

Diverse new Middle Jurassic Osmylopsychopidae (Neuroptera) from China shed light on the classification of psychopsoidea

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A well-preserved diverse fauna of fossil neuropterans of the family Osmylopsychopidae has been discovered at the Middle Jurassic locality of Daohugou, China. *Daopsychops dissectus* gen. et sp. nov., *D. clausus* gen. et sp. nov., *D. inanis* gen. et sp. nov., *D. bifasciatus* gen. et sp. nov., *D. cubitalis* gen. et sp. nov., *Eupypsochops ferox* gen. et sp. nov., *E. confinis* gen. et sp. nov., *Nematopsychops unicus* gen. et sp. nov., *Ochropsychops multus* gen. et sp. nov. and *Stenopteropsychops trifasciatus* gen. et sp. nov. are described. These new taxa allow a better understanding of the relationships between the psychopsoidea families Osmylopsychopidae, Psychopsidae and Brongniartiellidae. The type of the latter (*Brongniartiella gigas* from the Late Jurassic of Germany) is redescribed. The venation of the new genera of Osmylopsychopidae shows that Brongniartiellidae is a synonym of this family. Of the genera ascribed to Brongniartiellidae, only *Pseudopsychopsis* belongs to Osmylopsychopidae with certainty. *Gigantopsychops reticulatus* gen. et sp. nov. from Daohugou (Psychopsidae) is an important taxon providing a new insight into the definition of the family. Wings of Psychopsidae may be distinguished from those of Osmylopsychopidae by a combination of the following character states: in both wings, the costal space is very broad distally; Rs1 is not deeply forked; the distal nygma is lost; the distal R1 is straight, not curved posteriad; in the hind wing, 1r-m is short and straight. It is clear now that the family Osmylopsychopidae was a dominant psychopsoidea group during the Mesozoic, and Psychopsidae was relatively rare.

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Introduction

The systematics of Mesozoic psychopsoidea is very complicated and confused. This group of Neuroptera includes taxa with broad and multi-veined wings that are currently classified in five families, i.e. Osmylopsychopidae, Brongniartiellidae, Psychopsidae, Kalligrammatidae and Aetheogrammatidae (Makarkin *et al.* 2013). The difficulty in their classification is due mainly to the fact that psychopsoidea species are mostly fossil (predominantly Mesozoic), and often represented by poorly preserved, fragmentary or incomplete wings. Psychopsoidea are today only known from a small family, Psychopsidae (27 extant species), with a disjunct distribution in southern Africa, southern Asia and Australia (Oswald 1993a, 1994, 1995; Wang & Bao 2006). Kalligrammatidae and Aetheogrammatidae are easily distinguished from other psychopsoidea, whereas the Mesozoic members of the three other families (i.e. Osmylopsychopidae, Brongniartiellidae and Psychopsidae) hardly differ from each other. Moreover, it is quite possible that two other family-group taxa of

Mesozoic psychopsoidea might be valid: Triassopsychopinae based on *Triassopsychops* Tillyard from the Late Triassic (Carnian) of Australia (Tillyard 1922), and Glottidiidae based on *Glottopteryx* Makarkin & Archibald (= *Glottidia* Bode) from the Early Jurassic of Germany (Bode 1953; Makarkin & Archibald 2005). Also, there are other genera with broad wings currently considered as belonging to the Mesozoic family Prohemerobiidae, and fossil psychopsoidea taxa that have not been classified within any family. Given these circumstances, it is quite understandable why family placement of many fossil genera of psychopsoidea is so unstable.

The examination of numerous psychopsoidea from the Chinese Middle Jurassic locality of Daohugou shows that Osmylopsychopidae dominates this assemblage. Many of them are beautifully preserved complete forewings and hind wings. These fossils allow a much better understanding of the diagnostic characters and wing venation evolution of Osmylopsychopidae, and its relationship with other families, particularly Brongniartiellidae and Psychopsidae.

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Martynova (1949) established two closely related new families Osmylopsychopidae (as ‘Osmylopsychopsidae’) and Brongniartiellidae, designating *Osmylopsychops* Tillyard (Late Triassic of Australia) and *Brongniartiella* Meunier (Late Jurassic of Germany) as their type genera, respectively. This author assigned *Actinophlebia* Handlirsch, *Pterinoblattina* Scudder, *Mesopsychopsis* Handlirsch, *Paractinophlebia* Handlirsch (Jurassic of Germany and England) and *Epactinophlebia* Martynov (Late Jurassic of Kazakhstan) to Brongniartiellidae, and placed *Triassopsychops* Tillyard, *Archepsychops* Tillyard and *Protopsychoptis* Tillyard from the Late Triassic of Australia in Psychopsidae. Riek (1955) independently erected the new family Osmylopsychopidae comprised of *Osmylopsychops*, *Archepsychops* and *Mesopolystoechus* Martynov (Early/Middle Jurassic of Tajikistan). Later, he described the new genus *Petropsychops* Riek (Late Triassic of Australia) and assigned it together with *Protopsychoptis* to Osmylopsychopidae (Riek 1956). Fujiyama (1978) described the new genus *Kagapsychops* Fujiyama (Early Cretaceous of Japan) in Osmylopsychopidae, and Ponomarenko (1986, 1990) assigned to this family two other genera: *Pterinoblattina* Scudder (Early Cretaceous of England and Mongolia), and *Angaropsychops* Martynova (Early Cretaceous of Transbaikalia, Russia). Whalley (1988) followed Martynova (1949) in transferring *Actinophlebia* from Prohemerobiidae to Brongniartiellidae. Carpenter (1992) considered only *Archepsychops* and *Petropsychops* in this family (together with *Osmylopsychops*), and followed Martynova (1949) in an assignment of *Brongniartiella*, *Actinophlebia*, *Mesopsychopsis* and *Epactinophlebia* to Brongniartiellidae. Ponomarenko (1996) referred *Parhemerobius* Bode and *Actinophlebia* to Osmylopsychopidae. Makarkin & Archibald (2005) agreed that these two genera might indeed belong to Osmylopsychopidae. Jepson *et al.* (2009) assumed that some Cretaceous genera (e.g. *Grammapsychops* Martynova, *Embaneura* Zalesky and *Pulchroptionia* Martins-Neto) may belong to Osmylopsychopidae. Therefore, the family Osmylopsychopidae could occur from the Middle Triassic to the Late Cretaceous based on different authors.

It should be noted that most of these assignments were not founded on a solid family definition. Lambkin (1992) re-examined in detail the types of *Osmylopsychops spillerae* Tillyard and the two other fragmentary wings recorded by Riek (1956), and provided a more precise new reconstruction of its forewing venation. Recently, Lambkin (2014) reported new material of Osmylopsychopidae from the Triassic of Australia, including valuable new specimens of *Osmylopsychops* and *Petropsychops*, and described a new genus and species *Gayndahpsychops carsburgi* Lambkin from the early Middle Triassic of Australia. He treated *Archepsychops* as a genus of Osmylopsychopidae only preliminarily because it is known only from its fragmentary holotype, and considered

Protopsychoptis as Neuroptera *incertae sedis* as its holotype is too fragmentary to warrant further consideration. In the Lambkin (2014) paper, the genera *Osmylopsychops*, *Petropsychops* and *Gayndahpsychops* Lambkin were well documented with important information about their venation. Furthermore, he found that the new material of *Osmylopsychops* demonstrated a high degree of intra-specific variation in wing size and venation. This significant revision and detailed drawings allow for a clearer definition of Osmylopsychopidae, although the absence of photographs in the paper substantially decreases its value.

Hitherto, no fossil species of Osmylopsychopidae and Brongniartiellidae have been described from China. However, we may conclude based on descriptions of new taxa in this paper that *Undulopsychopsis alexi* Peng *et al.* from the Yixian Formation of China should be considered as belonging to Osmylopsychopidae, not Psychopsidae to which it was originally assigned (Peng *et al.* 2011). Also, judging from the illustrations, *Sinopsychops chengdeensis* Hong and *Beipiaopsychops triangulatus* Hong from the Middle Jurassic of China (Hong 1982, 1983) most probably belong to Osmylopsychopidae. These taxa are represented by poorly described fragmentary wings whose type specimens are now lost. Therefore, their taxonomic affinities within the family are currently impossible to establish.

In this paper, we describe from the Middle Jurassic of Daohugou five new genera and 10 new species of Osmylopsychopidae, and one new genus and species of Psychopsidae, the venation of which is similar in some characters to that of the former family. Additionally, we re-examine the holotype of the type species of Brongniartiellidae (based on many high-resolution photographs), and find that this family should be synonymized with Osmylopsychopidae.

Material and methods

All the specimens described here were collected from the Jiulongshan Formation in Daohugou village, Shantou Township, Ningcheng County, Inner Mongolia, China. Daohugou fossil-bearing beds contain abundant and diverse plants, insects and other animals (Ren *et al.* 2010), whose age is late Middle Jurassic (Bathonian/Callovian boundary, 165 Ma) according to $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP $^{206}\text{Pb}/^{238}\text{U}$ dating (Chen *et al.* 2004; see further details in Yang *et al.* 2012).

The type specimens are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (Dong Ren, Curator). The specimen of *Brongniartiella gigas* (type of Brongniartiellidae) is deposited in the Teylers Museum, Haarlem, the Netherlands. It was photographed in detail by Dr S. Bruce Archibald during his visit to this museum.

These specimens were examined using a Leica MZ 12.5 dissecting microscope and illustrated with the aid of a camera lucida attachment. The line drawings were prepared with CorelDraw X4 and final photographs were adjusted using Adobe Photoshop CS5.

We follow the traditional (*sensu* Wootton 2003) venational terminology of Comstock (1918) in the recent interpretation of Oswald (1993a, 1993b) and Archibald & Makarkin (2006).

Institutional abbreviations

CNU: College of Life Sciences, Capital Normal University, Beijing, China; **TM:** Teylers Museum, Haarlem, the Netherlands; **TAMUIC:** Texas A&M University Insect Collection, College Station, Texas, USA.

Anatomical abbreviations

1A–3A: first to third anal veins; **Cu:** cubitus; **CuA:** cubitus anterior; **CuP:** cubitus posterior; **hp:** humeral plate; **hv:** humeral veinlet (i.e. basalmost subcostal veinlet); **M:** media; **MA:** media anterior; **MP:** media posterior; **R1:** first branch of R; **Rs:** radial sector; **Rs1:** proximalmost branch of Rs. (We interpret ‘MA’ of Lambkin (2014) to be Rs1, and ‘MP’ as M, except from *Petropsychops superbus* Riek which is correctly labelled; see Yang *et al.* 2014 for further details regarding the MA/Rs1 problem).

Systematic palaeontology

Order **Neuroptera** Linnaeus, 1758

Family **Osmylopsychopidae** Martynova, 1949
(= *Brongniartiellidae* Martynova, 1949 syn. nov.)

Key to the genera of Osmylopsychopidae based on forewings

(*Archepsychops* is not included because of its fragmentary nature).

1. Outer gradate series of crossveins absent 1
 - Outer gradate series of crossveins present 5
2. M multi-branched, all its branches anteriorly directed *Petropsychops*
 - M proximally divided into two main branches MA and MP 3
3. Branches of CuA very long; longer than CuA before branching *Gayndahpsychops* Lambkin
 - Branches of CuA short; much shorter than CuA before branching 4

4. Sc and R1 distally fused *Osmylopsychops*
 - Sc and R1 distally separate *Undulopsychopsis* Peng *et al.*
5. Branches of Rs deeply dichotomously branched 6
 - Branches of Rs proximally parallel and distally branched 8
6. M forked slightly proximal to primary fork of CuP *Brongniartiella* Meunier
 - M forked clearly distal to primary fork of CuP 7
7. Sc and R1 distally fused *Daopsychops* gen. nov.
 - Sc and R1 distally separate connected by short crossvein *Eupyppsychops* gen. nov.
8. CuP forked in its distal half (shallowly) *Stenopteropsychops* gen. nov.
 - CuP forked in its proximal half (deeply) 9
9. CuP pectinate; Rs1 deeply forked with three-four branches *Nematopsychops* gen. nov.
 - CuP not pectinate, at most twice deeply branched; Rs1 simple for most length or at most once deeply forked 10
10. M forked slightly distad primary fork of CuA; Rs1 simple *Ochropsychops* gen. nov.
 - M forked proximad primary fork of CuA; Rs1 deeply forked *Pseudopsychopsis* Makarkin

Genus ***Daopsychops*** gen. nov.

Type species. *Daopsychops dissectus* sp. nov.

Included species. *D. dissectus* sp. nov., *D. clausus* sp. nov., *D. inanis* sp. nov., *D. bifasciatus* sp. nov. and *D. cubitalis* sp. nov.

Etymology. From Daohugou, and *-psychops*, a traditional ending of names of psychopoid genera. Gender masculine.

Diagnosis. Forewing relatively elongate with rather acute apex possessing at least several costal crossveins; many subcostal crossveins; distal nygma; complete outer (distal-most) series of crossveins; Sc and R1 fused distally; posterior and outer margins undulate; branches of Rs mostly deeply forked; Rs1 deeply forked (at least once); M forked much proximad origin of basalmost branch of CuA; MP with few dichotomous branches; CuP relatively long, entering posterior wing margin approximately at mid-point.

Comments. The genus is most closely related to *Eupyppsychops* from which it may be easily distinguished by Sc and R1 being distally fused (separate in *Eupyppsychops*), and M forked much proximad the basalmost branch of CuA (only slightly proximad the basalmost branch of CuA in *Eupyppsychops*).

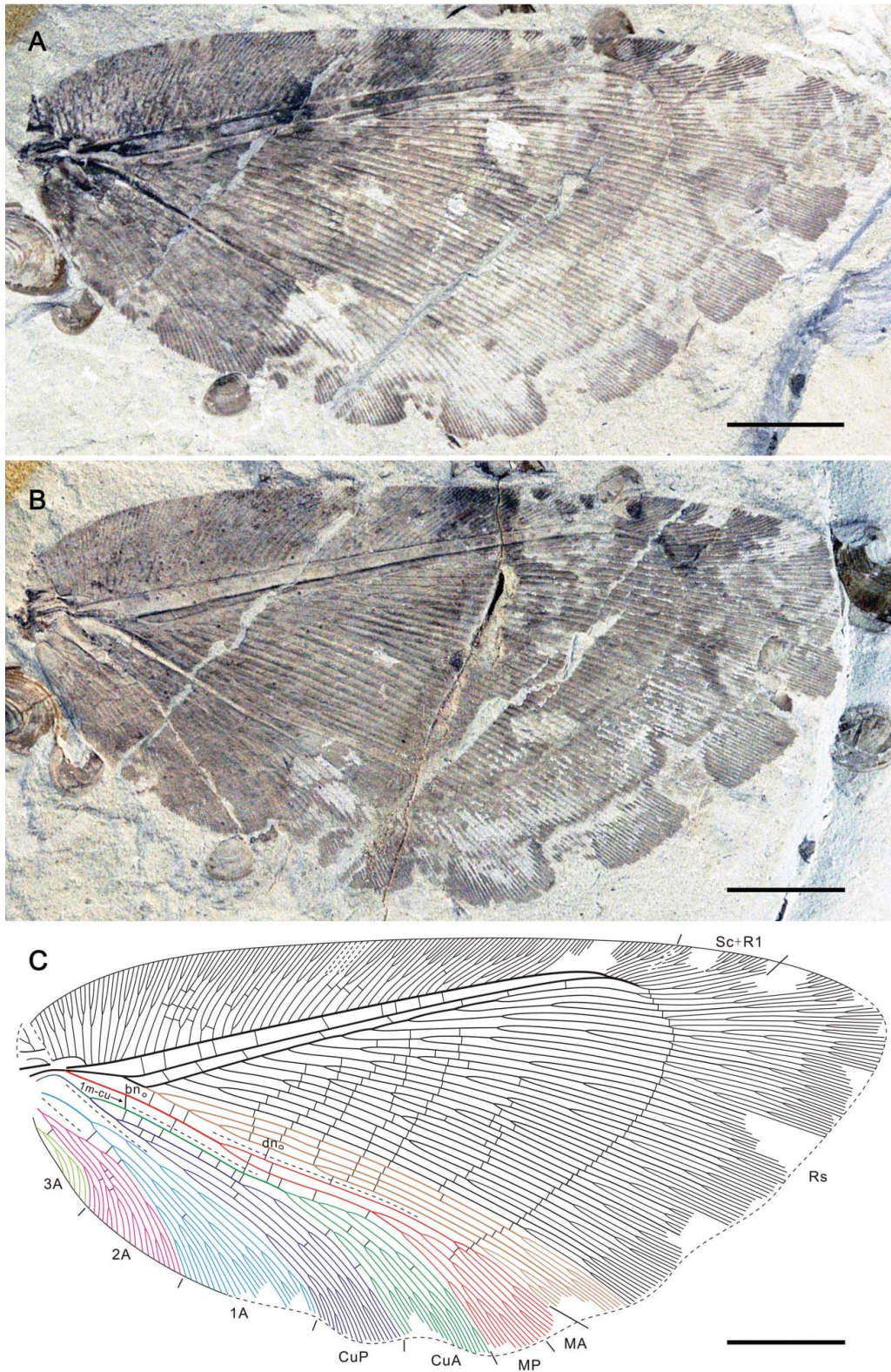


Figure 1. *Daopsychops dissectus* gen. et sp. nov., holotype, CNU-NEU-NN2011059P/C. **A**, photograph of the part; **B**, counterpart (converted to standard right view); **C**, line drawing of forewing venation. Scale bars: 5 mm.

Daopsychops dissectus sp. nov.

(Fig. 1)

Etymology. From the Latin *dissectus*, dissected, referring to the posterior and outer wing margins seeming to be divided into several parts.

Material. Holotype: CNU-NEU-NN2011059P/C, a nearly complete forewing.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from other species by the absence of costal gradate series of crossveins (present in *D. bifasciatus*, *D. inanis*) and crossveins in radial space arranged in six gradate series proximad outer (distalmost) series (irregularly spaced in *D. clausus*, *D. inanis*, *D. bifasciatus*, *D. cubitalis*).

