

Palaeontinidae (Insecta: Hemiptera: Cicadomorpha) from the Upper Jurassic Solnhofen Limestone of Germany and their phylogenetic significance

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Abstract – The Palaeontinidae (Insecta: Cicadomorpha) from the Upper Jurassic Solnhofen Limestone of Bavaria are revised. The diagnostic characters for three monotypic genera *Eocicada* Oppenheim, 1888, *Prolystra* Oppenheim, 1888 and *Archipsyche* Handlirsch, 1906 are reassessed based on newly discovered material. *Beloptesis gigantea* (Weyenbergh, 1874), *B. oppenheimi* Handlirsch, 1906, *Limacodites mesozoicus* Handlirsch, 1906, and *Protopsyche braueri* Handlirsch, 1906 are considered to be junior synonyms of *Prolystra lithographica* Oppenheim, 1888. *Eocicada lameerei* Handlirsch, 1908 is a junior synonym of *E. microcephala* Oppenheim, 1888. A key to the species of Solnhofen Palaeontinidae is presented. Solnhofen Palaeontinidae and most Cretaceous Palaeontinidae most probably form a monophyletic group based on the following characters: costal area narrow, vein RA branching from stem R basally, vein ScP not fused with vein RA, clavus much reduced and hindwing smaller. Furthermore, Solnhofen Palaeontinidae are probably basal to Cretaceous Palaeontinidae by the mesonotum lacking distinct longitudinal carinae. A fast succession from early to more derived Palaeontinidae took place during Late Jurassic times. Early Palaeontinidae declined sharply in the Late Jurassic, probably owing to the rise of newly evolved insectivorous animals like early birds and mammals. Late Palaeontinidae with better flight ability survived and became a dominant insect group during latest Jurassic times.

Keywords: Insecta, Palaeontinidae, Solnhofen, Late Jurassic, Germany.

1. Introduction

The Solnhofen Limestone of Bavaria, southern Germany, is one of the most famous Jurassic Fossil-Lagerstätten. It was deposited in the Tithonian stage of the Late Jurassic epoch, and represents a lagoonal environment located in the semi-arid subtropical belt (Barthel, Swinburne & Morris, 1990). The limestone yields abundant marine fossils, such as fishes, crinoids and ammonites (Barthel, Swinburne & Morris, 1990). Terrestrial organisms are much rarer and are represented by two theropod dinosaurs (*Compsognathus* and *Juravenator*) and some lizards, and species capable of flight, including the earliest bird *Archaeopteryx*, numerous pterosaurs and insects (Barthel, Swinburne & Morris, 1990; Kemp, 2001; Göhlich & Chiappe, 2006). Of the terrestrial fossils, insects are undoubtedly the most diverse group. Eleven orders have so far been described, although some taxa still await further investigation and interpretation (Frickhinger, 1994, 1999). As the only representative of Cicadomorpha within Hemiptera from Solnhofen, Palaeontinidae were first described by Weyenbergh (1874) as cicadas, and

later some new specimens were added by Oppenheim (1888) and Haase (1890). Since Handlirsch's (1906) synopsis of all Solnhofen Palaeontinidae comprising eight species within six genera, no detailed research has been made on these giant insects. However, because of poor preservation, the Solnhofen Palaeontinidae were misinterpreted with respect to their body morphology and wing venation by early researchers, although their outline was sometimes figured properly (Fig. 1). Therefore, the poor preservation and fallacious descriptions make the earlier systematic assignments of these specimens questionable: included in Lepidoptera by Handlirsch (1906); placed in Palaeontinidae by Carpenter (1932) and Hamilton (1992); excluded from 'Homoptera' by Evans (1956); and attributed to uncertain 'Homoptera' in the Treatise on Invertebrate Paleontology by Carpenter (1992). Up to now, the Solnhofen group is the best fossil record of Late Jurassic Palaeontinidae and the most important clue for understanding their diversification in the Cretaceous (Wang, Zhang & Szwedo, 2009). Therefore, an exhaustive reinvestigation and modern reinterpretation of their phylogenetic relationship and evolutionary significance is announced in the present work. Recently, some Middle Jurassic and Early Cretaceous

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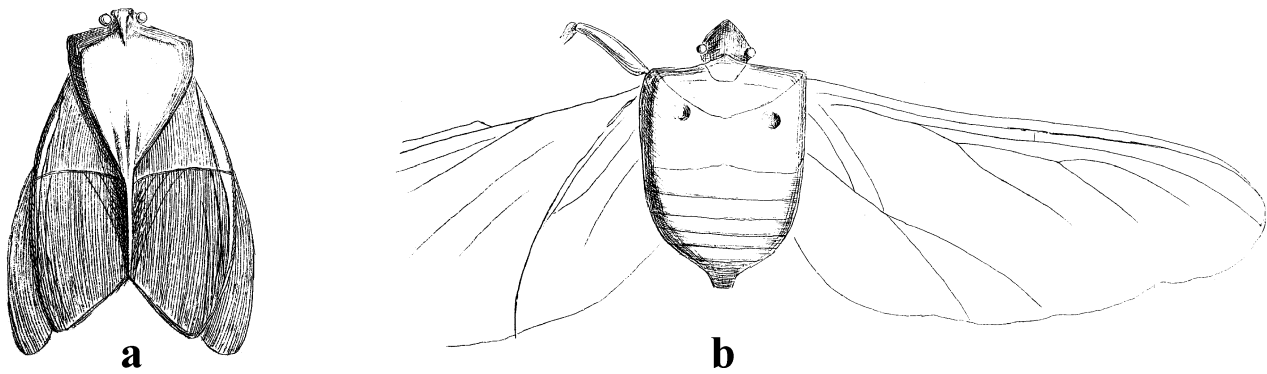


Figure 1. Drawings by Oppenheim (1888). (a) Holotype of *Prolystra lithographica*. (b) Holotype of *Eocicada microcephala*.

