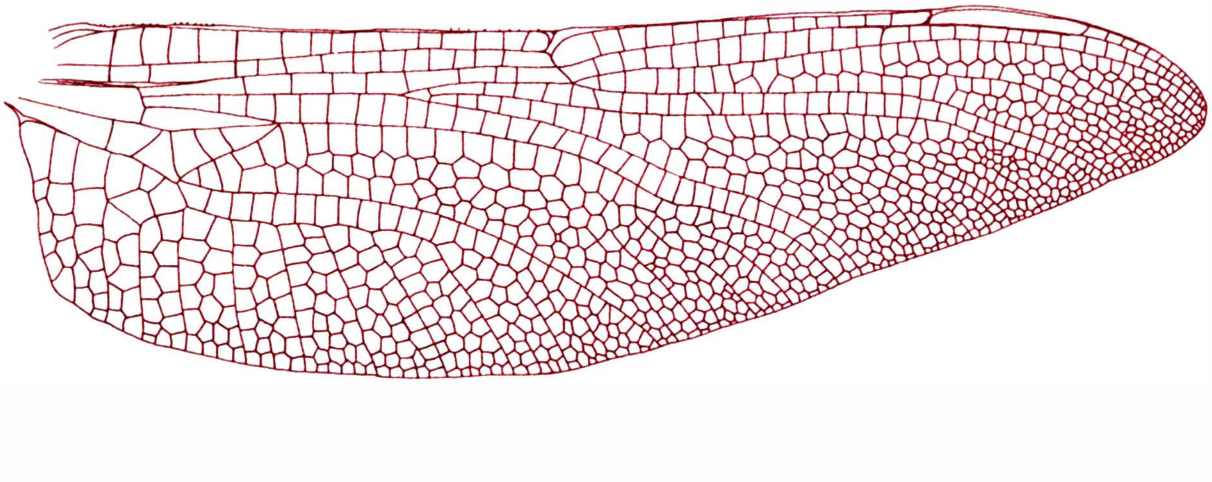
PALEONTOLOGIA LOMBARDA

Nuova serie Volume X

**André Nel, Günter Bechly, Edmund Jarzembowski &
Xavier Martínez-Delclòs**

A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida)



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Museo Civico di Storia Naturale di Milano

Milano 1998

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Nuova serie - Volume X

Società Italiana di Scienze Naturali
Museo Civico di Storia Naturale di Milano
Milano 1998

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Corso Venezia, 55 - 20121 Milano

Registrato al Tribunale di MIlano al n. 137 del 22/2/1992

Direttore responsabile Giovanni Pinna
Grafica editoriale Michela Mura

Stampa Litografia Solari, Peschiera Borromeo, luglio 1998

ISSN 1121-3361

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A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida)

Abstract - A new family, genus and species of Petalurida, *Cretapetalura brasiliensis* gen. nov. et sp. nov. (Cretapetaluridae fam. nov.) is described from the Lower Cretaceous Santana Formation of the Araripe Basin of Brazil, and a new subfamily, genus and species of Petalurida, *Pseudocymatophlebia hennigi* gen. nov. et sp. nov. (Pseudocymatophlebiinae subfam. nov. in Aktassiidae) is described from the Lower Cretaceous Weald Clay of England. A new species *Aktassia pritykinae* sp. nov. is described from the Lower Cretaceous of Mongolia. The description of new material enables us to revise the phylogenetic position of the genera *Protolindenia* Deichmüller 1886, *Aeschnogomphus* Handlirsch 1906, *Mesuropetala* Handlirsch 1906, and *Cymatophlebia* Deichmüller 1886 from the Upper Jurassic of Germany, and to designate neotypes for *Protolindenia wittei* and *Mesuropetala koehleri*. *Aeschnogomphus* and *Aktassia* Pritykina 1968 are considered to be sister-genera within the Petalurida - Aktassiidae (subfamily Aktassiinae stat. nov.). *Aeschnogomphus buchi* (Hagen 1848) is recognized as valid name for *Aeschnogomphus charpentieri* (Hagen 1848). *Mesuropetala*, formerly considered to be a petalurid, is regarded as a basal Aeshnoptera; and *Protolindenia*, formerly considered to be a gomphid, is transferred to the Petalurida, as most basal member of the stem-group of Petaluridae. The phylogenetic positions of *Mesuropetala auliensis* Pritykina 1968, *Mesuropetala costalis* Pritykina 1968, *Protolindenia aktassica* Pritykina 1968 (in *Kazakhophlebiella* gen. nov. et comb. nov.) and *Protolindenia deichmuelleri* Pritykina 1968 (in *Pritykiniella* gen. nov. et comb. nov.) (all Upper Jurassic taxa from Karatau, Turkestan, Russian Federation), are discussed. Also, the phylogenetic positions of *Miopetalura shanwangica* Zhang 1989 and *Miopetalura orientalis* (Hong 1985) (Middle Miocene of China) are discussed and these taxa are transferred from the Petaluridae to the Gomphides- Lindeniinae and Anisoptera *incertae sedis* respectively. The English Lower Cretaceous *Aeschnopsis perampla* (Brodie 1845) and *Cymatophlebiopsis pseudobubas* Handlirsch 1939 are revised, synonymised and considered to belong to Anisoptera *incertae sedis*. The Lower Cretaceous genus *Necrogomphus* Campion 1923 with two species *N. petrificatus* (Hagen 1850) and *N. jurassicus* (Giebel 1850) is revised and also referred to Anisoptera *incertae sedis*. The phylogenetic positions of *Protolindenia*, *Aeschnogomphus*, *Aktassia*, *Pseudocymatophlebia* gen. nov., and *Cretapetalura* gen. nov. within the Petalurida are discussed and a phylogenetic analysis of the fossil and extant Petalurida is presented. The Petalurida are identified as sister-group of all remaining extant Anisoptera (Euanisoptera). The new phylogenetic system of Anisoptera by Bechly (1996) is confirmed, and new phylogenetic definitions of the taxon names of Petalurida are proposed. The evolution and historical biogeography of Petalurida is discussed.

Résumé - Révision des libellules petalurides fossiles. (Insecta: Odonata: Anisoptera: Petalurida).

Une nouvelle famille, genre et espèce de Petalurida *Cretapetalura brasiliensis* gen. nov. et sp. nov., est décrit du Crétacé inférieur de la Formation Santana du bassin lacustre d'Araripe en Brésil, et une nouvelle sous-famille, genre et espèce de Petalurida, *Pseudocymatophlebia hennigi* gen. nov. et sp. nov. (Pseudocymatophlebiinae subfam. nov. *in* Aktassiidae) est décrit du Crétacé inférieur du 'Weald Clay' en Angleterre. Une nouvelle espèce *Aktassia pritykinae* sp. nov. est décrite du Crétacé inférieur de Mongolie. De plus, la description de nouveaux spécimens nous permet de réviser la position phylogénétique des genres *Protolindenia* Deichmüller 1886, *Aeschnogomphus* Handlirsch 1906, *Mesuropetala* Handlirsch 1906 et *Cymatophlebia* Deichmüller 1886 du Jurassique supérieur d'Allemagne, et de désigner des néotypes pour *Protolindenia wittei* et *Mesuropetala koehleri*. *Aeschnogomphus* et *Aktassia* Pritykina 1968 sont considérés comme des genres frères dans les Petalurida - Aktassiidae. *Aeschnogomphus buchi* (Hagen 1848) est reconnu comme nom valide en remplacement d'*Aeschnogomphus charpentieri* (Hagen 1848). *Mesuropetala*, antérieurement rangé dans les Petalurida, est considéré comme un Aeshnoptera. *Protolindenia*, antérieurement considéré comme un Gomphidae, est transféré dans les Petalurida, comme le plus basal représentant du groupe souche des Petaluridae. Les positions phylogénétiques de *Mesuropetala auliensis* Pritykina 1968, *Mesuropetala costalis* Pritykina 1968, *Protolindenia aktassica* Pritykina 1968 (= *Kazakhophlebiella* gen. nov. et comb. nov.) et *Protolindenia deichmuelleri* Pritykina 1968 (= *Pritykiniella* gen. nov. et comb. nov.) (taxons du Jurassique supérieur de Karatau, Turkestan, C.E.I.) sont discutées. Les positions phylogénétiques de *Miopetalura shanwangica* Zhang 1989 et *Miopetalura orientalis* (Hong 1985) (Miocène moyen de Chine) sont discutées et ces taxons sont transférés des Petaluridae dans les Gomphides - Lindeniinae et Anisoptera *incertae sedis* respectivement. Les genres du Crétacé inférieur d'Angleterre *Aeschnopsis perampla* (Brodie 1845) et *Cymatophlebiopsis pseudobubas* Handlirsch 1939 sont révisés, mis en synonymie et considérés comme un Anisoptera *incertae sedis*. Le genre du Crétacé inférieur *Necrogomphus* Campion 1923, avec deux espèces *N. petrificatus* (Hagen 1850) et *N. jurassicus* (Giebel 1850), est révisé et ses affinités phylogénétiques discutées. Les affinités phylogénétiques de *Protolindenia*, *Cretapetalura* gen. nov., *Pseudocymatophlebia* gen. nov., *Aktassia* et *Aeschnogomphus* au sein des Petalurida sont discutées et une tentative d'étude phylogénétique des Petalurida est proposée. Les Petalurida sont identifiés comme le groupe frère de tous les autres Anisoptera modernes (Euanisoptera). Le nouveau système phylogénétique des Anisoptera proposé par Bechly (1996) est confirmé. De nouvelles définitions phylogénétiques des noms taxonomiques au sein des Petalurida sont proposées. L'évolution et la biogéographie historique de Petalurida est discutée.

Riassunto - Revisione delle libellule fossili Petalurida (Insecta: Odonata: Anisoptera: Petalurida).

Vengono descritti una nuova famiglia, un nuovo genere ed una nuova specie di Petalurida del Cretacico inferiore della Formazione Santana (Araripe, Brasile): *Cretapetalura brasiliensis* gen. nov. et sp. nov (Cretapetaluridae fam. nov.) e una nuova sottofamiglia, genere e specie di Petalurida del Cretacico inferiore (Weald Clay) d'Inghilterra: *Pseudocymatophlebia hennigi* gen. nov. et sp. nov. (Pseudocymatophlebiinae subfam. nov. in Aktassiidae). La nuova specie *Aktassia pritykinae* è inoltre descritta del Cretacico inferiore di Mongolia. Lo studio di ulteriore materiale permette di riesaminare la posizione filogenetica dei generi *Protolindenia* Deichmüller 1886, *Aeschnogomphus* Handlirsch 1906, *Mesuropetala* Handlirsch 1906 e *Cymatophlebia* Deichmüller 1886 del Giurassico superiore di Germania, e di designare i neotipi di *Protolindenia wittei* e *Mesuropetala koehleri*. *Aeschnogomphus* e *Aktassia* Pritykina 1968 sono considerati sister-genera nell'ambito dei Petalurida Aktassiidae (sottofamiglia Aktassiinae stat. nov.). *Aeschnogomphus buchi* (Hagen 1848) è stabilito come nome valido per *Aeschnogomphus charpentieri* (Hagen 1848). *Mesuropetala*, ascritto in precedenza ai Petalurida, è considerato un Aeshnoptera primitivo; *Protolindenia*, ascritto in passato ai Gomfidi, è trasferito ai Petalurida, come rappresentante più primitivo del ceppo dei Petaluridae. Viene discussa la posizione filogenetica di *Mesuropetala auliensis* Pritykina 1968, *Mesuropetala costalis* Pritykina 1968, *Protolindenia aktassica* Pritykina 1968 in *Kazakhophlebiella* gen. nov. et comb. nov.) e *Protolindenia deichmuelleri* Pritykina 1968 (in *Pritykiniella* gen nov et comb. nov.), tutti del Giurassico superiore di Karatau, Turkestan, Federazione Russa. Vengono discusse anche le posizioni filogenetiche di *Miopetalura shanwangica* Zhang 1989 e *Miopetalura orientalis* (Hong 1985) (Miocene medio di Cina), e questi taxa sono trasferiti dai Petaluridae rispettivamente ai Gomfidi Lindeniinae e ad Anisoptera *incertae sedis*. Vengono revisionati e collocati fra gli Anisoptera *incertae sedis Aeschnopsis perampla* (Brodie 1845) e *Cymatophlebiopsis pseudobubas* Handlirsch 1939 (Giurassico inferiore d'Inghilterra), considerati sinonimi, ed il genere *Necrogomphus* Champion 1923 con le due specie del Cretacico inferiore *N. petrificatus* (Hagen 1850) e *N. jurassicus* (Giebel 1850). Viene discussa la posizione filogenetica nell'ambito dei Petalurida di *Protolindenia*, *Aeschnogomphus*, *Aktassia*, *Pseudocymatophlebia* gen. nov. e *Cretapleura* gen. nov., ed è presentata un'analisi filogenetica dei Petalurida fossili ed attuali. I Petalurida sono considerati come sister-group di tutti gli altri Anisotteri attuali (Euanisoptera). È confermato il recente sistema filogenetico degli Anisotteri proposto da Bechly (1996) e vengono fornite nuove definizioni filogenetiche dei taxa di Petalurida. Vengono infine discusse l'evoluzione e la biogeografia del gruppo.

Key-words: Petalurida, taxonomy, phylogeny, cladistics, fossil.

INTRODUCTION

Needham (1903: 739) established the family-group taxon Petalurinae as a subfamily within the Aeshnidae, together with the fossil Stenophlebinae and Aeschnidiinae and the extant Gomphinae, Aeshninae, Cordulegastrinae and Chlorogomphinae. This classification was also used in the famous work of Tillyard (1917). The petalurids were lifted to family rank as Petaluridae by Tillyard (1926) and even given the rank of a separate superfamily Petaluroidea by Carle (1982) and Pfau (1991). An alpha-taxonomic revision of extant Petaluridae is in progress by Andress (in prep) and by Carle (in prep.).

The alleged fossil Petaluridae represent a 'myth' because almost all the taxa that have been proposed to belong to this taxon are in fact unrelated to extant Petaluridae or at least of very uncertain position (Nel and Paicheler 1992; Carpenter *in* Rowe 1987: 119; Carle 1995; Bechly 1995, 1996).

Alleged Tertiary petalurids: Needham (1903) maintained that 'the Petalurinae are well represented among the Tertiary fossils of Europe', although no Tertiary dragonfly fossil had been assigned to the Petaluridae or their stem-group, with the sole exception of *Petalura acutipennis* Hagen 1859 (= *Petalura* ? *ovatipennis* Hagen 1859, which is a *nomen nudum* according to Nel and Paicheler 1992). The latter fossil has been proposed to be a Cordulegastridae *incertae sedis* by Nel and Paicheler (1992), but more probably represents a Gomphides - Lindeniinae, as already presumed by Handlirsch (1908: 899). More recently Zhang (1989: 29-31, 414, text-fig. 10-13, pl. 3, fig. 1) described the new fossil genus *Miopetalura* from the Miocene of Shanwang (Shandong Province, China) with the two species *M. shanwangica* and *M. orientalis*, not mentioned by Nel and Paicheler (1992) since they did not know of this publication. We have now the opportunity to discuss the phylogenetic position of these fossils, that were assigned to Petaluridae by Zhang (1989). Since we came to the conclusion that they are no petalurids either, there seems to be no Tertiary fossil record for Petalurida at all.

Alleged Mesozoic petalurids: it is a common belief among paleoentomologists, cited by many previous authors (e.g. Needham and Westfall 1955; Dunkle 1981; etc.), that petalurids were the dominant group of Mesozoic dragonflies. We therefore give here a brief chronological review of the systematic history of all the Mesozoic genera that have ever been considered to be members of the Petaluridae or their stem-group:

Handlirsch (1906) included the genera *Pheugothemis* Handlirsch 1906, *Mesogomphus* Handlirsch 1906 (= *Necrogomphus* Campion 1923), *Libellulium* Westwood 1854, and *Cymatophlebia* Deichmüller 1886 within the Gomphidae in the subfamily Cymatophlebiina (= Cymatophlebiinae), while he classified the genera *Aeschnogomphus* Handlirsch 1906, *Mesuropetala* Handlirsch 1906, and *Protolindenia* Deichmüller 1886 within Gomphidae in a new subfamily Protolindeniina (= Protolindeniinae). Carpenter (1932) transferred the Cymatophlebiinae and Protolindeniinae from the Gomphidae to the Aeshnidae, and considered *Mesuropetala* as subjective junior synonym of *Protolindenia*. Furthermore he transferred *Aeschnogomphus* to the Cordulegasterinae (sic). Handlirsch (1939) described two new taxa (which actually are *nomina nuda*) *Aeschnopsis perampla* (Brodie 1845) and *Cymatophlebiopsis pseudobubas* Handlirsch 1939 on the basis of two British Lower Cretaceous specimens figured by Brodie (1845), and placed them in Gomphidae too, without specification of a subfamily. Cowley (1942) designated the type species for the genera *Cymatophlebiopsis* and *Aeschnopsis*, which consequently are available names under his authorship, and placed the former genus in subfamily '?Cymatophlebiinae' (Gomphidae), and the latter genus in subfamily '?Protolindeniinae' (Gomphidae). Fraser (1957: 95) included the genera *Mesuropetala*, *Libellulium* and *Cymatophlebia* in the Petaluridae while he considered the genera *Pheugothemis*, *Pro-*

tolindenia and *Necrogomphus* to be Gomphidae, without further explanation. Pritykina (1968) also placed the genera *Mesuropetala* and *Cymatophlebia* in the Petaluridae, and *Protolindenia* in the Gomphidae, and described the new genus *Cymatophlebiella* Pritykina 1968 within Petaluridae. Furthermore she described the new family Aktassiidae (type genus *Aktassia* Pritykina 1968) from the Upper Jurassic of Kazakhstan, which is considered in the present study as a member of the stem-group of the Petaluridae. Lindley (1978) listed the genera *Mesuropetala*, *Protolindenia* and *Aeschnogomphus* as fossil Gomphidae; whereas Hennig (1981) agreed with Fraser (1957) that *Protolindenia* is a Gomphidae, while *Mesuropetala* and *Cymatophlebia* are representatives of the Petaluridae. Ponomarenko (1985: 136) apparently was the first author who ever considered *Protolindenia wittei* (Giebel 1860) to be a member of Petaluridae, although without any explanation. Pritykina (1986: 183) indicated the presence of still (?) undescribed Lower Cretaceous Petaluridae in west Mongolia. Carpenter (1992: 83) included the genera *Cymatophlebiella*, *Cymatophlebiopsis*, *Libellulium* (considered by him as subjective senior synonym of *Cymatophlebia*) and *Mesuropetala* in the Petaluridae, but mentioned that the family position of these taxa is uncertain. He classified *Protolindenia*, *Aeschnopsis* and *Aeschnogomphus* within Gomphidae, and considered *Necrogomphus* to be an Anisoptera *incertae sedis*. These views of Carpenter (1992) were accepted by Bridges (1994) in the most recent taxonomic catalogue of Odonata. Nel and Paicheler (1992) concluded that the phylogenetic position of all genera previously considered to be petalurids were uncertain and need a revision. They furthermore suggested that *Aeschnogomphus*, with the two Upper Jurassic species *A. intermedius* (Hagen 1848) and *A. charpentieri* (Hagen 1848), are probably not Petaluridae nor related to *Cymatophlebia*, but more probably related to Cordulegastridae. Ross and Jarzembowski (*in* Benton 1993) elevated the Protolindeniinae to family rank. Bechly (1993) also came to the conclusion that there are no certain fossil petalurids known, but Bechly (1995: 137) considered *Protolindenia wittei* to be the only fossil petalurid. He suggested the transfer of other *Protolindenia* spp. to the genus *Mesuropetala* and dismissed the synonymy of these two genera, that was proposed by Carpenter (1932) and Nel and Paicheler (1992). The genera *Mesuropetala*, *Cymatophlebiella*, *Cymatophlebiopsis* and *Libellulium* (treated by this author as synonym of *Cymatophlebia*) were considered by Bechly as Anisoptera *incertae sedis*, which might be united in a family Cymatophlebiidae and be possibly related to the Aeshnoidea (Austropetaliidae + Aeshnidae). Carle (1995: 397) mentions that 'at least one fossil petalurid is known from the Jurassic of Europe (*Protolindenia wittei*)'. Bechly (1996) proposed a new phylogenetic classification of all fossil and extant 'higher' taxa Odonatoptera, in which he classified Mesuropetalidae and Cymatophlebiidae (incl. Cymatophlebiinae with *Cymatophlebia*, and Valdaeshninae with *Valdaeshna* and *Hoyaeshna*) within the aeshnoid clade Aeshnoptera, while he regarded Protolindeniidae (*Protolindenia wittei*), Cretapetaluridae (mentioned by this author as nomen nudum and regarded to incl. *Aeschnopsis perampla* = *Cymatophlebiopsis pseudobubas*, *Necrogomphus jurassicus* erroneously synonymised with *Aeschnopsis*, and maybe *Nothomacromia*), Aktassiidae (*Aeschnogomphus* and *Aktassia*), and extant Petaluridae as members of the petalurid clade Petalurida. He regarded *Cymatophlebiella* and *Libellulium* as Anisoptera *incertae sedis*. As indicated in the 'Errata and Addendum'-section of Bechly (1996), his mentioning of Cretapetaluridae and *Cretapetalura brasiliensis* represents *nomina nuda*, since it was only accompanied by a reference to the then still unpublished present work. Lohmann (1996) erroneously regarded *Libellulium* as a junior (!?) synonym of *Cymatophlebia*, and regarded Cymatophlebiidae as sister-group of his Austropetaliidae (excl. *Archipetalia*) within his taxon Austropetaliata/Pan-Austropetaliidae. Based on a personal communication of Bechly, he mentions Aktassiidae and *Protolindenia* as Jurassic stem-group representatives of his Petalurata (together constituting the Pan-Petalurata). Bechly *et al.* (in prep.) revise all Mesozoic Aeshnoptera and basically confirm the conclusions of Bechly (1996). *Cymatophlebiella* is removed from the Cymatophlebiidae by Bechly *et al.* (in prep.) and is regarded as maybe the most basal group of Aeshnoptera. According to this work Cymatophlebiinae include *C. longialata* (Germar 1839), the type species of the genus *Cymatophlebia* Deichmüller 1886, *C. zdrzaleki* (Jarzembowski 1994) and *C. standingae* (Jarzembowski 1994), as well as three new species. *C. jurassica* Carpenter 1932 and *C. mongolica* Cockerell 1924 are excluded from *Cymatophlebia* and Cymatophlebiidae, since the latter have to be regarded as nomen dubium within Anisoptera *incertae sedis*, while the former represents a synonym of '*Morbaeschna muensteri*' *sensu* Needham 1907. The genus *Libellulium* Westwood 1854 (type species *L. agrias* Westwood 1854), formerly synonymised with *Cymatophlebia* by Fraser (1957), Hennig (1981), Carpenter (1992), Nel and Paicheler (1992), Bridges (1994), Bechly (1995), and Lohmann (1996) etc., is excluded from Cymatophlebiinae and regarded as a Cymatophlebiidae *incertae sedis*, most probably belonging to Valdaeshninae, which include *Valdaeshna*, *Hoyaeshna*, and a new species.

In the present work we revise all alleged and genuine fossil Petalurida, based on the previous publications, and a thourough study of the type material of *Necrogomphus*, *Aeschnopsis* and *Cymatophlebiopsis*, as well as of numerous specimens from the Upper Jurassic of Solnhofen belonging to *Protolindenia*, *Aeschnogomphus*, *Mesuropetala* and *Cymatophlebia* (a detailed revision of the latter two genera will be included in the large revision of all Mesozoic Aeshnoptera by Bechly *et al.* in prep.). Furthermore we describe two new Lower Cretaceous petalurids, from the Crato Member of Brazil and the Wealden of England.

In the following study we use the wing venation nomenclature of Riek (1976) and Riek and Kukalovà-Peck (1984), amended by Kukalovà-Peck (1991), Nel *et al.* (1993) and Bechly (1995, 1996). We follow the phylogenetic classification of Anisoptera proposed by Bechly (1996), amended by Bechly (1996b, website on the Internet, see below). For the systematic analysis and classification we follow the principles of consequent Phylogenetic Systematics (*sensu* Hennig 1966, 1981), rather than socalled 'mainstream-cladistics' (for reasons see Wägele 1994 and Boricki 1996). For all 'higher' taxon names of

Petalurida we provide for the first time phylogenetic definitions according to socalled 'phylogenetic taxonomy' after De Queiroz and Gauthier (1990, 1992).

Short sketch of the phylogenetic system of Anisoptera after Bechly (1996)

According to this new system, the Eurypalpida (= Libelluloidea *sensu* Fraser 1957) and Chlorogomphida (Hemeroscopidae + Chlorogomphoidea) are sister-groups in the monophylum Brachystigmata. The latter group and the Neopetaliidae are sister-groups in the monophylum Cristotibiata. Cristotibiata and Cordulegastrida (Zoraenidae + Cordulegastridae) together form the monophylum Cavilabiata (= Libelluloidea *sensu* Carle 1995). Cavilabiata and Gomphides (= Gomphidae *sensu* Fraser 1957 or Gomphoidea *sensu* Carle 1995) together form the monophyletic group Exophytica. The latter group and the Aeshnoptera (= Aeshnoidea *sensu* Carle 1995) are sister-groups in the monophylum Euanisoptera. Euanisoptera and Petalurida (Protolindeniidae + Cretapetaluridae + Aktassiidae + Petaluridae) are sister-groups in the monophylum Anisoptera (crown-group). The Aeshnoptera include the fossil Mesuropetalidae, the extant Austropetaliida (Archipetaliidae + Austropetaliidae), the fossil Cymatophlebioidea and the Euaeshnida (= Aeshnidae *sensu* Fraser 1957). The positions of the fossil families Liassogomphidae and Aeschnidiidae remain very uncertain although Carle's (1982) proposal that Aeschnidiidae could be the sister-group of all extant Anisoptera might well be correct. The attempted phylogenetic analysis by Nel and Martínez-Delclòs (1993b) of the Aeschnidiidae has recently demonstrated that we still lack strong synapomorphies with any other group of Anisoptera which hampers the determination of the correct phylogenetic position of the Aeschnidiidae. The presence of special cells below the cubito-anal vein basal of the discoidal triangle might represent a synapomorphy of Liassogomphidae and Aeschnidiidae (together: Aeschnidioidea) and maybe even Stenophlebiidae (together: Aeschnidioptera). Very detailed informations concerning this new classification of Odonata (including the used terminology of odonate wing venation) are available on the World Wide Web under the address (URL): http://members.aol.com/odonatadat/phylogeny/bechly.htm (Bechly 1996b).

In Bechly *et al.* (in press) a new family, genus and species is established for the adults that have previously been attributed to *Sona nectes* (Sonidae) by Pritykina (1986), and the names *Sona nectes* and Sonidae are restricted to the characteristical larvae, since the holotype is a larva. This restricted family-group taxon Sonidae probably represents a subjective junior synonym of Aeschnidiidae. In this work we have still retained the name Sonidae, but have put this family name in quotation marks ('Sonidae') when we refer to the adults, while we use 'Sonidae s.str.' it without quotation marks when we refer to the larvae. Likewise we preliminarily retain the name '*Morbaeschna muensteri*' *sensu* Needham (1907), although this name is invalid and will be replaced in Bechly *et al.* (in prep.).

SYSTEMATICS AND TAXONOMY

Genus *Miopetalura* Zhang 1989
(transferred from Petaluridae to Gomphides - Lindeniinae nov. sit.)

Type species: *Miopetalura shanwangica* Zhang 1989.

Further species: Zhang (1989) added a second species *Miopetalura orientalis* (Hong 1985) (= *Nasiaeschna orientalis* Hong 1985) to this genus, but this attribution is doubtful.

Amended diagnosis: as discussed below, the diagnosis proposed by Zhang would only be useful if this genus was a Petalurida indeed, but since it is more probably a Gomphides - Lindeniinae, the original diagnosis has to be amended. This genus is characterized as follows: 1) the presence of a broad three-celled forewing subtriangle; 2) the posteriorly open anal loop (reversal); 3) the crossed submedian cell; 5) the hindwing discoidal triangle is four-celled; 5) the IR2 is forked slightly distal of the oblique vein O; 6) the pterostigma is long and narrow, covering numerous cells; 7) the pterostigmal brace is reduced. Of these characters none is really diagnostic, since all of them also occur together in some extant Lindeniinae (e.g. *Diastatomma selysi* Schouteden 1934).

Miopetalura shanwangica Zhang 1989

1989 - *Miopetalura shanwangica* - Zhang, p. 29-31, p. 414; text-figs 10-12, pl. 3, fig. 1.

Holotype: specimen n° 820013; location unknown; an adult with three wings connected to the thorax and legs. No other specimens known.

Stratigraphic level: Middle Miocene, Shanwang Formation.

Type locality: Shanwang, 22 km east of the town of Linqu, Central Shandong Province, China.

Systematic position of *Miopetalura shanwangica*: Zhang (1989) characterized the genus *Miopetalura* within the Petaluridae (auct.) by the following characters: 1) the pterostigmal brace is lacking; 2) vein IR2 (IR3 *sensu* Zhang) has two long diverging branches; 3) the hindwing discoidal triangle is divided into four cells.

Characters 1 and 2 are very unusual for a non-Mesozoic petalurid and rather suggest a relationship with Cordulegastrida. None of the extant Petalurida lacks the pterostigmal brace whereas Cordulegastrida do. There is never any division of IR2 in Petalurida, but this structure is visible in nearly all Cordulegastrida (see Fraser 1929)

Polarity of character 1 (presence/absence of a oblique pterostigmal brace): Heterophlebioptera (= Heterophlebioidea *sensu* Nel *et al.* 1993), the probable sister-group of Anisoptera, and many Anisoptera (Liassogomphidae, Petalurida, Aeshnoptera, Gomphides, Neopetaliidae, and some other Cavilabiata) possess a oblique pterostigmal brace, just like Epiophlebiidae and many Zygoptera. The reduction and loss of this brace occurred in some aeschnidiid genera like *Gigantoaeschnidium* Nel and Martínez-Delclòs

1993, showing that the plesiomorphic condition in Aeschnidiidae is a fully developed brace (Nel and Martínez-Delclòs 1993). Thus, the presence of a oblique pterostigmal brace is probably a plesiomorphic condition within the Anisoptera and its absence an apomorphy. This hypothesis requires that reduction of the brace occurred three or four times by convergence within the [Heterophlebioptera + Anisoptera] in Aeschnidiidae, few Euaeshnida (e.g. *Brachytron*) and Gomphides (e.g. Epigomphidae), most Cordulegastrida and Chlorogomphida, and Eurypalpida. In extant Cordulegastrida, a oblique pterostigmal brace is present in some aberrant specimens of *Neallogaster luniferus* (Selys 1878), but it is vestigial and not very oblique (see fig. 1). Other Cordulegastrida have no differentiated pterostigmal brace. Within Gomphides - Lindeniinae the pterostigmal brace is reduced in *Diastatomma selysi* Schouteden 1934. The alternative hypothesis would imply that the development of a oblique pterostigmal brace occurred many times by convergence within Odonata. This is not only less parsimonious, but also a much less probable hypothesis from the viewpoint of evolutionary biology.

We therefore do regard the absence of the oblique pterostigmal brace as an apomorphic condition within the Anisoptera, but also regard this character as of very limited value because of the numerous convergences. Nevertheless, character 1 in the above list is a derived condition common to Cordulegastrida and *Miopetalura* absent in extant Petalurida, but present in the Upper Jurassic genus *Aeschnogomphus* which we place in the Petalurida - Aktassiidae.

Polarity of character 2 (division of IR2 into two 'branches'): the 'division' of IR2 into two branches is clearly an apomorphic condition in Cordulegastrida, but this character occurs convergently in some Gomphides (Lindeniinae), as well as in many 'derived' Euaeshnida (Aeshnidae s.str.), and even in some Synthemistidae, although only in a very rudimentary condition. The bifurcation of IR2 is very different in the Aeshnidae s.str., and somewhat different in the Lindeniinae. The bifurcation in Cordulegastrida lies basal of the oblique crossvein 'O', while the bifurcation in Lindeniinae lies slightly distal of this vein, and the bifurcation in Aeshnidae lies much distal of this vein. In *Miopetalura shanwangica*, the bifurcation is a only little distal of the oblique crossvein 'O'. Thus it suggest a closer relationship between *Miopetalura* and Gomphides -Lindeniinae, but certainly excludes Petalurida.

Polarity of character 3 (subdivision of the discoidal triangle): the division of the discoidal triangle into smaller cells occurred in several taxa in Aeschnidiidae, Petalurida, Cymatophlebiidae, Euaeshnida, some Gomphides (Lindeniinae), and a few Libellulidae, but is absent in Cordulegastrida. Since it is a rather homoplastic character, it is of limited value for the reconstruction of the phylogenetic position of *Miopetalura*.

Conclusion: Zhang's (1989) attribution of *Miopetalura* to the Petaluridae (auct.) was based on the long and narrow pterostigma covering many cells and the long, narrow and densely reticulated wings. These characters are also present in some Cordulegastrida (e.g. *Neallogaster latifrons* (Selys 1878)) and in some Gomphides (e.g. Lindeniinae). Zhang's photograph of the holotype of *M. shanwangica* clearly shows that the area between costal margin and RA distal of the pterostigma is not very narrow and crossed by relatively few veins, so that one of the main autapomorphic structures of the Petalurida is absent.

According to Zhang (1989: text-fig. 11) *M. shanwangica* has a posteriorly open anal loop. This apomorphic condition is present in some Petalurida but also in some Cordulegastrida, as well as in *Cymatophlebia* and some Gomphides, including some species within Lindeniinae.

The most surprising structure of *M. shanwangica* is the very broad, three-celled forewing subtriangle, as in the extant genus *Petalura*. All extant Cordulegastrida have a small undivided forewing subtriangle. This character, in *M. shanwangica* and extant *Petalura* spp., is also present in Liassogomphidae, Aeschnidiidae, Cymatophlebiidae (Nel *et al.* 1993; Bechly *et al.* in prep.), some Gomphides (Lindeniinae) and many Eurypalpida ('corduliids', Macrodiplacidae and Libellulidae). It is probably an apomorphic groundplan character (autapomorphy) of Anisoptera, which has been convergently reduced in some taxa.

Miopetalura shares with Petalurida only two characters which are also found in some Cordulegastrida (and Eurypalpida). The basic autapomorphic characters of the Petalurida are absent in *Miopetalura*. It shares with the Cordulegastrida three apomorphic characters, one of them (forking of IR2) absent in Petalurida, but like the other characters also present

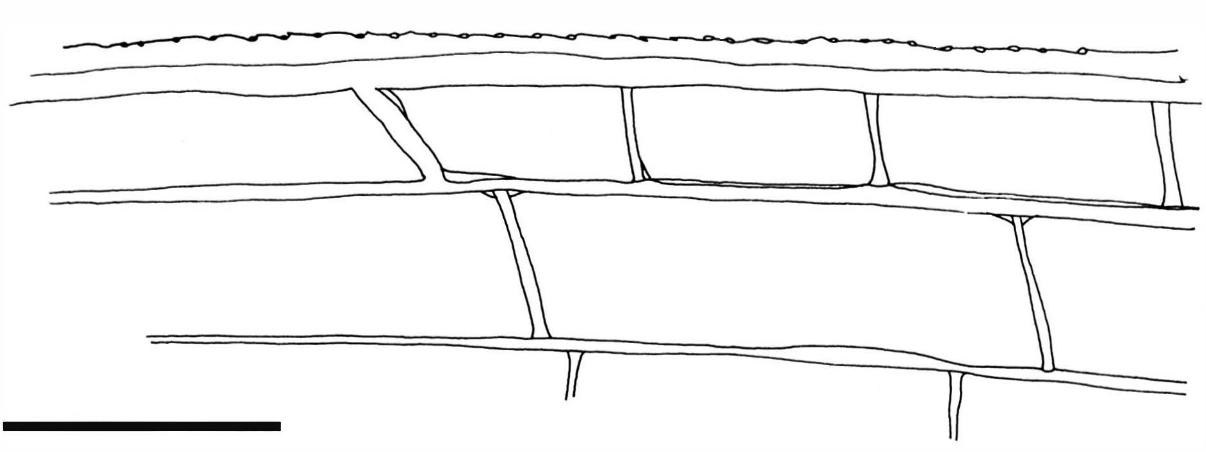

Fig. 1 - *Neallogaster luniferus* (Selys), pterostigmal brace region. Scale bar represents 1 mm.

in Gomphides - Lindeniinae. Altogether a relationship with Lindeniinae seems to be most probable, since the several characters, like the position of the IR2-fork, the four-celled discoidal triangle, the crossed submedian cell, and especially the three-celled forewing subtriangle, are strongly contradicting a relationship with Cordulegastrida, while they do support or at least do not contradict a position in Lindeniinae. Consequently we propose to transfer *Miopetalura* from the Petaluridae (auct.) to the Gomphides - Lindeniinae.

'*Miopetalura*' *orientalis* (Hong 1985)
= '*Nasiaeschna*' (?) *orientalis* Hong 1985 stat. rest.
(transferred from Petaluridae to Anisoptera *incertae sedis* nov. sit.)

1985 - *Nasiaeschna orientalis* - Hong, p. 16-18; text-figs 6-8, pl. 1, fig. 3, pl. 2, figs 1-2.
1989 - *Miopetalura orientalis* (Hong 1985) - Zhang, p. 30-31; text-fig. 13.
1994 - *Nasiaeschna orientalis* Hong - Nel *et al.*, p. 160.
1994 - *Nasiaeschna orientalis* Hong - Bridges, p. VII.174.

Holotype: specimen n° Sha D74/1002; location unknown; an adult with the forewing and hindwing preserved.

Stratigraphic level: Middle Miocene, Shanwang Formation.

Type locality: Shanwang, 22 km east of the town of Linqu, Central Shandong Province, China.

Further material: One larva, that was very doubtfully attributed to this species.

Systematic position of *Miopetalura orientalis*: Nel *et al.* (1994) discussed the position of this enigmatic species but they were not aware of Zhang's attribution to *Miopetalura*. Also, they considered that the larva figured by Hong (1985: 16, fig. 6) is poorly preserved and lacks characters for a certain attribution to the Aeshnidae (auct.) and to *Nasiaeschna* Förster 1900 in particular. Furthermore, there is no evidence for the conspecificity of the larva and adult anyway. Zhang (1989) described another aeshnid (*Mediaeschna matutina*) from the same outcrop, so the attribution of the larva is made even more uncertain, even if it would be an aeshnid larva indeed.

Hong (1985: 17, fig.7) illustrated the fore- and hindwing of his species. Nel *et al.* (1994) pointed out that the venation does not correspond to that of the genus *Nasiaeschna* and considered it as belonging to an aeshnid genus undetermined. Zhang attributed this species to the genus *Miopetalura* on the basis of the structure of the vein IR2. He considered that IR2 is forked. The vein which he considered to be the posterior branch of IR2 has been misidentified as Rspl by Hong (1985). From Hong's (1985) figure, the following characters of *M. orientalis* separate it from *Miopetalura shanwangica*: the pterostigmata are short and broad, not long and narrow; the pterostigmata are well braced obliquely; the hindwing anal loop is well closed posteriorly; the forewing subtriangle is unicellular; the reticulation is less dense.

These characters would be sufficient to exclude *M. orientalis* from *Miopetalura* if we adopt Hong's figure, but Zhang's (1989) figure of the hindwing contradicts Hong's interpretation: 1) the pterostigma and pterostigmal brace appear to be lacking; 2) the hindwing anal loop is posteriorly open; 3) the reticulation is very dense.

The fact that these two interpretations are so different shows that a re-examination of the specimens will be necessary before a more precise attribution of this species becomes possible. Until then, *M. orientalis* should be considered as an Anisoptera *incertae sedis*.

Genus *Necrogomphus* Campion 1923
(nec *Necrogomphus* Handlirsch 1939: 31)
= *Mesogomphus* Handlirsch 1906, nec *Mesogomphus* Förster 1906, nec *Mesogomphus* Davis 1883
(in Anisoptera *incertae sedis*)

Type species: *Necrogomphus petrificatus* (Hagen 1850) (Cowley 1934)

Further species: *Necrogomphus jurassicus* (Giebel 1856), that has to be excluded from the present genus. Jarzembowski (1991; 1992) has cited and figured a new undescribed fossil wing attributed to '*Mesogomphus* sp.' from the Lower Cretaceous, Lulworth Formation of southern England ('Fossil Forest').

Necrogomphus petrificatus (Hagen 1850)
Fig. 2

1845 - *Lindenia* - Brodie, p. 33; pl. 5, fig. 8.
1850 - *Gomphus petrificatus* - Hagen, p. 359.
1856 - *Libellula petrificata* (Hagen) - Giebel, p. 284.
1890 - *Aeshna petrificata* (Hagen) - Kirby, p. 168.
1895 - *Gomphus petrificatus* - Westwood, p. 391.
1906 - ? *Mesogomphus petrificatus* (Hagen) - Handlirsch, p. 592 (in Cymatophlebiinae, new genus name, but homonym).
1923 - *Necrogomphus petrificatus* (Hagen) -; Campion, p. 669 (*Necrogomphus* nom. subst. pro *Mesogomphus* Handlirsch).
1934 - *Necrogomphus petrificatus* (Hagen) - Cowley, p. 201 (designation of type species).
1939 - ? *Mesogomphus petrificatus* (Hagen) - Handlirsch, p. 153.
1957 - *Necrogomphus petrificatus* (Hagen) - Fraser, p. 93 (list, in Gomphidae).
1981 - *Necrogomphus petrificatus* (Hagen) - Schlüter, p. 40 (list, in Anisoptera *incertae sedis*).
1992 - *Necrogomphus petrificatus* (Hagen) - Carpenter, p. 85 (in Anisoptera family uncertain).
1992 - *Necrogomphus petrificatus* (Hagen) - Nel and Paicheler, p. 315-316 (position discussed).
1994 - *Necrogomphus petrificatus* (Hagen) - Bridges, p. VII.184.

Holotype: specimen n° I.12779, Brodie coll., Natural History Museum, London.

Stratigraphic level: Middle Purbeck, Lower Cretaceous.

Type locality: Teffont, Vale of Wardour, Wiltshire, England.

Revised description: only the basal half of a forewing is preserved. Length of preserved part, 22.3 mm; probable length of wing, 45 to 48 mm; width, 10 mm. Distance from base to nodus about 20.7 mm; distance from base to arculus, 3.4 mm. Many crossveins

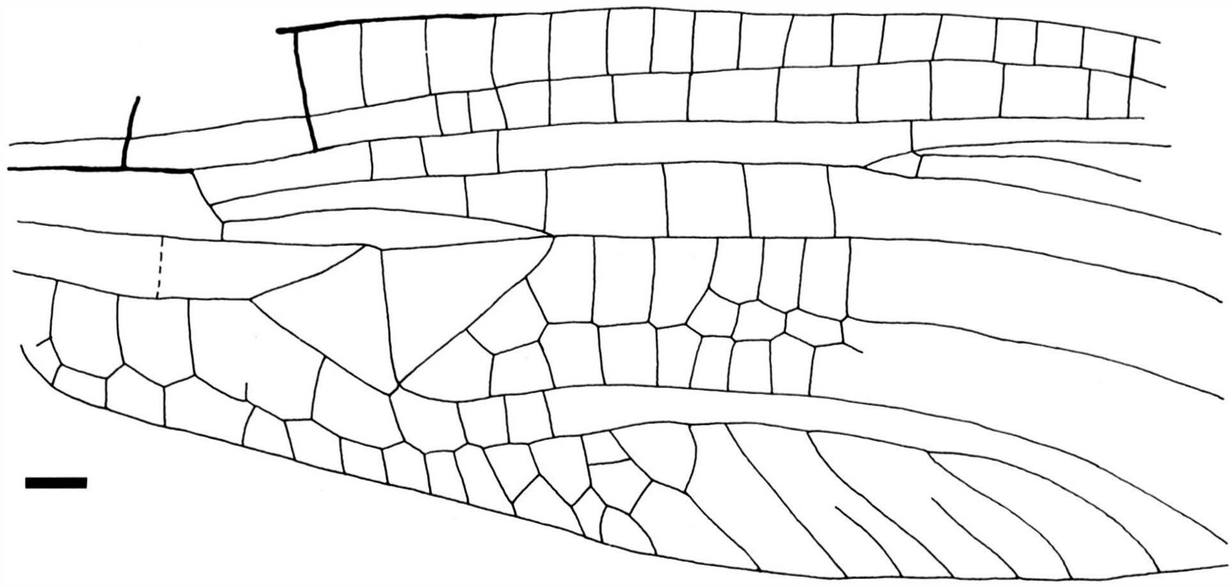

Fig. 2 - *Necrogomphus petrificatus* (Hagen 1850), holotype I.12779, Brodie coll., N.H.M., forewing. Scale bar represents 1 mm.

between RA and RP between arculus and RP3/4; only three of them being preserved, but their relative position indicates that they were more numerous. Five crossveins between RP and MA, between arculus and RP3/4. Two rows of cells just distal of discoidal triangle in postdiscoidal area, widened distally with three rows of cells at base of RP3/4. Mspl well-defined and nearly straight. MP gently curved . CuA well-defined. Area between MP and CuA somewhat broader near posterior wing margin. CuA with six or seven posterior branches, directed towards posterior margin. Cubito-anal area 2.5 mm wide. Number of rows of cells between CuA + AA and posterior margin unknown. Anal area between AA and posterior margin 2.2 mm wide, with two rows of cells. Unicellular discoidal triangle not transverse and very broad; length of its anterior side, 3.0 mm; of distal side, 3.7 mm; of basal side, 2.3 mm. Hypertriangles, median cell and submedian cell free (except for the CuP-crossing = 'anal-crossing' *sensu* Fraser 1957). A well-defined PsA (*sensu* Bechly 1995; = AA0 *sensu* Nel *et al*. 1993) separating submedian cell from unicellular subtriangle, 2.8 mm long and 1.9 mm wide. Two primary antenodal crossveins stronger than secondaries. Arculus between two primary antenodal crossveins, a little nearer Ax1 than Ax2. Posterior end of arculus strongly angled with respect to MA. Many secondary antenodal crossveins (more than sixteen) between costal margin and ScP, but fewer (about ten to twelve) corresponding antenodal crossveins between ScP and RA. No secondary crossvein preserved between Ax1 and Ax2.

Necrogomphus jurassicus (Giebel 1856)
Fig. 3

1845 - *Lindenia* sp. - Brodie, p. 33, pl. 5, fig. 9.
1850 - *Gomphus petrificatus* - Hagen, p. 359.
1856 - *Libellula jurassica* - Giebel, p. 284.
1890 - *Aeshna jurassica* (Giebel) - Kirby, p. 168.
1906 - ? *Mesogomphus jurassicus* (Giebel) - Handlirsch, p. 592 (in Cymatophlebiinae, new genus name, but homonym).
1939 - ? *Mesogomphus jurassicus* (Giebel) - Handlirsch, p. 153.
1992 - *Necrogomphus jurassicus* (Giebel) - Nel and Paicheler, p. 315-316 (position discussed).
1994 - *Necrogomphus jurassica* (Giebel) - Bridges, p. VII.123.
1996 - '*Aeschnopsis jurassicus* (= *Necrogomphus jurassicus*)' - Bechly, p. 380 (in Petalurida)

Holotype: specimen n° [I. 12782 + I.12778], Brodie coll., Natural History Museum, London.

Stratigraphic level: Middle Purbeck Beds, Lower Cretaceous.

Type locality: Teffont, Vale of Wardour, Wiltshire, England.

