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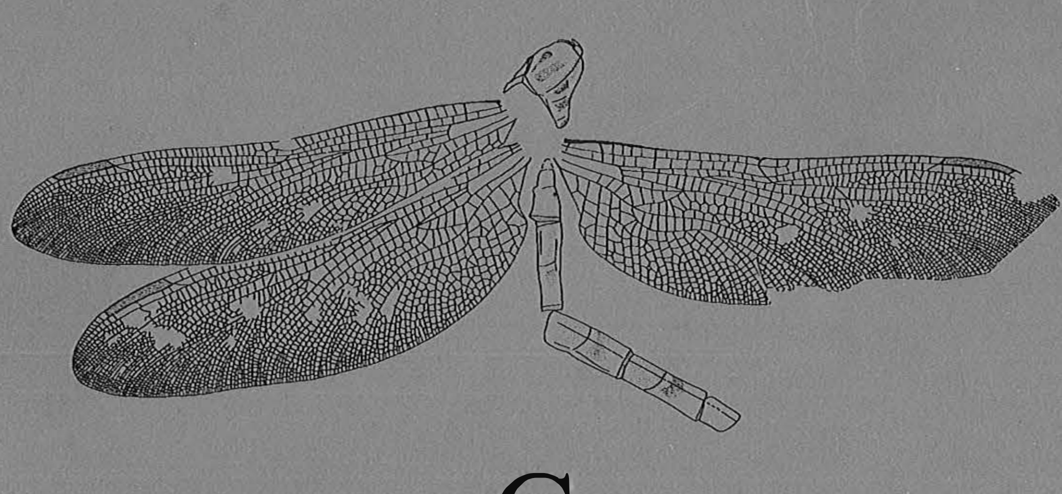

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Günter Bechly, André Nel, Xavier Martínez-Delclòs, Edmund A. Jarzembowski, Robert Coram, David Martill, Günther Fleck, François Escuillié, Max Martin Wisshak, Michael Maisch
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A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of numerous new taxa (Insecta: Odonata: Anisoptera)

Summary

All Mesozoic Aeshnoptera are revised and their phylogenetic relationships are reconstructed. The type species of the genus *Mesuropetala* is redescribed, and *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. is considered as its valid name instead of *Mesuropetala koehleri* (HAGEN, 1848). *Mesuropetala magna* sp. nov. is described from the Lower Cretaceous of Russia. "*Aeschna*" *antiqua* VAN DER LINDEN, 1827 and "*Aeschna*" *schmiedeli* GIEBEL, 1856 could be synonyms of *Mesuropetala muensteri* or *Protolindenia wittei*, and thus are here considered as nomina dubia in Anisoptera *incertae sedis*. *Cymatophlebiopsis pseudobubas* HANDLIRSCH, 1939 is regarded as junior subjective synonym of *Aeschnopsis perampla* (BRODIE, 1945), and the genus *Aeschnopsis* HANDLIRSCH, 1939 stat. restor. is transferred to Mesuropetalidae. *Necrogomphus jurassicus* (GIEBEL, 1856) from the Lower Cretaceous of England is attributed to the genus *Aeschnopsis*. Furthermore, two new species, *Aeschnopsis perkinsi* sp. nov. and *A. tischlingeri* sp. nov. are described from the Upper Jurassic of Germany. *Liupanshania* HONG, 1982 (*L. sijiensis* HONG, 1982) is transferred from Aeshnidae to a new family Liupanshaniidae fam. nov. that is regarded as sistergroup of Mesuropetalidae, and also includes the new taxa *Paramesuropetala gigantea* gen. et sp. nov. and *Araripeliupanshania annesusae* gen. et sp. nov. from the Lower Cretaceous of Brazil, *Paraliupanshania torvaldsi* gen. et sp. nov. and *P. rohdendorfi* sp. nov. from the lower Upper Cretaceous of Russia, and *Paraliupanshania britannica* sp. nov. from the Lower Cretaceous of England. *Progobiaeshna liaoningensis* gen. et sp. nov. is described from the Lower Cretaceous of China in a new family Progobiaeshnidae fam. nov. which is regarded as sistergroup of Aeshnida within Aeshnomorpha taxon nov. - Panaeshnida taxon nov. *Gobiaeshna* PRITYKINA, 1977 (*G. occulta* PRITYKINA, 1977) is preliminarily attributed to Progobiaeshnidae fam. nov. as well. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839) from the Upper Jurassic of Germany is redescribed and all Cymatophlebiidae are revised. Curious (autapomorphic) structures on the male abdomen of *Cymatophlebia* and *Rudiaeschna* are described in detail and their function is discussed. The phylogenetic position of Cymatophlebiidae within Anisoptera is discussed and seven new species are described: *Cymatophlebia kuempeli* sp. nov., *Cymatophlebia pumilio* sp. nov., *Cymatophlebia suevica* sp. nov., and *Cymatophlebia herrlenae* sp. nov. from the Upper Jurassic of Germany, as well as *Cymatophlebia purbeckensis* sp. nov., ?*Valdaeshna andressi* sp. nov., and *Prohoyaeshna milleri* gen. et sp. nov. from the Lower Cretaceous of England. "*Cymatophlebia*" *mongolica* COCKERELL, 1924 is transferred as nomen dubium to Anisoptera *incertae sedis*. *Libellulium* WESTWOOD, 1854 is rejected as synonym of *Cymatophlebia*, and its type species *L. agrias* WESTWOOD, 1854 is regarded as *nomen dubium*, probably belonging to Valdaeshninae subfam. nov. within Cymatophlebiidae. The two holotype specimens of *Cymatophlebia suevica* sp. nov., and *Cymatophlebia herrlenae* sp. nov. represent the first and currently sole fossil insect remains known from the Malm beta of the Swabian Alb in Southern Germany. These two new species furthermore have to be regarded as the oldest known crowngroup representatives of Anisoptera. With an estimated wing span of more than 220 mm, *Cymatophlebia suevica* sp. nov. and *Prohoyaeshna milleri* gen. et sp. nov. seem to represent the biggest Anisoptera and even the biggest crowngroup Odonata known at all. Rudiaeschnidae fam. nov. is proposed as new family for *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996 (Lower Cretaceous, China). This new family is regarded as sistergroup of Cymatophlebiidae and classified with the latter in a new superfamily Cymatophlebioidea stat. nov. *Paracymatophlebia splendida* gen. et sp. nov. from the Upper Jurassic of Kazakhstan is described in a new family Paracymatophlebiidae fam.

nov. which is regarded as sistergroup of Euaeshnida (together: Paneuaeshnida taxon nov.). Eumorbaeschnidae fam. nov. from the Upper Jurassic of Germany is proposed as most basal family of Euaeshnida, based on *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov. as "replacement" name for the aeshnid described by NEEDHAM (1907) under the incorrect name "*Morbaeschna muensteri*" because of a misidentified type species. The genus *Morbaeschna* NEEDHAM (1907) is synonymized with the genus *Mesuropetala*. *Anomalaeschna berndschusteri* gen. et sp. nov. (Lower Cretaceous, Brazil), *Paramorbaeschna araripensis* gen. et sp. nov. (Lower Cretaceous, Brazil), *Progomphaeschnaoides ursulae* gen. et sp. nov. and *Progomphaeschnaoides staniczeki* sp. nov. (Lower Cretaceous, Brazil), *Plesigomphaeschnaoides mongolensis* gen. et sp. nov. (Lower Cretaceous, Mongolia) and *Plesigomphaeschnaoides pindelskii* sp. nov. (Lower Cretaceous, England) are described within Neoaeshnida - Gomphaeschnidae in a new subfamily Gomphaeschnaoidinae subfam. nov. In the same group three new species, *Gomphaeschnaoides magnus* sp. nov., *Gomphaeschnaoides petersi* sp. nov., and *Gomphaeschnaoides betoreti* sp. nov. are described from the Lower Cretaceous of Brazil, together with a redescription of the type species *Gomphaeschnaoides obliquus*, including its previously unknown forewings and body. "*Gomphaeschna*" *paleocenica* and "*Gomphaeschna*" *danica* from the Palaeocene of Denmark are preliminarily transferred to the new genus *Plesigomphaeschnaoides* gen. nov. as well. *Sinojagoria imperfecta* gen. et sp. nov. is described from the Lower Cretaceous of China and regarded as most basal representative of Gomphaeschnaoidinae subfam. nov. ?*Gomphaeschna sibirica* sp. nov. and *Baissaeshna zherikhini* sp. nov. are described from the Lower Cretaceous of Russia. The genus *Cymatophlebiella* PRITYKINA, 1968 is excluded from Cymatophlebiidae and regarded as a basal Aeshnoptera *incertae sedis*; its type species *C. euryptera* PRITYKINA, 1968 is redescribed. Several taxonomic errors in LOHMANN (1996a-c) are corrected. Some general conclusions concerning the evolution and historic biogeography of Aeshnoptera are suggested, including an Mid-Jurassic Palaearctic origin and radiation of this monophylum.

Totally 26 genera and 52 species of fossil dragonflies are revised. The following new taxonomic decisions are found in this publication: 5 taxa nov., 5 fam. nov., 2 subfam. nov., 2 trib. nov., 12 gen. nov., 29 sp. nov., 8 syn. nov., 5 stat. nov., 6 comb. nov., 2 nom. correct., 3 stat. restor., 3 sensu nov., 5 pos. nov.

Key words: Insecta, Odonata, Anisoptera, Aeshnoptera, dragonflies, systematics, phylogeny, fossil, Upper Jurassic, Cretaceous, England, Wealden, Germany, Solnhofen, Nusplingen, Swabian Alb, Brazil, Araripe, China, Liaoning, Mongolia, Kazakhstan, Russia, Transbaikals.

Résumé

Une révision et étude phylogénétique des Aeshnoptera mésozoïques, avec description des nombreux nouvelles taxa (Insecta: Odonata: Anisoptera). - Tous les Aeshnoptera mésozoïques sont révisés et leur relations phylogénétiques réévaluées. L'espèce type du genre *Mesuropetala* est redécrite. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. est considérée comme nom valide en remplacement de *Mesuropetala koehleri* (HAGEN, 1848). *Mesuropetala magna* sp. nov. est décrit du Crétacé inférieur de Russie. „*Aeschna*" *antiqua* VAN DER LINDEN, 1827 et „*Aeschna*" *schmiedeli* GIEBEL, 1856 sont peut-être des synonymes des *Mesuropetala muensteri* out *Protolindenia wittei*, et donc sont ici considéré comme nomina dubia dans Anisoptera *incertae sedis*. *Cymatophlebiopsis pseudobubas* HANDLIRSCH, 1939 est considérée comme synonyme subjectif de *Aeschnopsis perampla* (BRODIE, 1945), et le genre *Aeschnopsis* HANDLIRSCH, 1939 stat. restor. est transféré aux Mesuropetalidae. *Necrogomphus jurassicus* (GIEBEL, 1856) du Crétacé inférieur anglais est attribué aux genre *Aeschnopsis*. En plus, deux nouvelles espèces, *Aeschnopsis perkinsi* sp. nov. et *A. tischlingeri* sp. nov. sont décrites du Jurassique supérieur d'Allemagne. *Liupanshania* HONG, 1982 (*L. sijiensis* HONG, 1982) est transféré des Aeshnidae vers une nouvelle famille Liupanshaniidae fam. nov., considérée comme le groupe frère des Mesuropetalidae, et comprend aussi les nouveaux taxa *Paramesuropetala gigantea* gen. et sp. nov. et *Araripeliupanshania annesusae* gen. et sp. nov. du Crétacé inférieur du Brésil, *Paraliupanshania torvaldsi* gen. et sp. nov. et *P. rohdendorfi* sp. nov. du Crétacé supérieur bas de Russie, et *Paraliupanshania britannica* sp. nov. du Crétacé inférieur d'Angleterre. *Progobiaeshna liaoningensis* gen. et sp. nov. est décrit du Crétacé inférieur de Chine, dans une nouvelle famille Progobiaeshnidae fam. nov., considérée comme le groupe frère des Aeshnida au sein des Aeshnomorpha taxon nov. - Panaeshnida taxon nov. *Gobiaeshna* PRITYKINA, 1977 (*G. occulta* PRITYKINA, 1977) est provisoirement attribué aux Progobiaeshnidae fam. nov. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839) du Jurassique supérieur d'Allemagne est redécrit. Tous les Cymatophlebiidae sont révisés. De curieuses structures autapomorphes portée par les abdomens des mâles de *Cymatophlebia* et *Rudiaeschna* sont décrites en détail et leur fonction est discutée. La position phylogénétique des Cymatophlebiidae au sein des Anisoptera est discutée et sept nouvelles espèces sont décrites: *Cymatophlebia kuempeli* sp. nov., *Cymatophlebia pumilio* sp. nov., *Cymatophlebia suevica* sp. nov. et *Cymatophlebia herrlenae* sp. nov. du Jurassique supérieur d'Allemagne, ainsi que *Cymatophlebia purbeckensis* sp. nov., ?*Valdaeshna andressi* sp. nov. et *Prohoyaeshna milleri* gen. et sp. nov. du Crétacé inférieur d'Angleterre. „*Cymatophlebia*" *mongolica* COCKERELL, 1924 est transférée comme nomen dubium dans les Anisoptera *incertae sedis*. La synonymie de *Libellulium* WESTWOOD, 1854 avec *Cymatophlebia* est rejetée; l'espèce type *L. agrias* WESTWOOD, 1854 est considéré comme un *nomen dubium*, probablement proche des Valdaeshninae subfam. nov. au sein des Cymatophlebiidae. Les deux spécimens holotypes de *Cymatophlebia suevica* sp. nov. et *Cymatophlebia herrlenae* sp. nov. représenter les premiers et actuellement seul insectes fossiles connu du Malm beta d'Alb Souabe d'Allemagne sud. Ces deux nouvelles espèces sont considérés comme les plus vieux représentants de „groupe couronne„ d'Anisoptera. Avec une estimé ouverture d'ailes de plus de 220 mm, *Cymatophlebia suevica* sp. nov. et *Prohoyaeshna milleri* gen. et sp. nov. semble de représenter les plus grandes Anisoptera et même les plus grandes représentants de „groupe couronne" d'Odonata connu en général. La nouvelle famille des Rudiaeschnidae fam. nov. est proposée pour *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996 (Crétacé inférieur, Chine). Cette nouvelle famille est considérée comme le groupe frère des Cymatophlebiidae et classée avec cette dernière dans la nouvelle superfamille des Cymatophlebioidea stat. nov. *Paracymatophlebia splendida* gen. et sp. nov. du Jurassique supérieur du Kazakhstan est décrit dans la famille nouvelle Paracymatophlebiidae fam. nov., considérée comme le groupe frère des Euaeshnida (réunis dans les Paneuaeshnida taxon nov.). Les Eumorbaeschnidae fam. nov. du Jurassique supérieur d'Allemagne sont proposés comme la famille la plus basale des Euaeshnida, basée sur *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov., désigné comme nom de remplacement pour l'aeshne décrit par NEEDHAM (1907) sous le nom incorrect „*Morbaeschna muensteri*" à cause d'une erreur d'identification de l'espèce type. Le genre *Morbaeschna* NEEDHAM (1907) est mis en synonymie avec le genre *Mesuropetala*. *Anomalaeschna berndschusteri* gen. et sp. nov. (Crétacé inférieur, Brésil), *Paramorbaeschna araripensis* gen. et sp. nov. (Crétacé inférieur, Brésil), *Progomphaeschnaoides ursulae* gen. et sp. nov. et *Progomphaeschnaoides staniczeki* sp. nov.(Crétacé inférieur, Brésil), *Plesigomphaeschnaoides mongolensis* gen. et sp. nov. (Crétacé inférieur, Mongolie) et *Plesigomphaeschnaoides pindelskii* sp. nov. (Crétacé inférieur, Angleterre) sont décrits au sein des Neoaeshnida - Gomphaeschnidae dans une nouvelle sous-famille Gomphaeschnaoidinae subfam. nov. Dans le même groupe, trois nouvelles espèces, *Gomphaeschnaoides magnus* sp. nov., *Gomphaeschnaoides petersi* sp. nov. et *Gomphaeschnaoides betoreti* sp. nov. sont décrites du Crétacé inférieur du Brésil, avec une redescription de l'espèce type *Gomphaeschnaoides obliquus*, dont les structures des ailes antérieures et du corps sont décrites pour la première fois. „*Gomphaeschna*" *paleocenica* et „*Gomphaeschna*" *danica* du Paléocène du Danemark sont, en première analyse, transférés dans le nouveau genre *Plesigomphaeschnaoides* gen. nov. *Sinojagoria imperfecta* gen. et sp. nov. est décrit du Crétacé inférieur de Chine et considéré comme le représentant le plus basal de Gomphaeschnaoidinae subfam. nov. ?*Gomphaeschna sibirica* sp. nov. et *Baissaeshna zherikhini* sp. nov. sont décrits du Crétacé inférieur de Russie. Le genre *Cymatophlebiella* PRITYKINA, 1968 est exclu des Cymatophlebiidae et considéré comme un Aeshnoptera basale *incertae sedis*; l'espèce type *C. euryptera* PRITYKINA, 1968 est redécrite. Plusieurs erreurs dans LOHMANN (1996a-c) sont corrigées. Quelques conclusions générales sur l'évolution de la biogéographie historique des Aeshnoptera sont proposées, y compris une origine paléarctique et une radiation de ce phylum au Jurassique moyen.

Tous ensemble 26 genres et 52 espèces des libellules fossiles sont revisées. Les nouvelles décisions taxonomiques suivantes sont trouvées dans cette publication: 5 taxa nov., 5 fam. nov., 2 subfam. nov., 2 trib. nov., 12 gen. nov., 29 sp. nov., 8 syn. nov., 5 stat. nov., 6 comb. nov., 2 nom. correct., 3 stat. restor., 3 sensu nov., 5 pos. nov.

Mots clefs: Insecta, Odonata, Anisoptera, Aeshnoptera, libellules, systématique, phylogénie, fossile, Jurassique supérieur, Crétacé, Angleterre, Wealden, Allemagne, Solnhofen, Nusplingen, Alb Souabe, Brazilie, Araripe, Chine, Liaoning, Mongolie, Kazakhstan, Russie, Transbaikals.

Zusammenfassung

Eine Revision und phylogenetische Untersuchung der mesozoischen Aeshnoptera, mit Beschreibung zahlreicher neuer Taxa (Insecta: Odonata: Anisoptera). - Alle mesozoischen Aeshnoptera werden revidiert und ihre phylogenetischen Verwandtschaftsbeziehungen rekonstruiert. Die Typusart der Gattung *Mesuropetala* wird wiederbeschrieben, und *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. wird an Stelle von *Mesuropetala koehleri* (HAGEN, 1848) als deren gültiger Name erkannt. *Mesuropetala magna* sp. nov. wird aus der Unterkreide Russlands beschrieben. „*Aeschna*" *antiqua* VAN DER LINDEN, 1827 und „*Aeschna*" *schmiedeli* GIEBEL, 1856 könnten Synonyme von *Mesuropetala muensteri* oder *Protolindenia wittei* sein, und werden hier somit als nomina dubia in Anisoptera *incertae sedis* erachtet. *Cymatophlebiopsis pseudobubas* HANDLIRSCH, 1939 wird als subjektives Juniorsynonym von *Aeschnopsis perampla* (BRODIE, 1945) angesehen und die Gattung *Aeschnopsis* HANDLIRSCH, 1939 stat. restor. zu den Mesuropetalidae gestellt. *Necrogomphus jurassicus* (GIEBEL, 1856) aus der Unterkreide Englands wird der Gattung *Aeschnopsis* zugeordnet. Außerdem werden zwei neue Arten, *Aeschnopsis perkinsi* sp. nov. und *A. tischlingeri* sp. nov., aus dem Oberen Jura Deutschlands beschrieben. *Liupanshania* HONG, 1982 (*L. sijiensis* HONG, 1982) wird von den Aeshnidae in eine neue Familie Liupanshaniidae fam. nov. überführt, die als Schwestergruppe der Mesuropetalidae angesehen wird, und auch die neuen Taxa *Paramesuropetala gigantea* gen. et sp. nov. und *Araripeliupanshania annesusae* gen. et sp. nov. aus der Unterkreide Brasiliens, *Paraliupanshania torvaldsi* gen. et sp. nov. und *P. rohdendorfi* sp. nov. aus der unteren Oberkreide Russlands, sowie *Paraliupanshania britannica* sp. nov. aus der Unterkreide Englands, umfasst. *Progobiaeshna liaoningensis* gen. et sp. nov. wird aus der Unterkreide Chinas in einer neuen Familie Progobiaeshnidae fam. nov. beschrieben, die als Schwestergruppe der Aeshnida innerhalb der Aeshnomorpha taxon nov. - Panaeshnida taxon nov. angesehen wird. *Gobiaeshna* PRITYKINA, 1977 (*G. occulta* PRITYKINA, 1977) wird vorläufig ebenfalls zu den Progobiaeshnidae fam. nov. gestellt. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839) aus dem Oberen Jura Deutschlands wird wiederbeschrieben und alle Cymatophlebiidae revidiert. Merkwürdige (autapomorphe) Strukturen am männlichen Abdomen von *Cymatophlebia* und *Rudiaeschna* werden detailliert beschrieben und deren Funktion diskutiert. Die phylogenetische Stellung der Cymatophlebiidae innerhalb der Anisoptera wird diskutiert und sieben neue Arten beschrieben: *Cymatophlebia kuempeli* sp. nov., *Cymatophlebia pumilio* sp. nov., *Cymatophlebia suevica* sp. nov. und *Cymatophlebia herrlenae* sp. nov. aus dem Oberen Jura Deutschlands, sowie *Cymatophlebia purbeckensis* sp. nov., ?*Valdaeshna andressi* sp. nov. und *Prohoyaeshna milleri* gen. et sp. nov. aus der Unterkreide Englands. „*Cymatophlebia*" *mongolica* COCKERELL, 1924 wird als nomen dubium zu den Anisoptera *incertae sedis* transferiert. *Libellulium* WESTWOOD, 1854 wird als Synonym von *Cymatophlebia* abgelehnt und die Typusart *L.*

agrias WESTWOOD, 1854 wird als *nomen dubium* angesehen, wahrscheinlich zu den Valdaeshninae subfam. nov. innerhalb der Cymatophlebiidae gehörend. Die zwei Holotypusexemplare von *Cymatophlebia suevica* sp. nov. und *Cymatophlebia herrlenae* sp. nov. stellen die ersten und bislang einzigen fossilen Insektenreste aus den Malm beta der Schwäbischen Alb in Süddeutschland dar. Diese zwei neuen Arten sind zudem als älteste bekannte Kronengruppenvertreter der Anisoptera anzusehen. Mit einer geschätzten Flügelspannweite von mehr als 220 mm scheinen *Cymatophlebia suevica* sp. nov. und *Prohoyaeshna milleri* gen. et sp. nov. die größten Anisoptera und sogar die größten Kronengruppen-Anisoptera zu sein, die überhaupt bekannt sind. Rudiaeschnidae fam. nov. wird als neue Familie für *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996 (Unterkreide Chinas) vorgeschlagen. Diese neue Familie wird als Schwestergruppe der Cymatophlebiidae angesehen und gemeinsam mit letzterer in einer neuen Überfamilie Cymatophlebioidea stat. nov. klassifiziert. *Paracymatophlebia splendida* gen. et sp. nov. wird aus dem Oberen Jura von Kasachstan in einer neuen Familie Paracymatophlebiidae fam. nov. beschrieben, die als Schwestergruppe der Euaeshnida angesehen wird (zusammen: Paneuaeshnida taxon nov.). Aus dem Oberen Jura Deutschlands werden die Eumorbaeschnidae fam. nov. als basalste Familie der Euaeshnida vorgeschlagen, basierend auf *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov., als „Ersatzname" für diejenige Aeshnide, die von NEEDHAM (1907) unter dem falschen Namen „*Morbaeschna muensteri*" beschrieben wurde, wegen einer Fehlbestimmung der Typusart. Die Gattung *Morbaeschna* NEEDHAM (1907) wird mit der Gattung *Mesuropetala* synonymisiert. *Anomalaeschna berndschusteri* gen. et sp. nov. (Unterkreide von Brasilien), *Paramorbaeschna araripensis* gen. et sp. nov. (Unterkreide von Brasilien), *Progomphaeschnaoides ursulae* gen. et sp. nov. und *Progomphaeschnaoides staniczeki* sp. nov. (Unterkreide von Brasilien), sowie *Plesigomphaeschnaoides mongolensis* gen. et sp. nov. (Unterkreide der Mongolei) und *Plesigomphaeschnaoides pindelskii* sp. nov. (Unterkreide von England) werden innerhalb der Neoaeshnida - Gomphaeschnidae in einer neuen Unterfamilie Gomphaeschnaoidinae subfam. nov. beschrieben. In der gleichen Gruppe werden die drei neuen Arten *Gomphaeschnaoides magnus* sp. nov., *Gomphaeschnaoides petersi* sp. nov. und *Gomphaeschnaoides betoreti* sp. nov. aus der Unterkreide Brasiliens beschrieben, ergänzt durch eine Wiederbeschreibung der Typusart *Gomphaeschnaoides obliquus*, einschließlich deren Vorderflügel und Körpers. „*Gomphaeschna*" *paleocenica* und „*Gomphaeschna*" *danica* aus dem Paläozän von Dänemark werden vorläufig ebenfalls zu der neuen Gattung *Plesigomphaeschnaoides* gen. nov. gestellt. *Sinojagoria imperfecta* gen. et sp. nov. wird aus der Unterkreide Chinas beschrieben und als basalster Vertreter der Gomphaeschnaoidinae subfam. nov. angesehen. ?*Gomphaeschna sibirica* sp. nov. und *Baissaeshna zherikhini* sp. nov. werden aus der Unterkreide Russlands beschrieben. Die Gattung *Cymatophlebiella* PRITYKINA, 1968 wird von den Cymatophlebiidae zu den basalen Aeshnoptera *incertae sedis* transferiert und deren Typusart *C. euryptera* PRITYKINA, 1968 wird wiederbeschrieben. Eine Reihe von taxonomischen Fehlern in LOHMANN (1996a-c) werden korrigiert. Einige allgemeine Schlussfolgerungen betreffend die Evolution und historische Biogeographie der Aeshnoptera werden erörtert, einschließlich eines mitteljurassischen, paläarktischen Ursprunges und Radiation dieses Monophylums.

Insgesamt werden 26 Gattungen und 52 Arten fossiler Großlibellen revidiert. Folgende neue taxonomische Entscheidungen finden sich in dieser Veröffentlichung: 5 taxa nov., 5 fam. nov., 2 subfam. nov., 2 trib. nov., 12 gen. nov., 29 sp. nov., 8 syn. nov., 5 stat. nov., 6 comb. nov., 2 nom. correct., 3 stat. restor., 3 sensu nov., 5 pos. nov.

Schlüsselwörter: Insecta, Odonata, Anisoptera, Aeshnoptera, Libellen, Systematik, Phylogenie, fossil, Oberer Jura, Kreide, England, Wealden, Deutschland, Solnhofen, Nusplingen, Schwäbische Alb, Brasilien, Araripe, China, Liaoning, Mongolei, Kasachstan, Russland, Transbaikals.

Contents

1. Introduction

Odonates or dragonflies *sensu lato* include about 5.600 fossil and extant species and are known since the lowermost Carboniferous (320 mybp). Although, they belong to the oldest groups of winged insects, and possess numerous "primitive" characters (symplesiomorphies), they also possess highly derived structures, such as the prehensile mask of the larvae, or the secondary genital apparatus of adult males. Anisoptera or dragonflies *sensu stricto* are known since the Lower Jurassic and include about half of the known odonate species. They now belong to the most popular insects, because of their relatively large size, their colourful appearance, their acrobatic flight capabilities, and their conspicuous mating behaviour ("mating wheel"). Fossil dragonflies belong to the most spectacular fossil insects and are very much desired by collectors. Therefore, the phylogeny of fossil dragonflies tends to raise a broader interest than the phylogenetic issues of many other insect groups.

Based on a broad phylogenetic analysis of fossil and extant odonates, BECHLY (1996, 1999a, b), recently proposed a new phylogenetic classification of Anisoptera, partly based on previous results by BECHLY (1995) and NEL *et al.* (1998). According to these results the most ancient groups of Pananisoptera seem to be Liassogomphidae, Aeschnidiidae, Petalurida, and Aeshnoptera (aeshnoid-like dragonflies) which are all rather common in the fossil record of the Mesozoic (NEL *et al.* 1994). NEL *et al.* (1993) and NEL & MARTÍNEZ-DELCLÒS (1993a) provided a first revision of the stemgroup clades Liassogomphidae and Aeschnidiidae. All alleged and genuine fossil Petalurida are revised by NEL *et al.* (1998). Our studies of numerous collections and the discovery of interesting new specimens now also allows a substantial and profound revision of all Mesozoic Aeshnoptera, including the description of numerous new taxa, as well as a phylogenetic analysis, and an attempt towards the solution of some complicated taxonomic problems, mainly concerning "*Morbaeschna*" *muensteri* (*sensu* NEEDHAM 1907) that is here redescribed under the new valid name *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov. Furthermore, our revision of the available material of Mesozoic Aeshnoptera also revealed that the aeshnoid-like dragonflies were much more diversified in the Upper Jurassic and Lower Cretaceous than previously expected: In this study we describe 12 new genera and 29 new species, as well as numerous higher taxa. Of some taxa (viz *Mesuropetala muensteri* comb. nov., *Cymatophlebia longialata*, *Eumorbaeschna jurassica* gen. et comb. nov., and *Gomphaeschnaoides obliquus*) we supply detailed descriptions and figures of several well-preserved specimens to provide evidence for the study of variability of wing venational characters in fossil dragonflies, which was hardly available before. In the past this aspect has been largely neglected, since only the type specimens have been described in detail, and even those often only rather briefly.

An important part of this work is the revision of the well-known genus *Cymatophlebia* DEICHMÜLLER, 1886. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839) is one of the most common dragonflies in the Upper Jurassic of Solnhofen (Bavaria, Germany). Consequently, it should be expected to represent one of the best known taxa, too, but this is not the case at all. NEL & PAICHELER (1992: 316-317) already mentioned several inconsistencies in the published figures and descriptions of *Cymatophlebia* by GERMAR (1839), MEUNIER (1898), HANDLIRSCH (1906-08), and CARPENTER (1932). Our studies of numerous male and female specimens in the collections of the Museum of Comparative Zoology in Cambridge, the Bayerische Staatssammlung für Paläontologie und Historische Geologie München in Munich, and the Jura-Museum in Eichstätt, as well as several other German official and private collections, allowed the clarification of several poorly known features of the venation and the unique abdominal lobes. On the basis of these observations we developed a more precise diagnosis of the genus *Cymatophlebia* and the family Cymatophlebiidae, as well as their position in the phylogenetic system of dragonflies. Furthermore, we have discovered five new species of *Cymatophlebia* and two new species of Cymatophlebiidae - Valdaeshninae subfam. nov., and we also propose the new family Rudiaeschnidae fam. nov. that seems to be the sistergroup of Cymatophlebiidae.

2. Material and methods

The results of this study are based on several years of thorough examination of many hundred fossil dragonfly specimens from various Mesozoic outcrops in numerous museums and private collections (see Table 1), mainly in Germany, France, England, Spain, Russia, Japan and the U.S.A. We indicated the deposition of all studied specimens, and we tried to provide collection numbers for all specimens, but this was not possible in several cases. However, such numbers are provided for all holotypes, almost all paratypes (with two exceptions), and most voucher specimens. The remaining specimens can be clearly recognized according to our descriptions and figures, even if no number should be available.

AMNH	American Museum of Natural History, New York, U.S.A.
BMBN	Booth Museum of Natural History, Brighton, U.K.
BMM	Bürgermeister Müller Museum, Solnhofen, Germany
BSP	Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany
CMNH	Carnegie Museum of Natural History, Pittsburgh, U.S.A.
JME	Jura-Museum, Eichstätt, Germany
GPIT	Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität, Tübingen, Germany
LEIUG	Leicester University Geology Department, Leicester, U.K.
MNEMG	Maidstone Museum & Art Gallery, Maidstone, Kent, U.K.
MB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
MNHN	Laboratoire de Paléontologie, Museum National d'Histoire Naturelle, Paris, France
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.
BMNH	Natural History Museum (ex British Museum of Natural History), London, U.K.
NMV	Naturhistorisches Museum Wien, Vienna, Austria
NSM	National Science Museum, Tokyo, Japan
PIN	Palaeoentomological Institute, Academy of Science, Moscow, Russia
SMF	Senckenberg Museum, Frankfurt, Germany
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
SMNS	Museum am Löwentor, Staatliches Museum für Naturkunde, Stuttgart, Germany
coll. BERGÉR	private collection and museum of Georg BERGÉR, Eichstätt, Germany
coll. BÜRGER	private collection of Peter BÜRGER, Bad Hersfeld, Germany
coll. KÜMPEL	private collection of Dieter KÜMPEL, Wuppertal, Germany
coll. LEICH	collection of Helmut LEICH at the "Fossilium" of the Zoological Garden, Bochum, Germany
coll. MURATA	private collection of Yasutaka MURATA, Kyoto, Japan
coll. *ms-fossil*	commercial collection of *ms-fossil*, Sulzbachtal, Germany
coll. ROCKERS	commercial collection of *PaleoSearch Inc.*, G.F. ROCKERS, Hays, U.S.A.
coll. TISCHLINGER	private collection of Helmut TISCHLINGER, Stammham, Germany

Table 1. Alphabetical list of used codens for collections.

Nearly all original drawings were made with a camera lucida, and most photographs were made with a SLR camera with macro-lens. A few drawings (e.g. of *Araripeliupanshania* gen. nov.) were made after macro-photographs, and some fossils have been scanned directly with a flatbed scanner. All drawings and photos have been scanned (300 * 600 dpi) and improved with the GIMP image processing software for Linux. Most measurements were taken from our figures (or from published figures) of the specimens, since the measurements are more facile and more precise from camera lucida drawings and/or macro photographs than from the original specimens, due to the effect of magnification. The measurements always refer to the maximum values, if not otherwise indicated (e.g. «width of forewing, 11 mm» refers to the broadest part of the forewing, contrary to «width of forewing at nodus, 9 mm»). The distances between nodus and pterostigma generally have been measured from the nodal furrow to the middle of the basal margin of the pterostigma, since the latter is distinctly oblique in most Anisoptera. The length of the pterostigma has been measured from the middle of the basal margin to the middle of the distal margin.

We use the wing venation nomenclature of RIEK (1976) and RIEK & KUKALOVÁ-PECK (1984), amended by KUKALOVÁ-PECK (1991), NEL *et al.* (1993) and BECHLY (1995, 1996) (see Table 2 and Text-Fig.1), and we follow the new phylogenetic classification of Anisoptera proposed by BECHLY (1996), amended by BECHLY (1999a, b). For the systematic analysis and classification we strictly follow the principles of consequent Phylogenetic Systematics (*sensu* HENNIG 1966, 1981), rather than so-called "numerical cladistics" (for reasons see WÄGELE 1994, BORUCKI 1996, and BECHLY 1999a, b). All recognized monophyla have been named, since we reject the sequencing of stemgroup representatives because of the logical and practical reasons described by WILLMANN (1989). For each proposed taxon of Aeshnoptera a recommended usage (list of included taxa) and a list of the concerning autapomorphies (the synapomorphies of its members) is provided. The assignment of formal categorical ranks has been omitted as far as possible (above the family group level) without violation of the International Rules of Zoological Nomenclature, because they are arbitrary and superfluous (WILLMANN 1989). The same applies to redundant taxa that have only been proposed in the family-group, in a few cases of genera that are sistergroups of higher taxa, since the family-group belongs to the so-called "obligatory" categorical ranks.

Although we concur with the time-biospecies concept (*sensu* HENNIG 1966), we of course had to apply a largely morphological species concept. The variability of wing venational characters among extant dragonfly species has been used as "rule of the thumb" criterion to estimate whether certain differences may be due to intraspecific variability, or have to be regarded as evidence for different specific identity. We tried to find autapomorphic characters for all proposed new species taxa, so that the latter should generally be monophyletic groups in case that they include several biospecies that could not be recognized from the fossil material.

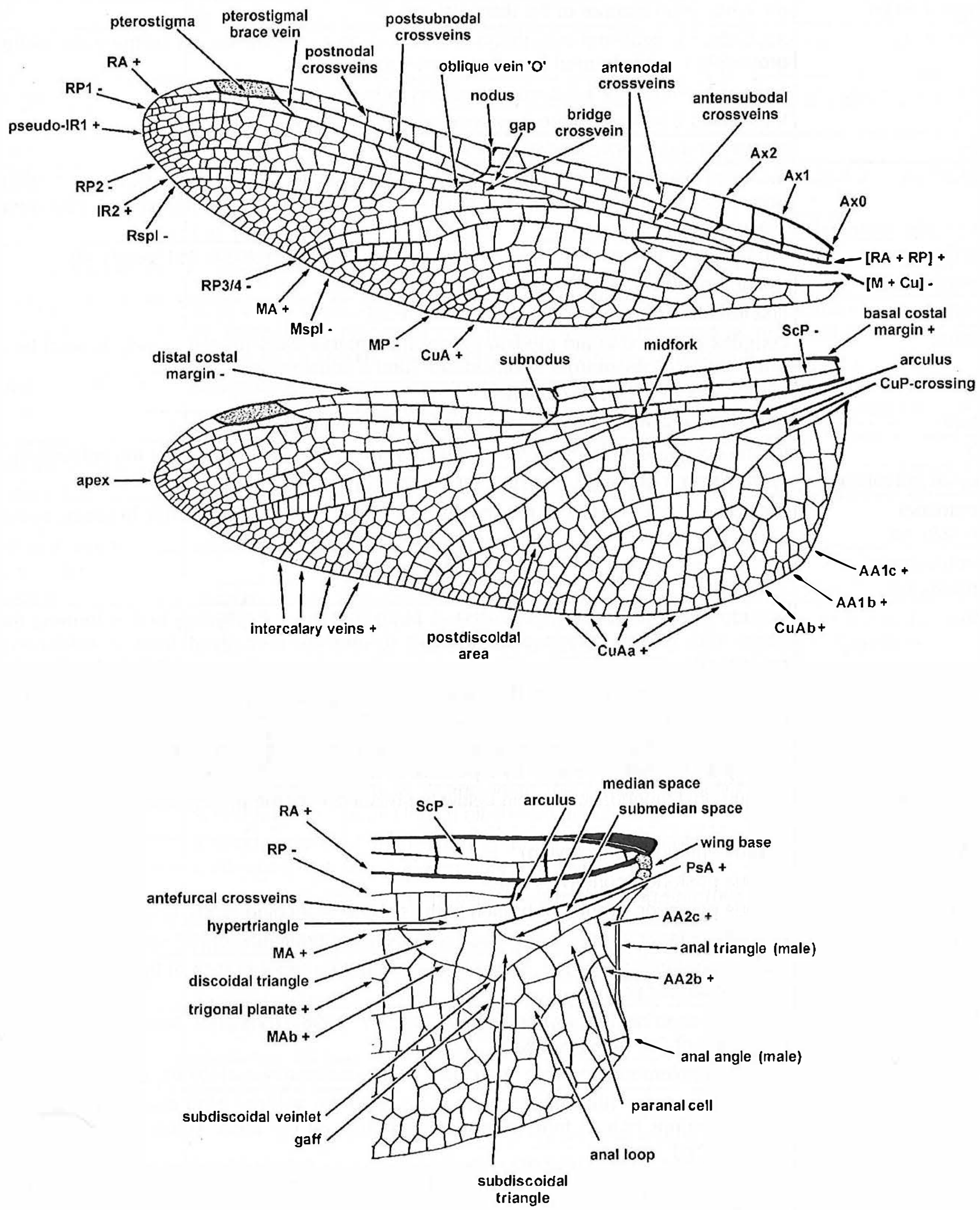
In case of doubtful attribution, a question mark is put in front of the concerning taxon. In case of doubtful attribution of a specimen to a certain species, the specific name is followed by a question mark. Presumably not monophyletic or otherwise invalid taxa are indicated by the use of quotation marks. The term *incertae sedis* is used to indicate taxa of uncertain phylogenetic position.