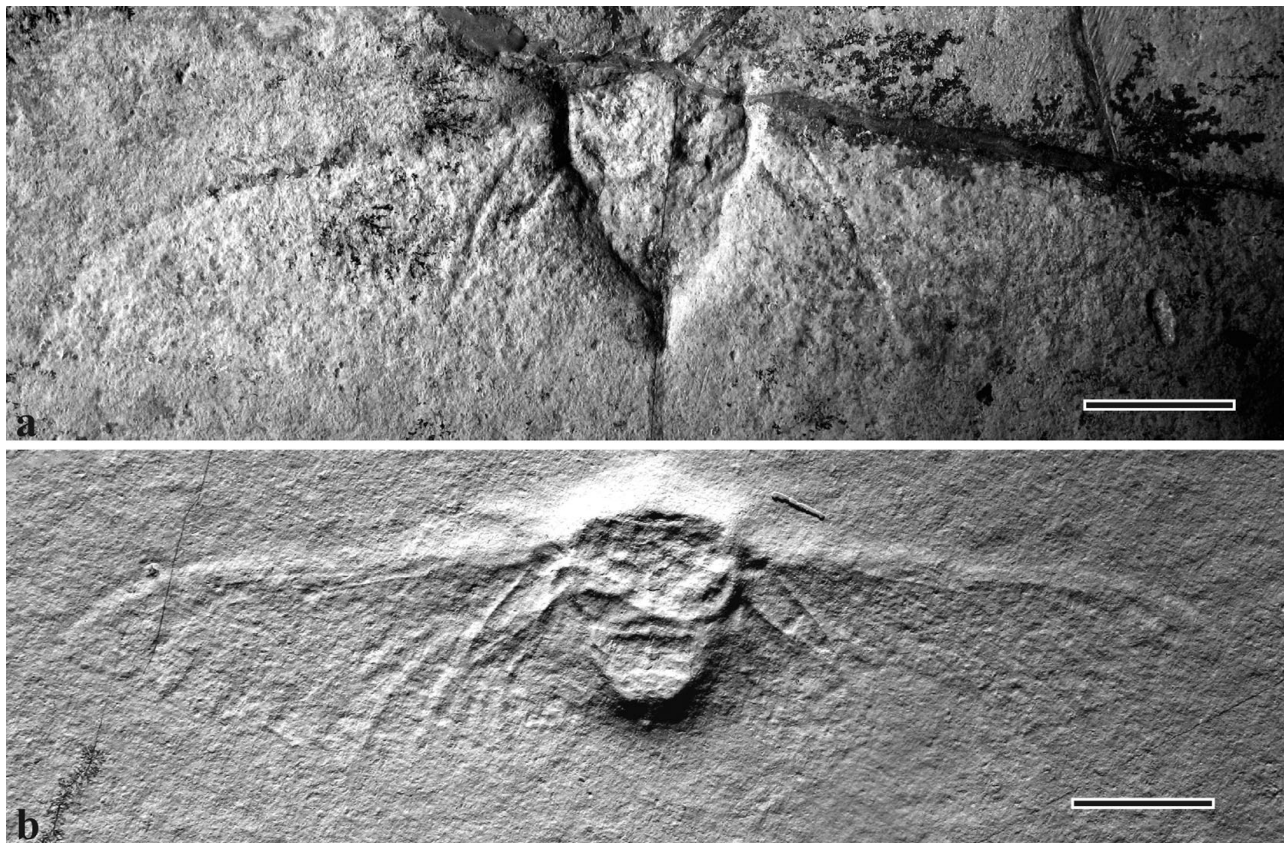


Figure 2. *Eocicada microcephala* Oppenheim, 1888. (a) JME SOS2050. (b) A well-preserved specimen deposited at the Museum Bergér. Scale bars represent 20 mm. For a colour version of this figure see online Appendix at <http://journals.cambridge.org/geo>.

palaeontinids from China and Brazil provided some new insights into important morphological structures and the evolution of Palaeontinidae (Menon, Heads & Martill, 2005; Wang, Ren & Shih, 2007; Wang, Zhang & Szwedo, 2009). These advancements paved the way for the present study of Solnhofen Palaeontinidae.

2. Material and methods

'Solnhofen fossil' represents any specimen from the Upper Jurassic Limestone of the Solnhofen area, Bavaria, southern Germany (Burnham, 2007). All fossils are preserved in lithographic limestones ('Plattenkalk'), which is a special type of fine-grained, flat-

cleaving limestone (Barthel, Swinburne & Morris, 1990). Although the fossils are from different outcrops and may be of slightly different ages, their general age is confined to the Early Tithonian, around 151 Ma (Kemp, 2001; Göhlich & Chiappe, 2006; Ogg, Ogg & Gradstein, 2008).

Up to now, almost all Solnhofen Palaeontinidae are preserved with body and wings (e.g. Figs 1, 2), even though some of them are strongly deformed. The preservation of articulated Palaeontinidae supports the previous conclusion that Solnhofen insects have relatively short drifting periods (Tischlinger, 2001), and that the bottom environment of the lagoon was very calm (Barthel, Swinburne & Morris, 1990).

However, most of the Solnhofen Palaeontinidae lost morphological details during diagenesis: wing colour patterns are invisible; the outer margin and apex of the forewings are sometimes destroyed; the wing venation, particularly the shape of the discal cell, is often unclear; and their bodies are sometimes strongly deformed.