Revised description: only the basal half of a hindwing is preserved. Length of preserved part, 23 mm; probable length of whole wing, 35 mm; width, 11.5 mm. Distance from base to nodus about 17.5 to 17.7 mm. Distance from base to arculus, 3.8 mm. Two primary antenodal crossveins stronger than secondaries. Only two secondary antenodal crossveins preserved. Nodus not preserved. Arculus between Ax1 and Ax2, very close to Ax1. Ax1 is only 0.4 mm basal of the arculus and Ax2 is 2.9 mm distal of Ax1. RP and MA well-separated in arculus. Posterior part of arculus at an obtuse angle with MA. No visible crossvein in area between RA and RP (between arculus and RP3/4). Only two distal crossveins between RP and MA (between arculus and RP3/4). Discoidal triangle elongate and divided into two cells; length of its anterior side, 2.5 mm; of its basal side, 1.4 mm; of its distal side, 3.1 mm. Anterior side of discoidal triangle reaching MAb 0.4 mm basal of division of MA into MA and secondary branch MAb. Hypertriangle looking more like a quadrangle than a triangle. Hypertriangle, median cell and submedian cell free of crossveins (except for CuP-crossing). A well-defined unicellular subtriangle separated from submedian cell by PsA, 1.8 mm long and 1.5 mm wide. Two rows of cells in postdiscoidal area just distal of discoidal triangle, distally strongly widened, (width near discoidal triangle, 2.6 mm; width at wing margin, about 7 mm), with about ten rows of cells near wing margin. No Mspl

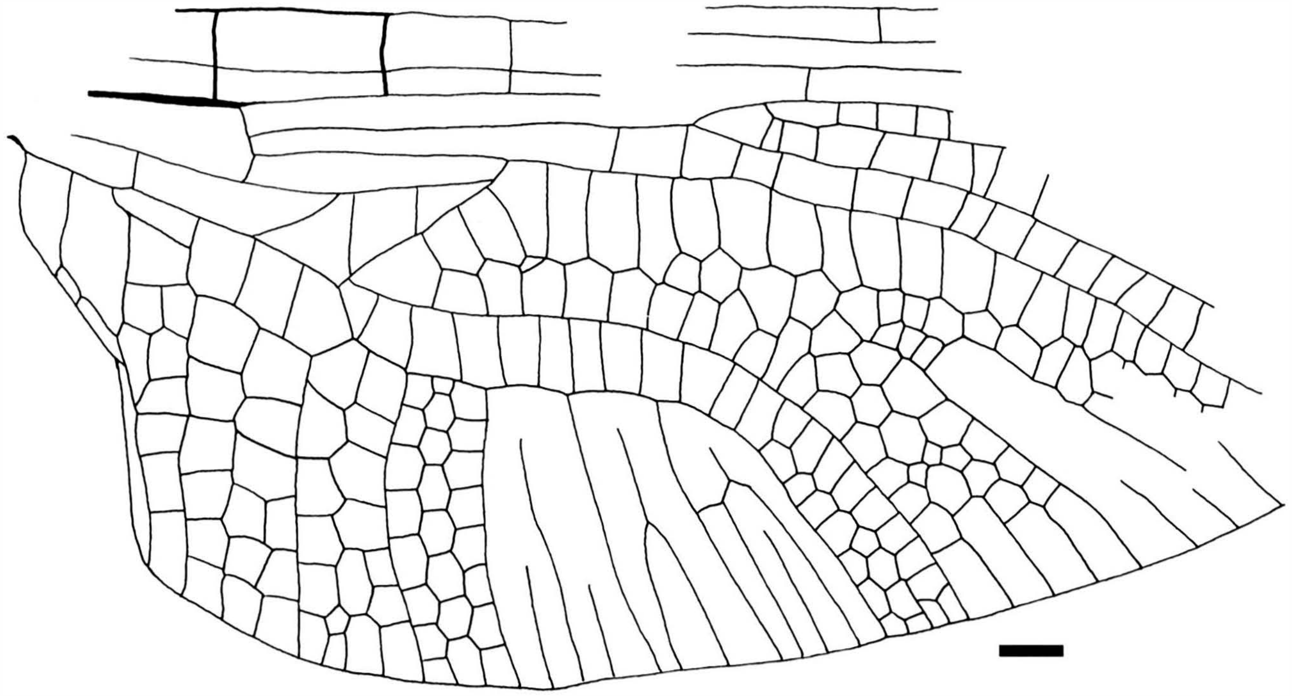

Fig. 3 - *Necrogomphus jurassicus* (Giebel 1856), holotype [I. 12782 + I.12778], N.H.M., hindwing. Scale bar represents 1 mm.

and only two secondary longitudinal veins in postdiscoidal area. Area between MP and CuA never widened, with one row of cells near discoidal triangle and two rows of cells opposite base of RP3/4. CuA and MP separating at posterior angle of discoidal triangle. Free portion of CuA (basal of fusion with AA) very short, 0.3 mm long, the gaff being 0.9 mm long. Most basal branch CuAb of CuA directed towards postero-anal angle of wing, fused with a posterior branch of AA and then deflected towards posterior wing margin. AA and CuAb delimiting a well-defined three-celled anal loop, distinctly longer than wide, 3.4 mm long and 1.4 mm wide, and closed posteriorly. CuAa divided into five parallel straight branches directed towards posterior margin. Cubito-anal area 5.4 mm wide, with up to eight rows of cells between CuAa and posterior wing margin. Only one paranal cell along AA between anal loop and anal triangle. Anal triangle well-developed, 3 mm long and 2 mm wide, divided into two main cells and two smaller cells along AP. Seven rows of cells in anal area between anal loop and posterior margin. Width of anal area, 6.7 mm. Many bridge-crossveins (Bqs), four of them being visible in basal half of the narrow bridge-space (Bqs-area) between RP, IR2 and subnodus. Bridge-space (Bqs-area) narrow.

Phylogenetic relationship between *N. petrificatus* and *N. jurassicus*: there is no evidence that *Necrogomphus petrificatus* and *Necrogomphus jurassicus* actually belong to the same genus because the two type specimens lack any synapomorphic characters. Indeed, some of the characters of *N. jurassicus* are really different from the corresponding characters in *N. petrificatus*. These include: the relative positions of the arculus and the first primary antenodal crossvein Ax1; the subtriangle of *N. petrificatus* is broader than in *N. jurassicus*; the discoidal triangle of *N. petrificatus* is broader than in *N. jurassicus*; the hypertriangle of *N. petrificatus* is triangular, whereas that of *N. jurassicus* is quadrangular; *N. petrificatus* has a Mspl but *N. jurassicus* lacks it.

Even, if other characters are accounted for by specific an/or fore-/hindwing differences, the lack of a well-defined Mspl in *N. jurassicus* and the presence in *N. petrificatus* suggest that these taxa belong to different genera. It is nearly impossible to determine the true relationship between these two species even if it is highly probable that they belong to different genera. However, it would not help to rename *N. jurassicus* because these fossil species are of little phylogenetic interest: their phylogenetic relationships are also nearly impossible to determine (see below).

Systematic position of *Necrogomphus petrificatus*: it is very difficult to assign this species to a known 'higher' taxon within Anisoptera because of the lack of the preserved structures in the distal half of the wing.

Comparison with Petalurida: the main differences to Petalurida are the well-defined Mspl and the unicellular subtriangle. Other characters are also found in Petalurida but are symplesiomorphies, especially the shape of the discoidal triangle. None of the preserved characters represents a putative synapomorphy with Petalurida.

Comparison with Cymatophlebiidae (*sensu* Bechly 1996 and Bechly *et al.*, in prep.): the well-defined Mspl, lack of any division of the subtriangles and discoidal triangles, and the narrow postdiscoidal area are the main differences from *Cymatophlebia*. These differences suggest that *N. petrificatus* is not related to the Cymatophlebiidae.

Comparison with Cordulegastrida, Austropetaliida and Neopetaliidae: the only perceptible difference with these taxa is the structure of the antenodal area: there is no secondary antenodal crossvein between the two primaries in *N. petrificatus*. They are numerous in Austropetaliida and Neopetaliidae and the crossvein Ax2 is in a distal position, well beyond the discoidal triangle.

Comparison with Euaeshnida: *N. petrificatus* differs from Euaeshnida by its non-elongate discoidal triangle and well-defined subtriangle.

Comparison with *Aktassia magna*: the Upper Jurassic species *Aktassia magna* Pritykina 1968 from Karatau (Russian Federation), is very different from *N. petrificatus* because of its very dense wing reticulation.

Comparison with Hemeroscopidae: this Lower Cretaceous taxon is based on one species, *Hemeroscopus baissicus* Pritykina 1977. A second species will be described soon from the Solnhofen limestone (Bechly *et al.*, in press). The forewing venation is very similar to *N. petrificatus*. The only visible difference is that the two primary antenodal crossveins of *Hemeroscopus* are separated by three secondaries and Ax2 is in a more distal position, on the level of the distal part of the discoidal triangle (Pritykina 1977).

Comparison with Gomphides: the main difference to Gomphides is the well-defined supplementary Mspl. Most others characters are present in that taxon too.

Comparison with 'Sonidae': the forewing of the only described adult 'Sonidae' (*Sona nectes* Pritykina 1986) is not very well-documented but it resembles *N. petrificatus*.

The lack of preservation precludes a reliable attribution of *N. petrificatus*. It could belong to Gomphides (incl. 'Sonidae') but also to Cordulegastrida, Austropetaliida or even to Hemeroscopidae (Chlorogomphida). Therefore it must be considered as Anisoptera *incertae sedis*.

In addition, N. *petrificatus* shows some resemblance to Lower Cretaceous *Araripegomphus cretacicus* Nel and Paicheler 1994 from Brazil. The differences between the two species are few: *Araripegomphus* has no Mspl and Ax2 is in a more distal position (Nel and Paicheler 1994). However, the known similarities between these two species do not support a phylogenetic relationship.

Systematic position of *Necrogomphus jurassicus*:

Comparison with Petalurida: the great number of bridge-crossveins (Bqs) and the narrow bridge-space (Bqs-area) could suggest a relationship with Petalurida. Most preserved characters of *N. jurassicus* are consistent with Petalurida. However, two main characters for this hypothesis are not found in all Petalurida: the longitudinal elongate anal loop is similar to *Cretapetalura*; the lack of any secondary antenodal crossveins between the two primaries is a character lacking in Petalurida, except that extant *Tanypteryx pryeri* (Selys 1889) rarely shows only two secondaries between the primary antenodals. The only autapomorphy of Petalurida which is absent in *N. jurassicus* is the very acute male anal angle. The holotype of *N. jurassicus* shows an anal triangle (it is clearly a male) but the anal angle is not sharply angular. A relationship of *N. jurassicus* with Petalurida consequently is not impossible but uncertain.

Comparison with Cymatophlebiidae (*sensu* Bechly 1996 and Bechly *et al.*, in prep.): *Cymatophlebia* differs from *N. jurassicus* in the following features: the anal loop of *Cymatophlebia* is posteriorly open and not elongate; the hindwing subtriangle of *Cymatophlebia* is three-celled; the hypertriangle of *Cymatophlebia* is triangular; the male anal angle of *Cymatophlebia* is much more angular; there are two posterior branches of AA between the anal loop and the anal triangle in male *Cymatophlebia* (instead of one in *N. jurassicus*). The main apomorphy of Cymatophlebiidae (presence of two specialized structures on the male third and fourth abdominal segments) is not preserved in *N. jurassicus*. Nevertheless, the structure of the anal loop, subtriangle and male anal angle of *N. jurassicus* strongly suggest that *N. jurassicus* is not a Cymatophlebiidae (*sensu* Bechly 1996 and Bechly *et al.*, in prep.).

Comparison with Cordulegastrida, Austropetaliida and Neopetaliidae: the elongate anal loop and the well-defined subtriangle of *N. jurassicus* are absent in Cordulegastrida. The main difference between *N. jurassicus* and the Austropetaliida and Neopetaliidae is the presence of an elongate anal loop.

Comparison with Euaeshnida: *N. jurassicus* differs from most Euaeshnida in the following points: *N. jurassicus* has a very weak Mspl; *N. jurassicus* has a well differentiated subtriangle (also present in Euaeshnida - Gomphaeschnidae); the anal loop of *N. jurassicus* is elongate (not more or less rounded or transverse), unlike all Euaeshnida but very much like *Aeschnopsis*, *Cretapetalura* gen. nov. and *Mesuropetala*.

Comparison with Gomphides: the elongate anal loop and the well-defined subtriangle of *N. jurassicus* can be found in some genera of Gomphides (e.g. the Lower Cretaceous genera *Cordulagomphus* Carle and Wighton 1990 and *Procordulagomphus* Nel and Escuillié 1994). All other characters of *N. jurassicus* are present in various extant genera of Gomphides: the elongate discoidal triangle and the numerous bridge-crossveins (Bqs) are found in *Ictinogomphus* Cowley 1934 and *Sieboldius* Selys 1854; the structures of the anal and cubito-anal, postdiscoidal and [MP-CuA] areas are similar to those of *Megalogomphus* Campion 1923; the extant genus *Malgassogomphus* Cammaerts 1987 also has numerous bridge-crossvein (Bqs) similar to those of *N. jurassicus* (Cammaerts 1987: figs 7-9).

Comparison with 'Sonidae': the preserved characters of the hindwing of the possible adult of *Sona nectes* are very similar to those of *N. jurassicus* with the following difference: *S. nectes* has only two bridge-crossveins (Bqs) but *N. jurassicus* has more than four. The alleged imagines of *Sona nectes* are most probably unrelated to the larva which represent the type of Pritykina (Bechly *et al.*, in prep.).

Nel (1991) and Bechly (1995, 1996) consider that 'Sonidae' are very closely related to the Gomphides, of even belonging to a subordinate group within Gomphides. Since all preserved characters of *N. jurassicus* can be found in various gomphid genera, its attribution to the Gomphides (incl. 'Sonidae') might be possible but there is no critical evidence for this hypothesis. However, this species is very different from the Upper Jurassic *Nannogomphus bavaricus* Handlirsch 1906 (Bechly, Nel and Martínez-Delclòs 1996) and the Lower Cretaceous genera *Cordulagomphus* and *Procordulagomphus*, by the very numerous bridge-crossveins (Bqs) and broader postdiscoidal area; it differs from the Lower Cretaceous *Araripegomphus cretacicus* Nel and Paicheler 1994 by its elongate posteriorly-closed anal loop (Nel and Paicheler 1994).

The great similarity between the preserved characters of *N. jurassicus* and *Aeschnopsis* seems to suggest a close relationship, that would imply the exclusion of *N. jurassicus* from the genus *Necrogomphus*. Because of the lack of informations concerning the relationships of *N. jurassicus*, it is a taxon of very little importance. Thus, it is not really necessary to create a new genus or to attempt to attribute it to another known genus, unless better material becomes available. A new species of *Mesuropetala*, known by two specimens [MCZ 6181a,b] and [MCZ 6197] in the collections of the Museum of Comparative Zoology (Harvard University, Cambridge), will be described in Bechly *et al.* (in prep.). The hindwing of this new species is nearly identical to that of *N. jurassicus*, with the only difference that there is only one row of cells between MP and CuAa till the wing margin in the hindwing. Since the latter character is variable in *Mesuropetala koehleri*, it could well be variable in this species too. Therefore *N. jurassicus* seems to be conspecific with this new species of *Mesuropetala* which would then have to be named *M. jurassicus*.

Genus *Aeschnopsis* Cowley 1942
(= *Cymatophlebiopsis* Cowley 1942 syn. nov.)
= *Aeschnopsis* Handlirsch 1939 (*nomen nudum*?)
= *Cymatophlebiopsis* Handlirsch 1939
(*nomen nudum*?)
(transferred from Gomphidae to Anisoptera
incertae sedis nov. sit.)

Type species: *Aeschnopsis perampla* (Brodie 1845) (= *Cymatophlebiopsis pseudobubas* Handlirsch 1939 syn. nov.); the type species for both genera were subsequently designated by Cowley (1942: 77-78). Nevertheless it is not quite clear that Cowley's opinion (followed by Bridges 1994) that the original names of Handlirsch represent *nomina nuda* is correct indeed, since he himself mentioned that Handlirsch may be considered to have given a generic description. According to Art. 69 IRZN the mere omission of the designation of a type species for a generic name established before 1931 does not make these names to *nomina nuda*.

Aeschnopsis perampla (Brodie 1845)
(= *Cymatophlebiopsis pseudobubas*
Handlirsch 1939 syn. nov.)
Figs 4-7

1845 - *Aeshna perampla* - Brodie, p. 33, pl. 5, fig. 7.
1850 - *Aeschna perampla* Brodie - Hagen, p. 362.
1856 - *Aeschna perampla* Brodie - Giebel, p. 412.
1890 - *Aeschna perampla* Brodie - Kirby, p. 173.
1906 - (Gomphidae?) *perampla* Brodie - Handlirsch, p. 593.
1939 - *Aeschnopsis perampla* (Brodie) - Handlirsch, p. 153 (new genus name, *nomen nudum*?).
1939 - *Cymatophlebiopsis pseudobubas* - Handlirsch, p. 153 (new genus name, *nomen nudum*?).
1942 - *Aeschnopsis perampla* (Brodie) - Cowley, p. 77-78 (subsequent designation as type species of *Aeschnopsis*, brief redescription, in Gomphidae - Protolindeniinae?).
1942 - *Cymatophlebiopsis pseudobubas* Handlirsch - Cowley, p. 78 (brief redescription).
1981 - *Aeschnopsis perampla* (Brodie) - Schlüter, p. 40 (in Anisoptera family uncertain).
1981 - *Cymatophlebiopsis pseudobubas* Handlirsch - Schlüter, p. 40 (in Anisoptera family uncertain).
1992 - *Aeshna perampla* Brodie - Carpenter, p. 81 (in Gomphidae, apparently similar to *Protolindenia*).
1992 - *Cymatophlebiopsis pseudobubas* Handlirsch - Carpenter, p. 83 (family assignment doubtful).
1992 - *Cymatophlebiopsis pseudobubas* Handlirsch - Jarzembowski, p. 176 (list).
1992 - *Aeschnopsis perampla* (Brodie) - Nel and Paicheler, p. 316 (position discussed).
1992 - *Cymatophlebiopsis pseudobubas* Handlirsch - Nel and Paicheler, p. 318 (position discussed).
1994 - *Aeschnopsis perampla* (Brodie) - Bridges, p. VII.182.
1994 - *Cymatophlebiopsis pseudobubas* Handlirsch - Bridges, p. VII193.
1996 - '*Aeschnopsis perampla* (= *Cymatophlebiopsis pseudobubas*)' - Bechly, p. 380 (in Petalurida).

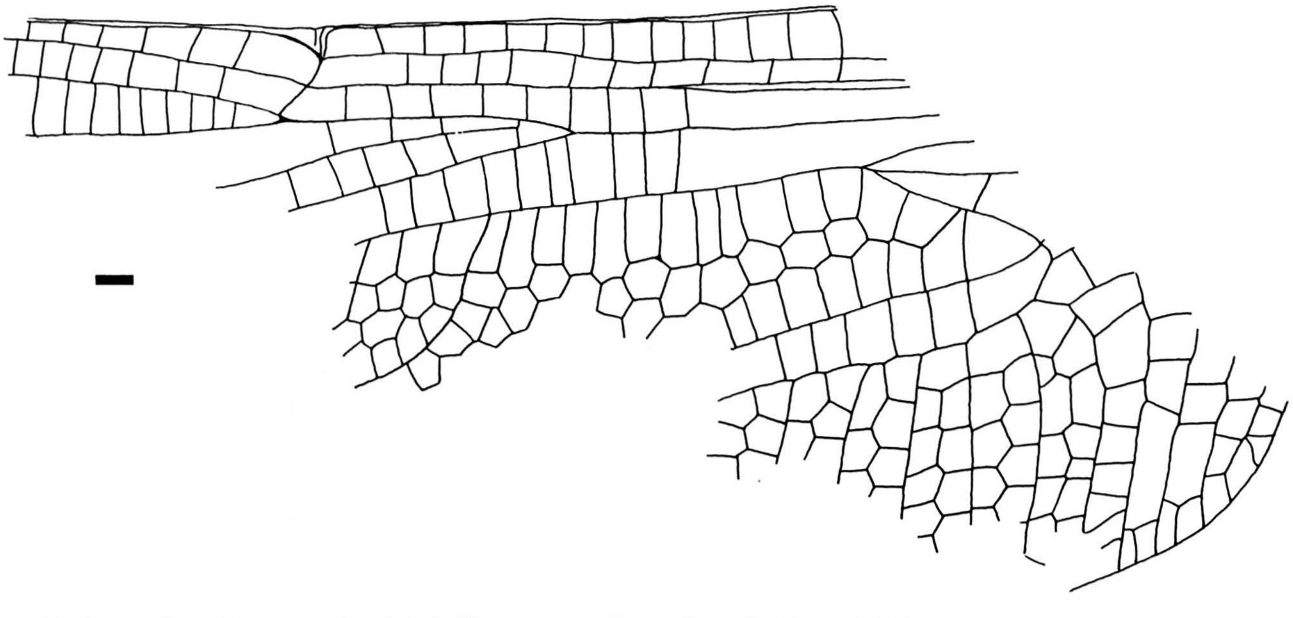

Fig. 4 - *Aeschnopsis perampla* (Brodie 1845), holotype I. 12780 N.H.M., hindwing. Scale bar represents 1 mm.

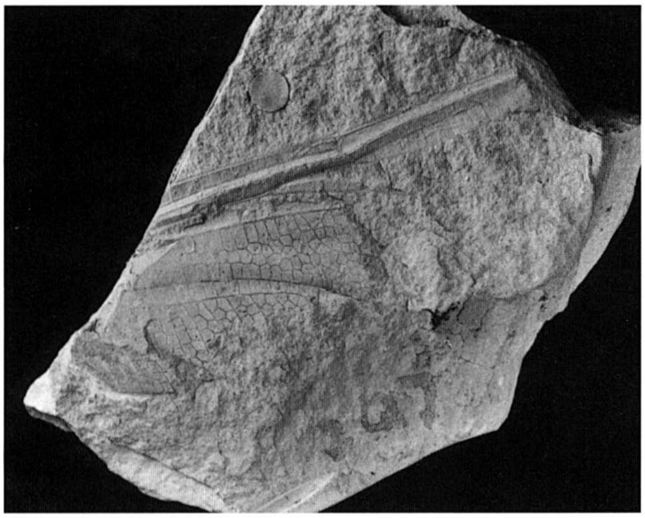

Fig. 5 - Photograph of *Aeschnopsis perampla* (Brodie 1845), holotype I. 12780, (X 5).

Holotype: *Aeschnopsis perampla* specimen I. 12780. The type of *Cymatophlebiopsis pseudobubas* is the specimen I. 3950, det. A.J. Ross, Brodie Coll., Natural History Museum, London.

Stratigraphic level: Lower-Middle Purbeck Beds, Lower Cretaceous.

Type locality: Teffont, Vale of Wardour, Wiltshire (*Aeschnopsis perampla*). Other locality. Durlston Bay, Dorset (*Cymatophlebiopsis pseudobubas*), England, U.K.

Redescription: I. 12780 is the imprint of the median part of a hindwing and I. 3950 is the basal half of a hindwing.

Specimen I. 12780 (holotype of *Aeschnopsis perampla*):

Wing is hyaline. Length of fragment, 39.0 mm; wing about 18 mm wide; distance from discoidal triangle to nodus, 16.2 mm. Postnodal crossveins probably numerous because six of them are present in the rather short preserved part of postnodal area; they are non-aligned with the corresponding postsubnodal crossveins below them, between RA and RP1. Antenodal crossveins numerous, with twelve secondary antenodals between the nodus and the second primary antenodal crossvein Ax2. Ax1 and the more basal secondary are not preserved. Ax2 is nearly on the level of the distal angle of discoidal triangle. Hypertriangle free of crossveins. Discoidal triangle crossed and very elongate; probable length of its basal side, 2.0 mm; of anterior side, 5.7 mm; actual length of distal side, 5.6 mm. Many crossveins in area between RA and RP between arculus and nodus but only the more distal ones being preserved. Three bridge-crossveins (Bqs) preserved but probably four or five. Three rows of cells in basal part of postdiscoidal area but no definite secondary longitudinal vein which would begin on distal side of discoidal triangle. Base of a well-defined Mspl preserved, beginning a little basal of nodus, opposite IR2. Area between Mspl and MA very broad, with four rows of cells, perhaps even more distally. Only one row of cells preserved in basal part of area between MP and CuAa, distal part being not preserved. Cubito-anal area very broad, with more than seven to eight rows of cells between CuAa and posterior wing margin. CuA divided into CuAa and CuAb. CuAa divided into six or seven or more posteriorly-directed parallel branches. CuAb postero-basally directed. CuAb and AA delimit a posteriorly-closed elongate anal loop, the basal part of which is not preserved, but which clearly seems to have been longitudinal elongate. Anal area broad, with up to eight rows of cells between AA and posterior margin of the wing. Postero-basal margin of the wing rounded. Area between RP1 and RP2 crossed by many straight crossveins.

Specimen I. 3950 (holotype of *Cymatophlebiopsis pseudobubas*):

Wing hyaline. Length of preserved part, 39.0 mm; wing 2.1 mm wide; distance from arculus to nodus, 20.2 mm; from discoidal triangle to nodus, 14.0 mm. Postnodal crossveins probably numerous because fourteen of them are preserved in basal half of postnodal area, non-aligned with corresponding postsubnodal crossveins below them. Antenodal crossveins numerous, eleven secondary antenodals between nodus and second primary antenodal crossvein Ax2. Ax1 not preserved but four secondary antenodals visible basal of Ax2. Ax2 nearly opposite distal angle of discoidal triangle. Hypertriangle free of crossveins,

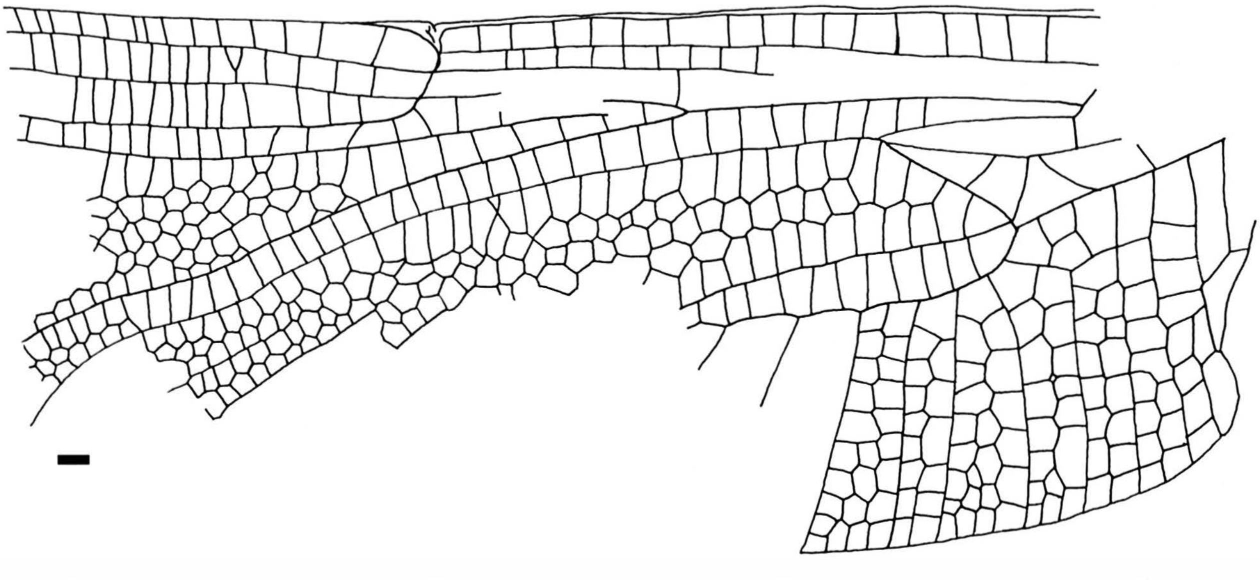

Fig. 6 - *Cymatophlebiopsis pseudobubas* Handlirsch 1939, holotype I. 3950 N.H.M., hindwing. Scale bar represents 1 mm.

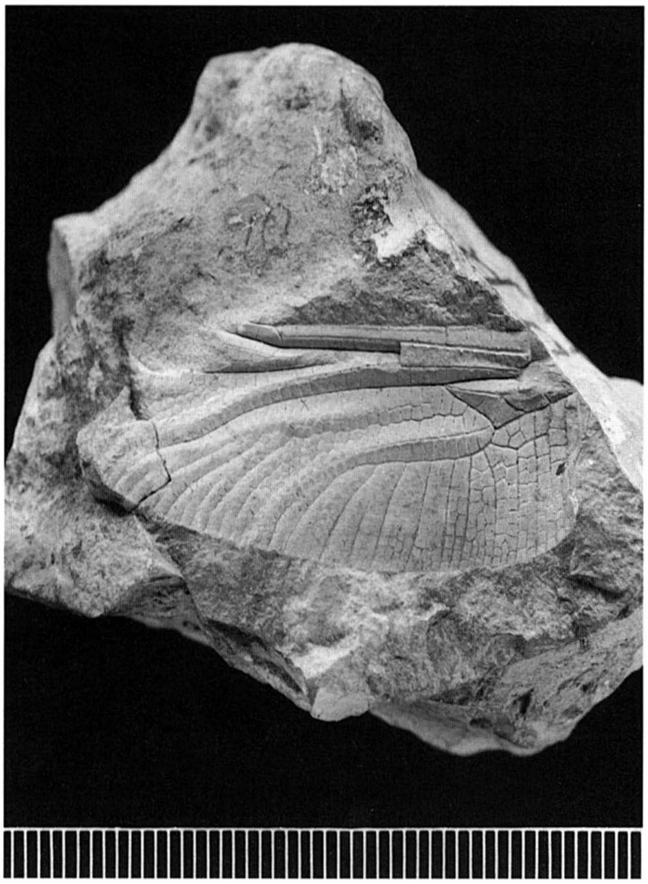

Fig. 7 - Photograph of *Cymatophlebiopsis pseudobubas* Handlirsch 1939, holotype I. 3950.

6.2 mm long and 1.1 mm wide. Discoidal triangle crossed and very elongate; length of its basal side, 2.1 mm; of anterior side, 4.5 mm; of distal side, 4.7 mm. MA and RP well-separated in the arculus, posterior part of arculus being well-angled with anterior part. Two bridge-crossveins (Bqs) preserved, there were probably four or five. Postdiscoidal area three-cells wide in its basal part, no definite secondary longitudinal vein which would begin on distal side of discoidal triangle. Base of a well-defined Mspl preserved beginning opposite nodus. Area between Mspl and MA very broad, with four or five rows of cells. Only one row of cells in basal part of area between MP and CuA and three rows in distal part. Cubito-anal area very broad, with ten rows of cells between CuAa and posterior wing margin. CuA divided into CuAa and CuAb. CuAa divided into seven posteriorly-directed subparallel branches. CuAb postero-basally directed. CuAb and AA delimit a posteriorly-closed, longitudinal elongate anal loop, 5.4 mm long and 1.9 mm wide, that is divided into five cells. Anal area broad, with eight or nine rows of cells between AA and posterior margin. Postero-basal margin of wing well-angled. Area between RP1 and RP2 crossed by many straight crossveins. Two oblique crossveins 'O' between IR2 and RP2, first one two cells distal of subnodus and second two cells distal of first one. No visible Rspl. If there was one, it must have been very weak and indistinct. Only one branch of AA between anal triangle and anal loop. A three-celled long and broad anal triangle. Median cell probably free of crossveins. Submedian cell only traversed by CuP-crossing. An oblique PsA delimiting an unicellular subtriangle, 2.7 mm long and 1.8 mm wide.

Comparison between *Aeschnopsis* and *Cymatophlebiopsis*: the preserved parts of the type specimens of *A. perampla* and of *C. pseudobubas* are very similar. The only differences are as follows: the Mspl of *A. perampla* originates in a slightly more basal position than in *C. pseudobubas*; the distance between the nodus and the discoidal triangle is a little greater in *A. perampla* than in *C. pseudobubas*; the branch CuAb of *A. perampla* is directed towards the wing base for a shorter length than in *C. pseudobubas*; the postero-anal margin of *A. perampla* is more rounded than in *C. pseudobubas*.

These differences cannot justify separate genera or species. The holotype of *A. perampla* is probably a female hindwing and that of *C. pseudobubas* a male hindwing, so that sexual dimorphism can readily explain the small differences between the two holotypes, especially in wing dimensions.

We propose a synonymy of *A. perampla* with *C. pseudobubas*. We chose the generic name *Aeschnopsis* because it is described three lines earlier than *Cymatophlebiopsis* in Handlirsch (1939: 153). This is consistent with Cowley (1942), who revised *Aeschnopsis* before *Cymatophlebiopsis*. The specific name *A. perampla* has priority over *A. pseudobubas* because it was published earlier by Brodie (1845).

Systematic position of *Aeschnopsis*:

Comparison with Gomphides: the great development of the cubito-anal, anal and postdiscoidal areas with a well-defined Mspl and the great number of postnodal and antenodal crossveins do not suggest any relationship with the Gomphides but there is no definite evidence of a relationship.

Comparison with Euaeshnida and Hemeroscopidae: *Aeschnopsis* shares with Euaeshnida a distinct Mspl and a broad area between it and MA plus an elongate discoidal triangle with a sigmoidal MAb (as in Gomphides - Hageniidae), but greatly differs from aeshnids in the following features: the anal loop is elongate; the anal loops of the Euaeshnida being more transverse, even those of the basal 'gomphaeschnine' grade of genera (Martin 1908-1909; Pritykina 1977; Wighton and Wilson 1986); the presence of two oblique crossveins 'O'. The presence of a PsA with a distinct unicellular subtriangle is probably an apomorphic ground-plan character of the Anisoptera (see: Jarzembowski and Nel 1996) that is retained in some Euaeshnida - Gomphaeschnidae but also some Gomphides, Petalurida, Austropetaliida, Brachystigmata: Chlorogomphida, etc. The Hemeroscopidae (probably Chlorogomphida) also show a broad transverse anal loop and they do not have a definite Mspl.

Comparison with *Aktassia magna*: the vestigial posteriorly open anal loop of *Aktassia magna* is a sufficient character for separation from *Aeschnopsis*.

Comparison with Cymatophlebiidae and Petalurida: the lack of any distinct vein Mspl in *Cymatophlebia* spp. renders the attribution of *Aeschnopsis* to Cymatophlebiidae (*sensu* Bechly 1996 and Bechly *et al.*, in prep.) difficult. Furthermore, the elongate anal loop of *Aeschnopsis* is very different from the posteriorly open and rounded anal loop of *Cymatophlebia*. The unicellular subtriangle and two-celled discoidal triangle of *Aeschnopsis* are very different from the corresponding structures of *Cymatophlebia*, too.

Cymatophlebiella euryptera Pritykina 1968 (Lower Cretaceous, Karatau, Russian Federation) differs from *Aeschnopsis* in the following characters: the anal loop is posteriorly open, weakly developed; the subtriangle is two-celled; the discoidal triangle is three-celled; there is no Mspl.

The lack of a preserved pterostigmal region in the two known wings of *A. perampla* makes a comparison with Petalurida difficult. The main difference is the presence of Mspl. The elongate anal loop differs from extant Petalurida, but is very similar to *Cretapetalura*, *Necrogomphus jurassicus*, and Mesuropetala. It might represent a synapomorphy of *Aeschnopsis* and *Cretapetalura* gen. nov., but this evidence is not very strong.

The affinities of *Aeschnopsis* cannot be determined with the currently available characters. This genus shares similarities and differences nearly equally with Cymatophlebiidae and Petalurida. It possibly belongs to a new, still undescribed family but the erection of such a group at this stage would not solve the problem of its phylogenetic relationships. Therefore, we refer *Aeschnopsis* to Anisoptera *incertae sedis*. *Necrogomphus jurassicus*, based on a hindwing, is very similar to *Aeschnopsis perampla* and maybe congeneric, but the lack of any strong synapomorphy render a confirmation of this hypothesis rather difficult. It remains possible that these taxa all belong to the same lineage as *Cretapetalura* gen. nov. (Cretapetaluridae fam. nov.), but only discovery of new and better preserved material could provide a convincing solution.

Genus *Mesuropetala* Handlirsch 1906
(*in* Aeshnoptera Bechly 1996,
Family Mesuropetalidae Bechly 1996)
(previously in Petaluridae)

Type genus: *Mesuropetala* Handlirsch 1906.

Type species: *Mesuropetala koehleri* (Hagen 1848), by subsequent designation by Cowley (1934).

Further species: Pritykina (1968) described *Mesuropetala costalis* and *Mesuropetala auliensis* from the Upper Jurassic of Karatau (C.I.S.). New species will be described in Bechly *et al.* (in prep.), who will also include '*Necrogomphus*' *jurassicus* (Giebel 1856) to this genus (see above).

Diagnosis: no complete diagnosis of this genus has previously been attempted. *Mesuropetala* can be distinguished from other Upper Jurassic Anisoptera genera by the combination of following features: wing dimensions similar to those of *Protolindenia wittei*, i.e. 47 to 51 mm long; oblique pterostigmal brace aligned with the basal side of pterostigma; pterostigma very elongate but not basally recessed; forewing discoidal triangle transverse but broad and two-celled, hindwing discoidal triangle longitudinal and unicellular; hypertriangles free of crossveins; well-defined subtriangles on all wings, those of forewings being three-celled whereas those of the hindwings are unicellular; anal loop longitudinal elongate, divided into two or three cells, and posteriorly well-closed but zigzagged; no well-defined vein Rspl or Mspl; two oblique crossveins 'O'; two primary antenodals stronger than the secondaries, separated by two to four secondaries; arculus nearer to Ax1 than to Ax2; Ax2 situated basally of distal angle of discoidal triangle; only a short IR1, distal of the pterostigma; MA and RP3/4 strongly parallel and undulate; IR2 and RP2 rather straight and strongly parallel, area between them being narrowed distally; CuA divided into five to seven parallel posterior branches; male cerci of *Mesuropetala koehleri* broad and foliate, like cerci of extant Petalurida (especially *Uropetala* and *Petalura*) and extant Euaeshnida - Polycanthagynini (incl. *Polycanthagyna erythromelas* McLachlan 1896 and maybe *Aeshna petalura* Martin 1908, according to G. Peters, pers. comm.), as suggested by Deichmüller (1886: pl. 4, figs 11-12).

Mesuropetala koehleri (Hagen 1848)
Figs 8-16

1848 - *Gomphus ? koehleri* - Hagen, p. 8.
1856 - *Libellula koehleri* (Hagen) - Giebel, p. 284.
1862 - *Gomphus ? koehleri* Hagen - Hagen, p. 139 (redescription).
1862 - *Petalura varia* Hagen - Hagen, p. 107 (syn. nov.).
1886 - *Uropetala koehleri* (Hagen) - Deichmüller, p. 52-56; pl. 4, fig. 3, 11-12 (redescription).
1897 - ? *Uropetala koehleri* (Hagen) - Meunier, p. 9; pl. 4, fig. 4 (figured).
1898 - *Petalura varia* Hagen - Meunier, p. 123.
1906 - *Mesuropetala koehleri* (Hagen) - Handlirsch, p. 588; pl. 47, fig. 9 (in gen. nov., a poor reproduction of Deichmüller's figure 3 is given.
1932 - *Protolindenia koehleri* (Hagen) - Carpenter, p. 113; fig. 7 (comb. nov., new fig.).
1934 - *Mesuropetala koehleri* (Hagen) - Cowley, p. 252 (subsequent designation as type species of *Mesuropetala*)
1957 - *Mesuropetala koehleri* (Hagen); Fraser, p. 95 (in Petaluridae).
1968 - *Mesuropetala koehleri* (Hagen); Pritykina, p. 49 (in Petaluridae).
1978 - *Mesuropetala koehleri* (Hagen) - Lindley, p. 345 (in Gomphidae).
1981 - *Mesuropetala koehleri* (Hagen) - Schlüter, p. 39 (in Petaluridae).
1985 - *Mesuropetala koehleri* (Hagen) - Ponomarenko, p. 136 (in Petaluridae).
1992 - *Mesuropetala koehleri* (Hagen) - Carpenter, p. 83 (in Petaluridae).
1992 - *Protolindenia koehleri* (Hagen) - Nel and Paicheler, p. 319 (position discussed).
1994 - *Mesuropetala koehleri* (Hagen) - Bridges, p. VII.127.
1996 - *Mesuropetala koehleri* (Hagen) - Bechly, p. 16, 382 (in Mesuropetalidae).

Holotype: the type specimen of Hagen has not been recently redescribed, and we were unable to find it in any of the numerous visited collections (incl. the coll. Hagen at MCZ!), thus its present location is unknown and it has to be regarded as lost. To finally settle the complex taxonomical problems described below, especially regarding the identity of the genus *Mesuropetala* and its distinction from *Protolindenia* (see below), of which the holotype of the type species has to be regarded as lost too, we decided to designate specimen [1846/Hagen 44] in the collection of the Museum of Munich (BSPGM) as neotype of *Mesuropetala koehleri* (Hagen 1848), according to Art. 75 IRZN. It comes from the same locality as the holotype and according to our comparison with the

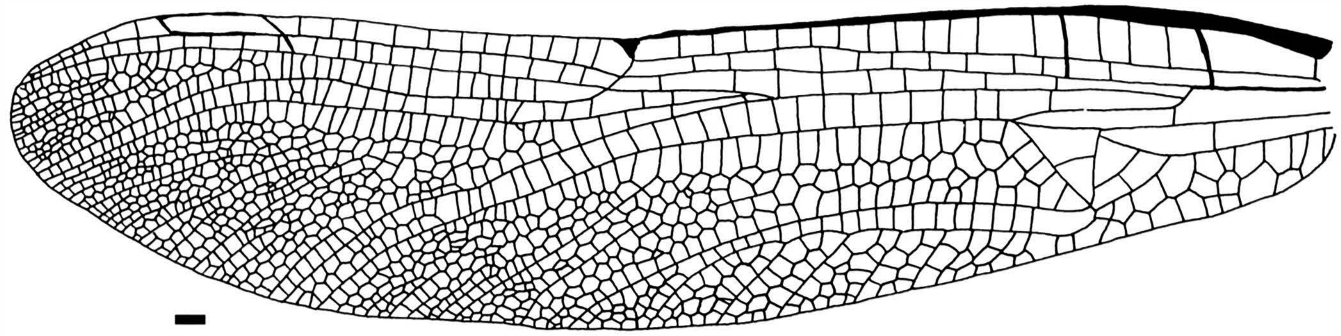

Fig. 8 - *Mesuropetala koehleri* (Hagen 1848), 1846 / Hagen 44, neotype, Museum of Munich, forewing. Scale bar represents 1 mm.

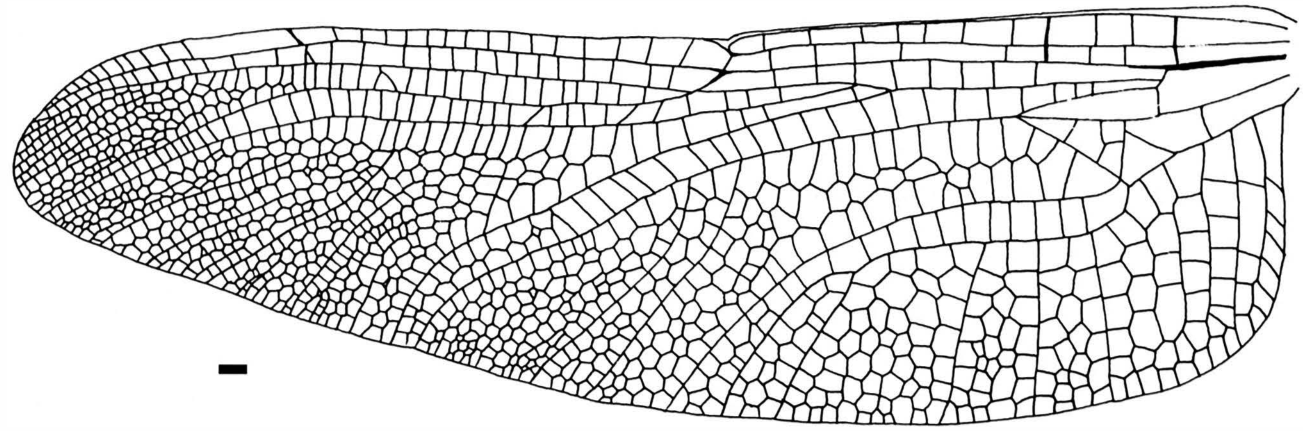

Fig. 9 - *Mesuropetala koehleri* (Hagen 1848), 1846 / Hagen 44, hindwing. Scale bar represents 1 mm.

available descriptions and figures it belongs to the same species.

Stratigraphic level: Upper Jurassic/Malm zeta/Tithonian, Lithographic Limestone.

Type locality: Solnhofen/Eichstätt, Bavaria, Germany.

Further material: Deichmüller (1886) redescribed and figured a specimen from the Museum of Dresden. Meunier (1897) mentioned the presence of some badly preserved specimens from the Musée Teyler (Haarlem). Carpenter (1932) partly figured the wing venation. His figure is based on the study of two specimens (n¡ 6194 and 1998) in the Museum of Comparative Zoology (Harvard University, Cambridge). Ponomarenko (1985) indicated the presence of some material in the Vienna Museum.

We had the opportunity to study a well preserved specimen [1846/Hagen 44], from the Museum of Munich (BSPGM), which we designated as neotype. Handlirsch (1906) considered that this specimen belonged to *Protolindenia wittei*, but it does not correspond to the figures of *P. wittei* given by Giebel, Hagen and Deichmüller, and it resembles the figures of *Mesuropetala koehleri* given by Deichmüller and Carpenter. Thus, this specimen does not belong to *P. wittei* but to *M. koehleri* (see below for a comparison between *P. wittei* and *M. koehleri*). The following study confirms this hypothesis.

As the holotype specimen of *Aeschna muensteri* Germar 1839 labelled [specimen AS VII 704/Syntyp. Origin. Germar, 1839, Taf. 23, fig. 12/Malm Zeta, Solnhofen, N°45/Aeschna Munsteri, Origin. Ex./Aeschna grandis ? Köhl./collection of the BSPGM, Munich] is very poorly preserved, the specific identity of *A. muensteri* and *Mesuropetala koehleri* is still uncertain, and a final solution of the complex taxonomical problems (also involving '*Morbaeschna muensteri*' *sensu* Needham 1907) will be attempted in Bechly *et al.* (in press).

In addition, there is a new specimen labelled [1966/64 Ei Bl] in the collection of the Jura-Museum (Eichstätt), and another labelled [1964 XXIII/ Anisoptera Gomphidae?] in the collection of the Museum of Munich (BSPGM). The latter specimen seems to belong to a new smaller species of *Mesuropetala* that will be described in Bechly *et al.* (in press). Two further well preserved specimens of *M. koehleri* have been located and studied by us in the collection of the Natural History Museum in Berlin (specimen [MB.J. 1441]) and the Museum of Comparative Zoology (Harvard University, Cambridge) (specimen [MZC 1998]). A further specimen from this collection [MCZ 6203] is rather important because it has a well preserved head with large approximate eyes. These specimens will all be described in detail in the forthcoming revision of Mesozoic Aeshnoptera by Bechly *et al.* (in prep.).

Systematic description:

Specimen [1846 a/b, Hagen 44], [neotype], Museum of Munich (BSPGM). Labelled [*Mesuropetala munsteri* Germ. O *M. koehleri* Hagen sp.]/[*Petalura Münsteri* Germ. sp., Leuchtenberg'sche Sammlung, Lithograph. Schiefer, Eichstädt].

A nearly complete female dragonfly with the wings in connection with the body. Two of the wings are complete and well preserved. The wings have been hyaline.

Forewing: length, 49.7 mm; width at nodus, 11.3 mm; distance from base to nodus, 25.8 mm; from nodus to pterostigma, 12.8 mm; distance from base to arculus, 5.0 mm. Pterostigma very elongate, 6.6 mm long, 0.8 mm wide, distinctly braced by a oblique crossvein, and covers numerous cells. Eleven postnodal crossveins visible between nodus and pterostigma (total number probably sixteen), non-aligned with corresponding postsubnodal crossveins; the most basal postnodal crossvein being slanted towards the nodus. Eighteen visible antenodal crossveins between costal margin and ScP, non-aligned with corresponding antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins stronger than other antenodal crossveins. Ax1 only 0.8 mm basal of the arculus; Ax2 7.2 mm distal of Ax1, on the level of the distal side of the discoidal triangle. Four secondary antenodal crossveins between ScP and costal margin, between the two primary antenodal crossveins, non-aligned with the three corresponding antenodal crossveins between ScP and RA. Ten antesubnodal crossveins visible in the space between the arculus and the subnodus, without a distinct 'cordulegastrid gap' (*sensu* Bechly 1995) directly basal of the subnodus (the apparent 'gap' in the basal third of the antesubnodal space is maybe partly an artefact of preservation). Three or four crossveins visible basal of the first oblique vein, including at least two bridge-crossveins (Bqs). Base of RP2 aligned with subnodus. Only one oblique crossvein 'O' visible, one and a half cells distal of subnodus (a second distal oblique vein might have been present too since this area is partly distorted). IR2 originates 5.2 mm and RP3/4 originates 6.5 mm basal of subnodus. No well-defined Rspl but three convex secondary veins in the distal part of the area between IR2 and RP3/4, originating on the zigzagging margin of a row of enlarged cells along IR2. RP2 and IR2 closely parallel, with always only one row of cells between them. Vein pseudo-IR1 distinct and originates beneath the distal end of the pterostigma. RP1 and RP2 closely parallel till the pterostigma, with only one row of cells between them. RP3/4 and MA parallel and gently undulating, with one row of cells between them (distally two rows). No Mspl but a row of enlarged cells along MA, and a distinct convex secondary vein in the distal postdiscoidal area, originating on MA. Postdiscoidal area not very widened distally, with three rows of cells distal of the discoidal triangle. Hypertriangle free of crossveins. Discoidal triangle very transverse and divided into two cells by a 'horizontal' crossvein; length of its anterior side, 3.4 mm; of basal side, 3.2 mm; of distal side, 4.6 mm; the distal side MAb being straight. Median cell free of crossveins. Submedian cell only traversed by CuP-crossing, 1.4 mm basal of arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subtriangle, max. 3.3 mm long and basally 2.7 mm wide (= length of PsA), divided into three cells. PsA meeting with MP + CuA somewhat below the basal angle of the discoidal triangle. One row of cells

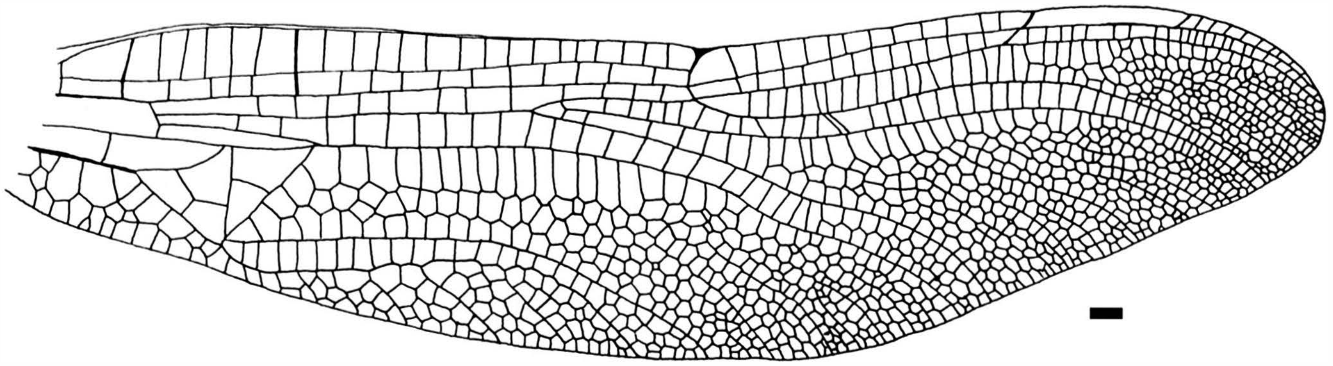

Fig. 10 - *Mesuropetala koehleri* (Hagen 1848), specimen 1966 / 64 Jura-Museum Eichstätt, forewing. Scale bar represents 1 mm.