The synonymy lists include all taxonomic references to the concerning taxon we could find. In accordance with RICHTER (1948) the reference to the valid original description of a taxon is indicated by an asterisk (*) in front; citations that refer to material that was studied by us are indicated by the letter "v" in front; specimens that have been identified without doubt are indicated by a point (.) in front; citations of specimens that are doubtfully attributed to the concerning taxon are indicated by a question mark (?) in front; citations of specimens that were incorrectly attributed to the concerning taxon are indicated by the letter "n" (for "non") in front; and citations that only mention the concerning taxa, but do not describe or feature actual specimens, are indicated by an italic publication year. All citations of articles of IRZN refer to the recent fourth edition of the code.

AA	Analis anterior (convex vein)
AAa	main branch of Analis anterior between PsA and subdiscoidal veinlet (CuA) (convex vein)
AA1b	the posterior branch of AA that is forming the basal margin of the anal loop in the hindwing (convex vein)
AA1c	the posterior branch of AA below PsA, basal of AA1b (convex vein)
AA2b	the posterior branch of AA that is forming the distal margin of the anal triangle in the male hindwing (convex vein)
AA2c	the posterior branch of AA that is dividing the anal triangle in the male hindwing (convex vein)
anal angle	kink in the postero-basal margin of the male hindwing
anal loop	area in the hindwing, anteriorly delimited by AA + CuP, distally delimited by the most basal posterior branch of CuA (CuAb), basally delimited by the most distal posterior branch of AA (AA1b), and posteriorly delimited by an enforced crossvein
anal triangle	triangular area at the base of the male hindwing, basally delimited by the basal wing margin, and distally delimited by the most basal posterior branch of AA (AA2b)
antefurcal crossveins	crossveins between RP and MA basal of midfork and distal of arculus
antenodal crossveins	crossveins between costal margin and ScP (first row), and between ScP and RA (second row), basal of nodus
antesubnodal crossveins	crossveins between RA and RP basal of subnodus and distal of arculus
arculus	composite structure near the wing base, the anterior part is formed by the base of RP + MA, the posterior part is formed by a crossvein (arcular crossvein or basal discoidal crossvein) that is homologous with the basal side of the quadrangle in Zygoptera
AP	Analis posterior (fused to the basal wing margin; originally a concave vein)
Ax0	basal brace (formed by the arched Subcosta anterior ScA and an aligned crossvein)
Ax1	basal primary antenodal crossvein
Ax2	distal primary antenodal crossvein
Bqs	bridge-crossveins (here restricted to the crossveins between RP and IR2 basal of subnodus, thus, not including all crossveins basal of the first oblique vein 'O')
concave vein (-)	a longitudinal vein that is running in the depression of a wing fold (low vein; not to be confused with a concave curvature of a vein)
convex vein (+)	a longitudinal vein that is running on top of a wing fold (high vein; not to be confused with the convex curvature of a vein)
CA	Costa anterior (part of the composite anterior wing margin; originally a convex vein)
costal margin (C)	the enforced anterior wing margin (the costal margin basal of the nodus is convex and formed by the fusion of CA, CP and ScA', while the costal margin distal of the nodus is neutral or concave and formed by the fusion of CA, ScA, and ScP)
CP	Costa posterior (part of the composite anterior wing margin basal of nodus; originally a concave vein)
CuA	Cubitus anterior (convex vein)
CuAa	the main branch of CuA in the hindwing, distal of its first branching (convex vein)
CuAb	the first posterior branch of CuA in the hindwing (convex vein)
cubito-anal crossvein	accessory crossveins in the submedian space (not including the CuP-crossing and PsA)
CuP-crossing	the crossvein-like vestige of the Cubitus posterior (= anal-crossing *sensu* TILLYARD and FRASER 1940; originally a concave vein)
discoidal triangle	a characteristical triangular cell (= triangle *sensu* auct.) in the discoidal area of Anisoptera
gaff	basal part of CuA between the subdiscoidal veinlet (CuA) and the first branching of CuA (convex vein)
gap	area without crossveins between two longitudinal veins which normally is traversed by crossveins (e.g. the "cordulegastrid-gap" basal of the subnodus in Cavilabiata and Gomphaeschnidae)

hypertriangle	triangular area anterior of the discoidal triangle
intercalary	secondary longitudinal vein that does not belong to the main longitudinal veins of the groundplan, but is formed from the cross-venation
IR1	(primary) Interradius 1 (convex intercalary vein between RP1 and RP2)
IR2	Interradius 2 (convex intercalary vein between RP2 and RP3/4)
MA	Media anterior (convex vein)
MAb	the distal side of the discoidal triangle (= MA2 *sensu* NEL & MARTÍNEZ-DELCLÒS 1993a), homologous with the distal discoidal vein (distal side of quadrangle) of Zygoptera (convex vein)
median space	area basal of the arculus, between RA + RP and M + Cu (also called basal cell)
membranule	membraneous area at the basal wing margin
midfork	first furcation of vein RP into RP1/2 and RP3/4
nodus	complex structure in the median part of the anterior wing margin, mainly formed by a break in the costal margin, a kink in ScP, and a nodal veinlet
MP	Media posterior (concave vein)
Mspl	Median Supplement (concave intercalary between MA and MP)
'O'	lestine oblique vein (one or two veinlets between RP2 and IR2 distal of the subnodus)
postdiscoidal area	area between MA and MP distal of the discoidal triangle
postnodal crossveins	crossveins between costal margin and RA distal of nodus (especially between nodus and pterostigma)
postsubnodal crossveins	crossveins between RA and RP distal of subnodus
PsA	pseudo-anal vein (= AA0 *sensu* NEL & MARTÍNEZ-DELCLÒS 1993a) that is forming the basal side of the subdiscoidal triangle (convex vein, derived from a cubito-anal crossvein)
pseudo-IR1	convex intercalary between RP1 and RP2, originating on RP1 near the pterostigma (convex vein)
pterostigma	sclerotized and pigmented area near the wing apex, between costal margin and RA, basally and distally delimited by a postnodal crossvein
pterostigmal brace vein	oblique postsubnodal crossvein below the basal side of the pterostigma
RA	Radius anterior (convex vein)
RP	Radius posterior (concave vein)
RP1	Radius posterior 1 (anterior branch of the second branching of RP; concave vein)
RP2	Radius posterior 2 (posterior branch of the second branching of RP; concave vein)
RP1/2	Radius posterior 1/2 (= RP' *sensu* BECHLY 1996) (anterior branch of the first branching of RP; concave vein)
RP3/4	Radius posterior 3/4 (= RP" *sensu* BECHLY 1996) (posterior branch of the first branching of RP; concave vein)
Rspl	Radial Supplement (concave intercalary vein between IR2 and RP3/4; concave vein)
ScA	Subcosta anterior (the main branch is fused to the anterior wing margin, but a small basal posterior branch forms the anterior portion of the basal brace Ax0; originally a convex vein)
ScP	Subcosta posterior (free basal of nodus, but fused to anterior wing margin distal of nodus; concave vein)
subdiscoidal triangle	triangular area postero-basal of the discoidal triangle, basally delimited by PsA and distally by the subdiscoidal veinlet
subdiscoidal veinlet	crossvein-like most basal part of CuA between the posterior angle of the discoidal triangle and the fusion with the Analis anterior AA (convex vein)
submedian space	area basal of the discoidal triangle
subnodus	oblique veinlet between RA and RP beneath the nodus
trigonal planate	strong secondary longitudinal vein (intercalary) that is originating at the angle of the distal side MAb of the discoidal triangle (convex vein)

Table 2. Alphabetical list of used wing venational abbreviations and terms (see Text-Fig. 1).



Text-Fig. 1. Terminology of dragonfly wing venation, after BECHLY (1996).

3. The problem of homoplasy in wing venational characters

The wing venational characters mentioned below are all very commonly used as diagnostic features, but are very homoplastic and thus alone represent rather weak phylogenetic evidence, although they may be useful in combination, or as additional evidence in connection with other stronger characters.

(1) Pterostigmal brace vein: In the groundplan of Anisoptera the pterostigma is well-braced by an oblique crossvein aligned with its basal side. This pterostigmal brace vein is more transverse and distally displaced in *Paraliupanshania torvaldsi* gen. et sp. nov. and in most Austropetaliida. It is also rather transverse in Progobiaeshnidae fam. nov., but still aligned with the basal side of the pterostigma. In *Prohoyaeshna* gen. nov. and *Hoyaeshna*, the pterostigmal brace vein is recessed basal of the pterostigma, convergent to *Hypopetalia* and the groundplan of Petalurida (e.g. *Protolindenia*). It is somewhat weakly developed in *Cymatophlebiella*, and seems to be completely reduced in *Paraliupanshania britannica* sp. nov. and *Brachytron*.

(2) Area between RP1 and RP2: In the groundplan of Aeshnoptera, RP1 and RP2 are basally closely parallel or even converging near the pterostigma with only a single row of cells basal of the pterostigma (preserved in most Mesuropetaloidea stat. nov. and most Euaeshnida including Eumorbaeschnidae fam. nov. and Gomphaeschnidae). Two (or more) rows of cells basal of the pterostigma are (secondarily) present in *Cymatophlebiella*, *Aeschnopsis perkinsi* sp. nov. and probably *A. tischlingeri* sp. nov., *Liupanshania*, Austropetaliida, Progobiaeshnidae fam. nov., Cymatophlebioidea stat. nov., Paracymatophlebiidae fam. nov., and some basal Aeshnodea (*Baissaeshna*, *Allopetalia*, *Boyeria*, *Petaliaeschna* and *Cephalaeschna*, but not in *Basiaeschna*). In some, but not all, of these taxa, the secondary increase of cell rows is correlated with a secondarily divergent course of RP1 and RP2 (e.g. *Aeschnopsis perkinsi* sp. nov. and *A. tischlingeri* sp. nov., *Liupanshania*, Archipetaliidae, *Gobiaeshna occulta*, Valdaeshninae subfam. nov., and Rudiaeschnidae fam. nov.). A slight secondary divergence of RP1 and RP2 is also present in *Baissaeshna*, *Petaliaeschna* and *Cephalaeschna*, and even in some of those Neoaeshnida that still have only a single row of cells between RP1 and RP2 basal of the pterostigma (e.g. *Alloaeschna*, *Progomphaeschnaoides* gen. nov., *Plesigomphaeschnaoides* gen. nov., and *Gomphaeschnaoides*).

(3) Course of RP2 and IR2: RP2 is undulated in *Paramesuropetala* gen. nov. and *Paraliupanshania* gen. nov., and in most Aeshnomorpha, although only weakly so in Austropetaliida and Rudiaeschnidae fam. nov. The undulation of RP2 is most strongly developed in Cymatophlebiidae (especially Cymatophlebiinae), Eumorbaeschnidae fam. nov., and some Gomphaeschnidae (e.g. *Paramorbaeschna* gen. nov. and *Linaeschna* MARTIN, 1908). Instead of this undulation there is a characteristical curvature of RP2 beneath the pterostigmal brace in Mesuropetalidae and Aeshnodea (reversal). IR2 is strongly undulated only in Cymatophlebiidae. Except for their distal parts, RP2 and IR2 are more or less parallel in the groundplan of Anisoptera, while they are distinctly not parallel in Rudiaeschnidae fam. nov. and Euaeshnida. The apparently parallel course of RP2 and IR2 in Euaeshnodea taxon nov. is caused by a secondary branch of IR2 that is developed in the area between RP2 and IR2 (secondarily reduced in *Boyeria* and *Oplonaeschna*). In Mesuropetalidae, RP2 and IR2 are more closely parallel than in the groundplan, even converging near the posterior wing margin.

(4) Oblique vein 'O': In the groundplan of Anisoptera there are two oblique veins 'O' between RP2 and IR2. This state is preserved Aeschnidiidae and Petalurida, and within Aeshnoptera in *Cymatophlebiella*, Mesuropetalidae, Cymatophlebioidea stat. nov., and at least some specimens of Eumorbaeschnidae fam. nov. The basal (lestine) oblique vein 'O' is only reduced in Austropetaliida, while the second distal oblique vein 'O' is convergently reduced in Liupanshaniidae fam. nov., Paracymatophlebiidae fam. nov., some specimens of Eumorbaeschnidae fam. nov., and all Neoaeshnida (convergent to all Exophytica).

(5) Rspl: An at least weakly defined Rspl belongs to the derived groundplan characters of Aeshnoptera. In most Mesuropetaloidea stat. nov., it is still a concave, but zigzagged, pseudo-Rspl. A well-defined Rspl is present in *Paraliupanshania* gen. nov. and both pairs of wings of Panaeshnida taxon nov., convergent to Aeschnidiidae and most Eurypalpida (except Synthemistidae and Gomphomacromiidae). The Rspl is strongly curved with several rows of cells between it and IR2 in *Paraliupanshania* gen. nov., Cymatophlebioidea stat. nov. (especially Cymatophlebiidae), and Aeshnidae (including *Oplonaeschna*), convergent to Aeschnidiidae and some Libellulidae. The Rspl is strictly parallel to IR2 with only a single row of cells between these two veins in most Mesuropetaloidea stat. nov. (except *Paramesuropetala* gen. nov. and *Paraliupanshania* gen. nov.) and most of the basal taxa of Euaeshnida (e.g. Eumorbaeschnidae fam. nov. and most Gomphaeschnidae, Brachytronidae, and Telephlebiidae stat. nov.). It is more or less

parallel to IR2, but with two or three rows of cells between these two veins in *Cymatophlebiella*, Austropetaliida, Progobiaeshnidae fam. nov., Paracymatophlebiidae fam. nov., and a few basal taxa of Neoaeshnida (e.g. Allopetaliidae stat. nov.).

(6) Mspl: A well-defined Mspl is present by convergence in *Paraliupanshania* gen. nov., some Cymatophlebiinae, and all Paneuaeshnida taxon nov., convergent to Aeschnidiidae and higher Eurypalpida (Corduliidae s.str., Macrodiplacidae, and Libellulidae). It is still somewhat less well-developed in Paracymatophlebiidae fam. nov. and Eumorbaeschnidae fam. nov., but strongly defined in all Neoaeshnida. In Paracymatophlebiidae fam. nov. and Eumorbaeschnidae fam. nov. the course of Mspl is somewhat irregular with up to two rows of cells between Mspl and MA, while in the groundplan of Neoaeshnida (Gomphaeschnidae, Brachytronidae, and Telephlebiidae stat. nov.) the Mspl is parallel to MA with only a single row of cells between these two veins (two rows in Allopetaliidae stat. nov.). The Mspl is strongly curved with several rows of cells between it and MA only in Aeshnidae (including *Epiaeschna* and *Oplonaeschna*), convergent to Aeschnidiidae and a few Libellulidae.

(7) Course of RP3/4 and MA: In the groundplan RP3/4 and MA are distally diverging, while they are closely parallel up to the wing margin in Mesuropetaloidea stat. nov., Valdaeshninae subfam. nov., and Euaeshnida (triple convergence). Furthermore, in the groundplan of Aeshnoptera, RP3/4 and MA are more or less undulated (convergent to the petalurid genus *Uropetala* and a few "corduliine" Eurypalpida, e.g. Macromiidae, *Idomacromia*, *Aeschnosoma* and *Libellulosoma*). This condition is convergently strongly reduced or completely suppressed (reversals) in *Aeschnopsis* (except the type species), Archipetaliidae, *Valdaeshna*, and all Aeshnodea. A stronger undulation is convergently present in Cymatophlebiidae, Paracymatophlebiidae fam. nov., and Eumorbaeschnidae fam. nov.

(8) Postdiscoidal area: The presence of at least three rows of cells in the basal part of the postdiscoidal area of both pairs of wings seems to be a symplesiomorphy of many basal Aeshnoptera with Liassogomphidae, Aeschnidiidae and Petalurida that is reversed to two rows in Exophytica, *Aeschnopsis perkinsi* sp. nov. and *A jurassica* (and in the hindwing of *M. muensteri* comb. nov.), *Araripeliupanshania* gen. nov., Austropetaliida taxon nov., and in the groundplan of Neoaeshnida (retained in Gomphaeschnidae, Brachytronidae and Telephlebiidae stat. nov., but again reversed to three rows of cells in Aeshnidae). The presence of three rows of cells in a few Lindeniidae (e.g. *Cacoides* and *Melanocacus*) and many Libellulidae (except Tetrathemistinae) probably is due to reversal as well. More than three rows of cells are present in *Paraliupanshania* gen. nov., most Cymatophlebiinae (except *Cymatophlebia purbeckensis* sp. nov., *C. pumilio* sp. nov., and *C. herrlenae* sp. nov.), *Prohoyaeshna* gen. nov., *Rudiaeschna limnobia*, and very few Aeshnidae with very dense wing venation (e.g. *Heliaeschna*).

(9) MAb and trigonal planate: In the groundplan of Anisoptera the distal side MAb of the discoidal triangle is straight, and there is no convex secondary vein (trigonal planate) originating on MAb in the basal postdiscoidal area. An angled MAb and trigonal planate is present by convergence in Liupanshaniidae fam. nov., *Valdaeshna*, and Neoaeshnida (slightly indicated already in Eumorbaeschnidae fam. nov.), as well as in Cretapetaluridae and in many Gomphides (e.g. Hageniidae and Lindeniidae).

(10) Discoidal triangle: In the groundplan of Anisoptera the forewing discoidal triangle is distinctly more transverse than the hindwing discoidal triangle which is more or less equilateral. This is indicated by the condition in Aeschnidiidae, Liassogomphidae, Petalurida, Mesuropetaloidea stat. nov., Gomphides, while the concerning state in Eurypalpida seems to be due to a reversal. Distinctly longitudinally elongated discoidal triangles in both wings represent a convergence of Aeshnomorpha taxon nov. and Cavilabiata (reversed in the hindwing of Chlorogomphidae and the forewing of Eurypalpida). A discoidal triangle that is divided into two cells by a single crossvein in both pairs of wings seems to represent the plesiomorphic state within Anisoptera, while free discoidal triangles or multicellular discoidal triangles represent alternative apomorphic states that have been realized by multiple convergence (e.g. the free hindwing discoidal triangle of *Mesuropetala muensteri* comb. nov., or the multicellular discoidal triangles of Liupanshaniidae fam. nov., *Cymatophlebiella euryptera*, *Hypopetalia pestilens*, and Panaeshnida taxon nov., reversed in Gomphaeschnidae except the most basal genus *Oligoaeschna*).

(11) Hypertriangle: The number of crossveins in the hypertriangle is very homoplastic within Anisoptera, but the most parsimonious interpretation suggests that a free hypertriangle belongs to the groundplan of Anisoptera and Aeshnoptera (retained in Mesuropetaloidea stat. nov.), while a two-celled hypertriangle belongs to the groundplan of Aeshnomorpha taxon nov., and a multicellular hypertriangle belongs to the groundplan of Panaeshnida taxon nov. (probably autapomorphies of the two mentioned groups), reversed in *Cymatophlebia purbeckensis* sp. nov. and *C. pumilio* sp. nov., Paracymatophlebiidae fam. nov., Gomphaeschnidae (except the most basal genus *Oligoaeschna*), and a few other taxa (maybe including *Eumorbaeschna jurassica* gen. et comb. nov. ?).

(12) Subdiscoidal triangle: The number of cells in the subdiscoidal triangle is a very homoplastic character within Anisoptera. The two- or three-celled forewing subdiscoidal triangles are most likely a symplesiomorphy within Anisoptera (e.g. Liassogomphidae, Aeschnidiidae, Petalurida and basal Gomphides - Lindeniidae), correlated with the plesiomorphic retained transverse shape of the forewing discoidal triangle in all these taxa. Since Cordulegastrida, Hemeroscopidae, Chlorogomphida, and Neopetaliidae have forewings with a longitudinal triangle and free subdiscoidal triangle, these states seem to be derived groundplan characters of Cavilabiata that are reversed in Eurypalpida (= Libelluloidea *sensu* FRASER 1957) which again have transverse forewing discoidal triangles (reversal) and partly also divided forewing subdiscoidal triangles. Within Aeshnoptera the divided forewing subdiscoidal triangles have been reduced Austropetaliida taxon nov. (reversed in *Hypopetalia pestilens*), *Valdaeshna surreyensis*, and in the groundplan of Euaeshnida. Contrary to the forewings, the subdiscoidal triangles of the hindwings probably have been unicellular in the groundplan of Anisoptera and Aeshnoptera, and became secondarily subdivided into two or three cells by convergence in *Cymatophlebiella euryptera*, *Progobiaeshna liaoningensis* gen. et sp. nov., *Hypopetalia pestilens*, and Cymatophlebioidea stat. nov. (reversed in *Valdaeshna surreyensis*), Eumorbaeschnidae fam. nov., and Aeshnidae. However, this hypothesis is rather uncertain, because this character is very homoplastic, and the alternative hypothesis of a divided hindwing subdiscoidal triangle in the groundplan of Panaeshnida taxon nov. (convergent to *Cymatophlebiella* and *Hypopetalia*; reversed in *Valdaeshna*, Gomphaeschnidae, Brachytronidae and Telephlebiidae stat. nov.) is nearly equally parsimonious.

(13) Cubito-anal crossveins: In the groundplan of Anisoptera there are no accessory cubito-anal crossveins between CuP-crossing and PsA. They are still absent in Cymatophlebiella, Mesuropetaloidea stat. nov. (except in *Aeschnopsis tischlingeri* sp. nov. and *Liupanshania*) and Austropetaliida. Such crossveins are present in *Aeschnopsis tischlingeri* sp. nov., *Liupanshania* and in most Panaeshnida taxon nov. (probably synapomorphy), but absent (reduced) in *Cymatophlebia pumilio* sp. nov. and *C. herrlenae* sp. nov., Paracymatophlebiidae fam. nov., Gomphaeschnidae (except in the forewing of *Oligoaeschna venusta*), Brachytron, and maybe in *Eumorbaeschna* gen. nov.

(14) PsA: A strongly defined pseudo-anal vein PsA is developed in both pairs of wings of Aeschnidiidae, the forewing of Petalurida, the forewing of Mesuropetaloidea stat. nov., both pairs of wings of *Aeschnopsis*, Austropetaliida and Cymatophlebiinae, both pairs of wings of Gomphides, and in the forewing of Eurypalpida. This character is obviously correlated with a transverse shape of the discoidal triangle and a well-defined subdiscoidal triangle. Therefore, PsA is more or less reduced towards a normal cubito-anal crossvein in most wings with longitudinally elongated discoidal triangles, such as the hindwing of Liupanshaniidae fam. nov., both pairs of wings of many Paneuaeshnida taxon nov., Cordulegastrida, Chlorogomphida, Neopetaliidae, and the hindwings of Eurypalpida. Within Aeshnoptera the strongest reduction is in the hindwings of Liupanshaniidae fam. nov., and in both pairs of wings of Valdaeshninae subfam. nov. and Aeshnodea which have the most elongated discoidal triangles. One of the rare exceptions from this rule is the hindwing of *Aeschnopsis perampla* (= *Cymatophlebiopsis pseudobubas*) which has a very elongated and narrow discoidal triangle, but also a very distinct PsA.

(15) Anal loop: In the groundplan of crowngroup Anisoptera (thus, excluding the basal taxa Aeschnidiidae and Liassogomphidae) there is a well-defined anal loop that is posteriorly well-closed and divided into four to six cells, and there is a rather short gaff. This is suggest by the well-defined anal loop in many Petalurida, most Aeshnoptera, most Gomphides, and nearly all Cavilabiata. In *Cymatophlebiella* and in the groundplan of Aeshnomorpha the gaff is slightly prolonged, although the anal loop is not enlarged. The anal loop is distinctly enlarged in *Progobiaeshna liaoningensis* gen. et sp. nov., *Hoyaeshna*, Rudiaeschnidae fam. nov., and Euaeshnida (especially in *Gomphaeschnaoides petersi* sp. nov. and in all Aeshnidae), correlated with a strong prolongation of the gaff. The anal loop is completely reduced in *Cymatophlebiella*, many specimens of *Cymatophlebia*, and most Liupanshaniidae fam. nov. (except *Araripeliupanshania* gen. nov.). In Paracymatophlebiidae fam. nov. the anal loop is still distinct, but the crossvein that is forming its posterior margin is not very strong. A unique very narrow and much longitudinally elongated anal loop is present in Mesuropetalidae (only Cretapetaluridae and Cordulagomphinae have a somewhat similar structure, but their anal loop is still distinctly different).

Some of these characters, e.g. the development of a well-defined and curved Rspl and Mspl, are so often convergently realized within Aeshnoptera that they could even be regarded as an underlying synapomorphy (*sensu* SAETHER 1979) or as a trend / tendency (*sensu* BRUNDIN 1968). Anyway, the phylogenetic hypotheses that are built on these homoplastic characters are only supported by relatively weak evidence. However, there is no other choice than using these weak characters as far as possible, since such wing venational characters mostly are the only available and usable characters for fossil dragonflies.

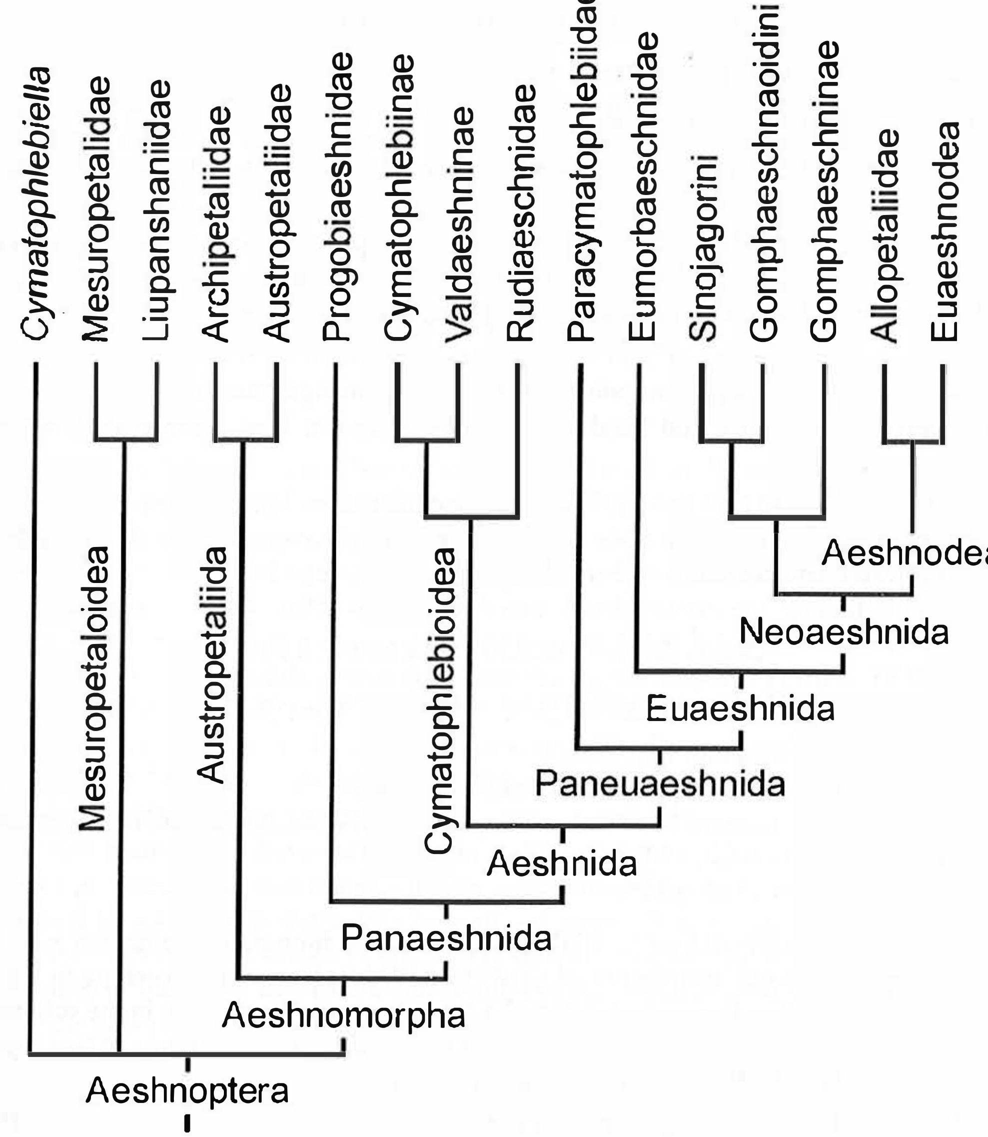
We therefore decided to build our system of fossil and extant aeshnoid dragonflies on all available characters, and used a priori weighting in all cases of character conflicts. We have mainly used uniqueness, congruence and homoplasy (compatibility and parsimony), and structural complexity as weighting criteria. Since these criteria cannot provide precise numerical weights, but only a somewhat vague greater trust in certain characters rather than in others, we preferred a "manual" (rather "mental") phylogenetic systematic analysis instead of a computer parsimony analysis (also see above). Counting steps, and favouring or rejecting certain cladograms because of insignificant differences in step-length would not make any sense in this context. This does not mean at all that we reject parsimony as a principle of choice between competing hypotheses. We only reject the reduction of parsimony to a simple search for shortest trees. Parsimony means minimizing all unnecessary ad hoc assumptions. We regard a tree that allows the interpretation of certain strong characters as homologous, at the cost of additional steps in very weak characters, as definitely more parsimonious than a somewhat "shorter" tree that has to interpret these strong characters as multiple convergences. Furthermore, if the topology of certain cladograms implies much more complicated evolutionary scenarios for certain structures or certain biogeographical patterns, these ad hoc hypotheses should be considered in a true parsimony analysis as well, and not only the number of steps that is minimally necessary to explain the character pattern. Independence of any evolutionary theories, that is often recommended by computer cladists, is no desirable property of biosystematic reasoning, since it boils down to ignorance of reality. Systematical biology and evolutionary research are mostly historical science rather than strict natural science *sensu* POPPER (1989), and therefore often involve hermeneutic procedures rather than falsificationism. The complex problems of phylogeny and evolution can neither be reduced to pseudo-objective computer algorithms that calculate statistics with precisely quantified values, nor can they be formulated as strictly falsifiable hypotheses. However, the concerning hypotheses and arguments can well be rationally discussed on the basis of the total available evidence and background knowledge. Hennigian Phylogenetic Systematics offers the theoretical foundation, methodology, and terminology for such rational discussions; nothing more and nothing less.

4. Systematic palaeontology of Mesozoic Aeshnoptera

Short sketch of the phylogenetic system of Anisoptera

According to the new phylogenetic system of BECHLY (1996, 1999a, b), the Eurypalpida (= Libelluloidea *sensu* FRASER 1957), Chlorogomphida, and Hemeroscopidae constitute the monophylum Brachystigmata. The latter group and the Neopetaliidae are sistergroups 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 alleged adult Sonidae belong to Gomphides, too, and seem to be closely related to Hageniidae, while the genuine Sonidae simply represent the larvae of Aeschnidiidae (therefore the alleged adult Sonidae are classified in a new family Proterogomphidae in BECHLY *et al.*, 1998). Exophytica and Aeshnoptera (= Aeshnoidea *sensu* CARLE 1995) are sistergroups in the monophylum Euanisoptera. Euanisoptera and Petalurida (Protolindeniidae + Cretapetaluridae + Aktassiidae + Petaluridae) are sistergroups in the monophylum Anisoptera (crowngroup). The Aeshnoptera (Text-Fig. 2) include the fossil Mesuropetalidae, the extant Austropetaliida taxon nov. (Archipetaliidae + Austropetaliidae), the fossil Cymatophlebioidea stat. nov. 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 sistergroup of all extant Anisoptera might well be correct. The attempted phylogenetic analysis by NEL & MARTÍNEZ-DELCLÒS (1993a) 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 could represent a synapomorphy of Liassogomphidae and Aeschnidiidae (together: Aeschnidioidea) and maybe even Stenophlebiidae (together: Aeschnidioptera), although such a

position would be in conflict with the evidence from several other characters which rather suggest a more basal position of Liassogomphidae (discoidal triangle not strictly triangular, no second oblique vein 'O', no well-defined PsA). Very detailed information 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.tripod.de/GBechly/phylosys.htm*, which will be regularly published on CD-ROM by BECHLY in SCHORR & LINDEBOOM (in press).



Text-Fig. 2. Phylogenetic tree of Aeshnoptera. For concerning synapomorphies see text.

Aeshnoptera BECHLY, 1996 (nec Aeshnoptera CRAMPTON, 1928)

Included groups: Mesuropetalidae BECHLY, 1996 and Aeshnomorpha taxon nov., and probably also the genera *Cymatophlebiella* PRITYKINA, 1968.

Wing venational autapomorphies: RP1 and RP2 basally parallel up to the pterostigma, thus, the area between these two veins is basally distinctly narrowed with only a single row of cells in-between in the groundplan (*contra* LOHMANN 1996c: 362); at least a weakly defined (zigzagged) Rspl is present; RP3/4 and MA more or less undulated.

Other autapomorphies: Abdominal terga with a medio-dorso-longitudinal fold or keel (secondarily reduced or suppressed within Austropetaliida taxon nov. and Gomphaeschnidae); compound eyes closely approximated or even contiguous.

Superfamily **Mesuropetaloidea** BECHLY, 1996 stat. nov.

Type genus: *Mesuropetala* HANDLIRSCH, 1906.

Included groups: Mesuropetalidae BECHLY, 1996 and Liupanshaniidae fam. nov.

Wing venational autapomorphies: Arculus shifted very close to the first primary antenodal Ax1; RP3/4 and MA closely parallel up to the wing margin in both pairs of wings.

Family Mesuropetalidae BECHLY, 1996

1996 Mesuropetalidae; BECHLY, p. 382

Type genus: *Mesuropetala* HANDLIRSCH, 1906.

Included genera: Including the two genera *Mesuropetala* HANDLIRSCH, 1906 and *Aeschnopsis* HANDLIRSCH, 1939.

Wing venational autapomorphies: RP2 and IR2 very closely parallel, even converging near the posterior wing margin; characteristical shape of the discoidal triangles, with the forewing discoidal triangle even more transverse than in the groundplan of Anisoptera; anal loop longitudinally elongated (convergent to Cretapetaluridae).

Other autapomorphies: Cerci (superior appendages) foliate (convergent to Cymatophlebiinae, Polycanthagynini including "*Aeschna*" *petalura*, and Petalurinae, but only known from *Mesuropetala muensteri* comb. nov.).

Discussion: BECHLY (1996) and NEL *et al.* (1998) already demonstrated that *Mesuropetala* which was previously mostly regarded as a fossil petalurid does not share any strong synapomorphies with Petalurida, while it does share several derived character states with Aeshnoptera (see above).

Genus *Mesuropetala* HANDLIRSCH, 1906

(= *Morbaeschna* NEEDHAM, 1907 jun. subj. syn. nov.)

1906 *Mesuropetala*; HANDLIRSCH, p. 588.
1907 *Morbaeschna*; NEEDHAM, p. 141 (jun. subj. syn. nov.).
1940 *Morbaeshna* TILLYARD & FRASER, p. 380 (unjustified emendation, jun. obj. syn. nov. of *Morbaeschna* NEEDHAM, 1907).
1998 *Mesuropetala*; NEL *et al.*, p. 15.

Type species: ?*Gomphus koehleri* HAGEN, 1848 from the Upper Jurassic of Solnhofen was fixed as type species of the genus by subsequent designation of COWLEY (1934a). However, according to BRIDGES (1994) the type method is probably rather by original indication (type by monotypy), since in the original description the single other species was only provisionally included in this genus. The valid name of this species is *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. according to our new synonymy.

Further included species: *M. auliensis* PRITYKINA, 1968 and ?*M. costalis* PRITYKINA, 1968 from the Upper Jurassic of Karatau (ex USSR)., and *M. magna* sp. nov. from the Lower Cretaceous of Transbaikals (Buryat Republic, ex USSR). HAGEN (1862: 107) synonymized "*Aeschna Wittei* GIEBEL", "*Aeschna antiqua* VAN DER LINDEN" and "*Aeschna Schmideli* GIEBEL" with "*P. Münsteri* GERMAR". HANDLIRSCH (1906: 589) provisionally classified "*Aeschna*" *schmiedeli* GIEBEL, 1856 (forewing length 55 mm, hindwing length 50 mm) in the genus *Mesuropetala*, too (followed by BRIDGES 1994). CARPENTER (1932: 113) suggested that "*Aeschna*" *schmiedeli* should better be «dropped from literature as an unrecognisable insect». The same applies to "*Aeschna*" *antiqua* VAN DER LINDEN, 1827 about which we only know the wing length of 46 mm, the mere citations of the name by HAGEN (1850: 362) and GIEBEL (1856: 279), and the statement of HAGEN (1862) that it could be identical with *Protolindenia wittei*, which is rather irrelevant regarding the fact that this author synonymized "*Aeschna Wittei* GIEBEL" with "*P. Münsteri* GERMAR", but regarded "*Gomphus Köhleri* HAGEN" as distinct species. Since "*Aeschna*" *antiqua* VAN DER LINDEN, 1827 and "*Aeschna*" *schmiedeli* GIEBEL, 1856 could either be synonyms of *Mesuropetala muensteri*, or *Protolindenia wittei*, we regard the two former taxa as nomina dubia in Anisoptera *incertae sedis*.

Diagnosis: No complete diagnosis of this genus has previously been attempted. A differential diagnosis for the two genera *Mesuropetala* and *Protolindenia* that have often been confused in the past is provided by NEL *et al.* (1998). *Mesuropetala* is distinguished from other Anisoptera genera (including *Paramesuropetala* gen. nov.) by the combination of following characters: Oblique pterostigmal brace aligned with basal side of pterostigma; pterostigma elongated, but not basally recessed; forewing discoidal triangle transverse and two-celled; hindwing discoidal triangle longitudinal and unicellular; hypertriangles free of crossveins; well-defined subdiscoidal triangles in all wings, those of forewings three-celled whereas those of hindwings unicellular; anal loop longitudinal elongated, divided into two or three cells, and posteriorly well-closed, but zigzagged; no well-defined Rspl or Mspl, but a distinct row of enlarged cells along posterior side of IR2 and MA that is delimited by a zigzagged pseudo-Rspl or pseudo-Mspl; two oblique veins 'O'; the two primary antenodal crossveins Ax1 and Ax2 are stronger than the secondary antenodal crossveins; two to four secondary antenodal crossveins between Ax1 and Ax2; arculus very close to Ax1; only a short pseudo-IR1 originating on RP1 beneath the distal side of the pterostigma or even distal of it (primary IR1 reduced); MA and RP3/4 parallel; IR2 and RP2 rather straight and distally converging; area between IR2 and RP2 narrow with always only a single row of cells; hindwing CuA divided into six to eight parallel posterior branches (including CuAb); no accessory cubito-anal crossveins between CuP-crossing and PsA; male hindwing with anal angle and three-celled anal triangle; cerci of both sexes broad and foliate, as already suggested by DEICHMÜLLER (1886: pl. 4, figs 11-12), and no visible spines on male cerci and epiproct (Text-Figs 8 and 10, Plate 5: Fig. 1); compound eyes large and approximated (Plate 4: Fig. 2), as already mentioned by HAGEN (1862: 139).

There are only few distinctions from the wing venation of the closely related genus *Aeschnopsis*: Pterostigma more strongly elongated (autapomorphy); hindwing discoidal triangle free (plesiomorphy); PsA less well-defined in the hindwing.