Handlirsch (1906) listed eight species of Solnhofen Palaeontinidae. These holotypes, except for three probably lost specimens, are still accessible. We examined several poorly preserved types using photographs, because detailed photos are clear enough to show the diagnostic characters. The holotypes of *Prolystra lithographica* and *Eocicada microcephala* (Fig. 1) were originally stored at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (BSPGM). In 1934, these two specimens, together with some other German fossil insects were borrowed by Friedrich E. Zeuner, when he worked at the British Museum of Natural History in London (BMNH). After World War II, some of Zeuner's specimens were returned to Germany by Walter G. Kühne, who deposited them at the Natural History Museum of Humboldt University in Berlin (ZMB). Unfortunately, we have not found these two holotypes in the collections above and perhaps they were lost in Germany or Britain during World War II. The holotype of *Beloptesis gigantea* is deposited at the Teylers Museum in Haarlem, Netherlands. It is poorly preserved and only a sketchy shape of body and wings is distinguishable. This specimen was examined for the present study via the photograph in Frickhinger (1994). The holotype of *Limacodites mesozoicus* and another poorly preserved palaeontinid specimen (BaJ1591 and BaJ1592) are housed at the Senckenberg Naturhistorische Sammlungen Dresden (SNSD). They were examined with help of detailed photos. Three holotypes (separately of *Archipsyche eichstattensis*, *Protopsyche braueri* and *Beloptesis oppenheimi*) from the Museum of Natural History, Vienna, Austria (NHMW) were also re-examined. The holotype of *Eocicada lameerei* was originally deposited at the 'Geological Institute of the Brussels University', but it has not been found yet. A poorly preserved specimen mentioned by Handlirsch (1906) was housed at the National Museum, Prague (NM), and was re-examined using detailed photos. Furthermore, eight new Solnhofen specimens, of which six are housed at the Jura Museum Eichstätt (JME), one at the Staatliches Museum für Naturkunde Stuttgart (SMNS), and one in a private collection (Museum Bergér in Eichstätt), were examined.

Each forewing reconstruction is based on several specimens. In drawings, dashed lines denote the nodal line in the forewing, and dotted lines indicate faintly seen and hypothesized missing veins. Considering that the nomenclature espoused by Becker-Migdisova (1949) has been used in most of the literature on palaeontinids, and in order to avoid taxonomic confusion, we followed the traditional terminologies with slight modifications (Wang, Zhang & Szewo, 2009).

3. Systematic palaeontology

Order HEMIPTERA Linnaeus, 1758
 Infraorder CICADOMORPHA Evans, 1946
 Superfamily PALAEONTINOIDEA Handlirsch, 1906
 Family PALAEONTINIDAE Handlirsch, 1906

Key to the species of Palaeontinidae from the Upper Jurassic of Germany:

- (1) Body slender; mesonotum almost as wide as abdomen; forewing small (length 33–36 mm): *Archipsyche eichstattensis*
 – Body sturdy; mesonotum wider than abdomen; forewing medium-sized or large (length > 40 mm)
 (2) Wings commonly folded; forewing medium-sized (43–46 mm): *Prolystra lithographica*
 – Wings commonly spread out; forewing large (65–75 mm): *Eocicada microcephala*

Genus *Eocicada* Oppenheim, 1888

Type species. *Eocicada microcephala* Oppenheim, 1888; by original designation and monotypy.

Type horizon and locality. Solnhofen Formation, Upper Jurassic (Early Tithonian); Eichstätt, Bavaria, Germany.

Revised diagnosis. Body robust. Mesonotum wider than abdomen. Forewing triangular, length 65–75 mm, maximum width (at the middle of wing) about 30 mm; vein Sc unbranched; veins RA, RP and M separating at one point; branch RP subparallel to branch RA; antenodal region trapezoid; postnodal region reduced; clavus narrow, less than one-third of wing length. Hindwing small, about half as long as forewing.

Eocicada microcephala Oppenheim, 1888
 Figures 2, 3b

- 1888 *Eocicada microcephala*: Oppenheim, p. 229, plate 31, fig. 30.
 1890 *Eocicada microcephala*: Haase, p. 16, fig. 6.
 1898 *Eocicada microcephala*: Meunier, plate 6, fig. 6.
 1906 *Eocicada microcephala*: Handlirsch, pp. 626–7, plate L, figs 7–9.
 1906 *Eocicada lameerei*: Handlirsch, p. 627, plate L, figs 10–12.
 1932 *Eocicada microcephala*: Carpenter, p. 121.
 1994 *Limacodites mesozoicus*: Frickhinger, pp. 152, fig. 303.
 1994 *Protopsyche braueri*: Frickhinger, p. 153, fig. 305.
 1999 *Limacodites mesozoicus*: Frickhinger, p. 60, fig. 107.

Examined material. JME SOS2050, a poorly preserved specimen, part and counterpart. A well-preserved specimen without collection number, part and counterpart, deposited at the Museum Bergér (private collection).

Description. Body length 31–33 mm (Table 1). Head small and subtriangular. Mesonotum length about 13 mm, width about 23 mm, without distinct longitudinal carinae. Abdomen pointed posteriorly. Forewing large. Nodal indentation clear, at basal 0.4 wing length. Branch RA departing from stem R+M at the same level of cross-vein r+m-cua, slightly recurved at nodal line, subparallel to costal margin beyond nodal line. Branch RP dividing from stem R+M at vein RA departing from stem R+M, arched anteriorly for remaining part. Stem M slightly bifurcating basal of nodal indentation. Stem M₁₊₂ branching into veins M₁ and M₂ at about the middle of wing. Branches M₁ and M₂ recurved posteriorly.