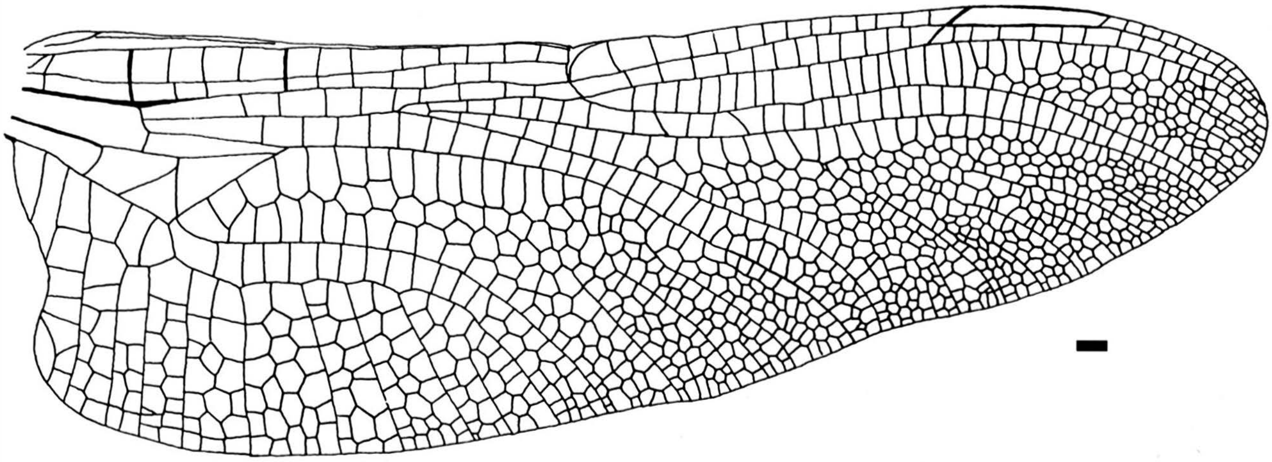

Fig. 11 - *Mesuropetala koehleri* (Hagen 1848), specimen 1966 / 64, hindwing. Scale bar represents 1 mm.

in the area between MP and CuA but distally these veins are diverging with five cells between them at posterior wing margin. MP reaching posterior wing margin somewhat distal of the level of the nodus, while CuA reaching posterior wing margin somewhat basal of the level of the nodus. Posterior branches of CuA well-defined but only four distal ones are preserved. Four or five rows of cells between CuA and posterior wing margin; max. width of cubito-anal area, about 2.9 mm. Anal area max. about 2.5 mm wide, below origin of PsA, with two or three rows of cells between AA and posterior wing margin.

Hindwing: length, 46.3 mm; width at nodus, 14.1 mm; distance from base to nodus, 20.3 mm, thus nodus in a rather basal position; distance from nodus to pterostigma, 15.0 mm; distance from base to arculus, 4.0 mm. Pterostigma very elongate, 6.1 mm long, 0.9 mm wide, distinctly braced by a oblique crossvein, and covering numerous cells. Fifteen postnodal crossveins between nodus and pterostigma, non-aligned with corresponding postsubnodal crossveins between RA and RP1; the most basal postnodal crossvein slanted towards the nodus. Twelve visible antenodal crossveins between costal margin and ScP (total number probably fourteen), non-aligned with corresponding antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Primary antenodal crossveins Ax1 and Ax2 stronger than others. Ax1 0.6 mm basal of the arculus, Ax2 about 5.9 mm distal of Ax1. Between the two primary antenodal crossveins, three or four secondary antenodal crossveins, non-aligned with corresponding antenodal crossveins. Eight antesubnodal crossveins visible in the space between arculus and subnodus, without a distinct 'cordulegastrid gap' (*sensu* Bechly 1995) directly basal of subnodus but with a 'gap' in basal part of antesubnodal space. Six crossveins basal of first oblique vein, including three bridge-crossveins (Bqs). Base of RP2 aligned with subnodus. Two oblique crossveins 'O', first one being three cells distal of subnodus and second five cells distal of first one. IR2 originates 5.0 mm and RP3/4 originates 5.9 mm basal of subnodus. No well-defined Rspl but three convex secondary veins in distal part of area between IR2 and RP3/4, originating on zigzagging margin of a row of enlarged cells along IR2. Distinct pseudo-IR1 originates beneath distal end of pterostigma. RP2 and IR2 closely parallel, with only one row of cells between them. RP1 and RP2 closely parallel till pterostigma, with only one row of cells between them. RP3/4 and MA parallel and gently undulating, with one row of cells between them (distally two rows). No well-defined Mspl but three convex secondary veins in distal part of postdiscoidal area, originating on zigzagging margin of a row of enlarged cells along MA. Postdiscoidal area distally widened, with two rows of cells directly distal of discoidal triangle. Hypertriangle free of crossveins (one or two apparent crossveins seem to be artefacts). Discoidal triangle free of crossveins and less transverse than that of forewing; its anterior side is 3.9 mm long, its basal side is 2.1 mm long; its distal side is 4.4 mm. long. Distal side of discoidal triangle (MAb) straight. Median cell is free of crossveins. Submedian cell, between MP + Cu and AA, only traversed by CuP-crossing, 1.4 mm basal of arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-

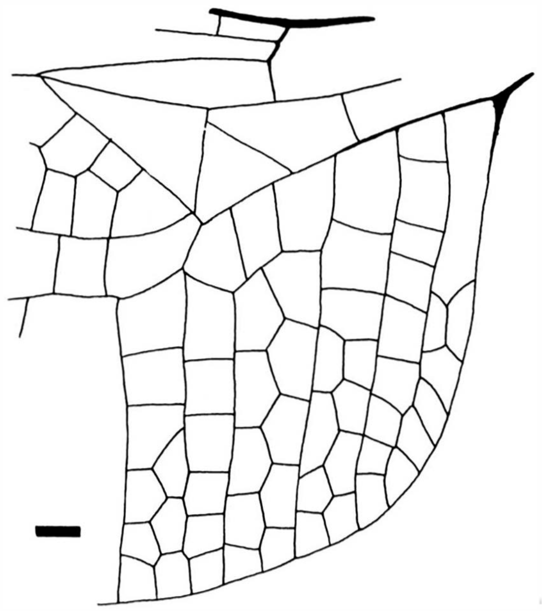

Fig. 12 - *Mesuropetala koehleri* (Hagen 1848), 1846 / Hagen 44, Museum of Munich, anal area of hindwing. Scale bar represents 1 mm.

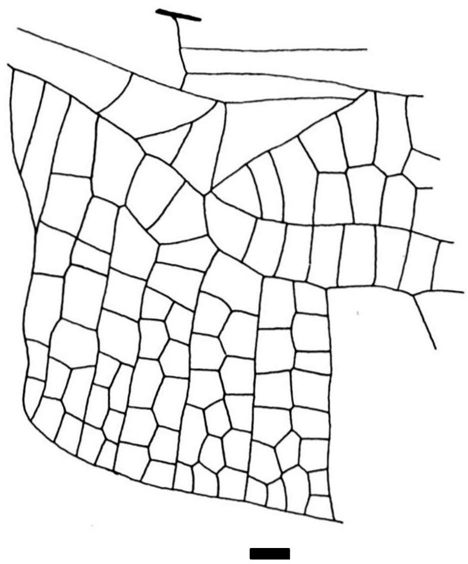

Fig. 13 - *Mesuropetala koehleri* (Hagen 1848), specimen 1966 / 64 Jura-Museum Eichstätt, anal area of hindwing. Scale bar represents 1 mm.

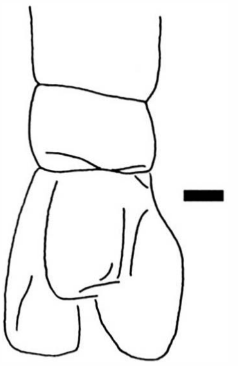

Fig. 14 - *Mesuropetala koehleri* (Hagen 1848), specimen 1966 / 64, female genital appendages. Scale bar represents 1 mm.

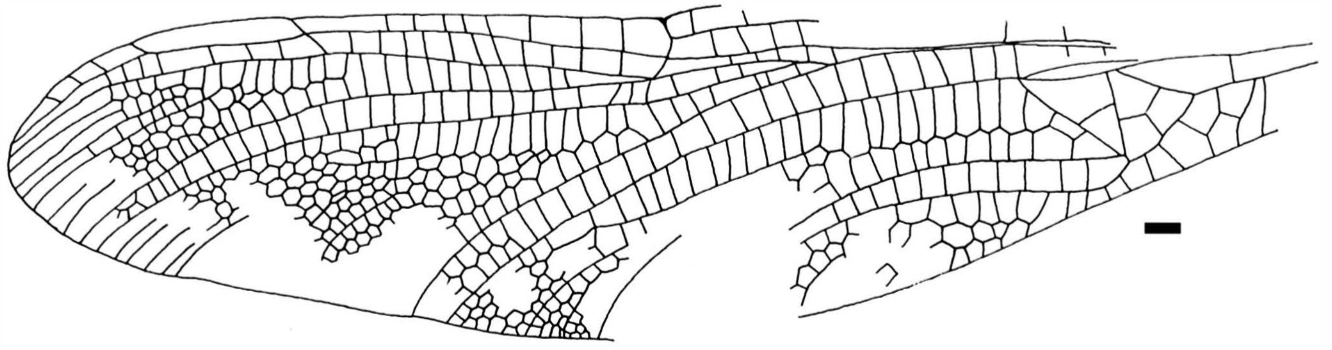

Fig. 15 - *Mesuropetala koehleri* (Hagen 1848), specimen 1964. XXIII, Museum of Munich, forewing. Scale bar represents 1 mm.

defined unicellular subtriangle, max. 2.0 mm long and basally 2.0 mm wide (= length of PsA). PsA meeting with MP + CuA slightly below basal angle of discoidal triangle. One row of cells in area between MP and CuA but, close to wing margin, these veins are somewhat diverging with two rows of cells between them. MP reaching posterior wing margin somewhat distal of level of nodus, while CuA reaching posterior wing margin opposite nodus. Six well-defined posterior branches of CuAa and a well-defined CuAb. Seven or eight rows of cells between CuA and posterior wing margin, max. width of cubito-anal area, 6.6 mm. Anal area broad, about 8.4 mm wide (below PsA), with seven rows of cells between AA and posterior wing margin. AA with four closely parallel and straight posterior branches. Anal loop longitudinal elongate, about 3.4 mm long and 1.6 mm wide, divided into three cells and posteriorly well-closed but zigzagged. Anal margin rounded. Neither an anal triangle nor an anal angle, thus it is a female specimen. No visible membranule.

Body length from head to the tip of the abdomen about 77 mm.

Abdomen never narrowed, 56 mm long, 4 mm wide. Two diverging valvula beginning under segment 8 and reaching apex of segment 9. Ovipositor not extending beyond apex of abdomen. Detailed structure of these valvulae unknown (e.g. presence or absence of spines), so it is impossible to indicate whether it was an endophytic or an exophytic egg layer.

Head 8 mm long, 8 mm wide. Compound eyes seem to be well-separated, 3 mm apart, but this rather seems to be due to a preservation in ventral view, since specimen [MCZ 6203], which is certainly conspecific and has a well-preserved head, clearly shows large approximated eyes. Detailed structure of head not preserved. Distance between head and base of forewings, 5 mm; width of thorax, 7 mm.

Comparison with the figure of *M. koehleri* in Carpenter (1932: fig. 7): there is no visible difference between the neotype specimen [1846/Hagen 44] and the composite figure of Carpenter based on the study of two specimens except the anal loop, which seems to be unicellular in the figure of Carpenter, but a comparison with other specimen clearly reveals that this is a drawing error due to the zigzagged hind margin of the anal loop in *Mesuropetala*: the anal loop in Carpenter's specimen is indeed two-celled!

Comparison with the figure of *M. koehleri* in Deichmüller (1886, pl. 4, fig. 3): the figure of Deichmüller is less precise than that of Carpenter' but all the figured characters are exactly identical to those of the neotype specimen [1846/Hagen 44]. Thus, the attribution of specimen [1846/Hagen 44] to *M. koehleri* is highly probable.

Comparison between *Protolindenia wittei* and *Mesuropetala koehleri*: Carpenter (1932: 112) synonymised the genus *Mesuropetala* with *Protolindenia*. Handlirsch (1906: 588-589) recognized three species in *Mesuropetala*, i.e. the type species (*M. koehleri*), ? *M. muensteri* and ? *M. schmiedeli* (Giebel 1856). Later, Fraser (1957: 95), Pritykina (1968: 49, 52), Schlüter (1981), Ponomarenko (1985), Carpenter (1992: 81, 83), Bridges (1994) and Bechly (1995) considered *Mesuropetala* and *Protolindenia* as separate genera without re-examining the material. They also considered *Mesuropetala* as a petalurid and *Protolindenia* as a gomphid, except for Bechly (1995). The impossibility of any direct comparison of the holotypes of *M. koehleri* and of *P. wittei* makes the comparison of the two species and the attribution of new specimens to them rather difficult. The wings and body dimensions of the two species are very similar (Handlirsch 1906). Carpenter (1932) gave the following diagnostic differences: *M. koehleri* is characterized by a much more transverse discoidal triangle in its forewing than *P. wittei* with the anterior side much shorter than the basal one.

After study of the available material and examination of the figures of Giebel, Hagen, Deichmüller and Carpenter the following differences are visible: the forewing discoidal triangle is two-celled in *M. koehleri* and three- to five-celled in *P. wittei*; there are three rows of cells in the hindwing area between CuAa and MP in *M. koehleri* and four to six rows of cells in *P. wittei*; IR1 is very short in *M. koehleri* and very long in *P. wittei*; the compound eyes are approximated in *M. koehleri* and widely separated in *P. wittei*; the male appendices (cerci) are foliate in *M. koehleri* and forcipate in *P. wittei*.

The figures of Giebel, Hagen, Deichmüller and Carpenter do not give any information concerning the position of the pterostigmal brace in the two species. If we follow these authors, the two species should not have any oblique pterostigmal brace. But, if the determinations of the specimen figured photographically by Carpenter (1992) and of specimens described herein are correct, *P. wittei* should have a oblique pterostigmal brace in a basal position (Bechly 1995). This is highly probable because all the other characters of these specimens agree with the description and the figure of the holotype of *P. wittei* given by Giebel (1860).

Thus, *P. wittei* has a oblique pterostigmal brace in a very basal position between the pterostigma and the nodus. On the other hand, the oblique pterostigmal brace of *M. koehleri* is clearly present but not basally displaced.

Systematic position of *Mesuropetala koehleri*:

M. koehleri was generally considered as a petalurid, although Nel and Paicheler (1992) and Bechly (1993, 1995) have considered this attribution to be far from certain. Following the redescription and study of the new material, it appears that the wing venation of this species has little to do with the Petalurida, as already suggested by Bechly (1996). All the autapomorphies of Petalurida are absent in *M. koehleri*: it has an elongate pterostigma but this character is of very relative value because the two basal Petalurida *Protolindenia* and *Cretapetalura* possess no yet possess really elongate pterostigmata; area between costal margin and RA distal of the pterostigma not narrow and only crossed by few veins; IR1 not elongate but very short; few bridge-crossveins (Bqs); bridge-space (Bqs-area) between RP, IR2 and the subnodus not narrowed; pterostigmal brace not basally recessed but clearly oblique.

All the common character states of Petalurida and *M. koehleri* can also be found in other groups: two oblique crossveins 'O' (only as rare aberration in Cordulegastrida, present in other basal Aeshnoptera like Cymatophlebiidae and most specimens of '*Morbaeschna muensteri*' *sensu* Needham 1907); well-defined subtriangles in fore- and hindwings (also present most Gomphides); many cells in the four wings reticulations; foliate male cerci (within Petalurida only distinct in *Petalura* and *Uropetala*, but also present in *Cymatophlebia* and Polycanthagynini incl. '*Aeshna*' *petalura* Martin 1908, according to G. Peters, pers. comm.). Thus, all these similarities could represent symplesiomorphies and convergences rather than putative synapomorphies of *Mesuropetala* with Petalurida.

The plesiomorphic characters visible in *M. koehleri* are also common to the Petalurida and Cordulegastrida, viz. the cubito-anal area is very long; Mspl and Rspl are lacking.

The attribution of *M. koehleri* to the Petalurida cannot be justified by any strong putative synapomorphies and this species shares no venational synapomorphy with the Cordulegastrida, Chlorogomphida, 'corduliids' and Libellulidae. *M. koehleri* shares no synapomorphic character with the extant Cordulegastrida. Its female ovipositor is shorter than in extant Cordulegastrida. It has a distinct pseudo-anal vein PsA, no trace of a secondary furcation of IR2 into two branches, and no vein Rspl. This last plesiomorphy is also present in extant Chlorogomphida, but *M. koehleri* has none of the autapomorphies of this taxon, i.e. reticulate median cell and submedian cell, very broad and posteriorly closed anal loop, presence of two rows of cells between CuA and MP, and highly derived structure of hindwing CuA.

The Euaeshnida always have well-defined Rspl and Mspl, unlike *M. koehleri*. The RP1 and RP2 are more or less parallel for a long distance (from the subnodus to the level of the pterostigma) in *M. koehleri* and most Euaeshnida (except *Allopetalia*).

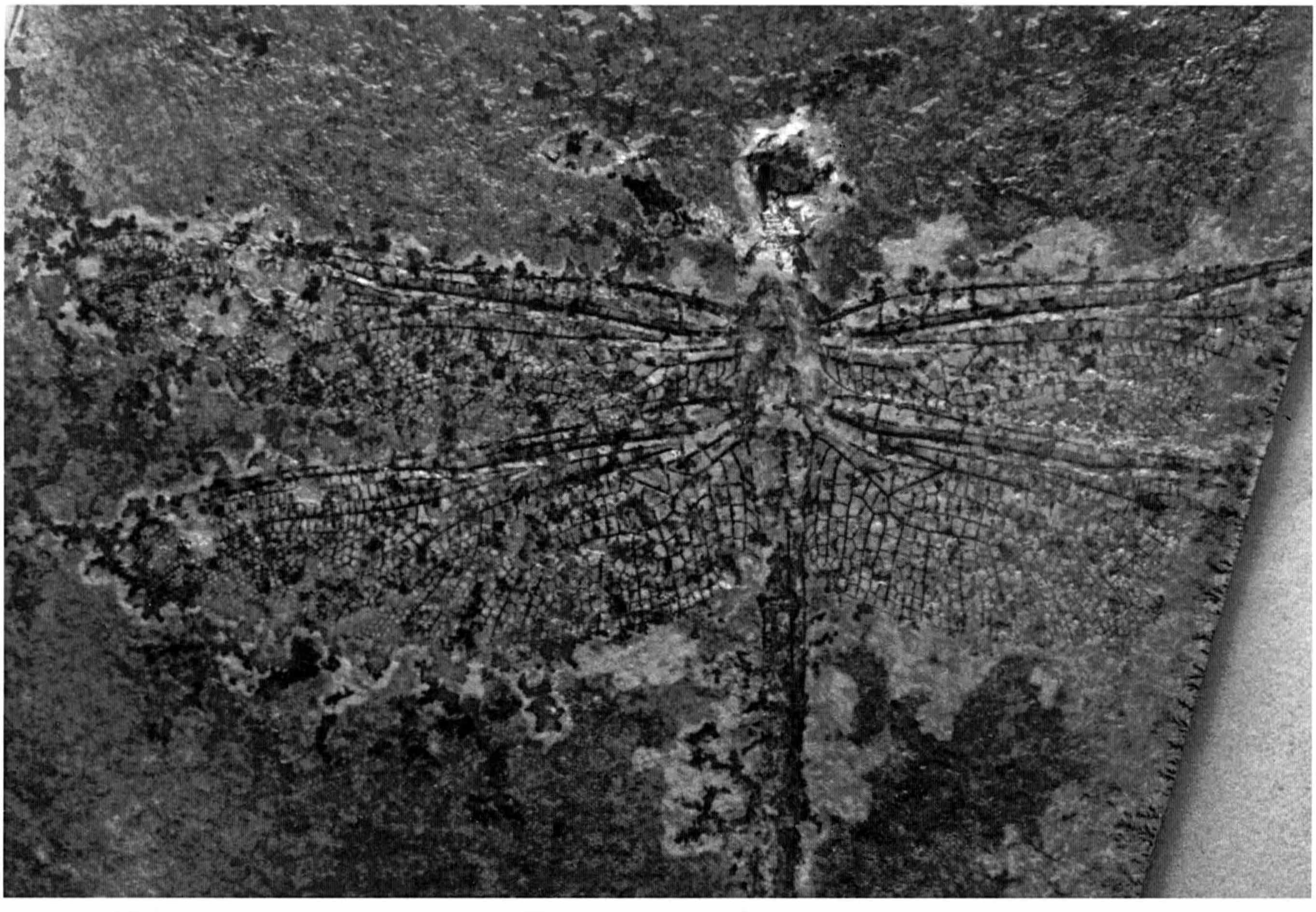

Fig. 16 - Photograph of *Mesuropetala koehleri* (Hagen 1848), neotype [1846 / Hagen 44].

In other Aeshnoptera (*Archipetalia* and *Cymatophlebia*) these veins are less parallel or have two rows of cells in the area between them, basal of the pterostigma. This character is without doubt derived but it is not unique within Anisoptera (present by convergence in a few Gomphides - Lindeniinae, the cordulegastrid genus *Anotogaster* and the chlorogomphid *Indorogomphus* Carle 1995). Nevertheless it is a rather convincing synapomorphy that demonstrates the relationship of *Mesuropetala* with Aeshnoptera, since a relationship with Lindeniinae is excluded by the absence of the forked IR2 (synapomorphy of Gomphoidinae and Lindeniinae) and the retained plesiomorphy of a second oblique crossvein 'O', which is autapomorphic absent in all Gomphides; the approximated compound eyes would agree with a position in Aeshnoptera or Cavilabiata, but exclude a position in Petalurida or Gomphides; a relationship with Cavilabiata (thus also Cordulegastrida) is excluded by the presence of numerous crossveins between RA and RP basal of the subnodus (no 'cordulegastrid gap' *sensu* Bechly 1995) and the absence of forked IR2. Therefore, it is more parsimonious to include *Mesuropetala koehleri* in a separate family Mesuropetalidae (see the phylogenetic discussion below), within the more basal Aeshnoptera (Bechly 1996; Bechly *et al.*, in prep.).

'*Mesuropetala*' *costalis* Pritykina 1968

Fig. 17-18

1968 - *Mesuropetala costalis* - Pritykina, p. 49-50; text-fig. 20, pl. 5, fig. 1.
1992 - *Mesuropetala costalis* Pritykina - Carpenter, p. 83.
1992 - *Protolindenia costalis* (Pritykina) - Nel and Paicheler, p. 320.
1994 - *Mesuropetala costalis* Pritykina - Bridges, p. VII.59.

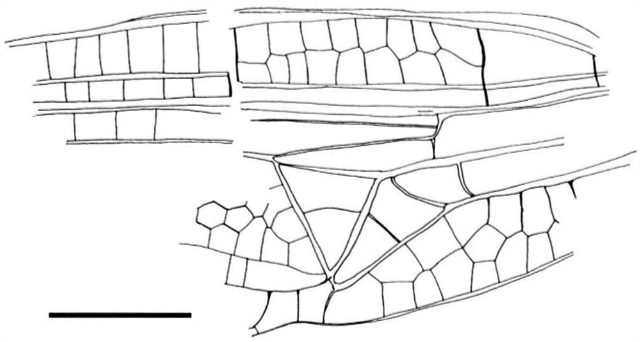

Fig. 17 - *Mesuropetala costalis* Pritykina 1968, specimen PIN 2239/20, holotype, forewing base. Scale bar represents 5 mm.

Holotype: specimen PIN 2239/20, the base of a forewing.

Stratigraphic level: Upper Jurassic.

Type locality: Karatau, Turkestan, C.I.S.

Systematic position: the preserved part of the typical wing provides little informations. Nevertheless, it is very similar to the same part of the forewing of *Mesuropetala koehleri*: the discoidal triangle is transverse and two-celled; the subtriangle is well-defined; the primary antenodals are stronger than the numerous secondaries; the postdiscoidal area is broad with

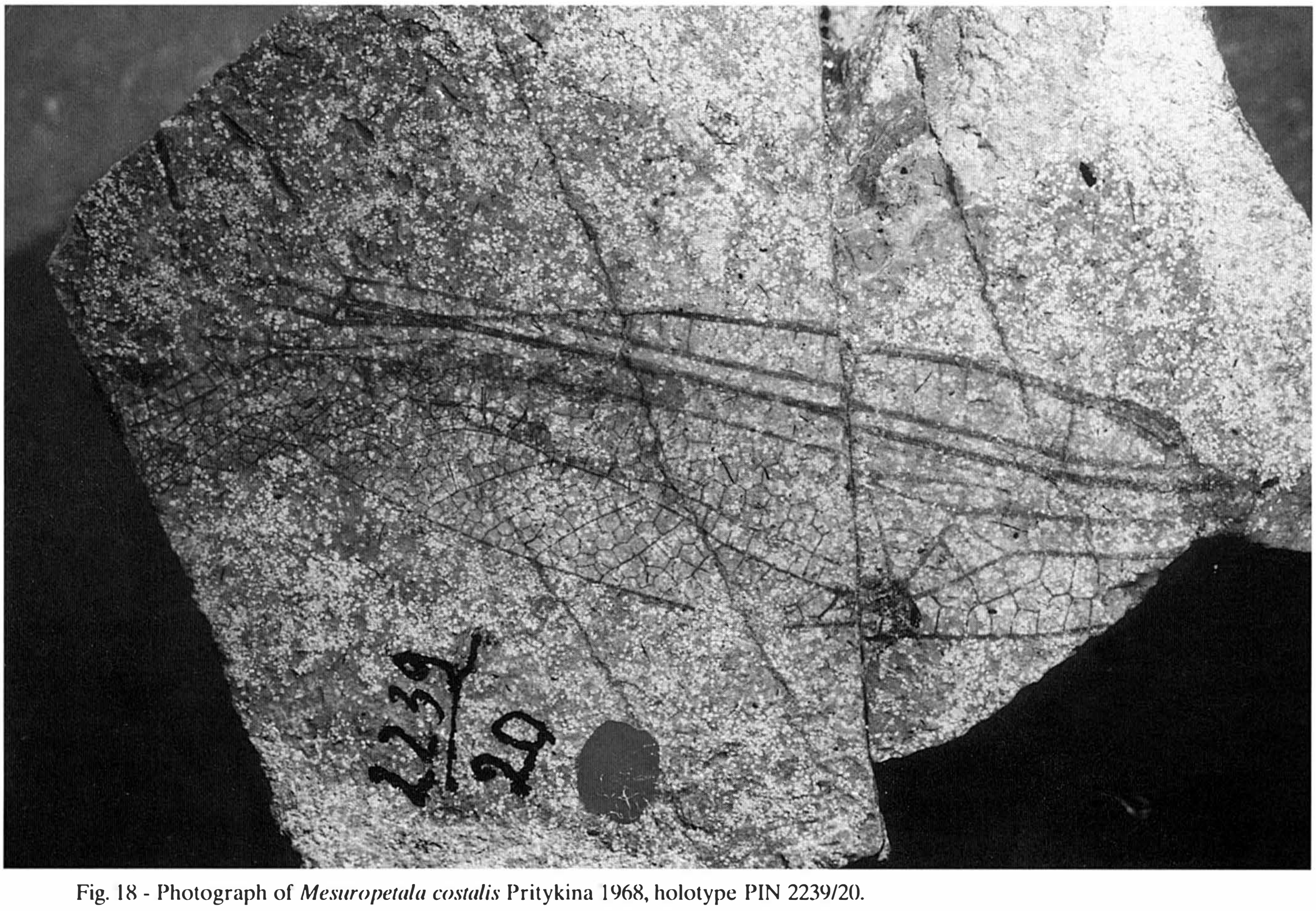

Fig. 18 - Photograph of *Mesuropetala costalis* Pritykina 1968, holotype PIN 2239/20.

three or four rows of cells distal of the discoidal triangle; CuA is long with seven posterior branches; the median cell and submedian cell (except for the CuP-crossing), and the hypertriangles are free of crossveins.

The main differences from *M. koehleri* are: antenodal cells between Ax1 and Ax2 divided into two cells so that there is a pseudo-vein in antenodal area; submedian cell two-celled instead of three-celled; postdiscoidal and cubito-anal areas broader. These differences are of specific significance and would justify the recognition of a separate species congeneric with *M. koehleri*.

However, a comparison of the corresponding characters in the forewing bases of extant Petalurida and extant Cordulegastrida (*Cordulegaster* Leach 1815) shows that there is no diagnostic character in this area of the forewings. It is highly probable that two different Mesozoic species belonging to Petalurida or Cordulegastrida would also have very similar forewing bases. Thus, the attribution of *M. costalis* to the same family or even genus as *M. koehleri* is somewhat uncertain.

Mesuropetala auliensis Pritykina 1968
Figs 19-21

1968 - *Mesuropetala auliensis* - Pritykina, p. 50-51; text-fig. 21, pl. 5, fig. 2.
1992 - *Mesuropetala auliensis* Pritykina - Carpenter, p. 83.
1992 - *Protolindenia auliensis* (Pritykina) - Nel and

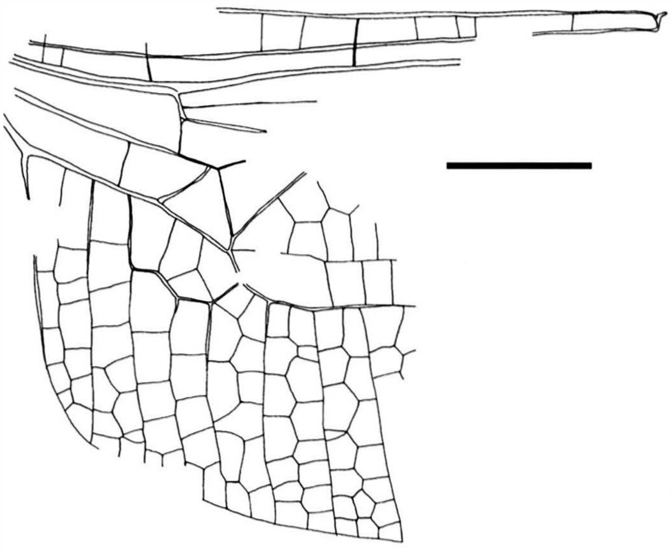
Fig. 19 - *Mesuropetala auliensis* Pritykina, 1968, specimen PIN 2239/21, holotype, hindwing base. Scale bar represents 5 mm.

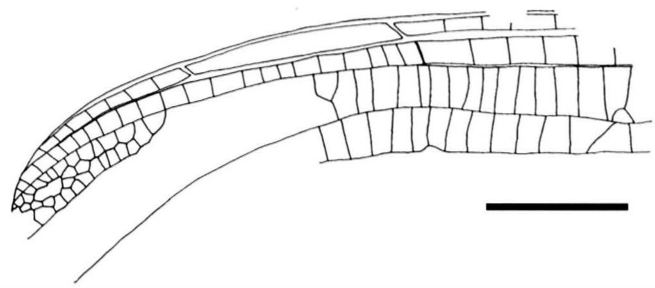
Fig. 20 - *Mesuropetala auliensis*, 2239/21, hindwing apex. Scale bar represents 5 mm.

Fig. 21 - Photograph of *Mesuropetala auliensis* Pritykina 1968, holotype PIN 2239/21.

Paicheler, p. 320.
1994 - *Mesuropetala auliensis* Pritykina - Bridges, p. VII.23.

Holotype: specimen PIN 2239/21, an incomplete hindwing.

Stratigraphic level: Upper Jurassic.

Type locality: Karatau, Turkestan, C.E.I.

Systematic position: by a direct reexam of the holotype of *M. auliensis*, we have found several characters not indicated by Pritykina (1968): the pterostigmal brace is opposite basal side of pterostigma, weakly oblique but stronger than other crossveins between RA and RP1. The anal loop is very similar to that of *M. koehleri*, viz. rather transverse, posteriorly well-closed and four-celled. Four secondary antenodal crossveins are preserved distal of Ax2, between costal margin and ScP, but without visible corresponding antenodal crossveins between ScP and RA.

Mesuropetala auliensis appears to be very similar to *M. koehleri*. The only visible differences are the longer pterostigma, covering more cells, and the more complete posterior closure of the anal loop. All other visible characters are identical in the two species. Thus, the generic attribution is valid and the specific differences substantiated.

Family Protolindeniidae Handlirsch 1906
Genus *Protolindenia* Deichmüller 1886
(in Petalurida Bechly 1996)

Type genus: *Protolindenia* Deichmüller 1886.

Type species: *Protolindenia wittei* (Giebel 1860).

Further species: Pritykina (1968) described two other species in this genus, *Protolindenia deichmuelleri* and *Protolindenia aktassica*, that have to be transferred to different genera.

Diagnosis: a diagnosis of this genus has never been attempted and is provided below. Wings dimensions similar to those of *Mesuropetala koehleri*, i.e. 47 to 51 mm long; a oblique pterostigmal brace present and basally recessed well-basal of pterostigma; area between costal margin and RA, distal of pterostigma, elongate and crossed by many veins; forewing discoidal triangle not transverse but nevertheless broad and three-celled; hindwing discoidal triangle longitudinal elongate and two- or three-celled; well-defined subtriangles on all wings, those of forewings being three-celled but those of hindwings unicellular; anal loop usually posteriorly open and small (3-4 cells); no distinct veins Rspl and Mspl; two oblique crossveins 'O'; two primary antenodals stronger than the secondaries, separated by two or three secondaries; arculus nearer Ax1 than Ax2; Ax2 basal of distal angle of discoidal triangle; IR1 very long and straight and originating well basal of pterostigma, below pterostigmal brace; MA and RP3/4 closely parallel and undulate near posterior margin; IR2 and RP2 relatively straight and closely parallel, area between them being narrowed distally; CuA divided into five to seven parallel posterior branches; distinct pseudo-anal PsA present in forewing; wings have been hyaline; female abdomen rather thick; male anal appendages not foliate; compound eyes distinctly separated.

Protolindenia wittei (Giebel 1860)
Figs 22-37

1860 - *Aeschna wittei* - Giebel, p. 127-132; pl. 1, fig. 1.
1862 - *Petalura* ? *wittei* (Giebel) - Hagen, p. 107, p. 133-136; pl. 13, fig. 3 (with some doubt, see the taxonomic remarks below).
1886 - *Protolindenia wittei* (Giebel) - Deichmüller, p. 37-42; pl. 4, figs 1-2, 9-10 (redescription in a new genus; figures of the type and of one new specimen).
1898 - *Protolindenia wittei* (Giebel) - Meunier, p. 118-119 (list of material in Munich).
1906 - *Protolindenia wittei* (Giebel) - Handlirsch, p. 589-590; pl. 47, fig. 10 (in Gomphida: Protolindeniina [sic] subfam. nov.; gives a poor reproduction of Deichmüller's figure 2).
1932 - *Protolindenia wittei* (Giebel) - Carpenter, p. 112 (in Aeshnidae: Protolindeniinae).
1942 - *Protolindenia wittei* (Giebel) - Cowley, p. 74, p. 77 (in Gomphidae: Protolindeniinae).
1957 - *Protolindenia wittei* (Giebel) - Fraser, p. 93 (lists, in Gomphidae).
1968 - *Protolindenia wittei* (Giebel) - Pritykina, p. 52 (in Gomphidae).
1978 - *Protolindenia wittei* (Giebel) - Lindley, p. 345 (in Gomphidae).
1981 - *Protolindenia wittei* (Giebel) - Schlüter, p. 40 (in Gomphidae).
1985 - *Protolindenia wittei* (Giebel) - Ponomarenko, p. 136 (in Petaluridae).
1992 - *Protolindenia wittei* (Giebel) - Carpenter, p. 81, p. 63; fig. 39 (figured, in Gomphidae).
1992 - *Protolindenia wittei* (Giebel) - Nel and Paicheler, p. 319 (position discussed).
1994 - *Protolindenia wittei* (Giebel) - Bridges, p. VII.253.
1995 - *Protolindenia wittei* (Giebel) - Bechly, p. 137 (in Petaluridae).

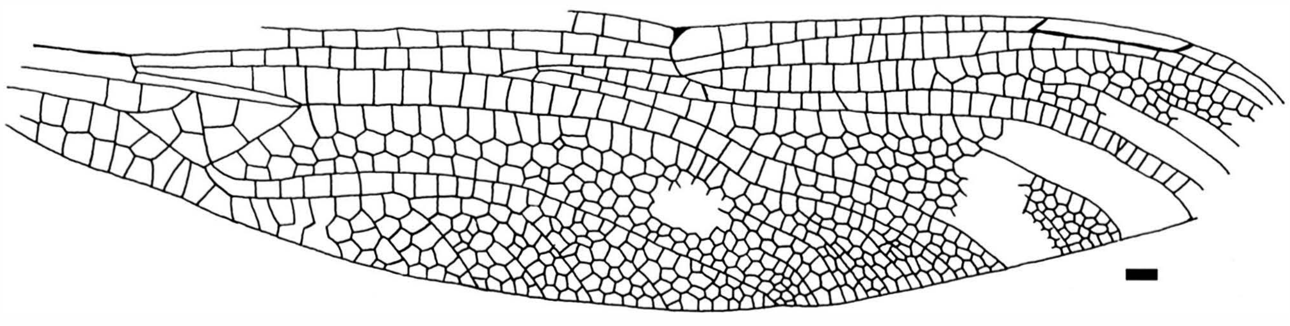

Fig. 22 - *Protolindenia wittei* (Giebel 1860), specimen SOS 2043, neotype, Jura-Museum Eichstätt, forewing. Scale bar represents 1 mm

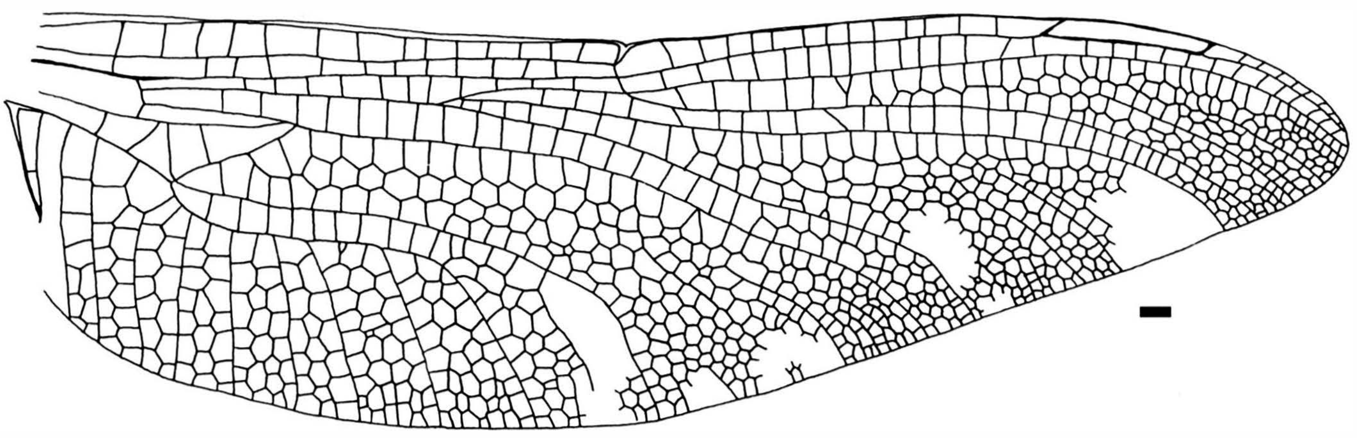

Fig. 23 - *Protolindenia wittei,* SOS 2043, hindwing. Scale bar represents 1 mm.

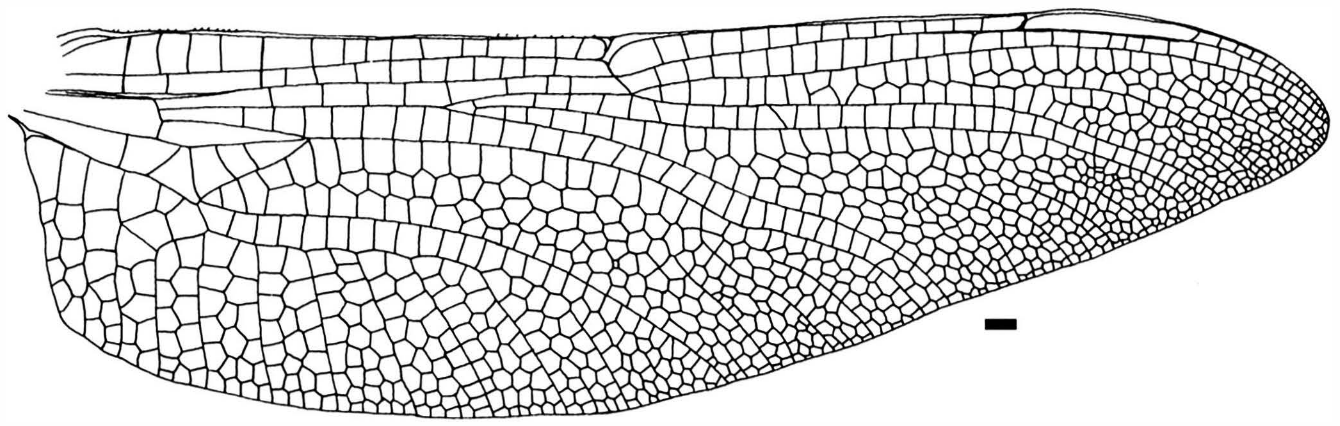

Fig. 24 - *Protolindenia wittei* (Giebel 1860), specimen 1965 IV, Museum of Munich, hindwing. Scale bar represents 1 mm.

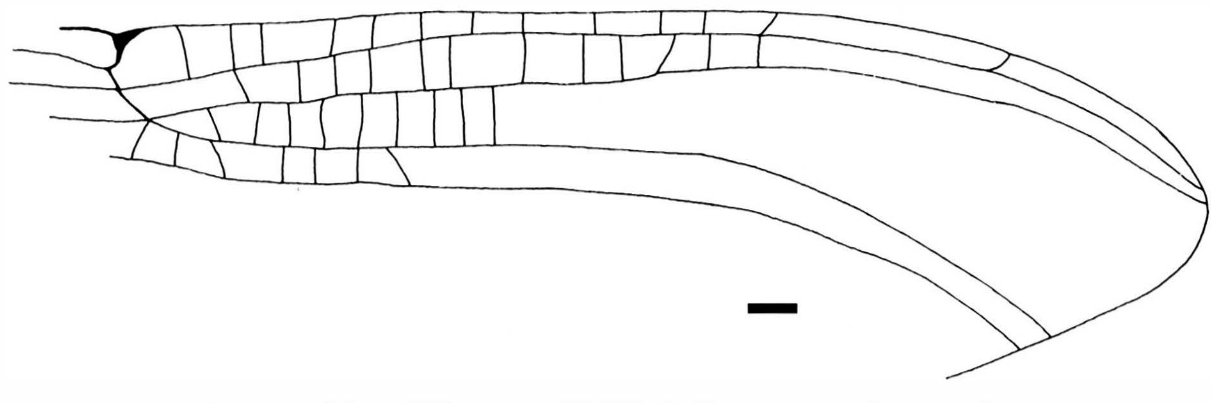

Fig. 25 - *Protolindenia wittei* (Giebel 1860), specimen BL 1957 79e, Jura-Museum Eichstätt, right hindwing, apical part. Scale bar represents 1 mm.

1996 - *Protolindenia wittei* (Giebel) - Bechly, p. 16, 380 (in Petaluridae).

Holotype: the type specimen of Giebel was located in 1860 in the collection Witte (Hannover, Germany). It has not been recently redescribed, and we were unable to find it in any of the numerous visited collections, thus its present location is unknown and it has to be regarded as lost. To finally settle the complex taxonomical problems described below, especially regarding the identity of the genus *Protolindenia* and its distinction from *Mesuropetala* (see above), of which the holotype of the type species has to be regarded as lost too, we decided to designate specimen [SOS 2043] in the collection of the Jura-Museum (Eichstätt) as neotype of *Protolindenia wittei* (Giebel 1860), according to Art. 75 IRZN. It comes from the same locality as the holotype and according to our comparison with the original description it belongs to the same species.

Stratigraphic level: Upper Jurassic/Malm zeta/Tithonian, Lithographic Limestone.

Type locality: Solnhofen/Eichstätt, Bavaria, Germany.

Further material: The location of the doubtfully attributed specimen figured by Hagen is also un-

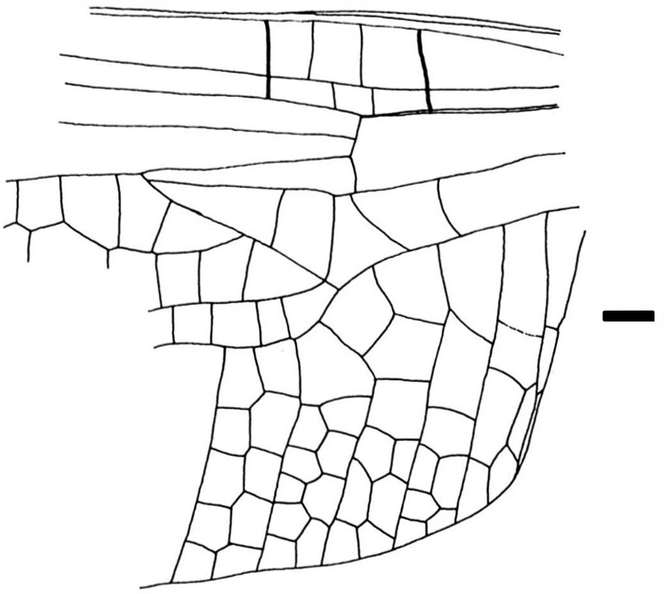

Fig. 26 - *Protolindenia wittei* (Giebel 1860), BL 1957 79e, left hindwing, basal part. Scale bar represents 1 mm.