Discussion: The genus "*Morbaeschna*" NEEDHAM, 1907 is based on "*Aeschna*" *muensteri* GERMAR, 1839 as type species (see below), since NEEDHAM (1907) erroneously believed that his specimen which he regarded as type of his new genus, was conspecific with *Aeschna muensteri* GERMAR, 1839. CARPENTER (1932: 113) suggested that the latter species should be dropped from the literature as an unrecognisable insect. This would of course not be compatible with the rules of nomenclature. Furthermore, our careful study of the holotype in Munich (BSP), which is very poorly preserved indeed, revealed that it is clearly not conspecific with NEEDHAM's new aeshnid, but very probably conspecific with ?*Gomphus koehleri* HAGEN, 1848 (see below), as was already suggested by HANDLIRSCH (1906: 589). Therefore, the new aeshnid of NEEDHAM remained unnamed, while ?*Gomphus koehleri* HAGEN, 1848 and "*Morbaeschna*" NEEDHAM, 1907 have to be regarded as junior subjective synonyms of "*Aeschna*" *muensteri* GERMAR, 1839 and *Mesuropetala* HANDLIRSCH, 1906, respectively (please note: In HANDLIRSCH's monograph the pages 1-640 with plates 1-36 have been published 1906, pages 641-1120 with plates 37-51 have been published 1907, and pages 1120-1430 have been published 1908). The aeshnid that was previously known under the incorrect name "*Morbaeschna muensteri*" (*sensu* NEEDHAM 1907) was renamed by us as *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov. (see below). TILLYARD & FRASER (1940) and FRASER (1957: 100) explicitly emended all names that are based on the genus *Aeshna* only because of their rejection of the emendation of the genus *Aeshna* FABRICIUS, 1775 to *Aeschna* by ILLIGER (1801: 126; this publication was indicated as being published in 1802 by STEINMANN 1997, and with author ANONYMOUS by BRIDGES 1994) and CHARPENTIER (1825: 24); consequently they introduced «*Morbaeshna* NEEDH.» as unjustified emendation of "*Morbaeschna*" NEEDHAM (TILLYARD & FRASER 1940: 380; FRASER 1957: 100), so that the former spelling has to be regarded as junior subjective synonym of the latter according to Art. 33.2.3 IRZN, since it is not in prevailing usage.

Mesuropetala muensteri (GERMAR, 1839) comb. nov.

(= *Mesuropetala koehleri* (HAGEN, 1848) jun. subj. syn. nov.)

Text-Figs 3-10, Plate 1: Figs 1-2, Plate 2: Figs 1-2, Plate 3: Figs 1-2, Plate 4: Figs 1-2, Plate 5: Figs 1-2, Plate 13: Fig. 2, Plate 33: Fig. 1

1826 «Libellulit»; KOEHLER, p. 231, pl. 7, fig. 3.
*v 1839 *Aeschna Münsteri* GERMAR, p. 215, pl. 23, fig. 12.
1840 «Libellulit»; CHARPENTIER, p. 172.
1848 *Gomphus? Köhleri* HAGEN, p. 8 (jun. subj. syn. nov.).
1848 *Cordulegaster? Münsteri*; HAGEN, p.8.
1850 *Cordulegaster Münsteri*; HAGEN, p.360.
1850 *Gomphus*? (*Lindenia*?) *Koehleri*; SELYS in SELYS & HAGEN, p. 366.

1856 *Diastatomma Münsteri* (GERMAR); GIEBEL, p. 276.
1856 *Libellula Köhleri* (HAGEN); GIEBEL, p. 284.
1862 *Gomphus Köhleri*; GIEBEL, p. 639.
1862 *Petalura*? *Münsteri* GERMAR; HAGEN, p. 107.
1862 *Aeschna Münsteri* GERM.; HAGEN, p. 137-138.
1862 *Gomphus*? *Köhleri* HAG.; HAGEN, p. 139 (brief redescription).
1862 *Petalura differenz* HAGEN, p. 107 (nomen nudum; synonymized by HANDLIRSCH 1906: 588, using the incorrect subsequent spelling *differens*).
1862 *Petalura varia* HAGEN, p. 107 (nomen nudum; synonymized by HANDLIRSCH 1906: 588).
1869 *Petalura differens* HAGEN; WEYENBERGH, p. 235.
1869 *Petalura varia* HAGEN; WEYENBERGH, p. 251.
1886 *Uropetala Münsteri*; DEICHMÜLLER, p. 41.
1886 *Uropetala Koehleri* (HAGEN); DEICHMÜLLER, pp. 52-56, pl. 4, fig. 3, 11-12 (redescription).
1890 *Uropetala Münsteri*; KIRBY, p. 172.
1897 ?*Uropetala Koehleri* (HAGEN); MEUNIER, p. 9, pl. 4, fig. 4.
1906 *Mesuropetala Koehleri* HAGEN; HANDLIRSCH, p. 588, pl. 47, fig. 9 (in gen. nov., gives a poor reproduction of DEICHMÜLLER's figure 3).
1906 ?*Mesuropetala Münsteri* GERMAR; HANDLIRSCH, p. 589.
1907 *Æschna muensteri* GERMAR; NEEDHAM, p. 141 (no demonstrably intentional emendation).
n 1907 *Morbaeschna muensteri* (GERMAR); NEEDHAM, p. 142.
v. 1932 *Protolindenia koehleri* (HAGEN); CARPENTER, p. 113, fig. 7 (comb. nov., new figure).
1934a *Mesuropetala koehleri* (HAGEN); COWLEY, p. 252 (subsequent designation of *M. koehleri* 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 & PAICHELER, p. 319 (position discussed).
1993 *Mesuropetala koehleri*; ROSS & JARZEMBOWSKI, p. 372 (in Petaluridae).
v. 1994 *Mesuropetala koehleri*; FRICKHINGER, p. 137, fig. 253 (the specimen in figure 252 from the private coll. SCHMITT / Frankfurt, which is erroneously labelled «*Libellulium longialatum*», is a *Mesuropetala* as well; see Plate 2: Fig. 2).
1998 *Mesuropetala koehleri* (HAGEN); NEL *et al.*, pp. 15-21, figs 8-16 (designation of neotype, new figures, new diagnosis and redescription, and position discussed).

Holotype: Type of *Aeschna muensteri* GERMAR is specimen no. [AS VII 794], BSP, Munich. The location of the holotype of *G. koehleri* HAGEN, 1848 is unknown, and even HAGEN (1862) already remarked that he could not find the type. Our study of the HAGEN collection at MCZ also did not yield any specimen that is indicated as the type of HAGEN, which has to be regarded as lost. Because of the taxonomic problems concerning the nomen dubium *G. koehleri* and the resulting uncertainties about the identity and distinction of the genus *Mesuropetala*, NEL *et al.* (1998) designated specimen no. [1846 a, b / HAGEN No. 44] in the Museum of Munich (BSP) as neotype of "*Gomphus*" *koehleri* HAGEN, 1848 (based on Article 75 IRZN). This latter specimen was erroneously regarded by HANDLIRSCH (1906: 589-590) as a specimen of *Protolindenia wittei* (GIEBEL, 1860), but it does not correspond to the figures of *P. wittei* given by GIEBEL (1860), HAGEN (1862) and DEICHMÜLLER (1886), and it closely resembles the figures of "*Mesuropetala koehleri*" given by DEICHMÜLLER (1886) and CARPENTER (1932). Thus, this specimen does not belong to *P. wittei*, but to "*M. koehleri*" (also see the recent revision of *Protolindenia* by NEL *et al.* 1998). A potential type of "*Gomphus*" *koehleri* HAGEN, 1848 could be specimen no. [MB. J. 1748] in the Museum für Naturkunde in Berlin which is part and counterpart of a complete dragonfly from the Solnhofen Limestone. It is labelled «*Mesuropetala koehleri* (HAGEN), vielleicht Typus von HAGEN, Eichstätt, Aus dem Nachlass von H.J. KOLBE - zool. Mus. Berlin (KUNTZEN) 15.10.40». A notice that is attached to the specimen states «Wahrscheinlich Original von HAGEN mit dem KOLBE enge persönliche Beziehungen hatte - an KOLBE gegeben, also wahrscheinliche Type oder Paratype - wahrscheinlich die Handschrift von HAGEN selbst. Aus dem Nachlaß v. H.J. KOLBE». Although from these statements it is theoretically possible that this specimen is the original type of *G. koehleri* HAGEN, this can never been proved

anymore. Furthermore, this specimen is not a *Mesuropetala* sp. (Aeshnoptera), but probably a *Protolindenia wittei* (Petalurida): Compound eyes widely separated; anal appendages not foliate; forewing discoidal triangle longitudinal; RP1 and RP2 basally not parallel, but diverging; forewing length 46 mm; hindwing length 43-44 mm; body length from head to the tip of the abdomen (including appendages), 72 mm. Therefore, we do not only regard the type status of this specimen as doubtful, but even consider its acceptance as holotype of *G. koehleri* as highly undesirable, since this would lead to substantial taxonomic confusion (also see NEL *et al.* 1998). In accordance with the provisions of the IRZN we reject this specimen as type of "*Gomphus*" *koehleri*.

TISCHLINGER (1994) erroneously listed «*Aeschna Münsteri* GERMAR», «*Mesuropetala Münsteri* GERM.», «*Petalura Münsteri* GERM.» and «*Diastatomme* (sic) *Münsteri* GERM.», as four different dragonfly species.

Other specimens: DEICHMÜLLER (1886) redescribed and figured a specimen from the Museum of Dresden, which still should be present in this collection according to LÖSER (pers. comm.). MEUNIER (1897) mentioned the presence of some poorly preserved specimens from the Musée Teyler (Haarlem). CARPENTER (1932) partly figured the wing venation (Text-Fig. 3). His figure is based on the study of the two specimens nos [MCZ 6194] and [MCZ 1998] in the Museum of Comparative Zoology in Cambridge. PONOMARENKO (1985) indicated the presence of some material in the Museum of Vienna (NMV).

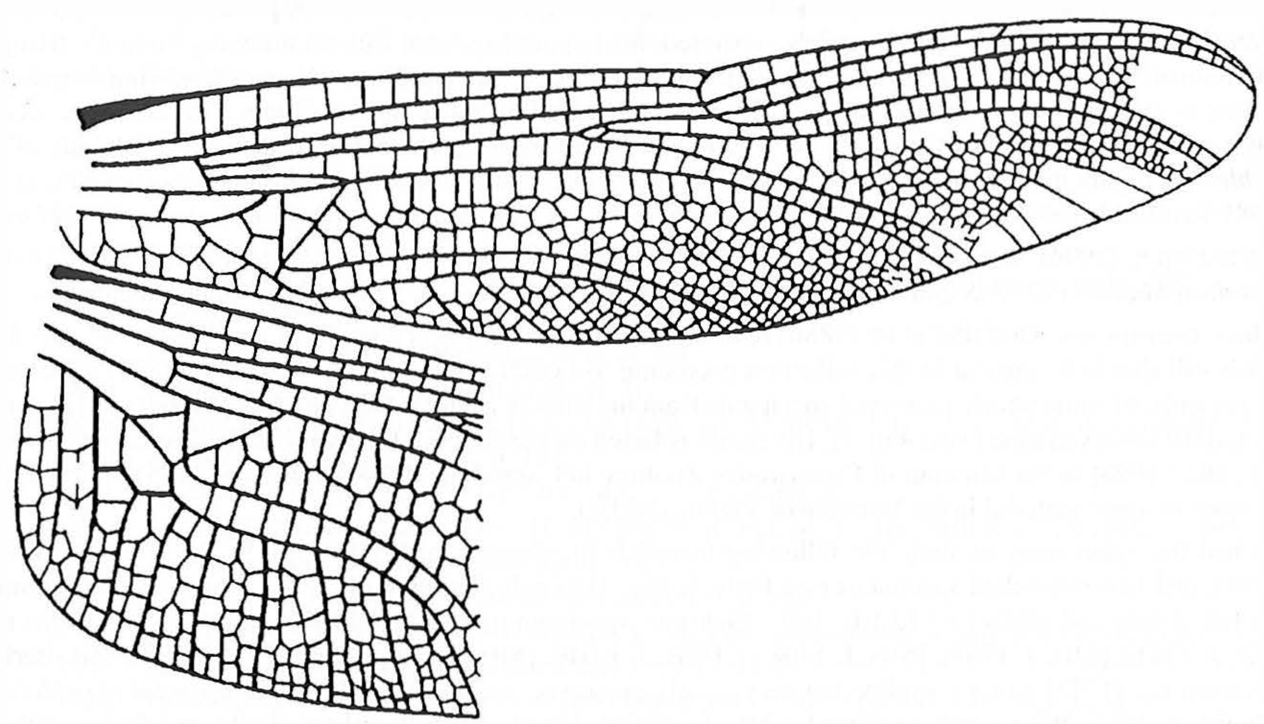
We had the opportunity to study the following material: Specimens nos [1998 a, b], [6203], [6204], [6296], [6194], and two unlabelled specimens (see Plate 5: Fig. 2) in coll. CARPENTER, MCZ, Cambridge; specimens nos [BL 1960] and [1966 / 64 Ei Bl], JME, Eichstätt; specimen no. [334], BMM, Solnhofen; specimens nos [MB. J. 1441], [MB. J. 1707], [MB. J. 1708 ?], [MB. J. 1710], [MB. J. 1711], and [MB. J. 1733], MB, Berlin; specimen no. [1235] and a complete but very poorly preserved specimen labelled [*Mesuropetala koehleri*, J. Schmitt, v. 1966, Wintershof, Eichstätt], SMF, Frankfurt. Finally we found three similar specimens without number in the collections of the Museum in Stuttgart (SMNS), but they are too poorly preserved to allow a definite attribution to this genus and species. The same applies to specimen no. [86/153] in coll. TISCHLINGER (Stammham) that was figured by TISCHLINGER (1996: fig. 16). We could also study a photograph of the single well-preserved male specimen of this taxon in coll. JUVYNS (Brussels), but since the owner is a fossil trader the future deposition of this important specimen is unfortunately uncertain.

Locus typicus: Solnhofen (note: The locus typicus of *G. koehleri* is Eichstätt), Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Diagnosis: This species has recently been revised in NEL *et al.* (1998), but the examination of further material made a new revision necessary. Based on a re-examination of the holotype of "*Aeschna*" *muensteri* GERMAR and the neotype of "*Gomphus*" *koehleri* HAGEN in the Museum of Munich (BSP), as well as the study of new specimens from the same Museum, the Museum of Comparative Zoology in Cambridge (MCZ), and the Museum für Naturkunde in Berlin, *Mesuropetala muensteri* comb. nov. can be characterized as follows: Wing length 47-49 mm; oblique pterostigmal brace below basal side of pterostigma; pterostigma extremely elongated (convergent to Petalurida); forewing discoidal triangle transverse, broad and two-celled; subdiscoidal triangles three-celled in forewings, but unicellular in hindwings; anal loop only two- or three-celled, longitudinal elongated, and posteriorly well-closed, but zigzagged; posterior row of distinctly larger pentagonal cells along IR2 and MA, but no well-defined Rspl or Mspl (concave, but indistinct and zigzagged pseudo-Rspl and pseudo-Mspl); two oblique veins 'O'; the two primary antenodal crossveins Ax1 and Ax2 are stronger than the secondary antenodal crossveins; about five secondary antenodal crossveins between Ax1 and Ax2 in forewings; arculus nearer to Ax1 than to Ax2; hindwing Ax2 situated on a level with distal angle of discoidal triangle; a distinct gap of antesubnodal crossveins immediately distal of arculus; pseudo-IR1 very short and originating distal of pterostigma; MA and RP3/4 strongly parallel and undulated; IR2 and RP2 rather straight and strongly parallel, area in-between distally narrowed; CuAa with five to six parallel posterior branches; compound eyes large and closely approximated; superior anal appendages (cerci) very broad and strongly foliate.

This species differs from *M. magna* sp. nov. by the much smaller size, from *M. auliensis* PRITYKINA, 1968 by smaller number of cells beneath the pterostigma (max. seven cells), and from ?*M. costalis* PRITYKINA, 1968 by the presence of only a single row of cells between costal margin and ScP and the three-celled subdiscoidal triangle in the forewing.



Text-Fig. 3. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MCZ 6194 + 1998 - female, right pair of wings (drawing after CARPENTER 1932: fig. 7; without scale).

Description

♦ Specimen no. BSP 1846 a, b / HAGEN No. 44; neotype of "*Gomphus*" *koehleri* HAGEN; female; labelled «*Mesuropetala munsteri* GERM. O *M. koehleri* HAGEN sp.», «*Petalura Münsteri* GERM. sp., LEUCHTENBERG'sche Sammlung, Lithograph. Schiefer, Eichstädt»

Text-Fig. 4, Plate I: Figs 1-2

A nearly complete adult female with the wings in connection with the body. Two of the wings are complete and well-preserved.

Body length from head to tip of abdomen 77 mm. Abdomen never narrowed, 56 mm long and 4 mm wide. Two diverging valvula beginning under segment VIII and reaching apex of segment IX; ovipositor not extending beyond apex of abdomen. Head 8 mm long and 8 mm wide. Compound eyes appear to be distinctly separated, 3 mm apart, but probably related to a preservation in ventral aspect, since specimen no. [MCZ 6203] which is certainly conspecific and has a well-preserved head, clearly shows large approximated eyes. Detailed structure of head not preserved.

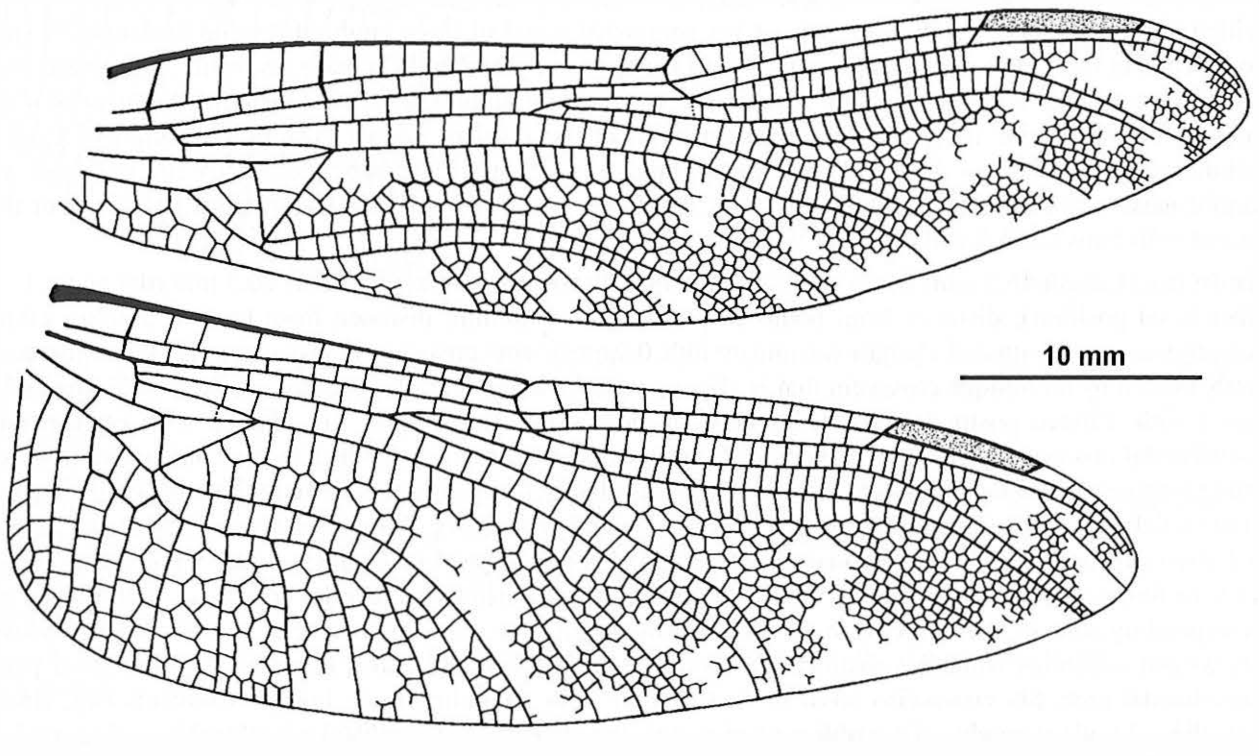
Forewing: Length 49.7 mm; width at nodus 11.3 mm; distance from base to nodus 25.8 mm; from nodus to pterostigma 12.8 mm; distance from base to arculus 5.0 mm. Pterostigma very elongated (length 6.6 mm; width 0.8 mm), and covering numerous cells. Pterostigma distinctly braced by an oblique crossvein that is aligned with its basal side. Pterostigma in a relatively basal position, at 60 % of distance between nodus and apex, and 79 % of whole length of wing. Eleven postnodal crossveins visible between nodus and pterostigma (total number probably sixteen), not aligned with corresponding postsubnodal crossveins. Most basal postnodal crossvein slanted towards nodus. Eighteen antenodal crossveins visible between costal margin and ScP, not aligned with antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Primary antenodal crossveins Ax1 and Ax2 stronger than secondary antenodal crossveins. Ax1 only 0.8 mm basal of arculus. Ax2 7.2 mm distal of Ax1, on a level with distal angle of discoidal triangle. Four secondary antenodal crossveins of the first row between the two primary antenodal crossveins, not aligned with the three corresponding antenodal crossveins in the second row. Ten antesubnodal crossveins visible in the space between arculus and subnodus without a distinct gap immediately basal of subnodus. The apparent gap in the basal third of the antesubnodal area is maybe partly an artifact of preservation. Three or four crossveins visible basal of first oblique crossvein, including at least two bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Only a single oblique vein 'O' visible, one and a half cells distal of subnodus. A second distal oblique vein could have been present,

too, since this area is partly distorted. IR2 originating 5.2 mm and RP3/4 6.5 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 the zigzagged margin of a row of enlarged cells along IR2. RP2 and IR2 closely parallel with always only a single row of cells in-between. Pseudo-IR1 well-defined and originating beneath distal side of pterostigma. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. RP3/4 and MA parallel and gently undulated with a single row of cells in-between (distally two rows). No Mspl, but a row of enlarged cells along MA, and a distinct convex secondary vein in distal part of postdiscoidal area, originating on MA. Postdiscoidal area not very widened distally with three rows of cells distal of discoidal triangle. Hypertriangle free of crossveins. Discoidal triangle very transverse and divided into two cells by a "horizontal" crossvein; length of anterior side 3.4 mm; of basal side 3.2 mm; of distal side MAb 4.6 mm. Distal side MAb straight. Median space free of crossveins. Submedian space 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 subdiscoidal triangle, max. 3.3 mm long and basally 2.7 mm wide (= length of PsA), divided into three cells. PsA ends on MP + CuA somewhat distal of basal angle of discoidal triangle. A single row of cells in basal part of area between MP and CuA. Distally MP and CuA are diverging with five cells in-between at posterior wing margin. MP reaching posterior wing margin somewhat distal of the level of nodus. CuA reaching posterior wing margin somewhat basal of the level of nodus. Posterior branches of CuA are well-defined, but only four distal ones preserved. Four or five rows of cells between CuA and posterior wing margin; max. width of cubito-anal area 2.9 mm. Anal area max. 2.5 mm wide (below 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 (the nodus is in a rather basal position); distance from nodus to pterostigma 15.0 mm; distance from base to arculus 4.0 mm. Pterostigma very elongated (length 6.1 mm; width 0.9 mm), and covering numerous cells. Pterostigma distinctly braced by an oblique crossvein that is aligned with its basal side. Pterostigma situated at 77 % of whole wing length. Fifteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Most basal postnodal crossvein slanted towards nodus. Twelve antenodal crossveins visible between costal margin and ScP (total number probably fourteen), not aligned with antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Primary antenodal crossveins Ax1 and Ax2 stronger than secondary antenodal crossveins. Ax1 0.6 mm basal of arculus; Ax2 5.9 mm distal of Ax1. Three or four secondary antenodal crossveins between the two primary antenodal crossveins, not aligned with corresponding antenodal crossveins in the second row. Eight antesubnodal crossveins visible in space between arculus and subnodus without a distinct gap immediately basal of subnodus, but with a gap in basal part of antesubnodal area. Six crossveins basal of first oblique vein, including three bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', the first three cells distal of subnodus and second five cells distal of first one. IR2 originating 5.0 mm and RP3/4 originating 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 the zigzagged margin of a row of enlarged cells along IR2. Pseudo-IR1 well-defined and originating beneath distal side of pterostigma. RP2 and IR2 closely parallel with always only a single row of cells in-between. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. RP3/4 and MA parallel and gently undulated with a single row of cells in-between (distally two rows). No well-defined Mspl, but three convex secondary veins in distal part of postdiscoidal area, originating on the zigzagged margin of a row of enlarged cells along MA. Postdiscoidal area distally widened with two rows of cells immediately distal of discoidal triangle. Hypertriangle free of crossveins (one or two apparent crossveins seem to be artifacts). Discoidal triangle free of crossveins and less transverse than that of forewing; length of anterior side 3.9 mm; of basal side 2.1 mm; of distal side MAb 4.4 mm. Distal side MAb straight. Median space free of crossveins. Submedian space 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 unicellular subdiscoidal triangle, max. 2.0 mm long and basally 2.0 mm wide (= length of PsA). PsA ends on MP + CuA slightly distal of basal angle of discoidal triangle. A single row of cells in area between MP and CuA, but close to wing margin they are somewhat diverging with two rows of cells in-between. MP reaching posterior wing margin somewhat distal of the level of nodus, while CuA reaches posterior wing margin on a level with 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, below PsA 8.4 mm wide with seven rows of cells between AA and posterior wing margin. AA with four closely parallel and straight posterior branches. Anal loop longitudinally elongated (length 3.4 mm; width 1.6 mm), divided into three cells and posteriorly well-closed, but zigzagged. Anal margin rounded with neither an anal triangle, nor an anal angle, thus, it is a female specimen. No visible membranule.

Comparison with the figure of *M. muensteri* (= *M. koehleri*) in CARPENTER (1932: fig. 7): There is no visible difference between specimen no. [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 specimens clearly reveals that this is a drawing error due to the zigzagged posterior side of the anal loop in *Mesuropetala*. The anal loop in CARPENTER's specimen is indeed two-celled.

Comparison with the figure of *M. muensteri* (= *M. koehleri*) in DEICHMÜLLER (1886, pl. 4, fig. 3): The figure of DEICHMÜLLER is less precise than that of CARPENTER (1932), but all the figured characters are exactly identical to those of specimen no. [1846 / HAGEN 44]. Thus, the attribution of specimen no. [1846 / HAGEN 44] to *M. muensteri* is highly probable.



Text-Fig. 4. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. Neotype of *G. koehleri* HAGEN BSP No. 44 - female, right pair of wings.

♦ Specimen no. BSP AS VII 794; type of "*Aeschna*" *muensteri* GERMAR; male ?; labelled «*Petalura* (*Mesuropetala*) *muensteri* GERM., Syntyp. u. Orig. GERMAR, 1839, Taf. 23, Fig. 12, Lithograph. Schiefer, Malm Zeta, Solnhofen / No 45, *Aeschna Munsteri* GERM., Origin. Ex., *Aeschna grandis* ? KÖHL., Solnhofen»

Text-Fig. 5, Plate 13: Fig. 2

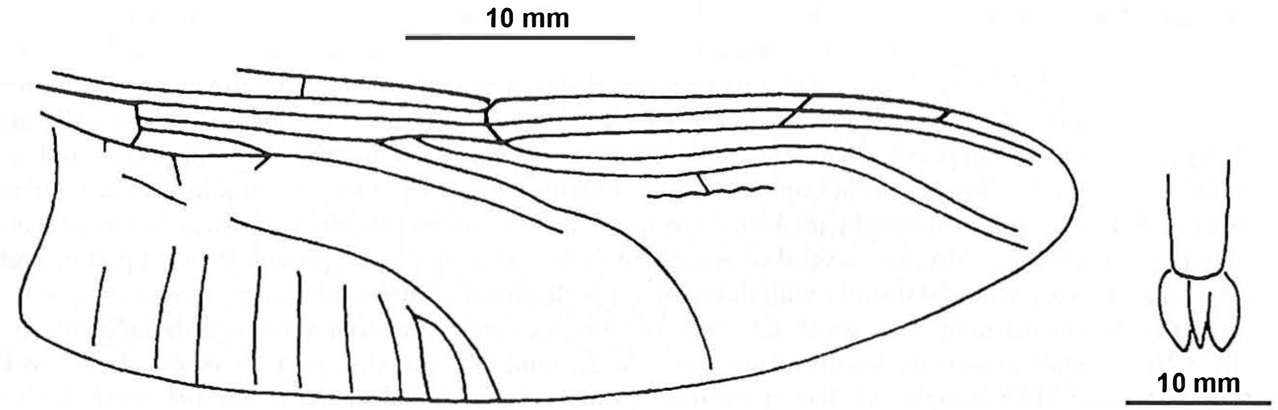
A very poorly preserved dragonfly with remnants of body and wings. Length from head to apex of the anal appendages, 85 mm. Abdomen (without anal appendages) 58 mm long and 4 mm wide. The paired superior appendages (cerci) are 5.4 mm long and foliate, and the unpaired inferior appendage (epiproct) is 4.8 mm long and conical. The anal appendages and the shape of the anal margin of the hindwing suggests that it is a male specimen, but this is not certain due to the poor preservation of the holotype, and due to the unknown female anal appendages of this species.

Forewing: Length 50 mm (erroneously stated to be 57 mm by HANDLIRSCH 1906: 589).

Hindwing: Length 46.3 mm; width at nodus 13.3 mm (largest width 14.1 mm). Only the right hindwing is sufficiently preserved to show some details (only visible with strong side light): Distance from base to nodus 20.1 mm; from nodus to pterostigma 13.7 mm. Pterostigma very elongated (length 6.3 mm) and distinctly braced. RP1 and RP2 basally closely parallel, even converging near pterostigma. RP1 and IR2 as well as RP3/4 and MA only slightly undulated and strictly parallel. A zigzagged pseudo-Rspl seems to be present, parallel to

IR2. Arculus angled, and bases of RP and MA distinctly separated at arculus. Hypertriangle basally rather wide. CuAa with about seven visible posterior branches.

Discussion: The visible wing venation, although very poorly preserved, strongly suggests that this specimen is conspecific with the neotype of *G. koehleri* HAGEN (see above), since it is the only known species from the same locality that has a comparable size and the same combination of characters (RP1 and RP2 closely parallel, pterostigma very long and braced, pseudo-Rspl, RP2 and IR2 closely parallel).



Text-Fig. 5. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. Type of *A. muensteri* GERMAR BSP AS VII 794 - right hindwing and anal appendages.

♦ Specimen no. BL 1960, JME

An almost complete specimen with body and wings, only the distal half of the right wings is missing. The wing venation agrees with the previously described specimens, including the presence of two oblique veins and the closely parallel veins RP1 and RP2. The forewing is 44 mm long and the hindwing 42 mm. The body length from head to the tip of the abdomen is 54 mm, including the foliate appendages that are 3 mm long.

♦ Specimen no. 1966 / 64 Ei Bl, JME; male

Plate 2: Fig. 1

Complete and well-preserved male (also figured in FRICKHINGER 1994: fig. 253). The wing venation of this specimen is very similar to specimen no. [1846 / HAGEN 44]

Forewing: Length 48.4 mm; width 11.6 mm; distance from base to arculus 5.9 mm; distance from base to nodus 25.6 mm; from nodus to pterostigma 11.9 mm. Pterostigma at 76 % of whole length of wing and covering six cells. Five secondary antenodal crossveins between Ax1 and Ax2.

Hindwing: Length 46.1 mm; width 15.1 mm; distance from base to arculus 5.2 mm; distance from base to nodus 20.9 mm; from nodus to pterostigma 13.7 mm. Pterostigma at 74 % of whole length of wing and covering nine cells. Hindwing discoidal triangle free of crossveins. Distal oblique vein 'O' double in hindwing (certainly an individual aberration). Wing base with anal angle and anal triangle, thus, it is a male specimen.

Male cerci and epiproct visible without spines. Cerci broadly foliate and rounded.

♦ Specimen no. MB.J. 1441, MB; female; labelled «Inv. Nr. 1995.4., *Mesuropetala koehleri* ~~*Cymatophlebia longialata*~~, Slg. KAUFMANN, 1995, Solnhofener Plattenkalk, Eichstätt, (in Ausstellung März 1996)»

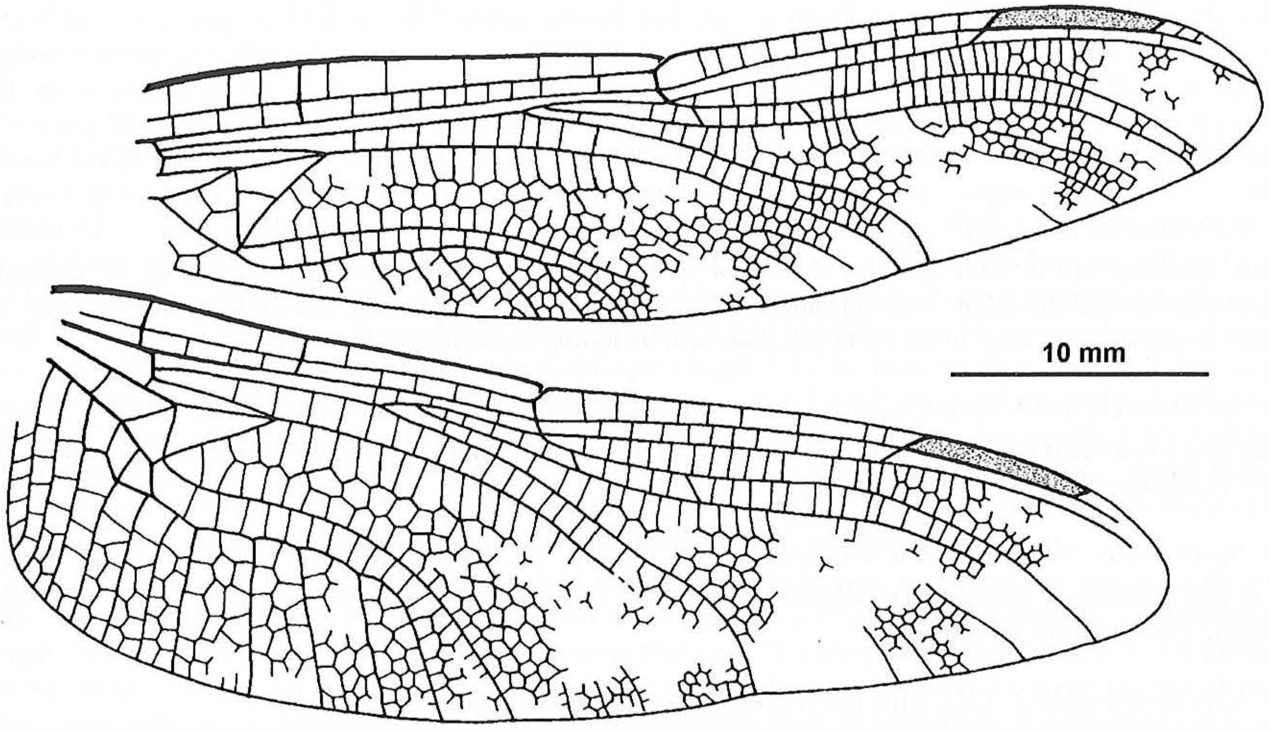
Text-Figs 6-8

An excellently preserved adult female with all for wings and parts of the body, including thorax and abdomen (width of segment VIII 2.3 mm; width of segment X 3.8 mm). The wing veins are traced by iron-oxide dendrites. The abdomen shows a medio-dorso-longitudinal crest along the abdomen (from the second to the eighth segment), but it is more like a sharp fold than a true carina, since its lateral margins are weakly defined and it has no spines. The superior appendages are well-preserved (length 5.2 mm; max. width 2.3 mm), strongly foliate with a distinct dorso-longitudinal crest.

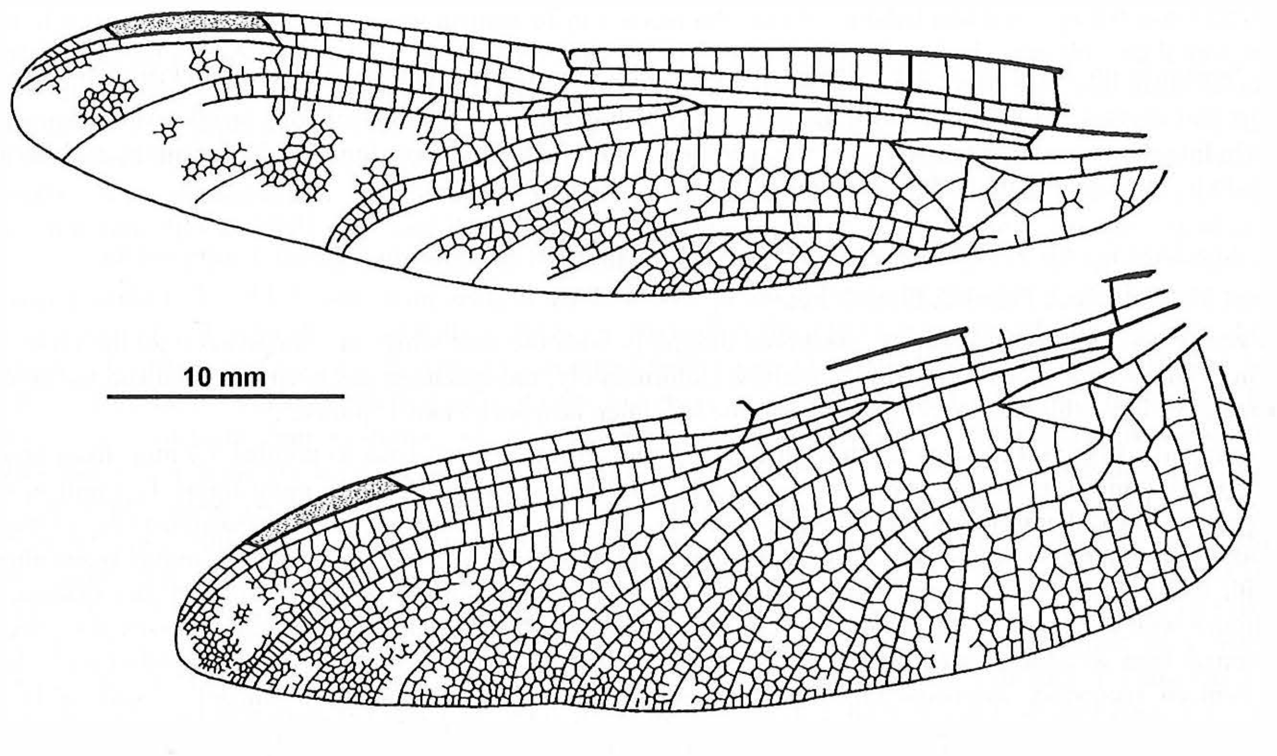
Forewing (based on the left forewing unless indicated otherwise): Length 49.0 mm; width at nodus 10.2 mm; distance from base to nodus 25.2 mm; from nodus to pterostigma 13.1 mm; distance from base to arculus 5.3 mm. Pterostigma very elongated (length 6.5 mm; width 0.8 mm), distinctly braced by an oblique crossvein, and probably covering numerous cells. Thirteen (right forewing twelve) postnodal crossveins visible between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Nineteen antenodal crossveins between costal margin and ScP, not aligned with antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Primary antenodal crossveins Ax1 and Ax2 stronger than other antenodal crossveins. Ax1 only 0.5 mm basal of arculus; Ax2 6.4 mm distal of Ax1, on a level with distal angle of discoidal triangle. Four secondary antenodal crossveins of the first row between the two primary antenodal crossveins, not aligned with corresponding antenodal crossveins in the second row. Only three preserved crossveins in antesubnodal area between arculus and subnodus (clearly an artifact of preservation). Five crossveins visible basal of first oblique vein, including at least four bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O' visible, 1.0 mm and 5.0 mm distal of subnodus. No well-defined Rspl, but a row of enlarged cells along IR2. Several convex secondary longitudinal veins in distal part of area between IR2 and RP3/4. RP2 and IR2 closely parallel with always only a single row of cells in-between. Vein pseudo-IR1 not preserved. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. RP3/4 and MA parallel and gently undulated with a single row of cells in-between (distally two rows). No Mspl, but a row of enlarged cells along MA, and several convex secondary longitudinal veins present in distal part of postdiscoidal area, not very widened distally with three rows of cells distal of discoidal triangle. Hypertriangle free of crossveins (length 6.1 mm; max. width 0.6 mm). Discoidal triangle very transverse and divided into two cells by a "horizontal" crossvein; length of anterior side 3.5 mm; of basal side 3.1 mm; of distal side MAb 4.8 mm. Distal side MAb straight. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.0 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 subdiscoidal triangle, max. 3.3 mm long and basally 2.9 mm wide (= length of PsA), divided into three cells. PsA ends at basal angle of discoidal triangle. A single row of cells in area between MP and CuA, but distally they are diverging with several cells in-between at posterior wing margin. MP reaching posterior wing margin on a level with nodus, while CuA reaches posterior wing margin somewhat basal of the level of nodus. About seven well-defined posterior branches of CuAa. Four or five rows of cells between CuA and posterior wing margin. Max. width of cubito-anal area 2.4 mm. Anal area max. 2.5 mm wide (below PsA) with two rows of cells between AA and posterior wing margin.

