* Poinar, 2006 was described from Dominican amber (Poinar, 2006). At the same time as this paper, an article on the neuropterid fauna of the Dominican and Mexican amber by Engel & Grimaldi is in press (Engel & Grimaldi, in press). There the authors describe two mantispids from Mexican and Dominican amber that are discussed in this paper as unidentified species.

REFERENCES

- Adams PA, Penny ND. 1992.** Review of the South American genera of Nothochrysinæ (Insecta: Neuroptera: Chrysopidae). In: Canard M, Aspöck H, Mansell MW, eds. *Current Research in Neuropterology. Proceedings of the Fourth International Symposium on Neuropterology*. Toulouse: privately printed, 34–41.
- Ansorge J. 1996.** Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlungen* **2**: 1–132.
- Ansorge J, Schlüter T. 1990.** The earliest Chrysopid: *Liasochrysa stigmatica* n. g., n. sp. from the Lower Jurassic of Dobbertin, Germany. *Neuroptera International* **6**: 87–93.
- Archibald SB, Makarkin VN. 2004.** New genus of minute Berothidae (Neuroptera) from Early Eocene amber of British Columbia. *Canadian Entomologist* **136**: 59–74.
- Aspöck U, Mansell MW. 1994.** A revision of the family Rhachiberothidae Tjeder, 1959, stat. n. (Neuroptera). *Systematic Entomology* **19**: 181–206.
- Aspöck U, Nemeschkal HL. 1998.** A cladistic analysis of the Berothidae (Neuroptera). *Acta Zoologica Fennica* **209**: 45–63.
- Blanchard CÉ. 1851.** Rafidianos. In: Gay C, ed. *Historia Fisica y Política de Chile, Zoología* **6**: 129–135.
- Briggs JC. 1987.** Antitropical distribution and evolution in the Indo-West Pacific ocean. *Systematic Zoology* **36**: 237–247.
- Briggs JC. 1995.** *Global Biogeography. Developments in Palaeontology and Stratigraphy*, Vol. 14. Amsterdam: Elsevier.
- Carpenter FM. 1992.** Superclass Hexapoda. In: Kaesler RA, ed. *Treatise on Invertebrate Paleontology, Part Royal, Arthropoda*, Vol. 4. Boulder, Colorado: Geological Society of America & Lawrence, Kansas, University of Kansas.
- Cockerell TDA. 1921.** Fossil arthropods in the British Museum. VI. Oligocene insects from Gurnet Bay, Isle of Wight. *Annals and Magazine of Natural History* **9**: 453–480.
- Comstock JH. 1918.** *The Wings of Insects*. Ithaca: Comstock Publishing Co.
- Cox CB, Moore PD. 2005.** *Biogeography: An Ecological and Evolutionary Approach*, 7th edn. Malden, Oxford: Blackwell Publishing.
- Darlington PJ Jr. 1957.** *Zoogeography. The Geographical Distribution of Animals*. New York: Wiley.
- Enderlein G. 1910.** Klassifikation der Mantispiden nach dem Material des Stettiner Zoologischen Museums. *Stettiner Entomologische Zeitung* **71**: 341–379.
- Engel MS. 2004.** Thorny lacewings (Neuroptera: Rachiberothidae) in Cretaceous Amber from Myanmar. *Journal of Systematic Palaeontology* **2**: 137–140.
- Engel M, Grimaldi D. In press.** The neuropterid fauna of Dominican and Mexican amber (Neuroptera: Megaloptera: Neuroptera). *American Museum Novitates*, in press.
- Eskov KY. 1987.** A new archaetid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called ‘Gondwanan’ ranges of recent taxa. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **175**: 81–106.
- Eskov KY. 1992.** Archaetid spiders from Eocene Baltic amber (Chelicerata: Araneida: Archaetidae) with remarks on the so-called ‘Gondwanan’ ranges of Recent taxa. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **185**: 311–328.