Description. Forewing sub-triangular, 37 mm long and 18 mm wide. Costal space very broad basally, narrowed towards apex; its width of narrowest part about twice width of adjacent subcostal and R1 spaces. More than 55 subcostal veinlets, mostly once or twice forked. Humeral veinlets strongly recurrent with six forked preserved branches. Subcostal space moderately broad at origin of Rs, slightly narrowed towards apex. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, fused near wing apex; Sc + R1 slightly curved posteriad for some distance, with eight forked veinlets. Rs with 15 primary branches; most of these deeply dichotomously branched. Rs1 deeply forked four times. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between posterior trace of Rs1 and its third proximal branches. M appears to originate from R at wing base; forked relatively far from wing base (at level of third fork of Rs1). MA nearly straight before end-twigging, MP slightly sinuate, both dichotomously branched distally. Cu well developed, forked near wing base. CuA pectinately branched distally, with four oblique dichotomously forked branches. CuP in general dichotomously branched, with six main branches; basalmost fork of CuP located slightly proximad basalmost fork of Rs1. Anal space well developed; 1A long, strongly dichotomously branched; 2A in general pectinately branched, with four branches; 3A few branched. Crossveins numerous: costal crossveins few and irregularly spaced, not forming gradate series; subcostal space with 10 crossveins; R1 space with eight crossveins; many radial crossveins arranged in six incomplete gradate series and one complete outer series from R1 to MP; between Rs1 and MA five preserved crossveins; between MA and MP two crossveins; between MP and CuA seven crossveins; crossveins between branches of Cu and in anal space scarce, irregularly spaced. Posterior and outer margins undulate. Macrotrichia on longitudinal veins poorly

preserved, long; macrotrichia on wing margins relatively short. Trichosors prominent along entire preserved margin. Wing membrane in general dark brownish, darkening from basal to distal portions; several pale patches along wing margins (especially along outer to posterior), and darkish stripe along outer margin proximad these patches; these alternating light and dark portions make the wing along outer margin seeming fractured.

Daopsychops clausus sp. nov.

(Fig. 2)

Etymology. From the Latin *clausus*, closed, referring to a loop-like duplication of one branch of Rs1 forming a closed cell.

Material. Holotype: CNU-NEU-NN2011061, a nearly complete forewing broken into two parts proximally, and with several dislocations of veins distally.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from other species by the absence of costal gradate series of crossveins (present in *D. inanis*, *D. bifasciatus*, *D. cubitalis*), and crossveins in radial space proximad outer (distalmost) gradate series irregularly spaced (arranged in several gradate series in *D. dissectus*).

Description. Forewing sub-triangular, 34 mm long as preserved (estimated complete length about 35–36 mm), 14.5 mm wide. Costal space enlarged basally, narrowed towards apex, its width of narrowest part about equal to width of adjacent subcostal and R1 spaces. More than 65 subcostal veinlets preserved, almost all twice or once forked, few forked three times or simple. Humeral veinlets strongly recurrent with seven forked preserved branches. Subcostal space at origin of Rs moderately broad, slightly gradually narrowed towards apex, in distal two thirds nearly equal to R1 space. Sc, R1 and Rs strong (stout). Sc and R1 approaching towards apex, fused near wing apex. Distal Sc, R1 and Sc + R1 slightly curved posteriad for some distance, with five forked veinlets. Rs with about 13 primary branches, mainly deeply dichotomously branched. Rs1 deeply forked four times. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between two posteriormost branches of Rs1. M appears to originate from R at wing base; forked relatively far from wing base (much distad second fork of Rs1). MA, MP nearly straight before end-twigging, both dichotomously branched distally. Cu well developed, forked near wing base. CuA pectinately branched distally, with four oblique dichotomously forked branches. CuP pectinately branched, with four strongly oblique branches, so that CuP space relatively narrow; basalmost fork of CuP located slightly proximad

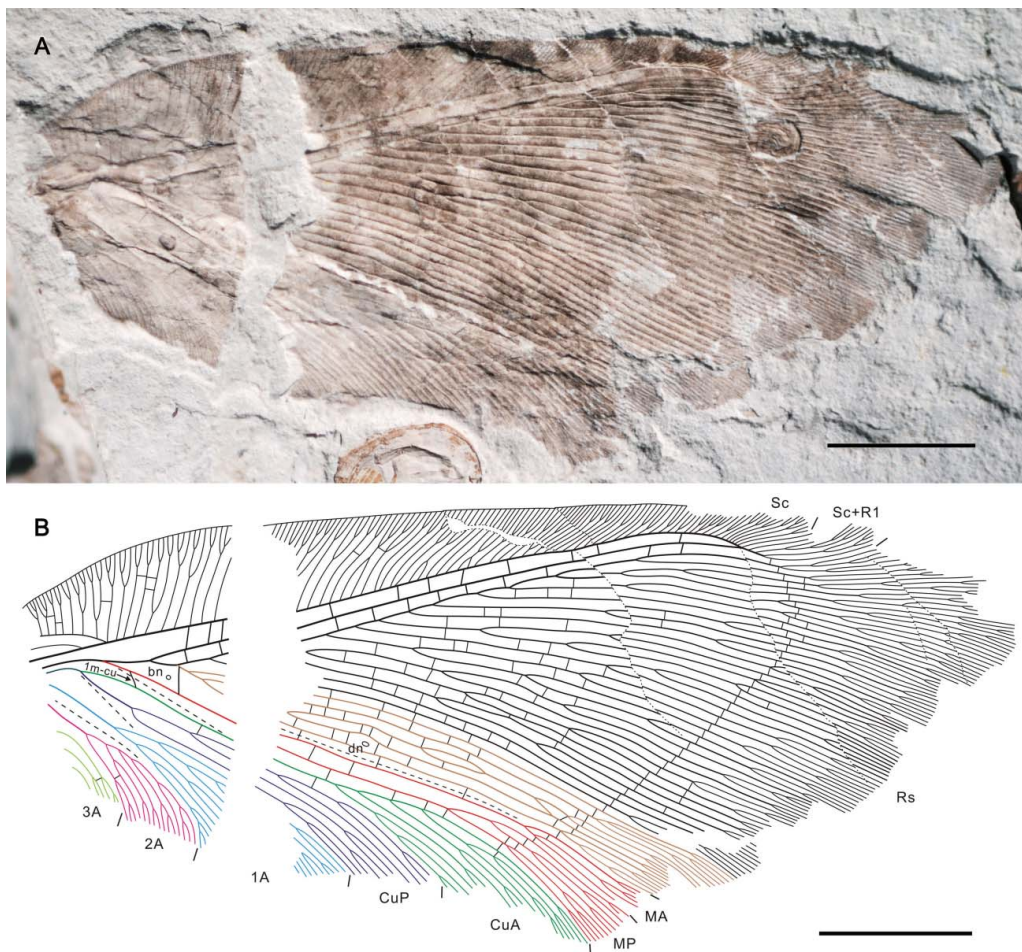


Figure 2. *Daopsychops clausus* gen. et sp. nov., holotype, CNU-NEU-NN2011061. **A**, photograph of specimen as preserved (converted to standard right view); **B**, line drawing of forewing venation. Scale bars: 5 mm.

basalmost fork of Rs1. Anal space well developed; 1A long, strongly dichotomously branched; 2A in general pectinately branched, with five branches; 3A incompletely preserved, probably few branched. Crossveins numerous: costal crossveins few and irregularly spaced, not forming gradate series; subcostal space with 11 crossveins; R1 space with 11 crossveins preserved; many radial crossveins irregularly spaced, others arranged in one complete outer series from R1 to CuA; few occasional crossveins preserved distad outer gradate series; between Rs1 and MA four preserved crossveins; between MA and MP two crossveins; between MP and CuA six preserved crossveins including oblique basal 1m-cu ('M5'); crossveins between branches of Cu and in anal space scarce, irregularly spaced. Posterior and outer margins not preserved. Macrotrichia on longitudinal veins almost not preserved; macrotrichia on wing margins relatively short. Trichosors prominent along costal margin. Wing membrane in general dark brownish medially, paler in basal and apical portions; several pale patches along wing margin (especially along outer margin).

Comments. There are several aberrations in the venation of the holotype: three pairs of subcostal veinlets in the costal space are fused with each other for some distance; one branch of Rs1 possesses a loop-like duplication forming a closed cell (alternatively, two branches of Rs1 are fused with each other for some distance forming a cell, and the posterior branch of these is fused again with other branch of Rs1 distally). Such aberrations sometimes occur in extant Hemerobiidae (e.g. Makarkin 1996, fig. 108).

Daopsychops inanis sp. nov.
(Figs 3–6)

Etymology. From the Latin *inanis*, empty, referring to the absence of a distinct wing colour pattern.

Material. Holotype: CNU-NEU-NN2011435P/C, a nearly complete forewing with wing apex missing. Paratype: CNU-NEU-NN2011073, a nearly complete forewing with wing apex and distal part missing. Paratype: CNU-NEU-

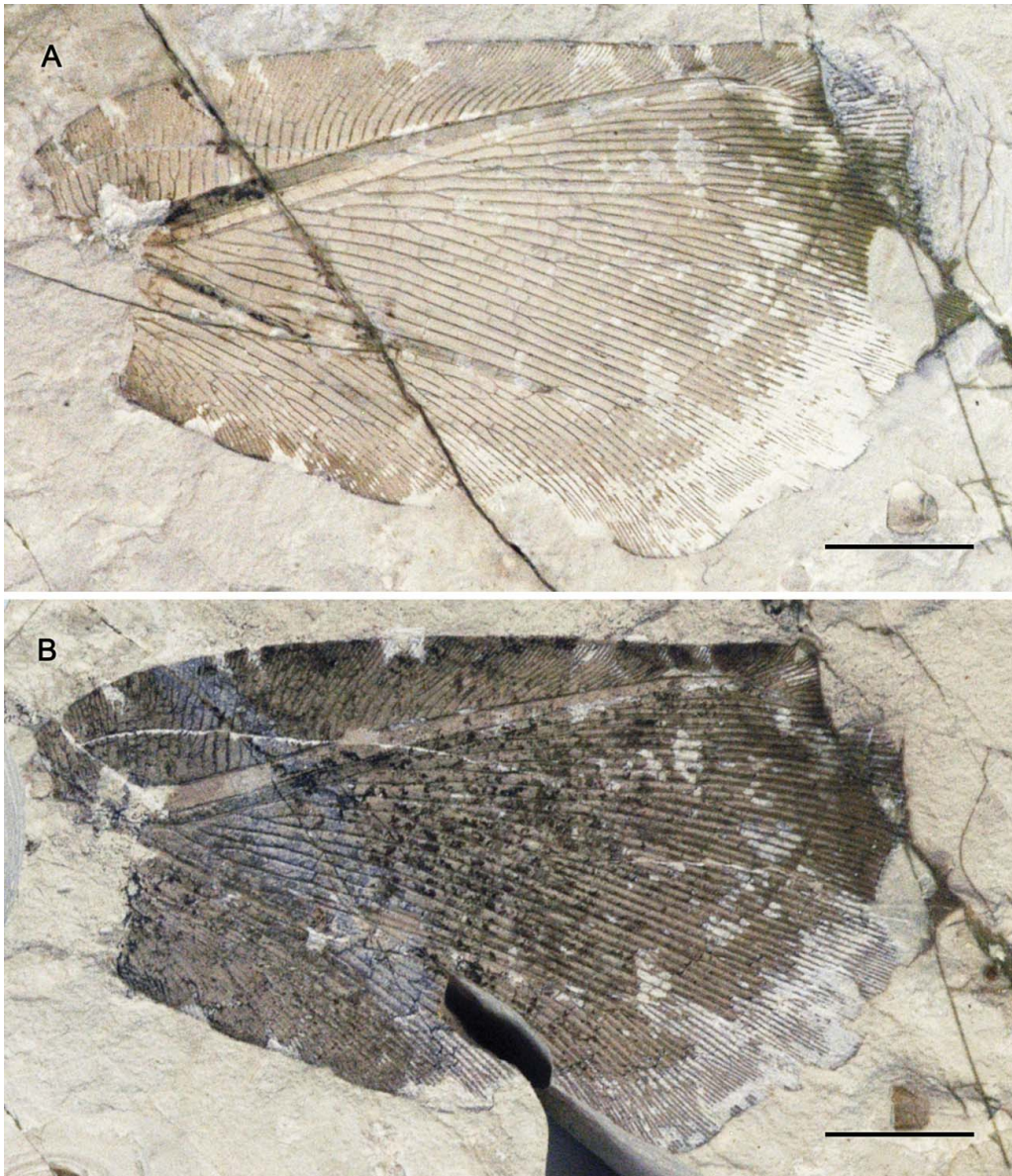


Figure 3. *Daopsychops inanis* gen. et sp. nov., photograph of holotype, CNU-NEU-NN2011435P/C. **A**, part (converted to standard right view); **B**, counterpart. Scale bars: 5 mm.

NN2011064, a nearly complete forewing with strong dislocations of veins proximally.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from other species by the presence of a costal gradate series of crossveins (absent in *D. dissectus*, *D. clausus*), and dark forewing lacking distinct colour pattern (colour pattern present in *D. dissectus*, *D. clausus*, *D. bifasciatus*, *D. cubitalis*).

Description of the holotype. Forewing (Figs 3, 4) quite elongate, sub-triangular, 32.5 mm long as preserved

(estimate complete length about 36–38 mm), 17.2 mm wide. Costal space broad basally, rather strongly narrowed towards apex, its width of the narrowest part nearly equal to width of adjacent subcostal and R1 spaces. More than 65 subcostal veinlets preserved, mostly once or twice forked, few simple. Humeral veinlets strongly recurrent, with three preserved forked branches. Subcostal space moderately broad proximally, slightly narrowed towards apex. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, fused near wing apex; Sc + R1 curved posteriad for some distance, with six forked veinlets. Rs with 11 primary branches, mostly deeply dichotomously branched. Rs1 once deeply forked. Two nygmata

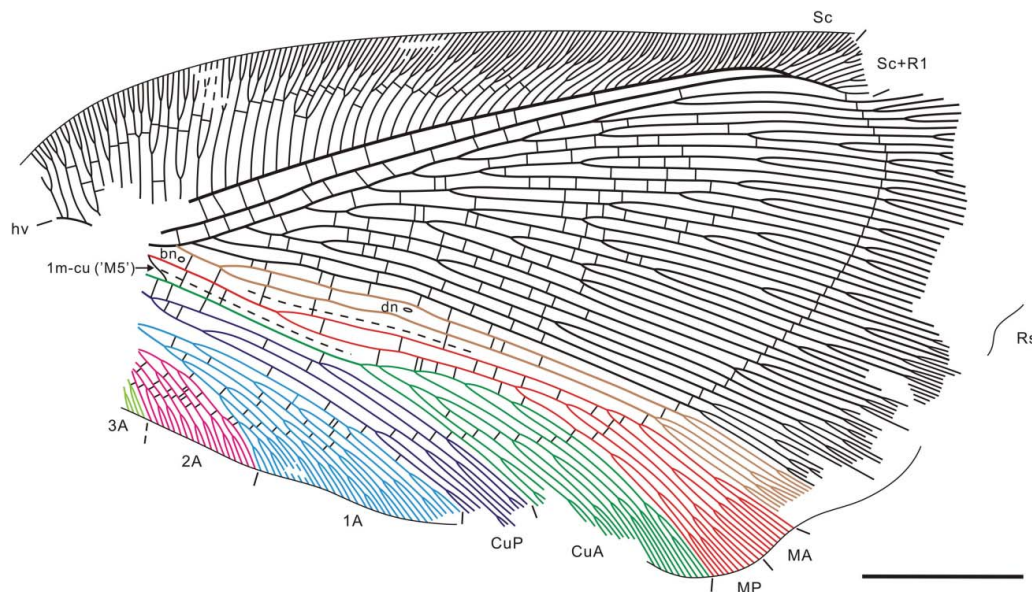


Figure 4. *Daopsychops inanis* gen. et sp. nov., holotype, CNU-NEU-NN2011435P/C, line drawing of forewing venation. Scale bar: 5 mm.

present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between two branches of Rs1. Wing base not preserved. M forked relatively far from wing base (much distad fork of Rs1). MA nearly straight before end-twigging, MP slightly sinuate, both dichotomously branched distally. Cu well developed. Anterior trace of CuA straight before its proximalmost branch, arched after; pectinately branched distally, with five oblique dichotomously forked branches (one deeply forked). CuP dichotomously branched, with four main branches; basalmost fork of CuP located slightly proximad basalmost fork of Rs1. 1A long, strongly dichotomously branched; 2A incomplete, in general pectinately branched, with four preserved branches; presumable 3A fragmentarily preserved. Crossveins numerous: most costal crossveins form gradate series running to centre of wing, other few and irregularly spaced; subcostal space with 13 crossveins; R1 space with 15 crossveins; radial crossveins arranged in one complete outer series from R1 to 3A, many others (proximad outer series) irregularly spaced; between Rs1 and MA five preserved crossveins; between MA and MP seven crossveins; between MP and CuA 12 crossveins, including long oblique 1m-cu; between branches of Cu and in anal space numerous, irregularly spaced crossveins (including ones of outer gradate series). Posterior and outer margins undulate. Macrotrichia on longitudinal veins almost not preserved; dense pits of lost sensilla in costal space arranged in two rows (Fig. 21C); macrotrichia on wing margins relatively short. Trichosors prominent along entire preserved margin. Membrane dark brown; areas near outer margin appear markedly paler.

Comments. Two additional specimens are assigned to this species, and considered here as paratypes.

The forewing CNU-NEU-NN2011073 (Fig. 5) is 33 mm long as preserved (estimated complete length about 35–37 mm), and 17.5 mm wide. It is assigned to *D. inanis* due to the similarity of the forewing venation and coloration to those of the holotype. We consider the more profusely branched Rs1 (three times deeply forked instead of one in the holotype) and the distal CuP as intraspecific variability.

The forewing CNU-NEU-NN2011064 (Fig. 6) is 28 mm long and 13.5 mm wide as preserved (estimated complete length about 30 mm, width 14 mm). This specimen is in general similar in the wing coloration and venation to those of the holotype. The differences between these specimens (e.g. the more profusely branched Rs1; the outer gradate series of crossveins poorly developed in the medial to anal spaces) are considered as intraspecific variability (the former character) or an artefact of preservation (the second character).

***Daopsychops bifasciatus* sp. nov.**
(Figs 7, 8)

Etymology. From the Latin *bis*, twice and *fasciatus*, banded, striped, referring to two white transverse bands (fasciae) in the forewing.

Material. Holotype: CNU-NEU-NN2011058P/C, an almost complete, beautifully preserved forewing. Paratype: CNU-NEU-NN2011217, an incomplete forewing deformed distally.