Hindwing (based on the left hindwing unless indicated otherwise): Length 45.6 mm; width at nodus 13.0 mm; distance from base to nodus 19.6 mm. Nodus in a rather basal position; distance from nodus to pterostigma 15.2 mm; distance from base to arculus 4.0 mm (4.6 mm in the right hindwing). Pterostigma very elongated (length 6.5 mm; width 0.9 mm), distinctly braced by an oblique crossvein, and covering numerous cells. Twelve or thirteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Only few secondary antenodal crossveins preserved in both rows, but they seem to have been numerous and not aligned. Primary antenodal crossveins Ax1 and Ax2 stronger than others. Ax1 0.4 mm basal of arculus (0.6 mm in right hindwing); Ax2 6.4 mm distal of Ax1. Three or four not aligned secondary antenodal crossveins between the two primary antenodal crossveins (right hindwing). Seven antesubnodal crossveins visible in space between arculus and subnodus without a distinct gap immediately basal of subnodus, but with a gap in basal part of antesubnodal area. Five crossveins basal of first oblique vein, including four bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.3 mm and 5.2 mm distal of subnodus (5.8 mm in right hindwing). No well-defined Rspl, but a row of enlarged cells along IR2 and several convex secondary longitudinal veins in distal part of area between IR2 and RP3/4. Pseudo-IR1 well-defined and originating beneath distal side of pterostigma. RP2 and IR2 closely parallel with always only a single row of cells in-between. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. RP3/4 and MA parallel and gently undulated with a single row of cells in-between (distally two rows). No Mspl, but a row of enlarged cells along MA and several convex secondary longitudinal veins in distal part of postdiscoidal area, distally widened with two rows of cells immediately distal of discoidal triangle. Hypertriangle free of crossveins (length 5.4 mm; max. width 0.8 mm). Discoidal triangle free of crossveins and much less transverse than that of forewing; length of anterior side 4.0 mm; of basal side 2.3 mm; of distal side MAb 4.6 mm. MAb straight. Median space free of crossveins; submedian space only traversed by CuP-crossing, 0.6 mm basal of arculus in left hindwing, and 1.5 mm in right hindwing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle, max. 1.9 mm long and basally 2.1 mm wide (= length of PsA). PsA ends at basal angle of discoidal triangle. A single row of cells in area between MP and CuA, but close to wing margin they are somewhat diverging with five cells in-between at posterior wing margin. MP reaching posterior wing margin on a level with nodus, while CuA reaches posterior wing margin somewhat basal of level of nodus. Six well-defined

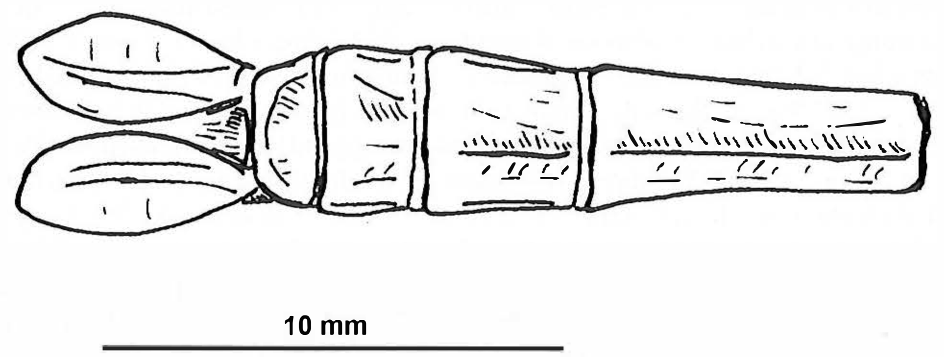
posterior branches of CuAa and a well-defined CuAb strongly bent. Seven rows of cells between CuA and posterior wing margin, max. width of cubito-anal area 6.0 mm. Anal area broad, below PsA 8.1 mm wide with six or seven rows of cells between AA and posterior wing margin. Anal loop longitudinal elongated, 3.8 mm long and 1.9 mm wide (4.0 mm long and 1.8 mm wide in right hindwing), divided into two cells (into three cells in right hindwing) and posteriorly well-closed, but zigzagged. Four parallel posterior branches of AA between CuAb and rounded anal margin. Neither an anal triangle, nor an anal angle, thus, it is a female specimen.



Text-Fig. 6. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MB.J. 1441 - female, right pair of wings.



Text-Fig. 7. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MB.J. 1441 - female, left pair of wings.



Text-Fig. 8. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MB.J. 1441 - female, anal appendages.

♦ Specimen no. MB.J. 1707, Slg. HÄBERLEIN 1880, MB

This specimen agrees with the other described specimens in all visible characters, including the elongated pterostigmata and the foliate anal appendages. The forewings are 47 mm long and the hindwings 45 mm. The body length from the head to the tip of the abdomen, including the anal appendages, is 79 mm.

♦ Specimen no. MB.J. 1708 a, b, MB; labelled «*Aeschna Münsteri* GERM., coll. MÜNSTER»

Part and counterpart of a very poorly preserved dragonfly with is either a *Mesuropetala muensteri* comb. nov., or a *Protolindenia wittei*.

♦ Specimen no. MB.J. 1710 a, b, MB; labelled «J.I. Quenst. Kat. 268 *Libellula bavarica*»

Part and counterpart of a complete dragonfly that agrees with the other described specimens in all visible characters. The wings are 47 mm long.

♦ Specimen no. MB.J. 1711, MB; labelled «*Diastatoma Münsteri* GERM.»

This specimen agrees with the other described specimens in all visible characters, including the elongated and three-celled anal loop and the basally parallel RP1 and RP2. The forewings are 52-53 mm long and the hindwings 51 mm. The body length from the head to the tip of the abdomen, excluding the anal appendages, is 73 mm.

♦ Specimen no. MB.J. 1733 a, b, MB; labelled «*Aeschnidium densum* HAGEN, Slg. HÄBERLEIN, Solnhofen»

Part and counterpart of a dragonfly that agrees with the other described specimens in all visible characters, including the elongated pterostigmata, the transverse and two-celled forewing discoidal triangle, and the free hindwing discoidal triangle. The forewing is 47 mm long.

♦ Specimen no. MCZ 1998; female ?; labelled «coll. HAEBERLEIN, Solenhofen, coll. CARPENTER»

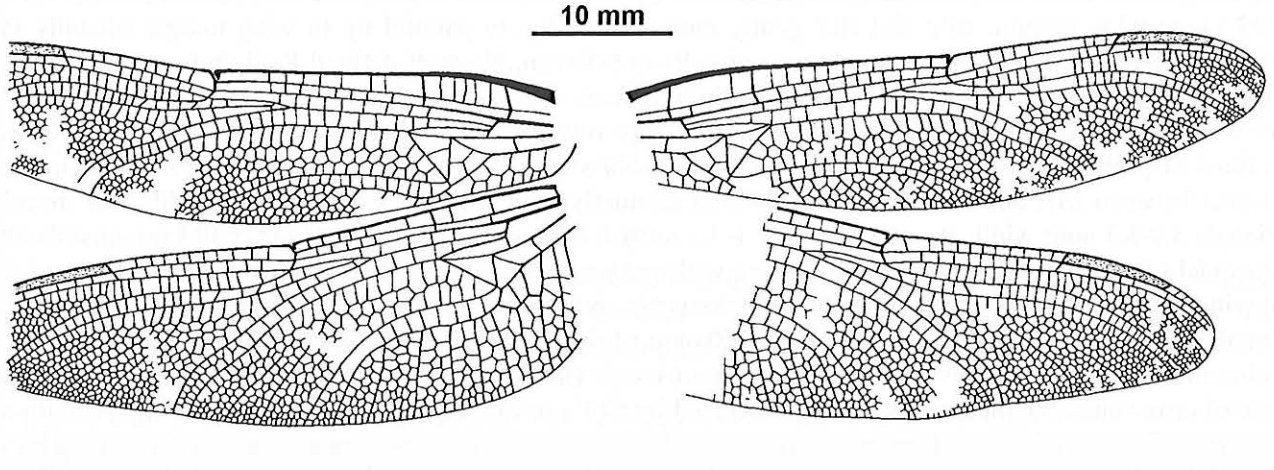
Text-Fig. 9, Plate 3: Figs 1-2, Plate 4: Fig. 1

A nearly complete and beautifully preserved dragonfly with the four wings in connection with the body. The wing veins are traced by iron-oxide dendrites. Unfortunately, the specimen has been damaged and the cracked parts have been glued together again, so that the specimen now looks like a "puzzle".

Forewing: Length 48.6 mm; width at nodus 10.9 mm; distance from base to arculus 5.7 mm; from base to nodus 25.7 mm in right forewing and 26.7 mm in left forewing; from nodus to pterostigma 12.1 mm in right forewing and 11.0 mm in left forewing (pterostigma in a relatively basal position). Pterostigma very elongated and covering more than five cells (length 6.9 mm; width 0.7 mm). A strong oblique pterostigmal brace aligned with basal side of pterostigma. Nine to elevén postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. Two primary antenodal crossveins stronger than secondary antenodal crossveins. Ax1 0.7 mm basal of arculus, Ax2 6.3 mm distal of Ax1. About seventeen secondary antenodal crossveins present, of which five secondary antenodal crossveins located between the two primary antenodal crossveins. Relatively numerous (at least nine or ten) antesubnodal crossveins between RA and RP. Apparently, a long gap of these crossveins immediately distal of arculus, and a short gap immediately basal of subnodus (the latter maybe rather an artifact of preservation). Arculus rather straight with bases of RP and MA distinctly separated at arculus. Two visible bridge-crossveins Bqs between IR2 and RP basal of subnodus. Midfork (base of RP3/4) 5.0 mm (right forewing) or 5.5 mm (left forewing) basal of nodus, and base of IR2 1.2 mm distal of midfork. RP2 aligned with subnodus. Two oblique veins 'O' between IR2 and RP2, the first 2.5 mm (right forewing) or 0.8 mm (left forewing) distal of subnodus, and the second 5.0 mm (right forewing) or 4.3 mm (left forewing) distal of subnodus. A very short pseudo-IR1 originating on RP1 two cells distal of pterostigma. Two to four rows of cells between pseudo-IR1 and RP1. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. Below basal side of pterostigma, RP1 and RP2 becoming divergent with distally six or seven rows of cells between pseudo-IR1 and RP2 along wing margin. RP2 and IR2 gently curved and closely parallel up to wing margin (distally even slightly converging) with only a single row of cells in-between. No well-defined Rspl, but a row of enlarged cells along posterior side of IR2, and two or three convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and slightly undulated with two rows of cells in-between near wing margin. No well-defined Mspl, but a row of enlarged cells along posterior side of MA, and one or two convex secondary veins in area between MA and MP. Postdiscoidal area distinctly widened near wing margin (width near discoidal triangle 3.2-3.3 mm; width at wing margin 7.1-7.5 mm). Three rows of cells in postdiscoidal area just distal of discoidal triangle. Area between MP and CuA widened near wing margin with six cells between MP and CuA at wing margin. Discoidal triangle distinctly transverse and divided into two cells by a longitudinal crossvein; length of anterior side 3.3 mm; of basal side 3.0 mm; of distal side MAb 4.5 mm. Hypertriangle free of crossveins and much more narrow than hindwing hypertriangle (length 5.8 mm; max. width 0.7 mm). Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.7-1.9 mm basal of arculus. Cubito-anal area max. 2.7 mm wide with four or five rows of cells between CuA and posterior wing margin. CuA with five well-defined parallel distal posterior branches. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle divided into three cells. Anal area max. 2.4 mm wide with two rows of cells between AA and posterior wing margin.

Hindwing: Length 46.2 mm; width at nodus 13.3 mm; distance from base to arculus 4.8 mm; from base to nodus 21.2 mm; from nodus to pterostigma 13.1 mm. Pterostigma in a relatively basal position, very elongated (length 7.9 mm; width 0.9 mm) and covering more than five cells. A strong oblique pterostigmal brace aligned with basal side of pterostigma. Ten or eleven postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. Only the distal primary antenodal crossvein (Ax2) preserved in left hindwing, on a level with distal angle of discoidal triangle. There are numerous secondary antenodal crossveins in both rows, not aligned with each other. Only five antesubnodal crossveins visible between RA and RP with a long gap of these crossveins immediately distal of arculus and immediately basal of subnodus (the latter could rather be an artifact of preservation). Arculus angled and bases of RP and MA distinctly separated at arculus. At least three crossveins between IR2 and RP basal of subnodus, including two bridge-crossveins Bqs. Midfork (base of RP3/4) 5.7 mm basal of nodus, and base of IR2 1.3 mm distal of midfork. Base of RP2 aligned with subnodus. Two oblique veins 'O', the first 1.2 mm (right hindwing) or 2.4 mm (left hindwing) distal of subnodus, and the second 5.9 mm (right hindwing) or 5.5 mm (left hindwing) distal of subnodus. A short pseudo-IR1 originating on RP1 slightly distal of pterostigma. About three rows of cells between pseudo-IR1 and RP1. RP1 and RP2 closely parallel up to pterostigma with only a single row of cells in-between. Below pterostigma, RP1 and RP2 becoming divergent with about six or seven rows of cells between pseudo-IR1 and RP2 near wing margin. RP2 and IR2 gently curved and closely parallel (distally even converging) with only a single row of cells in-between. No well-defined Rspl, but a row of enlarged cells along posterior side of IR2, and two or three convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and slightly undulated with two rows of cells in-between near wing margin. No well-defined Mspl, but a row of enlarged cells along posterior side of MA, and two convex secondary veins between MA and MP. Postdiscoidal area distinctly widened near wing margin with about twenty cells between MP and MA along posterior wing margin (width near discoidal triangle 3.3 mm; width at wing margin 8.3-8.8 mm). Only two rows of cells in postdiscoidal area just distal of discoidal triangle. Area between MP and CuA distally somewhat widened with four or five rows of cells at wing margin. Discoidal triangle longitudinally elongated and free of crossveins; length of anterior side 3.9 mm; of basal side 2.2 mm; of distal side MAb 4.5 mm. Hypertriangle free of crossveins and much broader than the forewing hypertriangle (length 5.1 mm; max. width 1.0 mm). Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.7 mm basal of arculus. Cubito-anal area max. 6.1 mm wide with six to eight rows of cells between CuA and posterior wing margin. CuAa with six parallel posterior branches. CuAb directed towards posterior wing margin. Anal loop longitudinal elongated, three-celled, and posteriorly well-closed, but zigzagged (length 4.0 mm; width 1.9-

2.9 mm). AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. AA with three preserved (totally probably four) parallel and straight posterior branches perpendicularly directed towards posterior wing margin. Anal area 8.3 mm wide with six rows of cells between AA and posterior wing margin. Basal part of anal area not preserved in both hindwings, but the anal margin seems to have been rounded, indicating that it is probably a female specimen.



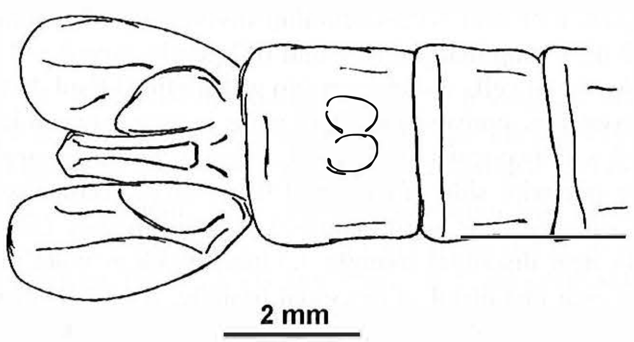
Text-Fig. 9. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MCZ 1998 - female ?, wings.

♦ Specimen no. MCZ 6203; male; labelled «coll. HAEBERLEIN, Solenhofen, coll. CARPENTER»

Text-Fig. 10, Plate 4: Fig. 2, Plate 5: Fig. 1

An almost complete male with four wings, head, one fore leg, thorax and complete abdomen. The wing venation is rather poorly preserved, but very similar to the other described specimens. Unfortunately, the wing bases which would be very interesting, since not yet known for male specimens of *Mesuropetala*, are destroyed. Wings 45 mm long. Body length from head to the tip of the abdomen (including appendages) 74 mm. Head well-preserved and clearly with large approximated compound eyes. Apex of abdomen rather well-preserved in dorsal aspect, showing foliate cerci (length 3.7 mm; width 1.7 mm) with a characteristic sculpturing (see Text-Fig. 10), as well as a conical epiproct that is 3.0 mm long, apically blunt and not bifid. Male gonopods (genital valvulae) also faintly visible (pressed through body), constituting the only evidence that this is indeed a male specimen.

The foliate cerci are also visible in specimen no. [MCZ 6194] and a further unnumbered specimen from MCZ (Plate 5: Fig. 2) which also has well-preserved legs with short spines on the femora and longer spines on the tibiae.



Text-Fig. 10. *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. MCZ 6203 - male, anal appendages.

♦ Specimen without number, coll. JUVYNS; male

Plate 33: Fig. 1

A complete and perfectly preserved male in the commercial collection of the fossil trader Mr Roland JUVYNS in Brussels (Belgium). The wings are outspread and the wing venation of all four wings is traced by iron oxide dendrites. Only the legs and the anal appendages are not visible. The first author has a photograph of this specimen, which shall have a wingspan of about 100 mm. The specimen is most important since it is the single known male *Mesuropetala* specimen with preserved hindwing bases: There is no posterior branch of AA between the anal loop and the anal triangle; the anal triangle is long and three-celled and smoothly curved (concavely indented) in the posterior half. A curious aberration in this specimen is the fact that the subdiscoidal triangle is normal (three-celled and widened with a curved posterior margin) in the right forewing, but narrow and two-celled with a straight posterior margin in the left forewing. Also most unusual is the circumstance that the discoidal triangles of both forewings are divided into three cells by two parallel horizontal crossveins. All other visible characters completely agree with the other described specimens.

Mesuropetala auliensis PRITYKINA, 1968

Text-Figs 11-13, Plate 5: Fig. 3

*v 1968 *Mesuropetala auliensis* PRITYKINA, pp. 50-51, text-fig. 21, pl. 5, fig. 2 (in Petaluridae).

1992 *Mesuropetala* ... PRITYKINA; CARPENTER, p. 83 (in Petaluridae).

1992 *Protolindenia auliensis* (PRITYKINA); NEL & PAICHELER, p. 320 (position discussed; due to a lapsus calami the names *Mesuropetala* and *Protolindenia* have been confused in this publication, so that *Protolindenia* is stated as original genus of *M. auliensis*, while *Mesuropetala* is indicated as new synonym, although it was clearly meant vice versa).

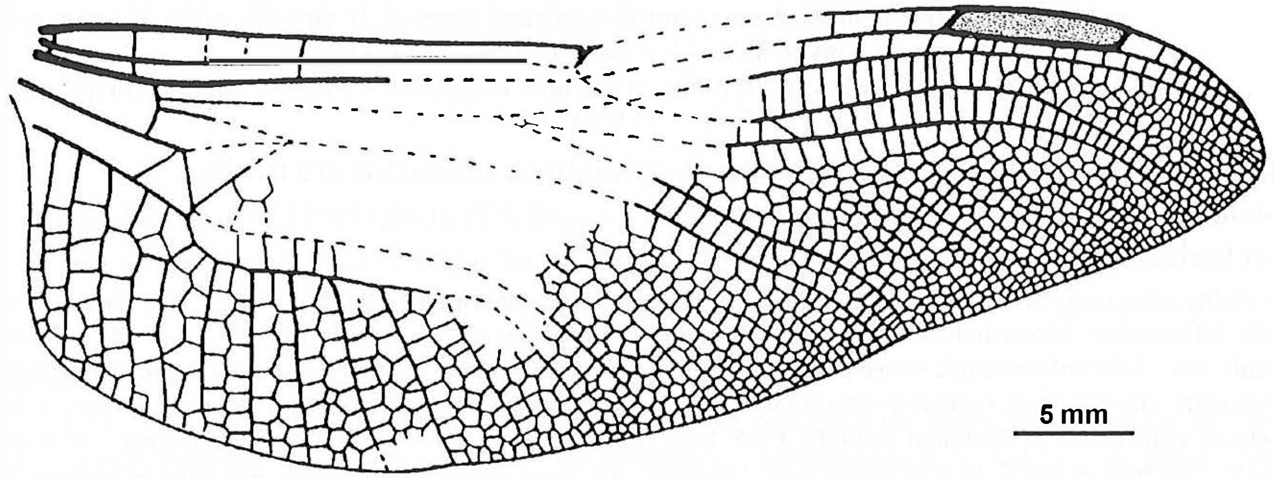
1998 *Mesuropetala auliensis* PRITYKINA; NEL *et al.*, pp. 22-23, figs 19-21 (redescription of type, position discussed).

Holotype: Specimen no. [2239 / 21], PIN, Moscow; a partly preserved hindwing of a female.

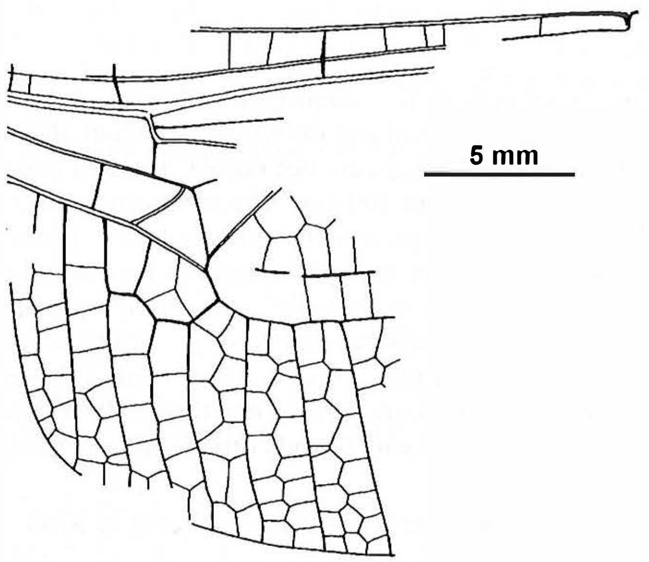
Locus typicus: Karatau, Turkestan, ex USSR.

Geological age: Upper Jurassic.

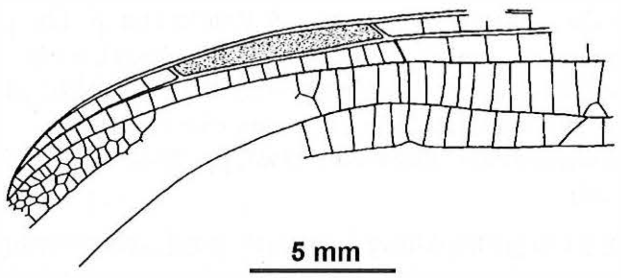
Mesuropetala auliensis appears to be very similar to *M. muensteri* comb. nov., they even share the characteristical anal loop and the very elongated pterostigma (synapomorphies). There are also at least three rows of cells in the basal part of the postdiscoidal area; Nevertheless, the hindwing of *M. auliensis* is distinctly larger (length of hindwing 52.8 mm) than that of *M. muensteri* comb. nov., and distinctly smaller than that of *M. magna* sp. nov. Its pterostigma is longer, covering more cells (eleven) than any of the other species. Its attribution to the genus *Mesuropetala* as a distinct species is strongly supported.



Text-Fig. 11. *Mesuropetala auliensis* PRITYKINA, 1968. Holotype PIN 2239 / 21 - male, hindwing (drawing after PRITYKINA 1968: text-fig. 21).



Text-Fig. 12. *Mesuropetala auliensis* PRITYKINA, 1968. Holotype PIN 2239 / 21 - male, hindwing base.



Text-Fig. 13. *Mesuropetala auliensis* PRITYKINA, 1968. Holotype PIN 2239 / 21 - male, hindwing apex.

?*Mesuropetala costalis* PRITYKINA, 1968

Text-Figs 14-15, Plate 5: Fig. 4

*v 1968 *Mesuropetala costalis* PRITYKINA, pp. 49-50, text-fig. 20, pl. 5, fig. 1 (in Petaluridae).
1992 *Mesuropetala* ... PRITYKINA; CARPENTER, p. 83 (in Petaluridae).
1992 *Protolindenia costalis* (PRITYKINA); NEL & PAICHELER, p. 320 (position discussed; due to a *lapsus calami* the names *Mesuropetala* and *Protolindenia* have been confused in this publication, so that *Protolindenia* is stated as original genus of *M. costalis*, while *Mesuropetala* is indicated as new synonym, although it was clearly meant vice versa).
1998 *Mesuropetala costalis* PRITYKINA; NEL *et al.*, pp. 21-22, figs 17-18 (redescription of type, position discussed).

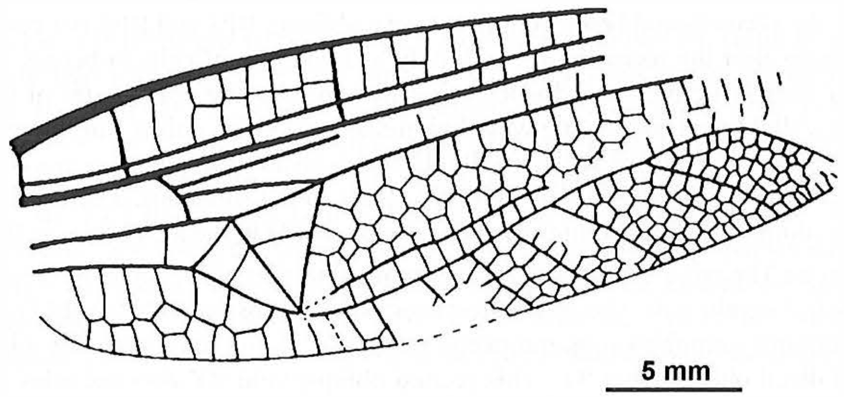
Holotype: Specimen no. [2239 / 20], PIN, Moscow; partly distorted basal half of a forewing.

Locus typicus: Karatau, Turkestan, ex USSR.

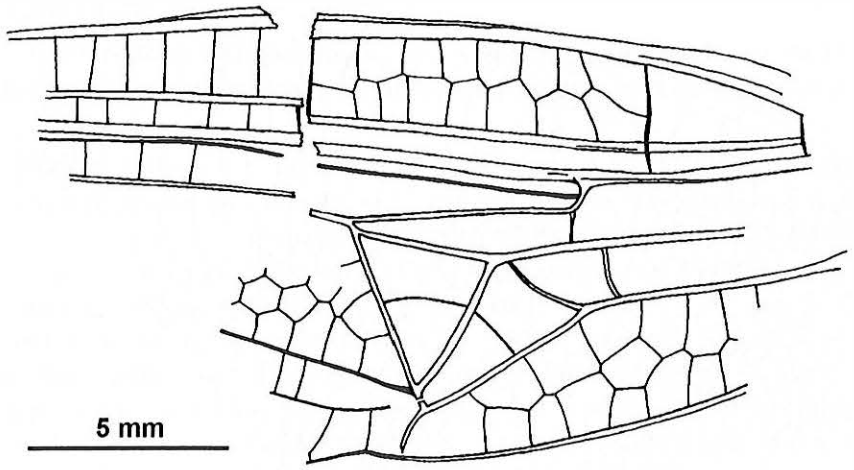
Geological age: Upper Jurassic.

In their recent revision NEL *et al.* (1998) showed that the preserved part of the holotypical forewing provides little information. Nevertheless, it is quite similar to the same part of the forewing of *Mesuropetala muensteri* comb. nov.: Discoidal triangle transverse and two-celled; subdiscoidal triangle well-defined; primary antenodal crossveins stronger than numerous secondary antenodal crossveins; postdiscoidal area broad with three or four rows of cells distal of discoidal triangle; CuA long with seven posterior branches; median space, submedian space, and hypertriangle free of crossveins. However, all these characters probably represent symplesiomorphies. ?*M. costalis* differs from all other species of Mesuropetalidae in the following forewing characters: First row of antenodal area between Ax1 and Ax2 divided into two rows of cells; subdiscoidal triangle two-celled; cubito-anal area somewhat broader; CuP-crossing and PsA very close (cubital cell short, as in Austropetaliida).

These differences certainly justify the recognition of a separate species, irrespective of its generic position. Its preliminary attribution to the genus *Mesuropetala* as a distinct species is quite possible, although by no means well supported, since there are only few diagnostic characters preserved. It could as well be a petalurid or gomphid, although there are also no fossil or extant species known which have two-celled discoidal and subdiscoidal triangles.



Text-Fig. 14. ?*Mesuropetala costalis* PRITYKINA, 1968. Holotype PIN 2239 / 20 - forewing base (drawing after PRITYKINA 1968: text-fig. 20).



Text-Fig. 15. ?*Mesuropetala costalis* PRITYKINA, 1968. Holotype PIN 2239 / 20 - forewing base.

Mesuropetala magna sp. nov.

Text-Fig. 16

Holotype: Specimen no. [1989 / 1461], PIN, Moscow; part and counterpart of the apical wing fragment.

Derivatio nominis: Latin expression for "big", because of the large size of this species.

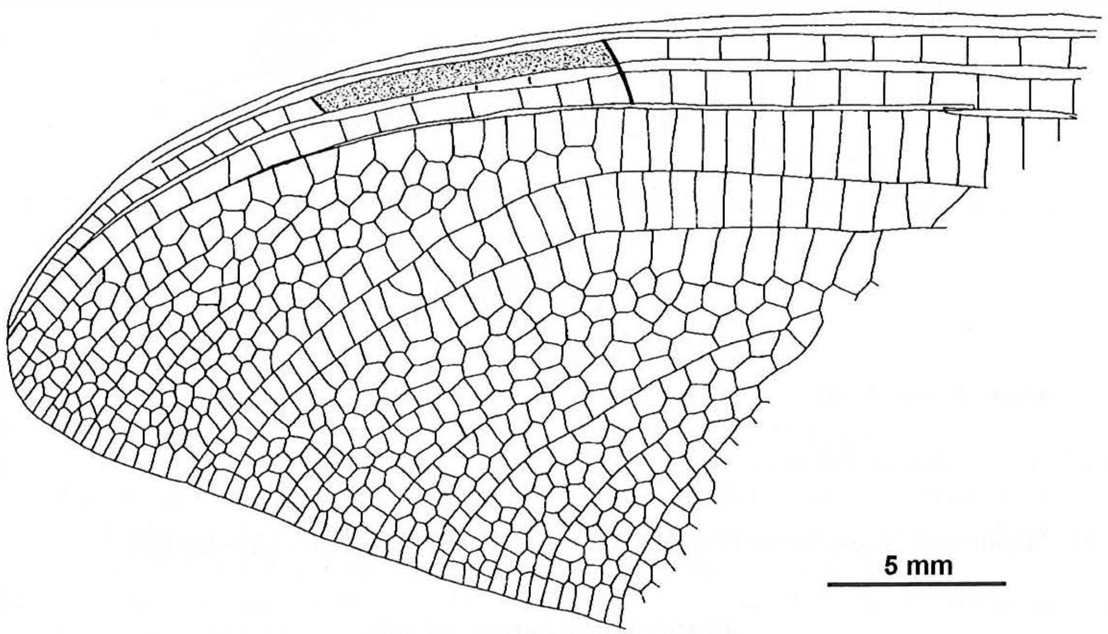
Locus typicus: Baissa, course of Bais at upper stream of Vitim River, Eravninsk region, Transbaikals, Buryat Republic, ex USSR.

Stratum typicum: Zazinsk Series, Lower Cretaceous ("Neocomian").

Diagnosis: The visible characters are very similar to the other species of the genus *Mesuropetala*. This new species is only differing in the following characters (probably autapomorphies): Very large size (wing length 69.0 mm); pterostigmal brace vein not very oblique; pseudo-IR1 rather weakly defined. It also differs from *M. auliensis* by the smaller number of cells beneath the pterostigma (seven instead of eleven cells).

Description: The apical part of a wing, only preserved distal of the second oblique vein 'O'. It cannot be clearly recognized if it is a fore- or a hindwing. However, RP3/4 and MA are not visible, since they end more basally, which indicates that it could rather be a hindwing. Length of the fragment 30.9 mm (total length probably 69 mm, estimated from the relative distance from basal side of pterostigma to apex, compared to the hindwing of *M. aaliensis*). The numerous postnodal crossveins are not aligned with the postsubnodal crossveins; there are sixteen postnodal crossveins distal of the pterostigma. The pterostigma is very elongated (length 8.6 mm; width 1.4 mm) and covers slightly more than seven cells; the pterostigma is distinctly braced by a strong vein, but the pterostigmal brace vein is not very oblique. RP1 and RP2 run parallel up to the pterostigma (even converging near the pterostigma) with only a single row of cells in-between; the primary IR1 is reduced and a rather weakly defined pseudo-IR1 originates on RP1 distinctly distal of the pterostigma; RP2 and IR2 are strictly parallel (even converging with their distal parts) with only a single row of cells in-between. An oblique vein 'O' is visible between RP2 and IR2 10.0 mm basal of the pterostigma. Because of this distal position, there was certainly a second oblique vein 'O' closer to the subnodus. There is no visible Rspl, but a row of enlarged cells along IR2. Several intercalary veins are visible in the area between IR2 and RP3/4.

Systematic position: The wing venation is nearly identical to that of the corresponding part of the wing of *Mesuropetala muensteri* comb. nov. The few differences (size, pterostigmal brace, IR1) are mentioned in the diagnosis. Some lindeniine gomphids (e.g. the extant genus *Cacoides*) have a similar wing venation, too, but never have a second distal oblique vein 'O'. This second oblique vein 'O' also excludes a position in Liupanshaniidae fam. nov. The character combination of this new species only occurs within the genus *Mesuropetala*, especially in the type species *M. muensteri* comb. nov. that also has a very elongated pterostigma and the row of enlarged cells along IR2 as derived similarities (putative synapomorphies). Therefore, this new species most likely represents the sister-species to the *M. muensteri* comb. nov. within the genus *Mesuropetala*.



Text-Fig. 16. *Mesuropetala magna* sp. nov. Holotype PIN 1989 /1461 - wing apex.

Genus *Aeschnopsis* HANDLIRSCH, 1939 stat. restor. (pos. nov.)

(= *Cymatophlebiopsis* HANDLIRSCH, 1939 stat. restor. and jun. subj. syn. nov.)

1939 *Aeschnopsis*; HANDLIRSCH, p. 153 (nom. rest. hic, not a nomen nudum).
1939 *Cymatophlebiopsis*; HANDLIRSCH, p. 153 (nom. rest. hic, not a nomen nudum, but a jun. subj. syn. nov. of *Aeschnopsis* HANDLIRSCH).
1942 *Aeschnopsis* COWLEY, pp. 77-78 (jun. obj. syn. nov. of *Aeschnopsis* HANDLIRSCH).
1942 *Cymatophlebiopsis* COWLEY, p. 78 (jun. obj. syn. nov. of *Cymatophlebiopsis* HANDLIRSCH, and jun. sub. syn. nov. of *Aeschnopsis* COWLEY in NEL *et al.*, 1998).
1992 *Aeschnopsis* HANDLIRSCH; CARPENTER, p. 81 (regarded by CARPENTER as valid).

1992 *Cymatophlebiopsis* HANDLIRSCH; CARPENTER, p. 83 (regarded by CARPENTER as valid).
1994 *Aeschnopsis* HANDLIRSCH; BRIDGES, p. III.1 (regarded by BRIDGES as nomen nudum).
1994 *Cymatophlebiopsis* HANDLIRSCH; BRIDGES, p. III.13 (regarded by BRIDGES as nomen nudum).
1994 *Aeschnopsis* COWLEY; BRIDGES, p. III.1 (regarded by BRIDGES as valid).
1994 *Cymatophlebiopsis* COWLEY; BRIDGES, p. III.13 (regarded by BRIDGES as valid).
1998 *Aeschnopsis* COWLEY 1942 (= *Cymatophlebiopsis* COWLEY 1942 syn. nov.); NEL *et al.*, pp. 12, 64 (regarded by the authors as valid).

Type species: *Aeschnopsis perampla* (BRODIE, 1845), by original indication (type by monotypy). COWLEY (1942) redescribed the two genera *Aeschnopsis* and *Cymatophlebiopsis*, since he regarded the concerning generic names of HANDLIRSCH (1939) as nomina nuda (followed by BRIDGES 1994, but not by CARPENTER 1992). This of course has to be regarded as invalid, since COWLEY himself mentioned that HANDLIRSCH has given a formal description. Therefore, he mainly based his decision on the omission of the designation of a type species. Indeed, Art. 13.3 IRZN requires the designation of a type species for all generic names established after 1930. However, according to Art. 68.3 IRZN the concerning type species have to be regarded as designated by monotypy by HANDLIRSCH (1939) since the concerning genera are monotypic. Therefore, HANDLIRSCH's generic names are well valid, and COWLEY's names have to be regarded as junior objective synonyms (even though they are not differing in spelling they are not homonyms, since they are not referring to a different taxon).

Further included species: *A. jurassica* (GIEBEL, 1856) pos. nov. from the Lower Cretaceous of England, and *A. tischlingeri* sp. nov. and *A. perkinsi* sp. nov. from the Upper Jurassic Solnhofen Limestone.

New diagnosis: The wing venation is very similar to *Mesuropetala*, only differing in the following characters: Pterostigma not extremely elongated (plesiomorphy, but not known in the type species and *A. jurassica*); hindwing discoidal triangle two-celled (autapomorphy); PsA strongly defined in both pairs of wings. The body characters are not yet known.

Aeschnopsis distinctly differs from *Cymatophlebia* in several important hindwing characters, e.g. the well-defined and longitudinally elongated anal loop, the unicellular subdiscoidal triangle, and the two-celled discoidal triangle.

Systematic position: Until recently (e.g. CARPENTER 1992: 83), most authors attributed the genus *Aeschnopsis* to Gomphidae and the genus *Cymatophlebiopsis* to Cymatophlebiinae. The genera *Aeschnopsis* and *Cymatophlebiopsis* have been revised and synonymized by BECHLY (1996) and NEL *et al.* (1998), and transferred to Anisoptera *incertae sedis*. BECHLY (1996) and NEL *et al.* (1998) considered a possible relationship with Cretapetaluridae, only because of the longitudinal shape of the anal loop, which is in fact quite different in Cretapetaluridae and thus not a convincing synapomorphy at all. A strong conflicting evidence against any position within Petalurida, and thus against a relationship with Cretapetaluridae, are the basally closely parallel veins RP1 and RP2 in the type species that also exclude the existence of a strongly prolonged primary IR1. A hypertrophied primary IR1 belongs to the groundplan of Petalurida, while basally parallel veins RP1 and RP2 represent a synapomorphy with Aeshnoptera. Because of several similarities with *Mesuropetala*, including at least one strong synapomorphy (viz longitudinally elongated and narrow anal loop), we here transfer the genus *Aeschnopsis* to Mesuropetalidae. This position is strongly confirmed by the discovery of two new species (*A. tischlingeri* sp. nov. and *A. perkinsi* sp. nov.) that share with the type species the two-celled discoidal triangle in the hindwing. Furthermore, there is no substantial conflicting evidence against this proposed new position of *Aeschnopsis*.