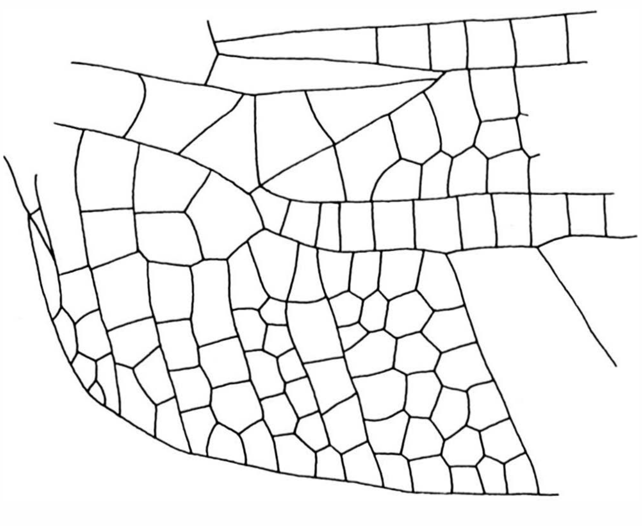

Fig. 27 - *Protolindenia wittei* (Giebel 1860), BL 1957 79e, right hindwing, basal part. Scale bar represents 1 mm

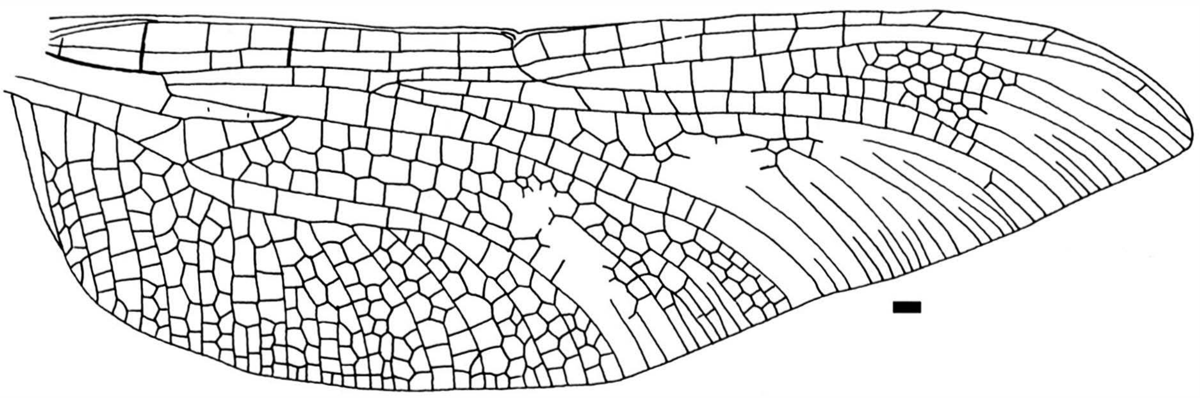

Fig. 28 - *Protolindenia wittei* (Giebel 1860), specimen SOS 1684, Jura-Museum Eichstätt, hindwing. Scale bar represents 1 mm.

known. The material of Deichmüller (1886) was in the Museum of Dresden. Carpenter (1932) cited three specimens in the Carnegie Museum and twenty-one in the Museum of Comparative Zoology (Harvard University, Cambridge). Carpenter (1992: 63, fig. 39) has figured a photograph of a very well preserved and complete male specimen (without indicating the collection). This specimen has previously been figured in several publications of the same author, and in some of them (e.g. Carpenter 1950) indicated as material from the Carnegie Museum. We have studied three new specimens from the Jura-Museum (Eichstätt) and one from the Museum of Munich (BSPGM). The well-preserved specimen [SOS 2043] from the Jura-Museum (Eichstätt) has been designated by us as neotype. We also found several specimens in the collection of the Natural History Museum in Berlin (specimens [MB.J. 1706]; [MB.J. 1709], very well preserved; [MB.J. 1713]; [MB.J. 1730]; and [MB.J. 676], in exhibition). A subsequent study of the specimens at the Museum of Comparative Zoology (Harvard University, Cambridge) confirmed the studies on the 'German' specimens, but did not lead to any 'surprising' further results (specimens: [MCZ 6184]; [MCZ 6182], eyes distinctly separated; [MCZ 6185]; [MCZ 6195]; [MCZ 6196]; [MCZ 6232 & 6233]; [MCZ 6262] & 'without number'; [MCZ 6266]; [MCZ 6267], well preserved thorax in dorsal view; [MCZ 6273 & 6274]; 4 further specimens without number could belong to *Protolindenia wittei* too, while all other specimens that were labelled '*Protolindenia*' have been incorrectly identified.).

Taxonomic remarks: the literature concerning this species is very confused probably because it is one of the more common species from the Upper Jurassic of Bavaria. Several new names and synonymies have been recognized during the past hundred years:

- Hagen (1862: 107), in his list of fossil Odonata from the Upper Jurassic of Bavaria synonymised *Aeschna* [sic] *schmiedeli* Giebel 1856 (= ? *Mesuropetala schmiedeli sensu* Handlirsch 1906) with his '*Petalura* ? *Wittei* '. Handlirsch (1906: 589) considered that they belong to different species and even genera because the former has longer wings than the latter. The exact status of '?*Mesuropetala schmiedeli*' is very uncertain.

- Weyenberg (1869), Deichmüller (1886: 37) and Handlirsch (1906: 589) listed '*Petalura münsteri*' figured by Hagen under *P. wittei.*

- Hagen (1862: 107, 137-138) also synonymised

Aeschna münsteri Germar 1839 (= *Cordulegaster münsteri* (Germar), Hagen 1848: 8-9) (= *Diastatomma münsteri* (Germar) Giebel 1856) with his '*Petalura wittei*'.

- '*A. münsteri*' was described by Germar (1839: 215, pl. 23, fig. 12) on the basis of a very poorly preserved specimen located in the Museum of Munich (BSPGM). Later, Handlirsch (1906: 589) considered that it was a different species and named it '?*Mesuropetala münsteri*'. Hagen (1862: pl. 13, fig. 3) figured a specimen under the name '*Petalura münsteri*' but named it '*Petalura* ? *wittei*' in the text (p. 133)! Deichmüller (1886: 37) and Handlirsch (1906) considered that this figured specimen was actually *Protolindenia wittei*. Later, Carpenter (1932: 113) commended that the type of '*Aeschna münsteri* ' is a very poorly preserved specimen and added that '*münsteri* and *schmiedeli* should be dropped from the literature as unrecognisable insects'. Even if Carpenter is right, some problems would remain:

1) what is the identity of the specimen figured by Hagen (1862: pl. 13, fig. 3)? This specimen is not Giebel's type of *P. wittei* but could it be conspecific with *P. wittei*?

2) Needham (1907) described a specimen that he considered to belong to the species '*Aeschna muensteri* Germar' in the Hagen collection at the Museum of Comparative Zoology (Harvard University, Cambridge) and named it '*Morbaeschna muensteri*' (Germar). Carpenter (1932: 113) wrongly considered that it was a '*Cymatophlebia* (*longialata*)'. This specimen is very different from *Cymatophlebia* and Cymatophlebiidae and is, in fact, a genuine Euaeshnida (Wighton and Wilson 1986; Bechly *et al*., in prep.). As the true '*Aeschna münsteri*' (or more correctly *muensteri*) is a different and unrecognisable species, the specimen described by Needham should be explicitly addressed as '*Morbaeschna muensteri*' *sensu* Needham 1907. The second author studied the original specimen of Needham (1907) at MCZ, and we have recently found three new undescribed specimens of '*Morbaeschna muensteri*' *sensu* Needham 1907 in the collection of the Jura-Museum (Eichstätt) which clearly show that this species is very different from *Protolindenia wittei* and from *Mesuropetala koehleri* (Bechly *et al*., in prep.). The complex taxonomical problems of '*Morbaeschna muensteri*' *sensu* Needham 1907, which in fact has to be regarded as unnamed (!), will be addressed in Bechly *et al.* (in prep.) with the establishment of a new name for this species.

The specimen of '*Morbaeschna muensteri*' *sensu* Needham 1907 from the Hagen collection at MCZ is definitely not the specimen figured by Hagen (1862: pl. 13, fig. 3) because it clearly has a wider area between IR2 and RP2, while the specimen figured in Hagen has a narrow area between IR2 and RP2.

We can conclude that: '*Morbaeschna*' *muensteri sensu* Needham 1907 is a genuine aeshnid that is different from *Protolindenia wittei*; the type of '*Aeschna münsteri* Germar 1839' is a very poorly preserved specimen and this species is an *incertae sedis*; however '*Aeschna münsteri* Germar 1839' is not the same species as '*Morbaeschna muensteri*' *sensu* Needham 1907; the identity of '*Aeschna münsteri* Germar 1839' with *Protolindenia wittei* is also unlikely, since the holotype has a basally parallel

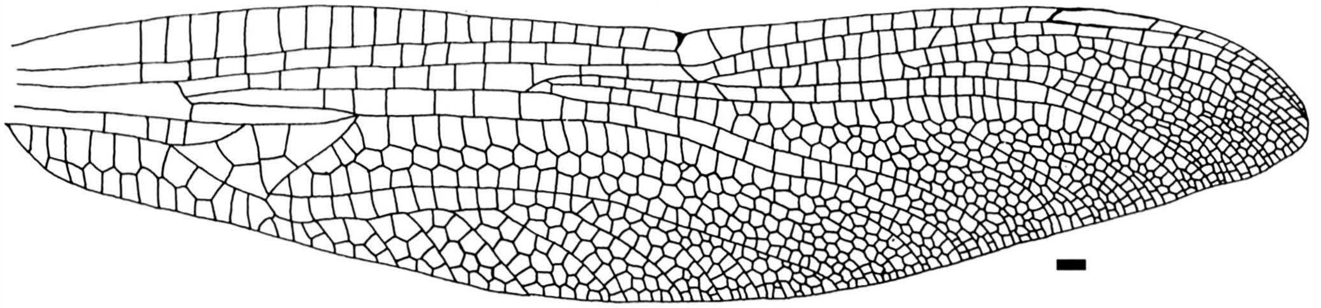

Fig. 29 - *Protolindenia wittei* (Giebel 1860), after Carpenter (1992), forewing. Scale bar represents 1 mm.

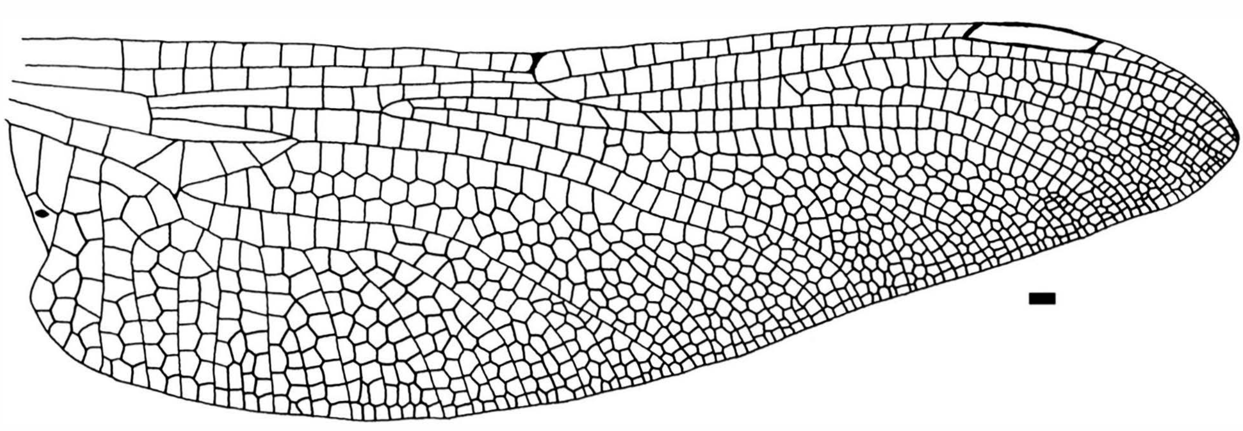

Fig. 30 - *Protolindenia wittei* (Giebel 1860), after Carpenter (1992), hindwing. Scale bar represents 1 mm.

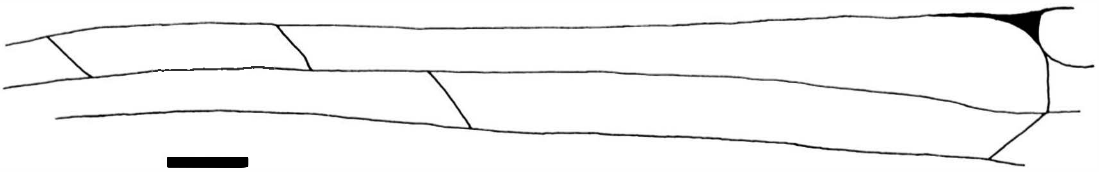

Fig. 31 - *Protolindenia wittei* (Giebel 1860), specimen n° 1 Berger-Museum, Eichstätt, female, postnodal areas, left forewing. Scale bar represents 1 mm.

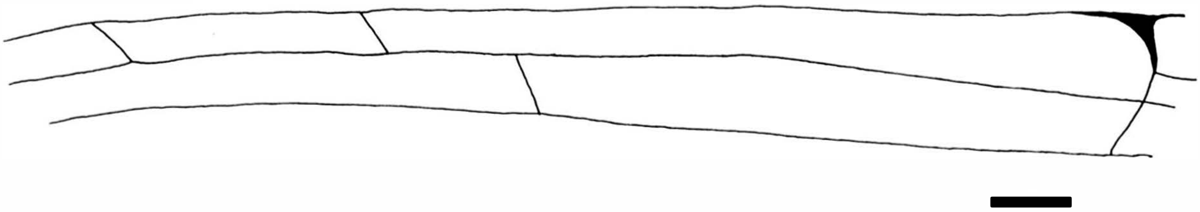

Fig. 32 - *Protolindenia wittei* (Giebel 1860), 1 Berger-Museum, left hindwing. Scale bar represents 1 mm.

RP1 and RP2 like *Mesuropetala koehleri* and unlike *Protolindenia wittei*; the specimen figured by Hagen (1862: pl. 13, fig. 3), and labelled *Protolindenia wittei* in his text, is still of uncertain systematic position. Only the figures of Giebel (1860), Deichmüller (1886) and Carpenter (1992) of *P. wittei* can be used with some certainty.

Systematic descriptions:

(A) specimen [SOS 2043], Jura-Museum, Eichstätt, [neotype].

Impression of a nearly complete specimen. The wings are well preserved and hyaline.

Forewing: length, 45.5 mm; width, 10.0 mm; ratio width/length, 0.21; distance from base to nodus, 23.2 mm; from nodus to pterostigma, 12.0 mm; from pterostigma to apex, 4.5 mm; from nodus to arculus, 18.8 mm. Pterostigma 5.6 mm long and 0.7 mm wide and rather narrow, with about four cells below pterostigma. Oblique pterostigmal brace not aligned with basal side of pterostigma but 1.4 mm (two cells) basally. About fourteen postnodal crossveins. Number of antenodal crossveins unknown but probably numerous. Two primary antenodal crossveins not preserved. Relative positions of the arculus and Ax1 undetermined. RP and MA well-separated in arculus. Posterior part of arculus not very angled with anterior part. Many crossveins between RP and RA basal of RP3/4 and between base of RP3/4 and nodus. Many crossveins between RP and MA basal of RP3/4. Six bridge-crossveins (Bqs). Discoidal triangle three-celled, not elongate and narrow; length of its anterior side, 3.6 mm; of distal side, 3.6 mm; of basal side, 2.5 mm. Anterior side of discoidal triangle joins MAb. Hypertriangle apparently free of crossveins. Median cell free of crossveins. Submedian cell traversed by CuP-crossing and by one supplementary cubito-anal crossvein. A well-defined PsA separating submedian cell from a nearly triangular three-celled subtriangle, the latter 3.2 mm long and 2.3 mm wide. Two rows of cells in anal area. CuAa divided into six posterior branches. CuAa comparatively long and reaching posterior wing margin opposite nodus. Seven rows of cells between CuAa and posterior wing margin. Area between CuA and MP widened near posterior wing margin with one row of cells behind discoidal triangle and six rows near posterior wing margin. Three rows of cells in postdiscoidal area distal of discoidal triangle. Two longitudinal zigzagged secondary veins parallel with MP and MA; the more costal of the secondary veins continues as a zigzagged concave vein (rudimentary Mspl?). One row of cells between Mspl and MA. Postdiscoidal area widened distally near posterior wing margin. Area between MA and RP3/4 widened near posterior wing margin developing three rows of cells. MA and RP3/4 closely parallel, and somewhat distal of nodus, undulate. RP2 originating at subnodus. Two oblique crossveins 'O'. A rudimentary zigzagged Rspl, parallel with IR2 in area between IR2 and RP3/4. One row of cells between Rspl and IR2. Area between IR2 and RP2 narrowed distally near posterior wing margin. IR2 gently curved. RP2 undulate a little basal of pterostigma. A long straight IR1 starting somewhat basal of pterostigmal brace. Three or four rows of cells in area between IR1 and RP2. Four or five rows of cells and two secondary longitudinal veins in area between IR1 and RP1.

Hindwing: length, 44.5 mm; width, 13.2 mm; width under nodus, 12.7 mm; distance from base to nodus, 20.3 mm; from nodus to pterostigma, 13.4 mm; from pterostigma to apex, 6.0 mm; from nodus to arculus, 15.6 mm. Pterostigma 5.9 mm long, 0.7 mm wide and rather narrow. About six cells below pterostigma. Oblique pterostigmal brace not aligned with basal side of pterostigma but 1.0 mm (one cell) basally (it can be easily distinguished from the other crossveins between RA and RP1 because of its obliquity). Thirteen visible postnodal crossveins, not strictly aligned with corresponding postsubnodal crossveins between RA and RP1. Fourteen antenodal crossveins. Two primary antenodal crossveins stronger than secondaries, with three secondaries between them. Arculus very near to Ax1. RP and MA well-separated in arculus. Posterior part of arculus not very angled with anterior part (MA). Seven crossveins between RP and RA basal of RP3/4 and four more crossveins between base of RP3/4 and nodus. Seven crossveins between RP and MA basal of RP3/4. Four bridge-crossveins (Bqs). Discoidal triangle very elongate and narrow, crossed

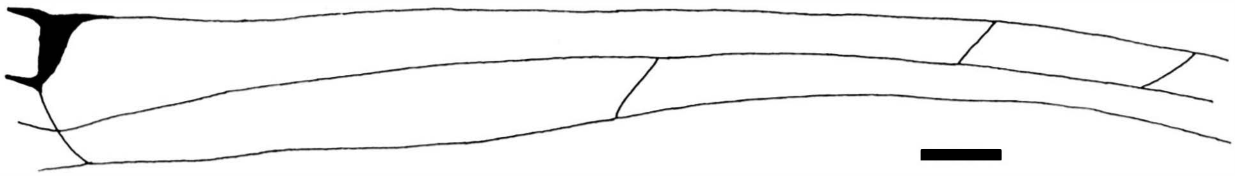

Fig. 33 - *Protolindenia wittei* (Giebel 1860), 1 Berger-Museum, right forewing. Scale bar represents 1 mm.

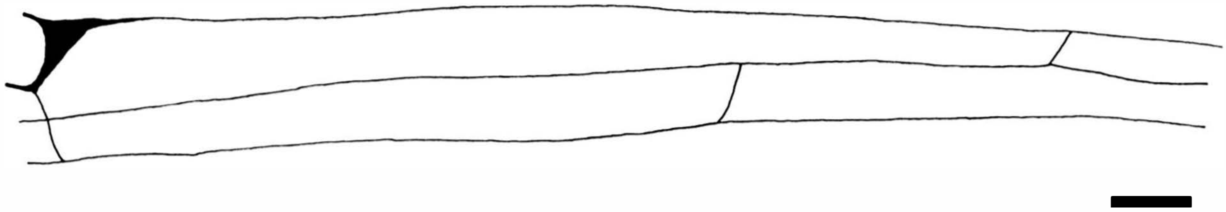

Fig. 34 - *Protolindenia wittei* (Giebel 1860), 1 Berger-Museum, right hindwing. Scale bar represents 1 mm.

by one vein; length of its anterior side, 4.2 mm; of distal side, 4.4 mm; of basal side, 1.9 mm. Anterior side of discoidal triangle ending on MA somewhat basal of division into main vein MA and secondary branch MAb, so that discoidal triangle with a small fourth side, 0.3 mm long. Hypertriangle free of crossveins. Median cell free of crossveins. Submedian cell only traversed by CuP-crossing. A well-defined PsA separating submedian cell from a nearly triangular unicellular subtriangle, 1.9 mm long and 1.7 mm wide. No anal triangle, thus it is a female. Two closely parallel posterior branches of AA. Seven or eight rows of cells in anal area. Width of anal area, 6.9 mm; width of cubito-anal area, 6 mm. CuAb a well-defined vein, directed postero-basally and making a pronounced curve towards posterior wing margin. CuAb not fused with any of posterior branches of AA. Anal loop vestigial (ill defined, posteriorly open and only three celled). CuAa divided into six posterior branches. CuA rather long and reaching posterior wing margin opposite nodus. Eight rows of cells between CuAa and posterior wing margin. Area between CuA and MP widened along posterior wing margin, these veins being separated by one row of cells distal of discoidal triangle and six rows near posterior wing margin. Two or three rows of cells developed in postdiscoidal area distal of discoidal triangle. Two longitudinal zigzagged secondary veins running parallel to MP and MA, the more anterior of these secondary veins continuing as a zigzagged and concave vein (rudimentary Mspl). One row of cells between Mspl and MA. Postdiscoidal area widened distally near posterior wing margin. Area between MA and RP3/4 distinctly widened near posterior wing margin with three rows of cells. MA and RP3/4 closely parallel, undulate somewhat distal of nodus. RP2 aligned with subnodus. Two oblique crossveins 'O'. A rudimentary zigzagged Rspl, parallel with IR2, in area between IR2 and RP3/4. One row of cells between Rspl and IR2. Area between IR2 and RP2 narrowed distally near posterior wing margin. IR2 a gently curved vein. RP2 undulate somewhat basal of pterostigma; IR1 a long straight vein beginning four cells basal of pterostigmal brace. Three or four rows of cells in area between IR1 and RP2. Four or five rows of cells and two secondary longitudinal veins in area between IR1 and RP1.

(B) specimen [1965 IV, Förstn.], Museum of Munich (BSPGM).

A complete hyaline hindwing. Length, 46.6 mm; width, 13.3 mm; width below nodus, 13 mm; distance from base to nodus, 21.1 mm; from nodus to pterostigma, 13.9 mm; from pterostigma to apex, 5.9 mm; from nodus to arculus, 15.5 mm.

Differences with neotype specimen [SOS 2043] are very few: length of pterostigma, 6.4 mm; width, 0.8 mm. Oblique pterostigmal brace two cells basal of pterostigma. Discoidal triangle divided by two crossveins. Anal loop better closed and four celled. No anal triangle and no anal angle, thus it is a female specimen. All other characters are identical in the two specimens.

(C) specimen [BL 1957 79e], Jura-Museum, Eichstätt.

Counterpart of two hindwings in connection with the body. Head, 5 mm long, 4 mm wide; abdomen, 50 mm long, 4 mm wide; distance between wings, 6 mm; length of hindwing, 41 mm; width, 12.5 to 13 mm. Abdomen never narrowed, cerci not very distinct but appearing long and narrow. Eyes well-separated. The differences with neotype specimen [SOS 2043] are very few: pterostigma 5.3 mm long and 0.6 mm wide. Oblique pterostigmal brace two cells basal of pterostigma. Only two secondary antenodal crossveins between primaries. No anal angle and anal triangle, thus it is a female. Anal loops three celled but of different shape: the right one is better closed than the left one. A secondary vein between CuAb and posterior branch of AA, posterior of anal loop in right wing but absent in left wing.

(D) [specimen SOS 1684], Jura-Museum, Eichstätt.

A complete hindwing with the main veins well-preserved but many crossveins and cells are not visible. Wing hyaline. Length, 45.0 mm; width, 14.0 mm; ratio width/length, 0.31; width below nodus, 13.3 mm; distance from base to nodus, 20.0 mm; from the nodus to the pterostigma, 18.0 mm; from the pterostigma to

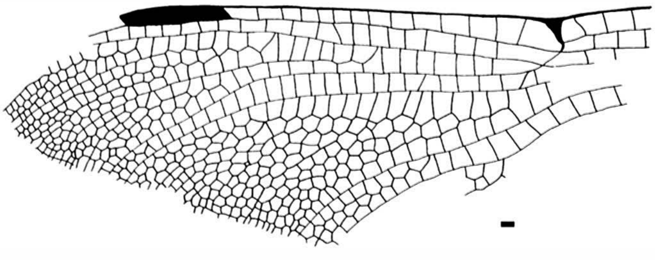

Fig. 35 - *Protolindenia wittei* (Giebel 1860), specimen 1964 XXIII oo, Museum of Munich, hindwing, apical half. Scale bar represents 1 mm.

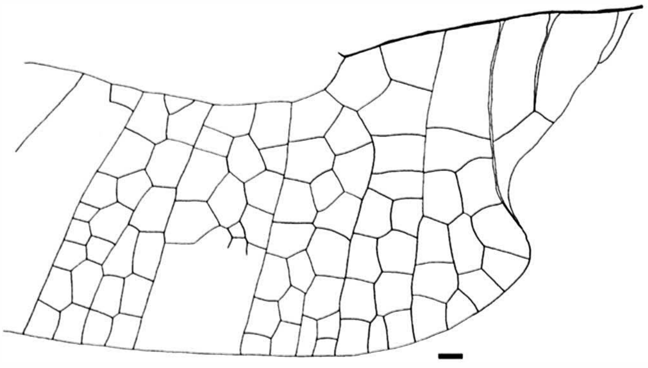

Fig. 36 - *Protolindenia wittei* (Giebel 1860), 1964 XXIII oo, cubito-anal area. Scale bar represents 1 mm.

the apex, 7.0 mm; from nodus to arculus, 14.0 mm. Differences with neotype specimen [SOS 2043] are very few: pterostigma 5.0 mm long and 0.8 mm wide and rather narrow; the exact number of cells which are covered by the pterostigma is unknown but is about three to six cells. Oblique pterostigmal brace not aligned with basal side of pterostigma but is 4.4 mm more basally than in the previous specimens. Exact number of postnodal crossveins unknown but ten of them visible; they are comparatively well-aligned with corresponding crossveins between RA and RP1. Exact number of antenodal crossveins unknown but twelve to fourteen visible. Two primary antenodal crossveins stronger than secondaries, with two secondaries between them. Only three crossveins present between RP and RA basal of RP3/4 and evidently three or four further crossveins between base of RP3/4 and nodus. Only two bridge-crossveins (Bqs) visible. Discoidal triangle very elongate and narrow and crossed by two veins; length of its anterior side, 4.3 mm; of distal side, 4.7 mm; of basal side, 1.6 mm. Hypertriangle apparently crossed by two crossveins. Anal loop vestigial (not very well-defined, posteriorly open, and five celled). CuAa divided into seven parallel posterior branches. No anal angle and no anal triangle but a membranule present (5.0 mm long and 0.3 mm wide), thus it is a female specimen.

(E) specimen figured in Carpenter (1992: 63, fig. 39) under the name of *Protolindenia wittei* (Giebel).

An impression of a complete dragonfly with two hindwings and two forewings in connection with the body. All the veins and the wing cells are clearly visible. The wings are hyaline. The differences to the neotype specimen [SOS 2043] are very few:

Forewing: length, 52.5 mm; width, 11.5 mm; width below nodus, 11.2 mm; distance from base to nodus, 26.5 mm; from nodus to pterostigma, 15.5 mm; from pterostigma to apex, 7.0 mm; from nodus to arculus, 20.0 mm. Pterostigma 4.5 mm long and 0.8 mm wide, rather narrow. About six cells below pterostigma. Oblique pterostigmal brace not aligned with basal side of pterostigma but 4.5 mm (five cells) basal. About seventeen visible postnodal crossveins. Twenty-three antenodal crossveins. Length of anterior side of discoidal triangle, 4.2 mm; of distal side, 4.3 mm; of basal side, 2.5 mm. Hypertriangle apparently divided by two crossveins. CuAa divided into seven posterior branches.

Hindwing: length, 50.0 mm; width, 15.0 mm; width below nodus, 14.0 mm; distance from base to nodus, 21.0 mm; from nodus to pterostigma, 15.5 mm; from pterostigma to apex, 7.0 mm; from nodus to arculus, 15.5 mm. Pterostigma 5.0 mm long and 0.8 mm wide, rather narrow. About six cells below pterostigma. Oblique pterostigmal brace 4.5 mm (five cells) basal of pterostigma. Seventeen visible postnodal crossveins, not strictly aligned with corresponding crossveins between RA and RP1. Fourteen antenodal crossveins. Two primary antenodal crossveins stronger than secondaries, with two secondaries between them. Length of anterior side of discoidal triangle, 4.5 mm; of distal side, 5.2 mm; of basal side, 1.7 mm. Hypertriangle apparently divided by two crossveins. Anal loop vestigial (not very well-defined, posteriorly open and four-celled). CuAa divided into seven posterior branches. A well-defined anal angle and a three-celled anal triangle, 4.5 mm long and 2.6 mm wide, thus it is a male specimen.

(F) specimen [1959/73 (b) K], Jura-Museum, Eichstätt.

A nearly complete specimen with the fore- and hindwings in connection with the thorax. The main wing veins are well-preserved but some cells are not visible. The wings were probably hyaline, with no visible trace of coloration. Head 7.5 mm long, 7.9 mm wide. Distance between eyes, 2 mm; eye width, 3 mm. Abdomen 56 mm long, 4.8 mm wide. Thorax 15 mm long, 6 mm wide. Forewing 52 mm long, 11 mm wide. Distance from base to nodus, 26 mm; from nodus to pterostigma, 15.3 mm; from nodus to arculus, 21.1 mm. Hindwing 50 mm long, 14.6 mm wide. Distance from base to nodus, 24 mm. Forewing identical to that of specimen figured by Carpenter (1992) except for its apparently unicellular subtriangle.

No visible difference with hindwing of specimen SOS 1684. Pterostigma 4.0 mm long and 0.8 mm wide, rather narrow. Exact number of cells covered by pterostigma unknown but there were probably about three to six cells. Oblique pterostigmal brace not aligned with basal side of pterostigma but eight cells basal. Postnodal and antenodal crossveins very numerous. Two primary antenodal crossveins stronger than secondaries, with two secondaries between them. Discoidal triangle very elongate, narrow and crossed by two veins; length of its anterior side, 4.0 mm; of distal side, 4.7 mm; of basal side, 1.9 mm. The hypertriangle apparently free of crossveins. Anal loop vestigial (not very well-defined, posteriorly open and five-celled). CuAa divided into seven parallel posterior branches. No anal angle and no anal triangle but instead a long membranule, thus it is a female specimen.

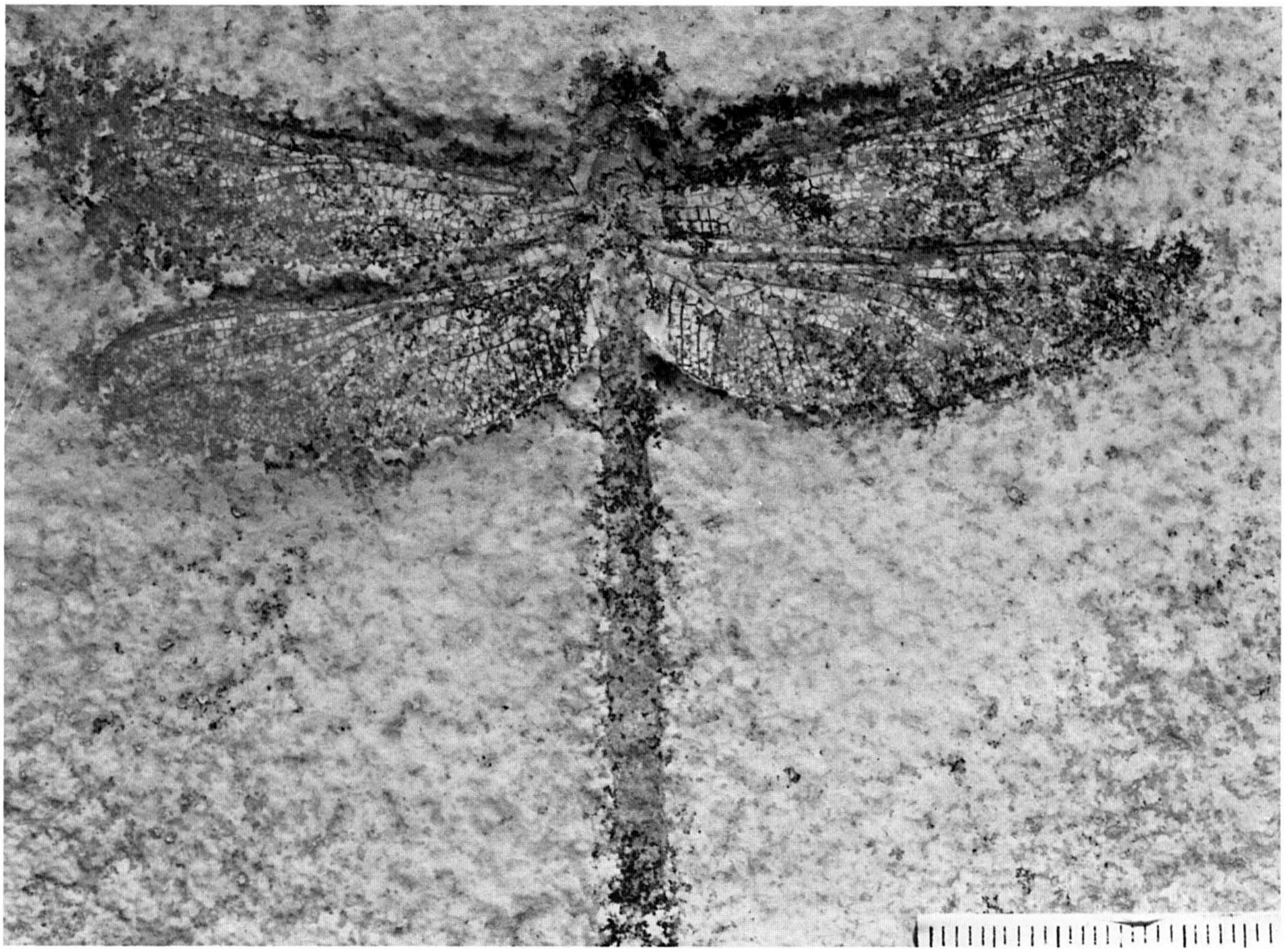

Fig. 37 - Photograph of *Protolindenia wittei* (Giebel 1860), neotype SOS 2043.

(G) specimen no. 1, Berger-Museum, Eichstätt.

This specimen is very similar to the precedent but is of great interest because it provides some evidence of the fact that the derived position of the oblique pterostigmal brace vein is rather variable in the different specimens of this species. The left fore- and hindwing braces are near the pterostigma, only two cells basal but the right fore- and hindwing braces are much more basal.

(H) specimen [1964 XXIII oo]/[Schernfeld], Museum of Munich (BSPGM).

A body with the hindwings and one forewing in connection with thorax. Wings are hyaline. Only the left hindwing is well-preserved. Length of hindwing, 42 mm; width, 15.0 mm; width below nodus, 13 mm; distance between base and nodus, 17 mm; between nodus and pterostigma, 13 mm; from pterostigma to apex, about 6 mm; from nodus to arculus, 13 mm. The differences to the neotype specimen [SOS 2043] are very few: pterostigma about 5 mm long, 0.7 mm wide, covering six cells. Pterostigmal brace four cells basal of pterostigma. Anal loop vestigial (ill defined, posteriorly open, and only three-celled). A wide three-celled anal triangle and a pronounced anal angle, thus it is a male specimen.

Comparison between the specimens: the only visible differences between these specimens, other than sex, are the variable number of cells between the pterostigmal brace and the pterostigma, the variable number of antenodal and postnodal crossveins and the more or less three- to five-celled anal loops. However, these characters are rather doubtful on specimen SOS 1684 because of its poor preservation. It is highly probable that it had more cells and crossveins than are preserved in the antenodal and postnodal areas. Also, the forewing subtriangle of specimen [1959/73(b) K] seems to be unicellular instead of three celled, like the specimen figured by Carpenter, but this can also be due to a poor preservation.

Comparison with the figure (type) in Giebel (1860: pl. 1, fig. 1) and the specimens figured by Deichmüller (1886): the figures of Giebel and Deichmüller are not very precise but they clearly show several interesting characters: there are two oblique crossveins 'O'; the long IR1 originates well basal of the pterostigma; the crossed submedian cell; the three-celled forewing and the unicellular hindwing subtriangles; the three- or four-celled forewing and the two-celled hindwing discoidal triangles; the posteriorly open anal loop; the parallel but curved RP3/4 and MA and the straight IR2 and RP2; the narrow area between IR2 and RP2.

All the characters visible in the figures of Giebel and Deichmüller are identical to those of the above specimens, except for the lack of any oblique pterostigmal brace. This omission can easily be dismissed as drawing error, due to the basally displaced position of this vein, although there is no definite proof. We therefore regard all these fossil dragonflies are conspecific and belong to *Protolindenia wittei.*

Systematic position of *Protolindenia wittei*: the presence of a long IR1, the two oblique crossveins 'O' and the basally-recessed oblique pterostigmal brace of *Protolindenia wittei* are apomorphic characters present in Petalurida.

The fore- and hindwing basal structures of *P. wittei* (subtriangles and discoidal triangles, anal loop, postdiscoidal and antenodal areas) are similarly present in extant Petalurida but also in Cordulegastrida and Austropetaliida. Thus, they are of less value.

The previous attribution of *Protolindenia wittei* to the Gomphidae is erroneous because of the pterostigmal characters (apomorphy) and the presence of two crossveins 'O' (plesiomorphy). The present transfer of *Protolindenia wittei* to the Petalurida is not based on many characters, but this had to be expected since there are not many autapomorphies in the wing venation of Petalurida. Anyway, all the apomorphic character states of *P. wittei* are also present in Petalurida, except the crossvein pattern in the forewing discoidal triangle which is probable autapomorphic. *P. wittei* shares with extant Petalurida the very cylindrical and stout female abdomen (more probably a symplesiomorphy regarding the same state in Aeschnidiidae and Isophlebiidae).

Genus *Pritykiniella* gen. nov.
(in Anisoptera *incertae sedis*,
previously in the genus *Protolindenia*)

Type species: *Protolindenia deichmuelleri* Pritykina 1968.

Etymology: in honour of Dr. Pritykina.

Diagnosis: diagnosis and figure see Pritykina (1968); autapomorphies: presence of three oblique crossveins 'O' between RP2 and IR2 (unique!); oblique crossvein 'O' very close to the subnodus).

Pritykiniella deichmuelleri (Pritykina 1968) comb. nov.
Figs 38-40

1968 - *Protolindenia deichmuelleri* - Pritykina, p. 52-5; text-fig. 23, pl. 5, fig. 4.

1992 - *Protolindenia deichmuelleri* Pritykina; Carpenter, p. 81.

1992 - *Protolindenia deichmuelleri* Pritykina - Nel and Paicheler, p. 319-320.

1994 - *Protolindenia deichmuelleri* Pritykina - Bridges, p. VII. 65.

1995 - 'die übrigen *Protolindenia*-Arten' - Bechly, p. 137 (position discussed and excluded from *Protolindenia*).

1996 - *Protolindenia (?) deichmuelleri* - Bechly, p. 16, 380 (in Anisoptera *incertae sedis*).

Holotype: specimen PIN 2239/22, a nearly complete hindwing.

Stratigraphic level: Upper Jurassic.

Type locality: Karatau, Kazakhstan, Ex. U.R.S.S.

Systematic position: Pritykina (1968) considered *P. deichmuelleri* as a gomphid. *P. deichmuelleri* can hardly be related to *Protolindenia wittei* because it lacks the main autapomorphic characters of Petalurida, viz. the pterostigma is not long and narrow but rather compressed and the pterostigmal brace is not basally recessed but aligned with the basal side of the pterostigma. Also, the base of IR1 is distinctly distal of the pterostigma, unlike *P. wittei*.

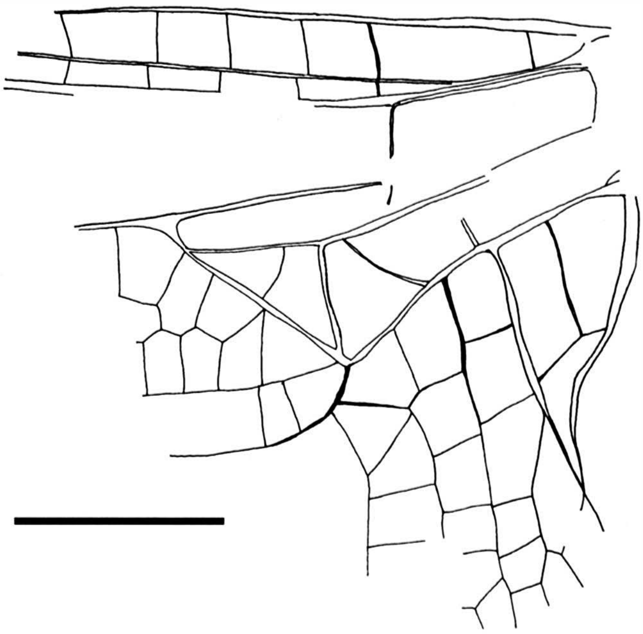

Fig. 38 - *Pritykiniella deichmuelleri* (Pritykina 1968), holotype PIN 2239/22, hindwing base. Scale bar represents 5 mm.

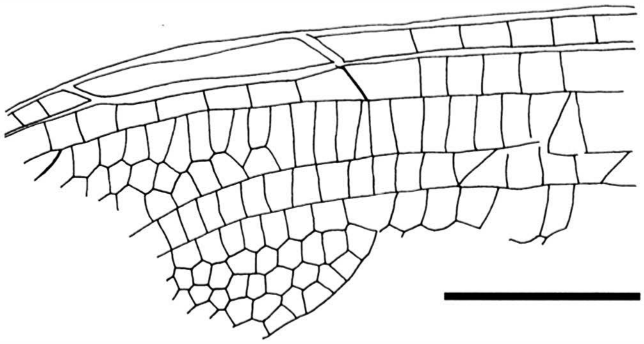

Fig. 39 - *Pritykiniella deichmuelleri* (Pritykina 1968), PIN 2239/22, hindwing apex. Scale bar represents 5 mm.

Also, *P. deichmuelleri* has three oblique crossveins 'O' instead of two, character we could confirm after a direct reexam of the holotype and which constitutes an unique autapomorphy in the Anisoptera. As the presence of more than one oblique crossvein is clearly a plesiomorphy, even this character cannot justify any relationship with the Petalurida. It seems not to be related to Euaeshnida because it has a well-defined subtriangle (plesiomorphy that is absent in hindwings of Euaeshnida) and a reduced anal loop that is posteriorly open (an apomorphy that never occurs in Euaeshnida).

It has to be excluded from the genus *Protolindenia* and to be transferred into a new genus *Pritykiniella* gen. nov. This new arrangement of course does not solve the problem of the phylogenetic relationship of this fossil.

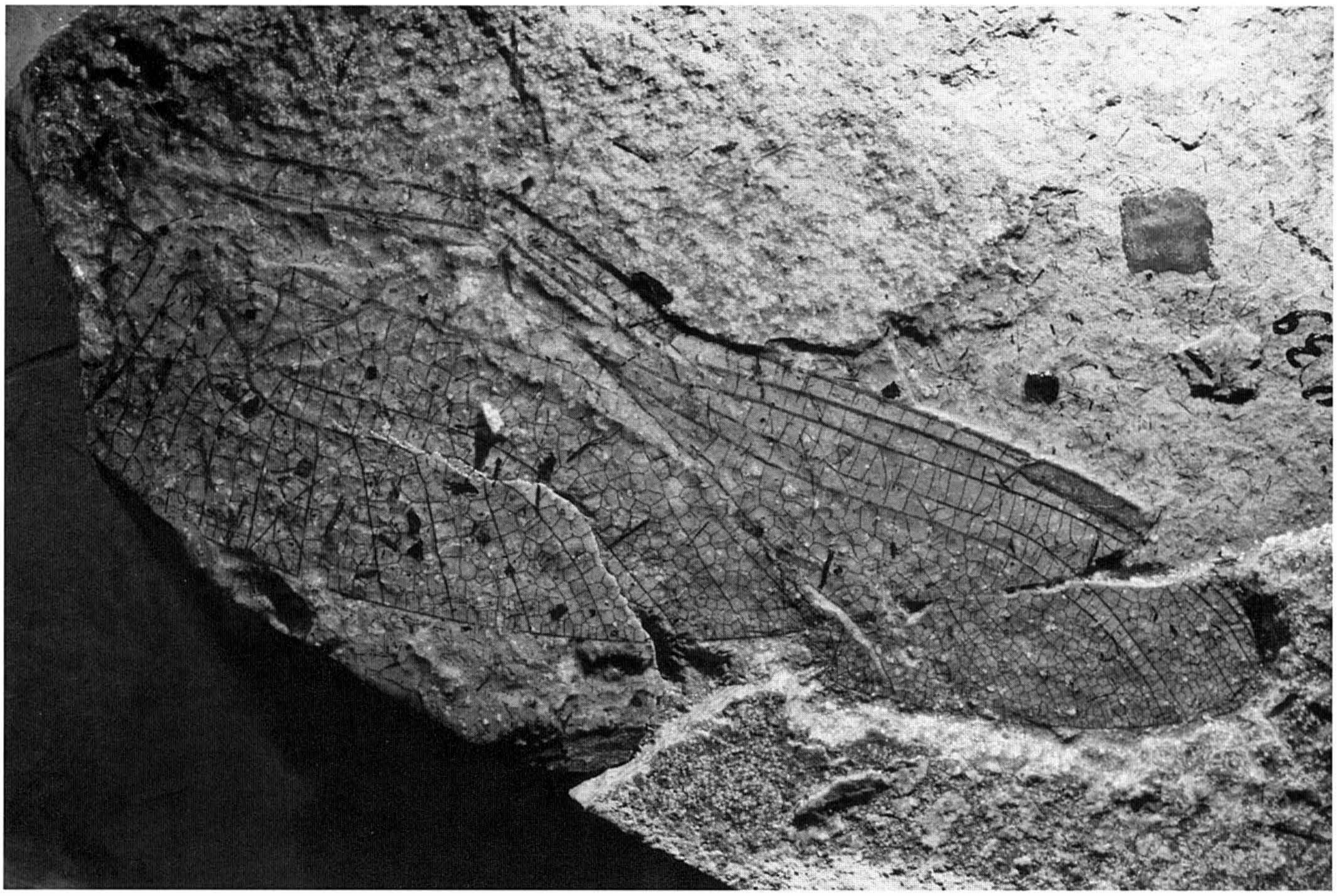

Fig. 40 - Photograph of *Pritykiniella deichmuelleri* (Pritykina 1968), holotype PIN 2239/22.

Genus *Kazakhophlebiella* gen. nov. (in Anisoptera *incertae sedis*, previously in the genus *Protolindenia*)

Type species: *Protolindenia aktassica* Pritykina 1968.

Etymology: after Kazakhstan.

Diagnosis: diagnosis and figure see Pritykina (1968); the strong reduction of the secondary antenodals and the 'libelluloid gap' in the postsubnodal crossveins, figured in Pritykina (1968, text-fig. 24) are artefacts of preservation.

Kazakhophlebiella aktassica (Pritykina 1968) comb. nov.

Figs 41-42

1968 - *Protolindenia aktassica* - Pritykina, p. 53-54; text-fig. 24, pl. 5, fig. 5.

1992 - *Protolindenia aktassica* Pritykina - Carpenter, p. 81.

1992 - *Protolindenia aktassica* Pritykina - Nel and Paicheler, p. 320.

1994 - *Protolindenia aktassica* Pritykina - Bridges, p. VII.6.

1995 - 'die übrigen *Protolindenia*-Arten' - Bechly, p. 137.

1996 - *Protolindenia (?) aktassica* - Bechly, p. 16, 380 (in Anisoptera *incertae sedis*).

Holotype: specimen PIN 2554/218, a nearly complete but very poorly preserved forewing. Pritykina noted the existence of three other specimens. We could have the opportunity to restudy the holotype and paratype PIN 2384/2 (costo-basal part of a forewing).

Stratigraphic level: Upper Jurassic.

Type locality: Karatau, Kazakhstan, Ex. U.R.S.S.

Systematic position: based on the illustration of Pritykina (1968: fig. 24), the holotype seems to possess an unique autapomorphic character within the Anisoptera, viz. only the two primary antenodal crossveins are complete in the antenodal area; the secondary antenodal crossveins being only present in the second row between ScP and RA, but completely absent in the first row between ScP and the costal margin. Paratype PIN 2384/2, although incompletely preserved, seems to belong to the same species because its preserved structures are identical to those of the holotype, viz. dimensions, postdiscoidal area, veins MA and RP3/4, submedian space, subtriangle, arculus, area between RP and MA. It is not possible to be absolutely accurate of the specific identity of the two specimens, because of their poor conditions but there is no evidence against this hypothesis. If so, paratype 2384/2 clearly has numerous secondary antenodal crossveins between costal margin and ScP distal of Ax2 and numerous corresponding antenodal crossveins between ScP and RA. It also has postsubnodal crossveins between RA and RP1 adjacent to the subnodus (no 'libellulid gap' *sensu* Bechly 1995, unlike in the text-figure 24 of the holotype in Pritykina (1968). The alleged 'libellulid gap' together with the absence of antenodal crossveins are simply due to the poor preservation of the holotype.