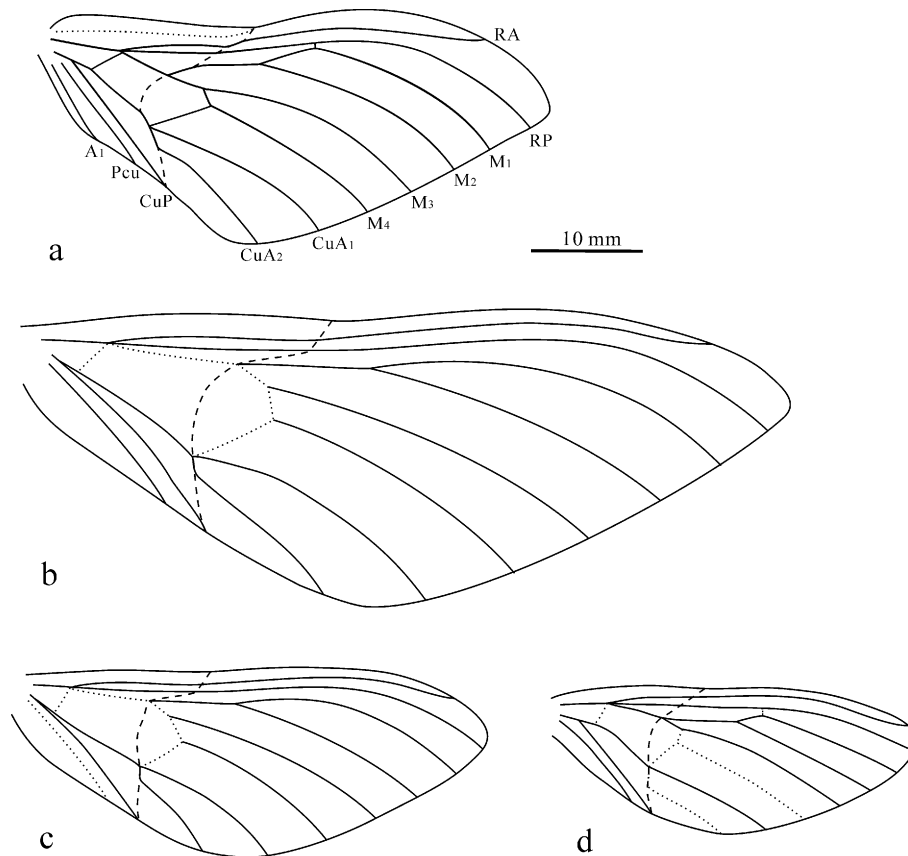


Figure 3. Reconstruction of forewings. (a) *Ilerdocossus fengningensis* (Ren, Yin & Dou, 1998) from the Early Cretaceous Yixian Formation of China. (b) *Eocicada microcephala*. (c) *Prolystra lithographica*. (d) *Archipsyche eichstattensis*. All to scale.

Table 1. Measurements of Solnhofen Palaeontinidae (in mm)

Specimen	Forewing length	Forewing width	Body length
JME SOS2050	~70	~34	~33
Private collection	74	27	~31
NHMW2007z0142/0002	44	23	33
NHMW2007z0142/0004	46	21	34
BaJ1591	43	23	33
SMNS specimen	45	20	34
NH4034	43	20	33
JME SOS4882	44	20	32
JME SOS3602			~30
JME SOS4881	>40		
NHMW2007z0142/0003	~32	~16	~23
BaJ1592	~35		~25
JME SOS1821	~35	16	25

Branch M_3 subparallel to branch M_2 . Branch M_4 directed posteriorly, geniculate at junction with cross-vein m_4 -cua, and then subparallel to vein M_3 . Branch CuA nearly straight, straight between cross-veins $r+m$ -cua and m_4 -cua, recurved at junction with cross-vein m_4 -cua, and then branching into veins CuA₁ and CuA₂ at about the same level of initial division of stem M. Discal cell large; antenodal region trapezoid, about twice as long as postnodal region. Branch CuP thick, dividing from stem Cu near base. Vein Pcu slightly arched.

Discussion. All the reported specimens of *E. microcephala* retain the same embedding position, in which the wings are spread out on each side of the body. These specimens

with the ‘butterfly’ position allow a detailed examination of wing size and wing venation. *E. microcephala* was erected and placed in the ‘Homoptera’ by Oppenheim (1888) on the basis of a poorly preserved specimen with forewings and hindwings spread. Later, Handlirsch (1906) erected *E. lameerei* based on a better preserved specimen, and distinguished it from the type species by the different forewing venation and the much smaller hindwing. Judging from the original description and photos, however, the forewing venation of *E. lameerei* is not distinctly different from that of *E. microcephala*. Furthermore, the hindwings of *E. microcephala* had not been correctly outlined by early researchers (see detailed discussion below). In fact, both *E. lameerei* and *E. microcephala* possess small hindwings which are about half as long as their respective forewings. The variation in the wing size probably demonstrates intraspecific differences, a common phenomenon in Mesozoic Palaeontinidae (Wang *et al.* 2008). Therefore, *E. microcephala* and *E. lameerei* are considered herein to belong to the same species, and *E. lameerei* is a junior synonym of *E. microcephala*.

Two well-preserved specimens were earlier attributed to *Limacodites mesozoicus* by Frickhinger (1994, fig. 303; 1999, fig. 107). However, judging from the original photograph and description, the large and triangular forewings (70–80 mm) indicate that the above two specimens belong to *E. microcephala*. Additionally, the specimen placed in *Protopsyche braueri* by Frickhinger (1994, fig. 305) is most probably attributed to *E. microcephala* by its wide body, large mesonotum and triangular forewings. This specimen is very similar to two specimens (JME SOS2050 and the specimen deposited at the Museum Bergér) described in the present work. The estimated length of its wing span

by Frickhinger (100 mm; in Frickhinger, 1994, p. 152) was probably erroneous.

Genus *Prolystra* Oppenheim, 1888

1888 *Prolystra* Oppenheim, p. 228.

1890 *Cicadite* Haase, p. 18.

1906 *Protopsyche* Handlirsch, p. 623.

1906 *Beloptesis* Handlirsch, p. 625.

Type species. *Prolystra lithographica* Oppenheim, 1888; by original designation and monotypy.

Type horizon and locality. Solnhofen Formation, Upper Jurassic (Early Tithonian); Eichstätt, Bavaria, Germany.

Revised diagnosis. Body robust. Mesonotum width about 20 mm, clearly wider than abdomen. Forewing triangular, length 43–46 mm; vein Sc unbranched; veins RA, RP and M separating at one point. Hindwing small; vein M 4-branched.

Discussion. The genus is similar to *Eocicada* by the robust body and wide mesonotum, but differs from the latter in having the medium-sized forewing.

Prolystra lithographica Oppenheim, 1888
Figures 3c, 4

1874 *Cicada gigantean*: Weyenbergh, p. 101, plate 3, fig. 4.

1888 *Prolystra lithographica*: Oppenheim, pp. 228–9, plate 31, fig. 1.

1890 *Cicadites gigantea*: Haase, p. 18, fig. 7.

1906 *Protopsyche braueri*: Handlirsch, pp. 623–4, plate XLIX, figs 17, 18.