Aeschnopsis perampla (BRODIE, 1845)

Text-Figs 17-19

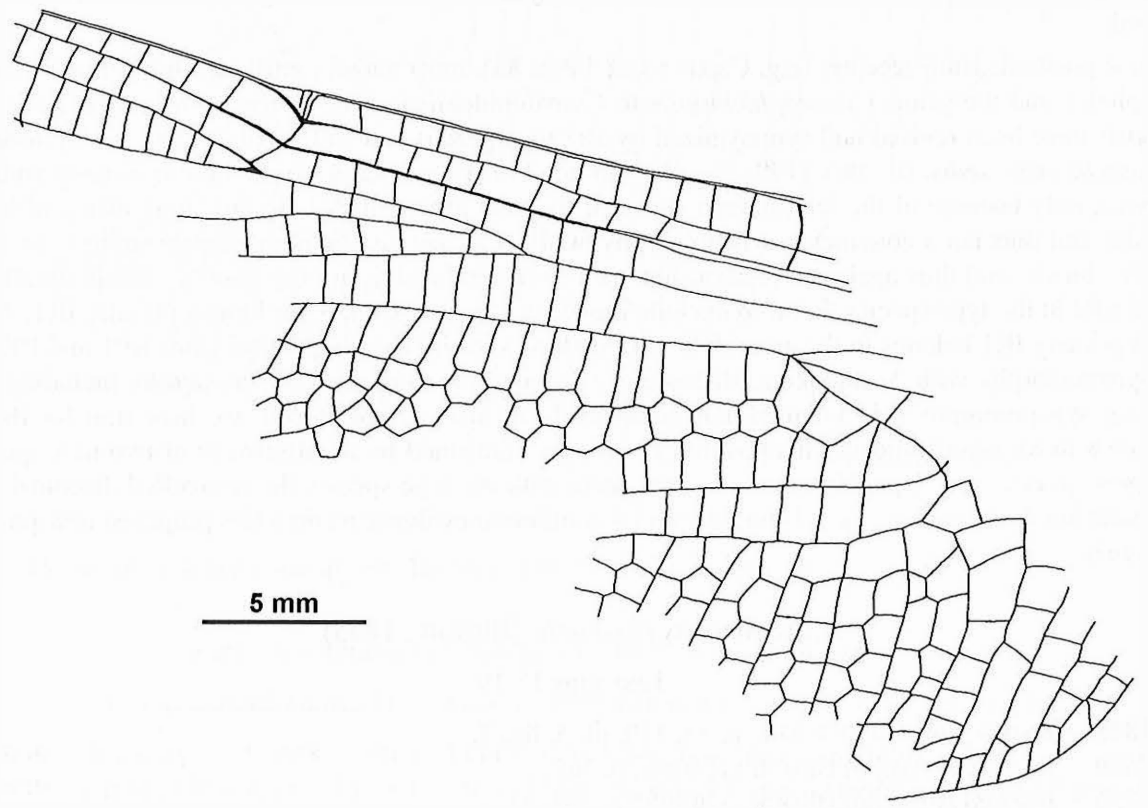
*v 1845 *Aeshna perampla* BRODIE, p. 33, 119, pl. 5, fig. 7.
1850 *Aeschna perampla* BRODIE; HAGEN, p. 362.
1856 *Aeschna perampla* BRODIE; GIEBEL, p. 281, 412.
1890 *Aeschna perampla* BRODIE; KIRBY, p. 173.
1906 (Gomphidae ?) *perampla* BRODIE; HANDLIRSCH, p. 593.
1939 *Aeschnopsis perampla* (BRODIE); HANDLIRSCH, p. 153 (new genus name, not a nomen nudum).
v 1939 *Cymatophlebiopsis pseudobubas*; HANDLIRSCH, p. 153 (new genus name, not a nomen nudum, in Gomphidae).

1942 *Aeschnopsis perampla* (BRODIE); COWLEY, pp. 77-78 (brief redescription, in Gomphidae - Protolindeniinae ?).
1942 *Cymatophlebiopsis pseudobubas* HANDLIRSCH; COWLEY, p. 78 (brief redescription, in Gomphidae - Cymatophlebiinae ?).
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 (in Petaluridae, family assignment doubtful).
1992 *Aeschnopsis perampla* (BRODIE); NEL & PAICHELER, p. 316 (position discussed).
1992 *Cymatophlebiopsis pseudobubas* HANDLIRSCH; NEL & PAICHELER, p. 318 (position discussed).
1993 *Cymatophlebiopsis pseudobubas* HANDLIRSCH; JARZEMBOWSKI, p. 176.
1994 *Aeschnopsis perampla* (BRODIE); BRIDGES, p. VII.182 (in Gomphidae).
1994 *Cymatophlebiopsis pseudobubas* HANDLIRSCH; BRIDGES, p. VII193 (in Petaluridae).
1996 "*Aeschnopsis perampla* (= *Cymatophlebiopsis pseudobubas*)"; BECHLY, p. 380 (in Petalurida).
v. 1998 *Aeschnopsis perampla* (= *Cymatophlebiopsis pseudobubas*); NEL *et al.*, pp. 12-15, figs 4-7 (synonymization and position discussed).

Holotype (of *Aeschnopsis perampla*): specimen I. 12780, BMNH, London; fragment of a female hindwing. The holotype of *Cymatophlebiopsis pseudobubas* is specimen I. 3950, det. A.J. ROSS, coll. BRODIE 1994, BMNH, London; fragment of a male hindwing.

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

Stratum typicum: Lower-Middle Purbeck beds, Lower Cretaceous, Berriasian.

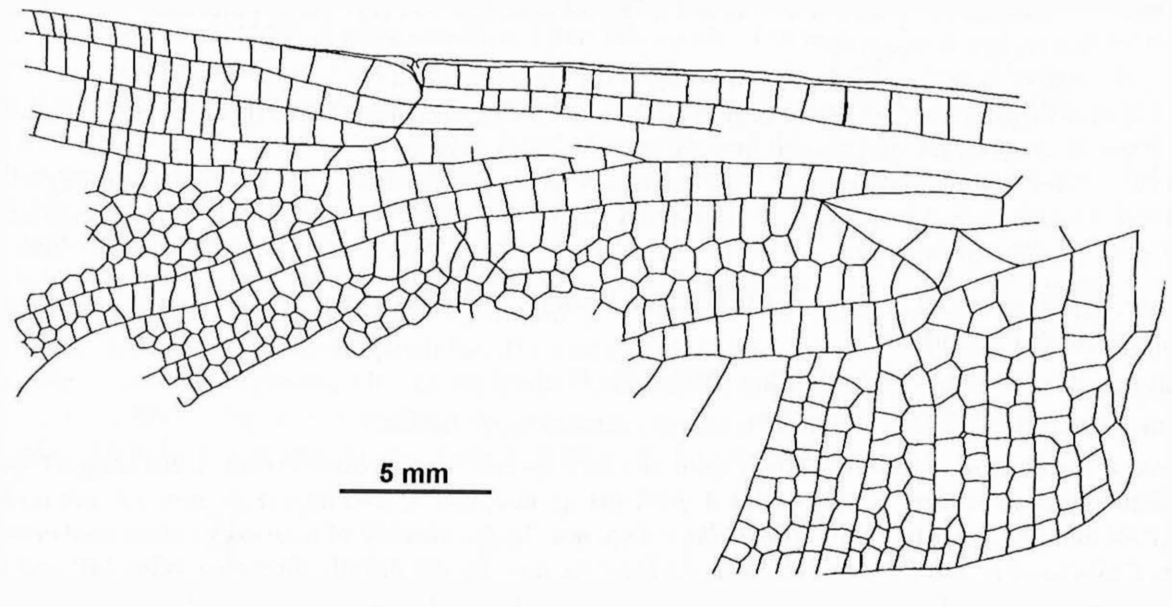


Text-Fig. 17. *Aeschnopsis perampla* (BRODIE, 1845). Holotype BMNH I. 12780 - female, left hindwing.

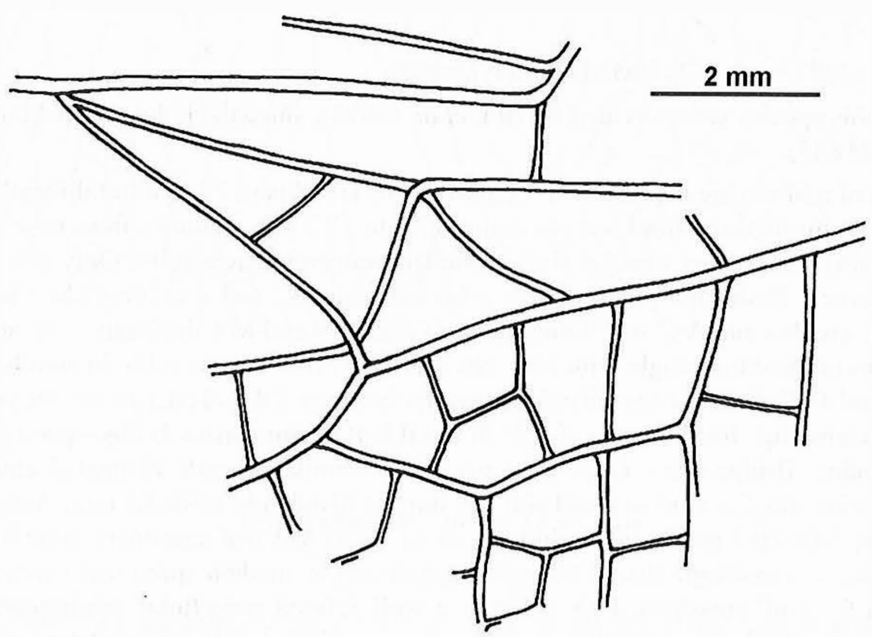
Diagnosis: The type species differs from all other species of the genus by the following hindwing characters: Discoidal triangle more longitudinally elongated and more narrow (autapomorphy); anal loop more elongated and divided into more than three cells (autapomorphy); cubito-anal area with up to ten rows of cells; RP3/4 and

MA smoothly undulated (plesiomorphy); RP1 and RP2 basally closely parallel (plesiomorphy; unknown in *A. jurassica*.). The relatively approximated position of the two oblique veins 'O' is a derived similarity with *A. perkinsi* sp. nov. (absent in *A. tischlingeri* sp. nov., but unknown in *A. jurassica*). The presence of three cell rows in the basal postdiscoidal area of the hindwing is a plesiomorphic difference to *A. jurassica* and *A. perkinsi* sp. nov. (unknown in *A. tischlingeri* sp. nov.), and the more distal position of Ax2 is a plesiomorphic difference to *A. jurassica*.

Redescription: The two holotypes have been recently redescribed by NEL *et al.* (1998).



Text-Fig. 18. *Aeschnopsis perampla* (BRODIE, 1845). Holotype of *Cymatophlebiopsis pseudobubas* HANDLIRSCH BMNH I. 3950 - male, left hindwing.



Text-Fig. 19. *Aeschnopsis perampla* (BRODIE, 1845). Holotype of *Cymatophlebiopsis pseudobubas* HANDLIRSCH BMNH I. 3950 - male, left hindwing base.

Aeschnopsis jurassica (GIEBEL, 1856) pos. nov.

Text-Fig. 20

(mandatory spelling change according to Art. 34 IRZN)

v 1845 *Lindenia* sp. BRODIE, p. 33, pl. 5, fig. 9.
1850 *Gomphus petrificatus*; HAGEN, p. 359 (incorrect attribution).
*v 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 & PAICHELER, pp. 315-316 (position discussed).
1994 *Necrogomphus jurassica* (GIEBEL); BRIDGES, p. VII.123.
1996 "*Aeschnopsis jurassicus* (= *Necrogomphus jurassicus*)"; BECHLY, p. 380 (in Petalurida).
1998 '*Necrogomphus*' (?)*jurassicus* (GIEBEL 1856); NEL *et al.*, pp. 9-12, 65, fig. 3 (redescription, position discussed).

Holotype: Specimen no. [I. 12782 + I.12778], coll. BRODIE, BMNH, London; part and counterpart of a basal fragment of a male (?) hindwing.

Locus typicus: Teffont, Vale of Wardour, Wiltshire, England.

Stratum typicum: Middle Purbeck beds, Lower Cretaceous, Berriasian.

Diagnosis: *Aeschnopsis jurassica* differs from all other species of the genus, except *A. tischlingeri* sp. nov., by its distinctly smaller size. It shares with *A. perkinsi* sp. nov. and *A. tischlingeri* sp. nov. the not undulated veins RP3/4 and MA. It differs from *A. tischlingeri* sp. nov. by the absence of accessory cubito-anal crossveins between CuP-crossing and PsA, and from *A. perkinsi* sp. nov. by the distally diverging veins MP and CuAa, and the wider cubito-anal area (eight rows of cells instead of six). A unique character (autapomorphy) of this species is the rather basal position of Ax2 in the hindwing, on a level with the basal half of the discoidal triangle. Whether the quadrangular shape of the hypertriangle is an autapomorphy, too, or only an individual aberration, can only be answered when further material becomes available. The unique structure of the anal triangle in the holotype almost certainly represents a teratological aberration, since it is most unusual for Anisoptera.

Description

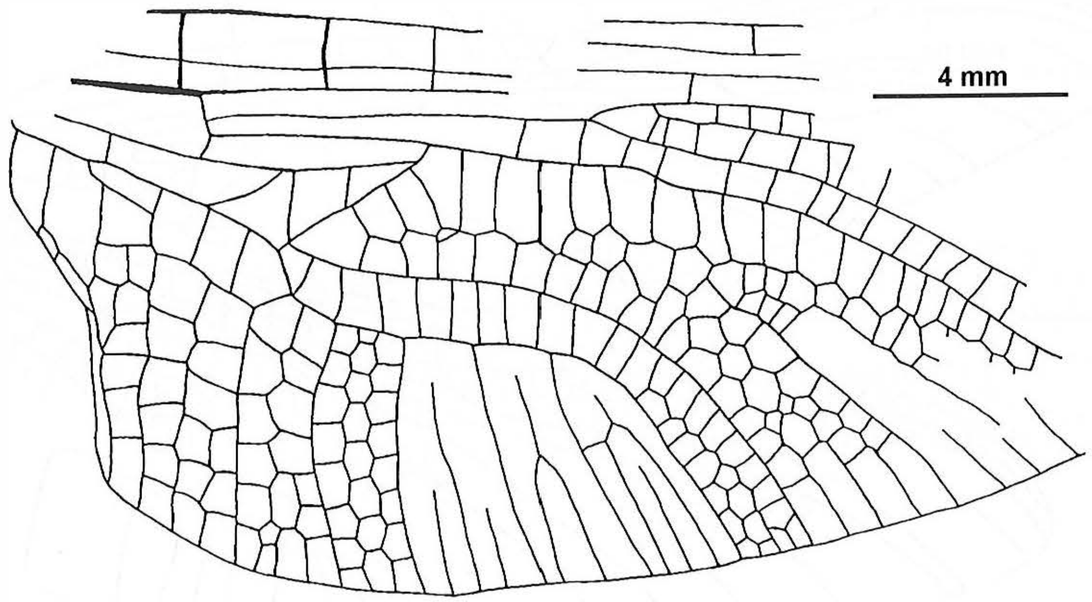
♦ Specimen no. I. 12782 + I.12778, BMNH; holotype; male ?

A redescription of this species was provided by NEL *et al.* (1998), since the holotype specimen was incorrectly figured by BRODIE (1845).

Only the basal half of a hindwing is preserved. Length of preserved part, 23 mm (total length of wing probably 35 mm); width 11.5 mm; distance from base to nodus 17.5 to 17.7 mm; distance from base to arculus 3.8 mm. Two primary antenodal crossveins stronger than secondary antenodal crossveins. 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 distinctly separated at arculus. Posterior part of arculus at an obtuse angle with MA. No antefurcal crossveins visible in area between RA and RP (between arculus and RP3/4). Only two distal crossveins between RP and MA (between arculus and RP3/4). Many bridge-crossveins Bqs, four of them visible in basal half of the narrow bridge-space (Bqs-area) between RP, IR2 and subnodus. Bridge-space (Bqs-area) narrow. Discoidal triangle elongated and divided into two cells; length of anterior side 2.5 mm; of basal side 1.4 mm; of distal side MAb 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 space and submedian space free of crossveins (except for CuP-crossing). PsA delimits a well-defined unicellular subdiscoidal triangle (length 1.8 mm; width 1.5 mm). 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 7 mm) with about ten rows of cells near wing margin. No Mspl and only two secondary longitudinal veins in postdiscoidal area. Area between MP and CuA never widened with a single row of cells near discoidal triangle and two rows of cells on a level with the 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, only 0.3 mm long, the gaff 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 (length 3.4 mm; width 1.4 mm), 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 a single elongated and narrow paranal cell along AA between anal loop and anal triangle. Anal triangle irregular and not very well-defined, 3 mm long and 2 mm wide, divided into two main cells and two smaller cells along the postero-basal wing margin (AP + AA''). Anal area max. 6.7 mm wide with up to seven rows of cells. The anal area and especially the "anal triangle" look very strange and would be absolutely unique among Anisoptera); therefore we rather consider this aberrant anal area as highly teratological, or maybe it was even a gynandromorph specimen.

Discussion: BECHLY (1996) already considered that this species belongs to *Aeschnopsis* because of several derived similarities (e.g. longitudinal anal loop, narrow bridge-space, etc.). NEL *et al.* (1998) recently demonstrated that there is no evidence that the holotype of *Aeschnopsis jurassica* (GIEBEL, 1856) belongs to the genus *Necrogomphus* CAMPION, 1923 and preliminarily transferred this species to Anisoptera *incertae sedis*. Our discovery of the new species *Aeschnopsis tischlingeri* sp. nov. and *A. perkinsi* sp. nov. (see below) also revealed the true position of *A. jurassica* in Mesuropetalidae, since the preserved part of the holotype is strikingly similar to the corresponding area in the hindwing of the mentioned new species. All the minor differences belong to the character range that occurs in the other known species of Mesuropetalidae as well. The basal position of the arculus very close to Ax1 in the hindwing, and the three-celled longitudinal anal loop are strong synapomorphies with Mesuropetalidae. The two-celled discoidal triangle indicates a position in *Aeschnopsis* rather than *Mesuropetala*. The not undulated veins RP3/4 and MA indicate a close relationship with *Aeschnopsis tischlingeri* sp. nov. and *A. perkinsi* sp. nov., and the small size, as well as several other similarities, could even indicate a sistergroup relationship with *A. tischlingeri* sp. nov.



Text-Fig. 20. *Aeschnopsis jurassica* (GIEBEL, 1856). Holotype BMNH I. 12782 + I. 12778 - male ?, right hindwing base.

Aeschnopsis tischlingeri sp. nov.

Text-Figs 21-22 A

? 1999 *Aeschnopsis tischlingeri* BECHLY; FRICKHINGER, p. 49, fig. 79 (nomen nudum).

Holotype: Specimen no. [1964 XX III x a, b], BSP, Munich; labelled «*Tarsophlebia eximia* (HAGEN), Ob. Malm, Plattenkalke, Schernfeld / Anisoptera Gomphidae ?». This type specimen should not be confused with specimen [BSP 1964 XIII oo] (erroneously indicated as «BSP 1964 XXIII oo» in NEL *et al.* 1998) which is a male *Protolindenia wittei*, or with specimen [BSP 1964. XXIII] which is an isolated *Stenophlebia* wing, or with specimen [BSP 1964 XXIII x] that was described and figured in NEL *et al.* (1998) under the name *Mesuropetala koehleri*, but obviously represents an *Aeschnopsis* sp., too (Fig. 22 B, Plate 6: Fig. 4).

Other specimen: A further putative specimen of this new taxon is present in coll. BÜRGER (Bad Hersfeld, Germany).

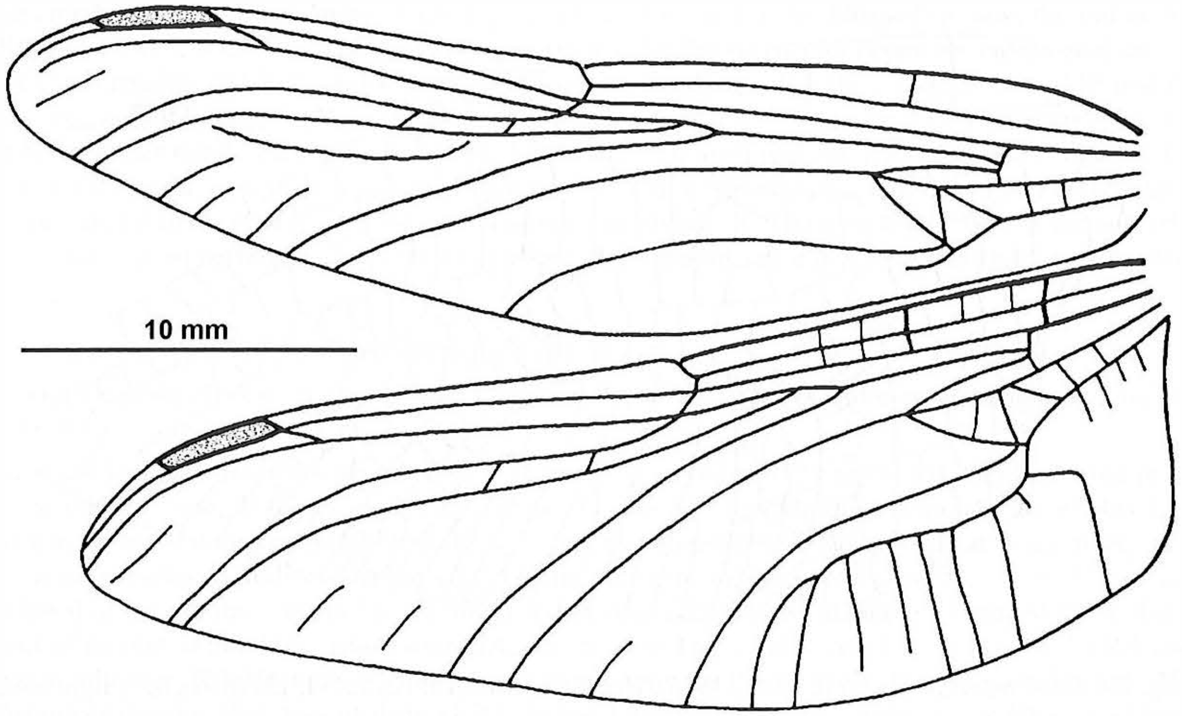
Derivatio nominis: Named in honour of Mr Helmut TISCHLINGER (Stammham), one of the foremost private collectors, preparators, and researchers of Solnhofen fossils.

Locus typicus: Schernfeld (near Solnhofen), Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

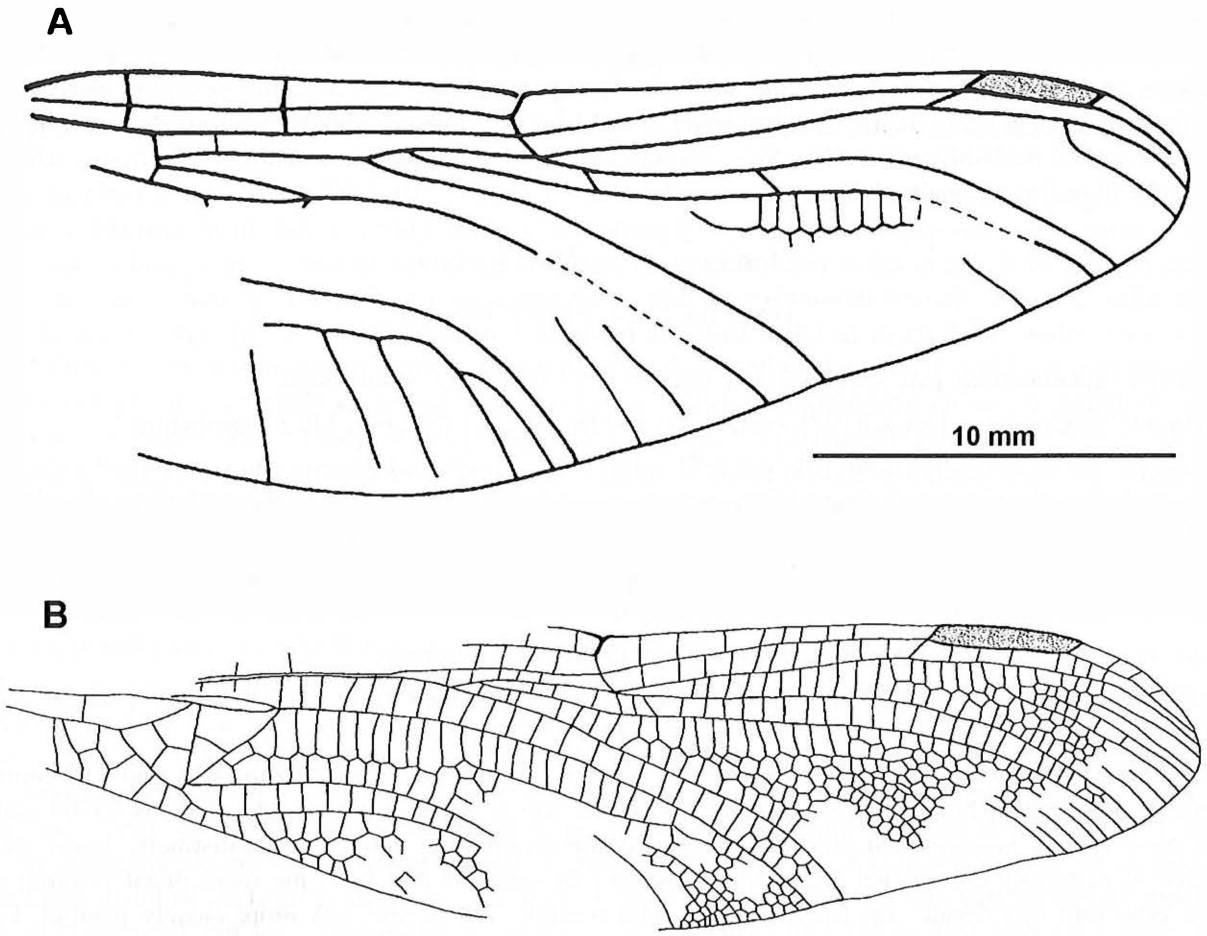
Diagnosis: This new species differs from all other species of the genus by the relatively widely separated (but still parallel) veins RP3/4 and MA, and the presence of an accessory cubito-anal crossvein between CuP-crossing and PsA in both pairs of wings. It also differs from all other species, except *A. jurassica*, by its much smaller size (forewing length only 34 mm). It shares with *A. perkinsi* sp. nov. the basally gently diverging veins RP1 and RP2, the relatively distinct pseudo-Rspl, and the not undulated veins RP3/4 and MA (also present in *A. jurassica*). Additionally to the above mentioned unique characters, this new species can be easily distinguished from *A. perkinsi* sp. nov. by the following hindwing characters: Less curved origin of RP1/2; more basal position of the crossvein that divides the discoidal triangle; CuAa and MP distally divergent; the two oblique veins 'O' are more widely separated.

Description: Part and counterpart of a female that is almost completely preserved except for the missing right forewing and the distorted anal area of the right hindwing. The main venational structures are clearly visible, but the cross-venation is not preserved, and the veins are not traced by iron-oxide dendrites. The body length from head to the tip of the abdomen is 54 mm.



Text-Fig. 21. *Aeschnopsis tischlingeri* sp. nov. Holotype BSP 1964 XX III x b - female, left pair of wings (counterpart).

Forewing: Length 34.0 mm; width at nodus 7.8 mm; distance from base to nodus 16.9 mm; from nodus to pterostigma 11.1 mm; distance from base to arculus 3.9 mm. Pterostigma elongated (length 3.3 mm; width 0.6 mm), distinctly braced by a very oblique crossvein, and probably covering several cells. Distal primary antenodal Ax2 3.3 mm distal of arculus. Other antenodal crossveins are not preserved. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.5 mm and 4.3 mm distal of subnodus. A zigzagged pseudo-Rspl is delimiting a row of enlarged cells along IR2. Two or three convex secondary veins in area between IR2 and RP3/4. RP2 and IR2 closely parallel with always only a single row of cells in-between. Pseudo-IR1 well-defined, but its basal part is not preserved (it probably originated beneath distal side of pterostigma). RP1 and RP2 gently diverging. RP3/4 and MA parallel and rather straight, but relatively widely separated. No Mspl visible. Postdiscoidal area not very widened distally (width near discoidal triangle 2.2 mm; width at wing margin 5.3 mm). The hypertriangle appears to be free of crossveins, but the cross-venation is only poorly preserved. Discoidal triangle very transverse (because of the poor preservation of the cross-venation it is not possible to verify if the discoidal triangle was divided or not); length of anterior side 1.9 mm; of basal side 1.7 mm; of distal side MAb 3.0 mm. Distal side MAb straight. Median space free. Submedian space traversed by an accessory cubito-anal crossvein between CuP-crossing (1.7 mm basal of arculus) and PsA. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle (because of the poor preservation of the cross-venation it is not possible to verify if the subdiscoidal triangle was divided or not), which is max. 1.5 mm long and basally 2.0 mm wide (= length of PsA). MP reaching posterior wing margin somewhat distal of level of nodus. CuA not preserved. Anal area max. 1.6 mm wide (below PsA).



Text-Fig. 22. A: *Aeschnopsis tischlingeri* sp. nov. Holotype BSP 1964 XX III x b - female, right hindwing (counterpart). B: *Aeschnopsis* sp., BSP 1964 XXIII - left forewing, without scale (note: This is not the same specimen as the holotype, although it has a very similar collection number).

Hindwing (description based on left hindwing unless stated otherwise): Length 33.0 mm; width at nodus 10.3 mm; distance from base to nodus 14.4 mm (the nodus is in a rather basal position); distance from nodus to pterostigma 12.3 mm; distance from base to arculus 3.9 mm. Pterostigma elongated (length 3.3 mm; width 0.6 mm), distinctly braced by a very oblique crossvein, and probably covering several cells. Two primary antenodal crossveins Ax1 and Ax2 stronger than others. Ax1 0.5 mm basal of arculus; Ax2 4.2 mm distal of Ax1. At least two secondary antenodal crossveins preserved between the two primary antenodal crossveins. Base of RP2 aligned with subnodus. Two oblique veins 'O', 2.7 mm and 5.5 mm distal of subnodus in left hindwing, and 1.3 mm and 6.1 mm distal of subnodus in right hindwing. A weakly defined and zigzagged Rspl, delimiting a row of enlarged cells along IR2 (only visible in right hindwing). At least two convex secondary veins in distal part of area between IR2 and RP3/4. Pseudo-IR1 well-defined and originating beneath distal side of pterostigma (only visible in right hindwing). RP2 and IR2 closely parallel with always only a single row of cells in-between. RP1 and RP2 gently diverging. RP3/4 and MA parallel and rather straight. No Mspl preserved, but two convex secondary veins present in distal part of postdiscoidal area (only visible in right hindwing). Postdiscoidal area distally somewhat widened (width near discoidal triangle 2.5 mm; width at wing margin 5.4 mm). Hypertriangle apparently free of crossveins, but the cross-venation is only poorly preserved. Discoidal triangle divided into two cells and much less transverse than that of forewing; length of anterior side 2.9 mm; of basal side 1.7 mm; of distal side MAb 3.5 mm. MAb straight. Median space free. Submedian space traversed by an accessory cubito-anal crossvein between CuP-crossing (1.7 mm basal of arculus) and PsA. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle (no crossveins are visible in the subdiscoidal triangle, but this could well be an artifact of preservation), max. 1.6 mm long and basally 1.6 mm wide (= length of PsA). PsA ends on MP + CuA somewhat basal of discoidal triangle. A single row of cells in area between MP and CuA, but close to wing margin they are somewhat diverging with two rows of cells in-between. MP reaching posterior wing margin somewhat distal of level of nodus, while CuA reaches posterior wing margin somewhat basal of level of nodus. Six well-defined posterior branches of CuAa and a well-defined CuAb which is strongly bent (basally directed towards wing base, distally directed towards wing margin). Max. width of cubito-anal area 4.4 mm. Anal area broad, below PsA 5.9 mm wide, and with four parallel posterior branches perpendicularly directed towards wing margin (only their bases preserved in left hindwing). Anal loop not preserved (according to the shape of CuAb it probably was similar to *A. perkinsi* sp. nov.). Anal margin rounded without anal triangle or anal angle, thus, it is a female specimen.

Aeschnopsis perkinsi sp. nov.

Text-Figs 23-24, Plate 6: Figs 1-3

Holotype: Specimen no. [MCZ 6180-6181], coll. CARPENTER, MCZ, Cambridge.

Paratype: Specimen no. [MCZ 6197], coll. HAEBERLEIN, coll. CARPENTER, MCZ, Cambridge.

Other specimens: Specimen no. [MCZ 6198] is less well-preserved, but agrees in size and all visible characters, including the characteristic anal loop and the row of enlarged cells along the posterior side of IR2 and MA. Like the type specimens it is from the Upper Jurassic Solnhofen Limestone.

Derivatio nominis: Named in honour of Dr Philip PERKINS (Cambridge) who kindly supported the studies of the first author at MCZ.

Locus typicus: Solnhofen, Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Diagnosis: This new species is very similar to *A. tischlingeri* sp. nov., including the RP1 and RP2 somewhat divergent, the distinct but zigzagged pseudo-Rspl in all wings, and the not undulated veins RP3/4 and MA (also present in *A. jurassica*). It differs from *A. tischlingeri* sp. nov. mainly by its distinctly larger size, the absence of accessory cubito-anal crossveins between CuP-crossing and PsA, the more distal position of the single crossvein that divides the hindwing discoidal triangle, RP3/4 and MA more closely parallel. Unique hindwing characters (putative autapomorphies) of this new species are the strongly pronounced curvature of the base of RP1/2, the distally converging veins MP and CuAa with only a single row of cells between these veins up to the wing margin, and the much more approximated positions of CuP-crossing and PsA. The more approximate position of the two oblique veins 'O' is a derived similarity to the type species (holotype of "*Cymatophlebiopsis pseudobubas*") that is absent in *A. tischlingeri* sp. nov., but unknown in *A. jurassica*. The presence of only two rows of cells in the postdiscoidal area of both pairs of wings is a unique state within Mesuropetalidae, but this character is unfortunately not sufficiently preserved in all other species of this family. *A. jurassica* also has two cell rows in the hindwing postdiscoidal area, but the forewing is not preserved. *A. perkinsi* sp. nov. differs from *A. jurassica* by the more distal position of Ax2 in the hindwing. Altogether, the character pattern suggests a close relationship with *A. tischlingeri* sp. nov. and *A. jurassica*.

Description

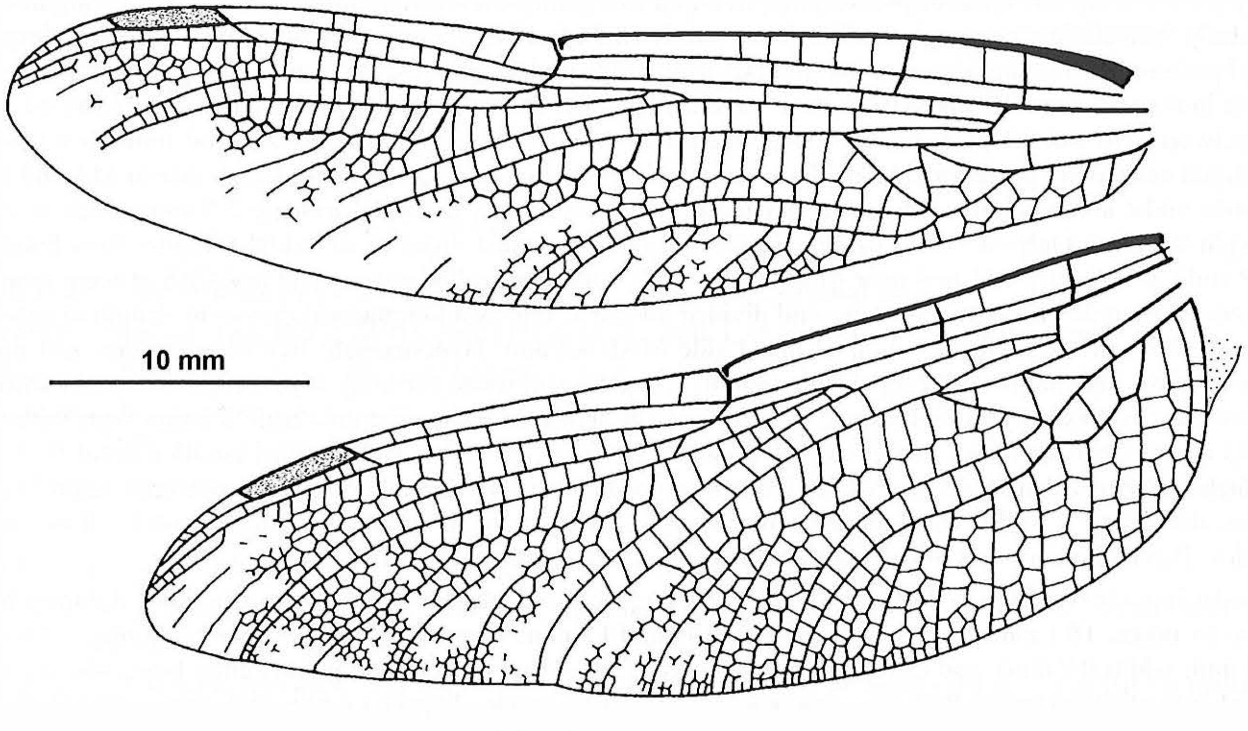
♦ Specimen no. MCZ 6180-6181; holotype; female; labelled «*Gomphus spec*., Solenhofen, Dr. KRANTZ»

Text-Fig. 23, Plate 6: Figs 1-2

Part and counterpart of a complete adult female with the four wings preserved. The veins are partly traced by iron-oxide dendrites. The body is only poorly preserved, except for the head which shows the large and approximated compound eyes.

Forewing (left): Length 44.2 mm; width at nodus 10.4 mm; distance from base to arculus 5.5 mm; from base to nodus 23.1 mm; from nodus to pterostigma 13.0 mm. Pterostigma not extremely elongated (length 4.2 mm; width 0.8 mm), and covering five cells. A strong and very oblique pterostigmal brace aligned with basal side of pterostigma. Probably numerous postnodal crossveins between nodus and pterostigma (but only four are preserved) not aligned with corresponding postsubnodal crossveins between RA and RP1. Most basal postnodal crossvein slanted towards nodus. Two primary antenodal crossveins stronger than secondary antenodal crossveins. Ax1 0.6 mm basal of arculus, and Ax2 4.7 mm distal of Ax1. Numerous secondary antenodal crossveins in both rows, not aligned with each other. Only three antesubnodal crossveins preserved between RA and RP, but they were probably more numerous. Arculus rather straight, and bases of RP and MA distinctly separated at arculus. At least two bridge-crossveins Bqs between IR2 and RP basal of subnodus. Midfork (base of RP3/4) 5.2 mm basal of nodus, and base of IR2 1.6 mm distal of midfork. RP2 aligned with subnodus. Two oblique veins 'O' between IR2 and RP2, a distinct first one 1.0 mm and a less distinct one 2.9 mm distal of subnodus. A short pseudo-IR1 originating on RP1 below distal part of pterostigma. Two or three rows of cells between pseudo-IR1 and RP1. RP1 and RP2 slightly divergent, but with only a single row of cells in-between up to slightly basal of pterostigma. RP2 and IR2 gently curved and closely parallel up to wing margin (distally even slightly converging) with only a single row of cells in-between. A rather distinct, but zigzagged Rspl present and limiting a row of enlarged cells along posterior side of IR2. Two or three convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and rather straight with only a single row of cells in-between. No true Mspl, but a weakly defined and strongly zigzagged vein present and limiting a row of enlarged cells along posterior side of MA. Two or three convex secondary veins in area between MA and MP. Postdiscoidal area strongly widened near wing margin (width near discoidal triangle 2.6 mm; width at wing margin 8.5 mm). Only two rows of cells in postdiscoidal area just distal of discoidal triangle. Area between MP and CuA slightly widened near wing margin with only three cells between MP and CuA at wing margin. Discoidal triangle distinctly transverse and divided into two cells by a longitudinal crossvein; length of anterior side 3.0 mm; of basal side 2.4 mm; of distal side MAb 4.4 mm. Hypertriangle free of crossveins and much more narrow than hindwing hypertriangle (length 5.8 mm; max. width 0.7 mm). Median space free. Submedian space only traversed by CuP-crossing, 1.4 mm basal of arculus. Cubito-anal area max. 2.9 mm wide with five rows of cells between CuA and posterior wing margin. CuA with five well-defined parallel distal posterior branches. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle divided into three cells. Anal area max. 2.0 mm wide (below PsA) with two rows of cells between AA and posterior wing margin.