- Eskov KY. 2002.** Geographical history of insects. In: Rasnitsyn AP, Quicke DLJ, eds. *History of Insects*. Dordrecht: Kluwer Academic Publishers, 427–435.
- Eskov KY, Golovatch SI. 1986.** On the origin of trans-pacific disjunctions. *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere* **113**: 265–285.
- Felder M, Harms F-J. 2004.** Lithologie und genetische Interpretation der vulkano-sedimentären Ablagerungen aus der Grube Messel anhand der Forschungsbohrung Messel 2001 und weiterer Bohrungen. *Courier Forschungsinstitut Senckenberg* **252**: 151–203.
- Franzen JL. 2005.** The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. *Annales de Paléontologie* **91**: 329–335.
- Goth K. 1990.** Der Messeler Ölschiefer – ein Algenlaminit. *Courier Forschungsinstitut Senckenberg* **131**: 1–143.
- Grimaldi DA. 1996.** *Amber: window to the past*. New York: Harry N. Abrams and the American Museum of Natural History.
- Grimaldi DA. 2000.** A diverse fauna of Neuropterodea in amber from the Cretaceous of New Jersey. In: Grimaldi DA, ed. *Studies on Fossil in Amber, with Particular Reference to the Cretaceous of New Jersey*. Leiden: Backhuys Publishers, 259–303.
- Grimaldi DA, Engel MS. 2005.** *Evolution of the Insects*. Cambridge: Cambridge University Press.
- Handlirsch A. 1906–08.** *Die Fossilen Insekten und die Phylogenie der Rezenten Formen*. Leipzig: Engelmann.
- Handschin E. 1959.** Beiträge zu einer Revision der Mantispiden (Neuroptera). I. Teil. Mantispiden des Musée Royal du Congo Belge, Tervuren. *Revue de Zoologie et de Botanique Africaines* **59**: 185–227.
- Harms F-J. 2002.** Steine erzählen Geschichte (n): Ursachen für die Entstehung des Messel-Sees gefunden. *Natur und Museum* **132**: 1–4.
- Hoffman KM. 2002.** Family Mantispidae. In: Penny ND, ed. *A Guide to the Lacewings (Neuroptera) of Costa Rica Proceedings of the California Academy of Sciences* **53**: 251–275.
- Hörschemeyer T. 1994.** Ein fossiler Tenebrionide *Ceropria? messelense* n. sp. (Coleoptera: Tenebrionidae: Diaperinae) aus dem Mitteleozän Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* **170**: 75–83.
- Hörschemeyer T, Wedmann S. 1994.** Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 1. *Courier Forschungsinstitut Senckenberg* **170**: 85–136.
- Illiger JKW. 1798.** Verzeichnis der Käfer Preussens, entworfen von Johann Gottlieb Kugelann, ausgearbeitet von

- Johann Karl Wilhelm Illiger. Mit einer Vorrede des Professors und Pagenhofmeisters Helwig in Braunschweig, und dem angehängten Versuche einer natürlichen Ordnungs- und Gattungs-folge der Insekten. Halle.
- Jarzembowski EA. 1980.** Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bulletin of the British Museum of Natural History (Geology)* **33**: 237–293.
- Jarzembowski EA. 1999.** British amber: a little-known resource. *Estudios del Museo de Ciencias Naturales de Álava* **14** **2**: 133–140.
- von Koenigswald W, Storch G. 1998.** *Messel. Ein Pompeji der Paläontologie*. Sigmaringen: Jan Thorbecke Verlag.
- Lambkin KJ. 1986a.** A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family I. General and Drepanicinae. *Australian Journal of Zoology (Supplementary Series)* **116**: 1–142.
- Lambkin KJ. 1986b.** A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family II. Calomantispidae and Mantispinae. *Australian Journal of Zoology (Supplementary Series)* **117**: 1–113.
- Leach WE. 1815.** Entomology. In: Brewster D, ed. *Edinburgh Encyclopaedia* **9**: 57–172.