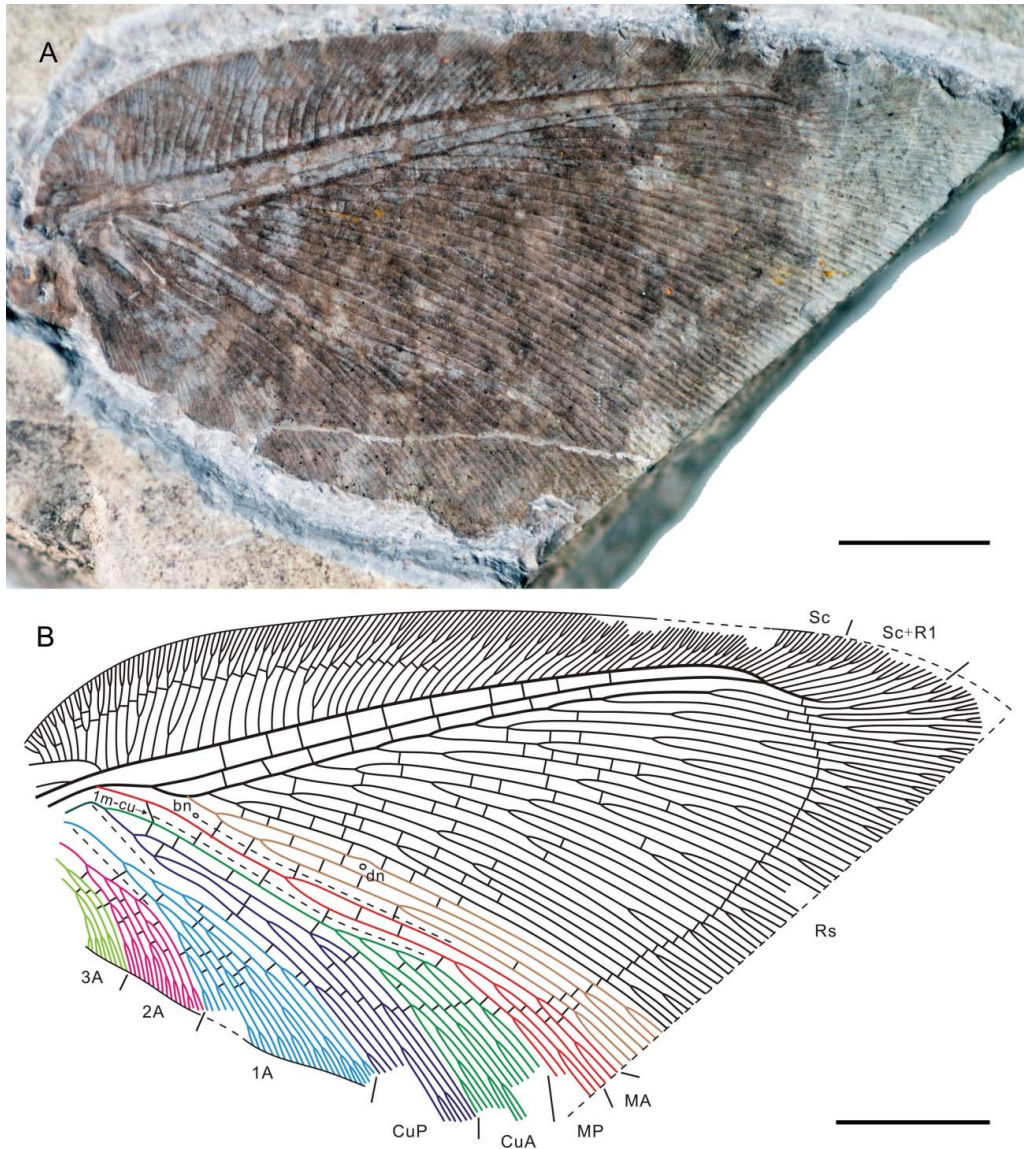


Figure 5. *Daopsychops inanis* gen. et sp. nov., paratype, CNU-NEU-NN2011073. **A**, photograph of specimen as preserved (converted to standard right view); **B**, line drawing of forewing venation. Scale bars: 5 mm.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from other species by the presence of two distinct pale transverse fasciae (bands) in forewing.

Description of the holotype. Forewing elongate, ovate; 29.5 mm long as preserved (estimated complete length about 31–32 mm), about 14.6 mm wide. Costal space very broad basally, narrowed towards apex; its width of narrowest part about twice width of adjacent subcostal and R1 spaces. Subcostal veinlets, almost all twice and single forked. Humeral veinlets strongly recurrent. Subcostal space broad at origin of Rs, gradually narrowed

towards apex, strongly narrowed basally. R1 space narrow. Sc, R1, Rs proximally stout. Sc + R1 or R1 rather strongly curved posteriad for some distance, with several forked veinlets. Rs with 13 primary branches; most of these deeply dichotomously branched. Rs1 profusely branched, with five deep forks. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma in strong dilation between two posterior branches of Rs1. M appears to originate from R at wing base; forked relatively far from wing base (at level of fourth fork of posterior trace of Rs1, much proximad branching of CuA). MA quite strongly dichotomously branched distally; branching pattern of MP not clear. Cu forked near wing base. CuA branched much distad fork of M; branching not clear. CuP long,

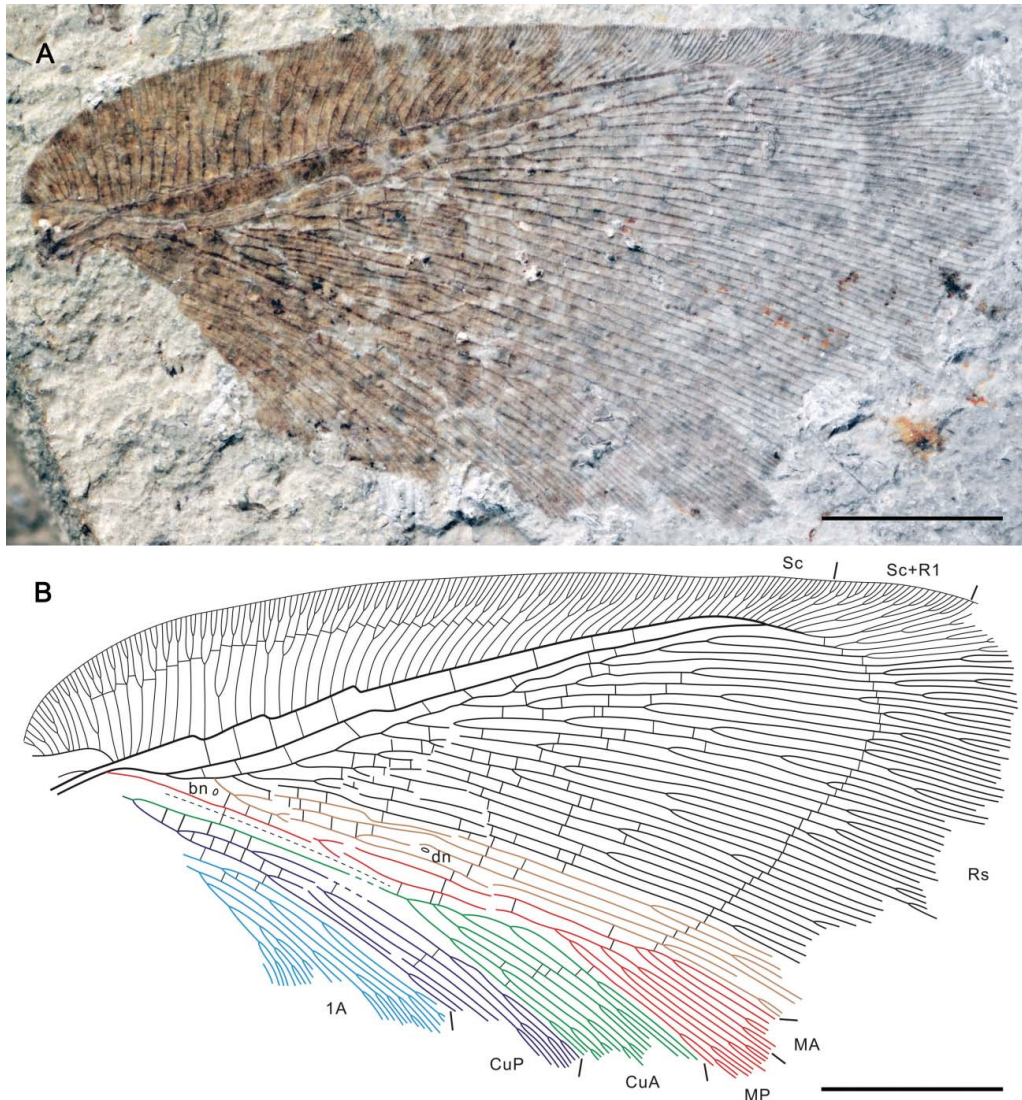


Figure 6. *Daopsychops inanis* gen. et sp. nov., paratype, CNU-NEU-NN2011064. **A**, photograph of specimen as preserved; **B**, line drawing of forewing venation. Scale bars: 5 mm.

incompletely preserved; probably entering posterior margin approximately at wing mid-point; branching pattern not clear, probably pectinate, with four very oblique branches; basalmost fork of CuP located proximad origin of Rs1. 1A long, strongly dichotomously branched; 2A incomplete, pectinately branched; 3A relatively well developed, with three long preserved branches. Crossveins numerous: many costal crossveins forming irregular gradate series; subcostal space with four crossveins in proximal portion; R1 space with eight preserved widely spaced crossveins; radial crossveins arranged in two probably complete gradate series from R1 to MP; outer series distad this comprised of weak crossveins; radial crossveins proximad outer series not numerous, spaced irregularly; between Rs1 and MA four preserved proximal crossveins; between MP and CuA three proximal crossveins, of these long, very oblique 1m-cu; crossveins

between branches of CuP, 1A and 2A irregularly spaced. Posterior wing margin slightly convex, probably not undulate; outer margin not preserved. Macrotrichia on longitudinal veins poorly preserved; macrotrichia on wing margins relatively short. Trichosors prominent along preserved margins. Wing membrane solid brown, with two distinct very pale transverse fasciae (proximal fascia complete; distal fascia from costal margin to about mid-point), two basal pale larger patches (one in area of humeral veinlets, another in area of basal CuP and 1A), and several small pale spots throughout wing.

Comments. The forewing of CNU-NEU-NN2011217 (Fig. 8) is 22.7 mm long and 15 mm wide as preserved (estimated complete length > 30 mm, width 15.5–16 mm). It is preliminary assigned to this species due to the strong similarity of its forewing colour pattern. Its

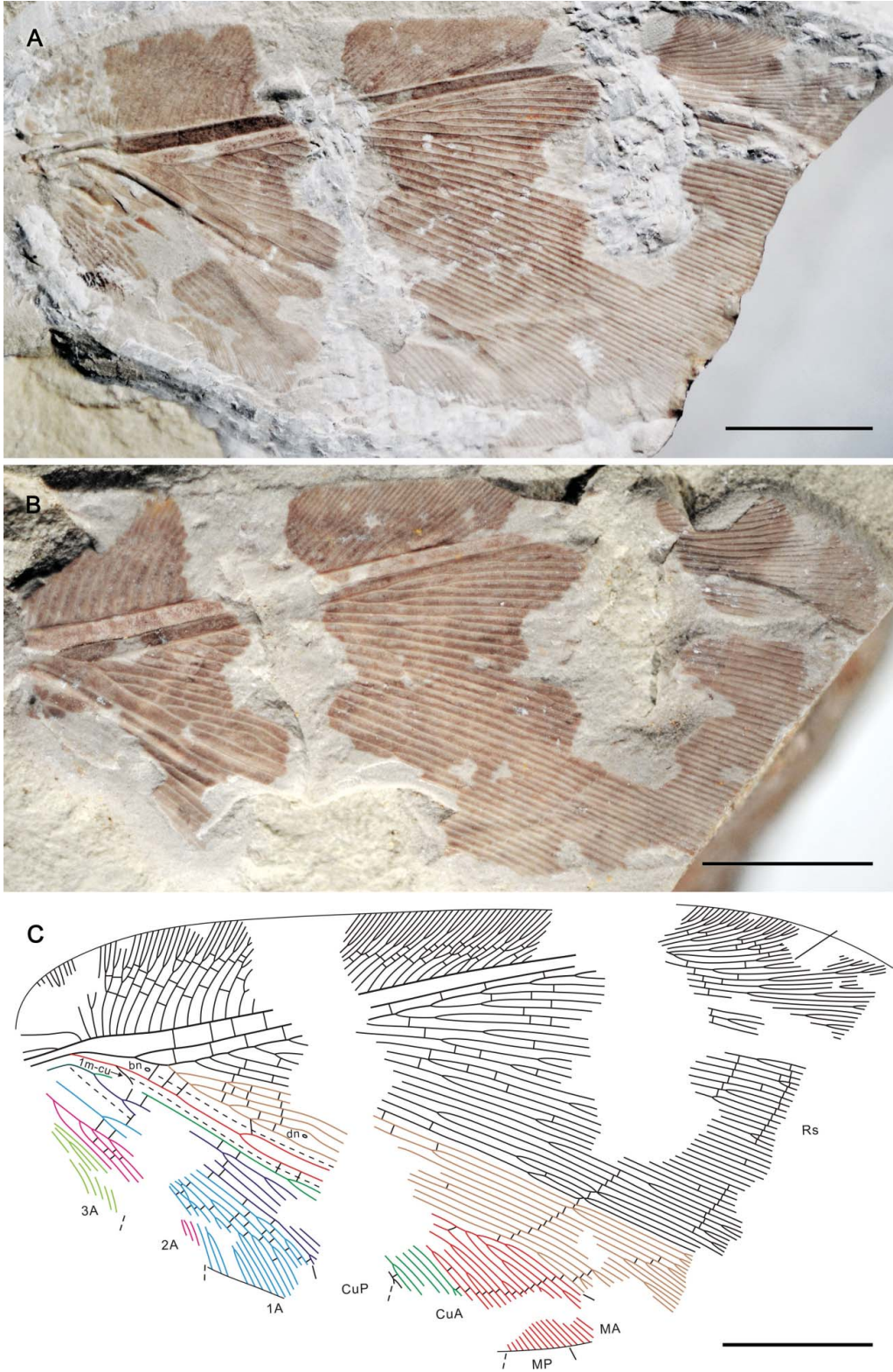


Figure 7. *Daopsychops bifasciatus* gen. et sp. nov., holotype, CNU-NEU-NN2011058P/C. **A**, photograph of the part (converted to standard right view); **B**, counterpart; **C**, line drawing of forewing venation. Scale bars: 5 mm.

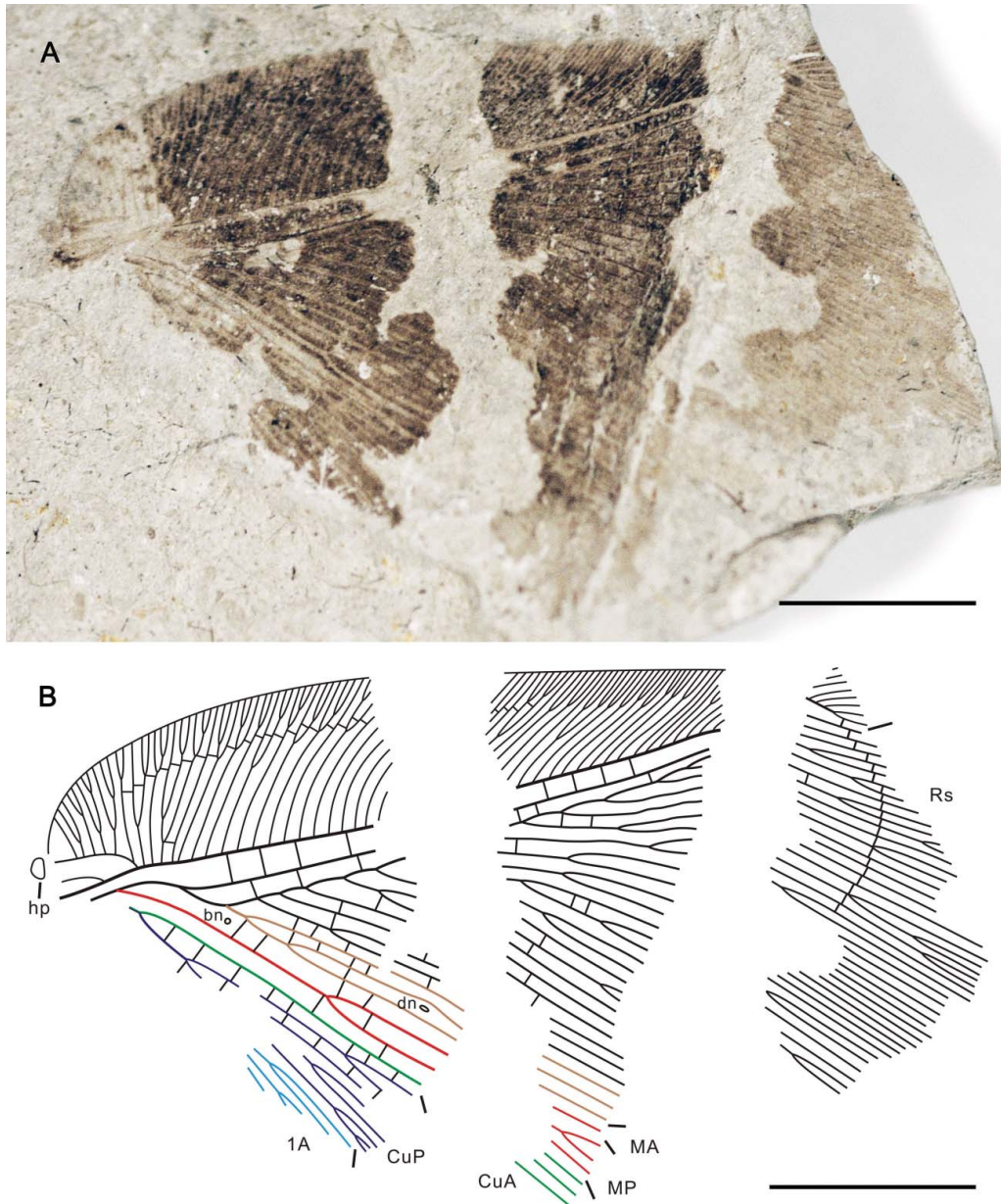


Figure 8. *Daopsychops bifasciatus* gen. et sp. nov., paratype, CNU-NEU-NN2011217. **A**, photograph of specimen as preserved; **B**, line drawing of forewing venation. Scale bars: 5 mm.

venation is also similar with that of the holotype, but differs in some details (e.g. Rs1 twice deeply forked; all costal crossveins are arranged in one gradate series).

***Daopsychops cubitalis* sp. nov.**
(Fig. 9)

Etymology. From the Latin *cubitalis*, cubital vein, referring to the strongly pectinately branched CuA in the forewing.

Material. Holotype: CNU-NEU-NN2011432P/C, four wings partly overlapping: a nearly complete forewing; a

central part of another forewing; poorly preserved incomplete hind wings.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from other species by possessing numerous crossveins distad outer gradate series (shared with *D. bifasciatus*), stronger pectinately branched CuA and fewer branched MA.