Hindwing (left): Length 42.5 mm; width at nodus 12.5 mm; distance from base to arculus 4.9 mm; from base to nodus 18.1 mm; from nodus to pterostigma 14.8 mm. Pterostigma not extremely elongated (length 4.4 mm; width 0.9 mm), and covering about five cells. A strong and oblique pterostigmal brace aligned with basal side of pterostigma. Probably numerous postnodal crossveins between nodus and pterostigma (but only six are preserved), not aligned with corresponding postsubnodal crossveins between RA and RP1. Two primary antenodal crossveins stronger than secondary antenodal crossveins. Ax1 0.7 mm basal of arculus, and Ax2 5.4 mm distal of Ax1, on a level with distal angle of discoidal triangle. Only two secondary antenodal crossveins preserved, but they were probably numerous in both rows and not aligned with each other. Basal brace Ax0 visible (probably formed by a posterior branch of ScA and an aligned crossvein; homologous with the costal brace of Ephemeroptera). Only a single antesubnodal crossvein visible between RA and RP, but they were certainly more numerous. Three bridge-crossveins Bqs between IR2 and RP basal of subnodus. Midfork (base of RP3/4) 4.9 mm basal of nodus, and base of IR2 0.8 mm distal of midfork. Base of RP2 aligned with subnodus. Only a single oblique vein 'O' visible, 1.3 mm distal of subnodus (maybe two oblique veins in right hindwing). A short pseudo-IR1 originating on RP1 below distal side of pterostigma. RP1 and RP2 slightly divergent, but with only a single row of cells in-between up to somewhat basal of pterostigma. Origin of RP1/2 at midfork strongly curved. RP2 and IR2 gently curved and closely parallel (distally strongly converging) with only a single row of cells in-between. A rather distinct, but zigzagged Rspl present and limiting a row of enlarged cells along posterior side of IR2. Three convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and rather straight with only a single row of cells in-between. No true Mspl, but a weakly defined and zigzagged vein present and limiting a row of enlarged cells along posterior side of MA. Three convex secondary veins between MA and MP. Postdiscoidal area distinctly widened near wing margin with much more than twenty-five cells between MP and MA along posterior wing margin (width near discoidal triangle 3.1 mm; width at wing margin 8.9 mm). Only two rows of cells in postdiscoidal area just distal of discoidal triangle. Area between MP and CuAa distally not widened, but distinctly narrowed with only two tiny cells in-between at wing margin. Discoidal triangle longitudinally elongated and divided into two cells by a distal transverse crossvein; length of anterior side 3.6 mm; of basal side 1.9 mm; of distal side MAb 4.3 mm. Hypertriangle free of crossveins and much broader than forewing hypertriangle (length 5.4 mm; max. width 0.8 mm). Median space free. Submedian space only traversed by CuP-crossing, 1.4 mm basal of arculus. Cubito-anal area max. 5.2 mm wide with six or seven rows of cells between CuA and posterior wing margin. CuAa with five parallel posterior branches. CuAb directed towards posterior wing margin. Anal loop longitudinally elongated (length 4.8 mm; width 1.6 mm), three-celled, and posteriorly well-closed, but zigzagged. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. AA with only three parallel and straight posterior branches perpendicularly directed towards posterior wing margin. Anal area 6.8 mm wide (below PsA) with six rows of cells between AA and posterior wing margin. Anal margin rounded without anal angle or anal triangle, thus, it is a female specimen. There seems to be a large membranule, but it is too poorly preserved to be certain about this character state.



Text-Fig. 23. *Aeschnopsis perkinsi* sp. nov. Holotype MCZ 6181 - female, left pair of wings.

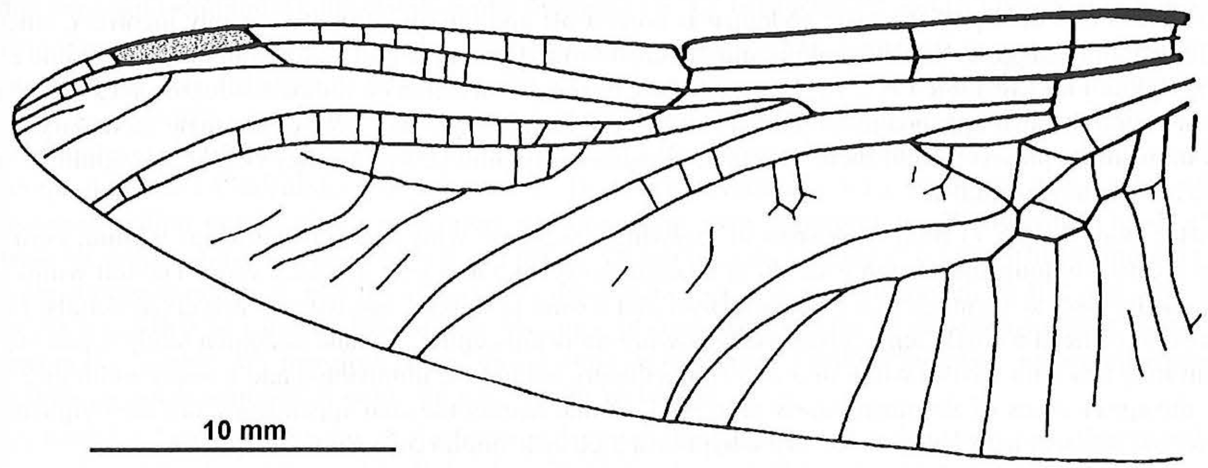
♦ Specimen no. MCZ 6197; paratype; male ?; labelled «*Protolindenia wittei* GIEBEL, coll. HAEBERLEIN, Solenhofen»

Text-Fig. 24, Plate 6: Fig. 3

The wing venation of this specimen is very similar to the holotype and only seems to differ by the presence of two oblique veins 'O' in both pairs of wings, even though these structures are only faintly preserved. Here we only describe the venation of the left hindwing which is better preserved than the other wings.

Hindwing: Length 38.8 mm; width at nodus 12.1 mm; distance from base to arculus 4.3 mm; from base to nodus 16.7 mm; from nodus to pterostigma 14.1 mm. Pterostigma not extremely elongated (length 4.3 mm; width 0.7 mm), and covering about five cells. A strong and oblique pterostigmal brace aligned with basal side of pterostigma. Numerous postnodal crossveins between nodus and pterostigma, of which only seven are preserved, and not aligned with corresponding postsubnodal crossveins between RA and RP1. Two primary antenodal crossveins stronger than secondary antenodal crossveins. Ax1 0.5 mm basal of arculus, Ax2 5.2 mm distal of Ax1, on a level with distal angle of discoidal triangle. No secondary antenodal crossveins preserved, but they were probably numerous in both rows and not aligned with each other. Basal brace Ax0 visible. No antesubnodal crossveins preserved between RA and RP, but they were certainly present. Only a single bridge-crossvein Bq preserved close to subnodus. Midfork (base of RP3/4) 4.3 mm basal of nodus, and base of IR2

0.8 mm distal of midfork. Base of RP2 aligned with subnodus. Two oblique veins 'O' visible, 2.0 mm and 3.9 mm distal of subnodus. A short pseudo-IR1 originating on RP1 below distal half of pterostigma. RP1 and RP2 basally slightly divergent, but becoming more strongly divergent below pterostigmal brace vein. Origin of RP1/2 at midfork strongly curved. RP2 and IR2 gently curved and closely parallel (distally strongly converging) with only a single row of cells in-between. A rather distinct Rspl present and limiting a row of enlarged cells along posterior side of IR2. At least two convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and rather straight with only a single row of cells in-between. No Mspl visible, but a row of enlarged cells along posterior side of MA, and at least one or two convex secondary veins between MA and MP. Postdiscoidal area distinctly widened near wing margin (width near discoidal triangle 2.9 mm; width at wing margin 8.3 mm). Area between MP and CuAa distally not widened, but distinctly narrowed. Discoidal triangle longitudinally elongated and divided into two cells by a distal transverse crossvein; length of anterior side 3.7 mm; of basal side 2.1 mm; of distal side MAb 3.8 mm. Hypertriangle free of crossveins and rather broad (length 4.8 mm; max. width 0.8 mm). Median space free of crossveins. Submedian space only traversed by CuP-crossing, 0.8 mm basal of arculus (unsafe, since only faintly preserved). Cubito-anal area max. 6.2 mm wide. CuAa with five parallel posterior branches. CuAb directed towards posterior wing margin. Anal loop longitudinal elongated, three-celled, and posteriorly well-closed, but zigzagged (length 4.5 mm; width 1.7 mm). AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. AA with probably three parallel and straight posterior branches perpendicularly directed towards posterior wing margin. Anal area 9.6 mm wide (below PsA). Basal part of anal area and anal margin not preserved, but the shape of preserved part suggests that it could rather be a male specimen.



Text-Fig. 24. *Aeschnopsis perkinsi* sp. nov. Paratype MCZ 6197 - male ?, left hindwing.

Mesuropetalidae indet.

(cf. *Mesuropetala muensteri* comb. nov. or *Aeschnopsis perkinsi* sp. nov.)

Plate 6: Fig. 5

v 1994 *Aeschnidium* sp.; RESCH, pp. 364-365 (with photograph).
v 1994 *Aeschnidium* sp.; FRICKHINGER, p. 135, fig. 246.
v 1996 *Mesuropetala* sp.; TISCHLINGER, p. 291, 294-295, fig. 3.
v 1999 *Mesuropetala muensteri* (GERMAR); FRICKHINGER, p. 53, fig. 88.

Material: Specimen no. [SMS 358], coll. Udo RESCH (Clausthal-Zellerfeld, Germany; ex coll. GRAUPNER, Planegg); two dragonflies in tandem position.

Locality: Eichstätt, Southern Frankonian Alb, Bavaria, Germany.

Stratum: Solnhofen Lithographic Limestone, Upper Jurassic, Malm zeta 2b, Lower Tithonian, *Hybonotum*-Zone.

Description: The fossil is preserved on a rectangular plate (213 mm * 249 mm) of lithographic limestone from Eichstätt and shows two complete Anisoptera with outstretched wings. The animals are both preserved in ventral aspect. Consequently the terms right and left in the description correspond to the opposite sides in the living animal. The wings are slender and apically falcate. Although all wings of both specimens are more or less complete, the wing venation is not preserved, and only some traces of the wing pleating allow the identification of the midfork (RP1/2, IR2, RP3/4) and the lower sector of the arculus (basal MA) in some wings. The position of the nodus can only be vaguely guessed from the shape of the fuzzy costal margin. There is no trace of Rspl or Mspl visible in any of the wings. Neither an anal loop, nor a discoidal triangle, hypertriangle or subdiscoidal triangle can be recognized in most wings, except in the left wings of the female which show a very indistinct preservation of the discoidal triangles: The forewing discoidal triangle apparently was somewhat transverse, while the hindwing discoidal triangle was slightly elongated. A distinct subdiscoidal triangle seems to be present in the forewing. A comparison of the present state of this fossil (FRICKHINGER 1999: fig. 88) with the original state (FRICKHINGER 1994: fig. 246) reveals that the fossil was subsequently treated to remove the dendrites and afterwards the male abdomen was incorrectly "reconstructed" with paint, since it is now more curved than in the figure of the untreated fossil.

Male: Wing span of forewings, apparently 93 mm, but this value is misleading, since the wings are twisted forward; wing span of hindwings, 94 mm; right forewing length 46 mm (the width cannot be measured because of fuzzy preserved posterior margin), left forewing length 44 mm (base probably partly covered by body imprint); greatest width 11 mm; right hindwing length 45 mm and greatest width 13 mm; left hindwing length 44 mm and greatest width 12.5 mm. Midfork 14 mm from wing base in right forewing and 13 mm in right and left hindwing. Base of left hindwing too poorly preserved to distinguish an anal angle, also because it is superimposed by the basal abdomen, but the right hindwing base exhibits a distinct anal angle which excludes any position within Aeschnidiidae. Head missing and thorax present, but poorly preserved. No legs visible. Male abdomen bent with its tip pointing toward the head-neck-region of female where it apparently ends. RESCH (1994) stated that the tip of the male abdomen is broken off and missing; this is probably incorrect, since the position strongly suggests that the male is still attached to the female occiput and pronotum (also visible on the photograph in FRICKHINGER 1994: fig. 246). Because of the preservation on the backside, the apex of the male abdomen with the anal appendages is hidden beneath the female body. The area of the male secondary genitalia is indistinctly preserved, but there is a faint elongated structure (2.8 mm long) visible that could be interpreted as vesicula spermalis.

Female: Body length 71 mm; wing span of forewings 98.5 mm; wing span of hindwings 92 mm; both forewings are 46 mm long and 11 mm wide; both hindwings are 44.5 mm long and 12.5 wide. The left wings show traces of the discoidal triangles (see above). Head and thorax preserved, but with no preserved details. Lateral of left side of head a single leg is preserved, showing no details either. Female abdomen straight and slender, 50 mm long and with a basal width of 3 mm (immediately behind the hindwings) and a distal width of 2.5 mm (near the apex). Apex of abdomen poorly preserved, so that neither the anal appendages, nor the ovipositor are visible, but it can at least be excluded that a hypertrophied aeschnidiid ovipositor was present.

Discussion: These two dragonflies in tandem position from the Solnhofen Limestone have been briefly described by RESCH (1994) and preliminarily identified as *Aeschnidium* sp. This plate which is also illustrated in FRICKHINGER (1994), apparently represents the single known case where a dragonfly tandem became fossilized. There exist two or three pieces of Tertiary amber with a male and female damselfly enclosed, but these did not remain connected with each other. Whereas the interpretation of the mentioned Solnhofen fossil as mating tandem is confirmed by our study, the preliminary determination proved to be erroneous: The specimens are no Aeschnidiidae, since the male has an anal angle and the female lacks the hypertrophied ovipositor. Although the wing venation is too poorly preserved to allow a precise determination based only on wing venational characters, the size and shape of the wings and the female abdomen also exclude *Aeschnidium* (wings broader and female abdomen shorter), *Urogomphus* (wing span much larger and abdomen much thicker), *Cymatophlebia* (wing span much larger), *Protolindenia* (female abdomen distinctly thicker), *Aeschnogomphus* (wing span much larger), *Nannogomphus* (wing span much smaller) and two new genera of Hemeroscopidae and Proterogomphidae (BECHLY *et al.* 1998) (wings distinctly shorter and much greater relative length of abdomen). The apparent shape of the discoidal triangles and the apparent lack of Rspl and Mspl furthermore contradict a position within Aeschnidiidae, Cymatophlebiidae and Euaeshnida (*Eumorbaeschna jurassica* gen. et comb. nov.), although this evidence is weak due to the poor preservation of the wings. If the fossil should not represent a new taxon, among the Solnhofen dragonflies only the genera *Mesuropetala* and *Aeschnopsis* remain as possibly congeneric, especially since all preserved characters perfectly agree with Mesuropetalidae. The size excludes *Aeschnopsis tischlingeri* sp. nov. and *Aeschnopsis jurassica*, thus, it most likely belongs to *Mesuropetala muensteri* comb. nov., or (less likely) to *Aeschnopsis perkinsi* sp. nov.

RESCH (1994) believed that this tandem probably was trapped on drying mud and thus should confirm the hypothesis that the Solnhofen paleo-environment was a tidal area of mud flats (recently again endorsed by RÖPER 1992 and GERHARD & RÖPER 1992) that were periodically exposed to the air. However, TISCHLINGER (1996) most convincingly demonstrated that the Solnhofen dragonflies must have been embedded in very calm water of considerable depth. At least for these limestone fossils the "deep water hypothesis (*sensu* KEUPP 1977 and BARTHEL 1978) must be the correct explanation for their genesis. This does of course not exclude the possible validity of the "tidal mud flat hypothesis" for other varieties of the so-called Solnhofen Limestones, which are much more diverse than previously believed (RÖPER & ROTHGAENGER1998).

Family Liupanshaniidae fam. nov.

Type genus: *Liupanshania* HONG, 1982.

Included genera: *Liupanshania* HONG, 1982, *Araripeliupanshania* gen. nov., *Paramesuropetala* gen. nov., and *Paraliupanshania* gen. nov.

Wing venational autapomorphies: Unique shape of the very elongated and narrow hindwing discoidal triangle (anterior side of discoidal triangle distally curved and ending on the anterior side MA of the hypertriangle; MAb is strongly sigmoidally curved with a very concave basal part and a strong angle in the distal part); hindwing discoidal triangle divided into at least three cells by parallel crossveins; forewing discoidal triangle divided into three cells (but only known in *Araripeliupanshania* gen. nov. and *Paramesuropetala* gen. nov.); both pairs of wings (but especially the hindwing) with a strong convex secondary longitudinal vein (trigonal planate) in the postdiscoidal area, originating at the angle of MAb (convergent to several other groups of Aeshnoptera and Gomphides); the distal second oblique vein 'O' between RP2 and IR2 is secondarily absent.

Systematic position: Liupanshaniidae fam. nov. share with Aeshnoptera the following synapomorphies: RP1 and RP2 basally strictly parallel, so that the area between these two veins is basally distinctly narrowed, with only a single row of cells in-between (reversed in *Liupanshania*); Rspl present; RP3/4 and MA are more or less undulated. On the other hand, the wing venation of Liupanshaniidae fam. nov. is very similar to that of the gomphid families Lindeniidae and Hageniidae. However, several character states are clearly contradicting any position within Gomphides and support a relationship with Aeshnoptera: Well-defined Rspl; closely approximate compound eyes (visible in *Araripeliupanshania* gen. nov.); long cerci and trifid epiproct (visible in *Araripeliupanshania* gen. nov.). Furthermore, the absence of a secondary branch of IR2 and MA would contradict a position in Lindeniidae, and the presence of numerous antefurcal crossveins would contradict a position in Hageniidae. We therefore regard the similarities of Liupanshaniidae fam. nov. with Lindeniidae and Hageniidae as convergences and suggest a position in Aeshnoptera.

Liupanshaniidae fam. nov. share with Aeshnomorpha taxon nov. and Panaeshnida taxon nov. the curved RP2, the more distinct Rspl, and the multicellular discoidal triangles, but differ in the transverse forewing discoidal triangle and the free hypertriangles. Especially the transverse forewing discoidal triangle clearly excludes a position within Aeshnomorpha taxon nov., but would not contradict a sistergroup relationship. The strongly defined and curved veins Rspl and Mspl in *Paraliupanshania* gen. nov. and *Paramesuropetala* gen. nov. must be regarded as convergence to Aeshnida, since the Rspl and Mspl are not curved in *Araripeliupanshania* gen. nov. and *Liupanshania*. The short gaff excludes a position within Progobiaeshnidae fam. nov., Valdaeshninae subfam. nov., and Euaeshnida. The reduced anal loop is a shared derived similarity of *Liupanshania* and *Paraliupanshania torvaldsi* gen. et sp. nov. with Austropetaliida taxon nov. and Cymatophlebiinae, but this has to be a convergence, since a well-defined anal loop is retained in *Araripeliupanshania* gen. nov. Likewise, the reduced and displaced pterostigmal brace of *Paraliupanshania* gen. nov. must be a convergence to Austropetaliida taxon nov. Both characters are highly homoplastic anyway, and thus of rather low phylogenetic significance. The unicellular hindwing subdiscoidal triangle is a plesiomorphic character state that is for example absent in Cymatophlebiidae and Rudiaeschnidae fam. nov. The reduction of the second distal oblique vein 'O' is a derived similarity with Neoaeshnida. Further derived similarities with Neoaeshnida include the parallel course of RP3/4 and MA up to the wing margin in both pairs of wings, and the convex secondary vein (trigonal planate) in the hindwing postdiscoidal area, correlated with an angled distal side MAb of the hindwing discoidal triangles. However, the small or even reduced anal loop and the short gaff would be absolutely unique and very unlikely reversals within Euaeshnida. Furthermore, the transverse forewing discoidal triangle contradicts a relationship with Euaeshnida anyway (see above).

Altogether, the evidence strongly suggests a position of Liupanshaniidae fam. nov. within Aeshnoptera, but not within Aeshnomorpha taxon nov. Because of two putative synapomorphies (arculus very close to Ax1, and RP3/4 and MA closely parallel up to the wing margin), even though these are rather weak characters, we advocate a sistergroup-relationship to Mesuropetalidae. Within Liupanshaniidae fam. nov. there are several curious convergences and parallelisms to higher Aeshnoptera. The convergent evolution of a well-defined Rspl and Mspl is foreshadowed in the pseudo-Rspl and pseudo-Mspl of *Mesuropetala* which probably belong to the groundplan characters of Mesuropetaloidea stat. nov.

Genus *Liupanshania* HONG, 1982 pos. nov.

Type species: *Liupanshania sijiensis* HONG, 1982, by original designation.

Diagnosis: This genus is distinguished by the following characters of the hindwing: The pterostigma is very long (autapomorphy); RP1 and RP2 are basally divergent with two rows of cells in-between basal of the pterostigma; RP2 not undulated; there is an indistinct Rspl closely parallel to IR2 with only a single row of cells in-between; hypertriangle free; the discoidal triangle is very elongated and narrow (of typical liupanshaniid shape), and divided into three cells; there is a strong convex secondary longitudinal vein (trigonal planate) originating on the angle of MAb in the postdiscoidal area; Mspl apparently absent or at least very indistinct; subdiscoidal triangle unicellular; there is a supplementary cubito-anal crossvein in the submedian space between CuP-crossing and PsA (autapomorphy); the gaff is short; the anal loop is reduced and posteriorly open.

Systematic position: The shape of the structure of the discoidal triangle is a unique derived similarity and probable synapomorphy with *Paraliupanshania* gen. nov. and *Araripeliupanshania* gen. nov. Otherwise the wing venation of *Liupanshania* is strikingly similar to the extant gomphid genus *Sieboldius* (Hageniidae). However, a very distinct difference are the numerous antefurcal (submedian) crossveins that even contradict a position in Hageniidae. Further significant distinctions from *Sieboldius* are the more pronounced Rspl and the number of cells in the discoidal triangle (three instead of two).

Araripeliupanshania gen. nov. from the Lower Cretaceous of Brazil has a very similar venation of the hindwing, but differs in the following characters: The anal loop is closed and three- to five-celled; there is no accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA; RP1 and RP2 are basally closely parallel with only a single row of cells in-between basal of the pterostigma; the pterostigma is somewhat shorter and more distinctly braced; there seems to be a weak and zigzagged Mspl parallel to MA with only a single row of cells in-between.

Liupanshania sijiensis HONG, 1982

Text-Fig. 25

* 1982 *Liupanshania sijiensis* HONG, 1982; HONG, pp. 61-63, text-fig. 48, pl. 5, figs 3-5.
1994 *Liupanshania sijiensis* HONG, 1982; NEL *et al.*, p. 181.

Holotype: Specimen no. [She 1001], P.R. China (the original description does not mention in which collection the type is deposited). The holotype is represented by the basal two-thirds of an isolated hindwing, but there is a second piece with an apical third of a wing, which probably is the counterpart of the type.

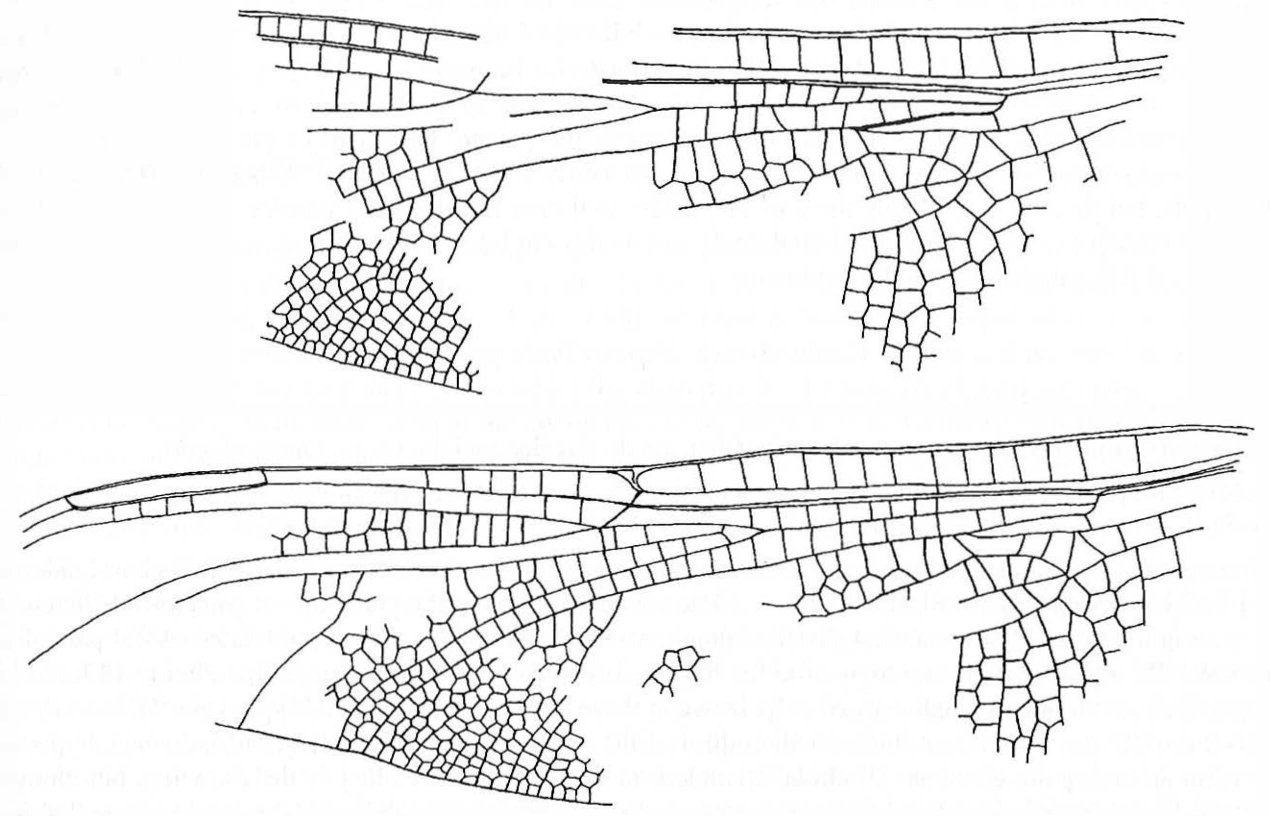
Locus typicus: Jiuquan Basin, Gansu province, P.R. China.

Geological age: Lower Cretaceous (the no. Hh-XXXV-5/2 that it is given in the original description represents a code for the stratigraphy and outcrop, which is not known to the authors).

Diagnosis: Same as for the genus.

Redescription: *Liupanshania sijiensis* HONG, 1982 is based on an isolated hindwing. Although this wing is rather well-preserved, the drawing provided in the original description is a poor reconstruction rather than a precise figure of the fossil specimen, since the anal area is completely figured although not preserved. Many "unusual" features obviously are based on drawing errors (see NEL *et al.* 1994), since they are in conflict with the characters visible on the corresponding photographs. Fortunately, on the photographic figures of the holotype many of the preserved characters can be recognized. Our redescription is based on these photographs.

A rather complete and well-preserved hindwing with main part of the cubito-anal and anal areas missing. No trace of coloration preserved, but the wing was probably hyaline.



Text-Fig. 25. *Liupanshania sijiensis* HONG, 1982. Holotype She 1001, Hh-XXXV-5/2. - hindwing (new figures after the photographs in HONG 1982: pl. 5, figs 3-5).

Hindwing: Length 64 mm; width 18 mm. Pterostigma very long and probably covering at least seven small cells. The pterostigmal brace is only faintly visible, but apparently was not very oblique. Numerous postnodal crossveins are visible between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. There were numerous antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Ax2 is clearly visible, on a level with distal angle of discoidal triangle, distinctly stronger than the secondary antenodal crossveins. Ax1 is faintly visible, somewhat basal of the arculus. There are about five secondary antenodal crossveins between Ax1 and Ax2. At least eight (maybe ten) antesubnodal crossveins are still visible in the median part of the area between arculus and subnodus, but they were probably much more numerous. Two visible bridge-crossveins Bqs visible basal of subnodus, but there were probably about four. There is an indistinct and zigzagged Rspl closely parallel to IR2 with only a single row of cells between it and IR2; there is at least one convex secondary vein originating on Rspl and reaching the posterior wing margin. Base of RP2 aligned with subnodus. The basal part of the area between RP2 and IR2 is very poorly preserved, so that the oblique vein 'O' is not clearly visible. RP2 and IR2 are closely parallel with only a single row of cells in-between, except near the wing margin where they seem to be separated by four rows of cells. RP1 and RP2 are basally slightly divergent with one to two rows of cells in-between basal of the pterostigma, but below the pterostigma they begin to diverge strongly with numerous rows of cells in-between. The pseudo-IR1 is very poorly preserved, but it might have originated distal of the pterostigma. RP3/4 and MA are parallel with a bulge near the posterior wing margin; there is only a single row of cells in-between, except in the bulged area near the wing margin, where they are separated by two rows of cells. Mspl is clearly absent, but there are two convex secondary veins in the distal postdiscoidal area, originating on MA and reaching the posterior wing margin. The postdiscoidal area is distally strongly widened with two rows of cells immediately distal of the discoidal triangle; there is a very strong secondary longitudinal vein (trigonal planate), originating at the strongly angled distal side MAb of the discoidal triangle (the distal part of this secondary vein is not preserved). MAb has a most peculiar structure, viz its basal part is strongly concave and its distal angle is strongly pronounced. The anterior side of the discoidal triangle is distally curved, too, and ends on the anterior side of the hypertriangle. The hypertriangle is free of crossveins. The discoidal triangle is very long, narrow and divided into three cells by two parallel crossveins in its basal half. Median space free of crossveins. Submedian space traversed by CuP-crossing and an accessory cubito-anal crossvein between it and PsA. AA divided into a weak, but oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting an indistinct and short unicellular subdiscoidal triangle. The main parts of MP and CuA are not preserved. The gaff is short. Three well-defined posterior branches of CuAa are visible, but there were probably more than six. The cubito-anal area is rather broad with more than six rows of cells between CuAa and the posterior wing margin. CuAb is directed towards the postero-basal part of the wing, but there is not crossvein-anastomosis with AA1b, thus, there is no posteriorly closed anal loop. Two posterior branches of AA are visible, but there were probably three of them. The anal area is only partly preserved, but was very broad. The anal margin (area of the potential anal angle and anal triangle) is not preserved, thus, it is not possible to recognize if it is a male or a female specimen.

Genus *Araripeliupanshania* gen. nov.

Type species: *Araripeliupanshania annesusae* sp. nov.

Derivatio nominis: After the type locality Chapada do Araripe and the genus *Liupanshania*.

Autapomorphies: Not unequivocal autapomorphies are yet known, even though there are sufficient diagnostic characters.

Diagnosis: Pterostigma elongated and braced by an oblique crossvein that is aligned with its basal side; RP1 and RP2 basally closely parallel with only a single row of cells up to the pterostigma; pseudo-IR1 distinct but short, originating on RP1 somewhat distal of the pterostigma; RP2 only slightly undulated; distal part of area between IR2 and RP2 with two rows of cells; Rspl and Mspl present but zigzagged, parallel to IR2 and MA, respectively, with only a single row of cells between these veins; only a single oblique vein 'O' near the subnodus; crossveins only present in the median third of the antesubnodal area, at least in hindwings; hypertriangles free in both pairs of wings; discoidal triangle transverse and three-celled in the forewing, but elongated (typical liupanshaniid shape) and three- to four-celled in the hindwing; subdiscoidal triangle two-celled in the forewing and unicellular in the hindwing; no accessory cubito-anal-crossvein between CuP-crossing and PsA; anal loop posteriorly well-closed and divided into three to five cells; membranule present; legs very short and stout; compound eyes dorsally approximated, but not meeting.

Systematic position: This new genus shares the following characters with the gomphid taxon Lindeniidae - Lindeniinae (compare e.g. *Lindenia tetraphylla* or *Sinictinogomphus clavatus*): Anal loop posteriorly closed, but only three-celled; no accessory cubito-anal crossveins between CuP-crossing and PsA; RP1 and RP2 basally strictly parallel with only a single row of cells in-between up to the pterostigma; the pterostigma is short and distinctly braced; the forewing discoidal triangle is transverse and three-celled with a two-celled subdiscoidal triangle; the hindwing discoidal triangle is longitudinally elongated with a distinct angle in its distal side MAb; a strong convex secondary longitudinal vein (trigonal planate) originates on the angle of MAb in the postdiscoidal area; relatively large size (forewing length 40.0 mm). However, the characters mentioned in the discussion on the systematic position of Liupanshaniidae fam. nov. (e.g. presence of Rspl and Mspl, and absence of a secondary branch of IR2 and MA) suggest that this new genus is not a gomphid but a basal member of Aeshnoptera. This is also strongly confirmed by the preserved body characters that are most untypical for Gomphides but agree very well with basal Aeshnoptera (e.g. Austropetaliida taxon nov.): The head is well-preserved and shows closely approximated, but not touching compound eyes; the cerci are very elongated and the epiproct is very broad and trifid.

Araripeliupanshania annesusae sp. nov.

Text-Figs 26-27, Plate 7: Figs 1-2, Plate 8: Figs 1-2, Plate 9: Figs 1-2, Plate 10: Figs 1-2, Plate 11: Fig. 1

v. 1998 *Araripeliupanshania annesuseae*; BECHLY, p. 62, fig. 30 (nomen nudum).

Holotype: Specimen no. [D 58], MB, Berlin.

Allo- and paratypes: Female specimen (allotype) no. [64345] (old number 72), SMNS, Stuttgart; specimen no. [64343] (old number K 38), SMNS, Stuttgart; specimen no. [M 56], coll. *ms-fossil* (scheduled to be purchased by SMNS); specimen no. [L 75], private coll. SCHWICKERT, Sulzbachtal; specimen without number, coll. MURATA, Kyoto (even though this specimen has no number, it can easily be recognized after our photograph).

Derivatio nominis: Named in honour of Mrs Annesuse SCHWICKERT (Sulzbachtal, Germany).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

Diagnosis: Same as for the genus.

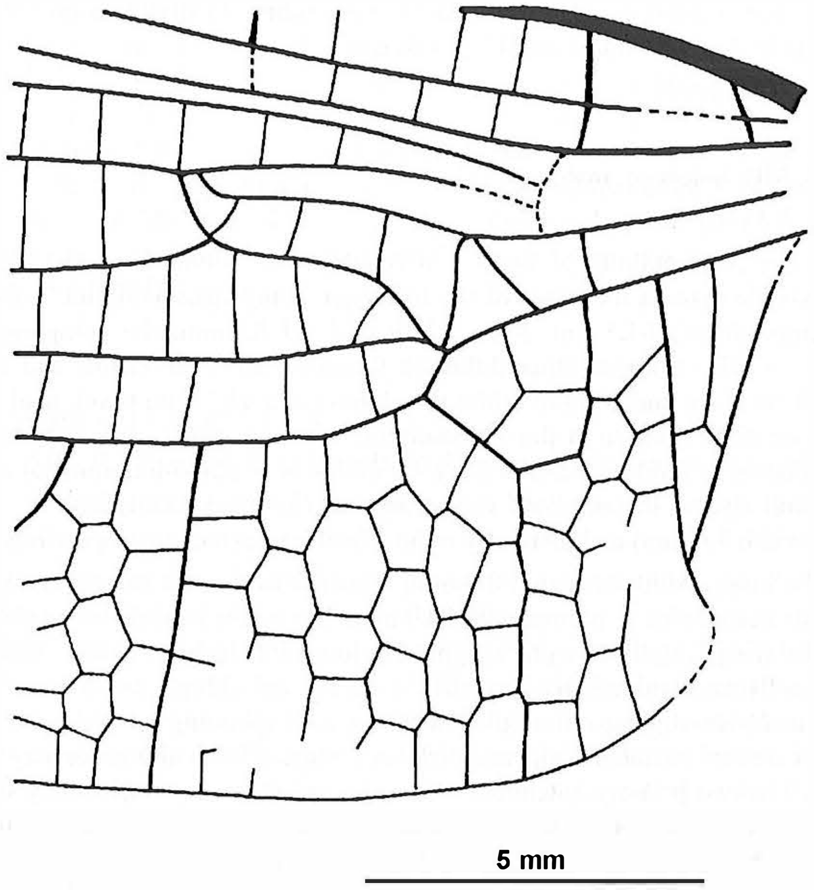
Description

♦ Specimen no. D 58, MB; holotype; male

Text-Figs 26-27, Plate 7: Figs 1-2

A well-preserved and complete male (also figured in ANONYMOUS 1998: 78, and BECHLY 1998), of which only the legs are not visible (except the bases of the forelegs). Wing span 85.6 mm. Total body length (including head and anal appendages) 64.5 mm. Max. width of head 8.2 mm; the compound eyes are distinctly approximated, but not touching (min. distance 0.8 mm); the three ocelli are visible and arranged in a triangle; the pterothorax is 11.0 mm long and 5.2 mm wide; the abdomen is 44.1 long (excl. anal appendages) and 3.0-3.3 mm wide; there is no distal dilation of the abdomen, but the basal part is distinctly constricted (min. width 1.0 mm) near the secondary genital apparatus; there seems to be a dorso-longitudinal abdominal carina; the anal appendages are well visible, the cerci are very elongated (length 3.2 mm) and the epiproct is very broad (length 2.1 mm; max. width 3.0 mm) and distinctly trifid (similar to extant austropetaliids).

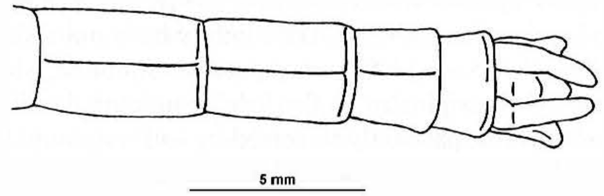
Forewing: Length 39.8 mm; width at nodus 8.8 mm; distance from base to arculus 4.1 mm. distance from base to nodus 21.1 mm; from nodus to pterostigma 10.9 mm. The nodus is of the normal Anisoptera-type and is situated at 53 % of the wing length. The pterostigma is elongated (length 3.7 mm; width 0.8 mm), covering about four and a half cells, and is distinctly braced by a strong and oblique brace vein. Nine postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Nineteen antenodal crossveins between costal margin and ScP, not aligned with the secondary antenodal crossveins between ScP and RA. The two primary antenodal crossveins are aligned and distinctly stronger with three not aligned secondary antenodal crossveins in-between in the right wing, and four of them in the left wing. Ax1 is 0.9 mm basal of the arculus, and Ax2 is 4.6 mm distal of Ax1 on a level with the middle of the discoidal triangle. The antesubnodal area is poorly preserved. Two bridge-crossveins Bqs visible basal of the subnodus. Base of RP2 aligned with subnodus. There is only a single oblique vein 'O', hardly a one cell (0.5 mm) distal of the subnodus in the right wing, but one and a half cell (1.1 mm) distal of the subnodus in the left wing. Rspl is rather well-defined and parallel to IR2 with only a single row of cells between it and IR2. Several convex secondary veins in the area between IR2 and RP2, originating on Rspl and reaching the posterior wing margin. RP2 and IR2 are parallel with a single row of cells in-between, except near the posterior wing margin. RP1 and RP2 run parallel up to the pterostigma (even converging near the pterostigma) with only a single row of cells in-between, but below the pterostigma they become divergent with two or more rows of cells in-between. The pseudo-IR1 is not very well visible, but obviously originates on RP1 distal of the pterostigma. RP3/4 and MA are parallel and only weakly undulated with a single row of cells in-between, except near the posterior wing margin (two rows of cells in-between). Mspl is clearly visible but zigzagged, and parallel to MA with a single row of cells between it and MA. Two convex secondary veins in the distal part of the postdiscoidal area, originating on Mspl and reaching the posterior wing margin; a convex secondary longitudinal vein in the basal part of the postdiscoidal area, originating at the slight angle of the distal side MAb of the discoidal triangle. The postdiscoidal area is distally strongly widened (width near discoidal triangle 2.6 mm; width at posterior wing margin 8.3 mm) with two rows of cells in the basal part and at least seventeen cells along the posterior wing margin. The hypertriangle is elongated and narrow (length 5.2 mm; max. width 0.6 mm), and free of crossveins; its costal margin is somewhat curved. The discoidal triangle is totally different from that of the hindwing, of normal triangular shape with three rather straight sides; it is transverse and divided into three cells (in both forewings); length of anterior side 2.8 mm; of basal side 2.6 mm; of distal side MAb 3.2 mm; its distal side MAb is only weakly angled. In both forewings MP originates precisely at the lower angle of the discoidal triangle. Median space free of crossveins; submedian space only traversed by CuP-crossing (1.0 mm basal of the arculus). The anal vein is divided into a well-defined anterior secondary branch PsA and a main branch AA; PsA delimiting an elongated subdiscoidal triangle that is divided into two cells by a crossvein. MP and CuA are closely parallel with a single row of cells in-between up to the posterior wing margin. MP reaches the posterior wing margin on a level with the nodus. CuA with about four rather well-defined posterior branches. The subdiscoidal veinlet is not shortened. There are up to three or four rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 2.3 mm. The anal area is relatively broad (max. width 2.3 mm) with two rows of cells between AA and the posterior wing margin. There might be a small membranule at the wing base.