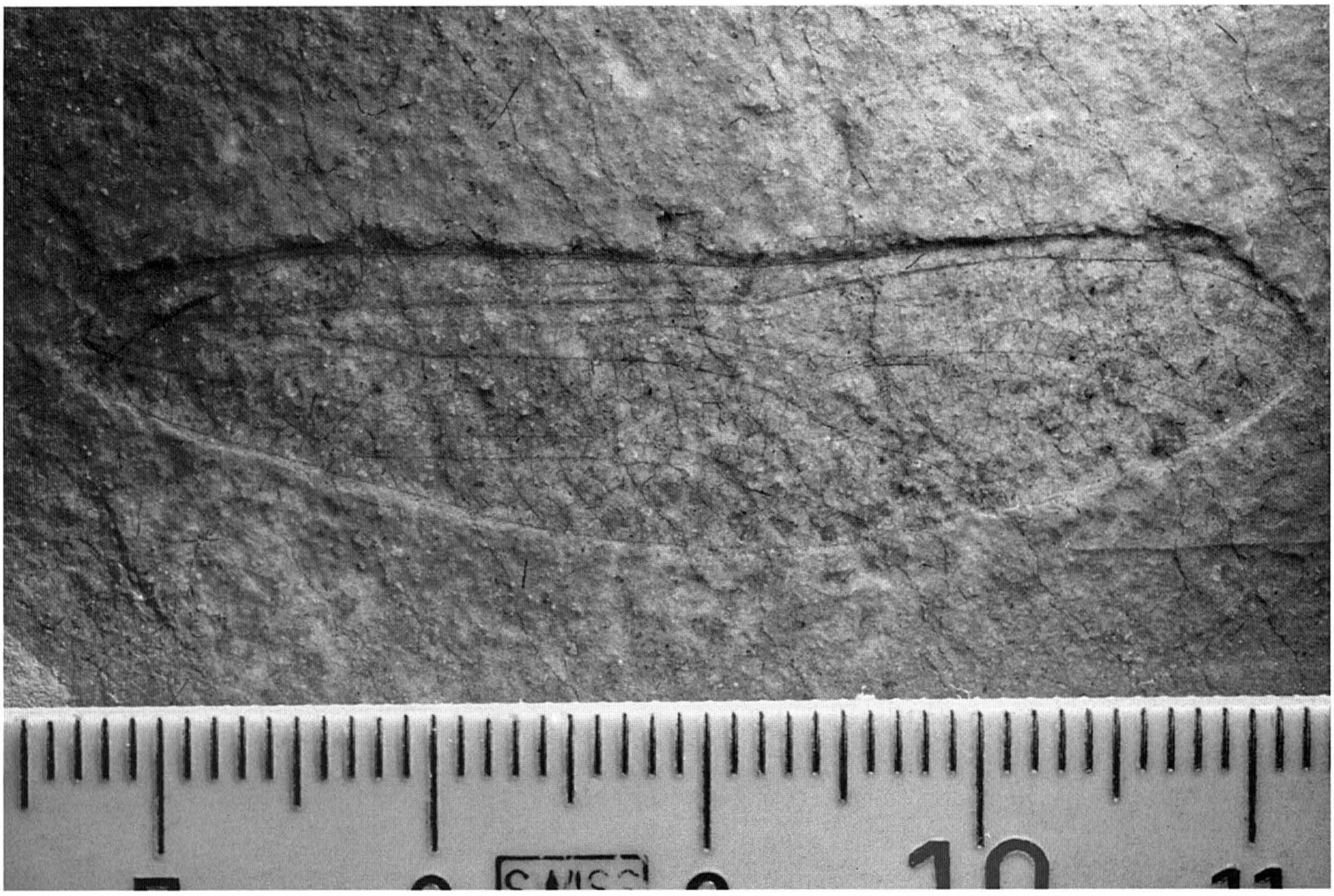

Fig. 41 - Photograph of *Kazakhophlebiella aktassica* (Pritykina 1968), holotype PIN 2554/218.

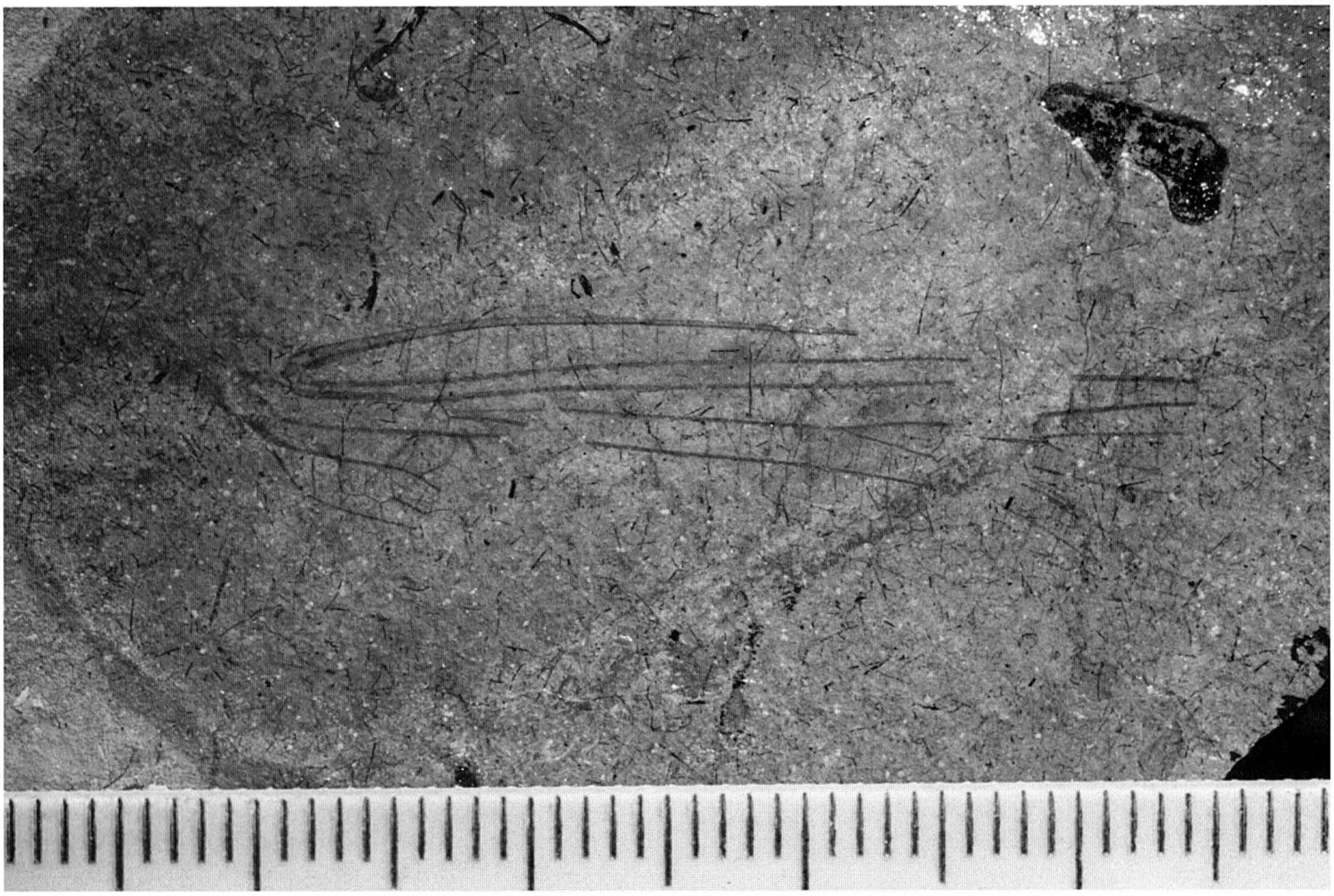

Fig. 42 - Photograph of *Kazakhophlebiella aktassica* (Pritykina 1968), paratype PIN 2384/2.

The pterostigma is not narrow, not elongate and not basally recessed; the pterostigmal brace is not basally recessed; there is only one oblique crossvein 'O'; the subtriangle is indistinctly defined. Contrary to *Protolindenia wittei*, *K. aktassica* lacks any synapomorphies with Petalurida and therefore must be excluded from *Protolindenia* and transferred to a new genus *Kazakhophlebiella* gen. nov.

P. aktassica might be related with Eurypalpida because they share a straight arculus with approximated origins of RP and MA; short pterostigma; relatively distal position of forewing nodus. These derived similarities could represent putative synapomorphies. Furthermore the forewing discoidal triangle is rather transverse too, correlated with a distinct multicellular subtriangle, but this character is also found in Liassogomphidae, Aeschnidiidae, Petalurida, Mesuropetalidae, and Gomphides (symplesiomorphy). Some characters seem to contradict a relationship with Eurypalpida, e.g. the presence of crossveins between RA and RP directly basal of the subnodus (no 'cordulegastrid gap' *sensu* Bechly 1995), the distally divergent RP3/4 and MA, the distinct pterostigmal brace. However, the derived states in all extant Chlorogomphida and Eurypalpida could rather be due to convergence, as is indicated by the discovery of a new fossil genus from Solnhofen (see: Bechly *et al.*, in press).

Finally, *P. aktassica* could belong to various families or even to a new one, still to be described. The discovery of further material is needed before any definite conclusions can be reached about this species.

Family Cretapetaluridae fam. nov.
(= Cretapetaluridae Bechly 1996 *nomen nudum*)

Type genus: *Cretapetalura* gen. nov.
Diagnosis: same as for type genus.

Genus *Cretapetalura* gen. nov.

Type species: *Cretapetalura brasiliensis* gen. nov. et sp. nov.

Etymology: after the Cretaceous and *Petalura*.

Diagnosis: a petalurid genus distinguished by the following features: a very broad area between RP1 and RP2; a very well-defined elongate anal loop in hindwing; a very angular distal side of hindwing discoidal triangle; a well-defined secondary longitudinal vein in basal part of postdiscoidal area; pterostigmal brace located midway between nodus and pterostigma; pseudo-anal vein PsA present and distinct in both wings.

Cretapetalura brasiliensis gen. nov. et sp. nov.
Figs 43-45

1996 - *Cretapetalura brasiliensis* - Bechly, p. 380 (*nomen nudum*).

Holotype: specimen i 9562, Museo Civico di Storia Naturale di Milano, Italy.

Stratigraphic level: Lower Cretaceous, Aptian (Maisey 1990; Martill *et al.* 1993).

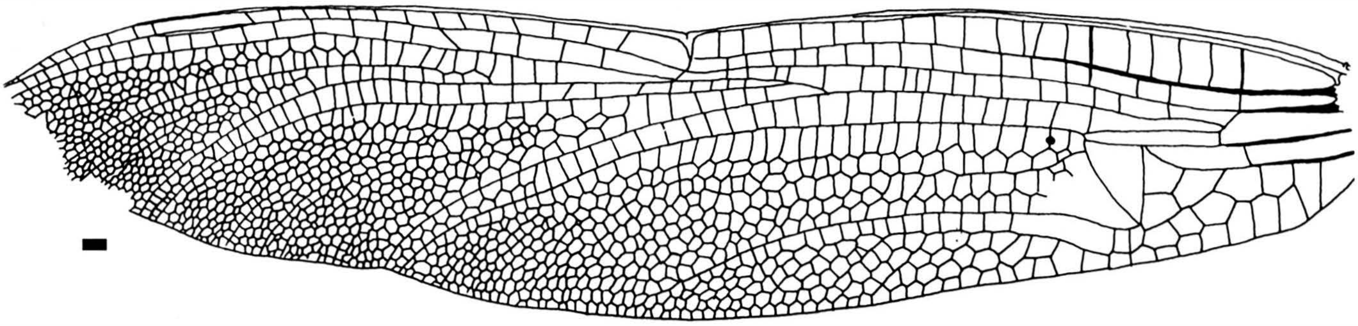

Fig. 43 - *Cretapetalura brasiliensis* gen. nov. et sp. nov., holotype i 9562, forewing. Scale bar represents 1 mm.

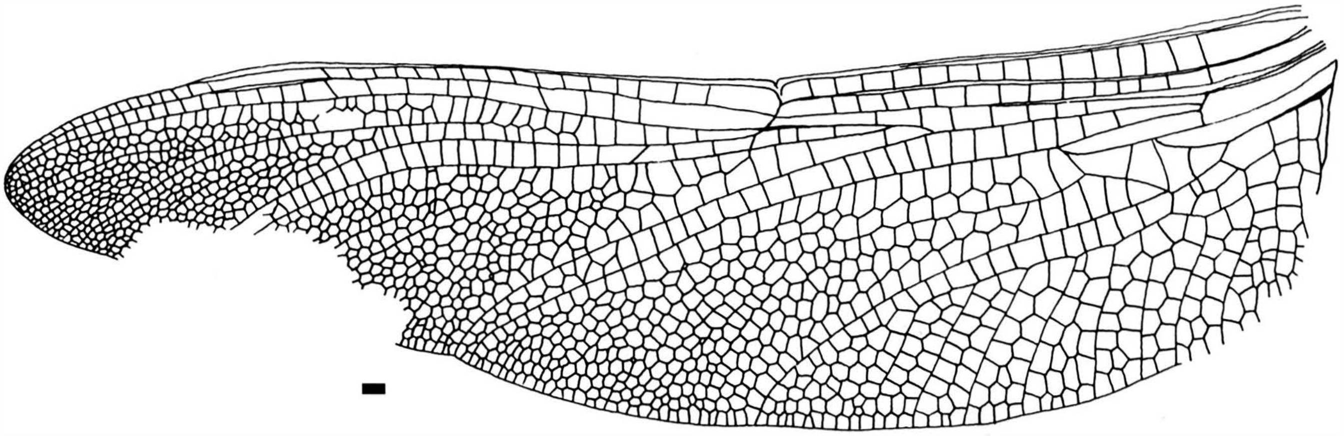

Fig. 44 - *Cretapetalura brasiliensis* gen. nov. et sp. nov., i 9562, hindwing. Scale bar represents 1 mm.

Type locality: Ceara, Crato Member, Santana Formation, near Nova Olinda, Araripe Basin, N.E. Brazil.

Etymology: after Brazil.

Description of holotype: a right hindwing and a left forewing still in connection with the thorax. The impressions of two incomplete legs are also preserved. The thorax and legs are very badly preserved and provide no useful information unlike the wings which are hyaline.

Forewing: length, 67.0 mm; maximal width, 14.5 mm; width at nodus, 14.0 mm; distance from base to nodus, 32.0 mm; from nodus to pterostigma, 21.4 mm; from nodus to arculus, 26.4 mm; from nodus to base of RP3/4, 6.0 mm; from nodus to base of IR2, 4.6 mm. Postnodal crossveins numerous (fourteen), and non-aligned with corresponding postsubnodal crossveins below them. Pterostigmal brace stronger and more oblique than other crossveins between RA and RP1. Pterostigmal brace in a very basal position, about midway between nodus and pterostigma, 8.8 mm and six postnodal crossveins from pterostigma. Pterostigma long and narrow, 5.0 mm long and 0.9 mm wide, parallel sided and covering three cells and two 1/2 cells. Pterostigma in a basal position, 8.5 mm from apex of wing. Probably about fourteen cells between costal margin and RA distal of pterostigma (nine visible). Nineteen antenodal crossveins between costal margin and ScP, not aligned with corresponding antenodal crossveins between ScP and RA. Two primary antenodal crossveins Ax1 and Ax2 slightly stronger than secondaries. Ax1 aligned with arculus. No antenodal crossvein in a more basal position. Four crossveins between Ax1 and Ax2 (distance between Ax1 and Ax2, 7.2 mm). Arculus straight, not 'broken', its posterior part being aligned with anterior part. RP and MA well-separated at their bases in arculus. Eighteen crossveins in area between RA and RP (between arculus and nodus), and eleven in area between MA and RP (between arculus and base of RP3/4). Although exact number undetermined, very numerous (probably more than seven) bridge-crossveins (Bqs). Bridge-space (Bqs-area) between RP and IR2 very narrow (0.5 mm wide), narrower than that of hindwing. Base of RP2 aligned with subnodus. An oblique crossvein 'O' just distal of base of RP2 and a supplementary oblique crossvein 4.6 mm away distally, between RP2 and IR2. Straight IR1 originating 11.0 mm distal of subnodus, below pterostigmal brace. Areas between RP1 and IR1 and between IR1 and RP2 very wide (with ten to thirteen rows of small cells). Area between RP2 and IR2 not widened distally, with only one row of cells except near posterior margin of wing. These two veins are closely parallel and slightly curved. Area between IR2 and RP3/4 very broad but without any clear Rspl. RP3/4 and MA closely parallel and only slightly curved, with one row of cells, except two rows near posterior wing margin. Postdiscoidal area distinctly wider near posterior wing margin. No distinct Mspl. Four rows of cells between MA and MP just distal of discoidal triangle. Discoidal triangle not elongate, but rather broad (length of anterior side, 2.8 mm; of distal side, 4.8 mm; of basal side, 3.6 mm). Distal side of discoidal triangle not straight but with a distinct angle. A well-defined secondary longitudinal vein originating at angle of distal side of discoidal triangle and distally vanishing in postdiscoidal area. Anterior side of discoidal triangle ending a little beyond hypertriangle. Discoidal triangle in a very distal position, 3.6 mm from arculus. Hypertriangle long and narrow, 6.6 mm long and 0.6 mm wide, free of crossveins. Median cell (m) free of crossveins. Submedian cell also free, with only CuP-crossing in its distal half, 0.9 mm basal of arculus. A distinct pseudo-anal vein PsA delimiting a subtriangle. Forewing subtriangle wider than hindwing one, being 3.8 mm long and 4.0 mm wide, divided into three cells. Main branch of AA which delimits its posterior side of subtriangle strongly angled with basal part of AA, so that PsA is aligned with basal part of AA. MP and CuA separating at posterior angle of discoidal triangle. Free portion of CuA very short, CuA being then fused with AA. Area between CuA + AA and MP narrow, 1.1 mm wide at base, with only one row of cells along its length. CuA + AA very long, with six parallel branches directed towards posterior wing margin, so that, cubito-anal area is very long and extending almost as far as nodus. Cubito-anal area moderately broad with up to seven rows of cells between CuA + AA and posterior wing margin. Anal area narrow, with two rows of cells between AA and posterior wing margin but without any posterior branch of AA crossing through it.

Hindwing: length, 67.0 mm; maximal width, 18.0 mm; width opposite nodus, 16.5 mm; distance from base to nodus, 27.0 mm; from nodus to pterostigma, 22.5 mm; from nodus to arculus, 21.0 mm; from nodus to base of RP3/4, 7.5 mm; from nodus to base of IR2, 5.5 mm. Postnodal crossveins numerous (fifteen), non-aligned with corresponding postsubnodal crossveins below them. Pterostigmal brace stronger and more oblique than other crossveins between RA and RP1. Pterostigmal brace in a very basal position, about midway between nodus and pterostigma, 10.0 mm from pterostigma, with eight postnodal crossveins between the two. Pterostigma long and narrow, 6.0 mm long and 0.9 mm wide, parallel sided and covering five cells. Pterostigma in a basal position, 11.5 mm from apex of wing, with about twenty cells between costal margin and RA distal of pterostigma. Fifteen antenodal crossveins between costal margin and ScP, not aligned with corresponding antenodal crossveins between ScP and RA. Two primary antenodal crossveins Ax1 and Ax2 a little stronger than secondary antenodal crossveins. Ax1 aligned with arculus, no antenodal crossvein in a more basal position. Four crossveins between Ax1 and Ax2, distance between Ax1 and Ax2, 7.4 mm. An obtuse angle between posterior part and anterior part of arculus. RP and MA well-separated at theirs bases in arculus, 0.3 mm apart. Seven or eight crossveins in area between RA and RP (between arculus and nodus), and in area between MA and RP (between arculus and base of RP3/4). Exact number of bridge-crossveins (Bqs) not visible but they were very numerous (more than five) in area between RP, IR2 and subnodus. Base of RP2 aligned with subnodus. One oblique crossvein 'O' just distal of base of RP2 and a supplementary oblique crossvein 4.6 mm more distally, between RP2 and IR2. IR1 originating 10.0 mm distal of subnodus, nearly below pterostigmal brace. IR1 a smoothly curved vein. One supplementary longitudinal vein in area between IR1 and RP1, distal of pterostigma. Areas between RP1 and IR1 and between IR1 and RP2 very wide, with ten to fourteen rows of small cells. Area between RP2 and

Fig. 45 - Photograph of *Cretapetalura brasiliensis* gen. nov. et sp. nov., holotype i 9562.

IR2 never widened, with only one row of cells; these two veins being closely parallel and slightly curved. Area between IR2 and RP3/4 very broad but without any clear Rspl. RP3/4 and MA closely parallel and nearly straight, with one row of cells, except two rows near posterior wing margin. Postdiscoidal area very broad towards posterior wing margin. No clear Mspl. Two or three rows of cells between MA and MP just distal of discoidal triangle. Discoidal triangle elongate, not broad (length of anterior side, 4.2 mm; of distal side, 5.2 mm; of basal side, 2.6 mm). Discoidal triangle divided into two cells by a crossvein. A distinct angle in distal side of discoidal triangle. A well-defined secondary longitudinal vein originating at angle on distal side of discoidal triangle and vanishing distally in postdiscoidal area. Anterior side of discoidal triangle terminating a little basal of distal angle of hypertriangle. Discoidal triangle in a very distal position, 2.6 mm from arculus. Hypertriangle long and narrow, 7.0 mm long and 0.8 mm wide, free of crossveins. Median cell free. Submedian cell free but CuP-crossing not preserved either. A strong oblique pseudo-anal vein PsA between AA and MP + CuA which defines a subtriangle, 3.3 mm long and 2.7 mm wide. Subtriangle divided into two cells by a crossvein. MP and CuA separating at posterior angle of discoidal triangle. Free part of CuA very short, CuA being nearly immediately fused with AA. CuA + AA clearly divided into a basally-directed branch CuAb and a distally-directed branch CuAa. Area between CuA + AA and MP narrow, 1.5 mm wide at base, with only one row of cells along it. CuAa very long, reaching the posterior margin opposite nodus, with six parallel branches directed towards posterior wing margin. Cubito-anal area long and very broad (6.6 mm wide) with seven to nine rows of cells between CuAa and posterior wing margin. CuAb and a posterior branch of AAa delimiting a well-defined posteriorly-closed anal loop, elongate, distinctly longer than broad, 3.8 mm long and 1.9 mm wide. Anal loop divided into five smaller cells. AAa directed towards posterio-basal part of wing. AA producing two other parallel branches (AAb and AAc) towards posterior wing margin. Anal area is very broad, 8.0 mm wide, with nine or ten rows of cells between AA and posterior wing margin. A distinct membranule, 1.0 mm long and 0.3 mm wide. Posterio-basal margin of wing damaged but apparently rounded, without any anal angle, and no anal triangle, thus it seems to be a female specimen.

Systematic position of *Cretapetalura* gen. nov.: the general appearance of the wings of *Cretapetalura brasiliensis* gen. nov. et sp. nov. is very similar to that of extant genera of Petalurida. But an attribution of a new taxon to the Petalurida rather than to Austropetaliida or Neopetaliidae, based only on wing characters, is contentious because the wing venation of these taxa is very similar and shows only few autapomorphic characters. For example, Carle and Louton (1994) demonstrated that in spite of wing venational similarities the genus *Neopetalia* Cowley 1934 has no phylogenetic relationship with the other genera formerly placed in the Neopetaliidae (Austropetaliidae *sensu* Carle and Louton), and belongs to the 'cordulegastroid' grade within Cavilabiata, having to be classified in a monotypic family Neopetaliidae (*sensu* Carle and Louton).

Nevertheless, *Neopetalia* does possess apomorphic ground-plan characters of Cavilabiata, like an elongated 'gaff' (basal part of hindwing CuA between the discoidal triangle and the furcation into CuAa and CuAb) and a 'cordulegastrid-gap' (*sensu* Bechly 1995) formed by the lack of crossveins between RA and RP directly basal of the subnodus, that are absent in *Cretapetalura* gen. nov. Likewise, Austropetaliida share several apomorphic features with the other Aeshnoptera, that are absent in *Cretapetalura* gen. nov., e.g. basally parallel veins RP1 and RP2, undulating veins RP2 and RP3/4 and MA, and longitudinal discoidal triangles of similar shape in both wing pairs. Therefore *Cretapetalura* gen. nov. clearly does neither belong to Neopetaliidae nor to Austropetaliida.

The present attribution of *Cretapetalura* gen. nov. to the Petalurida is mainly based on the following four synapomorphies within the Anisoptera: area between costal margin and RA distal of pterostigma very narrow and crossed by numerous veins; IR1 a very long and weakly curved vein originating about midway between nodus and pterostigma; areas between RP1 and IR1 and between IR1 and RP2 very broad, with about ten rows of cells (apomorphic character lacking in *Tanypteryx* Kennedy 1917 and *Tachopteryx* Selys 1859); the bridge-space (Bqs-area) very narrow, especially in forewing. This last character seems to be an autapomorphy of Petalurida, that is only absent in the genus *Tanypteryx*.

The following characters are also present in Petalurida but are not unique autapomorphies of this taxon.

A very long and narrow, more or less basally recessed pterostigma which is also present in the wings of some Aeschnidiidae, Anactina and Isophlebiida (e.g. *Dinosamarura tugnuica* Pritykina 1985 and *Anisophlebia helle* (Hagen 1862)). This specialisation is due to remarkable convergences (Nel *et al.* 1993).

The forewing and hindwing pterostigmal braces lying in a very basal position, about midway between the nodus and the pterostigma. Something similar to this distinct petalurid character is also present in some Euaeshnida (Anactina) and some Austropetaliida (*Hypopetalia*).

Two oblique crossveins 'O'. This petalurid character is also present in some aberrant specimens of *Cordulegaster* spp. (Cordulegastridae s.str.), in many Aeschnidiidae as well as in several fossil 'anisozygopteres' and Anisoptera and rather seems to represent a symplesiomorphy of basal Anisoptera;

A very well-defined forewing (three-celled) subtriangle. This character, which is present in nearly all extant Petalurida, is absent in Neopetaliidae and Austropetaliida. However, it is also present in Gomphides - Gomphoidinae and more 'derived' Eurypalpida ('corduliids' and Libellulidae);

The well-defined hindwing subtriangle limited by a PsA. This character is weakly developed in some genera of Petalurida but is absent in *Uropetala* Selys 1857 and *Petalura* Leach 1815. In *Phenes* Rambur 1842, *Tachopteryx* Uhler *in* Selys 1859 and *Tanypteryx* Kennedy 1917, this subtriangle is only unicellular, instead of being two-celled as in *Cretapetalura* gen. nov. The Aeschnidiidae, Gomphides - Gomphoidinae and Austropetaliida have better defined hindwing subtriangles as in *Cretapetalura* gen. nov.; the Austropetaliida and Neopetaliidae have a characteristic pattern of red brown costal spots. This derived character is probably lacking in *Cretapetalura* gen. nov., which is considered a plesiomorphic condition. The presence of this character in both Austropetaliida and Neopetaliidae which are clearly unrelated is almost certainly due to convergence, perhaps caused by mimicry (Carle and Louton 1994), although an evolutionary explanation for such a mimicry is not known at all.

Family Aktassiidae Pritykina 1968 sensu nov.
Subfamily Pseudocymatophlebiinae subfam. nov.

Type genus: *Pseudocymatophlebia* gen. nov.
Diagnosis: same as for type genus.

Genus *Pseudocymatophlebia* gen. nov.

Type species: *Pseudocymatophlebia hennigi* gen. nov. et sp. nov.

Etymology: after *Cymatophlebia* and 'pseudo-' to indicate the misleading similarities between this genus and the Cymatophlebiidae.

Diagnosis: a petalurid genus distinguished by the following features: wings very long with a dense meshwork of numerous cells; pterostigmal brace not very oblique and somewhat basally recessed; bridge-crossveins (Bqs) very numerous; no-well-defined Rspl nor Mspl but postdiscoidal area and area between IR2 and RP3/4 very wide with many cells; a secondarily very elongated and straight IR1 vanishing distally in area between RP1 and RP2 (autapomorphy), and not fused with the pseudo-IR1; crossveins between MA and RP3/4 and between IR2 and RP2 oblique towards base of wing; many crossveins in area between RA and RP basal of nodus.

Pseudocymatophlebia hennigi gen. nov. et sp. nov.
Figs 46-48

Material: Holotype specimen no. MNEMG 1996. 224 a,b, part and counterpart of a forewing. Paratypes specimens no. MNEMG 1996. 225a and 225b, a nearly complete forewing, and an antero-basal fragment of a hindwing; found X. Martínez-Delclòs, coll. E. Jarzembowski, Maidstone Museum & Art Gallery.

Stratigraphic level: Lower Cretaceous, Barremian, Upper Weald Clay.

Type locality: Smokejacks Brickworks (Ross and Cook 1995), Ockley, Surrey, UK.

Etymology: in honour of the late Prof. Willi Hennig, the founder of Phylogenetic Systematics.

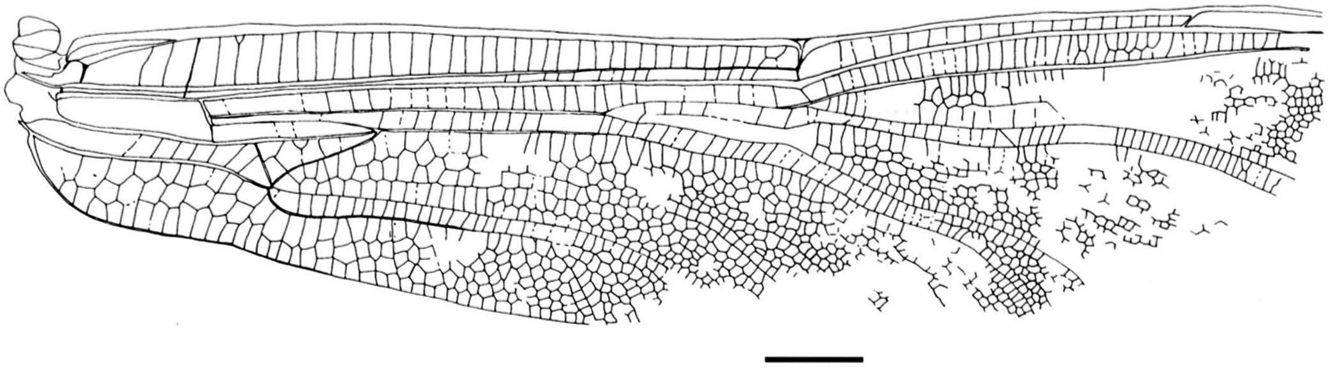

Fig. 46 - *Pseudocymatophlebia hennigi* gen. nov. et sp. nov., holotype 96. 225a MNEMG, forewing. Scale bar represents 5 mm.

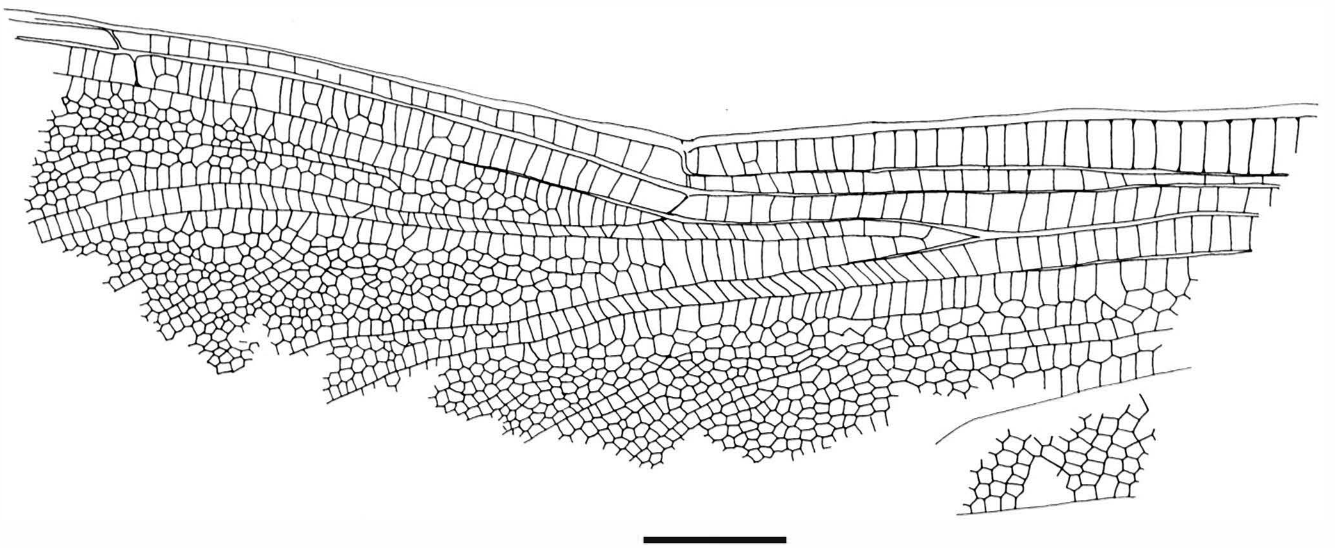

Fig. 47 - *Pseudocymatophlebia hennigi*, paratype 1996. 224a MNEMG, forewing. Scale bar represents 5 mm.

Description:

[specimen MNEMG 1996. 224], [holotype].

Part and counterpart of the median two-thirds of a forewing; length of fragment, 48.5 mm, probable total length of wing, 56.0 mm; width at nodus, about 14.2 mm. Distance from nodus to pterostigma, 20.8 mm. Pterostigma not completely preserved but probably very long and narrow, 1.0 mm wide. Pterostigmal brace weakly oblique and shifted 0.6 mm basal of basal side of pterostigma. Pterostigma covering many cells, six or more being visible. Very numerous (twenty-five) postnodal crossveins between nodus and pterostigma, non-aligned with corresponding postsubnodal crossveins. Some cells between RA and RP1 subdivided into two cells. Antenodal crossveins very numerous, twenty-eight of them being preserved, in the portion of the antenodal area between nodus and arculus. Antenodal crossveins between costal margin and ScP non-aligned with the antenodal crossveins between ScP and RA. ScP fused with costal margin at nodus. Very numerous (twenty-six visible) antesubnodal crossveins between RA and RP, distal of arculus and basal of subnodus. Bases of RP3/4 and IR2 10.8 and 8.8 mm basal of nodus. Numerous (fourteen) bridge-crossveins (Bqs) between RP, IR2 and base of RP2. Bridge-space (Bqs-area) very narrow, 0.5 mm wide. Base of RP2 aligned with subnodus. First oblique crossvein 'O' poorly preserved, 1.5 mm distal of subnodus. Second distal crossvein 'O' 8.9 mm distally. Crossveins between IR2 and RP2 very numerous, short and oblique. Crossveins between RP3/4 and MA very numerous and often oblique. RP2 and IR2 long and parallel, weakly curved, and preserved area between them not widened. RP3/4 and MA weakly curved but area between them gently widened distally, with about five rows of cells towards posterior wing margin. Area between IR2 and RP3/4 very wide, with numerous rows of cells but without any defined Rspl. Postdiscoidal area very wide, distally widened near wing margin, with numerous rows of cells but without any defined Mspl. Main branch of CuA not preserved but six (or more) rows of cells distally in cubito-anal area. Area between RP1 and RP2 very wide, with four rows of cells below second oblique crossvein 'O', RP1 and RP2 diverging distally, with ten rows of cells between them below pterostigma. A secondarily elongated and straight vein IR1, 7.3 mm long vanishing distally 2.9 mm basal of pterostigma. More distal pseudo-IR1 not preserved.

[specimen no. MNEMG 1996. 225a], [paratype]

Part and counterpart of a nearly complete forewing, with only the posterior margin partly destroyed; length of fragment, 67.8 mm, probable length of wing, about 78 mm; width at nodus, about 15.9 mm; distance from nodus to pterostigma, 19.6 mm; from base to nodus, 38.1 mm. Nodus clearly in a distal position. Pterostigma not completely preserved but probably very long and narrow, about 9.0 mm long and 0.9 mm wide. Pterostigmal brace weakly oblique and 0.5 mm basal of basal side of pterostigma. Pterostigma covering many cells (ten or eleven being visible). Very numerous (twenty-one) postnodal crossveins between nodus and pterostigma, non-aligned with corresponding postsubnodal crossveins. Some cells between RA and RP1 double. Antenodal crossveins very numerous, thirty-seven being preserved. Antenodal crossveins between costal margin and ScP non-aligned with corresponding antenodal crossveins between ScP and RA. ScP

Fig. 48 - Photograph of *Pseudocymatophlebia hennigi* gen. nov. et sp. nov., holotype 1996. 224.

fused with costal margin at nodus. Very numerous (twenty-eight visible) antesubnodal crossveins between RA and RP, distal of arculus and basal of subnodus. Bases of RP3/4 and IR2 10.4 and 8.3 mm basal of nodus, respectively. Numerous (ten plus) bridge-crossveins (Bqs) between RP, IR2 and base of RP2. Bridge-space (Bqs-area) very narrow, 0.9 mm wide. Base of RP2 aligned with subnodus. First oblique crossvein 'O' poorly preserved, about 2.0 mm distal of subnodus; second distal crossvein 'O' 8.1 mm distally. Crossveins between IR2 and RP2 very numerous, short and oblique. Crossveins between RP3/4 and MA very numerous and oblique. RP2 and IR2 parallel, weakly curved and the area between them is not widened. RP3/4 and MA weakly curved but area between them gently widened distally, with six to eight rows of cells towards posterior wing margin. Area between IR2 and RP3/4 very wide, with numerous rows of cells but without any defined Rspl. Postdiscoidal area also very wide, distally widened near wing margin, with numerous rows of cells but without any Mspl. Seven rows of cells in cubito-anal area. CuA with more than nine posterior branches. Area between RP1 and RP2 very wide, with three or four rows of cells below second oblique crossvein 'O'. RP1 and RP2 diverging distally, with six or seven rows of cells between them below pterostigma. A secondarily elongated and straight IR1, about 7.0 mm long, distally vanishing about 5.0 mm basal of pterostigma. More distal pseudo-IR1 not preserved. Discoidal triangle very narrow and elongate, divided into six small cells; length of its anterior side, 6.3 mm; of basal side, 2.3 mm; of distal side, 6.4 mm; distal side somewhat undulating but without any secondary longitudinal vein of postdiscoidal area originating at it. Hypertriangle 8.6 mm long and max. 0.9 mm wide, divided into small cells by two or more crossveins. Arculus 2.2 mm basal of discoidal triangle. Bases of RP and MA distinctly separated at arculus. Median cell free of crossveins. Submedian cell traversed by five crossveins, including CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subtriangle divided into two cells by a crossvein. Anal area rather wide, with three rows of cells between AA and posterior margin of wing.

[specimen MNEMG 1996. 225b], [paratype]

Part and counterpart of the costal margin of a hindwing, between the base and the nodus. It is poorly preserved.

Discussion: the two forewings and the fragment of a hindwing described above were found only 10 cm apart on the same parting, thus they probably belong to the same specimen. Furthermore the two forewings are very similar and can be considered as conspecific.

Systematic position of *Pseudocymatophlebia* gen. nov.: this new genus shows superficial similarities with the English Cymatophlebiidae *Cymatophlebia standingae*, *C. zdrzaleki*, *Valdaeshna* and a new genus and species of Valdaeshninae that will be described in Bechly *et al.* (in press) in their very long wings with numerous crossveins and cells. Nevertheless, it differs from these taxa as follows: 1) it has no defined Rspl; 2) RP2, IR2, RP3/4 and MA lack pronounced undulations; 3) RP1 and RP2 are basally distinctly divergent; 4) there are more bridge-crossveins (Bqs) in a distinctly narrower bridge-space (Bqs-area); 5) the pterostigmal brace is less oblique. Characters (1), (2) and (3) are symplesiomorphies of the Anisoptera, thus *Pseudocymatophlebia* gen. nov. does not share any synapomorphies with the Aeshnoptera or even Cymatophlebiidae. Character (4) and (5), together with the large size of the wings, with numerous cells, the distinct basal recession of the stigmal brace vein, and the straight and basally prolonged IR1, are rather strong synapomorphies with Petalurodea (*sensu* Bechly 1996; = Cretapetaluridae fam. nov. + Aktassiidae + Petaluridae). Within this group, it differs from *Cretapetalura* gen. nov. in possessing a true 'lestine' oblique vein (first basal crossvein 'O') not shifted basally (plesiomorphy), and sharing two synapomorphies with the Petaluroidea (= Aktassiidae + Petaluridae): the widening of the area between RP3/4 and MA near the posterior wing margin; and the undulating RP3/4. Within this group, it is an unique autapomorphy of *Pseudocymatophlebia* gen. nov. that the very long and straight-IR1 is vanishing distally and not fusing with the more distal pseudo-IR1. The very large number of tiny cells could be a synapomorphy with Aktassiidae that suggests a closer relationship with this family than with the Petaluridae. The well-defined pterostigmal brace is a plesiomorphic state also present in *Aktassia* (see below) but not in *Aeschnogomphus*. Thus, Pseudocymatophlebiinae subfam. nov. is here considered as the sister-group of Aktassiinae stat. nov., which shall only include the sister-genera *Aeschnogomphus* and *Aktassia*.

Subfamily Aktassiinae stat. nov.
(in Petalurida Bechly 1996,
Family Aktassiidae Pritykina 1968)

Type genus: *Aktassia* Pritykina 1968. Other genus. *Aeschnogomphus* Handlirsch 1906.

Type species: *Aktassia magna* Pritykina 1968, by original designation.

Aktassia magna Pritykina 1968
Fig. 49-50

1968 - *Aktassia magna* - Pritykina, p. 48-49 (in family Aktassiidae Pritykina 1968).
1992 - *Aktassia magna* Pritykina - Carpenter, p. 82.
1994 - *Aktassia magna* Pritykina - Bridges, p. VII.143.
1995 - *Aktassia magna* Pritykina - Bechly, p. 263 (close to Aeschnidiidae).
1996 - *Aktassia magna* Pritykina - Bechly, p. 16, 380 (in Petalurida).

Material: Holotype PIN 2384/4, part and counterpart of a single male hindwing incompletely preserved, paratype PIN 2066/25, the distal half of a wing.

Stratigraphic level: Upper Jurassic.

Type locality: Karatau, Kazakhstan, Ex U.R.S.S.

Description: *Aktassia magna* Pritykina 1968 is known from two specimens, only the holotype being figured and described by Pritykina (1968). Specimen 2066/25 shares with the holotype of *A. magna* all the structures of the common parts of their wings. Thus there is no evidence against its attribution to this species. Characters figured by Pritykina (1968, text-

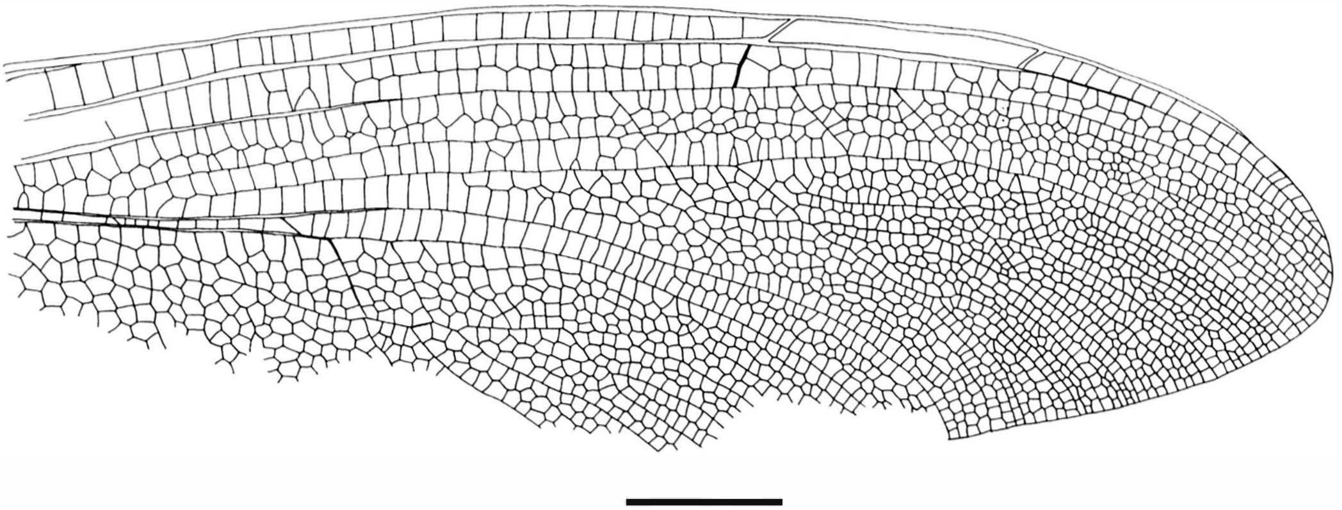

Fig. 49 - *Aktassia magna* Pritykina 1968, paratype PIN 2066/25, wing apex. Scale bar represents 5 mm.

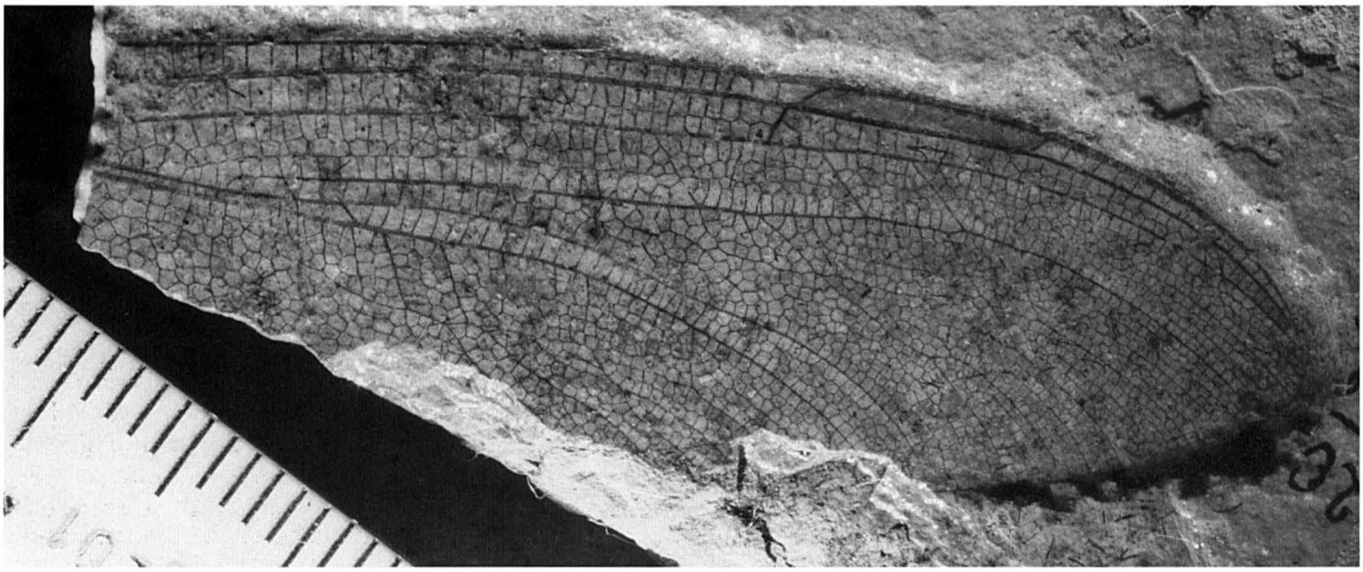

Fig. 50 - Photograph of *Aktassia magna* Pritykina 1968, paratype PIN 2066/25.

fig. 19) are exact but some features not preserved in the holotype are clearly visible in the paratype, i.e. pterostigmal brace is distinctly stronger than other postsubnodal crossveins but not very oblique. At least, two oblique crossveins 'O' present, in very distal positions. IR2 and RP2 very strongly approximate in their basal parts, minimal distance between them 0.2 mm. A rather well-defined Rspl, with five or six rows of cells between IR2 and Rspl. Cells in the areas between RP2 and RP1 and between IR2 and RP3/4 are arranged in polygonal groups limited by stronger secondary veins, three of these branched on RP1.

Discussion: most of the observable characters are plesiomorphies or autapomorphies. Therefore it is very difficult to determine the phylogenetic relationships of this enigmatic taxon. It shares with the Aeschnidiidae an extremely high density of cells, but this might be due to convergence since the discoidal triangles and cubito-anal areas of *Aktassia* and the Aeschnidiidae are very different (Nel and Martínez-Delclòs 1993). On the other hand *Aktassia* shares several apomorphic character states with *Aeschnogomphus* and other Petalurida (large and broad wings; narrow postnodal area with many cells distal of elongated pterostigma; very long and straight IR1; and widened area between RP1 and RP2), and appears to belong to the petalurid stem-group. Most probably, *Aktassia* represents the sister-genus of *Aeschnogomphus* with which it shares many wing venational 'similarities' including several apomorphic character states (giant size; straight posterior margin of the hindwing; very high density of cells; characteristic pattern of intercalary veins between RP2 and IR2 and between MA and MP). The differences in *Aktassia* are the shape of the hindwing and the shape of the discoidal triangle which might only be artefacts caused by tectonic deformation (longitudinal compression) of the fossil, also shown by the abnormally undulate anterior side and hypertriangle. *Aktassia* and *Aeschnogomphus* are best classified together in the family Aktassiidae within Petalurida. Differences from *Aeschnogomphus* are as follows: presence of two rows of cells between MP and CuA; presence of two rows of cells between RA and RP1 distal of nodus; presence of a weakly oblique pterostigmal brace.

Aktassia pritykinae sp. nov.
Figs 51-53

Holotype: specimen PIN 3664/471, two distal halves of wings on the same slab of rock, collected by the palaeontomological group of the JSMPE in 1976.

Stratigraphic level: Lower Cretaceous.

Type locality: Shin-Khuduk, Mid Gobi Aimak, about 40 km SW Undur-Shil Town, near Shin-Khuduk Well, outcrop 119, layer 3d, Mongolia.