Description. Forewing broadly ovate with rounded apex; 32 mm long, 16.5 mm wide. Costal space very broad

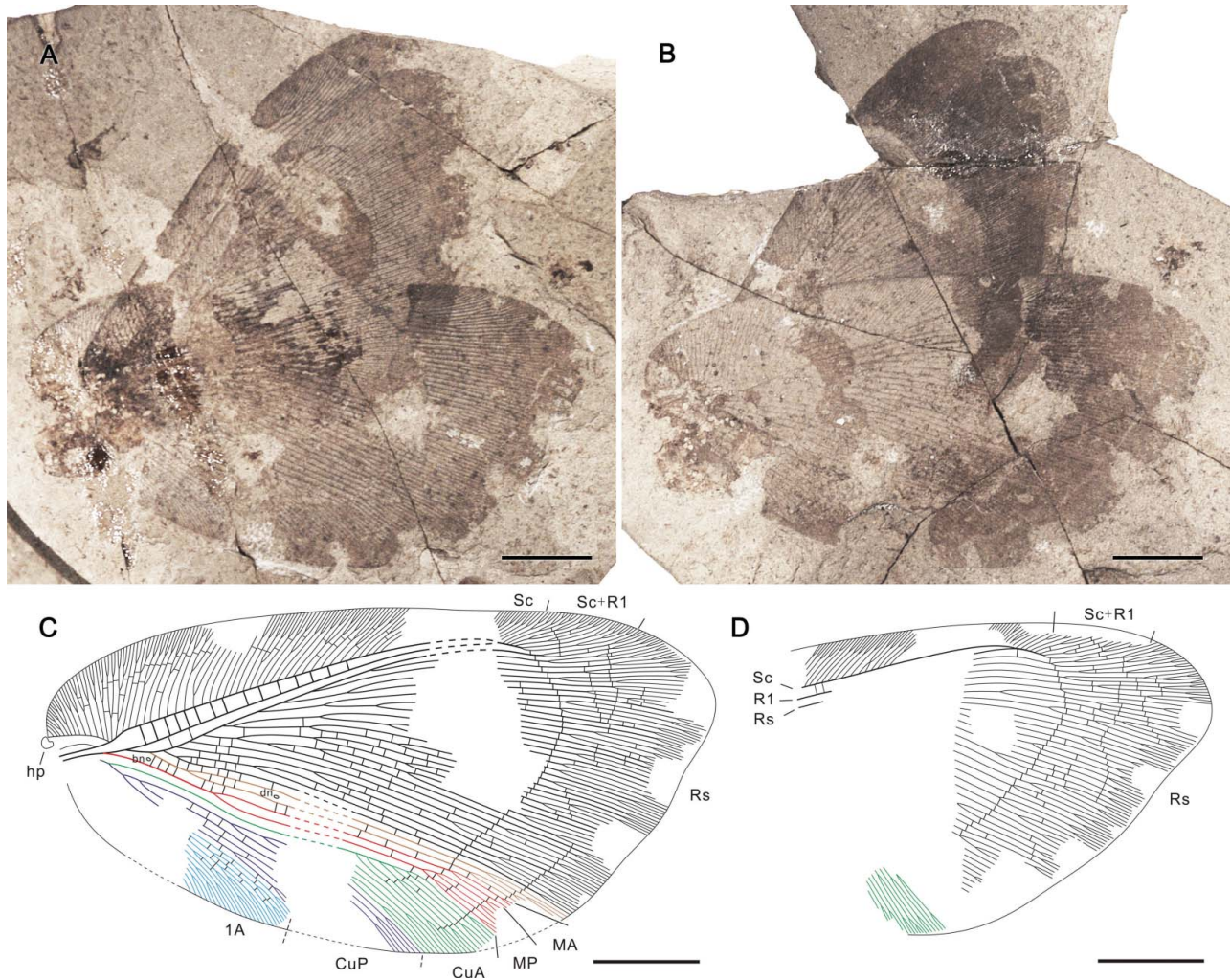


Figure 9. *Daopsychops cubitalis* gen. et sp. nov., holotype, CNU-NEU-NN2011432P/C. **A**, part (converted to standard right view); **B**, counterpart; **C**, venation of forewing; **D**, line drawing of hind wing venation. Scale bars: 5 mm.

basally, narrowed towards apex; its width of narrowest part about twice width of adjacent subcostal and R1 spaces. More than 45 subcostal veinlets, almost all twice and single forked. Humeral veinlets strongly recurrent with 13 branches, mainly forked. Humeral plate distinct, rounded. Subcostal space broad at origin of Rs, basally, gradually narrowed towards apex, strongly narrowed basally. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, fused near wing apex; Sc + R1 slightly curved posteriad for some distance, with at least six forked veinlets. Rs with 11 primary branches; most of these deeply dichotomously branched. Rs1 once deeply forked. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between two branches of Rs1. M appears to originate from R at wing base; forked relatively far from wing base (markedly distad fork of Rs1, much proximad branching of CuA). MA, MP nearly straight before end-twigging; both dichotomously branched distally. Cu

forked near wing base. CuA pectinately branched distally, with about seven oblique forked branches. CuP long, entering posterior wing margin after mid-point, pectinately branched, with four very oblique branches; basalmost fork of CuP located much proximad basalmost fork of Rs1. Anal space poorly preserved, probably only distal part of 1A visible. Crossveins numerous: most costal crossveins form one interrupted gradate series, others arranged irregularly; subcostal space with 15 preserved crossveins; R1 space with two preserved crossveins; radial crossveins arranged in one complete outer series from R1 to CuA, and several short series distad outer series; radial crossveins proximad outer series spaced irregularly; between Rs1 and MA 12 preserved crossveins; between MA and MP one distal preserved crossvein; between MP and CuA two crossveins; crossveins between branches of CuP and 1A irregularly spaced. Posterior wing margin slightly convex, not undulate; outer margin very slightly undulate. Macrotrichia on longitudinal veins dense,

moderately long to long; macrotrichia on wing margins relatively short. Trichosors prominent along preserved margin. Wing membrane in general dark brownish, probably with few pale patches.

Hind wing smaller than forewing, with narrower distal portion; 27.5 mm long, 15 mm wide. Costal space moderately broad; its width of narrowest part nearly twice width of adjacent subcostal and R1 spaces. Subcostal veinlets dense and forked; two subcostal veinlets touch each other forming X-like configuration. Sc and R1 fused near wing apex; Sc + R1 curved posteriad for some distance, with seven veinlets. In subcostal space two preserved crossveins; in R1 space one distal preserved crossveins; distal crossveins in radial space arranged in one outer series, and several short gradate series distad outer series. Outer margin slightly excised near apex.

Comments. This species is assigned to *Daopsychops* only preliminarily as its forewing apex is rounded, not elongate as in other species. The venation of *Daopsychops cubitalis* principally does not differ from that of other species. The forewing colour pattern and venation of this species are most similar to those of *D. bifasciatus*, but not so well preserved.

Genus *Eupypsychops* gen. nov.

Type species. *Eupypsychops confinis* sp. nov.

Included species. *E. confinis* sp. nov. and *E. ferox* sp. nov.

Etymology. From the Greek *eupys* [εὐρύς], ample, broad, and *-psychops*, a traditional ending of names of psychopoid genera, referring to broad wing with dense venation. Gender masculine.

Diagnosis. Forewing relatively elongate with rather acute apex possessing gradate series of costal crossveins; many subcostal crossveins; distal nygma; complete outer (distal-most) series of crossveins; undulate posterior and outer margins; Sc and R1 not fused distally; branches of Rs mostly deeply forked; Rs1 deeply forked at least three times; M forked only slightly proximad origin of basalmost branch of CuA; MP few dichotomously branched; CuP relatively long, entering posterior wing margin approximately at mid-point.

Comments. This genus is most similar to *Daopsychops*, but differs by Sc and R1 being separated distally, and M forked only slightly proximad the basalmost branch of CuA.

Eupypsychops confinis sp. nov. (Figs 10, 11)

Etymology. From the Latin *confinis*, adjacent, referring to the proximalmost branch of CuA originated near the fork of M.

Material. Holotype: CNU-NEU-NN2011063P/C, a nearly complete forewing (anal area missing).

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from *E. ferox* by specific colour pattern (large pale patches mainly in distal portion of wing).

Description. Forewing relatively elongate, broadly ovate, approximately 24.5 mm long, 12 mm wide. Costal space very broad basally, narrowed towards apex; its width of narrowest part over twice width of adjacent subcostal and R1 spaces. About 40 subcostal veinlets, mostly once or twice forked, few simple. Humeral veinlets strongly recurrent, with 11 branches (partly forked). Humeral plate distinct, rounded. Subcostal space moderately broad at origin of Rs, gradually narrowed towards apex, strongly narrowed basally. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, but not fused, connected by short distal crossvein; R1 apically slightly curved posteriad, with three forked veinlets. Rs with 14 primary branches; most of these deeply dichotomously branched. Rs1 deeply forked three times. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between branches of Rs1. M appears to originate from R at wing base; forked relatively far from wing base (slightly distad second fork of Rs1). MA nearly straight before end-twigging; MP slightly sinuate; both dichotomously branched distally. Cu forked near wing base. CuA pectinately branched distally, with five oblique dichotomously forked branches; proximalmost branch originated only slightly distad fork of M. CuP in general dichotomously branched, with five main preserved branches; basalmost fork of CuP located well proximad basalmost fork of Rs1. Anal space not preserved. Crossveins numerous: all costal crossveins form one gradate series running to centre of wing; subcostal space with eleven crossveins; R1 space with 11 crossveins; distal radial crossveins arranged in one complete outer series from R1 to CuP, other radial crossveins partly arranged in shorter gradate series, partly irregularly spaced; between Rs1 and MA two preserved crossveins preserved; between MA and MP three crossveins; between MP and CuA four crossveins. Posterior margin not preserved, outer margin slightly undulate. Preserved macrotrichia on longitudinal veins dense, very long; macrotrichia on wing margins relatively short. Trichosors prominent along all preserved margins. Wing membrane in general dark brownish, with numerous



Figure 10. *Eupyropsylops confinis* gen. et sp. nov., photograph of holotype, CNU-NEU-NN2011063P/C. **A**, part; **B**, counterpart (wetted with ethanol, converted to standard right view). Scale bars: 5 mm.

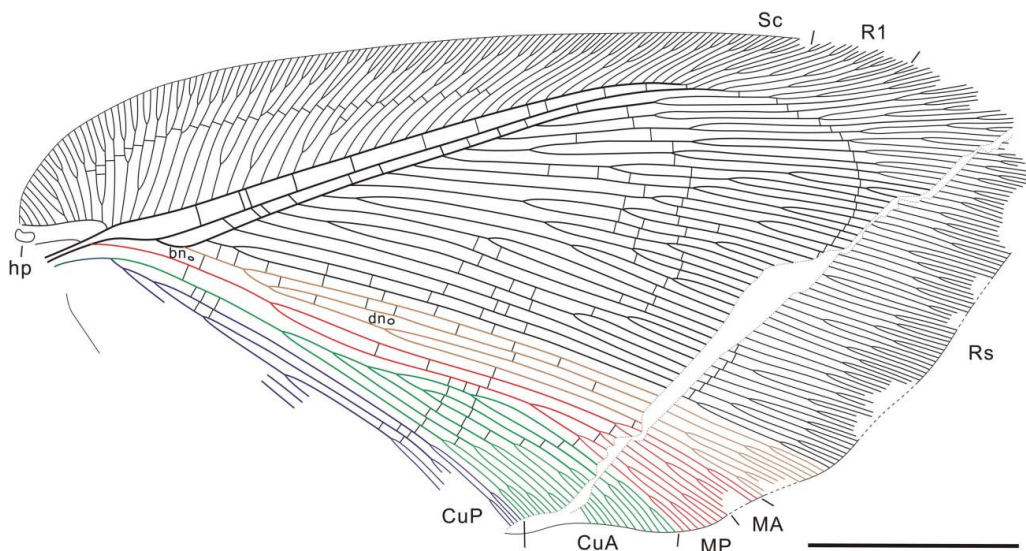


Figure 11. *Eupyropsylops confinis* gen. et sp. nov., holotype, CNU-NEU-NN2011063P/C, line drawing of forewing venation. Scale bar: 5 mm.

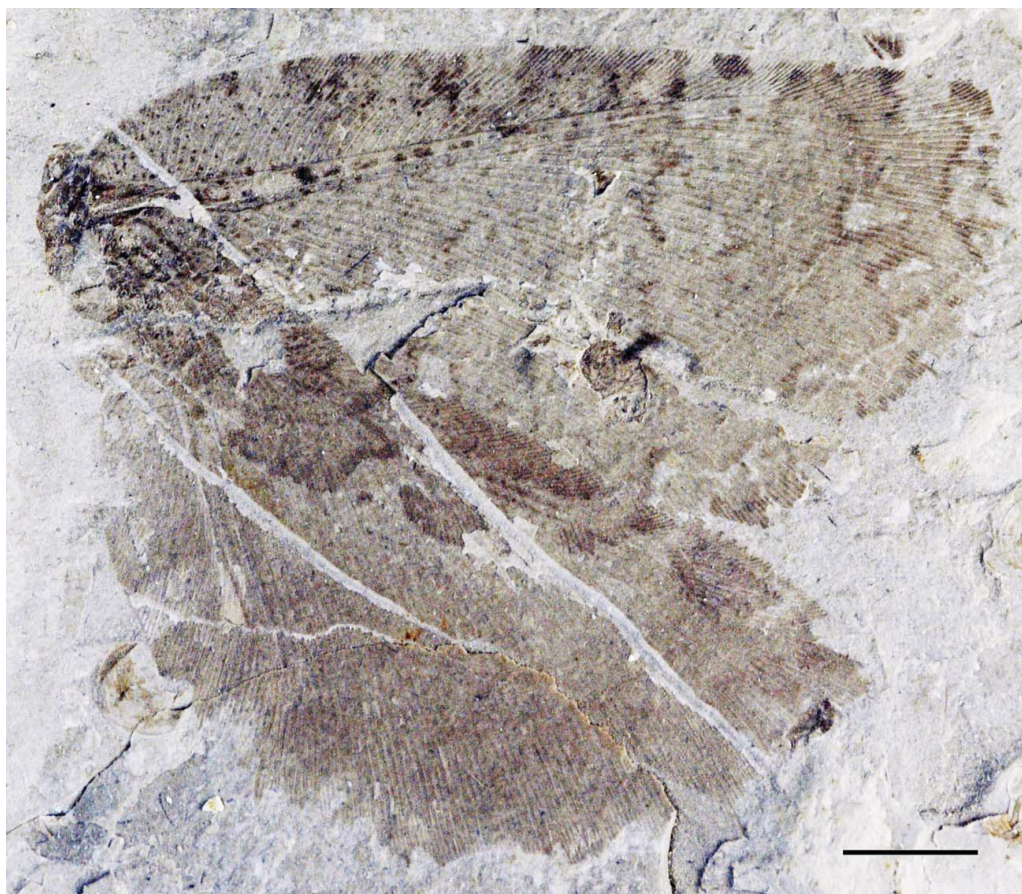


Figure 12. *Eupypsychops ferox* gen. et sp. nov., photograph of the holotype, CNU-NEU-NN99030. Scale bar: 5 mm.

small to large pale patches, mainly in distal portion of wing.

Eupypsychops ferox sp. nov.
(Figs 12, 13)

Etymology. From the Latin *ferox*, fierce, referring to the impressive visual effect due to the large size and dense venation.

Material. Holotype: CNU-NEU-NN99030, a nearly complete open forewing, and a fragmentary preserved other forewing and two hind wings overlapping.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. Can be distinguished from *E. confinis* by specific colour pattern (small pale patches narrowly margined with dark brown).

Description. Forewing broad, 35 mm long, 18.5 mm wide as preserved (estimated complete length about 37–38 mm, width about 19 mm). Costal space moderately broad at origin of Rs, narrowed towards apex, strongly

narrowed basally; width of narrowest part about twice width of adjacent subcostal and R1 spaces. About 50 subcostal veinlets, mostly twice and three times forked, few once forked or simple. Humeral veinlets strongly recurrent with eight (mostly forked) branches. Subcostal space moderately broad basally, narrowed towards apex. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex but not fused, connected by short crossvein near wing apex; both distally slightly curved posteriad for some distance. R1 with five forked veinlets distally. Rs with 15 primary branches, mostly deeply dichotomously branched. Rs1 deeply forked five times. Basal nygma in small cell near wing base between stem of Rs1 and M; distal nygma not preserved. M appears to originate from R at wing base; forked relatively far from wing base (slightly distad third fork of Rs1). Preserved parts of MA, MP nearly straight before end-twigging, both dichotomously branched distally. Cu well developed, forked near wing base. CuA pectinately branched distally, with four preserved oblique branches (one deeply dichotomously forked). CuP poorly preserved; basalmost fork of CuP located slightly proximad basalmost fork of Rs1. 1A, 2A incomplete; 1A long, probably pectinately branched. Crossveins numerous: most