- Linnaeus C. 1758.** *Systema Natura Per Regna Tria Naturae Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis, 10th edn*, Vol. 1. Holmiae: Salvii.
- Lutz H. 1986.** Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der 'Grube Messel' bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana Lethaea* **67**: 177–218.
- Lutz H. 1990.** Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* **124**: 1–165.
- Lutz H. 1991.** Autochthone aquatische Arthropoda aus dem Mittel-Eozän der Fundstätte Messel (Insecta: Heteroptera; Coleoptera; cf. Diptera-Nematocera; Crustacea: Cladocera). *Courier Forschungsinstitut Senckenberg* **139**: 119–125.
- Makarkin VN. 1990.** Novye setchatokrylye (Neuroptera) iz verkhnego mela Azii [New lacewings (Neuroptera) from the Late Cretaceous of Asia]. In: Akimov IA, ed. *Novosti Faunistiki I Sistematiki (News of faunistics and systematics)*. Kiev: Naukova Dumka. 63–68. (In Russian)
- Makarkin VN. 1995.** Notes on Palearctic Hemeroibiidae (Neuroptera). 1. Introduction and genus *Wesmaelius* Krüger, 1922. Part 1. Subgenus. *Wesmaelius Far Eastern Entomologist* **24**: 1–13.
- Makarkin VN. 1997.** Fossil Neuroptera of the Lower Cretaceous of Baisa, East Siberia. Part 5: Mantispidae. *Russian Entomological Journal* **5**: 91–93.
- Makarkin VN, Archibald SB. 2003.** Family affinity of the genus *Palaeopsychops* Andersen with description of a new species from Early Eocene of British Columbia (Neuroptera: Polystoechotidae). *Annals of the Entomological Society of America* **96**: 171–180.
- Makarkin VN, Menon F. 2005.** New species of the Mesochrysoptidae (Insecta, Neuroptera) from the Crato Formation of Brazil (Lower Cretaceous), with taxonomic treatments of the family. *Cretaceous Research* **26**: 801–812.
- McLachlan R. 1867.** New genera and species, of neuropterous insects and a revision of Mr. F. Walker's British Museum catalogue of Neuroptera, part ii (1853), as far as the end of the genus *Myrmeleon*. *Journal of the Linnean Society of London* **9**: 230–281.
- Mertz DF, Harms F-J, Gabriel G, Felder M. 2004.** Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. *Natur und Museum* **134**: 289–290.
- Mertz DF, Renne PR. 2005.** A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from ⁴⁰Ar/³⁹Ar dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg* **255**: 67–75.
- Navás L. 1909.** Mantispidos nuevos [I]. *Memorias de la Real Academia de Ciencias Y Artes de Barcelona* **3**: 473–485.
- Navás L. 1926.** Insectos exóticos Neuropteros y afines. *Brotéria (Zoológica)* **23**: 79–93.
- Navás L. 1928.** Insectos neotropicos. 3.a serie. *Revista Chilena de Historia Natural* **31**: 316–328.
- Nel A. 1989.** Deux nouveaux Mantispidae (Planipennia) fossiles de l'Oligocene du sud-est de la France. *Neuroptera International* **5**: 103–109.
- Nel A, Delclòs X, Hutin A. 2005a.** Mesozoic chrysopid-like Planipennia: a phylogenetic approach (Insecta: Neuroptera). *Annales de la Société Entomologique de France* **41**: 29–68.
- Nel A, Perrichot V, Azar D, Néraudeau D. 2005b.** New Rhachiberothidae (Insecta: Neuroptera) in Early Cretaceous and Early Eocene ambers from France and Lebanon. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **235**: 51–85.
- Ohl M. 2004.** Annotated catalog of the Mantispidae of the world (Neuroptera). *Contributions on Entomology, International* **5**: 131–262. (in collaboration with Oswald JD)
- Osborne R, Tarling D. 1995.** *The Historical Atlas of the Earth: a Visual Exploration of the Earth's Physical Past*. Glasgow: Viking, Bath Press Colourbooks.