Text-Fig. 26. *Araripeliupanshania annesusae* gen. et sp. nov. Holotype MB D 58 - male, hindwing base (drawing after photograph).

Hindwing: Length 38.2 mm; width at nodus 11.2 mm; distance from base to arculus 4.3 mm; distance from base to nodus 17.4 mm; from nodus to pterostigma 12.5 mm. The nodus is of the normal Anisoptera-type and is situated at 46 % of the wing length. The pterostigma is elongated (length 4.1 mm; width 0.9 mm), covering about four and a half cells, and is distinctly braced by a strong and oblique brace vein. About ten or eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. There were about ten antenodal crossveins between costal margin and ScP, not aligned with the secondary antenodal crossveins between ScP and RA. The two primary antenodal crossveins are aligned and distinctly stronger with two or three not aligned secondary antenodal crossveins in-between. Ax1 apparently close to the arculus, and Ax2 is 5.0 mm distal of Ax1, somewhat basal of the level of the distal end of the discoidal triangle. The antesubnodal area is poorly preserved. The arculus is angled. Two bridge-crossveins Bqs basal of the subnodus. Base of RP2 aligned with subnodus. There is only a single oblique vein 'O', one cell distal of the subnodus. Rspl is rather well-defined and parallel to IR2 with only a single row of cells in-between. At least two or three convex secondary veins in the area between IR2 and RP2, originating on Rspl and reaching the posterior wing margin. RP2 and IR2 run parallel with a single row of cells in-between, except near the posterior wing margin. RP1 and RP2 run parallel up to the pterostigma (even converging near the pterostigma) with only a single row of cells in-between, but below the pterostigma they become divergent with two or more rows of cells in-between. The pseudo-IR1 is very short and originates on RP1 distinctly distal of the pterostigma. RP3/4 and MA are parallel and only weakly undulated with a single row of cells in-between, except near the posterior wing margin (two rows of cells in-between). Mspl is clearly visible but zigzagged, and parallel to MA with a single row of cells between it and MA. Two convex secondary veins in the distal part of the postdiscoidal area, originating on Mspl and reaching the posterior wing margin; a strong convex secondary longitudinal vein in the basal part of the postdiscoidal area originates at the strong angle of the distal side MAb of the discoidal triangle. The postdiscoidal area is distally strongly widened (width near discoidal triangle 2.7 mm; width at posterior wing margin 8.2 mm) with two rows of cells in the basal part and at least sixteen cells along the posterior wing margin. The hypertriangle is elongated and narrow (length 5.1 mm; max. width 0.5 mm), and free of crossveins; its costal margin is somewhat curved. The discoidal triangle is longitudinal elongated, divided by three crossveins (in both hindwings), and has a very peculiar shape; length of basal side 1.8 mm; the

apical end of anterior side (length 4.1 mm) is bent and ends on the anterior side (MA) of the hypertriangle; its distal side MAb (length 4.6 mm) has a very peculiar structure, viz its basal part is very concave and its angle is very pronounced. In both hindwings MP is not precisely originating at the lower angle of the discoidal triangle, but is somewhat shifted anteriorly on MAb (MAb and MP shortly fused). Median space free of crossveins; submedian space only traversed by CuP-crossing, 0.7 mm basal of arculus. PsA is reduced to an oblique cubito-anal crossvein, delimiting a short and unicellular subdiscoidal triangle. MP and CuA run parallel with a single row of cells in-between, except near the posterior wing margin (two rows of cells in-between). MP reaches the posterior wing margin slightly basal of the level of the nodus. CuAa with five rather well-defined posterior branches; CuAb is well-defined. The subdiscoidal veinlet is very short and the gaff is not distinctly elongated. There are up to five rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 5.3 mm. The anal area is broad (max. width 6.6 mm) with up to seven rows of cells between AA and the posterior wing margin. The anal loop is well-defined by CuAb and AA1b, posteriorly closed by a strong veinlet, and divided into three cells (in both hindwings). There is no posterior branch of AA between the basal side of the anal loop (AA1b) and the distal side of the anal triangle (AA2b). There is a distinct anal angle, and a large three-celled anal triangle, thus, it is a male specimen.



Text-Fig. 27. *Araripeliupanshania annesusae* gen. et sp. nov. Holotype MB D 58 - male, anal appendages (drawing after photograph).

♦ Specimen no. 64345 (old number 72), SMNS; allotype; female

Plate 8: Figs 1-2

All wings, head, thorax, and the forelegs are preserved, but the complete abdomen is missing. The posterobasal margin of the hindwing is rounded without anal angle and anal triangle, thus, it is a female specimen. The wing venation is very similar to the holotype, but there seems to be a gap of crossveins in the distal part of the antesubnodal area in both pairs of wings. Length of forewing 38.7 mm; discoidal and subdiscoidal triangles three-celled. Length of hindwing 37.0 mm; distal side MAb of discoidal triangle strongly sigmoidal; anal loop four-celled; two posterior branches of AA between anal loop and anal margin; long and narrow membranule visible.

♦ Specimen no. 64343 (old number K 38), SMNS; paratype; male

Plate 9: Fig. 1

Head, thorax, three legs, and an isolate complete hindwing of a male. The head is max. 8.6 mm broad; the compound eyes are dorsally approximated (distance 0.9 mm). The legs are unusually short and stout, and there are no distinct spines visible: Length of profemur 4.9 mm (width 1.3 mm), of protibia 3.5 mm, of protarsus 2.4 mm; length of mesofemur 6.0 mm (width 1.5 mm), of mesotibia 4.6 mm, of preserved part of mesotarsus 2.0 mm; length of metafemur 5.2 mm (width 1.1 mm). The wing venation is perfectly preserved. Length of hindwing 39.8 mm; width at nodus 11.8 mm; distance from base to arculus 4.0 mm; distance from base to nodus 17.0 mm; from nodus to pterostigma 13.0 mm. The nodus is of the normal Anisoptera-type and is situated at 43 % of the wing length. The pterostigma is elongated (length 4.0 mm; width 0.9 mm), covering about four cells, and is distinctly braced by a strong and oblique brace vein. Nine postnodal crossveins between nodus and pterostigma, not aligned with the ten corresponding postsubnodal crossveins. Eleven antenodal crossveins between costal margin and ScP, not aligned with the nine secondary antenodal crossveins between ScP and RA. The two primary antenodal crossveins are aligned and distinctly stronger with three not aligned secondary antenodal crossveins in-between. Ax1 is 0.2-0.3 mm basal of arculus, and Ax2 is 5.3 mm distal of Ax1, slightly basal of the level of the distal end of the discoidal triangle. Five or six crossveins in the median part of the antesubnodal area; antesubnodal area with a long gap of crossveins in the basal third and the distal third. The arculus is very weakly angled. Two bridge-crossveins Bqs basal of the subnodus (but three crossveins basal of oblique vein 'O'). Base of RP2 aligned with subnodus. There is only a single oblique vein 'O', one cell distal of the subnodus. Rspl is zigzagged and runs parallel to IR2 with only a single row of cells in-between. Two strong convex secondary veins in the area between IR2 and RP2, originating on Rspl and reaching the posterior wing margin. RP2 and IR2 run parallel with a single row of cells in-between, except near the posterior wing margin. RP1 and RP2 run parallel up to the pterostigma (even converging near the pterostigma) with only a single row of cells in-between, but below the pterostigma they become divergent with two or more rows of cells in-between. The pseudo-IR1 is very short and originates on RP1 distinctly distal of the pterostigma. RP3/4 and MA are parallel and slightly undulated with a single row of cells in-between, except near the posterior wing margin (two rows of cells in-between). Mspl is weakly defined (zigzagged) and runs parallel to MA with a single row of cells between it and MA. Three convex secondary veins in the distal part of the postdiscoidal area, originating on Mspl and reaching the posterior wing margin; a strong convex secondary longitudinal vein in the basal part of the postdiscoidal area originates at the strong angle of the distal side MAb of the discoidal triangle. The postdiscoidal area is distally strongly widened (width near discoidal triangle 3.0 mm; width at posterior wing margin 8.2 mm) with two rows of cells in the basal part and numerous cells along the posterior wing margin. The hypertriangle is elongated and narrow (length 5.1 mm; max. width 0.8 mm), and free of crossveins; its costal margin is somewhat curved. The discoidal triangle is longitudinal elongated, divided into three cells by two crossveins, and has a very peculiar shape; length of basal side 1.8 mm; the apical end of anterior side (length 4.1 mm) is slightly bent and ends at the distal angle of discoidal triangle; the distal side MAb (length 4.5 mm) has a very peculiar structure, viz its basal part is very concave and its angle is very pronounced. MP originates at the lower angle of the discoidal triangle. Median space broad and free of crossveins; submedian space only traversed by CuP-crossing, 1.0 mm basal of arculus. PsA is reduced to an oblique cubito-anal crossvein, delimiting a short and unicellular subdiscoidal triangle. MP and CuA run parallel with a single row of cells in-between, but they diverge distally with two or more rows of cells in-between. MP reaches the posterior wing margin on a level with the nodus. CuAa with five well-defined posterior branches; CuAb is well-defined, too. The subdiscoidal veinlet is very short and the gaff is not distinctly elongated. There are up to five rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 5.5 mm. The anal area is broad (max. width 7.1 mm) with up to six or seven rows of cells between AA and the posterior wing margin. The anal loop is well-defined by CuAb and AA1b, posteriorly closed by a strong veinlet, and divided into three cells. There is no posterior branch of AA between the basal side of the anal loop (AA1b) and the distal side of the anal triangle (AA2b). There is a distinct anal angle, and a large three-celled anal triangle, thus, it is a male specimen. Along the basal side of the anal triangle there is a long membranule visible (length 6.5 mm; max. width 1.0 mm).

♦ Specimen no. M 56, coll. *ms-fossil*; paratype; female

Plate 9: Fig. 2

An isolated hindwing (length 36.3 mm). The wing venation agrees with the other type specimens. The rounded hind margin, without anal angle and anal triangle, shows that it is a female specimen.

♦ Specimen no. L 75, coll. SCHWICKERT; paratype; male

Plate 10: Figs 1-2

All wings, head, thorax, forelegs, and the basal half of the abdomen are preserved. The wing venation is very well visible. There is an anal angle and anal triangle in the hindwing, thus, it is a further male specimen. The wing venation is very similar to the holotype, but there also seems to be a gap of crossveins in the distal part of the antesubnodal area in both pairs of wings. Length of forewing 35.3 mm; discoidal and subdiscoidal triangles three-celled. Length of hindwing 34.1 mm; distal side MAb of discoidal triangle strongly sigmoidal; discoidal triangle three-celled; subdiscoidal triangle unicellular; anal loop five-celled; anal triangle broad and three-celled.

♦ Specimen without number, coll. MURATA, Kyoto; paratype; male

Plate 11: Fig. 1

A beautifully preserved isolated left hindwing of a male with the wing articulation and a fragment of the pterothorax. Size unknown, since this description is based on a photograph without scale. The nodus is of the normal Anisoptera-type and is situated at 45 % of the wing length. The pterostigma is elongated, covering about five cells, and is distinctly braced by a strong and oblique brace vein. About ten postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. There were about ten antenodal crossveins between costal margin and ScP, not aligned with the nine antenodal crossveins between ScP and RA. The two primary antenodal crossveins are aligned and distinctly stronger than the secondary antenodal crossveins; between Ax1 and Ax2 there are two secondary antenodal crossveins in the first row, and two or three of them in the second row, not aligned with each other; Ax1 is directly at the arculus, and Ax2 is on a level with the distal end of the discoidal triangle. Several antesubnodal crossveins are visible in the space between the arculus and the subnodus, but this area is not very well-preserved. The arculus is angled, and the bases of RP and MA are distinctly separated at arculus. Two bridge-crossveins Bqs basal of the subnodus. Base of RP2 aligned with subnodus. There is only a single oblique vein 'O', one and a half cell distal of the subnodus. Rspl is only weakly defined and parallel to IR2 with only a single row of cells in-between. At least two convex secondary veins in the area between IR2 and RP2, originating on Rspl and reaching the posterior wing margin. RP2 and IR2 run parallel with a single row of cells in-between, except near the posterior wing margin. RP1 and RP2 run parallel up to the pterostigma with only a single row of cells in-between, but below the pterostigma they become divergent with two or more rows of cells in-between. The pseudo-IR1 is very short and originates on RP1 about one cell distal of the pterostigma; one row of cells between pseudo-IR1 and RP1. RP3/4 and MA are parallel and only weakly undulated with a single row of cells in-between, but they diverge slightly near the wing margin with two rows of cells in-between. Mspl is weakly defined, zigzagged, and parallel to MA with a single row of cells between it and MA. Two convex secondary veins in the distal part of the postdiscoidal area, originating on Mspl and reaching the posterior wing margin; a strong convex secondary longitudinal vein in the basal part of the postdiscoidal area, originating at the strong angle of the distal side MAb of the discoidal triangle. The postdiscoidal area is distally strongly widened with two rows of cells in the basal part and about fifteen cells along the posterior wing margin. The hypertriangle is elongated and free of crossveins; its costal margin is somewhat curved. The discoidal triangle is longitudinal elongated, divided by two crossveins, and has a very peculiar shape; the apical end of anterior side is bent and ends on the anterior side (MA) of the hypertriangle; its distal side MAb has a very peculiar structure, viz its basal part is very concave and its angle is very pronounced. Median space free of crossveins; submedian space only traversed by CuP-crossing. PsA is reduced to an oblique cubito-anal crossvein, delimiting a short and unicellular subdiscoidal triangle. MP and CuA run parallel with a single row of cells between their basal parts, but two rows of cells between their distal parts. MP originates exactly at the lower angle of the discoidal triangle (contrary to the holotype) and reaches the posterior wing margin slightly basal of the level of the nodus. CuAa with five well-defined distal posterior branches, while the most basal posterior branch of CuAa is a zigzagged and weak vein; CuAb is well-defined. The subdiscoidal veinlet is rather short and the gaff is slightly elongated. There are up to five rows of cells between CuA and the posterior wing margin. The anal area is broad with six or seven rows of cells between AA and the posterior wing margin. The anal loop is well-defined by CuAb and AA1b, posteriorly closed by a strong veinlet, and divided into five cells. There is no posterior branch of AA between the basal side of the anal loop (AA1b) and the distal side of the anal triangle (AA2b). There is a distinct anal angle, and a large three-celled anal triangle that nearly reaches down to the anal angle, thus, it is a male specimen.

Genus *Paramesuropetala* gen. nov.

Type species: *Paramesuropetala gigantea* sp. nov.

Derivatio nominis: After the genus *Mesuropetala*, because of the similarity to this genus.

Wing venational autapomorphies: Very large size; pseudo-IR1 weakly developed; RP3/4 and MA more strongly undulated.

Diagnosis: This new genus is distinguished from related genera by the following combination of forewing characters: Very large size (wing length 66.0 mm); pterostigma elongated and braced, but the pterostigmal brace vein is not very oblique; RP1 and RP2 basally closely parallel with only a single row of cells up to the pterostigma; pseudo-IR1 indistinct and short, originating on RP1 somewhat distal of the pterostigma; RP2 distinctly undulated; distal part of area between IR2 and RP2 with two rows of cells; Rspl present, although somewhat weak and zigzagged, and curved with four or fiive rows of cells between it and IR2; RP3/4 and MA are distinctly undulated; Mspl is strongly zigzagged but concave with three rows of cells between it an MA; only a single oblique vein 'O' near the subnodus; hypertriangle free; discoidal triangle transverse and three-celled; subdiscoidal triangle three-celled; presence of a strong convex secondary longitudinal vein (trigonal planate) that originates on the straight distal side MAb of the discoidal triangle; no accessory cubito-anal-crossvein between CuP-crossing and PsA.

Systematic position: We consider *Paramesuropetala* gen. nov. as an Aeshnoptera because of the following putative synapomorphies: RP1 and RP2 basally strictly parallel, thus, the area between these two veins is basally distinctly narrowed with only a single row of cells in-between between the nodus and the pterostigma; Rspl is present; RP3/4 and MA more or less undulated. It shares with Mesuropetaloidea stat. nov. the arculus shifted very close to the first primary antenodal Ax1, the parallel RP3/4 and MA, and the very transverse forewing discoidal triangle, here all considered as synapomorphies. However, this new genus has some character states that seem to contradict a relationship with Mesuropetalidae, such as: (1) the presence of a relatively well-defined Rspl; (2) a distinctly undulated RP2; (3) a concave Mspl; (4) a strong convex secondary longitudinal vein (trigonal planate) in the postdiscoidal area originating on MAb; (5) only the basal oblique vein 'O' is present, close to the subnodus; (6) MP and CuA are closely parallel. Characters (1) and (2) are autapomorphies of the Aeshnomorpha taxon nov. Character (3) is an autapomorphy of the Aeshnida. Characters (4), (5) and (6) are more advanced conditions than in Austropetaliida taxon nov., Progobiaeshnidae fam. nov., Cymatophlebioidea stat. nov. and Eumorbaeschnidae fam. nov., but shared with Liupanshaniidae fam. nov. and Neoaeshnida. Within Liupanshaniidae fam. nov. all six characters are present in *Paraliupanshania* gen. nov. Nevertheless, characters 1-6 are all rather homoplastic and thus weak evidence, while the transverse forewing discoidal triangle, the three-celled subdiscoidal triangle, and the free hypertriangles represent strong evidence against a position in Aeshnomorpha taxon nov. or even in Aeshnida. The straight distal side MAb of the discoidal triangle also excludes a position in Euaeshnida. We therefore regard *Paramesuropetala* gen. nov. as a Liupanshaniidae fam. nov., most likely representing the sister-genus of *Paraliupanshania* gen. nov.

Paramesuropetala gigantea sp. nov.

Text-Fig. 28

1998 *Paramesuropetala gigantea*; BECHLY, p. 62 (nomen nudum).

Holotype: Specimen no. [MNHN-LP. R. 55194], coll. MARTILL, MNHN, Paris.

Derivatio nominis: After the large size, since it is the largest known dragonfly from Araripe.

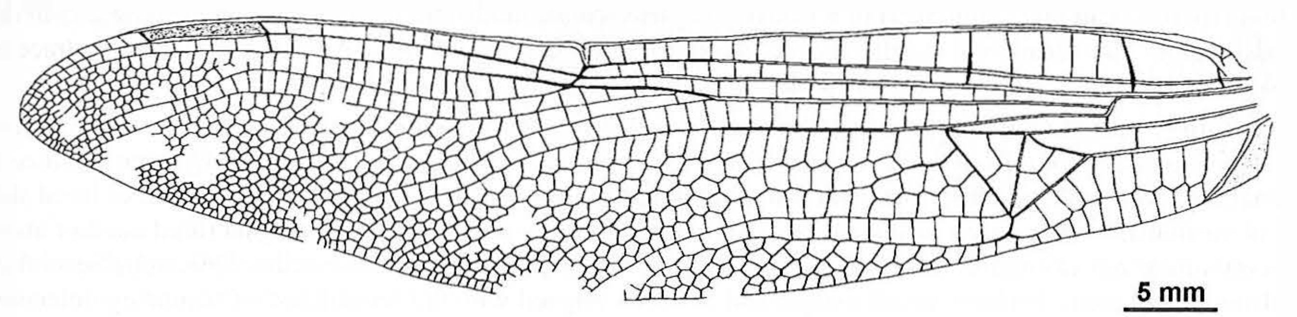
Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

Diagnosis: Same as for the genus.

Description: Imprint of a single complete forewing. No trace of coloration, the wing was probably hyaline.

Forewing: Length 66.6 mm; width at nodus 13.7 mm; distance from base to arculus 7.3 mm; distance from base to nodus 35.3 mm; from nodus to pterostigma 17.1 mm. Pterostigma very elongated (length 6.3 mm; width 1.0 mm), covering five cells, and braced by a weakly oblique crossvein that is aligned with its basal side. Pterostigma not in a basal position, at 55 % of distance between nodus and apex, and 80 % of whole length of wing. Eleven postnodal crossveins visible between nodus and pterostigma (total number probably twelve), not aligned with corresponding postsubnodal crossveins. Most basal postnodal crossvein slanted towards nodus. Twenty antenodal crossveins between costal margin and ScP, not aligned with antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Primary antenodal crossveins Ax1 and Ax2 aligned and stronger than the secondary antenodal crossveins. Ax1 is only 0.7 mm basal of arculus, and Ax2 is 8.7 mm distal of Ax1, somewhat basal of the distal angle of discoidal triangle. Four secondary antenodal crossveins of the first row between the two primary antenodal crossveins, but there is only a single corresponding antenodal crossvein visible in the second row. The basal brace Ax0 is visible. Twelve antesubnodal crossveins visible in the space between arculus and subnodus without a distinct gap immediately basal of subnodus, but with a long gap near arculus. RP and MA distinctly separated at arculus that is angled. Three bridge-crossveins Bqs basal of subnodus. Base of RP2 aligned with subnodus. Nodus of the normal Anisoptera-type. Only a single oblique vein 'O', one and a half cells (1.4 mm) distal of subnodus. IR2 originating 5.5 mm and RP3/4 (midfork) 7.5 mm basal of subnodus. A concave, but zigzagged Rspl that is curved with max. four or five rows of cells between it and IR2. RP2 and IR2 parallel with only a single row of cells in-between, except distal of the level of pterostigma (two to three rows of cells near the posterior wing margin). RP2 distinctly undulated on a level with pterostigma. Pseudo-IR1 well-defined, but short and basally zigzagged, originating on RP1 distinctly distal of pterostigma. RP1 and RP2 closely parallel up to pterostigma (even converging near pterostigma) with only a single row of cells in-between, but below the pterostigma they become strongly divergent two or more rows of cells in-between. RP3/4 and MA parallel and distinctly undulated with a single row of cells in-between (two rows near the posterior wing margin). A concave, but strongly zigzagged Mspl with three rows of cells between it and MA. Postdiscoidal area distinctly widened distally (width near discoidal triangle 4.7 mm; width at posterior wing margin 12.6 mm) with three or four rows of cells immediately distal of discoidal triangle. Hypertriangle free of crossveins (length 8.4 mm; max. width 0.9 mm). Discoidal triangle very transverse and divided into three cells; length of anterior side 4.1 mm; of basal side 4.2 mm; of distal side MAb 5.6 mm. Distal side MAb straight, but with a distinct convex secondary vein (trigonal planate) originating on it; the latter vein is vanishing in the distal part of the postdiscoidal area. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.6 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 three-celled subdiscoidal triangle, max. 4.7 mm long and basally 3.2 mm wide (= length of PsA). PsA is slightly curved and ends at basal angle of discoidal triangle. A single row of cells in area between MP and CuA. MP reaching posterior wing margin on a level with nodus. CuA reaching posterior wing margin somewhat basal of the level of nodus. Seven posterior branches of CuA are well-defined. Max. width of cubito-anal area 3.0 mm with max. five rows of cells between CuA and posterior wing margin. Anal area max. 3.9 mm wide (below PsA) with two rows of large cells between AA and posterior wing margin. Distinct membranule visible at the wing base.



Text-Fig. 28. *Paramesuropetala gigantea* gen. et sp. nov. Holotype MNHN-LP. R. 55194 - left forewing.

Genus *Paraliupanshania* gen. nov.

Type species: *Paraliupanshania torvaldsi* sp. nov.

Other species: *Paraliupanshania rohdendorfi* sp. nov. from the lower Upper Cretaceous of Russia like the type species, and *Paraliupanshania britannica* sp. nov. from the Lower Cretaceous of England.

Derivatio nominis: After *Liupanshania* to indicate the similarity between the two genera.

Diagnosis: This genus is characterized by the following features of the hindwing: A generally very dense cross-venation with numerous cells; RP1 and RP2 basally closely parallel with only a single row of cells up to the pterostigma; hypertriangle free; the discoidal triangle is divided into six cells and is of most peculiar shape, since the distal side MAb is nearly zigzagged with its basal part strongly concave and its distal angle extremely pronounced; the convex secondary vein (trigonal planate) that originates at the angle of MAb is very strong, even as strong as the main veins MA and MP, and stronger than Mspl, thus dividing the postdiscoidal area into two very distinct parts; Mspl is rather well-defined and more or less parallel to MA, but separated by two or three rows of cells from it.

Several further hindwing characters seem to be diagnostic for this new genus, too, but are unknown in *P. rohdendorfi* sp. nov., and partly also unknown in *P. britannica* sp. nov.: Pterostigma elongated and unbraced, since the pterostigmal brace vein is rather transverse and displaced one cell distal of basal side (convergent to Austropetaliida taxon nov.); pseudo-IR1 distinct and originating on RP1 beneath the distal side of the pterostigma; RP2 slightly undulated; distal part of area between IR2 and RP2 with four rows of cells; Rspl well-defined and strongly curved with about five rows of cells between it and IR2 (convergent to Progobiaeshnidae fam. nov., Cymatophlebioidea stat. nov., and Aeshnidae, including Oplonaeschna); only a single oblique vein 'O' near the subnodus; the postnodal and antenodal crossveins are very numerous; PsA is strongly reduced, and the unicellular subdiscoidal triangle is very small (convergent to Aeshnoclea); no accessory cubito-anal-crossvein between CuP-crossing and PsA; anal loop completely suppressed (potential synapomorphy with *Liupanshania* ?; convergent to Austropetaliida taxon nov. and Cymatophlebiinae).

Paraliupanshania torvaldsi sp. nov.

Text-Fig. 29, Plate 11: Figs 2-3

Holotype: Specimen no. [2383 / 14], PIN, Moscow.

Derivatio nominis: Named in honour of Dr h.c. Linus TORVALDS (Helsinki), initiator and main developer of the *Linux* operating system.

Locus typicus: Kzhyl-Zhar, Russia.

Geological age: Lower Upper Cretaceous, Turonian.

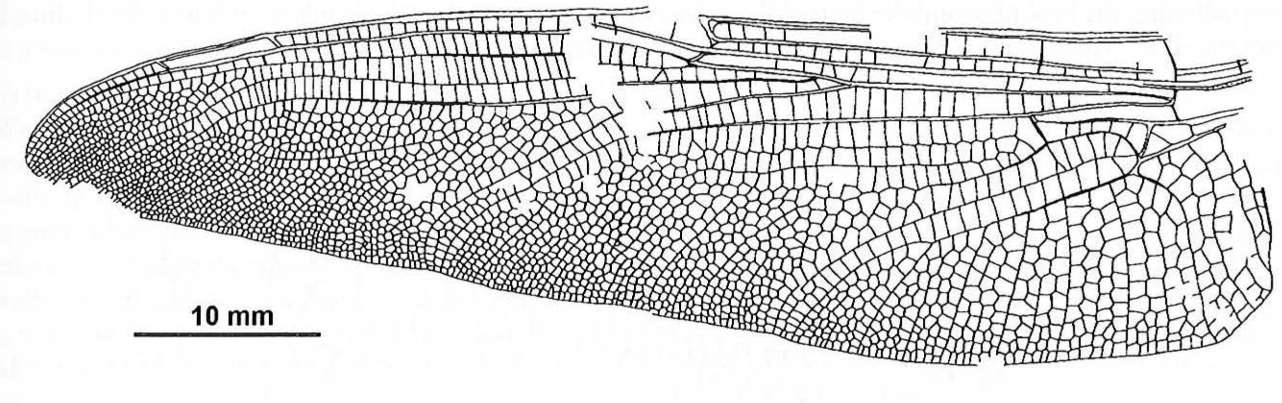
Autapomorphies: Same as for family.

Diagnosis: This species is distinguished by the following characters: There are two or three rows of cells between Mspl and MA instead of up to four in *P. rohdendorfi* sp. nov.; there are only two or three rows of cells between MP and CuA along the wing margin, instead of five or six in *P. rohdendorfi* sp. nov.; MP and CuA are reaching the posterior wing margin on a level with the midfork, while they reach the posterior wing margin near the level of the nodus in *P. rohdendorfi* sp. nov.

Description: Part and counterpart of a nearly complete female hindwing, partly broken at the base and in the nodal region. The venation is excellently preserved, even the small spines on RA + RP are visible. No trace of coloration preserved, but the wing was probably hyaline.

Hindwing: Length 66.6 mm; width at nodus 16.5 mm; distance from base to arculus 4.3 mm; distance from base to nodus 29.8 mm; from nodus to pterostigma 21.5 mm. Pterostigma elongated, covering seven small cells (length 6.3 mm; max. width 1.1 mm); pterostigmal brace not oblique and displaced one cell distal of basal side of pterostigma. Twenty-seven postnodal crossveins visible between nodus and pterostigma (total number about twenty-nine), not aligned with the thirty-one corresponding postsubnodal crossveins. Numerous secondary antenodal crossveins between costal margin and ScP, not aligned with the second row of secondary antenodal crossveins between ScP and RA. The primary antenodal crossveins are aligned and distinctly stronger with about four or five secondary antenodal crossveins in-between; Ax1 is aligned with arculus, and Ax2 is 7.4 mm distal of Ax1 on a level with distal angle of discoidal triangle. Basal brace Ax0 visible. Numerous antesubnodal crossveins in the area between the arculus and the subnodus, but they are rather incompletely preserved, so that it cannot be recognized if there was a gap near the subnodus or not. Arculus angled; the bases of RP and MA are shortly separated at arculus. Four bridge-crossveins Bqs basal of subnodus. Base of RP2 aligned with subnodus. There is only a single oblique vein 'O', two and a half cells (1.6 mm) distal of the subnodus. Rspl is very well-defined and strongly curved with up to six rows of cells between it and IR2. About five convex secondary longitudinal veins (intercalaries) in distal part of the area between IR2 (or Rspl) and RP3/4. RP2 and IR2 are more or less parallel with only a single row of cells in-between up to the level of pterostigma, but more distally there are up to four rows of cells between these veins; IR2 is curved on a level with pterostigma, and RP2 is even slightly undulated in this area. RP1 and RP2 are basally closely parallel (even converging near pterostigma) with only a single row of cells in-between up to the pterostigmal brace vein, but more distally they become strongly divergent with two or more rows of cells in-between. Pseudo-IR1 well-defined and originating on RP1 slightly distal of distal side of pterostigma. RP3/4 and MA are parallel and only weakly undulated with a single row of cells in-between, except between their strongly curved distal parts (two rows of cells). Mspl well-defined and originates about four cells distal of discoidal triangle, thus, it is in a basal position, straight and parallel to the basal MA with two (distally three) rows of cells between it and MA. MA and MP strongly divergent. Postdiscoidal area therefore distally extremely widened (width near discoidal triangle 3.6 mm; width at posterior wing margin 18.2 mm) with four rows of cells in the basal part of the postdiscoidal area, but with about fifty-five (!) small cells along the posterior wing margin; about five convex secondary longitudinal veins (intercalaries) in distal part of postdiscoidal area; very strong convex secondary longitudinal vein (trigonal planate), originating at the strongly pronounced angle of the distal side MAb of the discoidal triangle and distally becoming more indistinct and zigzagged, finally ending on MP; there are three rows of cells between the trigonal planate and MA, and one row of cells between it and MP. The hypertriangle is free of crossveins. The discoidal triangle is very long, narrow and divided into six cells by parallel crossveins; length of anterior side 6.4 mm; of basal side 1.9 mm; of distal side, 6.4 mm (rather the distance from distal angle to posterior angle of discoidal triangle than the true length of MAb); the anterior side of discoidal triangle is apically curved and ends on the anterior side of hypertriangle close to distal angle of discoidal triangle; MAb has a very peculiar structure, viz its basal part is very concave, its distal angle is very pronounced, and the part distal of the angle is straight. Median space free of crossveins. Submedian space only traversed by

CuP-crossing, 0.7 mm basal of arculus. PsA reduced to an oblique weak cubito-anal crossvein that is ending on the basal side of discoidal triangle; subdiscoidal triangle indistinct, very small and unicellular. MP and CuA run parallel with a single row of cells in-between, except near the posterior wing margin (two rows of cells); MP and CuA reach the posterior wing margin on a level with midfork. Subdiscoidal veinlet reduced, and gaff very short. CuAa with six well-defined posterior branches; CuAb is also well-defined and basally curved towards the wing base; the main branch of CuAa obliquely approaches the posterior wing margin; cubito-anal area max. 9.7 mm wide with up to ten or eleven rows of cells between CuAa and posterior wing margin. Anal area is broad (max. width 10.7 mm) with up to ten rows of cells between AA and posterior wing margin. Anal loop posteriorly open or rather completely reduced. AA with three posterior branches. Anal margin rounded without anal angle or anal triangle, thus, it is a female specimen.



Text-Fig. 29. *Paraliupanshania torvaldsi* gen. et sp. nov. Holotype PIN 2383 / 14 - female, left hindwing.

Paraliupanshania rohdendorfi sp. nov.

Text-Fig. 30

Holotype: Specimen no. [846 / 5], PIN, Moscow, collected 1951 by J.V. LEBEDEV, Tomsk Polytechnical Institute.

Derivatio nominis: Named in honour of the late Russian paleoentomologist Prof. Dr B. B. ROHDENDORF.

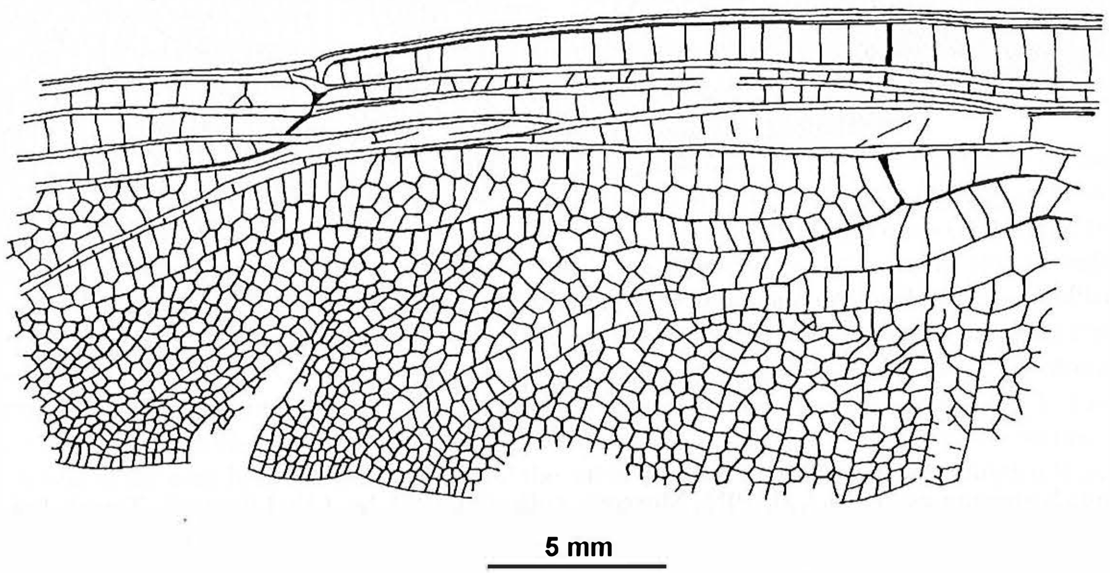
Locus typicus: Right side of Kem' River, 4 km upstream, Kholovskiy village, Yeniseysk District, Krasnoyarsk Province, Russia.

Geological age: Lower Upper Cretaceous, Cenomanian.

Diagnosis: This species is distinguished from the previous new species by the following characters: There are up to four rows of cells between Mspl and MA instead of two or three in *P. torvaldsi* sp. nov.; there are five or six rows of cells between MP and CuA along the wing margin, instead of two or three rows in *P. torvaldsi* sp. nov.; MP and CuA are reaching the posterior wing margin near the level of the nodus, instead of the level of the midfork in *P. torvaldsi* sp. nov. The size of the wing is 10 % smaller than in *P. torvaldsi* sp. nov.

Description: Part and counterpart of the median part of a hindwing. No trace of coloration preserved, but the wing was probably hyaline. Concerning the interpretation of our Text-Fig. 30 it should be noted that there the fossil is distorted.

Hindwing: Length of the fragment 31.6 mm (based on a comparison of the distance from Ax2 to nodus with *Paraliupanshania torvaldsi* gen. et sp. nov., the probable total length can be estimated as 60.3 mm); width at nodus 11.9 mm; distance from base to nodus, and from nodus to pterostigma, unknown. Pterostigma not preserved. There are seven basal postnodal crossveins preserved, all not very well-aligned with the corresponding postsubnodal crossveins. Twenty-five antenodal crossveins preserved between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the second primary antenodal crossvein Ax2 that is aligned and distinctly stronger (Ax1 is not preserved); there were at least six secondary antenodal crossveins between Ax2 and Ax1 (total number probably about eight). The antesubnodal area between arculus and subnodus, as well as the bridge-space (Bqs-area) are very poorly preserved. Base of RP2 aligned with subnodus. Oblique vein 'O' not preserved. Rspl not visible. RP3/4 and MA parallel and rather straight with a single row of cells in-between. Mspl well-defined and originating three cells distal of discoidal triangle; Mspl straight and parallel to MA with two to four rows of cells between it and MA. Postdiscoidal area distally extremely widened; there are three rows of cells immediately distal of the discoidal triangle and a very strong secondary longitudinal vein (trigonal supplement), originating at the very strongly angled distal side MAb of the discoidal triangle; there are three rows of cells between this secondary vein and MA, and one row between it and MP; this secondary vein is distally reaching MP. Hypertriangle not clearly visible. Discoidal triangle very elongated, narrow, and divided into six cells by parallel crossveins (basal part of discoidal triangle not preserved); its distal side MAb has a very peculiar structure, viz its basal part is very concave and its angle is very pronounced. Median space, submedian space, and subdiscoidal triangle not preserved. MP and CuAa run parallel with a single row of cells in-between, except near the posterior wing margin where these veins diverge and are separated by six cells at the posterior wing margin. MP reaches the posterior wing margin on a level with nodus. Seven well-defined posterior branches of CuA are visible. Cubito-anal area max. 5.4 mm wide with up to ten or eleven rows of cells between CuAa and the posterior wing margin. The anal area (including the anal loop and the area of the potential anal angle and anal triangle) is not preserved, thus, it is not possible to recognize if it was a male or a female specimen.



Text-Fig. 30. *Paraliupanshania rohdendorfi* sp. nov. Holotype PIN 846 / 5 - left hindwing (part).

Paraliupanshania britannica sp. nov.

Text-Fig. 31

Holotype: Specimen no. [016388], coll. Peter AUSTEN 21/8/91, BMBN, Brighton.

Derivatio nominis: After the type locality in Britain.

Locus typicus: Rudgwick Brickworks, near Horsham, West Sussex, England.

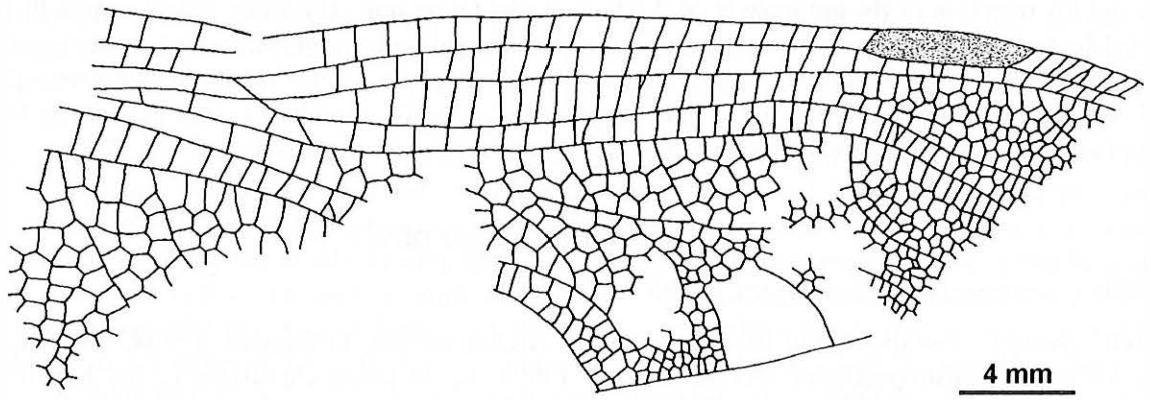
Stratum typicum: Upper Weald Clay, Lower Cretaceous, Barremian.