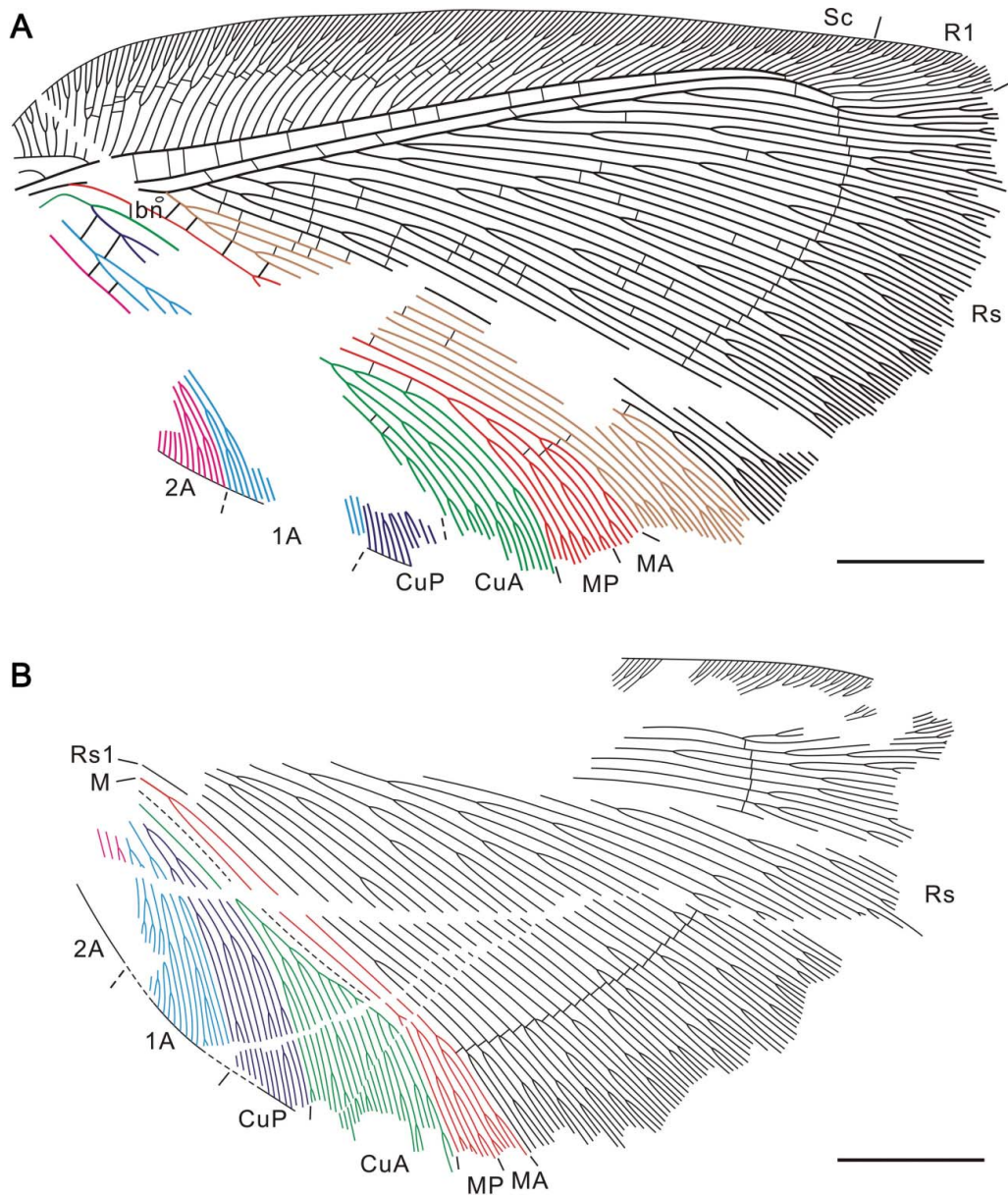


Figure 13. *Eupyropsychops ferox* gen. et sp. nov., line drawings of the holotype, CNU-NEU-NN99030. **A**, forewing; **B**, hind wing. Scale bars: 5 mm.

costal crossveins form one gradate series running to centre of wing, few other irregularly spaced; subcostal space with 14 crossveins; R1 space with seven crossveins preserved; radial crossveins arranged in one long outer series from R1 to MP, others (proximal this series) not numerous, irregularly spaced; between Rs1 and MA five preserved crossveins; between MP and CuA three preserved crossveins, including short, slightly oblique 1m-cu; between branches of Cu two distal preserved crossveins; in anal space two basal crossveins. Posterior margin probably slightly undulate; outer margin not preserved, probably undulate. Preserved macrotrichia on longitudinal veins dense, long; macrotrichia on wing margins

relatively short. Trichosors along costal margin prominent. Wing membrane in general dark brownish, colour pattern consists of indistinct irregularly spaced dark spots in costal and subcostal space, and several irregularly spaced pale patches narrowly margined with dark brown near outer margin.

Hind wing slightly shorter than forewing, broad; 31 mm long, 16 mm wide as preserved (estimated complete length about 33–34 mm, width 17 mm). Costal space, Sc, R1 and Rs poorly preserved. Subcostal veinlets dense, forked. Most branches of Rs deeply branched dichotomously. MA, MP nearly straight before end-twigging, both dichotomously branched distally. CuA pectinately



Figure 14. *Nematopsychops unicus* gen. et sp. nov., photograph of holotype, CNU-NEU-NN2011086P/C. **A**, part (converted to standard right view); **B**, counterpart. Scale bars: 5 mm.

branched distally, with nine oblique forked branches. CuP dichotomously branched, with four or five main branches. Anal space poorly preserved; 1A strongly dichotomously branched; 2A poorly preserved. Crossveins difficult to identify; at least some radial crossveins arranged in one outer series from R1 to MA. Trichosors prominent along preserved margins. Wing membrane in general dark brownish; colour pattern indistinct.

Genus *Nematopsychops* gen. nov.

Type and only species. *Nematopsychops unicus* sp. nov.

Etymology. From the Greek *nematinos* [νημάτινος], filiform, filamentous, and *-psychops*, referring to the prominent, mostly unbranched, and parallel longitudinal veins. Gender masculine.

Diagnosis. In both wings, no costal crossveins; Sc and R1 fused distally; only one (basal) subcostal crossvein; distal nygma absent; complete outer (distalmost) series of crossveins; branches of Rs (except Rs1) mostly shallowly forked; Rs1 deeply forked several times; MP few pectinate branches. In forewing, M forked only slightly

proximad origin of basalmost branch of CuA; CuP pectinate, relatively long entering posterior wing margin approximately at mid-point.

Comments. The genus is most closely related to *Ochropsychops* but may be easily distinguished from it by the absence of costal crossveins and only one (basal) subcostal crossvein; the radial crossveins proximad the outer gradate series are irregularly spaced; and CuA is pectinate, relatively long.

Nematopsychops unicus sp. nov.
(Figs 14, 15)

Etymology. From the Latin *unicus*, sole, referring to only one (basal) subcostal crossvein.

Material. Holotype: CNU-NEU-NN2011086P/C, a fragmentarily preserved thorax with two wings: a nearly complete forewing and hind wing; a fragmentarily preserved abdomen.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

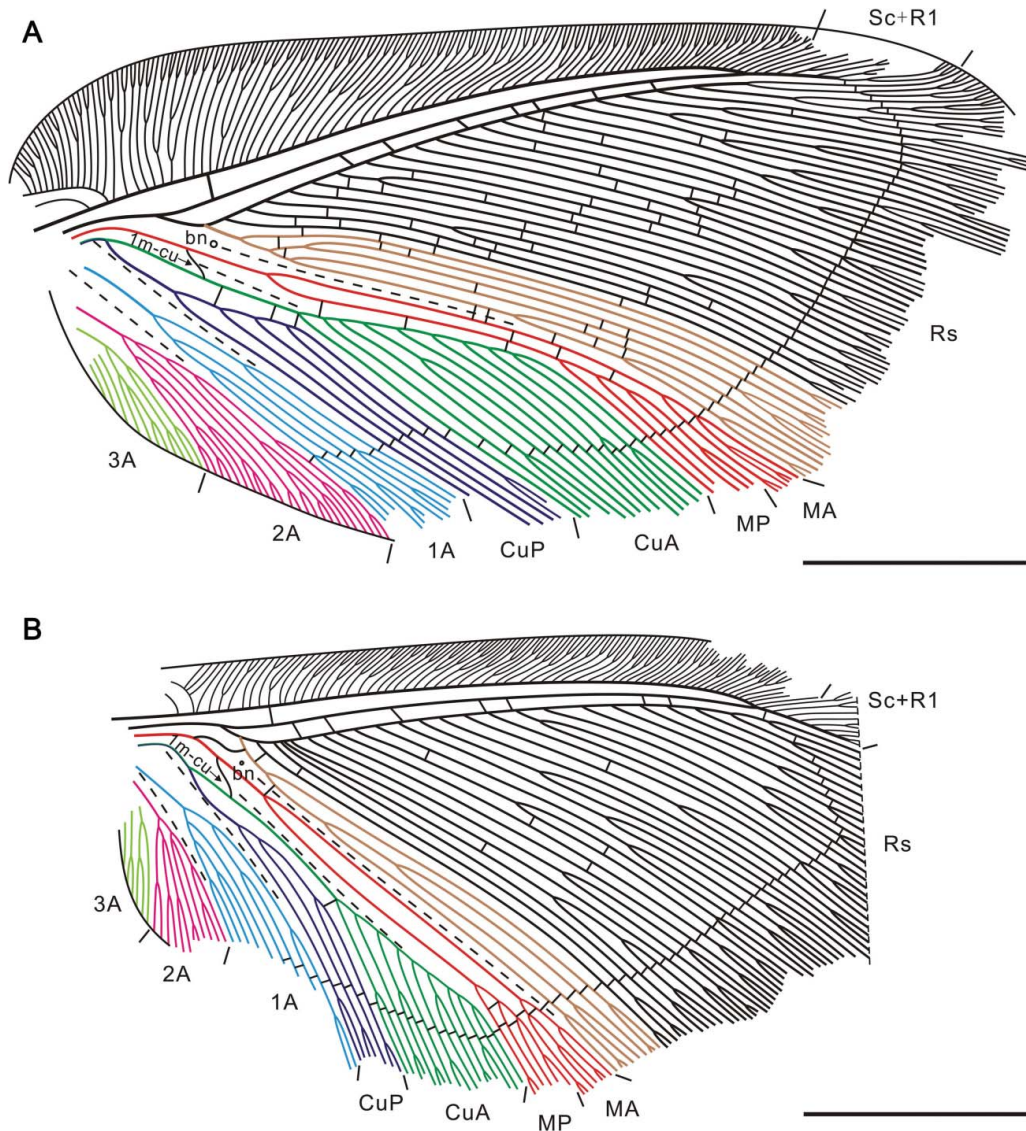


Figure 15. *Nematopsychops unicus* gen. et sp. nov., line drawings of holotype, CNU-NEU-NN2011086P/C. **A**, forewing; **B**, hind wing. Scale bars: 5 mm.

Diagnosis. As for the genus.

Description. Three (apparently distal) segments of abdomen short; their length about three times their width.

Forewing broadly ovate; approximately 23 mm long, 12 mm wide. Costal space very broad basally, narrowed towards apex; its width of narrowest part about twice width of adjacent subcostal and R1 spaces. More than 65 subcostal veinlets, mostly twice and three times forked, few once forked or simple. Humeral veinlets strongly recurrent with 14 mostly forked branches. Subcostal space broad at origin of Rs, gradually narrowed towards apex, strongly narrowed basally. R1 space narrow. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, fused near wing apex; Sc + R1 straight, not curved posteriad,

with seven veinlets. Rs with 23 primary branches; mostly shallowly forked, few of these deeply dichotomously branched. Rs1 deeply forked six times (proximad outer gradate series). Basal nygma near wing base between stem of Rs1 and M; distal nygma absent. M not fused basally with R; forked closer to wing base than in other genera (distad second fork of Rs1). MA slightly arched before end-twigging, dichotomously branched distally; MP slightly sinuate, few pectinately branched, with three branches. Cu well developed, forked near wing base. CuA regularly pectinately branched distally, with nine oblique long branches. CuP regularly pectinately branched, with four very long branches; basalmost fork of CuP located slightly proximad basalmost fork of Rs1. Anal space well developed; 1A long, dichotomously branched; 2A more

dichotomously branched than 1A; 3A few branched. Crossveins numerous: costal crossveins absent; subcostal space with only one basal crossvein; R1 space with seven crossveins; radial crossveins arranged in one complete long outer series from R1 to 1A, other radial crossveins irregularly spaced; between Rs1 and MA three preserved crossveins; between MA and MP three distal crossveins; between MP and CuA four crossveins, including long oblique 1m-cu; between CuA and CuP three basal crossveins; no crossveins detected in anal space. Posterior and outer margins mostly not preserved. Macrotrichia on longitudinal veins dense, moderately long (Fig. 21A); macrotrichia on wing margins relatively short. Trichosors prominent along preserved margins. Wing membrane dark brownish; colour pattern indistinct, except white crossveins of outer gradate series.

Hind wing sub-triangular, slightly smaller than forewing; 16.5 mm long, 10.4 mm wide as preserved (estimated complete length about 20 mm, 11 mm width). Costal space relatively broad for entire length, slightly dilated towards apex; its width of narrowest part about twice width of adjacent subcostal and R1 spaces. More than 60 subcostal veinlets, mostly once and twice forked, few simple. Humeral veinlets recurrent with three preserved branches. Subcostal space moderately broad at origin of Rs, slightly narrowed towards apex, strongly narrowed basally. R1 space slightly narrower than subcostal space. Sc, R1, Rs strong (stout). Sc and R1 approaching towards apex, fused apically; Sc + R1 straight, extending slightly posteriad for long distance, with eight preserved veinlets. Rs with 26 primary branches; many of these simple. Rs1 deeply forked three times. Basal nygma located near wing base between stem of Rs1 and M; distal nygma absent. M not fused with R basally; forked relatively far from wing base (distad first fork of Rs1). MA straight before end-twigging, dichotomously branched distally; MP slightly incurved, few pectinately branched, with three branches. Cu well developed, forked near wing base. CuA pectinately branched distally, with nine forked branches. CuP pectinately branched, with three branches; basalmost fork of CuP located slightly distad basalmost fork of Rs1. Anal space well developed; 1A, 2A strongly dichotomously branched; 3A few branched. Crossveins numerous: costal crossveins absent; subcostal space with only one basal crossvein; R1 space with seven crossveins; most radial crossveins arranged in one complete long outer series from R1 to 1A, few others irregularly spaced; three crossveins between Rs1 and MA, including long sigmoid basal 1r-m; between branches of MP one distal crossvein; basal crossvein 1m-cu long, slightly sigmoid; between CuA and CuP one crossvein. Macrotrichia as in forewing. Trichosors prominent along preserved margins. Wing membrane dark brownish, colour pattern indistinct, except pale crossveins of outer gradate series.

Genus *Ochropsychops* gen. nov.

Type and only species. *Ochropsychops multus* sp. nov.

Etymology. From the Greek *ochros* [ὀχρός], pale, and *-psychops*, a traditional ending of names of psychopoid genera, referring to pale colour of the wing membrane as preserved. Gender masculine.

Diagnosis. Forewing broad with obtuse apex possessing one gradate series of costal crossveins; many subcostal crossveins; distal nygma; complete outer (distalmost) series of crossveins; numerous radial crossveins proximad outer series arranged in several short series; Sc and R1 fused distally; Sc + R1 strongly curved posteriorly; posterior and outer margins not undulate; branches of Rs mostly shallowly forked; Rs1 only distally forked; M forked at level of origin of basalmost branch of CuA; MP pectinately branched; CuP relatively short, entering posterior wing margin well before mid-point.

Comments. *Ochropsychops* is most closely related to *Nematopsychops* but may be easily distinguished from it by the presence of costal crossveins, numerous subcostal crossveins, radial crossveins proximad the outer gradate series arranged to several gradate series, and CuA not pectinate, very short.

Ochropsychops multus sp. nov.

(Fig. 16)

Etymology. From the Latin *multus*, numerous, referring to radial crossveins arranged in many gradate series.

Material. Holotype: CNU-NEU-NN2011055P/C, a nearly complete forewing.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. As for the genus.

Description. Forewing sub-triangular; 32.5 mm long, 13.2 mm wide. Costal space very broad basally, narrowed towards apex; its width of narrowest part almost equal to width of adjacent subcostal and R1 spaces. More than 60 subcostal veinlets, mostly once forked or simple, few twice forked. Humeral veinlets strongly recurrent, with eight forked branches. Subcostal and R1 spaces relatively narrow, almost equal in width. Sc, R1, Rs strong (stout). Sc and R1 fused apically relatively abruptly; Sc + R1 strongly curved posteriad, with 12 mostly forked veinlets. Rs with 25 primary branches; most of these parallel, simple before end-twigging. Rs1 simple for most of its length, dichotomously forked distally. Two nygmata present: basal nygma located in small cell near wing base between stem of Rs1 and M; distal nygma between two most proximal branches of Rs. M appears to originate from R at wing

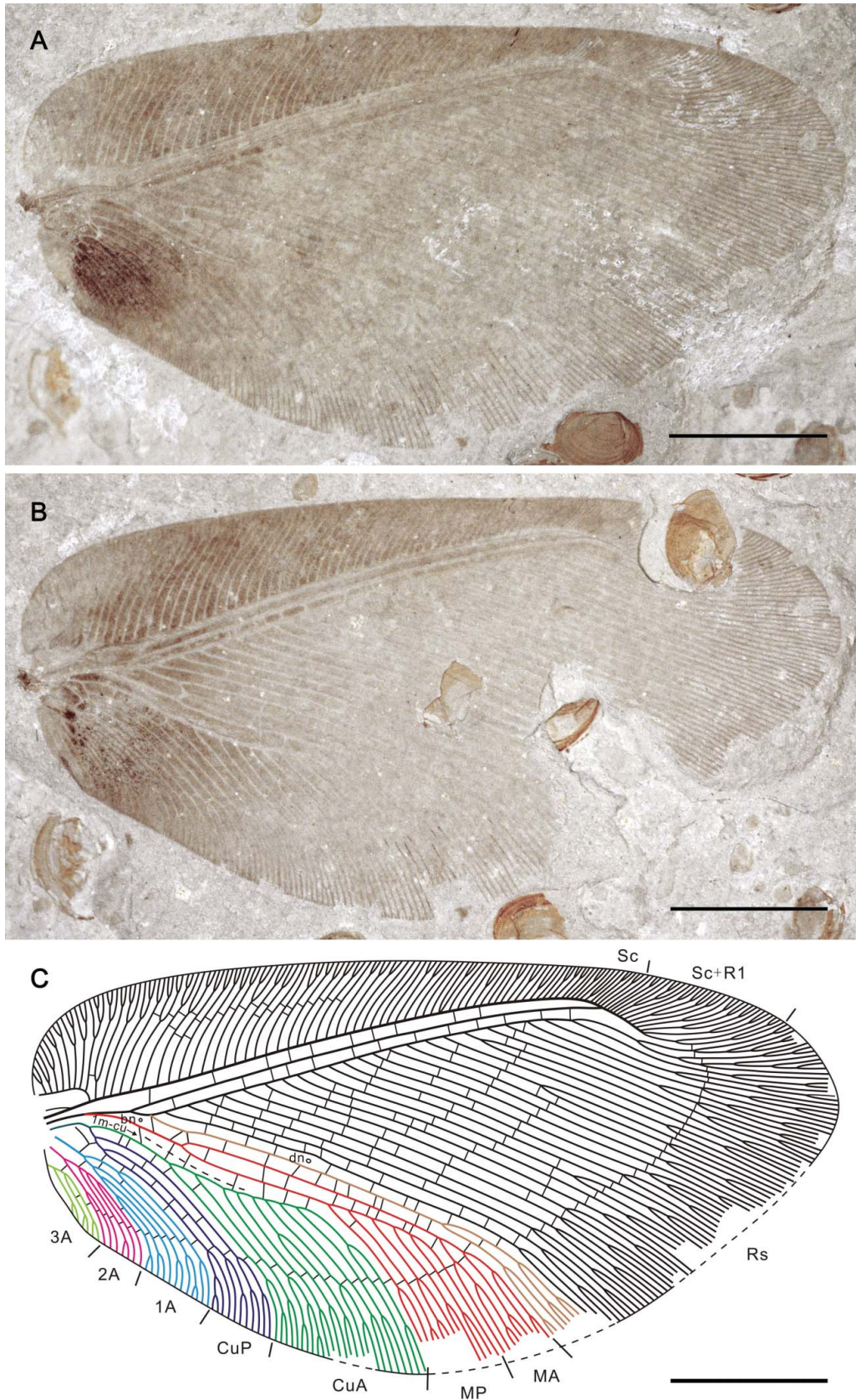


Figure 16. *Ochropsychoops multus* gen. et sp. nov., holotype, CNU-NEU-NN2011055P/C. **A**, part; **B**, counterpart (converted to standard right view); **C**, line drawing of forewing venation. Scale bars: 5 mm.

base; forked relatively close to wing base. MA nearly straight before end-twigging, dichotomously branched distally. MP slightly sinuate, pectinately branched distally, with five oblique forked branches. Cu forked near wing base. CuA relatively short, pectinately branched distally, with eight long forked branches; basalmost fork of CuA located at same level as fork of M. CuP short (entering posterior margin well before wing mid-point), few branched, with three long main branches, each dichotomously forked; basalmost fork of CuP located proximad origin of Rs. Anal space relatively poorly developed; 1A dichotomously branched; 2A pectinately branched, with

four branches; 3A few branched. Crossveins numerous: few costal crossveins form one short gradate series; subcostal space with 10 crossveins; R1 space with 13 crossveins; radial crossveins arranged in eight incomplete gradate series and one complete long outer series from R1 to 3A; between Rs1 and MA 13 crossveins; between MA and MP ten crossveins; between MP and CuA seven crossveins; crossveins between branches of Cu and in anal space not numerous, irregularly spaced (besides outer gradate series). Preserved macrotrichia on longitudinal veins in cubital and anal spaces dense, long; macrotrichia on wing margins short. Trichosors prominent along entire



Figure 17. *Stenopteropsychops trifasciatus* gen. et sp. nov., holotype, CNU-NEU-NN2011517. **A**, photograph of the part; **B**, line drawing of forewing venation. Scale bars: 5 mm.

margin. Wing membrane in general slight brownish, markedly darker proximally and in costal space.