- Oswald JD. 1993.** Revision and cladistic analysis of the world genera of the family Hemeroibiidae (Insecta: Neuroptera). *Journal of the New York Entomological Society* **101**: 143–299.
- Panfilov DV. 1980.** Novye predstaviteli setcharokrylykh (Neuroptera) iz yury Karatau [New representatives of lacewings (Neuroptera) from the Jurassic of Karatau]. In: Dolin VG, Panfilov DV, Ponomarenko AG, Pritykina LN. *Iskopayemye nasekomye mezozoya (Fossil Insects of the Mesozoic)*. Kiev: Naukova Dumka, 82–111. (In Russian.)
- Penny ND. 1982a.** Review of the generic level classification of New World Mantispidae (Neuroptera). *Acta Amazonica* **12**: 209–223.
- Penny ND. 1982b.** Neuroptera of the Amazon Basin. Part 3. Mantispidae. *Acta Amazonica* **12**: 415–463.
- Platnick NI, Nelson G. 1978.** Vicariant patterns and historical explanation in biogeography. *Systematic Zoology* **27**: 1–16.
- Platnick NI, Nelson G. 1981.** Systematics and biogeography: *Cladistics and Evolution*. New York: Columbia University Press.
- Poinar GO Jr. 1996.** Fossil velvet worms in Baltic and Domin-

- ican Amber: Onychophoran evolution and biogeography. *Science* **273**: 1370–1371.
- Poinar GO Jr. 2006.** *Feroseta priscus* (Neuroptera: Mantispidae), a new genus and species of mantidflies in Dominican amber. *Proceedings of the Entomological Society of Washington* **108**: 411–417.
- Poinar GO Jr, Poinar R. 1999.** *The Amber Forest: a Reconstruction of a Vanished World*. Princeton, New Jersey: Princeton University Press.
- Poivre C. 1981a.** Mantispides du Cameroun I. (Neuroptera, Planipennia). *Neuroptera International* **1**: 77–89.
- Poivre C. 1981b.** Mantispides du Cameroun II. Nouvelle description et morphologie externe comparée de *Sagittalata lugubris* et *S. jucunda* (Neuroptera, Planipennia). *Neuroptera International* **1**: 110–121.
- Poivre C. 1981c.** Morphologie Comparative et Systématique de Mantispides d'Afrique et d'Europe (Neuroptera, Planipennia). PhD Thesis, University of Nancy.
- Poivre C. 1985.** Mantispides du Cameroun. III. Nouvelle description de *Rectinerva braconidiformis* (Planipennia, Mantispidae). *Neuroptera International* **3**: 195–200.
- Ponomarenko AG. 2002.** Superorder Myrmeleontidea Latreille, 1802 (= Neuropteroidea Handlirsch, 1903). In: Rasnitsyn AP, Quicke DLJ, eds. *History of Insects*. Dordrecht: Kluwer Academic Publishers, 176–192.
- Ponomarenko AG, Shcherbakov DE. 2004.** New lacewings (Neuroptera) from the terminal Permian and basal Triassic of Siberia. *Paleontological Journal* **38**: S197–S203.
- Richter G, Baszio S. 2001a.** Traces of a limnic food web in the Eocene Lake Messel – a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* **166**: 345–368.
- Richter G, Baszio S. 2001b.** First proof of planctivory/insectivory in a fossil fish: *Thaumaturus intermedius* from the Eocene Lake Messel (FRG). *Palaeogeography, Palaeoclimatology, Palaeoecology* **173**: 75–85.
- Richter G, Wedmann S. 2005.** Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology* **223**: 147–161.
- Say T. 1824.** Order Neuroptera. In: Keating WH, ed. *Narrative of an Expedition to the Source of St Peter's River; Lake Winnepeck, Lake of the Woods and C and C Performed in the Year 1823, by Order of the Hon J C Calhoun, Secretary of War, Under the Command of Stephen H Long, Major U S T E*, Vol. 2. Philadelphia: Carey and Lea. 303–310.