Description: length of fragment 1, 46.1 mm (fig. 39), length of fragment 2, 33.1 mm (fig. 40), probable length of wing, about 90 mm; width at nodus, about 18 mm; distance from nodus to pterostigma, about 23 mm. Exact position of nodus unknown. Pterostigmata completely preserved, very long and narrow, that of fragment 1 being about 8.8 mm long and 1.8 mm wide, that of fragment 2 being about 11.1 mm long and 2.3 mm wide. Pterostigmal braces not oblique and opposite basal side of pterostigmata. Pterostigmata covering 13 or 14 cells. Area between costal margin and RA distal of pterostigma very long, with more than 17 crossveins. Very numerous (11 of them being visible in the small preserved portion of postnodal area) postnodal crossveins between nodus and pterostigma, non-aligned with corresponding postsubnodal crossveins. Few cells between RA and RP1 double. Antenodal area and bridge-space (Bqs-area) not preserved. Base of RP2 aligned with subnodus. First oblique crossvein 'O' poorly preserved, about 4.5 mm distal of subnodus; second distal crossvein 'O' present. Crossveins between IR2 and RP2 and between RP3/4 and MA very numerous. RP2 and IR2 parallel, weakly curved and the area between them is gently widened. RP3/4 and MA weakly curved but area between them gently widened distally, with six rows of cells towards posterior wing margin. Area between IR2 and RP3/4 very wide, with numerous rows of cells but without any defined Rspl. Postdiscoidal area also very wide, distally widened near wing margin, with numerous rows of cells but with a very rudimentary zigzagged Mspl. Area between RP1 and RP2 very wide, with three rows of cells below second oblique crossvein 'O'. RP1 and RP2 diverging distally, with five or six rows of cells between them below pterostigma. A secondarily elongated and straight IR1, not distally vanishing.

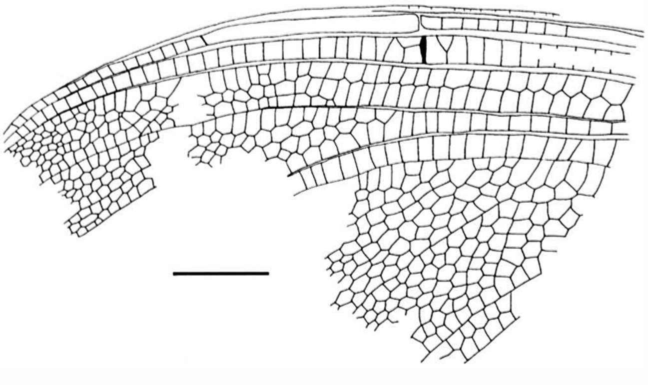
Fig. 51 - *Aktassia pritykinae* sp. nov., holotype PIN 3664/471, fragment 1, wing apex. Scale bar represents 5 mm.

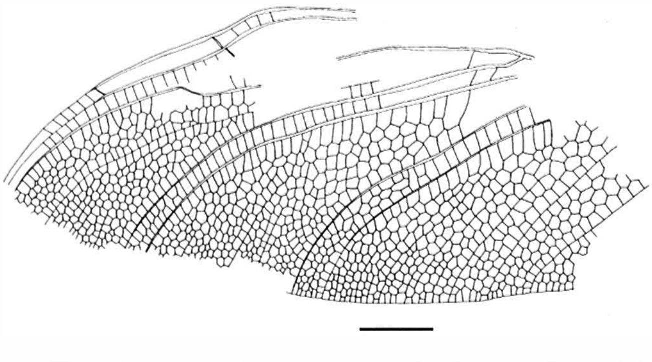
Fig. 52 - *Aktassia pritykinae* sp. nov., PIN 3664/471, fragment 2, wing apex. Scale bar represents 5 mm.

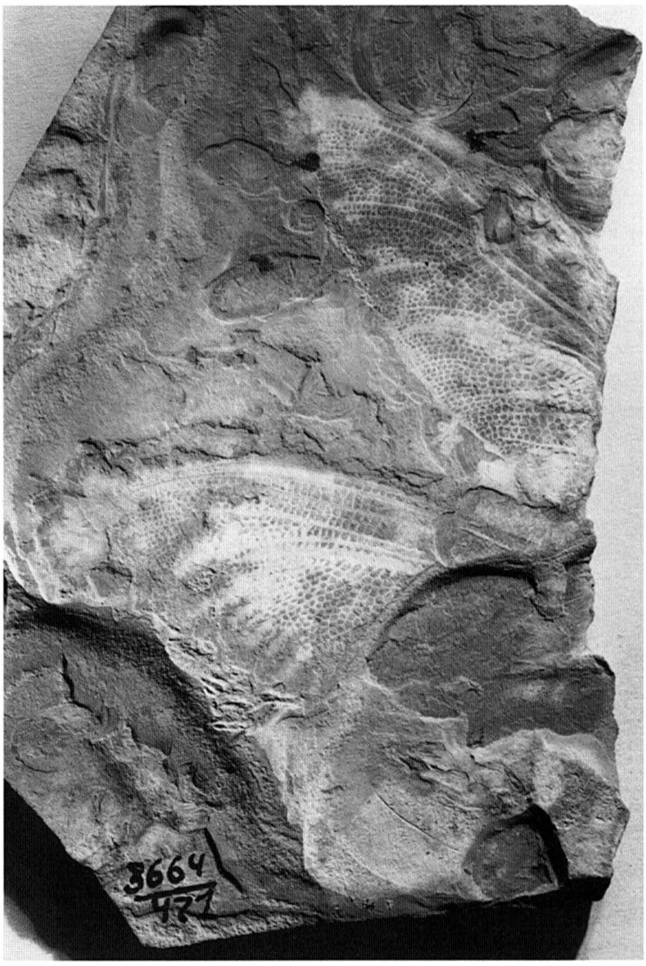

Fig. 53 - Photograph of *Aktassia pritykinae* sp. nov., holotype PIN 3664/471.

Discussion: because of their relative position, fragment 1 probably is a forewing and fragment 2 a hindwing. Thus, the forewing pterostigma is distinctly shorter than that of hindwing. *Aktassia pritykinae* sp. nov. shares with Aktassiinae the following synapomorphies: very long and broad wings with broad areas between main veins, very long pterostigmata, long area between costal margin and RA distal of pterostigma, very long and straight IR1, reaching the posterior margin. It shares with *A. magna* a symplesiomorphy, absent in *Aeschnogomphus*, i.e. the non-oblique pterostigmal brace is not reduced, distinctly stronger than other crossveins between RA and RP1, aligned with the basal side of the pterostigma. It differs from *A. magna* in the absence of a double row of cells in the area between RA and RP1 distal of the pterostigma. It does not share the autapomorphic characters of *Aeschnogomphus*, i.e. the distinctly basally recessed pterostigma and the very widened areas between MA and RP3/4 and IR2 and RP2 along the wing margin. Because of the fragmentary preservation, the affinities of *A. pritykinae* sp. nov. within Aktassiinae remain uncertain. We provisionally attribute it to *Aktassia* because of the great phenetic similarities in the preserved parts of the wing venations.

Genus *Aeschnogomphus* Handlirsch 1906
(in Petalurida Bechly 1996,
Family Aktassiidae Pritykina 1968)

Type species: Handlirsch (1906: 590) did not designate a type species of the genus. Cowley (1934: 249) subsequently designated *Aeschnogomphus charpentieri* (Hagen 1848) as type species although this species has been created after *Aeschnogomphus intermedius* (Münster *in* Germar 1839) and listed in second position in the work of Handlirsch (1906). He also did not mention '*Anax buchi*' Hagen 1848 at all, which has to be regarded as the valid name of *A. charpentieri* (Hagen 1848) (see below). However, this is absolutely in agreement with the provisions of Art. 69 IRZN, that allow any originally included nominal species to be chosen as type species by subsequent designation, for genus-group names that were established before 1931.

Amended diagnosis: no satisfactory diagnosis has been previously provided. This genus is well-characterized by the following features: wings very long (75 to 95 mm long); forewing discoidal triangle wide, divided into many cells; forewing subtriangle broad and three-celled; hindwing discoidal triangle three-celled and narrow; hindwing subtriangle unicellular; hindwing anal loop posteriorly open; hindwing cubito-anal area broad; no Rspl nor Mspl; two oblique crossveins 'O'; areas between RP3/4 and MA and between IR2 and RP2 distally widened; a long straight IR1; areas between IR1 and RP2 and between IR1 and RP1 very broad; antenodal and postnodal crossveins very numerous; pterostigma very long and narrow, and basally recessed; no oblique pterostigmal brace; area between costal margin and RA distal of pterostigma very narrow and long, with many crossveins.

Aeschnogomphus buchi (Hagen 1848) comb. nov.
(= *Aeschnogomphus charpentieri* (Hagen 1848)
syn. nov.)
Figs 54-58

1837 - '*Aeschna* od. *Libellula*' - Erichson in Buch, p. 135, pl. 3.
1840 - '*Libellulita dresdensis*' or '*Libellulites solenhofensis*' - Charpentier, p. 171, p. 180; pl. 48, fig. 1.
1848 - *Anax Buchi* - Hagen, p. 11.
1848 - *Aeschna* [sic] *Charpentieri* - Hagen, p. 11-12.
1856 - *Aeschna* [sic] *charpentieri* Hagen - Giebel, p. 278.
1856 - *Aeschna* [sic] *Buchi* Hagen - Giebel, p. 280.
1862 - *Anax Charpentieri* (Hagen) - Hagen, p. 140-141; pl. 14, fig. 1.
1862 - *Anax Buchi* Hagen - Hagen, p. 143-144 (in 'Calopteryginae', regarded as related to '*Aspasia*' or '*Amphitrite*').
1866 - *Anax Buchi* Hagen - Hagen, p. 82-96; pl. 3, fig. 2. (regarded as conspecific with *A. charpentieri*).
1890 - *Cordulegaster Dresdensis* Charpentier - Kirby, p. 171.
1897 - ? *Cordulegaster intermedius* Hagen - Meunier, p. 1; pl. 7, fig. 8.
1906 - (? *Stenophlebia*) *Buchi* (Hagen) - Handlirsch, p. 584. (in 'Anisozygoptera' *incertae sedis*)
1906 - *Aeschnogomphus Charpentieri* (Hagen) - Handlirsch, p. 590 (new genus name).
1934 - *Aeschnogomphus charpentieri* (Hagen) (= *Aeschnogomphus dresdensis* (Charpentier 1849)) - Cowley, p. 249 (subsequent designation as type species of *Aeschnogomphus*).
1979 - *Aeschnogomphus intermedius* - Malz and Schröder, p. 9, fig. 1.
1992 - *Aeschnogomphus charpentieri* (Hagen) - Carpenter, p. 81; fig. 50, 7.
1992 - *Aeschnogomphus charpentieri* (Hagen) - Nel and Paicheler, p. 310.
1994 - *Anax buchi* Hagen - Bridges, p. VII.39 (in *Stenophlebia*?).
1994 - *Aeschnogomphus charpentieri* (Hagen) - Bridges, p. VII.48.
1994 - *Aeschnogomphus dresdensis* (Charpentier) - Bridges, p. VII.73.
1996 - *Aeschnogomphus charpentieri* (Hagen) - Bechly, p. 16, 380 (in Aktassiidae).

Holotype: Charpentier (1840: 180) did not describe and gave no formal name to this species in his paper written in Latin. His 'name' '*Libellulita dresdensis*' is just a descriptive term for a fossil dragonfly in the collection of the Museum in Dresden, and not intended as a formal taxonomic name, as already correctly recognized by Handlirsch (1906), *contra* Bridges (1994) who erroneously regarded '*Aeschna*' (sic) *dresdensis* Charpentier 1840 as a valid name. Thus, the first available name is that of Hagen (1848). Charpentier and Hagen (1848: 12) indicated that the holotype is located in the Museum of Dresden (maybe the plate is still there). The counter-plate is specimen [MCZ 6176] in the collection of the Museum of Comparative Zoology (Harvard University, Cambridge). Hagen (1866: 95) recognized that his species '*Anax charpentieri*' Hagen 1848 is synonymous to '*Anax buchi*' Hagen 1848, which was published in the same paper, and used the latter name for this species. Our study of both holotypes confirmed their conspecific status (the holotype of *A. buchi* is specimen [MB.J. 841 a,b] in the Natural History Museum in Berlin). According to the 'principle of the first reviser' (Art. 24 IRZN) Handlirsch (1906) designated *A. buchi* as the valid name and *A. charpentieri* as invalid subjective synonym.

Stratigraphic level: Upper Jurassic/Malm zeta/Tithonian, Lithographic Limestone.

Type locality: Solnhofen/Eichstätt, Bavaria, Germany.

Further material: Charpentier's (1840) figure of the type is not precise. Later, Hagen (1862: 140) described a specimen from the Krantz collection in Bonn. Meunier (1897: 11, pl. 7, fig. 8) figured a specimen from the Musée Teyler (Haarlem) which he named *Cordulegaster intermedius* Hagen, but he also indicated the presence of specimens that he named *Cordulegaster intermedius* Deichmüller. Handlirsch (1906: 590) synonymised *Cordulegaster intermedius* Hagen *sensu* Meunier (1897) with *Aeschnogomphus charpentieri*. The specimen figured by Meunier (1897)

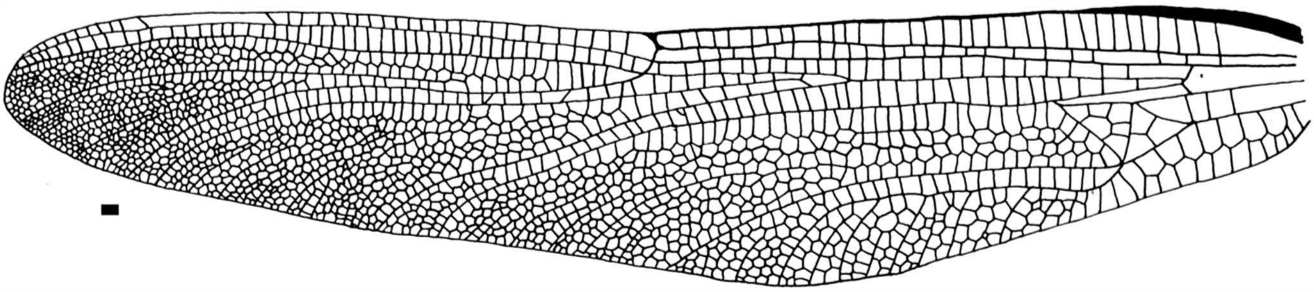

Fig. 54 - *Aeschnogomphus buchi* (Hagen 1848), specimen [9-6, Malm Ú 2] Jura-Museum Eichstätt, forewing. Scale bar represents 1 mm.

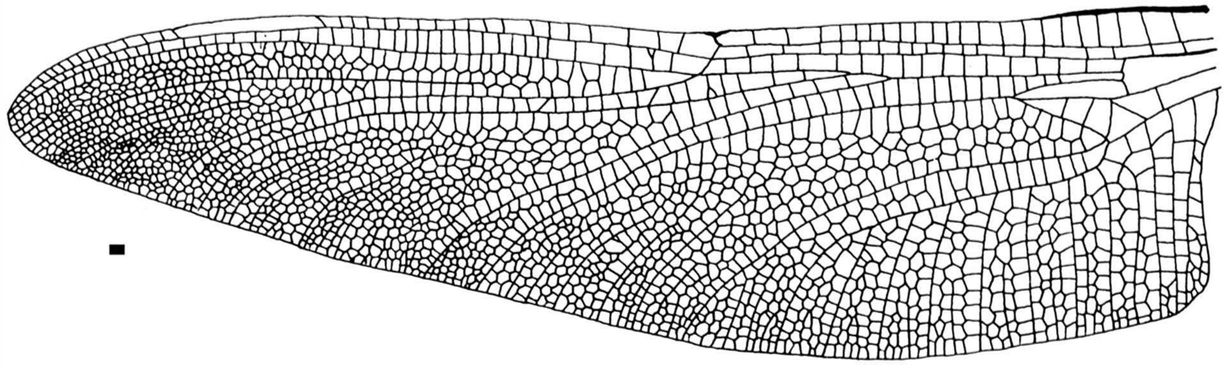

Fig. 55 - *Aeschnogomphus buchi* (Hagen, 1848), [9-6, Malm Ú 2], left hindwing. Scale bar represents 1 mm.

is in a very poor state of preservation and nearly useless for description.

We studied the following material: specimen [9-6, Malm Ú 2], Jura-Museum, Eichstätt, Germany; specimen [1984. I. 158], Museum of Munich (BSPGM), Germany; specimen [MB.J. 841 a, b], holotype of '*Anax*' *buchi* Hagen 1848, Natural History Museum in Berlin; specimen [MB.J. 1722 a,b] in the same collection; specimen [MCZ 6176], holotype of '*Anax*' *charpentieri* Hagen 1848, Museum of Comparative Zoology (Harvard University, Cambridge).

Descriptions:

(A) Specimen [9-6, Malm Ú 2], Jura-Museum, Eichstätt.

Part and counterpart of a nearly complete and very well preserved specimen with the four wings well displayed, labelled: [ob. Zwicklage] [*Aeschnogomphus intermedius* (*charpentieri* Hagen 1848)]. The specimen was figured in Malz and Schröder (1979: p. 9, fig. 1) under the name *Aeschnogomphus intermedius*.

Forewing: length, 74.3 mm; width, 14.8 mm; width below nodus, 13.6 mm; distance from base to nodus, 36.7 mm; from nodus to pterostigma, 21.3 mm; from pterostigma to apex, 11. 1 mm; from nodus to arculus, 30.2 mm. Pterostigma long and narrow, 8.6 mm long and 0.7 mm wide, basally recessed at about 56 % of distance between nodus and apex, the basal margin being more oblique than the distal one. Its anterior and posterior margins not flattened. Pterostigma covering nine cells. No oblique pterostigmal brace. Postnodal crossveins very numerous (twenty-three to twenty-five), and non-aligned with corresponding postsubnodal crossveins. Nodus normal, with ScP fusing with costal margin at nodus. Subnodus not very oblique. IR1 long, first weakly zigzagged and becoming very straight distally till wing margin. Area between IR1 and RP1 very broad with more than seven rows of very small irregular cells. Area between IR1 and RP2 broader with about twenty rows of cells and three secondary longitudinal veins. RP2 aligned with subnodus. Two oblique crossveins 'O' between RP2 and IR2. Their positions are not very stable because there are six cells between them on the right forewing and only five on the left forewing. First crossvein 'O' about four cells distal of subnodus. One row of cells in area between RP2 and IR2 and distally two and three rows near posterior wing margin. That area is distally widened but less than the area between RP3/4 and MA near wing margin. RP2 and IR2 gently curved and reaching posterior wing margin in a oblique angle. IR2 originating 8.5 mm and RP3/4 10.9 mm basally of nodus. One cell between these veins at their bases. More than eight bridge-crossveins (Bqs) between RP and IR2 basal of subnodus. Many (about twenty-five) crossveins between RA and RP between nodus and arculus and between RP and MA basal of the RP3/4. No Rspl. Area between IR2 and RP3/4 very wide with many small cells and no secondary longitudinal vein. RP3/4 and MA undulate on the level of the two oblique crossveins 'O'. Area between RP3/4 and MA distally greatly widened with about seven rows of cells between these veins along wing margin. No Mspl but only weakly defined secondary veins in postdiscoidal area. Three or four rows of cells in postdiscoidal area distal of discoidal triangle. Postdiscoidal area widened distally with about thirty rows of cells between MA and MP near wing margin. Discoidal triangle very broad, nearly equilateral and divided into five or six cells; the anterior side is 4.2 mm long, the distal side 4.9 mm long and the basal side 3.2 mm long. Hypertriangles and median cells free of crossveins. Submedian cell distally crossed by three

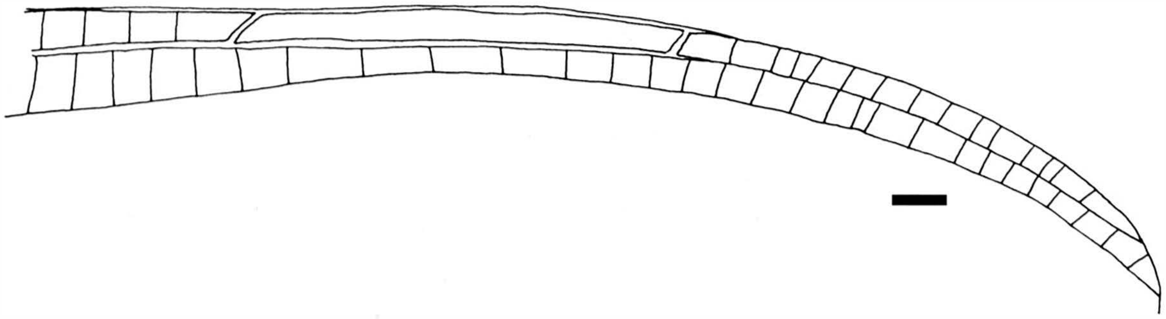

Fig. 56 - *Aeschnogomphus buchi* (Hagen 1848), specimen [9-6, Malm Ú 2], pterostigma, forewing. Scale bar represents 1 mm.

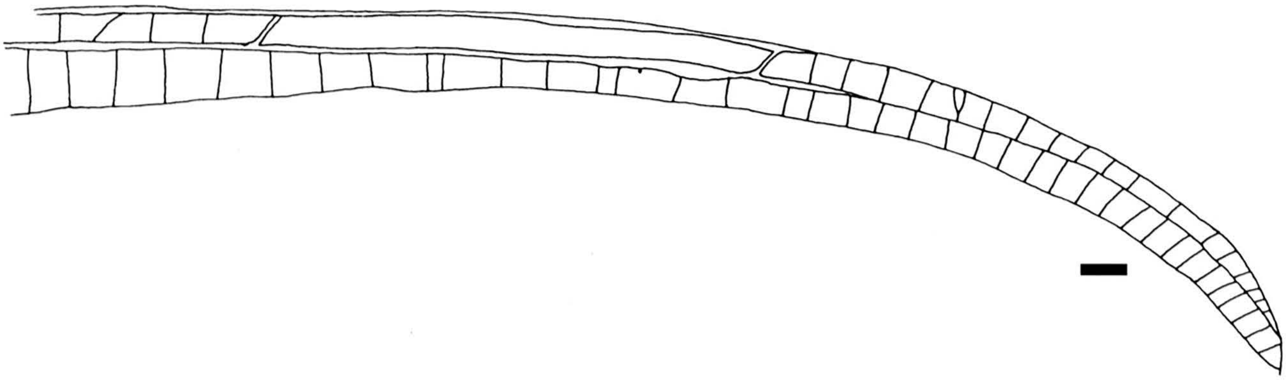

Fig. 57 - *Aeschnogomphus buchi* (Hagen 1848), [9-6, Malm Ú 2], pterostigma, hindwing. Scale bar represents 1 mm.

crossveins, including CuP-crossing which cannot be distinguished from others. A distinct pseudo-anal vein PsA separating submedian cell from a three-celled subtriangle, 4.2 mm long and 2.7 mm wide. Two rows of cells in anal area between base and AAa. MP and CuA separated in posterior angle of discoidal triangle. Area between CuA and MP widened distally near wing margin, with four or five rows of cells near wing margin, just like the area between RP3/4 and MA. MP gently curved. CuA a well-defined eight-branched vein. Branches of CuA parallel and reaching posterior wing margin. Five or six rows of cells in cubito-anal area which is 4.2 mm wide. Arculus angled. More than thirty crossveins in antenodal area. two of secondary antenodal crossveins look stronger than others because they are well-aligned with corresponding crossveins between ScP and RA. Nearly all other antenodal crossveins between ScP and costal margin not aligned with corresponding antenodal crossveins between ScP and RA. Arculus two cells beyond Ax1, about midway between Ax1 and Ax2.

Hindwing: length, 70.7 mm; width, 19.6 mm; width below nodus, 18.3 mm. Distance from base to nodus, 29.2 mm; from nodus to pterostigma, 22.2 mm; from pterostigma to apex, 14.5 mm; from nodus to arculus, 23.4 mm. Pterostigma long and narrow, 8.9 mm long and 0.8 mm wide, basally recessed at about 54 % of distance between nodus and apex. Its basal side is less oblique than its distal one. Anterior and posterior sides not widened. Pterostigma covering ten cells. No oblique pterostigmal brace. Only eighteen to twenty postnodal crossveins, less numerous than in forewing. Corresponding postsubnodal crossveins between RA and RP1 non-aligned with postnodal crossveins. Nodus normal, with ScP fusing with costal margin at nodus. Subnodus not very oblique. IR1 a long vein at first zigzagged for a short distance and then becoming very straight distally till wing margin. Area between IR1 and RP1 very broad with five rows of very small irregular cells. Area between IR1 and RP2 broader with about twenty rows of cells. RP2 aligned with subnodus. Two oblique crossveins 'O' between RP2 and IR2, with seven cells between them. First 'O' three cells distal of subnodus. One row of cells in area between RP2 and IR2 basally and distally two or three rows near posterior wing margin. Area between RP2 and IR2 widened distally but less than area between RP3/4 and MA. RP2 and IR2 gently curved and reaching posterior wing margin obliquely. IR2 originates 7.7 mm and RP3/4 9.9 mm basal of nodus. Five bridge-crossveins (Bqs) between RP and IR2 basal of subnodus. Many (nearly sixteen) crossveins between RA and RP in areas between nodus and arculus and between RP and MA basal of base of RP3/4. No Rspl. A very wide area between IR2 and RP3/4, with many small cells and no secondary vein. RP3/4 and MA somewhat undulate on the level of the two oblique crossveins 'O'. Area between RP3/4 and MA distally greatly widened with about seven rows of cells between these veins near wing margin. No Mspl. Three or four rows of cells in postdiscoidal area distal of discoidal triangle. Postdiscoidal area distinctly widened along wing margin with about thirty rows of cells between MA and MP. Very oblique discoidal triangle longitudinal elongate and distinctly narrower than that of forewing; it is divided into three cells by two parallel crossveins, its anterior side being 5.3 mm long, the distal side 5.4 mm long and the basal side 2.4 mm long. Hypertriangle and median cell free of crossveins. Submedian cell distally tra-

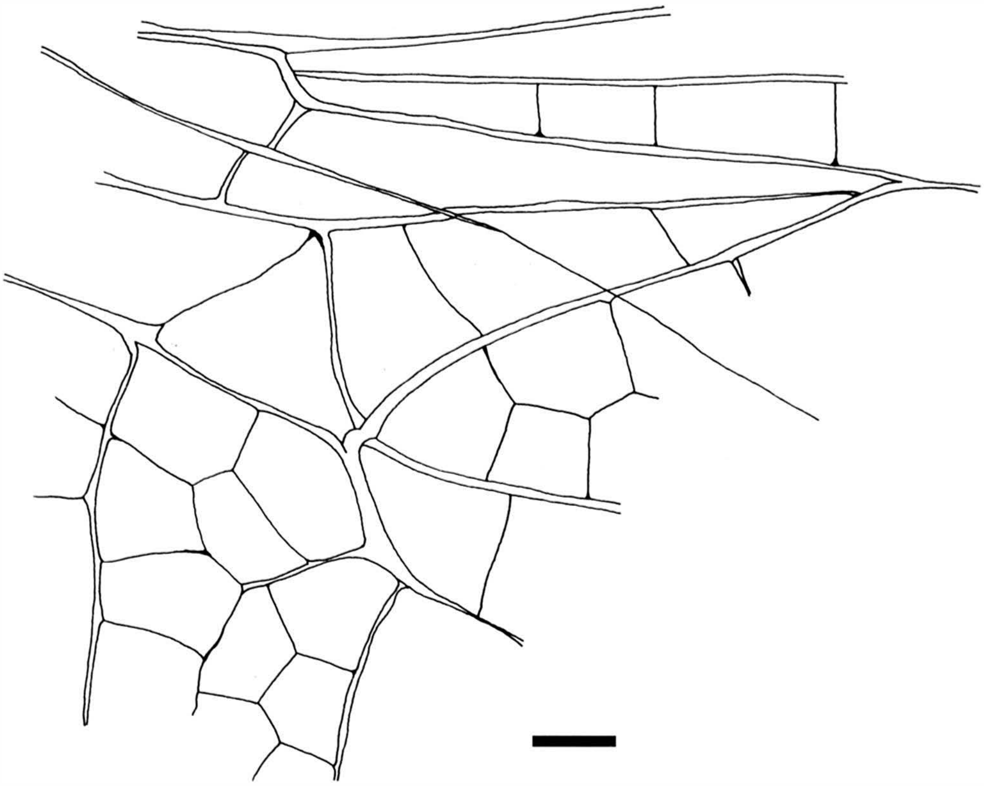

Fig. 58 - *Aeschnogomphus buchi* (Hagen 1848), specimen [9-6, Malm Ú 2], discoidal triangle, right hindwing. Scale bar represents 1 mm.

versed by CuP. A distinct pseudo-anal vein PsA separating submedian cell and a well-defined subtriangle, but PsA and subtriangle less distinct than in forewing. Subtriangle unicellular, 2.5 mm long and 1.7 mm wide. Twelve rows of cells in anal area below AA. Three posterior branches of AA perpendicular to main branch of AA, closely parallel, straight and directed towards posterior wing margin. MP and CuA separated in posterior angle of discoidal triangle. Area between CuA and MP distally widened near wing margin, with ten rows of cells and three secondary veins near posterior wing margin, like in area between RP3/4 and MA. MP gently curved. CuA a well-defined nine-branched vein. Eight distal branches of CuA nearly straight, parallel and reaching posterior wing margin. Nine or ten rows of cells in cubito-anal area, 9.0 mm wide. CuAb directed towards proximo-posterior part of wing. Anal loop vestigial (three-celled and posteriorly open). Arculus less angular than in forewing. About twenty-six antenodal crossveins. Two primary antenodal veins Ax1 and Ax2 stronger than secondaries. Almost all other antenodal crossveins between costal margin and ScP not well-aligned with corresponding antenodal crossveins between ScP and RA. Arculus one cell distal of Ax1, nearer Ax1 than Ax2. Anal wing margin rounded, without any anal angle nor anal triangle, thus it is a female specimen.

Genital organs: two long cerci, 8.3 mm long, rather narrow, nearly four times longer than wide. No visible ovipositor behind tenth abdominal segment.

Abdomen not very well-preserved. The segmentation is not very distinct but it seems that the last segments (seven to nine) are somewhat broader than others.

Head and thorax are not preserved.

(B) Specimen [1984. I. 158, *Aeschnogomphus intermedius*], Museum of Munich (BSPGM).

A nearly complete dragonfly but its wing venation is not very well-preserved. The specimen is labelled as [*Aeschnogomphus intermedius*].

Forewing: length, 79.2 mm; width, 18.0 mm; distance from base to nodus, 45.6 mm; from nodus to apex, 33.6 mm. Hindwing length, 74.4 mm; width, 18.6 mm; distance from base to nodus, 37.2 mm; from nodus to apex, 37.2 mm. The preserved parts of wing venation, especially main veins and discoidal area, are similar to those of specimen [9-6, Malm Ú 2], except for the hindwings bases: there is an anal angle and an anal triangle, similar to those of the specimens figured by Meunier (1898) and Nel and Paicheler (1992: fig. 9). It is thus a male.

Abdomen 75.6 mm long; maximal width, 8.4 mm; minimal width, 4.8 mm. The secondary genital organs of the second abdominal segment are not preserved but those of the tenth segment are clearly visible. Two long and narrow parallel-sided cerci (8.8 mm long and 2 mm wide), twice longer than tenth segment. Also a triangular epiproct (= 'lame supra-anale' *sensu* Aguesse 1968), 2 mm long and 2.5 mm wide, distinctly shorter than cerci.

(C) Specimen [MB.J. 841 a,b], [holotype of *Anax buchi* Hagen], Natural History Museum in Berlin.

This specimen is labelled: [Malm, Solnhofen, coll. L. v. Buch], [? *Stenophlebia Buchi* (Hagen)], [Orig. Erichson (1839: Zur Abbildung der Libelle von Solenhofen. - In: v. Buch, L. (1839): über den Jura von Deutschland. (gelesen 1837). - Abh. kgl. Akad. Wiss. Berlin (für 1837), S. 135, Taf. 3 (*Aescha* oder *Libellula*)], [Orig. Hagen (1866): Pal. XV, Fig. 2 (*Anax*

Buchi)], [Orig. Handlirsch (1906-1908): Die fossilen Insekten ..., S. 584 (? *Stenophlebia*) *Buchi* Hagen]

It is a part and counter-part of a complete specimen, with poorly preserved wing venation, but which clearly belongs to *Aeschnogomphus*. Based on a reexamination of this type of '*Anax Buchi*' Hagen (1966: 39) himself correctly recognised that his earlier opinion that it should be a Calopteryginae (*sensu* Hagen) is wrong, and that the type of his '*Anax charpentieri*' is a male specimen of '*Anax Buchi*'. The body length of this specimen is 96 mm (incl. the elongate cerci). Forewing length 79 mm. Hindwing CuAa with seven posterior branches. A hindwing longitudinal elongate discoidal triangle. RP3/4 and MA somewhat undulate. RP2 and IR2 gently curved, but not undulate. IR1 very long and straight. no Rspl or Mspl.

A further specimen [MB.J. 1722 a,b] of *A. buchi* is in the collection of the Natural History Museum in Berlin. It is a part and counter-part, and labelled [*Aeschnogomphus charpentieri* Hagen, Redenbacher'sche Sammlung]. The hindwing length is 78 mm, and the body length 123 mm (incl. 8 mm anal appendages).

Specimen [MCZ 6176], [holotype of '*Anax*' *charpentieri* Hagen], Museum of Comparative Zoology (Harvard University, Cambridge).

In the collections of MZC, we found the counterpart of the holotype of '*Anax*' *charpentieri*. It is labelled as follows: [MCZ 6176, Coll. Carpenter, Type], [*Anax Buchi* Erichs. mas., Palaeont. X. pl. 14. f. 1 and XV., page 39. N°8 Type, counterpart, Solenhofen, Dr. Krantz], [*Anax Buchii*, Doppelplatte zu *A. charpentieri*, Palaeont. T. X t. 14 f. 1]. Wing length about 80 mm, and preserved characters of wing venation clearly show that it is conspecific with the type of *A. buchi* (Hagen 1848), described above (see: Hagen 1848, 1862, 1866).

Also at MCZ we found a further important specimen of *Aeschnogomphus buchi*, with a forewing 85 mm long. The specimen was described (but not illustrated) by Hagen (1866: 95) and is labelled as follows: [MCZ 6177, Coll. Carpenter, Type],[*Anax Buchi* Erichs., Paleont. XV. p. 39., No. 22. Type, Solenhofen, Dr. Krantz].

Aeschnogomphus intermedius (Münster *in* Germar 1839)

1839 - *Aeschna* [sic] *gigantea* (*intermedia*) - Münster *in* Germar, p. 216; pl. 23, fig. 13.
1848 - *Anax intermedius* (Germar) - Hagen, p. 10.
1850 - *Anax intermedius* (Germar) - Selys-Longchamps, p. 361.
1862 - *Anax intermedius* (Germar) - Hagen, p. 142.
1869 - *Petalura intermedia* (Germar) - Weyenberg, p. 251.
1886 - *Cordulegaster* (?) *intermedius* (Münster) - Deichmüller, p. 45-4; pl. 4, fig. 7.
1898 - *Cordulegaster intermedius* Münster - Meunier, p. 119; pl. 5, fig. 11.
1906 - *Aeschnogomphus intermedius* (Hagen) - Handlirsch, p. 590; pl. 47, fig. 11-12.
1932 - *Aeschnogomphus intermedius* (Hagen) - Carpenter, p. 114; fig. 8. (new figure; in Cordulegasterinae).
1979 - *Aeschnogomphus intermedius* (Hagen) - Malz and Schröder, p. 42-43; fig. 25.
1985 - *Aeschnogomphus intermedius* (Hagen) - Ponomarenko, p. 136.
1992 - *Aeschnogomphus intermedius* (Hagen) - Nel and Paicheler, p. 310.
1994 - *Aeschnogomphus intermedius* (Münster) - Bridges, p. VII.118.
1994 - *Aeschnogomphus intermdius* (sic) (Hagen) - Bridges, p. VII.117.

Holotype: specimen AS VII 795 labelled [orig. Germar 1837, taf. 23, fig. 13], collection of the Museum of Munich (BSPGM). The holotype is a very poorly preserved specimen. Only the main veins of the wings are more or less visible and the venation is nearly useless because the crossveins are not preserved. The body is also of little use and the head is not preserved. Deichmüller (1886: 47) attempted to compare his material with the holotype described by Germar (1839). It will probably never be possible to be absolutely certain about the specific identity of the holotype with the better material described subsequently, since the only diagnostic character would be the size.

Stratigraphic level: Upper Jurassic/Malm zeta/Tithonian, Lithographic Limestone.

Type locality: Solnhofen/Eichstätt, Bavaria, Germany.

Specific differences between *A. intermedius* and *A. buchi* (= *A. charpentieri*): Hagen (1862: 140) indicated that the hindwing of *A. charpentieri* is 75 mm long. Handlirsch (1906: 590) considered that *A. charpentieri* would be characterized by a wing length between 76 and 80 mm and that *A. intermedius* would be characterized by a wing length between 90 and 95 mm. The wings of the holotype specimen AS VII 795 of *A. intermedius* are 88 to 90 mm long. The wings lengths of the specimen figured in Meunier (1898) under the name *C. intermedius* are unknown because Meunier neglected to give any scale or dimensions. Carpenter (1932: 114) mentions five specimens in the collection of the Carnegie Museum (nos. 3822, 3821, 5111-5112, 5113, and 1221) and one fine specimen [MCZ 1997] in the collection of the Museum of Comparative Zoology (Harvard University, Cambridge). We did not find the latter specimen at MCZ, but two specimens of *Aeschnogomphus spec.* without number. Anyway, Carpenter (1932: 114) indicated that the forewing lengths of the specimens of *A. intermedius* that he examined were between 90 and 95 mm. Malz and Schröder (1979: fig. 25) figured the photograph of an remarkably well-preserved male specimen whose forewing length is 95 mm and hindwing length 88 mm (specimen [ASV 38], Museum of Munich (BSPGM)). The forewings of the specimen MNHN-LP-R. 54379 in the Muséum national d'Histoire Naturelle (Paris) described by Nel and Paicheler (1992: 310-314, fig. 5-8) and tentatively placed near the genus *Aeschnogomphus*, are 95 mm long and the hindwings are 86 mm long.

We found four specimens in the collection of the Natural History Museum in Berlin: [MB.J. 1649] with a forewing length of 96 mm; [MB.J. 1651 a,b], Coll. Kaufmann (leg. Kaufmann 1974), hindwing length 88-89 mm; [MB.J. 1744], received in exchange 1901, forewing length 91 mm, hindwing length 86 mm, body length (incl. head and appendages) 125 mm; [MB.J. 1745], Coll. Kaufmann (right wing pairs supplemented by a cast 7.2.53), forewing length 94-95 mm, hindwing length 88 mm, body length 123 mm, hindwing with much more elongate and narrow discoidal triangle and much less distinct subtriangle and PsA than the forewing. We also found two further specimens in this collection, but these are two badly preserved to allow a specific attribution: [MB.J. 1723], only a large body fragment, but with the distinct anal appendages of *Aeschnogomphus*; [MB.J. 1724].

The specimen R. 54379 and the specimens figured by Meunier (1898) and by Malz and Schröder (1979) differ from the material described and figured by Carpenter (1932) in the presence of a crossed discoidal triangle and the absence of any antenodal crossveins basal to the primary Ax1 (Nel and Paicheler 1992: 314). The specimen [9-6, Malm Ú 2], although smaller than the preceding material, also shows the same differences compared with Carpenter's figure. The figures of Deichmüller (1886) and Handlirsch (1906-1908) are useless for solving this problem because they are not precise enough. Hagen's (1862: pl. 14, fig. 1) illustration of *A. charpentieri* shows a crossed hindwing discoidal triangle and no antenodal crossveins basal of Ax1.

Is the material figured by Carpenter a different species from the already known two spp. of *Aeschnogomphus* , or is Carpenter's figure imperfect? Unfortunately we did not find Carpenter's specimen [MCZ 1997] in the collections of MCZ. This problem remains unsolved and the attribution of new material to a definite species of *Aeschnogomphus* is rather uncertain and mainly based on the wing dimensions. At least it can be regarded as very unlikely that a single species has wing lengths variable between 75 mm and 96 mm, since something similar does not occur in any known extant species. A potential wing venational character that could differentiate *A. buchi* and *A. intermedius* might be the anal area of the forewing: this area has basally three rows of cells and two rows of cells beneath the discoidal triangle in *A. intermedius* (see: Malz and Schröder 1979: fig. 25); but it has basally two rows of cells and only one row of cells beneath the discoidal triangle in *A. buchi* (see: Plate III, fig. 1; also see Malz and Schröder 1979: fig. 1).

Systematic position of *Aeschnogomphus*:

Sexual dimorphism: specimen [9-6, Malm Ú 2] is obviously a female because of the lack of the anal angle and anal triangle on the hindwings. The specimen of *Aeschnogomphus* sp. figured by Meunier (1898) from the Museum of Munich (BSPGM) (Nel and Paicheler 1992: fig. 9) and the specimen [1984. I. 158] have an anal angle and anal triangle. These structures are characteristic for male ['anisozygopteres' + Anisoptera] (Nel *et al.* 1993) except for a few Euaeshnida (Anactina), the Anauriculida (*Hemicordulia* + Macrodiplacidae + Libellulidae) and one genus of Cordulegastrida (*Anotogaster* Selys 1854; see Fraser 1929; Lohmann 1992), and most probably the Aeschnidiidae (Nel and Martínez-Delclòs 1993). Therefore the absence of these features in specimens of other taxa can be regarded as diagnostic for female specimens, namely specimen [9-6, Malm Ú 2] and also specimen MNHN-LP-R. 54379 studied by Nel and Paicheler (1992).

Female genitalia and appendages: the female specimen R. 54379 lacks any preserved genital organ at the end of the abdomen. Specimen [9-6, Malm Ú 2] has no hypertrophied ovipositor longer than the tenth abdominal segment, which is a plesiomorphic condition relative to the hypertrophied ovipositors of extant Cordulegastrida (Fraser 1929).

The hypertrophied ovipositor, although a derived character, is present in some other Anisoptera which are not directly related to the Cordulegastrida: the fossil Aeschnidiidae but also some Synthemistidae and Libellulidae like *Sympetrum Cordulegaster* or *Uracis ovipositrix* (Kennedy 1917: 519, fig. 144), the Mesozoic Tarsophlebiidae (Nel *et al.* 1993). The female of the Upper Jurassic Zygoptera: Steleopteridae have similar hypertrophied ovipositors (Nel, unpubl. pers. obs.). This derived structure has clearly been developed by convergence in at least five different groups and its phylogenetic value is less important than previously supposed. Nevertheless, its absence in *Aeschnogomphus* does not prove that it could not be related to the Cordulegastrida.

The female cerci are different from those of extant Petalurida, which are very wide and spinose, but are similar to those of many female Euaeshnida, which could of course also be a convergence or even a symplesiomorphy.

Male appendages: the male specimen [1984. I. 158] from Museum of Munich (BSPGM) is the first described one which has sufficiently well-preserved male appendages of the tenth abdominal segment. These structures are different from those of the male of the extant species of Cordulegastrida because the cerci lack any spine and are very long, more than three times longer than the epiproct which is triangular not truncate in shape (Fraser 1929; Aguesse 1968; Carle 1983). The male cerci are also very different from those of extant Petalurida which are very wide and spinose. Most probably this type of cerci represents an autapomorphy that is correlated with the large size of this taxon (difficulty of a stable tandem formation).

The genital appendages of *Aeschnogomphus* appear of little use because they represent either plesiomorphic or autapomorphic conditions within Petalurida or Cordulegastrida. The very long female and male cerci look like those of some Euaeshnida (*Aeshna* spp. for example). The polarity of the character (cerci three times longer than epiproct) is still somewhat uncertain, although it rather seems to be a plesiomorphic state, regarding its occurrence in Gomphides and Euaeshnida, but also in Isophlebioptera and Heterophlebioptera, the sister-group of Anisoptera (Nel *et al.* 1993, pers. obs.).

The other body characters (thorax, head) are not sufficiently known and of little use, except for the eyes, which seem to be distinctly separated, like in Petalurida, but unlike Cordulegastrida.

Venational characters: Nel and Paicheler (1992: 314) considered that *Aeschnogomphus* could be related to the Petalurida (called by them Petaluroidea) rather than to Cordulegastrida on the basis of two venational characters: the pterostigma is somewhat basally recessed, very long and narrow (possible apomorphy of the Petalurida); no Rspl and Mspl. The latter character is of little use because it is probably symplesiomorphic. Further similarities are: presence of two oblique crossveins 'O', contrary to Cordulegastrida, but this is a symplesiomorphy too, since present in numerous basal Anisoptera (Aeschnidiidae, Mesuropetalidae, Cymatophlebiidae); presence of a well-defined and broad three-celled subtriangle in the forewing. This last character is also visible in the Miocene genus *Miopetalura* whose position is rather uncertain. This character is obviously correlated with a transverse forewing discoidal triangle and might be a ground-plan character of Anisoptera, since it is also present in Liassogomphidae, Aeschnidiidae, Mesuropetalidae, basal Gomphides (Lindeniidae), many 'corduliids', Macrodiplacidae and Libellulidae. However, several apomorphic characters indeed suggest a relationship with Petalurida: Bridge-space (Bqs-area) relatively narrow (not present in the Cordulegastrida); a straight long IR1 well basal of pterostigma (not present in the Cordulegastrida); very elongate pterostigmata; large wings with numerous cells. The lack of any division of IR2 into two branches is a plesiomorphic condition present in the Petalurida and *Aeschnogomphus*. In Cordulegastrida, IR2 is more or less bifurcate. The lack of any oblique pterostigmal brace is a derived similarity with Cordulegastrida, but very homoplastic since also realised in some Aeschnidiidae, Chlorogomphida, 'corduliids', and Libellulidae. All the other extant and fossil Petalurida, except *Aktassia*, have a oblique pterostigmal brace. But the convergent development of this character in several groups of Anisoptera suggests that this could also have occurred in the Petalurida. In this taxon, the pterostigmal brace is more or less basally recessed, and its position is varying in different genera. Thus, this character, which could suggest a relationship between *Aeschnogomphus* and Cordulegastrida, is probably the result of convergence. Some Cordulegastrida still show a oblique pterostigmal brace, e.g. *Neallogaster luniferus*. *Neallogaster* differs greatly from *Aeschnogomphus* in other venational characters and is very probably not related.

Aeschnogomphus shares with Petalurida at least four apomorphic venational characters, but only one with Cordulegastrida. Furthermore there are several potential synapomorphies with *Aktassia*, within Petalurida - Aktassiidae (see above). Therefore, the attribution to the Petalurida (or more precisely to the stem-group of extant Petaluridae) is the most probable hypothesis, and this is confirmed by our phylogenetic analysis below. The presence of another petalurid, *Protolindenia wittei* (Giebel 1860) contemporary with *Aeschnogomphus* spp., shows that the petalurid lineage was already well-established by the Late Jurassic.

CLADISTIC ANALYSIS OF PETALURIDA

Cladistic analysis

The present phylogenetic analysis is based on the methods of Phylogenetic Systematics as described by Hennig (1966) and Ax (1987). We first performed a numerical cladistic analysis, and than critically re-evaluated the evidence for all clades on the basis of an appropriate character weighting (using criteria like compatibility and complexity), because we completely agree with the general critic of socalled 'computer cladism' by Wägele (1994) and Boricki (1996). We selected 52 morphological characters of 16 taxa and performed a parsimony analysis with the computer-software PAUP 3.1 and MACCLADE 3.0. The characters were equally weighted, and not treated as irreversible; the multistate characters were treated as ordered (for a theoretical justification see Lipscomb 1992), except character '45' (shape of male epiproct, unordered). The 'heuristic' search option of PAUP (heuristic search options: general: minimal trees only, collapse zero-length branches; starting trees: get by stepwise addition, swap on minimal trees only; stepwise addition: closest; branch swapping: nearest-neighbour interchanges, save all minimal trees - mulpars, steepest descent) has been used to calculate unrooted most parsimonious trees (MPT's). The resulting 3 MPT's have been a posteriorly rooted with an all-zero-outgroup (Lundberg-rooting with a hypothetical ancestor = hypanc) and a semistrict and majority rule consensus (50 %) were calculated, which

Table 1 - Data matrix of the cladistic analysis of the genera of Petalurida.