Genus *Stenopteropsychops* gen. nov.

Type and only species. *Stenopteropsychops trifasciatus* sp. nov.

Etymology. From the Greek *stenos* [στενος], narrow, *pteron* [πτερον], wing and *-psychops*, a traditional ending of names of psychopoid genera, referring to narrow forewing of the type species. Gender masculine.

Diagnosis. Forewing relatively narrow with pale transverse fasciae; costal space relatively narrow basally; Rs1 originated from R before Rs proper; M forked relatively close to wing base; CuP simple, only with marginal fork; 1A relatively few branched.

Stenopteropsychops trifasciatus sp. nov.
(Figs 17, 18)

Etymology. From the Latin *tres*, three, and *fasciatus*, banded, striped, referring to three white transverse bands (fasciae) in the forewing.

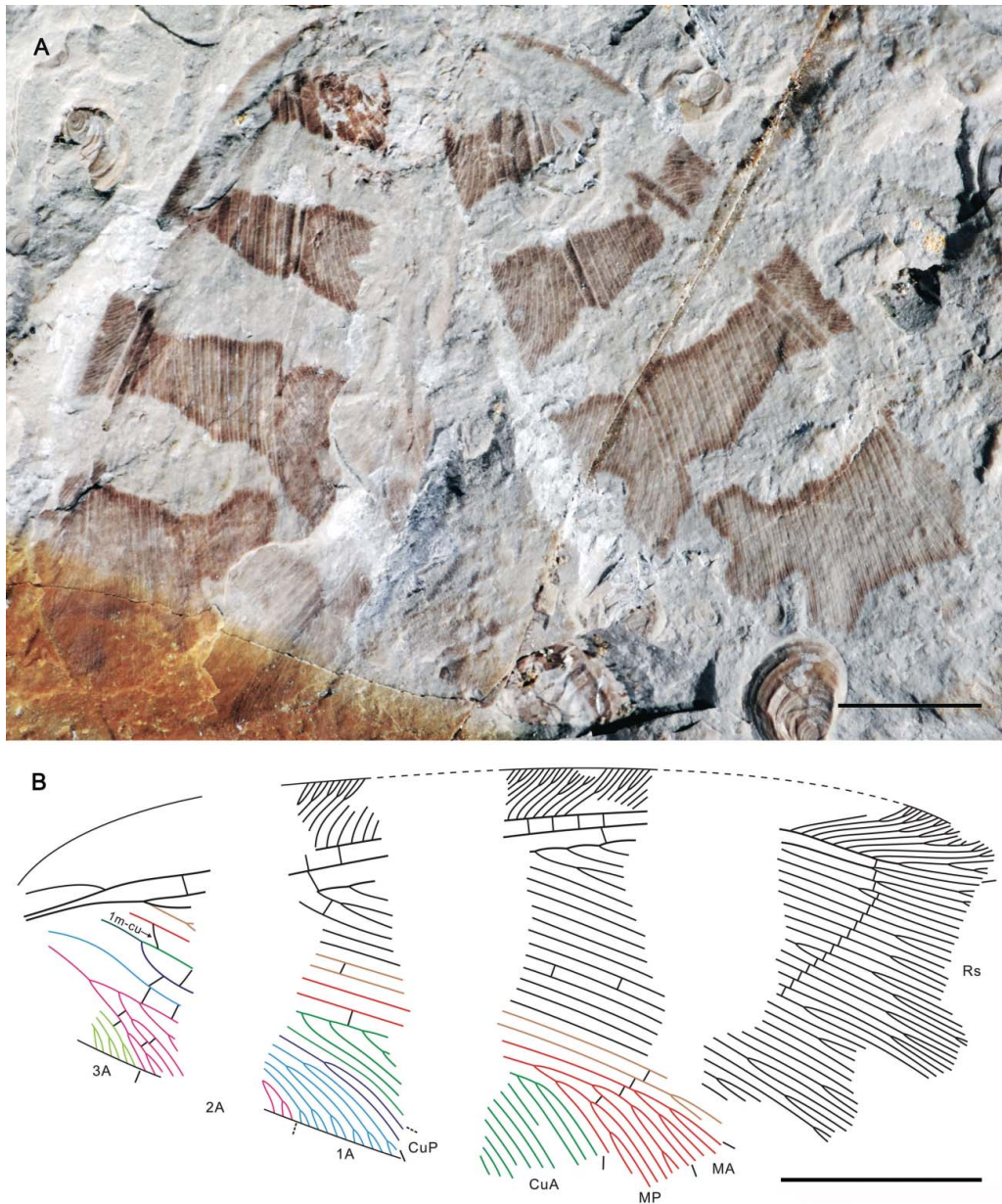


Figure 18. *Stenopteropsychops trifasciatus* gen. et sp. nov., paratype, CNU-NEU-NN99037. **A**, photograph of specimen as preserved; **B**, line drawing of forewing venation. Scale bars: 5 mm.

Material. Holotype: CNU-NEU-NN2011517, two nearly complete forewings. Paratype: CNU-NEU-NN99037, two almost complete forewings.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic), Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. As for the genus.

Description of the holotype. Forewing elongate, 26 mm long, 11 mm wide. Costal space relatively narrow, broadest at basal fascia, narrowed basally and towards apex; its width of narrowest distal part once and half width of adjacent subcostal and R1 spaces. All subcostal veinlets once or three times forked. Humeral veinlets not preserved. Subcostal and R1 spaces relatively narrow, almost equal in width. Sc, R1, Rs strong (stout). Distal Sc and R1 not preserved; Sc + R1 or R1 straight, directed slightly posterior, at least with eight forked veinlets. Rs with 16 primary branches; most of these parallel, simple before end-twigging. Rs1 originated before Rs proper, once very deeply forked. Nygmata not detected. M forked close to wing base. MA, MP slightly sinuate before end-twigging; MA dichotomously branched distally; MP pectinately branched distally, with four–five forked branches (one of these deeply forked). Cu forked near wing base. CuA pectinately branched, with at most seven branches (at least two of these deeply forked); basalmost fork of CuA located very proximally but distad fork of M. CuP relatively short (entering posterior margin well before wing mid-point), simple (with only shallow marginal fork). Anal space relatively poorly developed; 1A dichotomously branched; 2A pectinately branched, with six–seven branches; 3A poorly preserved. Crossveins not numerous: no costal crossveins and subcostal crossveins detected; R1 space with two proximal preserved crossveins; most radial crossveins arranged in one complete outer series from R1 to MP, other few radial crossveins irregularly spaced; between Rs1 and MA two closely spaced short proximal crossveins; between MA and MP two distal crossveins; between MP and CuA three preserved crossveins, including 1m-cu almost perpendicular to CuA; between CuA and CuP three crossveins; between CuP and 1A two proximal crossveins; between 1A and 2A two crossveins; crossveins between branches of CuA, 1A and 2A not detected except one occasional in 2A space. Posterior and outer margins not undulate. Few preserved macrotrichia on longitudinal veins long (Fig. 21B); macrotrichia on wing margins short. Trichosors prominent along preserved margins. Wing membrane brownish with several white patches and fasciae, mostly with a narrow dark brownish margin: three complete transverse broad fasciae; large basal patch fused with basalmost fascia in costal space; large apical patch; three small spots near costal, outer, and posterior margins in distal half of wing.

Comments. The forewing CNU-NEU-NN99037 (Fig. 18) is 26 mm long and 10.5 mm wide, i.e. slightly narrower than the holotype. It assigned to this species as a paratype due to a very similar colour pattern, but its venation differs in some details: several subcostal crossveins are present, Rs1 is originated from Rs near its origin, CuP is more deeply forked distally, and 1m-cu is long and oblique.

Genus *Brongniartiella* Meunier, 1897

Type species. *Brongniartiella problematica* Meunier, 1897 (= *Ricania gigas* Weyenbergh, 1869), by monotypy.

Revised diagnosis. Forewing broad, large (up to 57 mm long); costal space comparatively narrow; subcostal veinlets mostly shallowly forked near margin; posterior and outer margins not undulate; branches of Rs mostly deeply forked; Rs1 once deeply forked; M forked at level of primary fork of CuP; distal nygma apparently present; complete outer distalmost gradate series of crossveins present; cubital and anal spaces relatively narrow. Hind wing broad, sub-triangular; posterior and outer margins not undulate; Sc + R1 (or R1) slightly gently curved posteriorly.

Comments. This genus is the type of the family Brongniartiellidae. Besides the type species, another species (*Brongniartiella inconditissima* Handlirsch from the same locality) was assigned to the genus by Handlirsch (1906–1908).

Brongniartiella differs from all similar genera described herein by the outer gradate series crossing the CuA space relatively close to origins of the branches of CuA, and M forked slightly proximad the primary fork of CuP.

Brongniartiella gigas (Weyenbergh, 1869) (Fig. 19)

1869 *Ricania gigas* Weyenbergh: 270; pl. 35, fig. 23.

1897 *Brongniartiella problematica* Meunier: 238; pl. 11, fig. 25.

1906–1908 [1906] *Brongniartiella problematica* Meunier; Handlirsch: 606.

Redescription. Forewing ovate, sub-triangular, approximately 55 mm long as preserved (estimated complete length above 56–57 mm), 25 mm wide. Costal space relatively narrow; slightly narrowed towards apex. Subcostal veinlets evenly curved proximally, strongly bent to apex distally; mostly shallowly forked. Humeral veinlet recurrent, probably with at least six branches. Subcostal space broad at least in central part; probably with several crossveins. R1 space broad, at least basally. Posterior branches of Rs deeply dichotomously forked;

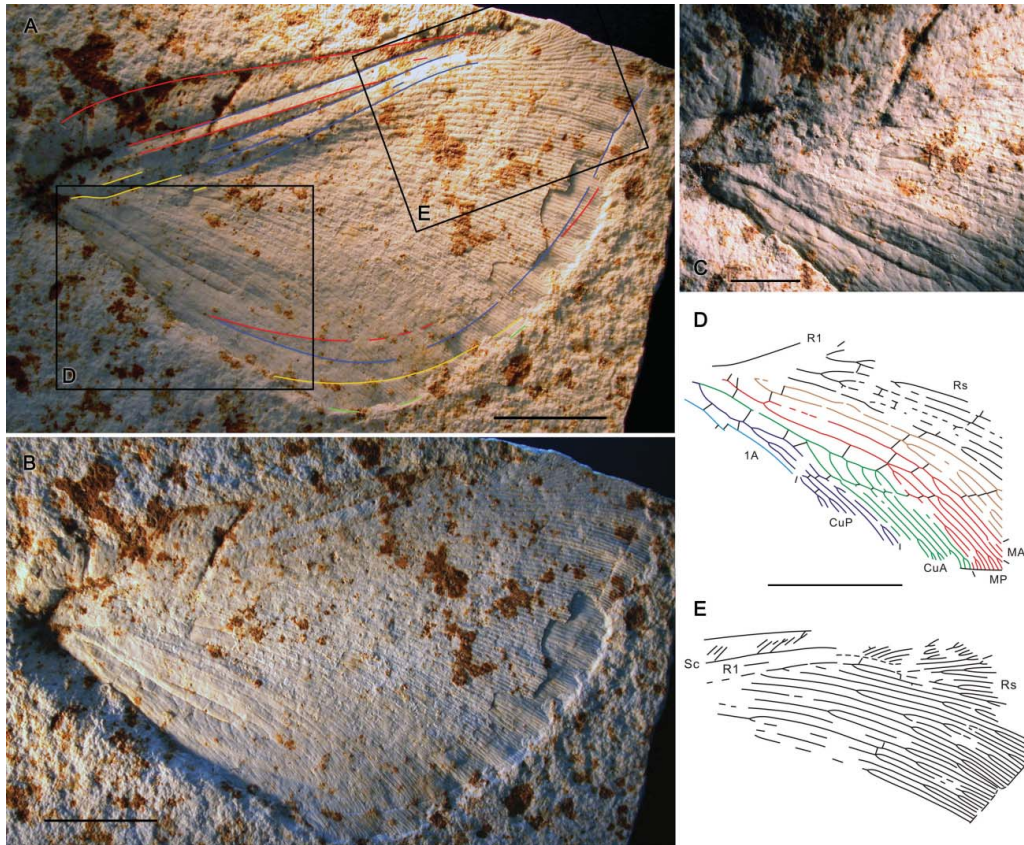


Figure 19. *Brongniartiella gigas* (Weyenbergh, 1869), holotype, TM 15411. **A**, photograph of specimen as preserved; wing outline and main elements of right forewing are shown by red lines; right hind wing by blue; left forewing by yellow; and left hind wing by green; **B**, photograph of specimen under lighting from the opposite direction; **C**, base of wings; **D**, preserved left forewing venation (as located on Fig. 20A); **E**, preserved right hind wing venation (as located on Fig. 20A). Scale bars: 10 mm (A, B, D, E), 5 mm (C).

R_s1 deeply forked. Distal nygma probably present located at dilation of R_s1 space. M forked relatively close to wing base; MA, MP parallel to each other before branching; MA forked proximad outer gradate series, both branched shallowly forked. MP more deeply branched, in general dichotomously; forked three times proximad outer gradate series. Cu forked near wing base. CuA nearly straight until distalmost branch, pectinately branched, with five shallowly forked branches. CuP in general few dichotomously forked; basalmost fork of CuP located at level of fork of M. 1A fragmentarily preserved, long. Crossveins relatively scarce: no costal crossveins detected; subcostal space with few preserved crossveins; radial crossveins arranged in two gradate series: outer series running at least from R_s5 to CuP (distal wing areas unclear), and another series proximad outer series at least from R_s4 to MA; other few radial crossveins in proximal wing portion irregularly spaced; crossveins in radiomedial to anal spaces few, irregularly spaced. Trichosors apparently present amongst at least outer margin, poorly visible. Wing coloration not preserved.

Hind wing broad, sub-triangular, about 50 long (estimated), 24.5 mm wide. Costal space relatively narrow. Preserved subcostal veinlets in distal part strongly bent, at last some shallowly forked. Subcostal space relatively broad. Sc + R₁ or R₁ slightly curved posteriad for some distance, with at least five forked veinlets. R₁ space broad. Branches of R_s in distal part mainly deeply dichotomously forked. Few preserved radial crossveins in distal part belong most probably to outer gradate series. Venation of proximal wing part largely not preserved. Wing coloration not preserved.

Material. Holotype: TM 15411 (formerly 6448) four wings overlapping: only proximal part of the costal space of the right forewing is relatively well preserved; only proximal part of the left forewing is well preserved (Fig. 19D); distal part of the right hind wing is relatively well preserved (main portion of this is shown in Fig. 19E); the left hind wing is poorly preserved, only an area of its torus is visible. Central portions of the specimen are poorly preserved due to the left forewing and right hind wing overlapping.

Type locality and horizon. Late Jurassic; Solnhofen, Germany.

Comments. F. Meunier wrote by hand in ink on the reverse of the holotype of *Ricania gigas*: “Brongniartiella problematica F. Meunier / N.B. On ne sait à quel ordre appartient cette aile d’insecte / F. Meunier (1896).” Therefore, the synonymy of these two species is objectively based on the single specimen.

Family **Psychopsidae** Handlirsch, 1906

Genus ***Gigantopsychops*** gen. nov.

Type and only species. *Gigantopsychops reticulatus* sp. nov.

Etymology. From the Greek *gigas* [γίγας, -αντος], gigantic, huge, and *-psychops*, a traditional ending of names of psychopsoid genera, referring to the large size of the forewing. Gender masculine.

Diagnosis. Forewing very broad, large (more than 40 mm long); costal space dilated apically; no costal gradate series; Sc and R1 fused distally; M deeply forked close to wing base, dichotomously branched occupying large area; radial crossveins numerous and irregularly arranged; CuP with very few dichotomous branches; basal crossveins between CuA and CuP, CuP and A1, 1A and 2A reticulate.

Comments. This genus greatly differs from other fossil psychopsids mainly by the large wing size, the dichotomously branched M occupying a large area, and the very few branched CuP.

Gigantopsychops reticulatus sp. nov.
(Fig. 20)

Etymology. From the Latin *reticulatus*, reticular, referring to reticulated crossveins near wing base.

Material. Holotype: CNU-NEU-NN2011040P/C, a nearly complete forewing.

Type locality and horizon. Jiulongshan Formation (Middle Jurassic); Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Diagnosis. As for the genus.