1906 *Prolystra lithographica*: Handlirsch, pp. 624–5, plate XLIX, figs 20–23.

1906 *Beloptesis oppenheimi*: Handlirsch, pp. 625–6, plate L, figs 3–5.

1906? *Beloptesis gigantea*: Handlirsch, p. 626, plate L, fig. 6.

1994 *Beloptesis gigantea*: Frickhinger, p. 152, fig. 301.

1994 *Eocicada lameerei*: Frickhinger, p. 152, fig. 302.

Examined material. NHMW2007z0142/0002 (holotype of *Protopsyche braueri*); NHMW2007z0142/0004 (holotype of *Beloptesis oppenheimi*); BaJ1592, NH4034, JME SOS4882, complete but poorly preserved; JME SOS3602 (part and counterpart) and JME SOS4881, both incomplete and strongly deformed; and a poorly preserved specimen without collection number deposited at SMNS.

Description. Body length 30–34 mm (Table 1). Head small and subtriangular. Mesonotum without distinct longitudinal carinae. Abdomen pointed posteriorly. Forewing medium-sized. Branch RA departing from stem R+M at the same level of cross-vein r+m-cua. Stem M slightly bifurcating basal of nodal indentation. Stem M₁₊₂ branching into veins M₁ and M₂ at about the middle of wing. Discal cell large and antenodal region trapezoid. Branch CuP thick, dividing from stem Cu near base.

Discussion. *P. lithographica* is the most common palaeontinid from Solnhofen. Contrary to *E. microcephala*, most of the *P. lithographica* specimens possess the wings folded at the body. Handlirsch (1906) erected four species based on the poorly preserved specimens with wings folded, but at the same time he suggested that *Prolystra lithographica*,

Beloptesis oppenheimi and ?*Beloptesis gigantean* were probably the same species. After re-examining the holotype, Frickhinger (1994) also regarded ?*Beloptesis gigantea* as an invalid species. Furthermore, because Handlirsch (1906) regarded them as Lepidoptera, he misinterpreted the wing venation, and even added some veins in his reconstructions (such as Handlirsch, 1906, plate XLIX, figs 15, 23). Evidently, the diagnostic characters showed by Handlirsch (1906) are not valid. Based on our re-examination, it is impossible to assign these specimens to different taxa and, therefore, they are regarded now as members of only one species.

A specimen with deformed forewings was originally placed in *E. lameerei* by Frickhinger (1994, fig. 302). However, the wing size (about 50 mm in Frickhinger, 1994) indicates that the individual belongs to *P. lithographica*.

Genus *Archipsyche* Handlirsch, 1906

1906 *Limacodites* Handlirsch, p. 622.

Type species. *Archipsyche eichstattensis* Handlirsch, 1906; by original designation and monotypy.

Type horizon and locality. Solnhofen Formation, Upper Jurassic (Early Tithonian); Eichstätt, Bavaria, Germany.

Revised diagnosis. Body slender, length about 25 mm. Mesonotum almost as wide as abdomen. Forewing triangular, length about 33–36 mm, width about 16 mm; vein Sc unbranched; veins RA, RP and M separating at one point; branch CuA bifurcating basal of the level of nodal indentation.

Discussion. *Archipsyche* is different from other Solnhofen genera by the smaller forewing (Handlirsch, 1906; Carpenter, 1932). Because of the lack of detailed venational characters, a thorough comparison is currently impossible.

Archipsyche eichstattensis Handlirsch, 1906
Figures 3d, 5

1906 *Archipsyche eichstattensis*: Handlirsch, p. 624, plate L, figs 1, 2.

1906 *Limacodites mesozoicus*: Handlirsch, pp. 622–3, plate XLIX, figs 12–15.

1999 *Eocicada lameerei*: Frickhinger, p. 61, fig. 106.

Examined material. NHMW2007z0142/0003, holotype, poorly preserved, part and counterpart; BaJ1591 (holotype of *Limacodites mesozoicus*), wings unclear and body strongly deformed, part and counterpart; JME SOS1821, wings and body clear, part and counterpart.

Description. Body slender, length about 25 mm (Table 1). Mesonotum width about 10 mm. Forewing small, with distinct nodal indentation. Branch RA departing from stem R+M at the same level of cross-vein r+m-cua. Stem M slightly bifurcating basal of nodal indentation. Stem M₁₊₂ branching into veins M₁ and M₂ at about middle of wing. Branch CuA branching into veins CuA₁ and CuA₂ at about the same level of initial division of stem M. Discal cell large. Branch CuP thick, dividing from stem Cu near base. Vein Pcu slightly arched.

Discussion. The specimen attributed to *A. eichstattensis* by Frickhinger (1994, fig. 300) is an alder fly (Neuroptera). The specimen placed in *E. lameerei* by Frickhinger (1999, fig. 106) probably belongs to *A. eichstattensis*, with its narrow body and small, short forewings.