Taxa / characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Petalura	3	1	?	2	2	1	1	0	1	0	2	2	2	0	1	0	2	1	2	0	0	0	2	4
Uropetala	3	1	0	2	2	1	1	0	1	0	1	2	2	0	1	0	2	1	2	0	0	0	2	1
Phenes	2	1	1	1	2	2	1	0	1	1	1	2	2	0	1	0	2	0	2	0	0	0	2	3
Tachopteryx	1	1	1	2	1	1	1	0	1	0	2	2	1	0	1	0	0	0	2	0	0	0	1	2
Tanypteryx	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1
Cretapetalura	2	1	?	1	0	1	1	0	0	0	0	0	1	0	1	0	2	1	1	0	0	0	0	3
Pseudocymatophlebia	2	1	?	?	0	?	?	0	?	?	0	0	0	0	1	0	0	1	1	1	0	0	1	3
Aeschnogomphus	3	2	?	2	0	1	?	1	1	1	0	1	1	0	1	0	0	1	1	1	0	0	1	1
Aktassia	3	2	?	?	?	1	?	0	0	0	0	0	2	0	1	0	?	?	?	1	0	0	1	?
Protolindenia	0	1	?	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1
Mesuropetala	0	1	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Aeschnopsis	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	0	1	0	0	?	1	?	?
Pritykiniella	1	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	?	?
Kazakhophlebiella	0	1	?	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Cymatophlebiella	0	1	?	?	?	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	?	?
Cymatophlebia	2	1	?	2	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0	2	2	0	0
Austropetalia	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

had an identical topology. A priori weighting of certain morphological characters (characters '16', '18', '36', '39', '42', '45', and '48') with double weight did not change the result. A posteriori successive re-weighting (5 times) using the Retention Index RI as measure of best fit (base weight = 1000) also gave the same result concerning all relevant taxa. The position of the dubious fossils *Pritykiniella* gen. nov., *Kazakhophlebiella* gen. nov., *Cymatophlebiella*, *Aeschnopsis* (= *Cymatophlebiopsis*, new synonymy) could not be resolved unambiguously; therefore they have been omitted from the further considerations and regarded as Anisoptera *incertae sedis*. After exclusion of the uninformative characters '14', '25' and '41', the presented cladogram does have a step-length = 133, a Consistency Index CI = 0.59 and a Retention Index RI = 0.58. When certain wing venational characters that have been suspected to be very unreliable because they are very simple and rather variable and homoplastic (characters '4', '17', '26', '27', '29', and '35') were deleted too, the resulting values improved significantly (step-length = 104, CI = 0.63, RI = 0.63) which confirms the initial hypothesis that these characters are more affected by homoplasy. Particularly the Petalurida are notorious for their very inconstant and variable wing venational characters, especially of the crossveins (Needham and Westfall 1955: 67; Ray Andress, pers. comm.). Consequently an analysis using only wing venational characters would more likely support a wrong phylogeny than a total evidence analysis, which was preferred by us for this reason, although this has the consequence that the number of missing entries increases significantly for all fossil taxa.

The result of this analysis is supporting our earlier preliminary findings (Nel and Paicheler 1992; Bechly 1993, 1995, 1996) that all fossil taxa that have been previously assigned to the Petaluridae (auct.) are not related to this taxon at all, while several true fossil Petalurida have formerly been classified within Gomphidae (auct.). Concerning the extant Petalurida, the result of the computer analysis would corroborate the traditional classification by Fraser (1957) which was also used in the most recent taxonomic catalogues of the Odonata (Davies and Tobin 1985; Bridges 1994). According to this analysis the Tanypteryginae (*sensu* Fraser 1957; only *Tanypteryx*) and Petalurinae (*sensu* Fraser 1957; all remaining extant petalurids) would seem to be monophyletic, while the Tachopteryginae (*sensu* Fraser 1933; *Tanypteryx* + *Tachopteryx*) and Petalurinae (*sensu* Fraser 1933; all remaining extant petalurids) would have to be regarded as paraphyletic (*contra* Carle 1995: 397). Nevertheless, the phylogenetic relationships of the fossil and extant Petalurida are far from certain. Quite well supported is the basal position of all the fossil taxa in the stem-group of Petaluridae, and the sister-group relationship of *Uropetala* and *Petalura*. Although the present numerical cladistic analysis favours a paraphyly of the remaining petalurid genera, there exists considerable evidence that rather suggests that *Tanypteryx*, *Tachopteryx* and *Phenes* form a clade (characters '3', '18', and especially character '42'), with the latter two genera being sister-groups (characters '39', '48' and '52'). On the other hand, several apomorphic characters are present only in *Tanypteryx* and *Tachopteryx* (characters '1', '28', '31', '36' and '45'), and these two genera were thus regarded as sister-groups by Fraser (1933) and Carle (1995: 397), who regarded *Phenes* as sister-group to the clade [*Petalura* + *Uropetala*]. This relationship of the latter three genera was also suggested by our most parsimonious cladogram, which only differs in the most basal position of *Tanypteryx* instead of a sister-group relationship of *Tanypteryx* and *Tachopteryx*. Although our most parsimonious cladogram is distinctly shorter (ca. ten steps) than the mentioned alternative phylogenies, there is substantial conflicting evidence for which cladistic parsimony alone does not seem to be a very satisfying solution. Many of the characters that support the alternative hypotheses do not represent very strong evidence, since they are either homoplastic characters, reductions, correlated characters, characters of uncertain polarity or characters that are insufficiently investigated, and most of the apparent plesiomorphies of *Tanypteryx* could easily represent reversals that are correlated with a secondarily reduced size. Since there remains strong evidence (e.g. the ventral

25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
0	2	1	0	2	0	0	2	1	1	0	0	1	0	2	1	0	0	1	2	1	1	1	3	1	?	0	?
0	1	1	0	0	0	0	2	2	1	1	0	1	0	0	1	0	0	1	2	1	1	1	3	1	1	0	1
0	1	1	0	1	0	0	2	2	1	1	0	1	0	2	2	1	1	1	1	3	1	0	1	1	1	0	2
1	2	1	1	1	0	1	2	2	1	0	1	1	0	1	1	0	1	1	1	2	1	0	1	1	0	0	2
0	1	0	1	1	0	1	2	2	1	0	1	1	0	0	1	0	2	1	1	2	1	0	2	1	1	1	1
0	1	1	2	1	1	2	1	0	1	0	2	?	0	?	?	?	?	?	?	?	?	?	?	1	0	1	?
1	3	?	?	0	?	0	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	3	2	0	1	0	0	2	1	1	1	0	?	1	?	?	?	?	0	0	?	?	?	?	?	?	?	?
?	?	2	0	?	?	0	2	1	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	3	2	0	1	0	1	0	0	1	1	0	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?
0	1	2	0	1	0	0	0	0	1	0	0	?	0	?	?	?	?	?	2	?	?	?	?	?	?	?	?
?	?	1	0	?	0	0	?	0	?	0	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	1	0	?	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	3	?	?	?	?	0	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	1	0	?	0	0	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	3	2	0	1	1	0	0	0	1	0	1	0	0	?	?	?	?	0	1	0	0	?	?	?	?	?	?
0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

metathoracic tubercle) in favour of a clade [*Tanypteryx* + (*Tachopteryx* + *Phenes*)] instead of a paraphyletic position of these genera, we decided to prefer this hypothesis over the most parsimonious cladogram of the numerical cladistic analysis. A manual evaluation of the character pattern with the program MacClade furthermore revealed that the putative sister-group relationship of *Cretapetalura* and all extant Petalurida, which resulted from the PAUP-analysis, is not supported by any convincing synapomorphies although clearly favoured by the parsimony algorithm. Since there is some evidence (e.g. character '32', state 2) that rather supports a sister-group relationship of Aktassiidae and all extant Petalurida, we decided to correct this discrepancy in our presented phylogenetic tree and the referring phylogenetic classification. The resulting phylogenetic tree of Petalurida (Fig. 59) is completely compatible with the proposal of Bechly (1996). We amended this phylogenetic tree and classification by the new stem-group petalurid *Pseudocymatophlebia hennigi* gen. nov. et sp. nov., in a new subfamily within Aktassiidae. The remaining uncertainties concerning the phylogenetic relationships within Petalurida might be solved by the future discovery of new characters with sufficient complexity and the functional analysis of more characters as base for an adequate character-weighting.

Character listing

(1) wing length smaller than 50 mm, wings not falcate = 0;

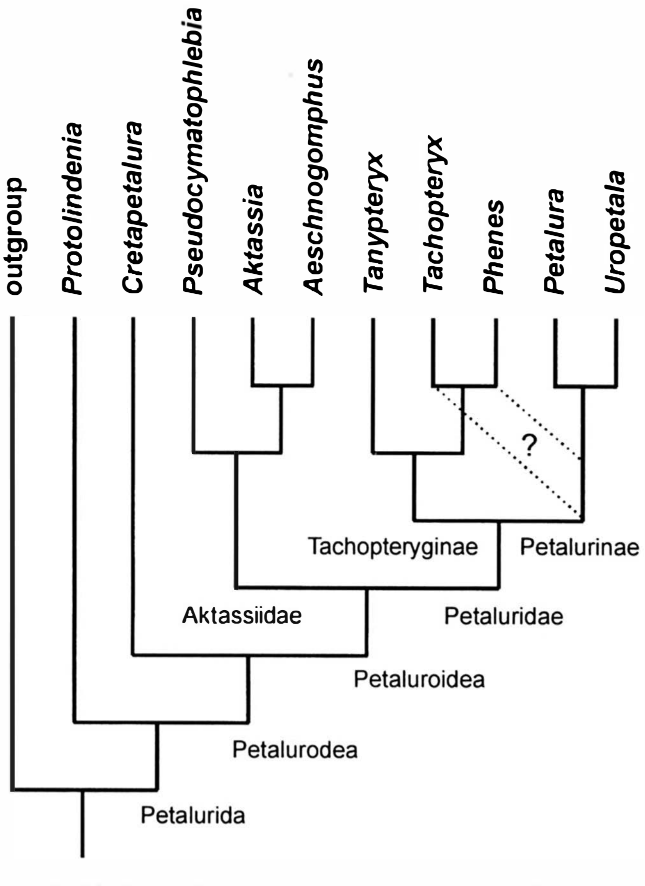

Fig. 59 - Phylogenetic tree of fossil and extant Petalurida.

wing length somewhat bigger than 50 mm, wings falcate and slender = 1;
wing length bigger than 50 mm, wings falcate and very slender =2;
wing length bigger than 65 mm, wings falcate and very slender = 3.

(2) number and density of cells in both wings is
not unusual = 0;
distinctly higher than normal = 1;
extremely high = 2

(3) the spines on the wing veins, especially the main longitudinal veins, are
normal = 0;
distinctly stronger than in other Anisoptera = 1.

(4) in the forewing the two primary antenodal crossveins between costal margin and ScP are separated by
two or three secondary antenodals = 0;
four or five secondary antenodals = 1;
five or six (rarely seven) secondary antenodals = 2.

(The polarity of this character is somewhat uncertain and it is very variable, especially within *Tanypteryx*).

(5) in the forewing the antenodal area is not shorter than the postnodal area = 0;
the forewing antenodal area is slightly shorter than the postnodal area = 1;
the forewing antenodal area is distinctly shorter than the postnodal area = 2.

(This character is synonymous with the character 'relative position of the nodus distal or basal of 50 % of the wing length'.)

(6) the postnodal area of both wings is
normal (not narrowed) = 0;
very narrow, with many cells distal of the pterostigma = 1;
very narrow, with many cells distal of the pterostigma and a pseudo-ScP is present = 2.

(7) the relative position of the pterostigmal brace is
at much more than 75 % of the wing length = 0;
at much less than 75 % of the wing length = 1.

(The position of the pterostigmal brace midway between the nodus and the apex is a synapomorphy of all Petalurida which is convergently present in some Aeschnidiidae, *Hoyaeshna cretacica* and Anactina. The character combination in stem-group petalurids *Protolindenia* and *Cretapetalura* suggests that this basal shift of the pterostigmal brace has been the primary cause of the successive secondary elongation of the pterostigma which seems to have followed its brace with its basal margin, while its distal margin remained static, contrary to Fraser (1957: 94). This character state in *Aeschnogomphus* is unknown because the pterostigmal brace is secondarily absent in this taxon. In the austropetaliid *Hypopetalia* the pterostigmal brace is also shifted somewhat basally of the pterostigma, but is still situated in a very distal position in the wing.)

(8) the pterostigmal brace is
present and distinct = 0;
absent or indistinct = 1.

(9) the relative position of the basal margin of the pterostigma is
at much more than 75 % of the wing length = 0;
at much less than 75 % of the wing length = 1.

(10) the relative position of the distal margin of the pterostigma is
at more than 85 % of the wing length = 0;
at less than 85 % of the wing length = 1.

(11) the relative length of the pterostigma is
normal (less than 11 % of the wing length) = 0;
long (ca. 12-17 % of the wing length) = 1;
very long (ca. 18-20 % of the wing length) = 2.

(12) the pterostigma of both wing pairs are
not significantly elongated and narrow (less than 9 times longer than broad) = 0;
very elongated and narrow (10-12 times longer than broad) = 1;
extremely elongated and narrow (12-16 times longer than broad) = 2.

(This character is not identical with the preceding character.)

(13) IR1 in both wing pairs is
basally not well-defined, i.e. a more or less zigzagged vein = 0;
a well-defined, less zigzagged and rather long vein = 1;
a very well-defined, straight and long vein = 2.

(14) at least in the forewing, RP2 is
distinct and straight = 0;
distally indistinct and zigzagged = 1.

(State 1 is an unique autapomorphy of *Kazakhophlebiella*.)

(15) especially in the forewing, the area between RP1 and RP2 is
not expanded (not more than 8 or 9 rows of cells) = 0;
very expanded (many more than 8 or 9 rows of cells) = 1.

(16) the longitudinal RP2 and IR2 are
parallel and rather straight, the area between RP1 and RP2 is not narrowed = 0;
more or less parallel but RP2 is distinctly undulate and the area between RP1 and RP2 is basally narrowed = 1.

(State 1 is an apomorphic ground-plan character of Aeshnoptera, see Bechly (1996) and Bechly *et al.*, in prep.)

(17) the position of the true basal oblique crossvein 'O' is usually
distal of the subnodus (separated by two cells or more) = 0;
closer to the subnodus (separated by *ca.* 1.5 cells) = 1;
very close to the subnodus (separated by only one cell) = 2.

(State 2 is a rather variable character, especially within the genera *Tanypteryx* and *Tachopteryx*).

Table 2 - Relative positions of the stigmal margins and the stigmal braces in some Anisoptera genera. the percentages are relative to the whole wing length; fw: forewing; hw: hindwing; bas. stigm. margin: basal stigmal margin; dist. stigm. margin: distal stigmal margin.

Taxon	**stigmal brace**	**bas. stigm. margin**	**dist. stigm. margin**	**stigma lenght/width**	**stigma length in %**
Phthitogomphus angulatus	78% / ?	80% / ?	89% / ?	04,5*	09,5% / ?
Aeschnidium densum	73% / 73%	73% / 73%	83% / 84%	04,0*	09,5% / 10,0%
Aktassia magna	? / 78%	? / 78%	? / 88%	06,0*	? / 10,5 %
Aeschnogomphus intermadius	? / ?	76% / 73%	86% / 84%	10,0*	09,5% / 11,0%
Protolindenia wittei	71% / 67%	80% / 78%	88% / 88%	06,5*	07,5% / 10,0%
Cretapetalura brasiliensis	66% / 60%	81% / 75%	88% / 84%	07,0*	07,5% / 09,0%
Tanypteryx hageni	72% / 68%	72% / 68%	87% / 87%	09,5*	14,0% / 17,0%
Tachopterix thoreyi	72% / 68%	72% / 68%	87% / 87%	12,0*	17,0% / 20,0%
Phenes raptor	67% / 63%	71% / 68%	83% / 81%	13,0*	12,0% / 15,0%
Uropetala carovei	70% / 67%	72% / 70%	87% / 85%	15,0*	14,0% / 16,0%
Petalura gigantea	68% / 67%	70% / 68%	88% / 88%	16,0*	18,0% / 21,0%
Mesuropetala koehleri	80% / 76%	81% / 77%	89% / 86%	05,0*	08,5% / 09,0%
Pritykiniella deichmuelleri	? / 78%	? / 79%	? / 91%	06,0*	? / 13,0%
Kazakhophlebiella aktassica	80% / ?	81% / ?	89% / ?	04,5*	09,0% / ?
Cymatophlebiella euryptera	? / 79%	? / 80%	? / ?	?	? / ?
Cymatophlebia longialata	79% / 77%	80% / 78%	89% / 87%	05,0*	09,0% / 10,0%
Austropetalia patricia	85% / 80%	83% / 78%	90% / 88%	06,0*	07,5% / 10,0%
Aeshna cyanea	82% / 81%	83% / 82%	89% / 88%	04,0*	05,5% / 06,5%
Anax imperator	73% / 69%	74% / 70%	85% / 83%	09,0*	11,5% / 13,0%
Sona nectes	77% / 74%	78% / 77%	89% / 88%	07,0*	10,5% / 11,5%
Hagenius brevistylus	79% / 76%	80% / 77%	90% / 89%	06,0*	10,5% / 12,5%
Hameroscopus baissicus	81% / 78%	82% / 79%	92% / 91%	06,0*	09,5% / 11,0%
Cordulegaster boltoni	? / ?	81% / 78%	91% / 90%	09,0*	09,5% / 11,5%
Neopetalia punctata	81% / 80%	80% / 79%	91% / 91%	05,5*	11,0% / 12,0%
Chlorogomphus campioni	83% / 82%	84% / 84%	91% / 90%	05,0*	07,0% / 07,5%
Synthemis claviculata	85% / 84%	86% / 85%	93% / 93%	04,0*	08,0% / 08,5%
Macromia magnifica	84% / 82%	85% / 83%	91% / 89%	03,5*	06,0% / 06,0%
Oxygastra curtisi	83% / 81%	83% / 81%	90% / 88%	04,0*	07,0% / 07,0%
Macrodiplax cora	88% / 86%	87% / 85%	93% / 91%	03,5*	05,5% / 06,0%
Orthetrum brunneum	83% / 81%	82% / 80%	93% / 91%	04,0*	09,5% / 10,5%
Anisoptera	**fw / hw**	**fw / hw**	**fw / hw**	**Ø fw & hw**	**fw / hw**

(18) a distal supplementary well-defined crossvein 'O' between RP2 and IR2 is
missing = 0;
present = 1;
present, plus a third oblique crossvein 'O' = 2.

(The presence of two crossveins 'O' is a symplesiomorphy of the Petalurida, which is absent as an apomorphy in the genera *Tanypteryx*, *Tachopteryx* and *Phenes* (*contra* Tillyard 1922: 2). Two oblique crossveins 'O' are also present in *Aeschnogomphus*, but unfortunately this character state is unknown for *Aktassia*. A second oblique crossvein 'O' is also present probably by convergence ('anisozygopteres') or symplesiomorphy (Anisoptera) in the following fossil 'anisozygopteres' and Anisoptera (Bechly 1995, 1996): *Selenothemis liadis, Oreophlebia lata, Xanthohypsa tillyardi, X. praeclara, Leptaeschnidium latum (and* several other Aeschnidiidae; Nel, unpubl.), *Petalura* (?) *acutipennis, Mesuropetala muensteri, Valdaeshna surreyensis, Cymatophlebia longialata, Cymatophlebia zdrzaleki, Cymatophlebiella euryptera, Pritykiniella deichmuelleri. P. deichmuelleri* even has a third oblique crossvein 'O' between RP2 and IR2 as an unique autapomorphy. Rarely extant Austropetaliida, Euaeshnida and Cordulegastrida also have a second oblique crossvein 'O' as an aberration, but apparently never in all wings (Tillyard 1922: 47). The homoplastic distribution of this character shows that it is not of great phylogenetic significance and because the presence of two oblique crossveins 'O' probably represents a ground-plan character of the Anisoptera (Bechly 1996; *contra* Bechly 1995), the occasional aberrations in extant Anisoptera can easily be explained as atavistic structures.)

(19) the bridge-space (Bqs-area) between RP and IR2 basal of the subnodus is
of normal width = 0;
distinctly narrowed = 1;
extremely narrow (especially in the forewing) = 2.

(20) the veinlets and intercalary veins between RP2 and IR2, IR2 and RP3/4, and MA and MP are
absent or of 'normal' shape = 0;
present and show a characteristic pattern = 1.

(21) an intercalary Rspl in both wing pairs is
absent = 0;
present and parallel to IR2, with one row of cells between the two veins = 1;
strongly curved, with several rows of cells between Rspl and IR2 = 2.

(As Rspl are absent in the Heterophlebioptera, sister-group of the Anisoptera (Nel *et al.* 1993), and many groups of Anisoptera (Liassogomphidae, Gomphides, Cordulegastrida, Chlorogomphida, Neopetaliidae), the Rspl does not seem to belong to the ground-plan of Anisoptera (*contra* Lohmann 1995). It is here interpreted as an synapomorphy of most Aeshnoptera (incl. Austropetaliida and Cymatophlebiidae), which has convergently evolved in Aeschnidiidae and Eurypalpida.)

(22) an intercalary Mspl is
absent = 0;
present (not curved) = 1;
present and strongly curved = 2.

(As Mspl are absent in the Heterophlebioptera, sister-group of the Anisoptera (Nel *et al.* 1993), and many groups of Anisoptera (Liassogomphidae, Gomphides, Cordulegastrida, Chlorogomphida, Neopetaliidae), the Mspl does not seem to belong to the ground-plan of Anisoptera either. Probably it has also convergently evolved in Aeschnidiidae, Euaeshnida and Eurypalpida.)

(23) development of the area between RP3/4 and MA:
in the forewing, the area between RP3/4 and MA is not widened near the posterior wing margin, with less than three rows of cells. Both veins are not distinctly curved distally and MA is only slightly undulate = 0;
in the forewing the area between RP3/4 and MA is somewhat widened near the posterior wing margin, with more than three rows of cells. Both veins are only slightly curved distally and MA is only slightly undulate = 1;
in the forewing the area between RP3/4 and MA is widened near the posterior wing margin, with more than three rows of cells. Both veins are distinctly curved distally and MA is strongly undulate = 2.

(This last character might be very susceptible to homoplasy.)

(24) shape of the discoidal triangle in forewing
the anterior side is longer than the basal side, the discoidal triangle being of similar shape to that of the hindwing = 0;
the anterior side is longer than the basal side but the discoidal triangle is of different shape to that of the hindwing = 1;
the anterior side is about as long as the basal side and the discoidal triangle is of different shape to that of the hindwing = 2;
the anterior side is shorter than the basal side and the discoidal triangle is of different shape to that of the hindwing and transversely elongate = 3;
the anterior side is much shorter than the basal side and the discoidal triangle is of very different shape to that of the hindwing and transversely elongate = 4.

(Maybe an apomorphic ground-plan character of Petalurida, but anyway a very homoplastic character, which is also present in the derived state in *Mesuropetala* (basal Aeshnoptera), most Gomphides and all Eurypalpida. Contrary to the statement of Fraser (1957: 94), the discoidal triangles in fore- and hindwing are dissimilar in all Petalurida except *Uropetala*. In the ground-plan of Anisoptera the forewing discoidal triangles are somewhat more transverse than the slightly longitudinal elongate hindwing discoidal triangles, but this character state seems to be enforced in Petalurida, convergent to Gomphides and Eurypalpida.)

(25) the basal side of the forewing discoidal triangle is
straight = 0;
sigmoidal = 1.

(26) in the forewing the discoidal triangle is usually
free of crossveins (unicellular) = 0;
divided into two cells by a crossvein = 1;
divided into three (or sometimes four) cells by two (or sometimes three) parallel crossveins = 2;
at least divided into three cells by three crossveins that build a 'Ypsilon' = 3.

(A very variable character of low phylogenetic significance).

(27) the hindwing discoidal triangle is usually
free of crossveins (unicellular) = 0;
divided into two cells by a crossvein = 1;
at least divided into three cells by two parallel crossveins = 2.

(Like the preceding character very variable and of low phylogenetic significance, although the free hindwing discoidal triangle seems to be an autapomorphic reversal in *Tanypteryx*, since in the ground-plan of Anisoptera and in all other Petalurida the discoidal triangle is divided.)

(28) the distal side of the hindwing discoidal triangle is
not angular = 0;
angular = 1;
very strongly angular = 2.

(This character is strongly correlated with character 32.)

(29) the forewing subtriangle is
of 'normal' shape and free of crossveins or only two-celled = 0;
somewhat broader and three-celled = 1;
very broad and at least four- or five-celled = 2

(A homoplastic character of low phylogenetic significance. In *Tanypteryx*, the forewing subtriangle is usually three-celled, but rarely two-celled, and the number of cells in *Petalura* is very variable).

(30) the hindwing subtriangle is
of 'normal' shape and free of crossveins = 0;
broader and at least two-celled = 1.

(31) a strong secondary longitudinal vein in the basal part of postdiscoidal area is
absent = 0;
present = 1;
present and very strongly developed = 2.

(This character is strongly correlated with character 29.)

(32) in the hindwing MP reaches the posterior wing margin
distinctly distal of the nodus = 0;
only slightly distal of the nodus = 1;
on the level of the nodus, or even somewhat basally = 2.

(33) development of CuAa in the hindwing:
CuAa is very long, divided into more than five posterior branches and reaches the posterior wing margin on the level of the nodus; the area between CuAa and MP is not significantly widened near the posterior wing margin = 0;
CuAa is shorter, mostly only divided into four to five posterior branches; the area between CuAa and MP is widened near the posterior wing margin = 1;
the hindwing CuAa is much shorter, divided into two or three (rarely four) posterior branches; the area between CuAa and MP is widened near the posterior wing margin = 2.

(The shortening of CuAa is an apomorphic state that convergently evolved in most major clades of Anisoptera, and thus seems to be a general evolutionary trend within Anisoptera. Consequently such a character is other rather low weight for a phylogenetic analysis.).

(34) development of a pseudo-anal vein PsA in the forewings:
no secondary PsA is formed by a specialized crossvein in the submedian area, distally of the CuP-crossing = 0;
a secondary PsA is formed by a specialized crossvein in the submedian area, distally of the CuP-crossing, thus AA is apparently bifurcated, with its secondary anterior branch terminating at the basal edge of the discoidal triangle = 1.

(A distinct PsA is present in Liassogomphidae, Aeschnidiidae, Petalurida, Mesuropetalidae, Austropetaliida (especially *Hypopetalia*), Cymatophlebiidae, basal Euaeshnida ('gomphaeschnine' grade, incl. '*Morbaeschna muensteri*' *sensu* Needham 1907), most Gomphides, some Chlorogomphida (*Chlorogomphus brunneus* Oguma 1926), and in all Eurypalpida. It seems to be correlated with a transverse shape of the discoidal triangle and the character pattern suggests that it belongs to the ground-plan of Anisoptera (Jarzembowski and Nel 1996; Bechly 1996; *contra* Bechly 1995), and is secondarily reduced in a few Gomphides (Hageniidae), most 'derived' Euaeshnida (especially Anactina) and Cordulegastrida because of their longitudinal elongation of the discoidal triangle in both wings.)

(35) in both wing pairs one (or more) supplementary cubito-anal crossvein(s) in the submedian cell between the CuP-crossing and PsA is (are) usually
absent = 0;
present = 1.

(This character is quite homoplastic and variable, especially in the genus *Tachopteryx*, and consequently of low phylogenetic significance.)

(36) the anal loop in the hindwing is
missing or at least posteriorly open = 0;
present and posteriorly closed, but rounded and about as long as broad = 1;
present and posteriorly closed, but elongated (distinctly longer than broad) = 2.

(According to Bechly (1996) an anal loop seems belong to the ground-plan of Anisoptera (*contra* Bechly 1995), because of the presence of an unicellular anal loop in Heterophlebioptera, sister-group of Anisoptera (Nel *et al.* 1993), and because of the presence of a similar anal loop in all major clades of Anisoptera. Within Anisoptera, it obviously has been convergently reduced many times (in Liassogomphidae, Aeschnidiidae, some Gomphides, some 'corduliids' and Libellulidae). The longitudinal elongated anal loop is an autapomorphy of *Cretapetalura*, which is also present in *Aeschnopsis* (= *Cymatophlebiopsis*) and *Necrogomphus jurassicus*, and in Mesuropetalidae. This character could indicate a phylogenetic relationship of some of these taxa, but could also be due to convergence. The number of cells in the anal loop is variable and not of much phylogenetic significance, at least within Petalurida.)

(37) the hindwing membranule is
present and distinct = 0;
present but strongly reduced = 1.

(38) the posterior margin of the hindwing is
distinctly indented at the end of the RP3/4 and MA = 0;
more or less straight between the apex and CuAa = 1.

(39) the pattern of body-coloration is
black and yellow, with well-defined markings = 0;
dark brown and cream coloured, with somewhat less-defined markings = 1;
brown, blackish brown or greyish, with ill-defined markings = 2.

(40) the antero-dorsal surface of the occiput is
flat = 0
distinctly bulged = 1
distinctly bulged, and supplied with two posterior tubercles = 2

(41) lateral spurs at the prealar ridge on the mesothorax are
absent = 0;
present = 1.

(42) the metapoststernum of the metathorax is
normal (flat) = 0;
somewhat expanded and rather hairy = 1;
extremely expanded and very hairy =2.

(The presence of a ventral metathoracic tubercle (Fraser 1933) is an unique and apomorphic character in the genera *Tanypteryx*, *Tachopteryx* and *Phenes* which probably represents a synapomorphy for this group according to Mr. Ray Andress, pers. comm. On the other hand it cannot be excluded that the large metathoracic tubercle of *Tanypteryx* could represent a ground-plan character of Petalurida, while the small tubercle of *Tachopteryx* and *Phenes* could represent an intermediate stage in the reduction of this structure which is finally completely absent in *Petalura* and *Uropetala*.)

(43) the abdomen, especially in the female, is
more or less slender (often basally constricted and distally compressed) = 0;
thick, stout and always cylindrical, without any constriction or compression = 1.

(44) the shape of the male cerci (appendices superiores) is as follows:
cerci of normal shape (not expanded distally) = 0;
cerci at least somewhat foliate = 1;
cerci very foliate = 2.

(45) the shape of the male epiproct (appendix inferior):
epiproct not divaricate = 0;
epiproct divaricate = 1;
epiproct divaricate and distally very broad = 2;
epiproct very wide, much longer than the cerci = 3.

(A divaricate epiproct is also present in *Epiophlebia* and has to be considered as a ground-plan character of Anisoptera, that was convergently transformed into a trifurcate or an unifurcate epiproct several times within Anisoptera, *contra* Lohmann 1995, 1996.)

(46) the female ovipositor is
not strongly curved upwards = 0;
strongly curved upwards = 1.

(47) emergence behaviour is
of 'normal' type, without peculiarities = 0;
highly derived (expansion of the abdomen precedes that of the wings) = 1.

(48) type of larval habitat and tunnelling-behaviour:
aquatic (no semi-terrestrial life and no burrowing in tunnels) = 0;
semi-terrestrial, but without burrowing in tunnels = 1;
semi-terrestrial, with excavation of simple tunnels = 2;
semi-terrestrial, with excavation of complex tunnels = 3.

(The absence of tunnelling behaviour in *Tachopteryx* and *Phenes* seems to be a synapomorphic reversal in these two taxa. Although Winstanley (1982: 304) still regarded the larval behaviour as insufficiently known, the non-tunnelling behaviour of the two mentioned genera seems to be rather certain according to Dunkle (1981:192) and Jurzitza (1989:15). According to Andress (pers. comm.), *Phenes* is now reared in captivity in Argentina and definitely is semi-terrestrial but does not at all burrow tunnels indeed. The character state in *Protolindenia* is unknown but there could be some weak evidence of a possibly aquatic larval lifestyle for *Cretapetalura* if *Nothomacromia sensibilis* (Carle and Wighton 1990) from the Cretaceous of Brazil should represent a cretapetalurid larva, since this fossil larva must have been truly aquatic according to the circumstances of fossilisation in the limestone. However, according to Bechly *et al.* (in press) *Nothomacromia* might be unrelated to Petalurida and could rather represent a member of Sonidae s.str. (see below).)

(49) the side lobes (labial 'palps') of the larval mask
are not expanded, or strongly expanded and distinctly concave = 0;
are somewhat expanded (unique quadrate shape!), a only slightly concave = 1.

(State 1 seems to be a synapomorphy of all extant Petalurida plus possibly *Cretapetalura* if the fossil larva *Nothomacromia sensibilis* should be related to *Cretapetalura*, rather than to Sonidae s.str. The very widened side lobe of the strongly concave mask in the Cavilabiata is really dissimilar and more probably convergently evolved with the only slightly concave mask of the Petalurida. Nevertheless in cannot be ruled out that the larval mask might represent a synapomorphy of Petalurida and the Cavilabiata, although this is strongly contradicted by the evidence that supports a sister-group relationship of Gomphides and Cavilabiata, since all Gomphides still possess the flat plesiomorphic type of larval mask; see below, and see Bechly (1996) and Lohmann (1995, 1996).)

(50) a robust dorso-lateral spur which overlaps the base of the movable hook on the side lobes (labial 'palps') of the larval mask is
absent = 0;
present = 1.

(51) the larval antennae are robust and
seven-jointed = 0;
six-jointed = 1.

(52) paired, hairy, lateral tubercles ('Zottenhöcker') on the larval abdominal segments are
absent = 0;
tufts of stiff setae present, but apparently no tubercles = 1;
comprise setal tufts which are supported by distinct abdominal tubercles = 2.

Type specimens

Since there seems to exist a considerable confusion and lack of information about the deposition of the type specimens of most species of alleged or true Petalurida, we have compiled the following review of the present state of knowledge:

Protolindenia wittei (Giebel 1860) (holotype: apparently lost; neotype designated in this work, specimen [SOS 2043], Jura-Museum, Eichstätt, Germany).

Cretapetalura brasiliensis gen. nov. et sp. nov. (holotype: specimen [i 9562] in the Museo civico di Storia Naturale di Milano, Italy).

Nothomacromia sensibilis (Carle and Wighton 1990) (holotype: in A.M.N.H., New York, U.S.A.).

Aktassia magna Pritykina 1968 (holotype: specimen [PIN 2384/4] in the Palaeontological Institute, Moscow/Russia).

Aeschnogomphus buchi (Hagen 1848) (holotype: specimen [MB.J. 841 a,b] in the Natural History Museum in Berlin, Germany).

Aeschnogomphus charpentieri (Hagen 1848) (invalid subjective synonym of *A. buchi*) (holotype: plate maybe in the Museum of Dresden, Germany; the counter-plate is specimen [MCZ 6176], collection of the MCZ, Harvard University, Cambridge, U.S.A.).

Aeschnogomphus intermedius (Münster *in* Germar 1839) (holotype: specimen [AS VII 795], collection of the BSPGM, Munich, Germany).

Pseudocymatophlebia hennigi gen. nov. et sp. nov. (holotype: specimen [MNEMG 1996. 224 a,b])

Tanypteryx hageni (Selys 1879) (holotype: apparently lost according to Carl Cook (pers. comm.); most probably in the Royal Institute of Natural Sciences Brussels, Belgium, according to Ray Andress pers. comm.).

Tanypteryx pryeri (Selys 1889) (holotype: no information; maybe in IRSN in Brussels, Belgium, according to Mr. Ray Andress, pers. comm.).

Tachopteryx thoreyi (Hagen 1857) (holotype: apparently lost according to Carl Cook (pers. comm.); we did not find it at MCZ, but only the following note in the drawer with *Tachopteryx* [*Tachopteryx thoreyi* Hagen. Type missing? Muttkowski lists it in MCZ. I could not find it. R.W. Garrison 1980]; maybe in IRSN, Brussels, Belgium, according to Mr. Ray Andress, pers. comm.).

Phenes raptor raptor Rambur 1842 (holotype: in private collection of Marchal; the present location of the collection is unknown; Mr. Ray Andress (pers. comm.) supposed it could be in NMNH, Paris, France, but we were unable to find it there).

Phenes raptor centralis Jurzitza 1989 (holotype: in private collection of Dr. Jurzitza, Germany).

Petalura gigantea Leach 1815 (Type: definitely lost; formerly in N.H.M., London, U.K.)

Petalura hesperia Watson 1958 (holotype: in the West Australia Museum, Perth, Australia)

Petalura ingentissima Tillyard 1907 (holotype: in N.H.M., London, U.K.; lectotype designated by Kimmins 1969)

Petalura pulcherrima Tillyard 1913 (holotype: in N.H.M., London, U.K.; lectotype designated by Kimmins 1969)

Uropetala carovei (White 1846) (holotype: in N.H.M., London, U.K)

Uropetala chiltoni Tillyard 1921 (holotype: in New Zealand Arthropod Collection, DSIR, Auckland, New Zealand)

PHYLOGENY AND EVOLUTION OF PETALURIDA

Systematic position of the Mesuropetalidae

Mesuropetala lacks nearly all the autapomorphies of Petalurida, but does have petal-shaped appendices superiores, transverse forewing discoidal triangles and two oblique crossveins 'O' like *Petalura* and *Uropetala*. Nevertheless these characters are not of great phylogenetic significance since they are either symplesiomorphies and/or very homoplastic within Anisoptera. Especially the presence of two oblique crossveins 'O' seems to belong to the ground-plan of Anisoptera since they are meanwhile also known from Aeschnidiidae and Cymatophlebiidae, and several other taxa, including '*Morbaeschna muensteri*' *sensu* Needham 1907 (Euaeshnida). Consequently this symplesiomorphic similarity cannot be used to demonstrate any phylogenetic relationship. The basally narrowed wing area between RP1 and RP2 with only one row of cells represents a relatively strong synapomorphy of *Mesuropetala* and the other Aeshnoptera. Several further characters support this position too (e.g. closely approximated eyes, RP3/4 and MA undulate, etc.), while they contradict a position in Petalurida (Bechly 1996; Bechly *et al.*, in prep.).

Systematic position of the Cymatophlebiidae

Cymatophlebia longialata, which apparently has foliate appendices too, is definitely no Petalurida and has to be classified within a separate family Cymatophlebiidae (Bechly 1993, 1995; Bechly *et al.*, in prep.), which almost certainly has to be included into the Aeshnoptera (also incl. Mesuropetalidae, Austropetaliida, and Euaeshnida). Within the Euaeshnida the Polycanthagynini (*Polycanthagyna spp.*, and probably also including '*Aeshna*' *petalura*, according to G. Peters, pers. comm.) also possess very foliate appendices, like *Mesuropetala* too. According to Bechly (1995) and Lohmann (1996) cymatophlebiids and austropetaliids could be sister-groups, based on the very distal position of the oblique crossvein 'O' and the strongly undulate course of the RP2 (parallel to IR2) as potential synapomorphies. However the interpretation of the former character is rather doubtful, and the homology and polarity of the second character is doubtful too, since an undulate RP2 is present in some basal Euaeshnida (e.g. '*Morbaeschna muensteri*' *sensu* Needham 1907), but also in some Gomphides (e.g. *Cacoides* Cowley 1934) and in several 'derived' Libellulidae (e.g. *Libellula* and *Pantala* Hagen 1861). Therefore Cymatophlebiidae cannot be included in Austropetaliida on the basis of such weak and doubtful evidence (further arguments against this relationship will be presented by Bechly *et al.*, in prep.).

The male Cymatophlebiidae have very strange outgrowths, which are clearly visible on the third abdominal segment of nearly all specimens and on the fourth segment of a recently discovered specimen (Bechly *et al.*, in prep.). These structures of the third and the fourth segments, although superficially similar, are in fact very different of the latero-ventral outgrowths of the abdominal tergum of the second segment at the male secondary genital apparatus of some Austropetaliida (e.g. *Hypopetalia*), also present in some male Macromiidae and Libellulidae. The main difference is that they appear to have been movable, according to their different position in different specimens. Some extant Eurypalpida (*Apocordulia macrops* Watson 1980) have long spinous hamuli on second segment which are extending under the third segment, but these are never so long and they never extend under the fourth segment. Consequently, the abdominal outgrowths of Cymatophlebiidae are not homologous with the hamuli of the second abdominal segment of other male Anisoptera (Bechly *et al.*, in prep.). These structures are autapomorphies of the Cymatophlebiidae and are probably ventro-lateral outgrowths of the abdominal terga, similar but of course not homologous to such outgrowths on the male terminal abdominal segments in some extant Gomphides (e.g. Lindeniinae). The function of these structures remains enigmatic but they were probably related to the mating comportment.

Phylogenetic position of Petalurida within Anisoptera

The Anisoptera constitute one of the best supported monophyla of Odonata (Asahina 1954; Hennig 1981; Trueman 1991, 1996; Pfau 1991; Bechly 1993, 1995; Nel *et al.* 1993; Nel and Martínez-Delclòs 1993; Carle and Louton 1994; Carle 1995; Lohmann 1995, 1996). Within Anisoptera all the taxa that possess a spoon-shaped larval mask (Cordulegastrida, Neopetaliidae, Chlorogomphida, Synthemistidae, 'Gomphomacromiidae', Macromiidae, 'corduliids', Macrodiplacidae and Libellulidae) constitute a well-supported monophylum too (Fraser 1957; Hennig 1981; Bechly 1995; Carle and Louton 1994; Carle 1995; Lohmann 1995, 1996; *contra* Pfau 1991 and Nel and Martínez-Delclòs 1993), which has been named Cavolabiata by Lohmann (1996; based on a suggestion of Bechly) and for which Bechly (1996) proposed the name Cavilabiata. The phylogenetic relationships within Cavilabiata are discussed in Carle (1995), Lohmann (1995, 1996), May (1995, and in prep.), Bechly (1996) and Bechly *et al.* (in press.).

There is some agreement that the fossil Liassogomphidae and Aeschnidiidae might have are more basal position than any extant group of Anisoptera (Handlirsch 1906-1908; Carle and Louton 1994; Carle 1995; Bechly 1995, 1996; *contra* Nel and Martínez-Delclòs 1993) but there is still no strong evidence for this hypothesis.

The biggest problem of Phylogenetic Systematics of Anisoptera remains the question which of the basal extant groups represents the sister-group to all remaining extant Anisoptera. The referring 'candidates' Petalurida (Petaluridae auct.), Aeshnoptera (Austropetaliida and Aeshnidae auct.) and Gomphides (Gomphidae auct.) have been previously united in a paraphyletic superfamily 'Aeshnoidea'. This latter taxon would only be monophyletic if it would be restricted to include only the fossil Mesuropetalidae and Cymatophlebiidae, and the extant Austropetaliida and Euaeshnida (Aeshnidae auct.). A close phylogenetic relationship of Austropetaliida and Euaeshnida is supported by several putative synapomorphies (both discoidal triangles elongate; RP1 and RP2 basally parallel; Rspl present; compound eyes approximated; elongated larval prementum; hamuli posteriores reduced; ligula L-shaped, etc.) (Carle 1995; Bechly 1996; Bechly *et al.*, in prep.; *contra* Lohmann 1995, 1996). The evidence for a position of Cymatophlebiidae within Aeshnoptera is based on some derived wing venational similarities as potential synapomorphies (e.g. presence of a distinct Rspl, and the undulate or curved course of RP2, correlated with a basally narrowed area between RP1 and RP2).

Nearly all possible trees for the basal splitting events within Anisoptera have been previously proposed by different authors and we therefore briefly discuss at least the alternatives that have been based on phylogenetic-systematic reasoning:

A) Heidemann and Seidenbusch (1993: 181) postulated that Euaeshnida (= Aeshnidae auct.) and Gomphides (and probably the Petalurida, that are not mentioned by these authors) together represent the sister-group of all Anisoptera with a spoon-shaped mask (Cavilabiata). They believe that the larval mask of Euaeshnida and Gomphides shows several synapomorphic character states: (1) labial 'palps' reduced in size and situated in the same level as the prementum; (2) indentions along the inner margin of the labial 'palps' reduced; (3) anterior margin of prementum supplied with a fringe of setae; (4) premental setae reduced.

We regard all these character states as symplesiomorphies since this interpretation is strongly supported by an outgroup comparison with *Epiophlebia* and basal Zygoptera. The strong indentions of the labial 'palps' are interpreted by Bechly (1995) as autapomorphy of Zygoptera, that is convergently and quite differently present in Cavilabiata. The presence of premental setae almost certainly represents a multiple convergence of some 'derived' subgroups of Zygoptera with the most 'derived' group of Anisoptera (Cavilabiata).

B) Pfau (1991; followed by Nel and Paicheler 1992) maintained that the Palanisoptera *sensu* Pfau (Aeshnoptera) represent the most basal branch of Anisoptera, while all remaining Anisoptera constitute a monophylum (Neanisoptera *sensu* Pfau) that can be divided into two monophyletic sister-groups, the Petaluroidea *sensu* Pfau (Petalurida + Gomphides + 'cordulegastroids') and the Libelluloidea *sensu* Pfau (Eurypalpida). This hypothesis is solely based on the structure of the male sperm vesicle ('functional penes') and completely neglects the mentioned overwhelming conflicting evidence for a monophyly of all Anisoptera that do possess a spoon-like larval mask (Cavilabiata). Pfau (1991) claimed that only the Palanisoptera retained an open sperm furrow in the sperm vesicle, while all Neanisoptera have closed this furrow and developed a distal sperm chamber. Recently Lohmann (1995, 1996) could demonstrate that a distal sperm chamber is present in Austropetaliida and that the development of the sperm furrow is quite homoplastic, since it was independently closed several times within Petalurida, Euaeshnida, and the 'exophytic' Anisoptera. According to Lohmann (1995, 1996) an open sperm furrow is retained in some Petalurida, all Austropetaliida and many Euaeshnida. We therefore regard Pfau's arguments in favour of a most basal position of Aeshnoptera as unconvincing.

The cladistic analysis of Nel and Martínez-Delclòs (1993) came to no conclusive results concerning the basal branching sequence in Anisoptera, but weakly supported the monophyly of the Petaluroidea (*sensu* Pfau). Nevertheless this analysis was very preliminary and largely based on wing venational characters, that are very liable to homoplasy.

C) Lohmann (1995, 1996) also divided the Anisoptera into Palanisoptera and Neanisoptera, but he restricted the Palanisoptera to include only the Gomphaeschnata and Aeshnata (= Euaeshnida), while he classified his Austropetaliata (= Austropetaliida) as most basal branch of the Neanisoptera. According to this author, the sister-group of Austropetaliata shall be a monophylum called Entoflexata, that contains the Petalurata (Petalurida) and the Exophyticata (Exophytica), which include the sister-groups Gomphata (Gomphides) and Cavolabiata (Cavilabiata). The alleged autapomorphies of Neanisoptera (*sensu* Lohmann). Although we agree concerning the monophyly of his Palanisoptera, Exophyticata and Cavolabiata, we do not believe in the monophyly of his Neanisoptera and Entoflexata. He proposed the following autapomorphies for his Neanisoptera: (1) wing space between AA1b and AA2b (*sensu* Bechly 1995) prolonged; (2) male sperm vesicle with a distal sperm chamber (incl. different structures termed by the author 'bulbus spermalis', 'buccula spermalis' and 'ductus bulbosus') and fused lobes of the terminal segment; (3) adult males with a trifurcate epiproct; (4) larvae with lateral lobes on all segments.

These alleged autapomorphies are dismissed by us for the following reasons: the development of the wing space between AA1b and AA2b is extremely homoplastic and completely useless as character for the reconstruction of the phylogeny within Anisoptera. Furthermore this character seems to have an opposite polarity as indicated by the character state in Liassogomphidae (see: Nel *et al.* 1993). The male sperm vesicle occurs in two different states within Anisoptera (Euaeshnida and all other Anisoptera), but since this character complex is plesiomorphic absent in the outgroup (Zygoptera and *Epiophlebia*) it cannot be polarised with any confidence. A secondary reduction of the mentioned structures in Euaeshnida cannot be excluded and furthermore is strongly suggested by the evidence in favour of a sister-group relationship between Austropetaliida and Euaeshnida (Carle 1995; also see above). Lohmann (1995, 1996) weights the presence of a sperm chamber very high and denies the probability of a reduction in Euaeshnida because he interprets this structure as an advanced device in sperm competition ('sperm aspirator'). We regard this interpretation as not supported by any evidence and speculative. We believe that the removal of foreign sperm is achieved in all Odonata by 'rubbing out' the female spermathecae and bursa with external structures of the functional 'penes' (ligula in Zygoptera, hamuli posteriores in *Epiophlebia*, and vesicula spermalis in Anisoptera), and interpret the sperm chamber as an accessory ejaculatory device (Lindeboom, pers. comm.; also see Carle 1995). The development of the male epiproct is very homoplastic in Anisoptera and an equally parsimonious interpretation (9 steps) is possible if a bifurcate epiproct is assumed in the groundplan of Anisoptera and 'Neanisoptera', which was convergently transformed into a trifurcate epiproct (in Petalurida, Austropetaliida, some Cordulegastrida, Neopetaliidae and some 'Gomphomacromiidae') or unifurcate epiproct (in some Euaeshnida, Synthemistidae and Libellulidae). We therefore dismiss this character as inconclusive. Finally the larval character seems rather dubious since it is very homoplastic (uncertain homology and polarity).

Lohmann (1995, 1996) proposed the following characters as potential autapomorphies of his Entoflexata: (1) different mode of tibial flexion in hind legs ('entoflexate' hind tibiae); (2) presence of a sexual dimorphism in the outer tibial spines on the mid- and hind legs; (3) male sperm vesicle with paired dorsal processes on the third segment, correlated with enlarged female spermathecae; terminal flagellae on the fourth segment of the male sperm vesicle are secondarily absent (only in mentioned in Lohmann 1995); (4) females with a reduced ovipositor, correlated with a non-endophytic oviposition; (5) larvae with a shortened prementum (only mentioned in Lohmann 1995).