Description. Forewing very broad; 41 mm long, 27 mm wide as preserved (estimated complete length about 43 mm, width 30 mm or more). Costal space broad, dilated towards apex; its width of apical part (near fusion of Sc and R1) over three times width of adjacent subcostal and R1 spaces. More than 60 subcostal veinlets, mostly simple as preserved, few once forked. Humeral veinlet not preserved, but probably well developed judging from arrangement of basalmost subcostal veinlets. Subcostal

space narrow. R1 space slightly wider than subcostal space. Sc, R1, Rs strong (stout). Sc and R1 fused apically; Sc + R1 nearly straight, continues course of R1, with five forked veinlets. Rs originated far from wing base, nearly straight for entire length; with 27 primary branches; posterior branches parallel to each other, shallowly forked; anterior branches mainly deeply dichotomously branched. Rs1 originated from R before Rs proper, simple, with loop-like duplication forming basal closed cell, anastomized with anteriormost branch of M at wing mid-point. Basal nygma in small cell near wing base between stem of Rs1 and M; distal nygma absent. M deeply forked close to wing base, dichotomously branched occupying large area; posterior trace of M anastomized with CuA distally. MA, MP hard to identify. Cu well developed, forked at wing base. CuA convex, strongly pectinately branched, with 15 oblique forked branches. CuP concave proximally, very few branched, in general dichotomously, with two main branches. Anal space well developed; 1A long, strongly dichotomously branched; 2A pectinately branched, with eight long preserved branches. Crossveins numerous: costal crossveins few and irregularly spaced, not forming gradate series; subcostal space with 10 crossveins; R1 space with 14 crossveins; radial, radiomedial, medial, and cubital crossveins dense, irregularly spaced, not arranged in series, decreased in number from basal to distal wing portions, absent in distalmost parts; mediocubital crossveins (between M and CuA) widely spaced, 12 detected; crossveins between branches of 1A, 2A scarce, irregularly arranged; basal crossveins between CuA and CuP, CuP and A1, 1A and 2A reticulate. Preserved macrotrichia on longitudinal veins in proximal part of wing dense, very long (Fig. 21D). Wing margins not preserved. Wing membrane dark brown; colour pattern absent.

Discussion

The beautifully preserved specimens described above from the Chinese Middle Jurassic locality of Daohugou pose some important questions regarding the systematics of psychopsoids. This material (and additional material not reported here) shows that Osmylopsychopidae was clearly a dominant psychopsoid group at least in the Middle Jurassic of Daohugou. The comparison of newly established genera with the type of Brongniartiellidae indicates that the latter family is a synonym of Osmylopsychopidae. Furthermore, the new taxa allow a new approach to solving the problem of how to distinguish the Mesozoic Osmylopsychopidae and Psychopsidae.

Triassic Osmylopsychopidae

The Triassic Osmylopsychopidae are characterized by the following forewing character states (based on

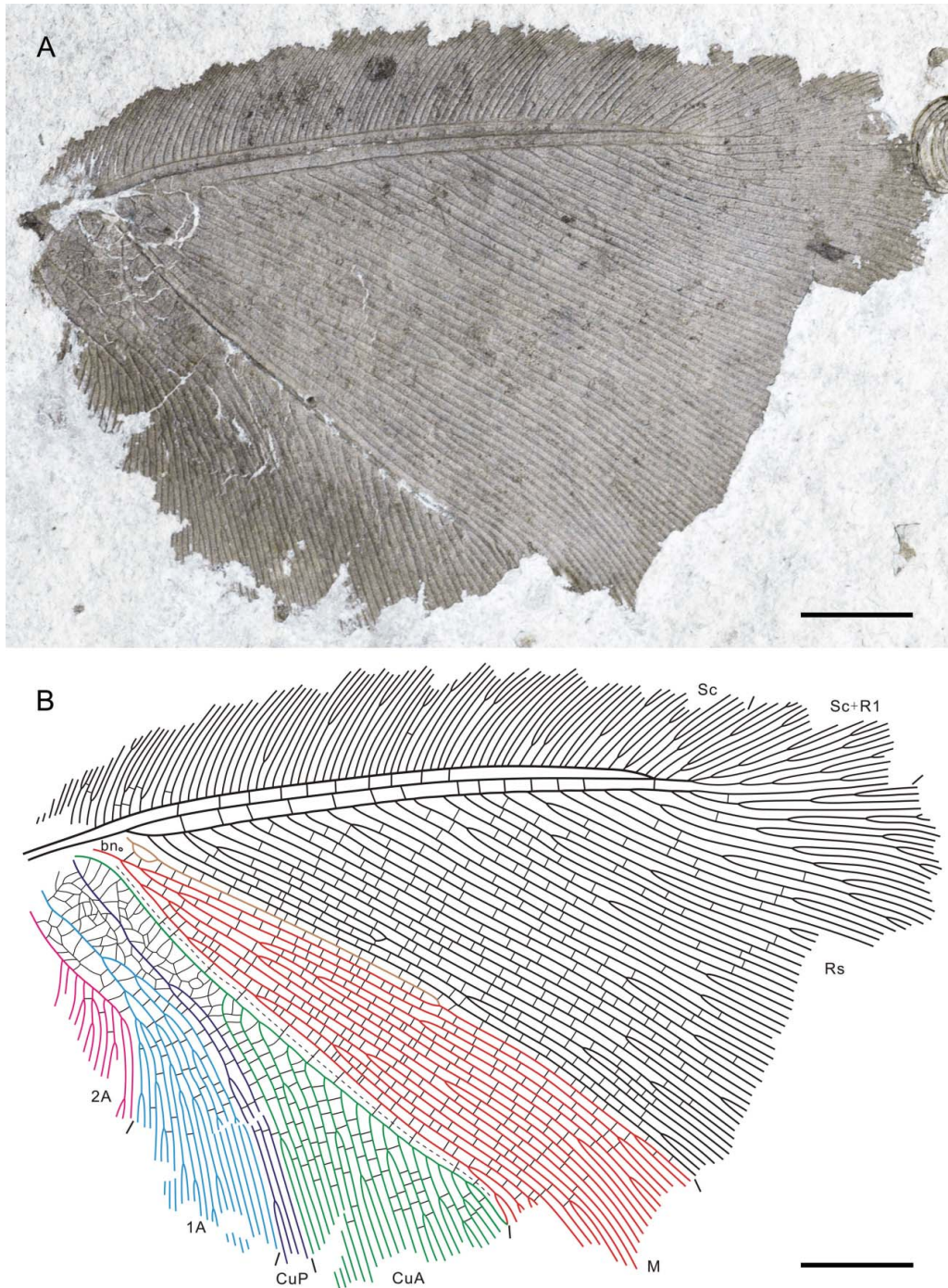


Figure 20. *Gigantopsychops reticulatus* gen. et sp. nov., holotype, CNU-NEU-NN2011040P/C. **A**, photograph of the part; **B**, line drawing of forewing venation. Scale bars: 5 mm.

Ellenberger *et al.* 1952; Lambkin 1992, 2014; Shcherbakov 2008; VM pers. obs.): (1) the costal space is strongly broadened basally and narrowed towards the apex; (2) the humeral vein is recurrent and branched; (3) Sc and R1 are fused distally; (4) Rs1 is occupying a large area and deeply profusely branched; (5) CuA is in general pectinately branched; (6) CuP is few (often

dichotomously) branched; (7) anal veins (A1, A2) are profusely and dichotomously branched; (8) no dense crossvenation, including (8a) scarce costal crossveins, (8b) few crossveins between Sc and R1, and (8c) no well-defined gradate series in the radial space, i.e. radial crossveins are few or rather numerous (i.e. in *Petropsychops*), randomly scattered or forming a number of short

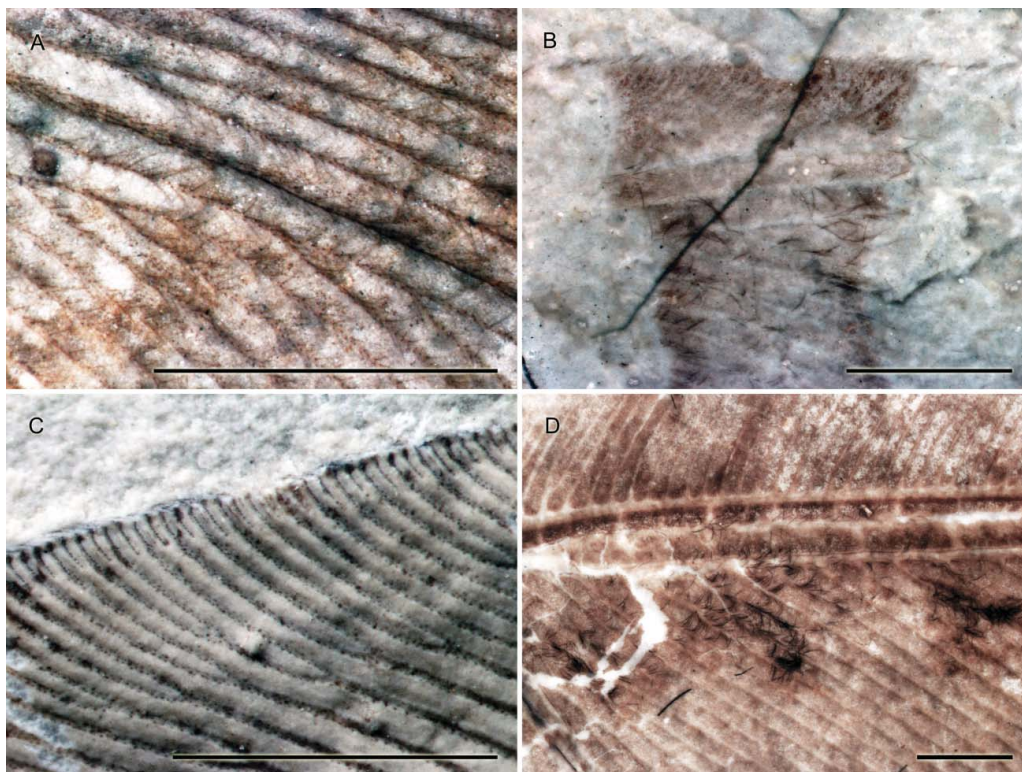


Figure 21. Wing trichiation of Osmylopsychopidae (A–C) and Psychopsidae (D) from Daohugou. **A**, the holotype of *Nematopsychops unicus* gen. et sp. nov., counterpart. **B**, the paratype of *Stenopteropsychops trifasciatus* gen. et sp. nov. **C**, *Daopsychops inanis* gen. et sp. nov., part. **D**, the holotype of *Gigantopsychops reticulatus* gen. et sp. nov., counterpart (converted to standard right view). Photographs of A, B and D are wetted with ethanol. Scale bars: 2 mm.

irregular gradate series, not arranged into long gradate series; (9) the distal nygma is present.

The venation of Osmylopsychopidae strongly differs from that of other Permian and Triassic Neuroptera (i.e. Permithonidae, Archeosmylidae, Mesoberothidae). These differences include in particular a number of derived character states, e.g. (1), (2), (4), (5), (7). Of these, state (4) is a putative autapomorphy of Osmylopsychopidae. Although this condition is present in some younger Hemerobiidae, there is some evidence that this family is an offspring of osmylopsychopid-like taxa and therefore these states in the two families might be homologous.

These characteristics are shared (with the exception of a few states in some species) by all genera from the Middle to Late Triassic of Australia (i.e. *Osmylopsychops*, *Archeopsychops*, *Petropsychops* and *Gayndahpsychops*), *Osmylopsychops radialis* Ellenberger *et al.* from the Late Triassic of France, and undescribed taxa from the Middle/Late Triassic Madygen Formation of Kyrgyzstan (Tillyard 1919b, 1923; Riek 1956; Ellenberger *et al.* 1952; Lambkin 1992, 2014; Shcherbakov 2008; VM pers. obs.). The family was widely distributed across Pangaea.

The hind wings are unknown in the Triassic Osmylopsychopidae (however, see below comments on *Triassopsychops superbus* Tillyard).

High diversity of the Middle Jurassic Osmylopsychopidae and the evolution of its venation

The osmylopsychopid affinity of the new genera of Osmylopsychopidae described above is undoubted. This is supported by the presence of most character states found in the Triassic Osmylopsychopidae, including one putative autapomorphy of the family (i.e. the deeply branched Rs1). All described species are certainly closely related. However, some of them lack a few of the character states found in the Triassic Osmylopsychopidae, and some possess new character states. This allows us a better understanding of the wing venation of the family, and to consider some evolutionary trends in the Middle Jurassic Osmylopsychopidae compared with Triassic ones.

The Daohugou species provide the family diagnosis with hind wing character states. The hind wing of *Nematopsychops unicus* is especially well preserved (Fig. 14B) and shows that in this family all forewing character states (except state 1) are also present in the hind wing. There is one additional character, i.e. the basal crossvein 1r-m is long and sigmoid (Fig. 22F). This condition is plesiomorphic in Neuroptera (Winterton & Makarkin 2010; Yang *et al.* 2012), but it is important for distinguishing Osmylopsychopidae and Psychopsidae (see

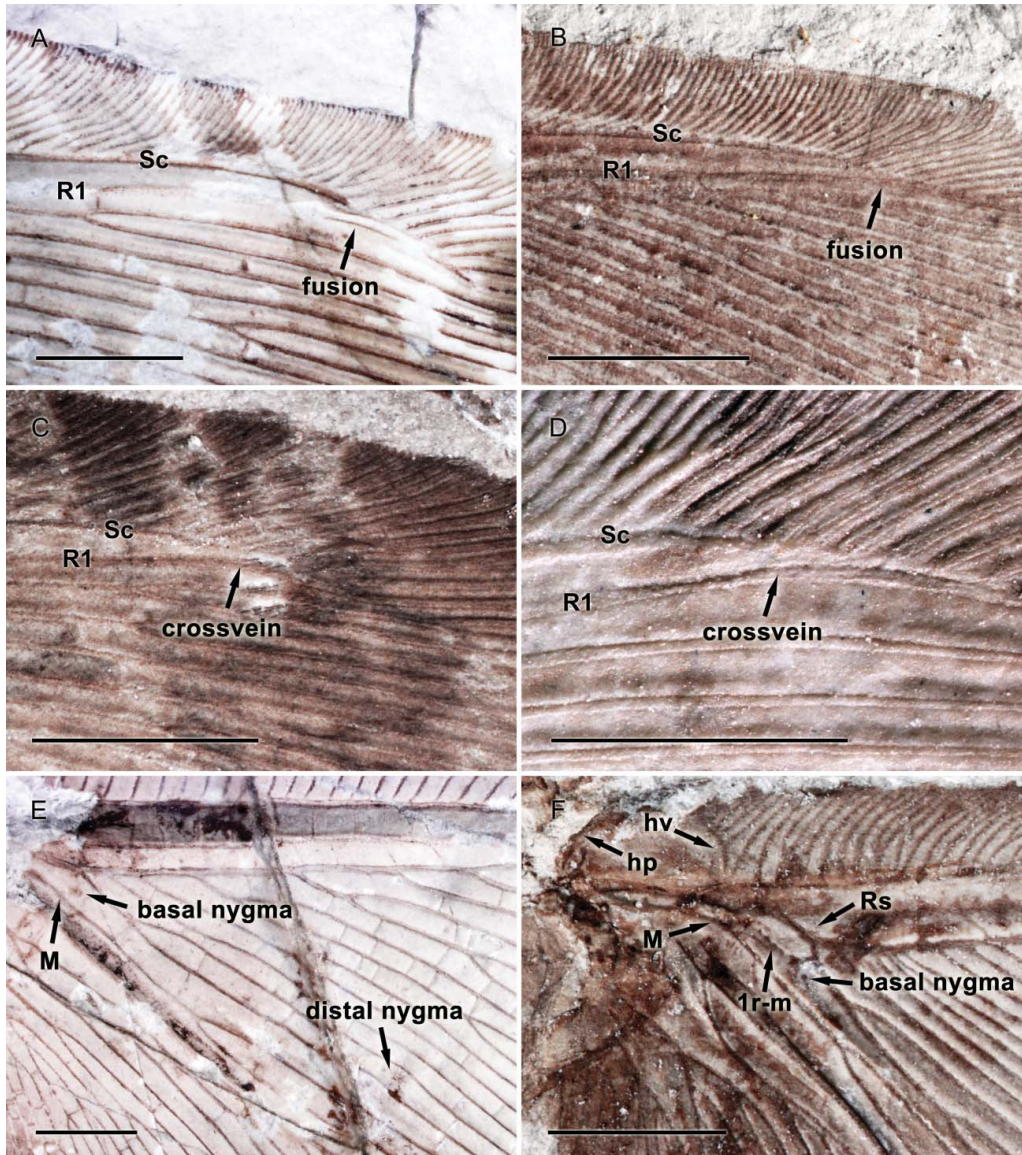


Figure 22. Apical and basal portions of the forewings (A–E) and hind wings (F) of Osmylopsychopidae from Daohugou. **A**, the holotype of *Daopsychoys inanis* gen. et sp. nov., part. **B**, the holotype of *Nematopsychoys unicus* gen. et sp. nov., part (converted to standard right view). **C**, the holotype of *Eupypsychoys confinis* gen. et sp. nov., part. **D**, the holotype of *E. ferox* gen. et sp. nov. **E**, the holotype of *D. inanis* gen. et sp. nov., part. **F**, the holotype of *N. unicus* gen. et sp. nov., counterpart. Scale bars: 2 mm.

below). A sigmoid 1r-m is also present in all the undescribed isolated hind wings of Osmylopsychopidae from Daohugou.

Wing margins. Many larger wings of Osmylopsychopidae from Daohugou possess undulate outer and posterior wing margins. This is particularly characteristic of *Daopsychoys dissectus*, *D. inanis* and *Eupypsychoys confinis* (Figs 1, 4, 11). The undulate wing margin is common amongst Mesozoic extinct families with large wings, such as Parakseneuridae and Saucrosmylidae, known also mainly from Daohugou (Yang *et al.* 2012, figs 1, 3, 16, 19; Liu *et al.* 2013, fig. 2). This wing margin construction together with their colour pattern may serve a special

function, for example, for concealing the insect in the Jurassic forest.

Wing trichiation. The veins of the Daohugou Osmylopsychopidae were very probably covered with dense and moderately long to very long macrotrichia like the extant and Jurassic Psychopsidae (Fig. 21A, B, D). Unfortunately, these macrotrichia are not preserved in the majority of wings (Fig. 21C).