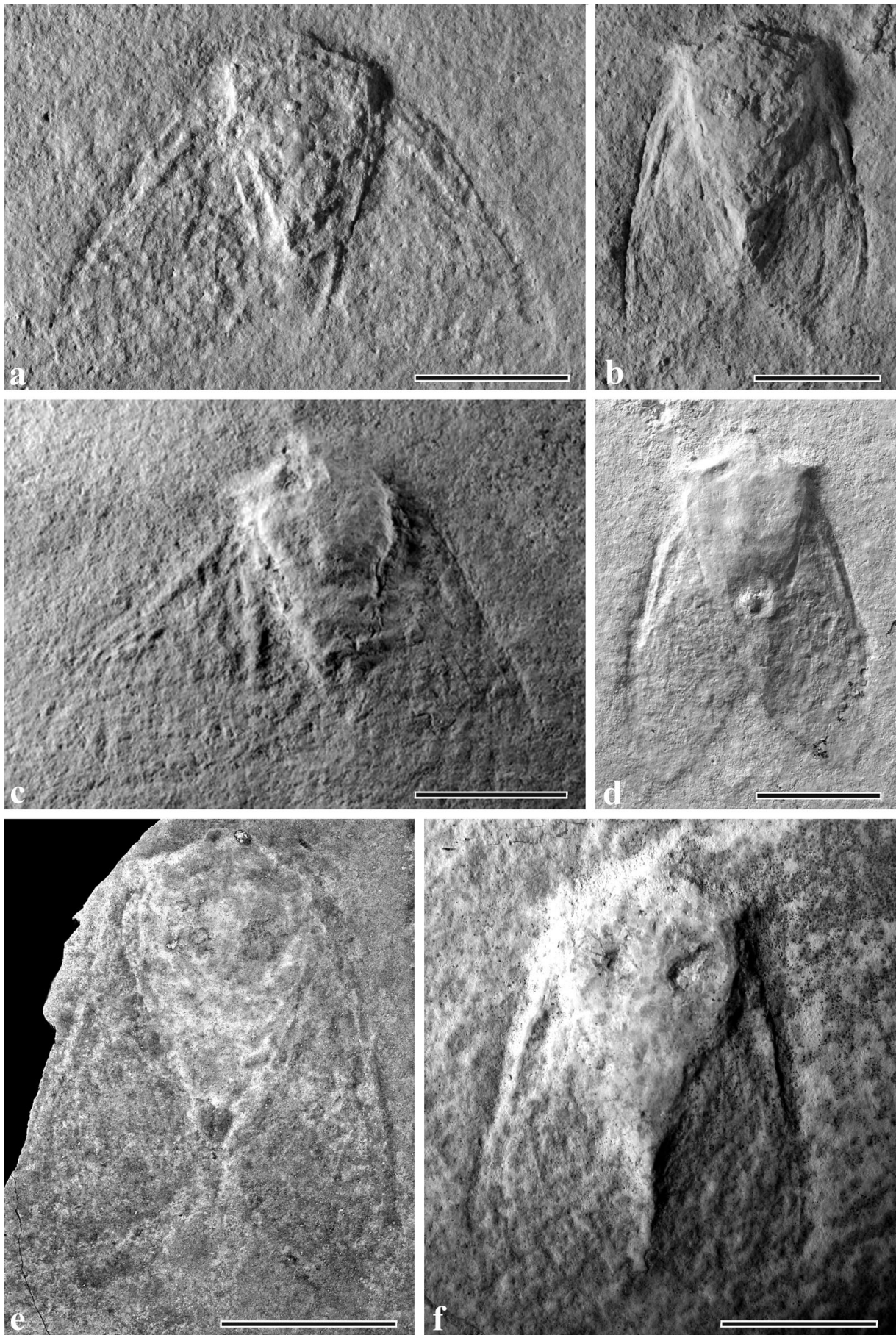


Figure 4. *Prolystra lithographica* Oppenheim, 1888. (a) NHMW2007z0142/0002. (b) NHMW2007z0142/0004. (c) BaJ1592. (d) NH4034. (e) JME SOS4882. (f) A poorly preserved specimen deposited at SMNS. Scale bars represent 20 mm. For a colour version of this figure see online Appendix at <http://journals.cambridge.org/geo>.



Figure 5. *Archipsyche eichstattensis* Handlirsch, 1906. (a) Holotype, NHMW2007z0142/0003. (b) BaJ1591. (c) JME SOS1821. Scale bars represent 20 mm. For a colour version of this figure see online Appendix at <http://journals.cambridge.org/geo>.

4. Discussion

Based on forewings and hindwings, Mesozoic Palaeontinidae are divided into two groups: early Palaeontinidae (most living in the Jurassic) and late Palaeontinidae (most living in the Cretaceous) (Wang, Zhang & Szwedo, 2009). Solnhofen Palaeontinidae are clearly more closely related to the late Palaeontinidae, and together with the Cretaceous taxa they most probably form a monophyletic group based on the following characters (Figs 3, 6): 1, forewing with costal area narrow; 2, vein RA branching from stem R basally; 3, vein ScP not fused with vein RA; 4, clavus much reduced; 5, hindwing smaller. A definite result awaits a future cladistic analysis.

Palaeontinidae possesses both a narrow pronotum and a large mesonotum (Fig. 2; Ren, Yin & Dou, 1998; Wang, Zhang & Fang, 2008). Cretaceous Palaeontinidae possesses a particular mesonotum with some longitudinal

carinae. For example, *Ilerdocossus* from the Lower Cretaceous of Spain and China have a mesonotum with about 15 longitudinal carinae (Wang, Zhang & Fang, 2008). Brazilian Palaeontinidae also preserve some longitudinal mesonotal carinae (Menon & Heads, 2005, fig. 1B; Menon, Heads & Martill, 2005, fig. 5a). However, these carinae are completely absent or only weakly developed in Jurassic Palaeontinidae. In addition, no trace of longitudinal carinae has been discovered from well-preserved Solnhofen Palaeontinidae (e.g. Figs 2b, 4b). Therefore, the presence of distinct longitudinal mesonotal carinae is probably a synapomorphy of Cretaceous Palaeontinidae (character 6 in Fig. 6) and Solnhofen Palaeontinidae are basal to the Cretaceous taxa because their mesonotum is lacking distinct longitudinal carinae.

Triassic Dunstaniidae and early Palaeontinidae retain large hindwings (Wootton, 2003; Wang, Zhang & Szwedo,