- Schaal S, Ziegler W, eds. 1992.** *Messel. An Insight Into the History of Life and of the Earth*. Oxford: Clarendon Press.
- Schmidt-Kittler N, ed. 1987.** International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene – Mainz, February 18th–21st 1987. *Münchener Geowissenschaftliche Abhandlungen (a)* **10**: 1–312.
- Scotese CR. 2003.** Plate tectonic maps and Continental drift animations. PALEOMAP Project website: <http://www.scotese.com>
- Shcherbakov DE. 2000.** Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permian-Triassic crisis. *Paleontological Journal* **34**: S251–S267.
- Tjeder B. 1959.** Neuroptera-Planipennia. The Lace-wings of Southern Africa. 2. Family Berothidae. In: Hanström B, Brinck P, Rudebec G, eds. *South African Animal Life Results of the Lund University Expedition in 1950–51.*, Vol. 6. Stockholm: Almqvist & Wiksell. 256–314.
- Tröster G. 1991.** Eine neue Gattung der Elateridae (Insecta: Coleoptera) *Macropunctum* gen. n. aus der Messel-Formation des unteren Mittel-Eozän der Fundstätte Messel. *Courier Forschungsinstitut Senckenberg* **139**: 99–117.
- Tröster G. 1993a.** Fossile Schnellkäfer der Gattung *Lanelater* Arnett 1952 (Coleoptera, Pyrophorinae, Agrypnini) aus dem Eozän der Grube Messel bei Darmstadt. *Senckenbergiana Lethaea* **73**: 49–60.
- Tröster G. 1993b.** Wasserkäfer und andere Raritäten – Neue Coleoptera-Funde aus den mitteleozänen Tonsteinen der Grube Messel bei Darmstadt. *Kaupia–Darmstädter Beiträge zur Naturgeschichte* **2**: 145–154.
- Tröster G. 1993c.** Zwei neue mitteleuropäische Arten der Gattung *Tenomerga* Neboiss 1984 aus dem Mitteleozän der Grube Messel und des Eckfelder Maeres (Coleoptera: Archostemata: Cupedidae). *Mainzer Naturwissenschaftliches Archiv* **31**: 169–176.
- Tröster G. 1994.** Fossile Elateridae (Insecta: Coleoptera) aus dem Unteren Mitteleozän (Lutetium) der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* **170**: 11–64.
- Wappler T. 2003.** New fossil lace bugs (Heteroptera: Tingidae) from the Middle Eocene of the Grube Messel (Germany), with a catalog of fossil lace bugs. *Zootaxa* **374**: 1–26.
- Wappler T, Andersen NM. 2004.** Fossil water striders from the Middle Eocene fossil sites of Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift* **78**: 41–52.
- Wappler T, Engel MS. 2003.** The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* **77**: 908–921.
- Wedmann S, Hörnschemeyer T. 1994.** Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae und Agrilinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 2. *Courier Forschungsinstitut Senckenberg* **170**: 137–187.
- Westwood JO. 1852.** On the genus *Mantispa*, with descriptions of various new species. *Transactions of the Entomological Society of London* **1**: 252–270.
- Whalley PES. 1983.** *Fera venatrix* gen. & sp. n. (Mantispidae) from amber in Britain. *Neuroptera International* **2**: 229–233.
- Willmann R. 1990.** The phylogenetic position of the Rhachiberothinae and the basal sister-group relationships within the Mantispidae (Neuroptera). *Systematic Entomology* **15**: 253–265.
- Willmann R. 1994.** Die phylogenetische Position ursprünglicher Mantispidae (Insecta, Planipennia) aus dem Mesozoikum und Alt-Tertiär. *Verhandlungen des Vereins für Naturwissenschaftliche Unterhaltung zu Hamburg* **34**: 177–203.
- Wootton RJ. 2003.** Wings. In: Resh VH, Carde RT, eds. *Encyclopedia of Insects*. London: Academic Press, 1186–1192.