Position of Rs1. In the vast majority of the Triassic species (including the undescribed specimens) Rs1 originates from R before Rs proper. The only exception is *Petropsychoys superbus* whose Rs1 originates from Rs proper

(Lambkin 2014, fig. 9). The majority of described species from Daohugou also have this condition of Rs1. Only the osmylopsychopid *Stenopteropsychops trifasciatus* and the psychopsid *Gigantopsychops reticulatus* have the former state (Figs 17, 20). A similar condition is present in some Kalligrammatidae, Ithonidae and Dilaridae, but in these taxa Rs1 is shallowly forked.

Branching of Rs1. Rs1 is usually deeply profusely branched in all described Triassic species. In the Daohugou species, this varies greatly, from being simple for most of its length with few distal branches (e.g. *Ochropsychops multus*), deeply forked once (e.g. *Stenopteropsychops trifasciatus*), to deeply forked three to five times (most other species).

Branching of Rs branches. In the vast majority of the Triassic Osmylopsychopidae the branches of Rs (except Rs1) are mainly simple before the terminal branching ('end-twigging'), i.e. not deeply forked, and almost parallel to each other (state A). The only exception is *Petropsychops superbus* whose Rs branches are mostly deeply forked, and therefore divergent towards the wing margins (state B) (Lambkin 2014, fig. 9). Both states occur in the Daohugou Osmylopsychopidae: *Daopsychops* and *Eupypsychops* have state B, and *Ochropsychops* and *Nematopsychops* state A (although few branches in the latter genera are deeply forked).

Distal Sc and R1. In all known Triassic Osmylopsychopidae these veins are distally fused. This condition remains in the majority of the Middle Jurassic species from Daohugou (Fig. 22A, B). However, in two species of the genus *Eupypsychops*, Sc and R1 approach each other but are not fused (Fig. 22C, D). The forewing venation of this genus is otherwise very similar to that of *Daopsychops*. This fact suggests that some psychopoid species whose Sc and R1 are not fused (e.g. *Actinophlebia*) may belong to Osmylopsychopidae. It pertains especially to *Actinophlebia* sp. from the Early Jurassic of Germany (Ansorge 1996, fig. 52), which possesses most osmylopsychopid features but its Sc and R1 are widely separated distally. Sc and R1 are also not fused in the Early Cretaceous *Undulopsychopsis alexi* (Peng *et al.* 2011), which is most like the species of *Eupypsychops*.

Outer gradate series of crossveins. This series runs along the outer to the posterior margins of the wing connecting the branches of Rs to 1A (at the most). It is present in all species from Daohugou (described above) and *Brongniartiella*, to a somewhat varying extent of development. Such a series is not detected in the described Triassic Osmylopsychopidae, but present in one undescribed species from the Madygen Formation (VM pers. obs.).

Nygmata. Two nygmata (basal and distal) are present in all new genera from Daohugou except *Nematopsychops*.

The basal nygma is located between Rs and M near the wing base; the distal nygma is placed between branches of Rs1 or between Rs1 and Rs2 (as in *Ochropsychops multus*) (Fig. 22E). The basal nygma is not detected in the described Triassic Osmylopsychopidae, but it is located in the same place as in Daohugou species in one undescribed species from the Madygen Formation (VM pers. obs.). The distal nygma in the Triassic Osmylopsychopidae vary in location. In *Osmylopsychops* and *Gayndahpsychops* it is placed anteriorly between Rs3 and Rs5. In undescribed osmylopsychopid specimens from the Madygen Formation, it is located between Rs1 and Rs2, and Rs2 and Rs3. In *Petropsychops*, however, the presumed distal nygma is located between the branches of Rs1, similar to the species from Daohugou.

Brongniartiellidae

The examination of *Brongniartiella gigas* from the Late Jurassic of Solnhofen in Germany (i.e. the type of Brongniartiellidae) clearly shows that the venation of this species does not principally differ from that of the newly described species of Osmylopsychopidae, especially *Daopsychops* and *Eupypsychops*. *Brongniartiella* shares with these genera the following character states: in the forewing, the likely presence of a distal nygma; the presence of a long outer gradate series of crossveins; the dichotomously forked branches of Rs; the deeply forked Rs1; the very similar configurations of MA, MP, CuA and CuP; in the hind wing, R1 (or Sc + R1) is curved posteriorly distally. In general, the wing shape and other visible venation are fully concordant with those of the genera of Osmylopsychopidae. Therefore, Brongniartiellidae is here synonymized with Osmylopsychopidae.

Earlier speculations of the composition and the stratigraphical distribution of Brongniartiellidae (e.g. Martynova 1949, 1962; Zherikhin 1978, 1980; Whalley 1988; Carpenter 1992; Ansorge 1996) were essentially based on incomplete or inadequate original descriptions of the type genus and other genera assigned to this family. Seven Mesozoic genera were treated as belonging to Brongniartiellidae by these authors: *Actinophlebia*, *Epactinophlebia*, *Brongniartiella*, *Mesopsychopsis*, *Paractinophlebia*, *Parhemerobius* and *Pterinoblattina*. The vast majority of species in these genera are represented by poorly preserved or incomplete wings.

Makarkin (2010) proposed to include in the family only the type genus and *Pseudopsychopsis* Makarkin (Early Cretaceous of Transbaikalia, Russia) until other 'brongniartiellid' genera were revised. *Pseudopsychopsis* shares with *Brongniartiella* many character states, e.g. the forewing is broad-oval; the costal space is narrowed towards apex; both the subcostal and R1 spaces broad; few crossveins in the subcostal space; Rs1 is deeply forked; CuA is pectinately branched; CuP is few

branched; the long outer gradate series of crossveins is present. Therefore, it is reasonably assumed that the genus *Pseudopsychopsis* also belongs to Osmylpsychopidae, but the determination of family affinities of other 'brongniartiellid' genera is in need of special research.

The Late Triassic *Triassopsychops superbus*

Triassopsychops superbus from the Late Triassic (Carnian) Blackstone Formation in Australia is thought to be the oldest true psychopsoid (Lambkin 2014), and the only species of Psychopsidae known from the Triassic. It is represented by two specimens, the holotype and a small wing fragment (Lambkin 2014). This species occupies a key position when considering the age of Psychopsidae and earlier divergence of Osmylpsychopidae and Psychopsidae.

Lambkin (2014, fig. 3) considered the wing fragment ACC I.100 as a forewing of *Triassopsychops superbus*. However, the analysis of his drawing and description shows that it might be actually a hind wing: the costal space is not dilated towards the wing base; 1r-m is long and sigmoid; M is very basally divided into MA (= Lambkin's MP) and the basally convex MP (= Lambkin's CuA); CuA (= Lambkin's CuP) is concave. The concave CuA is a feature of a hind wing (Makarkin *et al.* 2009), as well as the long sigmoid 1r-m. The broad costal space is not characteristic of the hind wings of most Neuroptera; however, it is observed in some psychopsoids. The broad costal space of the hind wing is present in many psychopsids, in particular in *Cretapsychops decipiens* Peng.

The holotype of this species is possibly also a hind wing: this wing has very similar venation of respective portions to the wing fragment ACC I.100, although the holotype wing is broken, partially crumpled and flattened, i.e. convexity/concavity relationships of veins are not preserved (Lambkin 2014). If these wings are really conspecific, *Triassopsychops* belongs actually to Osmylpsychopidae (not Psychopsidae) due to the presence of the distal nygmata, a sigmoid vein 1r-m, and the deeply branched Rs1 (= Lambkin's MA and posteriormost branch of Rs). In any case, the family affinity of this species is unclear, and it cannot be considered as belonging to Psychopsidae without further examination.

Extant Psychopsidae

The extant Psychopsidae have been revised (globally or regionally) several times (i.e. Tillyard 1919a; Krüger 1922; Kimmins 1939; Tjeder 1960; New 1989; Oswald 1993a). These studies and the examination of specimens in collections allowed the characterization of their wing venation.

The venation of extant members of the family is characterized by the following character states (Fig. 23): the forewing is broad with longitudinal veins, subcostal veinlets and margins with dense long macrotrichia; the costal space

is very broad throughout (width in the pterostigmal region more than two times the combined width of the adjacent Sc and R1 spaces); the humeral veinlet is recurrent, pectinately branched; the subcostal space has several crossveins; Sc is distally connected by a strong cross-vein with R1 or these veins anastomosing; distal part of R1 (after fusion with Sc or distalmost subcostal crossveins) is usually straight, not curved posteriad (its posterior trace continues the course of the proximal part of R1), with few branches, not or only a few pectinate; branches of Rs are not deeply forked and approximately parallel to the posterior margin; crossveins in the radial space are arranged mostly in 2–3 gradate series; M with two or more deep branches, none of them are pectinately branched distally; CuA and CuP are pectinately branched; 1A is multi-branched.

The hind wing is somewhat (or distinctly) smaller and narrower than the forewing. The venation is in general similar to that of the forewing. The basal crossvein 1r-m is relatively short and straight, sometimes slightly oblique (e.g. *Silveira* Navás; especially strong oblique in some specimens of *S. marshani* McLachlan).

Oswald (1993a) identified two forewing character states as synapomorphies of the Psychopsidae: numerous subcostal crossveins, and very broad costal space in the pterostigmal region. The presence of *vena triplica* (i.e. a complex character formed by Sc, R1 and Rs running parallel to the pterostigmal region, then anastomosed or connected by two distal crossveins between them) was excluded by him from a list of familial synapomorphies. The structure of *vena triplica* is constructed similarly in all extant psychopsid genera (see Tjeder 1960, figs 328–333) and might in principle be considered as synapomorphic for these genera, but we agree with arguments of Oswald (1993a, p. 41) that this is a complex feature consisting of several individual character states.

The following wing character states might be considered as putative synapomorphies of Psychopsidae: (1) the costal space is very broad distally; (2) the distal nygma is lost; (3) 1r-m is short and straight in the hind wing. Also, the distal configuration of R1 (or Sc + R1) is very characteristic of Psychopsidae, but the polarity of this character is hard to determine. These conditions do not occur in a presumed family ground plan of Osmylpsychopidae.

Fossil Psychopsidae

A diagnosis of the whole family (uniting both extant and fossil taxa) was provided by Jepson *et al.* (2012). Based on the venation in extant members, they characterized the psychopsid wing by a combination of the following character states: the costal space very broad throughout; the subcostal space with more than four crossveins; R1 with few branches distally, usually not pectinate; crossveins in the radial space usually arranged in two or three series; CuA and CuP pectinately branched in most species.

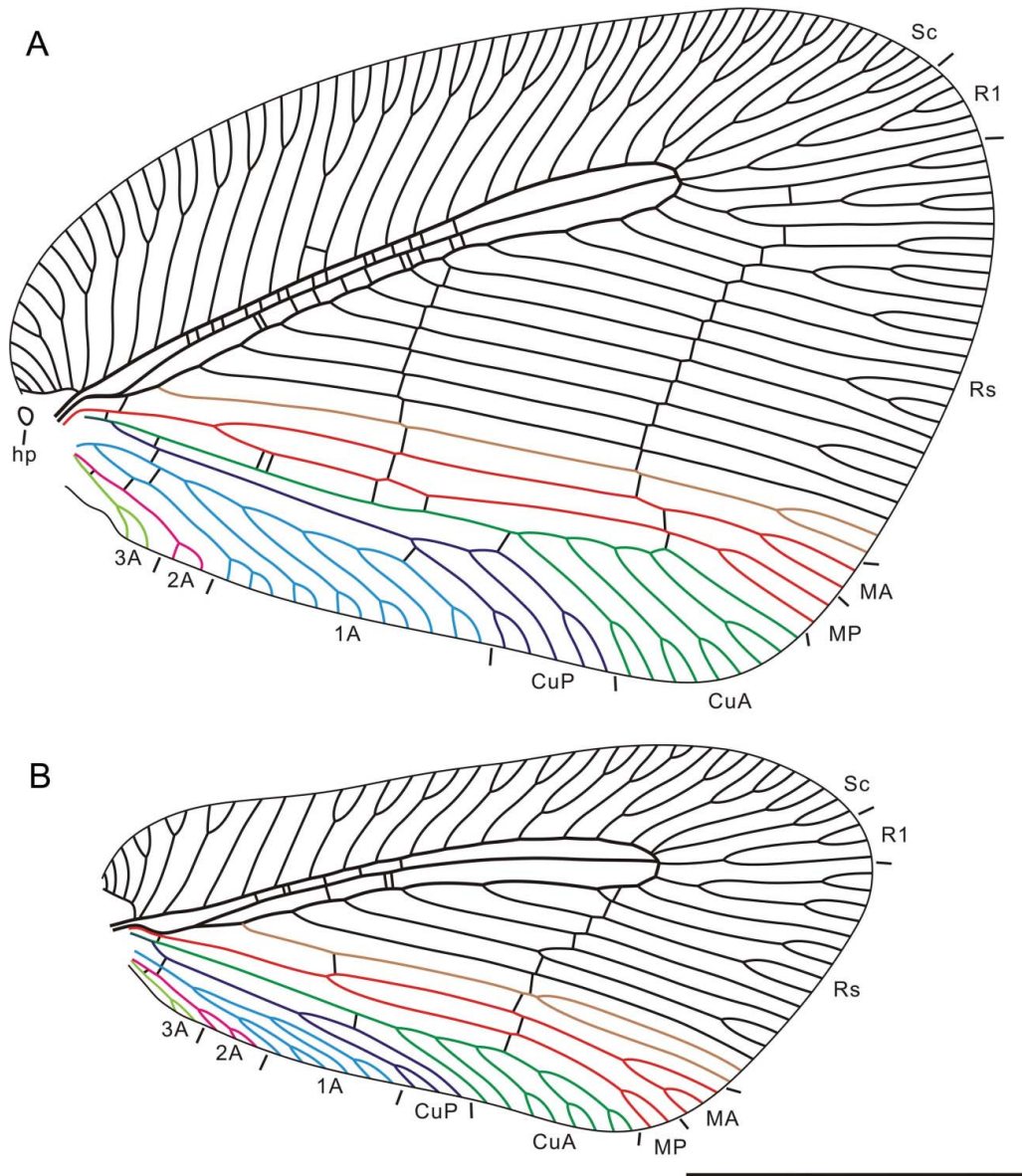


Figure 23. Wing venation of the extant *Balmes birmanus* (McLachlan, 1891) from Yunnan Province, China (TAMUIC). **A**, forewing; **B**, hind wing. Scale bar: 5 mm.

New taxa described above show that numerous subcostal crossveins are often present in Osmolypsychopidae; therefore, we exclude this condition from the list of diagnostic features of Psychopsidae.

Gigantopsyrops reticulatus is of great importance as a species whose wing characters are beautifully preserved. It possesses some character states (particularly, the configuration of M, R1, Rs1 and the costal space) allowing it to be assigned to the family Psychopsidae with confidence. It is one of oldest species in the family. The structure of M is most similar to that of the extant *Megapsyrops illidgei* Froggatt (see New 1989, fig. 196). Such a dichotomous M, as in this species, never occurs in Osmolypsychopidae. Therefore, the deeply dichotomous M might be

included in a list of characters which define the family Psychopsidae. *Gigantopsyrops reticulatus* shows also that in psychopsids CuP can be non-pectinate, and crossveins in the radial space can be irregularly arranged. The pectinate CuP as found in the extant Psychopsidae is probably a derived condition evolving within the family from the dichotomous CuP. Therefore, the pectinate CuP and radial crossveins arranged in series are not characteristics of all members of the family.

In summary, we may conclude (in particular, after the discovery of *Gigantopsyrops reticulatus*) that the wings of Psychopsidae may be distinguished from those of Osmolypsychopidae by a combination of the following character states: in both wings, [1] the costal space is very

broad distally (width in the pterostigmal region more than two times the combined width of the adjacent Sc and R1 spaces); [2] Rs1 is not deeply forked; [3] the distal nygma is lost; [4] the distal R1 (after distalmost subcostal crossveins or its fusion with Sc) is straight, not curved posteriorly (its posterior trace continues the course of proximal R1); in the hind wing, [5] 1r-m is short and straight in the hind wing.

Only one fossil genus has typical family venation, i.e. similar to that of extant members, possessing all the character states of the extant species: *Propsychopsis* Krüger from the Late Eocene of Baltic amber (Krüger 1923; MacLeod 1971). *Litopsychopsis* Engel & Grimaldi (latest Cenomanian Burmese amber) is poorly preserved with very incomplete wings. The fragmentary preserved venation possesses only the character states of the extant species, e.g. [1] and [4], all crossveins in the radial space are arranged in gradate series; CuA is pectinate (Engel & Grimaldi 2008, fig. 4).

The venation of all other known fossil genera differs from that of the extant Psychopsidae in some of the character states. *Baisopsychops* Makarkin (Early Cretaceous of Transbaikalia, Russia) most resembles the extant representatives; it is assigned to Psychopsidae based on the presence in this genus of state [1]–[4], but it has the non-pectinate CuP, and subcostal crossveins are not detected (Makarkin 1997).

Besides *Gigantopsychops reticulatus*, another species is known from Daohugou, *Cretapsychops decipiens*, which was assigned to Psychopsidae (Peng *et al.* 2010). Its venation and colour pattern are most similar to *Baisopsychops*, but it has some forewing features not characteristic of Psychopsidae: MA and R1 are pectinately branched; R1 is slightly curved posteriorly; the costal space is slightly narrowed towards the apex. In general, the venation of *Cretapsychops decipiens* is intermediate between that of Osmylopsychopidae and Psychopsidae. Theoretically, it may be considered in both families, as an advanced taxon of Osmylopsychopidae, or as a primitive taxon of Psychopsidae. Further investigations of this species (particularly its hind wing venation) should resolve this problem.

Many other Cretaceous species are considered as belonging to Psychopsidae (e.g. Jepson *et al.* 2009, 2012; Makarkin 2010; Makarkin *et al.* 2012). Also some species are known from the Jurassic (e.g. Martynova 1949, 1962; Panfilov 1980). Their venation greatly differs from that of extant members. Unfortunately, all of them are represented by incomplete wings, not allowing detailed comparison.

Conclusion

The families Osmylopsychopidae and Psychopsidae are undoubtedly closely related to each other. The new taxa described in this paper are very important in

distinguishing them. It is clear now that the family Osmylopsychopidae was a dominant psychopsoid group during the Mesozoic (at least in the Triassic to Jurassic), and Psychopsidae was relatively rare, at least in the Jurassic. The diversity of Psychopsidae was higher in the Early Cretaceous, but psychopsid affinities of these taxa are in need of confirmation. One of the main crucial periods in the evolution of Neuroptera is the terminal Triassic to Early Jurassic. Psychopsoids were quite diverse during this interval. Many of them are of uncertain family position due to their incomplete nature or poor preservation of their wings. Further examination of psychopsoids of that period should help to ultimately resolve their classification.

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