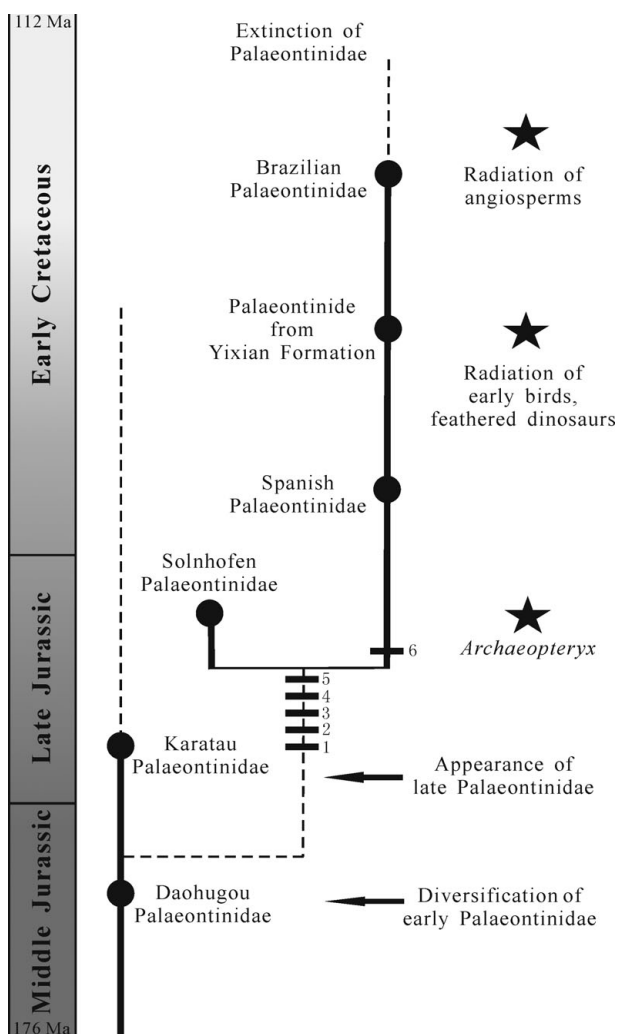


Figure 6. The evolution of late Mesozoic Palaeontinidae. Five synapomorphies of Late Palaeontinidae and one synapomorphy of Cretaceous Palaeontinidae. 1, forewing with costal area narrow; 2, vein RA branching from stem R basally; 3, vein ScP not fused with vein RA; 4, clavus largely reduced; 5, hindwing smaller, about half length of its forewing; 6, mesonotum with distinct longitudinal carinae. The time scale is from Ogg, Ogg & Gradstein (2008).

2009). For example, the ratio of forewing/hindwing length of most Middle Jurassic Palaeontinidae is about 1.5 (Fig. 7d; Wang *et al.* 2008). However, late Palaeontinidae (including Solnhofen representatives) possess small hindwings about only half the length of their forewings. Due to the decrease of the hindwing size, the forewing and hindwing jointly form a distinct triangular shape when coupled together (Fig. 2). In Solnhofen Palaeontinidae, the forewing and hindwing are sometimes so closely coupled that they look like a single wing (Fig. 2). This is the reason why early researchers did not distinguish them correctly when they drew some poorly preserved Solnhofen specimens (Fig. 1b).

The hindwings in the Hemiptera are held together with forewings by a wing-coupling apparatus during flight (Gorb & Perez-Goodwyn, 2003). In singing cicadas, forewing and hindwing are locked together by the wing-coupling fold of the forewing and the wing-coupling lobe

of the hindwing (Ossiannilsson, 1950; D'Urso & Ippolito, 1994). This type of wing-coupling apparatus was found in most extant Cicadomorpha (J. Chu, unpub. Master thesis, Univ. Wyoming, 1971; Dworakowska, 1988), and was also clearly observed in excellently preserved palaeontinids from the Middle Jurassic of Daohugou (Fig. 7). This apparatus consists of a longitudinal groove (wing-coupling fold) on the hind margin of the forewing clavius, situated near the junction of vein Pcu and hind margin, and of a hook (wing-coupling lobe) on the anterior margin of the hindwing, situated somewhat distally of the nodal indentation of the latter. The wing-coupling fold represents a deflexed part of the hind margin of the forewing, and the wing-coupling lobe is an upwards retroflected part of the anterior margin of the hindwing. During flight, the wings were held together by the wing-coupling lobe catching the wing-coupling fold. In the forewing, vein Pcu thickens and veins A₁ and A₂ end in the hind margin to strengthen the structure of the wing-coupling fold. In the hindwing, veins Sc and RA₁ terminate in the anterior margin basal and distal of the wing-coupling lobe, respectively, to strengthen the structure of wing-coupling lobe as well. The connection between the hindwing and the forewing can also be observed in some palaeontinids which retain the original buoyant position (Fig. 7d; Menon, Heads & Martill, 2005). The cicada-like coupling apparatus was probably present in all palaeontinids. These structures probably provide some useful information for the phylogenetic system of hemipterous insects (D'Urso & Ippolito, 1994). However, detailed structures of the coupling apparatus were not observed in Palaeontinidae so far. Besides the cicada-like coupling apparatus, the Triassic Dunstaniidae (represented by *Fletcheriana triassica* Evans, 1956) and most Jurassic Palaeontinidae possess another type of wing-coupling mechanism. They retain an elliptical or subtriangular forewing overlapped with a round hindwing, showing a butterfly-like overlap (amplexi-form): the wide clavus of the forewing is overlapped by the wide costal area of the hindwing by air pressure during flight (Wootton, 2003). The amplexi-form was modified in latest Jurassic Palaeontinidae because Solnhofen Palaeontinidae possessed a forewing with a narrow clavus (character 4 in Fig. 6) and a smaller hindwing (character 5 in Fig. 6).

The evolution of wing structures and flight performance of Palaeontinidae was analysed by Wootton (2003), whose conclusion was further supported by the newly discovered Palaeontinidae from the Middle Jurassic and Early Cretaceous (Wang, Zhang & Szwed, 2009). The triangular forewings, reduced hindwings and modified amplexi-form show that late Palaeontinidae evolved from moderately versatile to highly versatile flyers (Wootton, 2003). Furthermore, the presence of a reduced costal area and the rigid basal leading edge of the forewings of late Palaeontinidae also indicate an improvement of the flight ability (Wang, Zhang & Szwed, 2009). The so-far last known assemblage of early Palaeontinidae occurred in the Middle–Upper Jurassic Karabastau Formation (Callovian to Oxfordian–Kimmeridgian) of Karatau, southern Kazakhstan (Polyansky & Doludenko,