These alleged autapomorphies of Entoflexata are also dismissed by us as unconvincing. As already mentioned the polarity of the structures of the male sperm vesicle is unclear because of the absence in the outgroup, thus the petalurid type of sperm vesicle in all Entoflexata could as well be interpreted as symplesiomorphy. The absence of flagellae is an invalid character, since such flagellae are present in most Gomphides (including the very basal Lindeniinae). The reductions in the female ovipositor are quite different in Petalurida than in Exophyticata, since the latter have reduced the metagonapophyses and lost all ovipositor muscles, while the metagonapophyses and all muscles are retained in Petalurida, that do possess a complete ovipositor and only have a somewhat weakened musculature. The exophytic mode of oviposition and the correlated reductions in the ovipositor musculature are easily explained as convergence in Petalurida, since this character complex is tightly correlated with the autapomorphic semi-terrestrial larval habitat (see below). The elongate larval prementum of extant Aeshnoptera is regarded by us as synapomorphy, while the short prementum in other Anisoptera represents a symplesiomorphy. This opposite interpretation of the character polarity is indicated by the shape of the prementum in basal groups of the Calopterygoidea (e.g. Amphipterygidae), Coenagrionoidea (e.g. 'Megapodagrionidae') and the Epiophlebiidae. Furthermore the monophyly of Entoflexata is contradicted by the mentioned evidence for a monophyly of Aeshnoptera (incl. Austropetaliida) and the evidence for a most basal position of Petalurida (see below). In our opinion this conflicting evidence outweighs the only remaining evidence for a monophyly of Entoflexata ('entoflexate' hind tibiae and sexual dimorph tibial spines).

D) In several recent publications by F.L. Carle (Carle 1982, 1986, 1995; Carle and Louton 1994), it was proposed that the Gomphoidea *sensu* Carle (Gomphides) represent the most basal branch of extant Anisoptera, successively followed by the Petaluroidea *sensu* Carle (Petalurida), Aeshnoidea *sensu* Carle (Aeshnoptera), and the Libelluloidea *sensu* Carle (Cavilabiata). We disagree with this phylogenetic position of Gomphides, although we agree with the branching sequence of all other Anisoptera in Carle's phylogenetic reconstruction. Carle (1995) proposed the following synapomorphies for all non-gomphid Anisoptera: (1) proventriculus (gizzard) with denticles grouped posteriorly; (2) sclerotized proventricular lobes mound or tooth-like; (3) larval abdominal segments 4 and 5 secondarily without antero-lateral apodemes; (4) larval second molar segment of mandible with basal articulation lost.

Lohmann (1995, 1996) demonstrated that only the last character is valid, and that this is more parsimoniously explained as autapomorphic reversal in Gomphides. Some basal Euaeshnida (e.g. *Boyeria* and *Caliaeschna*) still have a gomphid-like proventriculus, consequently the proposed synapomorphy does not belong to the ground-plan of non-gomphid Anisoptera. The finger-like larval abdominal apodemes are quite different from the crest-like apodemes in *Epiophlebia* and more probably represent a gomphid autapomorphy, as already indicated by Carle (1995) himself. We completely agree with the referring arguments of Lohmann (1995, 1996), although we do not agree with his alternative phylogeny either (see above).

In the following chapter we explain the reasons why we do regard Petalurida as sister-group of all remaining extant Anisoptera, as suggested by Bechly (1993, 1995, 1996).

Plesiomorphic ground-plan characters of Petalurida

All extant Petaluridae do exhibit a unique set of many plesiomorphic characters, which most probably also represent plesiomorphic ground-plan characters of Petalurida: (1) the pterostigmata are distinctly braced (symplesiomorphy of Petalurida with Aeshnoptera, Gomphides and Neopetaliidae. The pterostigmal brace has been independently reduced in Aeschnidiidae (in part), Cordulegastrida, Chlorogomphida and Eurypalpida); (2) two primary antenodal crossveins ('brackets') are present and distinct from the secondaries, and the two rows of secondary antenodal crossveins are non-aligned (symplesiomorphy of all non-libelluloid Anisoptera); (3) Rspl and Mspl are plesiomorphic absent (symplesiomorphy of Petalurida, Gomphides, Cordulegastrida, Neopetaliidae and Chlorogomphida). A Rspl and Mspl evolved convergently in Aeschnidiidae, Aeshnoptera and Eurypalpida; (4) the hindwing CuA with at least 4 pektinate posterior branches (symplesiomorphy of Petalurida with all non-Eurypalpida within Anisoptera); (5) the arculus is angled and the sectors of the arculus are not stalked because RP and MA have distinctly separate origins at the arculus. A stalked arculus probably evolved four times within Eurypalpida, and a straight arculus evolved convergently in Gomphides, Chlorogomphida and Eurypalpida (Bechly *et al.*, in prep.); (6) the male hindwing has a distinct anal angle, correlated with distinct auricles on the second abdominal segment of the male abdomen (symplesiomorphy of all Anisoptera, convergently reduced in Aeschnidiidae, Anactina (Euaeshnida), *Anotogaster* (Cordulegastrida), and Anauriculida (*Hemicordulia* + Macrodiplacidae + Libellulidae); (7) the compound eyes are widely separated, and an intraocellar lobe is absent (a symplesiomorphy of Petalurida and Gomphides). Approximated eyes and an intraocellar lobe evolved convergently in Aeshnoptera and Cavilabiata (Bechly 1996; Lohmann 1995, 1996; *contra* Carle 1995); (8) a complete ovipositor is present, including all six muscles (Pfau 1991) (symplesiomorphy of Petalurida and Aeshnoptera), although oviposition is not endophytic but 'endosubstratic' like the oviposition in Cordulegastrida (convergence); (9) the male sperm vesicle without terminal flagellae. This could be a further unique plesiomorphy of Petalurida, but flagellae could also be secondarily absent, since they are reduced in some Euaeshnida and Gomphides and all Cavilabiata. The asymmetric flagellae in 'derived' Eurypalpida certainly are non-homologous new (or regained) structures; (10) in tandem formation the male appendices superiores still partly engage the female pronotum (unique symplesiomorphy of Petalurida with Aeshnoptera) (Tillyard 1917); (11) the plesiomorphic invaginated type of germ-band is still present (Ando 1962) (symplesiomorphy of Petalurida and Euaeshnida, while Gomphides and Cavilabiata have a partly invaginated and sigmoidal germ band as synapomorphy). The ellipsoidal eggs and gravity dependent rotation of the embryo have been convergently evolved in Gomphides and Exophytica, correlated with their non-endophytic oviposition; (12) an 'upright' mode of emergence (zygopteroid style) without the 'hanging back' resting position of most 'derived' Anisoptera. (Note: this seems to be a very doubtful character which is not even characteristic for petalurids according to St. Quentin and Beier (1968: 29-30); the 'hanging back' position is present in Calopterygidae, Epiophlebiidae, *Petalura*, Euaeshnida, Cordulegastrida and Eurypalpida, while the 'upright mode' is present in Lestinoidea, Coenagrionoidea, *Tanypteryx* and Gomphides); (13) the larval mask is not strongly concave with a median cleft (except *Tachopteryx*) and the prementum lacks setae, at least in the later instars (symplesiomorphy of Petalurida, Aeshnoptera and Gomphides). The fact that the molar lobe on the larval mandible is furnished with teeth (Carle and Louton 1994) must be a plesiomorphy too because such teeth are also present in Gomphides (Watson 1956) and Zygoptera; (14) all the larval antennomeres (7, except *Tanypteryx* with 6) are thick (non-filiform) which is a plesiomorphy according to Needham and Westfall (1955: 27) (unique plesiomorphy of Petalurida); (15) there is an eight-folded proventriculus (unique plesiomorphy of Petalurida; 16 folds in most Zygoptera and Epiophlebiidae, 32 in Amphipterygidae, 8 in Lestoidea by autapomorphic convergence, and 4 in all other Anisoptera by synapomorphy); (16) the larvae are incapable of locomotion by jet-propulsion because the necessary abdominal muscles are primarily absent (as in Zygoptera and *Epiophlebia*). Nevertheless water can be expelled from the rectal chamber by action of the rudimentary (not vestigial) transverse muscles of segment 6 (Rowe 1987: 125). The absence of jet-prop-locomotion and the transverse muscle 5 probably represents a unique plesiomorphy of Petalurida. A transverse muscle 5 belongs to the ground-plan of all non-petalurid Anisoptera, while a transverse muscle 4 might represent an autapomorphy of Cavilabiata (*contra* Carle 1995 and Lohmann 1995, 1996). Austropetaliida have secondarily lost all transverse muscles and therefore are unable of jet-prop-locomotion too (reversal).

Within Anisoptera the latter three character states are uniquely retained in the Petalurida, which are identified by this evidence as the most basal branch of extant Anisoptera (Calvert 1893; Tillyard 1922; Needham 1951; Fraser 1957; Bechly 1993, 1995; *contra* Pfau 1991; Carle 1995; Lohmann 1995, 1996). The broad body size of most petalurids might be plesiomorphic too considering the size of aeschnidiids, aeshnids, 'basal' gomphids (e.g. *Hagenius*) and cordulegastrids. The small size of *Tanypteryx* seems to be an autapomorphy of this genus, which also shows a considerable regressive trend in its wing venation (many reversals). A potential autapomorphic feature of the Petalurida could have been the chromosome number n = 9 or 10, because we disagree with Kiauta (1967, 1972) that the ancestral state was n = 9. (A phylogenetic re-interpretation of Kiauta's data clearly indicates that the ancestral state was n = 13 or 14). However, Jensen and Mahanty (1978) demonstrated that the earlier chromosome counts for *Uropetala* were erroneous and that the true value for this genus is also n = 13, thus representing the plesiomorphic character state too.

The small number of only ten extant petalurid species and their amphinotic distributional pattern are characteristical for rather basal groups. The closed sperm furrow in the male sperm vesicle (vesicula spermalis *sensu* Pfau 1991) and the exophytic mode of oviposition (correlated with egg-shape) are most parsimoniously interpreted as convergences of Petalurida with some Euaeshnida and all other 'exophytic' Anisoptera (Carle 1995; Lohmann 1995, 1996). The special type of sperm chamber of Petalurida, Gomphides and Cordulegastrida (Pfau 1991) is probably a plesiomorphic ground-plan character of Anisoptera which is secondarily reduced in Euaeshnida (*contra* Lohmann 1995, 1996) and transformed in Eurypalpida (Carle 1995). On the other hand, one could argue that petalurids have secondarily lost their ability for jet-propulsion (convergent to Austropetaliida), because of their semi-terrestrial larval habitat (Lohmann 1995, 1996). However, considering the total evidence we think it is much more likely that the jet-propulsion ability was primarily absent.

The highly specialized larval habit could have been the only adaptational niche in which a non-jet-prop Anisoptera could escape the selective pressure of the more advanced jet-propelled larvae (Dunkle 1981: 197). The same explanation may apply to the circumstance that 'anisozygopteres' only survived as two extant relict species. Nevertheless, the common occurrence of various 'anisozygopteres' and Petalurida with various representatives of the more advanced groups of Anisoptera with jet-propelled larvae during the very long period of the Upper Jurassic and Lower Cretaceous seems to contradict this hypothesis. Maybe, changes in the lake palaeo-ecology (composition of the aquatic flora) during the mid Cretaceous could also have been important.

Since our phylogenetic analysis confirms the basal position of Petalurida, we endorse the following proposal of Bechly (1996) for a new phylogenetic systematisation of Anisoptera:

- Anisoptera
  - Petalurida
  - Euanisoptera
    - Aeshnoptera
    - Exophytica
      - Gomphides
      - Cavilabiata
        - Cordulegastrida
        - Cristotibiata
          - Neopetaliidae
          - Brachystigmata
            - Chlorogomphida
            - Eurypalpida

The alleged plesiomorphy of semi-terrestrial larvae

Concerning the question, whether terrestrial larvae are plesiomorphic or apomorphic for Petalurida, we think that there is a lot of evidence in favour of the latter hypothesis, that terrestrial larvae are almost certainly an autapomorphy of Petalurida. The alternative hypothesis of Fraser (1957: 95), St. Quentin (1962: 184) and Dunkle (1981: 197) that terrestrial larvae are plesiomorphic for Anisoptera, is very unlikely and also unparsimonious because: (1) rectal gills are not only present in the larvae of Epiophlebiidae and Anisoptera, but also in the larvae of Zygoptera, although in a somewhat more plesiomorphic state (three rectal folds without tracheation). In any case, these structures seem to be functional, since zygopteroid larvae can breath very well when the caudal gills are broken, and probably homologous. This represents strong evidence for an aquatic larva as groundplan-character of all extant Odonata; (2) the terrestrial larvae of *Megalagrion* McLachlan 1883 (Coenagrionidae), *Pseudocordulia* Tillyard 1909 ('corduliids'), *Oligoaeschna* Selys 1889, *Telephlebia* Selys 1883 and *Antipodophlebia* Fraser 1960 (Euaeshnida) are without doubt secondarily terrestrial and can be seen as models for the same evolutionary trend in petalurids; (3) if one would assume that the groundplan of Anisoptera includes primarily terrestrial larvae, one would be forced to assume at least a triple convergent evolution of aquatic larvae in Zygoptera, Epiophlebiidae and Anisoptera. This is not only unparsimonious, but seems quite unlikely too (Askew 1988: 11); (4) the oldest known Odonata larva from the Triassic of Australia (Rozefelds 1985) looks like a synlestid larva and was certainly aquatic (correlation [structure - function] *sensu* Bryant and Russell 1992). From this period we know only very 'primitive' imaginal Odonata which cannot be assigned to any extant suborder with certainty. These facts could support the hypothesis that an aquatic 'Zygoptera-like' larva might be regarded as ancestral for all extant Odonata larva types. Of course, this fossil only tells us that 'Zygoptera-like' larvae did exist in the Triassic, nothing more is actually proven by this single specimen; (5) the fact that the larva of *Epiophlebia* is morphologically 'intermediate' between the zygopteroid type of larva and the anisopteroid type of larva is further support for the hypothesis that aquatic larvae are symplesiomorphic and homologous for all Odonata: Zygoptera + 'anisozygopteres' + Anisoptera (nothing can be inferred for the Protodonata, Archizygoptera and other Permo-Triassic Odonatoptera). This is also supported by a Jurassic Odonata larva from Russia (Pritykina 1985), which appears to possess zygopteroid anal appendages (foliate caudal gills) as well as an anisopteroid branchial basket; possibly associated imagines had wings of 'anisozygopteroid'-tarsophlebiid type (Crowson 1985: 100); (6) According to Kukalovà-Peck (1983, 1991, and pers. comm.), a yet undescribed fossil meganeurid larva from the Carboniferous of Mazon Creek shows abdominal leglets, similar to extant Euphaeidae and Polythoridae. Even if Kukalovà-Peck should have erroneously interpreted the leglets of this extraordinary fossil 'giant dragonfly' as respiratorial devices, it could be concluded from the structure of the larval mask that even Carboniferous 'protodonates' already had aquatic larvae, which would then belong to the ground-plan of Odonatoptera (remark: since adult non-meganeurid Odonatoptera have been recently discovered in the Carboniferous of England and U.S.A. (unpubl. findings of Jarzembowski, Nel and Bechly), it should be noted that Odonata-like Carboniferous larvae do not necessarily represent true Meganisoptera, although the size of the referring larva seems to exclude Protozygoptera).

The presence of functional tracheae and vestigial spiracles in Odonata larvae (Calvert 1929: 924; Fraser 1957: 95) is no conflicting evidence, because it could be as well explained by the presence of terrestrial larvae in the ground-plan of the Hexapoda, maybe still preserved in the ground-plan of Pterygota, but not necessarily anymore in the ground-plan of Odonatoptera or Odonata (Bechly 1995).

Fossil larvae of Petalurida

Previously no fossil dragonfly larvae have been assigned to the Petaluridae (auct.) or their stem-group. The only potential 'candidate' seems to be a fossil anisopteroid larva from the Lower Cretaceous Santana Formation in Brazil, that has been described as *Pseudomacromia sensibilis* (Pseudomacromiidae) within the Aeschnidioidea by Carle and Wighton (1990: 62-67). Since *Pseudomacromia* Carle and Wighton 1990 is an invalid junior homonym of *Pseudomacromia*, the generic name of *P. sensibilis* was replaced with *Nothomacromia* by Carle (1995), and Pseudomacromiidae was consequently replaced with Nothomacromiidae in the same publication. The previous arguments in favour of a position of the referring fossil larva within Aeschnidioidea have been shown to be unconvincing or even invalid by Nel and Martínez-Delclòs (1993b: 84). A petalurid relationship of this fossil larva is suggested by the unique shape of the labial 'palps' (a potential synapomorphy) and the exceptionally thick antennae (unique symplesiomorphy of Petalurida within extant Anisoptera). Its macromiid-like body most closely resembles the larva of *Tachopteryx*, which also has only six antennal segments (by convergence?). As the only known imaginal petalurid of Cretaceous age has been found in the same Formation in Brazil, it would be reasonable to suppose that this fossil could represent a possible larva of Cretapetaluridae (even a generic or even specific synonymy with *Cretapetalura brasiliensis* could not be excluded). If *Nothomacromia sensibilis* would indeed represent a larva of Cretapetaluridae, its preservation of in a limnic sediment would indicate that the stem-group petalurids of the Mesozoic probably did not yet possess the semi-terrestrial larval habitat of the extant crown-group representatives. However, according to Bechly *et al.* (in press) *Nothomacromia sensibilis* agrees with the alleged larvae of Hemeroscopidae (Pritykina 1977) and the larval Sonidae s.str. (Pritykina 1986) in the absolutely unique forcep like paraprocts (please note: the adults that have been previously attributed to *Sona nectes* by Pritykina are classified in a new family, genus and species by Bechly *et al.* in press). Therefore there is the strong possibility that all these larvae belong to a common family Sonidae s.str., which might represent the larvae of Stenophlebioidea or even more probably of Aeschnidiidae, according to Bechly *et al.* (in press).

Scarcity in the fossil record of Petalurida

Naturally one would expect to find a good Mesozoic fossil record of such an archaic group as the Petalurida. But although many authors have stated that 'petalurids have been the dominant group of Mesozoic dragonflies' (Needham and Westfall 1955: 67; Dunkle 1981: 189), only a few fossil taxa can be positively assigned to the stem-group of extant Petaluridae, while all previously considered fossil petalurids are not related to this group at all (see: Rowe 1987: 119; Nel and Paicheler 1992; Bechly 1993, 1995). Lower or Mid Jurassic and Tertiary fossil Petalurida are completely unknown (*contra* Needham 1903: 739). This may be due to the following four reasons: (1) petalurids are, and maybe always have been, a comparatively rare group and consequently are rarely fossilised; (2) the semi-terrestrial larval habitat is an ecological niche removed from aquatic sediments which makes fossilisation very unlikely; at least for crown-group petalurids which already possessed this derived way of life; (3) it is very difficult to recognize a fossil petalurid, because this taxon has only a few autapomorphic characters which are likely to become fossilised; (4) Tertiary species may have been restricted to circum-tropical biotas (amphinotic distribution) and the referring deposits are only poorly known.

Stem-group representatives of extant Petaluridae

Only *Protolindenia wittei*, *Cretapetalura* gen. nov., *Pseudocymatophlebia* gen. nov., *Aktassia* and *Aeschnogomphus* share the apomorphic characters of Petalurida, while the latter are absent in all fossils that have been previously assigned to the Petaluridae (auct.), including the four genera cited by Carpenter (1992). Most of these fossils should be better classified as 'Anisoptera *incertae sedis*' until further evidence is available (Nel and Paicheler 1992). *Kazakhophlebiella aktassica* and *Pritykiniella deichmuelleri* (classified in *Protolindenia* by Pritykina 1968) do not possess these synapomorphies too and therefore cannot be classified with *Protolindenia wittei* in the same genus *Protolindenia*, because *P. wittei* is the type species of this genus. For the same reason the genera *Protolindenia* and *Mesuropetala* cannot be synonyms, contrary to Carpenter (1932) and Nel and Paicheler (1992).

Aeschnopsis perampla (= *Cymatophlebiopsis pseudobubas*) and '*Necrogomphus*' (?) *jurassicus* are incompletely preserved fossils and must preliminarily be regarded as Anisoptera *incertae sedis*. Nevertheless the observable character states would not contradict a petalurid relationship of *Aeschnopsis*, especially with *Cretapetalura* which also shows the characteristical and derived shape of the anal loop.

Proposed phylogenetic system of Petalurida

Based on the numerical cladistic analysis and its phylogenetic interpretation, as well as on the 'manual' phylogenetic analysis of Bechly (1996), the following classification is proposed, which basically agrees with that of Bechly (1996). All recognized monophyla have been named, since we reject the sequencing of stem-group representatives because of the logical and practical reasons described by Willmann (Willmann 1989). The assignment of formal hierarchical ranks has been omitted whenever possible without violation of the International Rules of Zoological Nomenclature, because they are absolutely arbitrary and more or less superfluous (Willmann 1989). Each supraspecific taxon name is phylogenetically defined according to the rules of socalled 'phylogenetic taxonomy' (De Queiroz and Gauthier 1990, 1992), and a list of the putative autapomorphies is provided for all these taxa too.

Petalurida Bechly 1996 (= Pan-Petalurata *sensu* Lohmann 1996)

Phylogenetic definition: the most inclusive clade that contains *Petalura gigantea* Leach 1815 but none of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition of pan-monophylum).

Included sister-groups: Protolindeniidae Handlirsch 1906 and Petalurodea Bechly (1996).

Autapomorphies: postnodal space very narrow, with many cells distal of pterostigma; stigmal brace shifted in the basal two-third of the wing, midway between node and apex (convergent to some Aeschnidiidae, *Hoyaeshna* and Anactina); IR1 is a very well-defined, rather straight, and very long vein in both wing pairs (convergent to Austropetaliida, a few Aeshnidae and Neopetaliidae; reversed in *Tanypteryx*; even if the long IR1 of Petalurida and Austropetaliida should be regarded as a symplesiomorphy, because of the long IR1 in many 'anisozygopteres' and nearly all Zygoptera, the extreme state in Petalurida would still be a valid autapomorphy); the wing space between RP1 and RP2 (especially in forewings) is strongly expanded, with much more than 8-9 rows of cells (reversed in *Tanypteryx*; some Cymatophlebiidae also have more than 8 rows of cells between RP1 and RP2, although the corresponding area is not significantly expanded); the forewing pseudoanal vein PsA is hypertrophied and the subtriangle is widened, correlated with a more transverse forewing discoidal triangle (convergent to Eurypalpida and some Gomphides); forewing subtriangle divided by crossveins (convergent to Italoansida, the group of all libelluloid dragonflies with a boot-shaped anal loop); in both wing pairs more than two rows of cells in the basal part of the postdiscoidal area between the level of the distal angle of the discoidal triangle and that of the midfork (convergent to Aeschnidioptera, Mesuropetalidae, Cymatophlebiidae, '*Morbaeschna muensteri sensu* Needham 1907, Aeshnidae, few Lindeniidae like *Cacoides* and *Melanocacus*, and many Libellulidae, except Tetrathemistinae; reversed in *Tanypteryx*); in male hindwings the CuAb is very distinctly curved at its base, strongly approaching the secondary anal vein AA1b.

Family Protolindeniidae Handlirsch 1906

Phylogenetic definition: the most inclusive clade that contains *Protolindenia wittei* (Giebel 1860) but neither *Petalura gigantea* Leach 1815 nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included species: *Protolindenia wittei* (Giebel 1860) (a phylogenetic definition and list of autapomorphies of the genus *Protolindenia* Deichmüller 1886 should not be given until further genera are described in this family).

Autapomorphies: anal loop completely reduced (only a weak character, since convergently evolved in Aktassiidae, *Phenes* and Petalurinae).

Petalurodea Bechly 1996

Phylogenetic definition: the most inclusive clade that contains *Petalura gigantea* Leach 1815 but neither *Protolindenia wittei* (Giebel 1860) nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included sister-groups: Cretapetaluridae fam. nov. and Petaluroidea Needham 1903 (*sensu* Bechly 1996).

Autapomorphies: wings falcate and very slender, and distinctly longer than 50 mm (convergent to some other Odonatoptera, e.g. *Cymatophlebia*; reversed in *Tanypteryx*); the bridge-space (Bqs-area) between RP and IR2 basal of the subnode is distinctly narrowed (reversed in *Tanypteryx*); the hindwing MP is at least somewhat shortened, and terminating at the posterior margin max. slightly distal of the nodus.

Cretapetaluridae fam. nov.

Phylogenetic definition: the most inclusive clade that contains *Cretapetalura brasiliensis* gen. nov. et sp. nov. but neither *Petalura gigantea* Leach 1815 nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included species: *Cretapetalura brasiliensis* gen. nov. et sp. nov. (a phylogenetic definition and list of autapomorphies of the genus *Cretapetalura* gen. nov. should not be given until further genera are definitely included in this family). Maybe also including *Aeschnopsis perampla* (= *Cymatophlebiopsis pseudobubas*).

Autapomorphies: the true lestine oblique vein (basal oblique vein between RP2 and IR2) is shifted basally (convergent to *Phenes* and Petalurinae), only separated by one cell from the subnode; the distal side MAb of the hindwing discoidal triangle is strongly angulated, correlated with a very distinctly developed convex secondary vein in the postdiscoidal area (convergent to Euaeshnida and Gomphides); the hindwing subtriangle is widened and traversed by a crossvein (convergent to *Cymatophlebiella*, *Hypopetalia*, *Cymatophlebia*, and *Progomphus*); hindwing anal loop longitudinal elongated (convergent to Cordulagomphinae); larvae with tiny eyes, six-segmented antennae, very long legs, and elongated paraprocts (all these larval characters only refer to *Nothomacromia sensibilis*, which might rather be a Sonidae s.str. than a member of Petalurida according to Bechly *et al.* (in press).

Superfamily Petaluroidea Needham 1903 (*sensu* Bechly 1996)

Phylogenetic definition: the most inclusive clade that contains *Petalura gigantea* Leach 1815 but neither *Cretapetalura brasiliensis* gen. nov. et sp. nov. nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included sister-families: Aktassiidae Pritykina 1968 (sensu nov.) and Petaluridae Needham 1903 (*sensu* Bechly 1996).

Autapomorphies: pterostigmata elongated; in the forewing the area between RP3/4 and MA is somewhat widened near the posterior wing margin, with more than 3 rows of cells (reversed in Tanypterygini); RP3/4 is undulate and distally strongly diverging from MA (reduced in Tanypterygini); the hindwing MP is distinctly shortened, and terminating at the posterior margin on the level of the nodus, or even somewhat basal of the nodus.

Family Aktassiidae Pritykina 1968 (sensu nov.)

Phylogenetic definition: the most inclusive clade that contains *Aktassia magna* Pritykina 1968 but neither *Petalura gigantea* Leach 1815 nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included sister-subfamilies: Pseudocymatophlebiinae subfam. nov. and Aktassiinae Pritykina 1968 (stat. nov.).

Autapomorphies: very dense wing venation with a distinctly increased number of cells (convergent to Aeschnidiidae).

Subfamily Aktassiinae Pritykina 1968 (stat. nov.)

Phylogenetic definition: the most inclusive clade that contains *Aktassia magna* Pritykina 1968 but neither *Pseudocymatophlebia hennigi* gen. nov. et sp. nov. nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included sister-genera: *Aeschnogomphus* Handlirsch 1906 and *Aktassia* Pritykina 1968.

Autapomorphies: wings longer than 65 mm (convergent to Petalurinae); IR1 is secondarily very long and straight (reversal); characteristical pattern of veinlets and intercalary veins between RA and RP1, RP2 and IR2, IR2 and RP3/4, and MA and MP; anal loop completely reduced (unknown for *Pseudocymatophlebia* gen. nov., thus maybe an autapomorphy of Aktassiidae; convergent to Protolindeniidae, *Phenes* and Petalurinae); the posterior margin of the hindwings is remarkably straight between CuAa and the apex (unknown for *Pseudocymatophlebia* gen. nov., thus maybe an autapomorphy of Aktassiidae).

Aeschnogomphus Handlirsch 1906

Phylogenetic definition: the most inclusive clade that contains *Aeschnogomphus buchi* (Hagen 1848) but neither *Aktassia* Pritykina 1968 nor any of the type species of the other petalurid genera mentioned in this work, and any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included species: *A. buchi* (Hagen 1848) [invalid synonyms: *A. charpentieri* (Hagen 1848), and '*Libellulita dresdensis*' Charpentier 1840, which is no formal name anyway] and *A. intermedius* (Münster *in* Germar 1839).

Autapomorphies: the distal margin of the pterostigmata is recessed, situated at less than 85 % of the wing length (convergent to *Phenes*, Isophlebiida, Aeschnidiidae and Anactina); giant size; distinct type of adult anal appendages; female abdomen relatively slender (the stout female abdomen of the other fossil and extant petalurids seems to be a symplesiomorphy with Isophlebiidae and Aeschnidiidae).

Aktassia Pritykina 1968

Phylogenetic definition: the most inclusive clade that contains *Aktassia magna* Pritykina 1968 but neither *Aeschnogomphus buchi* (Hagen 1848) nor any of the type species of the other petalurid genera mentioned in this work, and any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included species: *Aktassia magna* Pritykina 1968 and *Aktassia pritykinae* sp. nov.

Autapomorphies: presence of two rows of cells between MP and CuAa in the hindwing; presence of two rows of cells between RA and RP1 distal of the nodus; submedian cell (between CuP-crossing and pseudo-anal vein PsA) traversed by crossveins (convergent to Aeschnidiidae).

Subfamily Pseudocymatophlebiinae subfam. nov.

Type genus: *Pseudocymatophlebia* gen. nov.

Phylogenetic definition: the most inclusive clade that contains *Pseudocymatophlebia hennigi* gen. et sp. nov. but neither *Aktassia magna* Pritykina 1968 nor any of the type species of the other type genera of the Anisoptera families *sensu* Fraser (1957) (stem-based definition).

Included species: *Pseudocymatophlebia hennigi* gen. nov. et sp. nov. (a phylogenetic definition and list of autapomorphies of the genus *Pseudocymatophlebia* gen. nov. should not be given until further genera are described in this family).

Autapomorphies: IR1 is vanishing distally, and not fused with the short pseudo-IR1.

Petaluridae Needham 1903 (*sensu* Bechly 1996) (= Petalurata *sensu* Lohmann 1996)

Phylogenetic definition: the least inclusive clade that contains the Recent genera *Tanypteryx*, *Tachopteryx*, *Phenes*, *Petalura* and *Uropetala* (node-based definition of crown-group).

Included sister-subfamilies: Tachopteryginae Fraser 1933 (sensu nov.) and Petalurinae Needham 1903 (*sensu* Bechly 1996).

Autapomorphies: in forewings the antenodal space as slightly shorter than the postnodal space (nodus situated basal of 50 % of the wing length); all pterostigmata extremely elongated and narrow (at least 12-17 % of wing length, and at least 10 times longer than broad; convergent to Isophlebiidae), since their basal margins are shifted basally to the stigmal brace (convergent to Isophlebiida, some Aeschnidiidae, and Anactina), therefore the pterostigmata also appear to be curved; hindwing CuAa somewhat shortened, ending distinctly basal of the level of the nodus (convergent to numerous other groups within Anisoptera; reversed in *Tachopteryx*?); membranule of hindwings strongly reduced; anal angle of male hindwings very acute (reversed in *Tachopteryx*); major wing veins with very strong spines (unsafe, since homoplastic and unknown for the fossil petalurids); adult head with a bulged occiput (Needham and Westfall 1955; according to Carle and Louton (1994) a trapezoidal occiput shall be a characteristic of all extant Petalurida but, since this shape of the occiput is correlated with the separated position of the compound eyes, it has to be regarded as symplesiomorphy of Petalurida and Gomphides); spatulate shape of the end hooks of the adult labial palps (Carle 1995); adult males with the epiproct truncate, distally broadened and divaricate (Carle and Louton 1994; retained in a very similar state in *Tanypteryx* and *Tachopteryx*, but strongly transformed in *Phenes* and *Uropetala*); cerci of adult males (appendices superiores) distally expanded, thus at least somewhat foliate; female ovipositor strongly curved upwards (Carle 1995) and with a weakly developed musculature (Pfau 1991), correlated with the an endosubstratic oviposition, which is again correlated with the derived semiterrestrial larval habitats; posterior-dorsal margin of the posterior larval abdominal segments with paired medio-lateral tubercles with prominent tufts of stiff setae (according to Schmidt (1941: 235) these 'Zottenhöcker' are at least present in *Tachopteryx*, *Phenes*, *Petalura* and maybe *Uropetala*; the presence in *Uropetala* was later corroborated by Rowe (1987: 121 and fig. 64); and Asahina (1954, cited in Needham and Westfall 1955: 69, fig. 36) demonstrated its presence in *Tanypteryx*); ventro-medial yellow hair brush of between the larval terminalia around the anus (Carle 1995; according to Schmidt (1941: 235) at least known from *Tachopteryx*, *Phenes*, *Petalura*); the lateral lobes ('palps') of the larval prehensile mask are somewhat expanded and of characteristical quadrate and slightly concave shape (this character could be a synapomorphy with Cretapetaluridae fam. nov. if the fossil larva *Nothomacromia sensibilis* should be related to this family); larval prehensile mask broadened with a prementum that is abruptly narrowed basally and has a triangular projected anterior margin (Carle and Louton 1994; Carle 1995); larval prehensile mask with reduced endhook of the lateral lobes ('palps') (Carle and Louton 1994); presence of a robust dorso-lateral spur that is overlapping the base of the movable hook on the lateral lobes ('palps') of the larval prehensile mask (Carle and Louton 1994, Carle 1995; present in *Tanypteryx*, *Tachopteryx*, *Phenes* and *Uropetala*, but reduced in *Petalura*; contrary to Williamson (1900) and Lohmann (1996: 237) *Tachopteryx* does have this spur too (Byers 1930; Dunkle 1989)); tibiae of the final instar larvae have strong spurs and apical burrowing hooks (Carle 1995), correlated with their burrowing behaviour (reversed in *Tachopteryx* and *Phenes* that do not burrow tunnels); leaf-mimicry of the larva, correlated with their cryptic, semi-terrestrial lifestyle; terminalia forming a dorsally directed vent (Carle and Louton 1994, Carle 1995); reduced dentition of the gizzard, with only one or two (max. six) blunt teeth on each of the eight lobes (Fraser 1957; Carle 1995; Lohmann 1995, 1996).

Remark: the mentioned non-wing venational characters are mostly unknown in the fossil petalurids and therefore could represent autapomorphies for more inclusive monophyla within Petalurida. Nevertheless, they are derived ground-plan characters of all extant Petaluridae compared to any other group of extant dragonflies.

Tachopteryginae Fraser 1933 (sensu nov.) (= Tanypteryginae *sensu* Bechly 1996)

Phylogenetic definition: the most inclusive clade that contains *Tachopteryx thoreyi* (Hagen 1857) but not *Petalura gigantea* Leach 1815 (stem-based definition).

Included sister-tribes: Tanypterygini Tillyard and Fraser 1940 (*sensu* Bechly 1996) and Tachopterygini Fraser 1933 (*sensu* Bechly 1996).

Autapomorphies: distal accessory oblique vein suppressed (unique within Petalurida); the metapoststernum on the venter of the adult metathorax is more or less expanded and hairy ('ventral metathoracic tubercle').

Tanypterygini Tillyard and Fraser 1940 (*sensu* Bechly 1996)

Phylogenetic definition: the most inclusive clade that contains *Tanypteryx hageni* (Selys 1879) but neither *Tachopteryx thoreyi* (Hagen 1857) nor *Petalura gigantea* Leach 1815 (stem-based definition).

Included sister-species: *T. hageni* (Selys 1879) and *T. pryeri* (Selys 1889) (a phylogenetic definition and list of autapomorphies of the genus *Tanypteryx* Kennedy 1917 should not be given until further genera are described in this family).

Autapomorphies: wings reduced in size (wings shorter than 50 mm), correlated with several further reductions and reversals in the wing venation (decreased number of cells; IR1 shorter and zigzagged; wing space between RP1 and RP2 not expanded, with less than 8-9 rows of cells; bridge-space (Bqs-area) less narrowed; at least the hindwing discoidal triangle is not traversed by any crossveins, etc.); in the forewing the field between RP3/4 and MA is not widened near the posterior wing margin (reversal); the forewing veins RP3/4 and MA are not curved distally, and MA is not undulate (reversal); the distal side MAb of the hindwing discoidal triangle is slightly angled, correlated with the development of a weak convex secondary vein in the postdiscoidal area (convergent to *Tachopteryx*, but much less distinct than in *Cretapetalura*, Euaeshnida and Gomphides); basal part of postdiscoidal area only with two rows of cells (reversal); larval antennae only six-segmented (convergent to *Nothomacromia*); adult 'ventral metathoracic tubercle' hypertrophied.

Tachopterygini Fraser 1933 (*sensu* Bechly 1996)

Phylogenetic definition: the most inclusive clade that contains *Tachopteryx thoreyi* (Hagen 1857) but neither *Tanypteryx hageni* (Selys 1879) nor *Petalura gigantea* Leach 1815 (stem-based definition).

Included sister-genera: *Tachopteryx* Uhler *in* Selys 1859 and *Phenes* Rambur 1842.

Autapomorphies: dull body coloration, convergent to *Petalura* (the black yellow colour pattern is most probably a symplesiomorphy of *Tanypteryx* and *Uropetala* with Epiophlebiidae, Gomphides, Cordulegastrida, Synthemistidae and Macromiidae; the statement by Fraser (1957: 95) that this type of coloration is only present in *Tanypteryx* is wrong because it is quite significant in *Uropetala*.); hairy lateral tubercles ('Zottenhöcker') of the larval abdomen very distinct; larvae secondarily not burrowing tunnels.

Tachopteryx Uhler *in* Selys 1859

Phylogenetic definition: the most inclusive clade that contains *Tachopteryx thoreyi* (Hagen 1857) but neither *Phenes raptor* Rambur 1842 nor any of the type species of the other petalurid genera mentioned in this work (stem-based definition).

Included species: *T. thoreyi* (Hagen 1857).

Autapomorphies: pterostigmata further prolonged (ca. 18-20 % of the wing length); basal side of the forewing discoidal triangle sigmoidally curved; male hindwings with a very obtusely angulated anal angle (Needham and Westfall 1954); the distal side MAb of the hindwing discoidal triangle is slightly angled, correlated with the development of a weak convex secondary vein in the postdiscoidal area (convergent to *Tanypteryx*, but much less distinct than in *Cretapetalura*, Euaeshnida and Gomphides).

Phenes Rambur 1842
Phylogenetic definition: the most inclusive clade that contains *Phenes raptor* Rambur 1842 but neither *Tachopteryx thoreyi* (Hagen 1857) nor any of the type species of the other petalurid genera mentioned in this work (stem-based definition).

Included species: *P. raptor* Rambur 1842, with the two subspecies *Phenes raptor raptor* Rambur 1842 and *Phenes raptor centralis* Jurzitza 1989.

Autapomorphies: presence of a short pseudo-ScP in the basal postnodal space (Fraser 1948); the distal margin of the pterostigmata is recessed too, situated at less than 85 % of the wing length (convergent to *Aeschnogomphus*, Isophlebiida, Aeschnidiidae and Anactina); anal loop completely reduced (convergent to Protolindeniidae, Aktassiidae, and Petalurinae); the true lestine oblique vein (basal oblique vein between RP2 and IR2) is shifted basally, only separated by one and a half cells from the subnode (convergent to Cretapetaluridae fam. nov. and Petalurinae); adult occiput with distinct postero-dorsal tubercles; presence of a strong lateral spur at the mesothoracic prealar ridge; unique type of adult male anal appendages (cerci forked and epiproct very large and strongly angulated), which is even visible in the larvae (Needham and Bullock 1943).

Petalurinae Needham 1903 (*sensu* Bechly 1996)
Phylogenetic definition: the most inclusive clade that contains *Petalura gigantea* Leach 1815 but not *Tanypteryx hageni* (Selys 1879) (stem-based definition).

Included sister-genera: *Petalura* Leach 1815 and *Uropetala* Selys 1857.

Autapomorphies: wings longer than 65 mm (convergent to Aktassiidae); anal loop completely reduced (convergent to Protolindeniidae, Aktassiidae, and *Phenes*); the true lestine oblique vein (basal oblique vein between RP2 and IR2) is shifted basally, only separated by 1,5 cells from the subnode (convergent to Cretapetaluridae and *Phenes*); cerci of adult males very broad and foliate (convergent to *Mesuropetala*, *Cymatophlebia*, *Polycanthagyna erythromelas* and '*Aeshna*' *petalura*, which could be a Polycanthagynini too, according to G. Peters, pers. comm.); unique type of emergence (Winstanley 1982: 306; expansion of the abdomen is preceding that of the wings); larvae burrowing more complex tunnels.

Petalura Leach 1815
Phylogenetic definition: the most inclusive clade that contains *Petalura gigantea* Leach 1815 but neither *Uropetala carovei* (White 1846) nor any of the type species of the other petalurid genera mentioned in this work (stem-based definition).

Included species: *P. gigantea* Leach 1815, *P. hesperia* Watson 1958, *P. ingentissima* Tillyard 1907, and *P. pulcherrima* Tillyard 1913.

Autapomorphies: dull body coloration, convergent to Tachopterygini (the black yellow colour pattern is most probably a symplesiomorphy of *Tanypteryx* and *Uropetala*; see above); the robust dorso-lateral spur that is overlapping the base of the movable hook on the lateral lobes ('palps') of the larval prehensile mask in the other extant Petaluridae is secondarily absent.

Uropetala Selys 1857
Phylogenetic definition: the most inclusive clade that contains *Uropetala carovei* (White 1846) but neither *Petalura gigantea* Leach 1815 nor any of the type species of the other petalurid genera mentioned in this work (stem-based definition).

Included sister-species: *U. carovei* (White 1846) and *U. chiltoni* Tillyard 1921.

Autapomorphies: we did not find any evident autapomorphies, although these probably exist, since the genus certainly is monophyletic, as is strongly indicated by its biogeographic isolation (endemic to New Zealand) and the great phenetic similarity of the two included species.

Anisoptera incertae sedis

Aeschnopsis Cowley 1942
invalid obj. syn. *Aeschnopsis* Handlirsch 1939 *nomen nudum*?; subj. syn -. *Cymatophlebiopsis* Cowley 1942, *Cymatophlebiopsis* Handlirsch 1939 *nomen nudum*?.
- *A. perampla* (Brodie 1845) (subj. jun. syn. *C. pseudobubas* Handlirsch 1939)
(maybe Petalurida - Cretapetaluridae, but insufficient evidence for a positive attribution)

Nothomacromiidae Carle 1995
(invalid synonym: Pseudomacromiidae Carle and Wighton 1990)
Nothomacromia Carle 1995
(nom. subst. pro *Pseudomacromia* Carle and Wighton 1990 which is a junior homonym of *Pseudomacromia* Kirby 1889, what makes the generic name *Pseudomacromia* Carle and Wighton 1990 and the respective family-group name Pseudomacromiidae invalid).
- *N. sensibilis* (Carle and Wighton 1990)
(probably a subjective junior synonym of Aeschnidiidae)

Anisoptera incertae sedis (probably no Petalurida)

Libellulium Westwood 1854
- *L. agrias* Westwood 1854
(Since the holotype was only a poor fragment and seems to be lost, this taxon has to be regarded as a *nomen dubium*. The few visible characters, e.g. undulating RP2 and IR2, suggest a position in Cymatophlebiidae, but certainly do not justify a synonymy with *Cymatophlebia*, especially since there is some evidence that it could rather be a member of Valdaeshninae than of Cymatophlebiinae, according to Bechly *et al.*, in prep.).

Pritykiniella gen. nov.
- *P. deichmuelleri* (Pritykina 1968) comb. nov.
(Originally described in the genus *Protolindenia* Deichmüller 1886)

Kazakhophlebiella gen. nov.
- *K. aktassica* (Pritykina 1968) comb. nov.

(Originally described in the genus *Protolindenia* Deichmüller 1886)

Cymatophlebiella Pritykina 1968
- *C. euryptera* Pritykina 1968

(Lacking the potential synapomorphies of Cymatophlebiidae, like Rspl, undulate RP2 and IR2, etc., but maybe a very basal representative of Aeshnoptera because of the basally parallel veins RP1 and RP2, and the undulating RP3/4 and MA).

Necrogomphus Campion 1923 (nec *Necrogomphus* Handlirsch 1939)
- *N. petrificatus* (Hagen 1850)
- '*Necrogomphus*' (?) *jurassicus* (Giebel 1856)

('*N.*' *jurassicus* is most probably belonging to the genus *Mesuropetala*, according to Bechly *et al*, in prep.).

Historical biogeography

The extant Petaluridae exhibit a transpacific distributional pattern *(Tanypteryx* in Japan and the western U.S.A.; *Phenes* in Chile and Argentina; *Uropetala* in New Zealand and *Petalura* in Australia) with the sole exception of *Tachopteryx thoreyi,* which is probably a secondary immigrant in the eastern U.S.A. (Schmidt 1941: 235). Some characters and the biogeographical distribution would suggest that the genera *Phenes*, *Petalura* and *Uropetala* might form a monophyletic subgroup with a classic East Gondwana pattern of distribution. On the other hand there is substantial conflicting evidence that rather supports a sister-group relationship of *Phenes* and *Tachopteryx* which would then belong to a rather old Pan-American clade of Petaluridae. The only definite stem-group petalurids are from the Upper Jurassic of Germany and Kazakhstan, and the Lower Cretaceous of Brazil and England, thus neither of transpacific nor of Gondwana distribution at all. They indicate a minimum age or 'terminus post quem non' (Hennig 1966) of the Petalurida of 150 m. ya (Malm z).

The resulting cladogram of our computer analysis would suggest the hypothesis that the last common stem species of crown-group Petaluridae was a member of a formerly wider spread taxon inhabiting a northern Pacific area in the Cretaceous. Subsequently, the crown-group Petaluridae spread around the Pacific Ocean, giving rise to different species with an amphinotic distribution by dispersal and extinction, with *Tanypteryx* as a first branch with a plesiotypic distribution, then *Tachopteryx* which spread to the eastern U.S.A., followed by *Phenes* which spread to southern South America, from there an unknown ancestor of [*Petalura* + *Uropetala*] spread via the Antarctic land bridge to Australia, were *Petalura* branched of, and finally *Uropetala* reached New Zealand, probably by aerial dispersal. On the other hand the phylogeny preferred by us on the basis of an appropriate character weighting would suggest two independent dispersal routes: one route leading from a northern pacific area (*Tanypteryx*), to the eastern U.S.A. (*Tachopteryx*) and down to Patagonia (*Phenes*), and a second route of uncertain northern Pacific origin leading to an Australian clade (*Petalura*) and a subsequent aerial dispersal from Australia to New Zealand (*Uropetala*). The strange fact that petalurids are absent on Tasmania is curious but not an obstacle, since it might be explained by simple contingence (Ray Andress, pers. comm.), just like the absence of Austropetaliida from New Zealand although they are present in Patagonia, Australia and Tasmania. *Protolindenia*, *Cretapetalura*, and *Aeschnogomphus* + *Aktassia* successively branched from the stem line before the rise of extant Petaluridae and consequently were not confined to the circum-Pacific biota, representing random samples of the former widespread stem-group of the Petaluridae. Carle's (1995: 397) hypothesis of a northern (Tachopteryginae) and southern (Petalurinae) clade as result of an alleged trans-pangaeian montane dispersal in the Mesozoic is in conflict with both alternative phylogenies as well as with the fossil record, and therefore has to be regarded as rather dubious.

ACKNOWLEDGEMENTS

We are most grateful to Dr. Günter Viohl (Director of the Jura-Museum, Eichstätt), Prof. Giovanni Pinna (Director of the Museo Civico di Storia Naturale, Milano), Dr. Helmut Mayr (Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich), Dr. Erika Pietrzeniuk (Museum für Naturkunde, Berlin), Dr. Gerd Dietl and Dr. Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart), Dr. Philip Perkins (MCZ, Cambridge), Dr. Vladimir Zherikhin (Director of the Russian Palaeoentomological Laboratory, Moscow) for their friendly support and loan of the material for this study. Our sincere thanks to Ray Andress (London, UK) for numerous personal communications on petalurid morphology, systematics and biogeography, and to Dr. Erich Weber (Inst. Zoology, Univ. Tübingen, FRG), who made many helpful comments on an early draft of this manuscript. Furthermore we thank Rosser Garrison (Azusa, CA, U.S.A.) and Carl Cook (Center, KY, U.S.A.) for informations concerning the present location of holotypes. Also, thanks to Mr. P. Crabb (NHM) for the photographs of NHM material.

This study forms part of a dissertation project of the second author G. Bechly which is financed by the 'Graduiertenförderung' of the state Baden-Württemberg (Germany). It was supported by DGICYT (Promocion General del conocimiento, PB93-0284), the European Union (Human Capital and Mobility Program, CHRXCT930164) and the European Science Foundation Project of Workshop 'Fossil Insects', for X. Martínez-Delclòs, A. Nel and E.A. Jarzembowski. It is PRIS contribution n° 000 for E.A. Jarzembowski.

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A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida)
Paleontologia Lombarda della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano
Nuova serie - Volume X - 1998

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