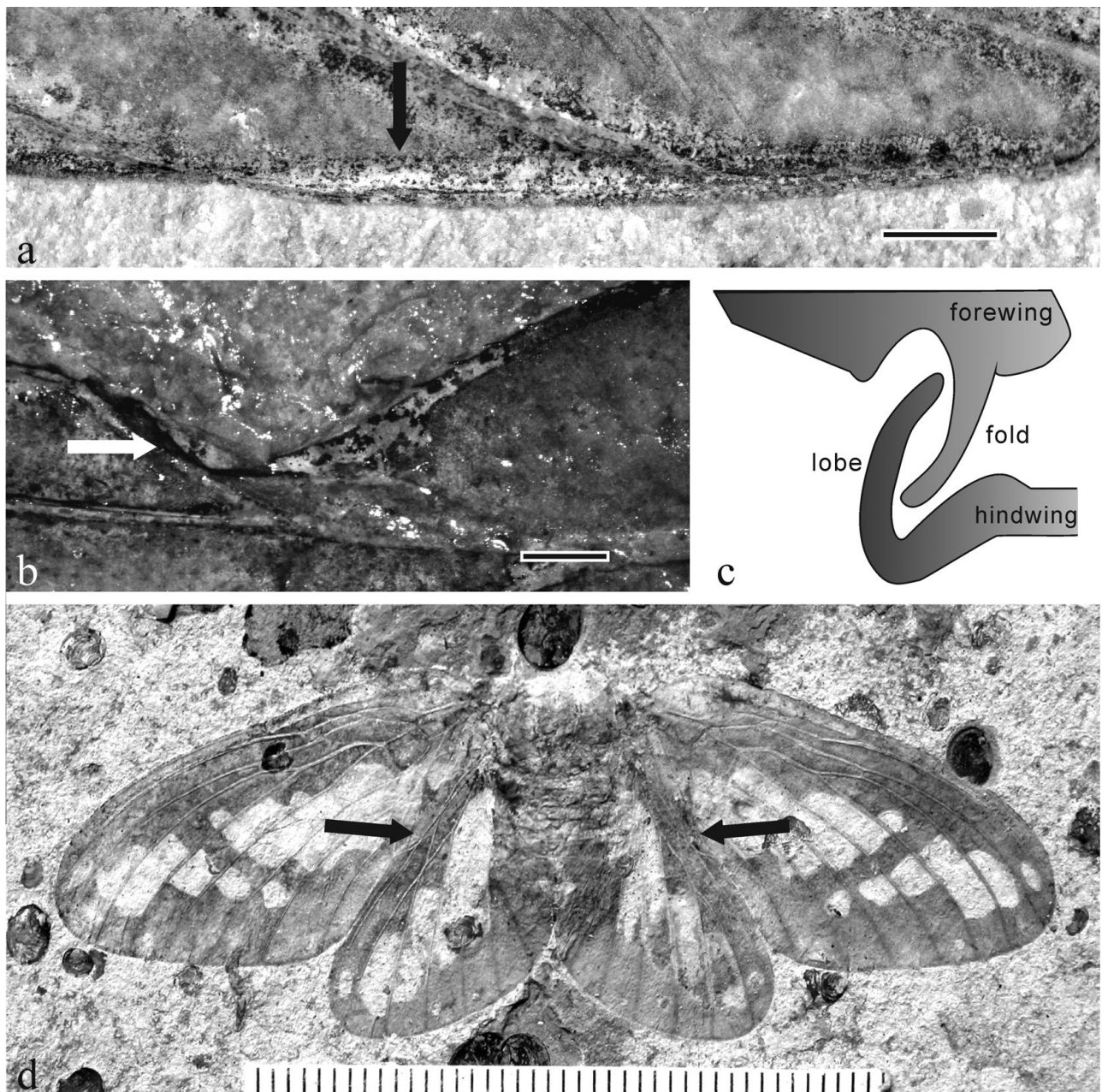


Figure 7. The wing-coupling structures of Palaeontinidae. For a colour version of this figure see online Appendix at <http://journals.cambridge.org/geo>. (a) The longitudinal groove (wing-coupling fold) on the hind margin of the clavus of the forewing (*Palaeontinodes* cf. *shabarovi* Martynov, 1937, NIGP140541). (b) The hook (wing-coupling lobe) on the anterior margin distal of the nodal indentation of the hindwing (*Suljuktocossus coloratus* (Wang, Zhang & Fang, 2006), NIGP140539). Scale bars represent 1 mm in (a) and (b). (c) Diagrammatic explanation of the functioning of wing-coupling mechanism. (d) The hindwing is locked with the forewing by the wing-coupling apparatus (*Sinopalaecossus* sp., NIGP150277). All fossils are from the Middle Jurassic of Daohugou, Inner Mongolia, China. Each tick on scale bar is 1 mm.

1978; Kirichkova & Doludenko, 1996; Wang, Zhang & Fang, 2007). After the Late Jurassic, the fossil record of early Palaeontinidae is very poor. Only one probable specimen was found in the Lower Cretaceous Yixian Formation (Wang, Zhang & Fang, 2010). Late Palaeontinidae probably originated in the Middle or Late Jurassic (Menon & Heads, 2005; Menon, Heads & Szwedo, 2007). Given the correct age of the Karabastau Formation, a rapid succession of palaeontinid assemblage occurred during Late Jurassic times. Interestingly, this evolutionary event was almost coeval with the appearance

of earliest birds (Fig. 6). *Archaeopteryx* from Solnhofen was an insectivorous predator with weak or moderate flight ability (Chiappe & Dyke, 2006; Burnham, 2007; Mayr *et al.* 2007). A Late Jurassic 'flight race' may have taken place between Palaeontinidae and early birds like *Archaeopteryx*. The sharp decline of early Palaeontinidae was probably due to intense predation pressures of newly evolved insectivorous animals like early stem lineage representatives of birds (e.g. *Archaeopteryx*), or small, short-tailed, manoeuvrable pterosaurs (Unwin, 2003), or early mammals which already passed through major

radiations in the Mid- and Late Jurassic (e.g. Luo, 2007). Solnhofen fossils indicated that late Palaeontinidae with better flight ability survived and became a dominant insect group during latest Jurassic times.

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