Diagnosis: The wing venation is nearly identical to the corresponding part of the wing in the type species *Paraliupanshania torvaldsi* gen. et sp. nov., with exception of the following few characters: Pterostigmal brace vein completely absent (autapomorphy); only about twenty postnodal crossveins (instead 27-29); max. five rows of cells. between Rspl and IR2 (instead of max. six rows); up to three rows of cells between RP3/4 and MA near the posterior wing margin (instead of only two rows).

Description: Part and counterpart of a relatively well-preserved fragment of the distal half of a hindwing. Length of fragment, 41 mm (compared to the type species, the corresponding parts of the wing are of identical size, so that the total length of the hindwing probably was also 66 mm); distance from nodus to pterostigma 22.3 mm. Pterostigma 5.6 mm long and max. 1.2 mm wide, covering seven cells, and unbraced. Only three distal secondary antenodal crossveins are preserved between costal margin and ScP and between ScP and RA, not aligned with each other. Twenty postnodal crossveins visible between nodus and pterostigma (total number probably twenty-one), not aligned with corresponding postsubnodal crossveins between RA and RP1. RP1 and RP2 are closely parallel up to the pterostigma with only a single row of cells in-between. Below basal side of

pterostigma RP1 and RP2 become divergent with two or more rows of cells in-between. A short pseudo-IR1 originates slightly distal of the pterostigma. Two or three rows of cells between pseudo-IR1 and RP1, and four or five rows between pseudo-IR1 and RP2. RP2 and IR2 run parallel up to the pterostigma with only a single row of cells in-between, but below the pterostigma they become somewhat divergent with two rows of cells in-between; RP2 and IR2 are distinctly undulated. RP2 is aligned with the subnodus. Only a single oblique vein 'O', one and a half cells (1.6 mm) distal of the subnodus. A well-defined and curved Rspl with up to five rows of cells in the area between Rspl and IR2 (max. width of this area 3.4 mm). Several convex secondary veins originating on Rspl and reaching the posterior wing margin. Two bridge-crossveins Bqs are visible basal of the subnodus; MA and RP3/4 are only weakly undulated and more or less parallel with only a single row of cells in-between, but near the posterior wing margin they become slightly divergent with two to three rows of cells in-between. No distinct Mspl is visible, but there are at least two convex secondary longitudinal veins in the distal postdiscoidal area, originating on MA somewhat basal of the level of the nodus and reaching the posterior wing margin. The wing base, the discoidal area, and the cubito-anal area are not preserved.

Systematic position: The following similarities with *Paraliupanshania* gen. nov. clearly show that this new Wealden species is not a Cymatophlebiidae but a Liupanshaniidae fam. nov.: Pterostigmal brace vein more or less reduced (synapomorphy with *Paraliupanshania* gen. nov.); RP1 and RP2 basally closely parallel, even converging near the pterostigma, and with only a single row of cells between RP1 and RP2 up to the pterostigma (plesiomorphy that is absent in all Cymatophlebioidea stat. nov.); RP2 smoothly undulated but IR2 relatively straight (synapomorphy with *Paramesuropetala* gen. nov. and *Paraliupanshania* gen. nov.); Rspl well-defined and strongly curved (synapomorphy with *Paramesuropetala* gen. nov. and *Paraliupanshania* gen. nov.); only a single oblique vein 'O' near the subnodus (synapomorphy with Liupanshaniidae fam. nov.); RP3/4 and MA parallel and only weakly undulated. Also the size and the other visible characters are extremely similar to *Paraliupanshania* gen. nov., e.g. pseudo-IR1 originating beneath the distal side of pterostigma, and pterostigma elongated and covering about seven cells, etc. The fact that no Mspl is visible is no conflicting evidence, since the basal postdiscoidal area where the Mspl is located in the two Russian species, is not preserved in the Wealden species.



Text-Fig. 31. *Paraliupanshania britannica* sp. nov. Holotype BMB 016388 - right hindwing.

Aeshnomorpha taxon nov.

1991 "Palanisoptera"; PFAU, p. 132 (nec Palanisoptera LOHMANN, 1995, 1996a).
1996 Aeshnata; BECHLY, p. 382 (nec Aeshnata LOHMANN, 1996a).

Included groups: Austropetaliida taxon nov. and Panaeshnida taxon nov.

Wing venational autapomorphies: Forewing discoidal triangle longitudinal elongated, like that of the hindwing, therefore the discoidal triangles of both pairs of wings are of similar shape; hypertriangles divided by at least one crossvein (reversed within Gomphaeschnidae and a few other taxa); RP2 at least slightly undulated (reversed in Archipetaliidae and some fossil Gomphaeschninae like *Alloaeschna* and *Gomphaeschnaoides*; modified to a characteristical curvature in Aeshnodea, *contra* LOHMANN 1996c); Rspl better defined; gaff at least slightly prolonged (somewhat reduced in Cymatophlebiinae, correlated with the reduction of the anal loop).

Other autapomorphies: Presence of at least a small intraocellar lobe in adults (convergent to Cavilabiata, *contra* CARLE 1995); male secondary genitalia (in the groundplan) include a lamina anterior with elongated median cleft (CARLE 1996), a short L-shaped ligula (CARLE 1995, 1996) with the antero-ventral face developed into a sharp edged valve separator (CARLE 1996), hamuli anteriores lamellate and directed medially (CARLE 1996), and hamuli posteriores strongly reduced in size (CARLE 1995, 1996) (however, as already suggested by LOHMANN 1996c, some of these genital characters are ambiguous or even dubious, while at least the reduced hamuli posteriores are certainly not a symplesiomorphy, *contra* LOHMANN 1996c); larval prehensile mask with an elongated prementum (this is certainly not a symplesiomorphy, *contra* LOHMANN 1996c, since the prementum in larval austropetaliids and aeshnids is distinctly longer than in *Epiophlebia* and in fossil larvae of Isophlebiidae and Aeschnidiidae); larval epiproct typically bifurcate apically (CARLE 1996); larval compound eyes produced forward, being widest anterior to antennal bases (CARLE 1996); proventricular lobes of gizzard small and mound-like with eight or fewer clustered teeth (CARLE 1996); presence of a true dorso-longitudinal carina (not only a sharp fold) on at least some of the adult abdominal terga (convergent to Tarsophlebiidae and Laterocarinida; reduced in some Archipetaliidae and in *Gomphaeschna*).

LOHMANN (1996a) mentions several alleged symplesiomorphies that should indicate a position of austropetaliids and aeshnids basal of Petalurida and Exophytica ("ektoflexate" hind tibiae, no sexual dimorphism in the armature of the mid and hind tibiae, and terminal segment of male vesicula spermalis less fused and without processus dorsales, correlated with smaller female spermathecae). We regard all these states as ambiguous or even dubious characters that are not yet sufficiently investigated and documented. If they are correct at all, they could rather represent reversals, since BECHLY (1996) and NEL *et al.* (1998) recently demonstrated with strong evidence a more basal position of Petalurida.

The non wing venational characters are mostly unknown in Mesuropetaloidea stat. nov. and therefore could also represent autapomorphies of Aeshnoptera.

Discussion: We preferred to give a new name to this monophylum, since the previous name Aeshnata BECHLY, 1996 could lead to confusion with the junior homonym Aeshnata LOHMANN, 1996a, which was used by the latter author for a very different monophylum (Aeshnodea in the present publication). This risk of confusion would be aggravated by LOHMANN's use of the suffix "-ata" as a standardized suffix for his high-level sistergroups, and his rejection of the monophyly of Aeshnomorpha taxon nov. The name Palanisoptera PFAU, 1991 is rejected by us because it was proposed as preliminary informal name, and because of its conjunction with the probably erroneous hypothesis that all other extant Anisoptera do form a monophyletic group (Neanisoptera PFAU, 1991). Furthermore, the name Palanisoptera was recently used by LOHMANN (1996a) for a very different monophylum (Euaeshnida), too, which could again lead to considerable confusion.

Austropetaliida taxon nov.

1996a Austropetaliata; LOHMANN, p. 228.

Included groups: Archipetaliidae BECHLY, 1996 (= Archipetaliidae LOHMANN, 1996a; = Archipetaliinae CARLE, 1996) and Austropetaliidae (*sensu* BECHLY 1999a, b). Detailed classification see BECHLY (1996, 1999a, b).

Wing venational autapomorphies: Series of five to eight reddish costal spots (convergent to Neopetaliidae; CARLE & LOUTON 1994, CARLE 1995, 1996), including an apical spot and a spot in the middle of the postnodal space (contrary to Neopetaliidae); pterostigmata secondarily shortened, and the pterostigmal brace vein not aligned with its basal side; IR1 very long (convergent to Petalurida and Valdaeshninae subfam. nov.); the insertions of the CuP-crossing and PsA on the anal vein AA are very close to each other; basal true lestine oblique vein 'O' reduced or completely suppressed (there is only a single distinct oblique vein 'O' between RP2 and IR2 in a very distal position, probably homologous with the distal accessory oblique vein).

Other autapomorphies: Larval labrum strongly widened distally (CARLE 1995, 1996); massive ventro-lateral development of larval occipital ridge massive (CARLE 1995, 1996); larval femora dorsally excrescent, supplied with tubercles (SCHMIDT 1941, CARLE 1995, 1996); larval transverse abdominal muscles completely suppressed (CARLE 1995, 1996), therefore larvae secondarily unable of jet-propulsion; larvae with extensively granulate body surface (CARLE 1996); larva with lateral abdominal lobes on all abdominal segments (CARLE 1995, 1996); larval cerci shorter than half of the length of the ventral margin of the 10th abdominal segment (LOHMANN 1995, 1996a); terminal segment of vesicula spermalis pendulous with sickle-like paired flagellae (CARLE 1995); epiproct of adult males developed as a very broad and apically trifid plate (FRASER 1933) with the median lobe much larger than the lateral lobes; cerci of adult males short and foliate (FRASER 1933); males with the ventral margin of the second abdominal tergite expanded as genital lobes (LOHMANN 1996a, based on an uncited personal information by the first author); leaf-like lateral expansions of abdominal terga VII and VIII (CARLE 1996; but maybe not belonging to the groundplan).

Discussion: Although the name "Austropetaliata" was already proposed for this clade by LOHMANN (1995, 1996a), we do not use this name for the following two reasons: (1) LOHMANN is using the suffix "-ata" explicitly to give equal suffixes to sistergroups, while we reject this goal as purely formalistic; (2) since this clade was previously addressed under the family-group name Austropetaliidae we preferred a name which sounds similar and which allows the further use of the vernacular expression "austropetaliids". Out of the same reasons we preferred the names Aeshnida, Petalurida, and Gomphides, instead of LOHMANN's names Palanisoptera (including Gomphaeschnata and Aeshnata), Petalurata, and Gomphata.

The Austropetaliida are still completely unknown in the fossil record (*contra* LOHMANN 1996a). The phylogeny of the included genera has been recently discussed by BECHLY (1996, 1999a, b), LOHMANN (1996a, c), and CARLE (1996). In the first part of his paper LOHMANN (1996a: 228-232) proposed a phylogeny which is fundamentally different from the phylogeny proposed by the two other authors: His taxon Austropetaliata is composed by the two alleged sistergroups Archipetaliidae and Pan-Austropetaliidae. Pan-Austropetaliidae shall include Cymatophlebiidae and Austropetaliidae, while the latter are divided into Austropetaliinae and Hypopetaliinae (only *Hypopetalia*). However, several shortcomings and errors in LOHMANN (1996a) could cause considerable confusion:

(1) For Archipetaliidae, LOHMANN cites as only potential autapomorphy «Flügel am Vorderrand mit vier Flecken zwischen Nodus und Basis» although this could rather be a plesiomorphy, since this state is also present in *Hypopetalia*. Nevertheless, Archipetaliidae are well supported as monophylum by the characters mentioned in BECHLY (1996) and CARLE (1996). Archipetaliidae LOHMANN, 1996a (published on 13^{th} June, and indicated as "n. fam.") is a junior objective synonym of Archipetaliinae BECHLY, 1996 (published on 15^{th} May), since they are both family-group taxa that are based on the same type genus.

(2) For Pan-Austropetaliidae, LOHMANN cites one potential autapomorphy «Flügeladern RP2 und IR2 verlaufen undulierend gegen den Flügelhinterrand». This character is incorrect, since IR2 is not undulated in any extant Austropetaliata (*sensu* LOHMANN). A more or less undulated RP2 is also present in basal aeshnids (e.g. *Eumorbaeschna* gen. nov., *Gomphaeschna*, *Paramorbaeschna* gen. nov., *Linaeschna*) and therefore most likely represents a symplesiomorphy that has been convergently reduced in *Archipetalia* and higher aeshnids (Aeshnodea).

(3) For Cymatophlebiidae LOHMANN (1996a) cites three potential autapomorphies of which one («Brückenader "oblique vein" nicht vorhanden») is clearly incorrect, since all Cymatophlebiidae have two very distinct oblique veins as a symplesiomorphy. The other two characters are more or less synonymous and furthermore not present in all Cymatophlebiidae. His statement «Als plesiomorphes Grundplanmerkmal weist die Gruppe noch getrennte Komplexaugen auf» is again wrong, since *Cymatophlebia* has strongly confluent eyes like an extant aeshnid (see below). Apparently the author's statement is not based on the study of fossil material, but rather on the notoriously unreliable descriptions and drawings of HANDLIRSCH (1906-08). His initial statement that Cymatophlebiidae only include the two species *Cymatophlebia longialata* (GERMAR 1839) and *C. agrias* (WESTWOOD 1854) is incorrect as well. *Libellulium agrias* WESTWOOD, 1854 is a *nomen dubium* (see below), while four further species have been described in the genus *Cymatophlebia* that are not mentioned by LOHMANN at all. Furthermore, if *L. agrias* is regarded as congeneric with *Cymatophlebia* by LOHMANN, the valid generic name would of course have to be *Libellulium* WESTWOOD, 1854 and not *Cymatophlebia* DEICHMÜLLER, 1886 (this error was obviously copied from HANDLIRSCH 1906: 592). LOHMANN erroneously indicated his Cymatophlebiidae as a taxon sensu nov. although he did not change the composition of this taxon at all, but only its phylogenetic position. The new ranking of Cymatophlebiidae as family, indicated by LOHMANN (1995: 60) as being based on a personal communication by BECHLY (1995), has to be regarded as questionable, since LOHMANN (1996a) did not indicate it as intentional by a "status nov." remark. Besides, the correct publication date for Cymatophlebiidae is not HANDLIRSCH, 1909 [sic], but HANDLIRSCH, 1906.

(4) For Austropetaliidae, LOHMANN cites two potential autapomorphies, of which the second («Flügeladern RP2 und IR2 verlaufen undulierend gegen den Flügelhinterrand») was already cited by himself in the same paper as autapomorphy of Pan-Austropetaliidae.

(5) For Austropetaliinae, LOHMANN cites a single potential autapomorphy («Thoraxseiten mit gelben oder grünen Streifen») which is clearly a plesiomorphy, as was correctly recognized by CARLE (1996). The

strong evidence presented in BECHLY (1996) and CARLE (1996) shows that the Austropetaliinae (*sensu* LOHMANN) are paraphyletic. Hypopetaliinae LOHMANN, 1996a is a junior subjective synonym of Phyllopetaliini BECHLY, 1996, since the latter include the genus *Hypopetalia*.

Conclusion: The inclusion of Cymatophlebiidae in crowngroup Austropetaliata LOHMANN, 1996a, as well as the different phylogeny of Austropetaliidae in LOHMANN (1996a), are based on an insufficient character analysis with numerous errors, and a neglect of conflicting evidence, and therefore have to be dismissed. It must be emphasized that all phylogenetic analyses are depending on a careful character analysis of fossil material rather than literature, irrespective if the resulting evidence is analysed "by hand" (rather by brain) or with computer-parsimony programs. Likewise the position of Austropetaliata as sistergroup of all remaining extant Anisoptera, except Aeshnata (*sensu* LOHMANN), has been recently dismissed by BECHLY (1996, 1999a, b) and by NEL *et al.* (1998) for the same reasons. In his "first postscript" to the mentioned publication LOHMANN (1996c) adopted the proposed phylogeny of extant Austropetaliidae by BECHLY (1996) and CARLE (1996), but did not mention the Cymatophlebiidae.

In his publication, LOHMANN (1996c: 363) maintained that the publication date of BECHLY (1996) would not be 15th May 1996, as indicated on the cover of the journal, but rather 31th July 1996, since only a single copy should have been available at the original date and the complete edition should have been available not before end of July 1996. However, this statement was based on a "private investigation" which did not include any consultation of the author and publisher of the referring publication. Consequently, LOHMANN (1996c) claimed the priority of the new names Archipetaliidae LOHMANN, 1996a (published 13th June), Araripegomphidae LOHMANN, 1996a (published 13th June), and Condaliidae LOHMANN, 1996c (published 12th September). However, this change of the publication date of BECHLY (1996) was not warranted, since indeed seven copies were available on the original publication date and partly already distributed on 17th May 1996 (including one copy to the *Zoological Record*), 19th May 1996, and 3rd June 1996. The complete edition was available since 30th May 1996. Thus according to the International Rules of Zoological Nomenclature (fourth edition) Art. 8.1.3 and 21.4, the correct publication date of *Petalura* special vol. 2 is 15th May 1996, as stated on the cover.

Panaeshnida taxon nov.

Included groups: Progobiaeshnidae fam. nov. and Aeshnida BECHLY, 1996.

Wing venational autapomorphies: Rspl strongly defined (not zigzagged) in both pairs of wings; hypertriangles divided by several parallel crossveins; discoidal triangles divided into more than two cells; submedian space divided by one or more accessory cubito-anal crossveins between CuP-crossing and PsA.

Family Progobiaeshnidae fam. nov.

Type genus: *Progobiaeshna* gen. nov.

Included genera: Currently only including the type genus *Progobiaeshna* gen. nov., and tentatively also the genus *Gobiaeshna* PRITYKINA, 1977.

Wing venational autapomorphies: Pterostigmata relatively short, and pterostigmal brace vein perpendicular, not oblique like the basal side of the pterostigma; pseudo-IR1 strongly reduced (very short and originating distinctly distal of the pterostigma); anal loop pentagonal, enlarged and divided into nine cells, correlated with a more pronounced elongation of the gaff (unknown in *Gobiaeshna*); several rows of cells between IR2 and Rspl which are more or less parallel; hindwing subdiscoidal triangle two-celled.

Diagnosis: In addition to the above mentioned autapomorphies of Progobiaeshnidae fam. nov., this new fossil family is diagnosed by the presence of the autapomorphies of Aeshnoptera (viz RP1 and RP2 basally parallel; MA and RP3/4 undulated) and Aeshnomorpha taxon nov. (viz both discoidal triangles longitudinal and of similar shape; RP2 more or less undulated; Rspl present; RP3/4 and MA distinctly divergent near the wing margin) and Panaeshnida taxon nov. (viz discoidal triangles and hypertriangles divided by crossveins; anal loop enlarged; accessory cubito-anal crossvein), and by the absence of the autapomorphies of Mesuropetalidae (see above), Austropetaliida taxon nov. (viz no costal spots; primary IR1 not hypertrophied; both oblique veins present and in "normal" position) and Aeshnida (see below), except the five-celled discoidal triangles which could represent a potential synapomorphy with Aeshnida. Further diagnostic characters are: RP2 and IR2 are only weakly undulated and strictly parallel with only a single row of cells in-between; there are two oblique veins 'O' between IR2 and RP2 (symplesiomorphy); Mspl is absent (symplesiomorphy); the very long veins MP and CuA (the latter with about seven posterior branches in both wings) that are distally diverging; absence of any angle or curve in the straight distal side of the discoidal triangle (symplesiomorphy); subdiscoidal triangles divided into two cells in both pairs of wings; three rows of cells in the basal postdiscoidal area of both pairs of wings; there is no secondary longitudinal vein in the postdiscoidal area originating on the distal side of the discoidal triangle (symplesiomorphy); PsA delimiting a distinct subdiscoidal triangle, but rather looking like an oblique cubito-anal crossvein than like a secondary anterior branch of AA.

Systematic position: The character pattern clearly demonstrates that this new family belongs to the Aeshnoptera - Aeshnomorpha taxon nov., as sistergroup of Aeshnida (see autapomorphies of Panaeshnida taxon nov.). The obvious similarities between the wing venation of Progobiaeshnidae fam. nov. and the wing venations of Rudiaeschnidae fam. nov. and Austropetaliida taxon nov. are due to numerous symplesiomorphies that are of considerable importance for the reconstruction of the groundplan of Aeshnomorpha taxon nov.

Because of the incomplete and relatively poor preservation of the holotype of *Gobiaeshna occulta* PRITYKINA, 1977 we decided to create a new genus for the well-preserved holotype of *P. liaoningensis* sp. nov., and to choose this genus as type genus of the new family Progobiaeshnidae fam. nov. Although *Gobiaeshna* corresponds very well to the diagnosis of this new family, its inclusion can only be tentative, since several important characters are not preserved in the holotype.

Genus *Progobiaeshna* gen. nov.

Type species: *Progobiaeshna liaoningensis* sp. nov.

Diagnosis: As for type species.

Progobiaeshna liaoningensis sp. nov.

Text-Fig. 32, Plate 12: Figs 1-2

Holotype: Specimen no. [63398], SMNS, Stuttgart.

Derivatio nominis: After the provenance of the type from the province Liaoning.

Locus typicus: Liaoning Province, P.R. China (unfortunately a more precise locality can not be given, since the specimen was purchased from a Chinese fossil trader on a fossil fair in Stuttgart).

Geological age: Lower Cretaceous, Aptian (SMITH et al. 1995, WELLNHOFER 1997).

Diagnosis: This new species is very similar to *Gobiaeshna occulta* PRITYKINA, 1977 (including the not oblique pterostigmal brace vein), but shows the following differences in the forewing: Only a single row of cells between the parallel parts of RP1 and RP2 instead of two rows in *G. occulta*; about thirteen secondary antenodal crossveins distal of Ax2 instead of only nine in *G. occulta* (but the latter number is based on the "reconstruction" of PRITYKINA, since not all antenodals are preserved in the holotype); and about five secondary antenodal crossveins between Ax1 and Ax2 instead of only three in *G. occulta*; PsA reduced to a simple crossvein in submedian space, instead of being distinctly stronger than the other cubito-anal crossveins.

Description

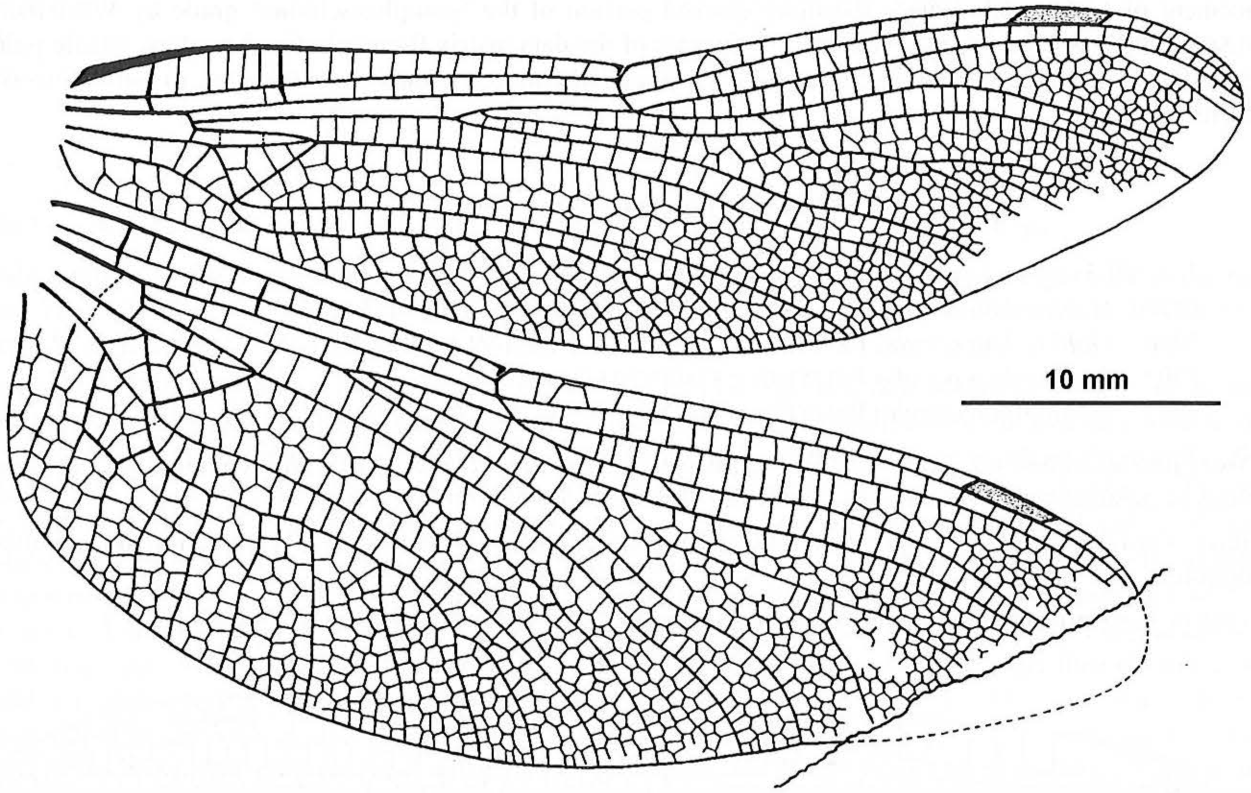
♦ Specimen no. 63398, SMNS; holotype; female

[original label «140, Libelle, Jura (145 Ma), Liaoning, VRC»]

A well-preserved female with a well-preserved right pair of wings, in connection with the pterothorax, and one preserved fore leg (on the backside of the plate there is a distal half of the abdomen of a large Ephemeroptera larva). The right pairs of wings is nearly completely preserved, only the apex of the hindwing is missing, while the left pair of wings is completely missing. The wings were probably hyaline. The pterothorax is rather well-preserved, and one fore leg is well-preserved, too, including the tiny spines and the "cleaning brush" (Plate 12: Fig. 2).

Forewing: Length 45.8 mm; width at nodus 11.0 mm; distance from base to nodus 21.3 mm; from nodus to pterostigma 15.5 mm; distance from base to arculus 4.8 mm. Pterostigma relatively short (length 3.4 mm; width 0.7 mm), and covering less than four cells. Pterostigmal brace vein enforced and aligned with basal side of pterostigma, but it is perpendicular and not oblique like the basal side of pterostigma. Fourteen or fifteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Twenty antenodal crossveins visible between costal margin and ScP, not aligned with second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. The most distal secondary antenodal crossvein between costal margin and ScP is slanted towards the nodus. Ax1 and Ax2 are stronger than the other antenodal crossveins; Ax1 is 1.4 mm basal of the arculus; Ax2 is 5.2 mm distal of Ax1. There are at least five secondary antenodal crossveins of the first row between the two primary antenodal crossveins, apparently not aligned with the corresponding antenodal crossveins of the second row. No antesubnodal crossveins preserved in the space between the arculus and the subnodus, but they were probably numerous. Four crossveins preserved basal of the first oblique vein, including at least two bridge-crossveins Bqs, but probably there were four of five of the latter. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.3 mm and 4.8 mm distal of the subnodus. Rspl somewhat weakly defined and parallel to IR2, but with two or three rows of cells in-between. Two convex secondary veins originating on Rspl. RP2 and IR2 closely parallel with only a single row of cells in-between up to the level of pterostigma (distally two rows of cells). RP2 hardly undulated. No primary IR1, and pseudo-IR1 strongly reduced and originating far distal of pterostigma. RP1 and RP2 basally closely parallel with only a single row of cells in-between, but 4.0 mm basal of the pterostigma they become divergent with two or more rows of cells in-between. RP3/4 and MA parallel and gently undulated with a single row of cells in-between up to the level of the second oblique vein, but distally there are two rows of cells in-between, and near the wing margin they are distinctly divergent. Neither a Mspl, nor any other secondary vein in postdiscoidal area that is widened distally (width near discoidal triangle 2.5 mm; width at wing margin 4.7 mm) with three rows of cells immediately distal of the discoidal triangle. Hypertriangle (length 4.6 mm; max. width 0.6 mm) seems to be divided by two crossveins, but these are only faintly preserved. Discoidal triangle longitudinally elongated and divided into five cells; length of anterior side 3.9 mm; of basal side 2.2 mm; of distal side MAb 3.9 mm; the distal side MAb is straight. Median space free of crossveins. One accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA. CuP-crossing 1.5 mm basal of arculus. Vein PsA reversed to an oblique cubito-anal crossvein, thus, not looking like a secondary branch of AA; PsA ends at the basal angle of the discoidal triangle. Subdiscoidal triangle rather well-defined, max. 2.0 mm long and basally 1.5 mm wide (= length of PsA), and divided into two cells by a crossvein. A single row of cells in the area between MP and CuA, but distally they become distinctly divergent with about nine cells in-between along the posterior wing margin. MP reaches the posterior wing margin far distal of the level of nodus (even distal of the level of the second oblique vein). CuA also reaches the posterior wing margin distinctly distal of the level of nodus, between the level of the first and the second oblique vein. Seven or eight well-defined posterior branches of CuA. There are max. five or six rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 3.6 mm. The anal area is max. 1.9 mm wide (below the origin of PsA) with two rows of cells between AA and the posterior wing margin.

Hindwing: Length 45.7 mm; width at nodus 15.1 mm; distance from base to nodus 18.8 mm, thus, the nodus is in a rather basal position; from nodus to pterostigma 18.7 mm; distance from base to arculus 4.5 mm. Pterostigma relatively short (length 3.4 mm; width 0.7 mm), and covering three and a half cells. Pterostigmal brace vein enforced and aligned with the basal side of pterostigma, but it is perpendicular and not oblique like the basal side of pterostigma. Seventeen postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Fourteen antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. The primary antenodal crossveins Ax1 and Ax2 are stronger than the others, but Ax2 is rather indistinct as an artifact of preservation. Ax1 is 1.3 mm basal of the arculus. Ax2 seems to be 5.7 mm distal of Ax1. Between the two primary antenodal crossveins, there are at least four secondary antenodal crossveins in the first row, not aligned with the corresponding antenodal crossveins of the second row. Seven antesubnodal crossveins preserved in the space between the arculus and the subnodus, but there were probably at least twelve of them. Six crossveins basal of the first oblique vein, including five bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.9 mm and 6.1 mm distal of the subnodus. Rspl somewhat weakly defined and more or less parallel to IR2, but with two to five rows of cells in-between. At least one convex secondary vein originating on Rspl. No primary IR1, and pseudo-IR1 is not visible either, although it might have originated very distally (as in the forewing), since the apex of the wing is not preserved. RP2 and IR2 are closely parallel with only a single row of cells in-between. RP1 and RP2 are basally closely parallel with only a single row of cells in-between, but 4.0 mm basal of the pterostigma they become divergent with two or more rows of cells in-between. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4) with a single row of cells in-between up to the level of the second oblique vein, but distally there are two rows of cells in-between, and near the wing margin they are distinctly divergent with four or five cells in-between. No Mspl, but on MA originates a single secondary vein in the distal postdiscoidal area. The postdiscoidal area is distally widened (width near discoidal triangle; 3.1 mm; width at wing margin 5.6 mm) with three rows of cells immediately distal of the discoidal triangle. The hypertriangle seems to be divided by one or two crossveins (length 5.2 mm; max. width 0.9 mm). Discoidal triangle longitudinally elongated (same shape as that of the forewing), and divided into six cells; length of anterior side 4.4 mm; of basal side 2.7 mm; of distal side MAb 4.1 mm; the distal side MAb is straight. Median space free of crossveins, although there is a faint structure on a level with Ax1 that could be interpreted as a weakly preserved crossvein. The submedian space seems to be only traversed by the CuP-crossing, 1.4 mm basal of the arculus, but this is uncertain, since the area is rather weakly preserved. PsA is more oblique than in the forewing, but still less well-defined than in the groundplan of Anisoptera, rather looking like a cubito-anal crossvein than like a secondary branch of AA. Subdiscoidal triangle distinct, max. 2.7 mm long and basally 1.7 mm wide (= length of PsA), and divided into two cells by a crossvein. PsA ends at basal angle of discoidal triangle. A single row of cells in the area between MP and CuA, but distally they become distinctly divergent with five cells in-between along the posterior wing margin. MP reaches the posterior wing margin far distal of the level of nodus (on a level with the second oblique vein), and CuA reaches the posterior wing margin distinctly distal of the level of nodus, too (on a level with the first oblique vein). Seven well-defined posterior branches of CuAa and a well-defined CuAb. There are max. nine or ten rows of cells between CuAa and the posterior wing margin, max. width of cubito-anal area 6.7 mm. Anal area broad, below PsA 7.5 mm wide with eight rows of cells between AA and posterior wing margin. Pentagonal anal loop large (length 2.9 mm; width 3.0 mm), divided into nine cells, and posteriorly well-closed. Only a single posterior branch of AA between the wing base and the basal side of the anal loop, below the CuP-crossing. Anal margin rounded. There is neither an anal triangle, nor an anal angle, thus, it is a female specimen.



Text-Fig. 32. *Progobiaeshna liaoningensis* sp. nov. Holotype SMNS 63398 - female, right pair of wings.

Genus *Gobiaeshna* PRITYKINA, 1977

Type species: *Gobiaeshna occulta* PRITYKINA, 1977, by original designation.

Diagnosis: As for type species.

Systematic position: *Gobiaeshna* shows great similarities in its preserved characters with *Progobiaeshna* gen. nov., including several putative synapomorphies, like the perpendicular pterostigmal brace vein, and the reduced pseudo-IR1. Distinctions from *P. liaoningensis* sp. nov. are listed in the diagnosis of the latter species. Nevertheless, there are several characters of *P. liaoningensis* sp. nov. that are unknown in *G. occulta*, such as the absence of a Mspl, and the course of the distal parts of the main longitudinal veins. Furthermore, there is also a great similarity of *Gobiaeshna* with *Cymatophlebia purbeckensis* sp. nov. Unfortunately, only the basal part of the forewing of *C. purbeckensis* sp. nov. is known. Differences between *P. liaoningensis* sp. nov. and *C. purbeckensis* sp. nov. are as follows: Mspl is absent; the very long veins MP and CuA that are distally diverging (both symplesiomorphies, unknown in *Gobiaeshna*); third enforced and aligned antenodal crossvein absent in the forewing. Other characters of the wing base are very similar in the two species, but as they are most likely symplesiomorphies, they are no valid evidence for a close relationship of the two species. Furthermore, the preserved characters clearly indicate a position of *C. purbeckensis* sp. nov. in Cymatophlebiinae (see below), while this can certainly be excluded for *P. liaoningensis* sp. nov. At least the structure of the short and unbraced pterostigma, and also the closely parallel course of RP2 and IR2, contradicts a position of *Gobiaeshna* in Cymatophlebiinae as well. Nevertheless, because of the great similarities between the three taxa and the lack of preservation of the area of the potential Mspl in *Gobiaeshna*, the attribution of *Gobiaeshna occulta* to Progobiaeshnidae fam. nov. has to be regarded as somewhat preliminary.

Irrespective of the phylogenetic position of *Gobiaeshna*, either in Cymatophlebiidae, or rather in Progobiaeshnidae fam. nov., this genus certainly cannot be regarded as a synonym of *Baissaeshna*, contrary to the speculations of WIGHTON & WILSON (1986: 520), since *Baissaeshna* shares the apomorphic characters of [Aeshnida - Euaeshnida - Neoaeshnida - Aeshnodea] that are absent or unknown in *Gobiaeshna*, and absent in Progobiaeshnidae fam. nov. and Cymatophlebiidae. Important differences between *Gobiaeshna* and *Baissaeshna* are the very oblique pterostigmal brace in *Baissaeshna*, and the presence of three rows of cells between IR2 and RP2 in *Baissaeshna*, instead of only one in *Gobiaeshna*. The hypothetical (and almost certainly incorrect) placement of *Gobiaeshna* within the more derived portion of the "gomphaeschnine" grade by WIGHTON & WILSON (1986) was based on several insufficiencies of the data matrix (homoplastic characters, unsafe polarities, unknown states), and the exclusion of *Cymatophlebia* from the analysis which led to partly incorrect polarities.

Gobiaeshna occulta PRITYKINA, 1977

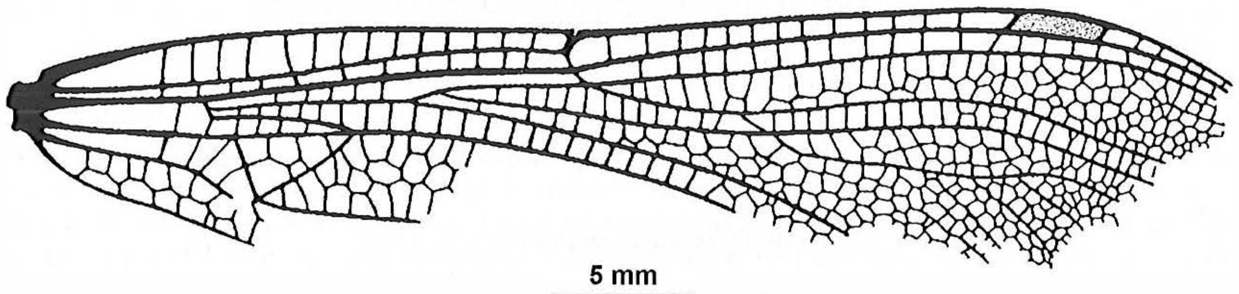
Text-Figs 33-36, Plate 12: Figs 3-4, Plate 13: Fig. 1

*v 1977 *Gobiaeshna occulta* PRITYKINA, p. 87, text-fig. 4, pl. 2, figs 1-3.
1986 *Gobiaeshna occulta* PRITYKINA, 1980 [sic]; WIGHTON & WILSON, p. 507.
1992 *Gobiaeshna occulta* PRITYKINA; CARPENTER, p. 82.
1994 *Gobiaeshna occulta* PRITYKINA, 1977; NEL *et al.*, p. 176.

Holotype: Specimen no. [3145 / 672], PIN, Moscow; part and counterpart of an incomplete forewing with destroyed posterior and nodal areas of the wing.

Locus typicus: bore-well (pit ?) of Anda-Khuduk 2, Ubur-Khangaisk aimak, Ushgiin-Nur mountains. Mongolia.

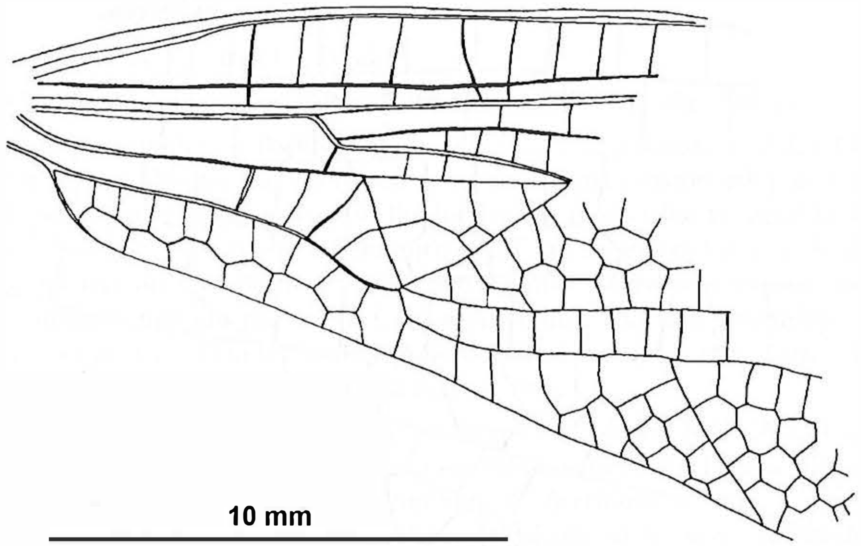
Stratum typicum: Anda-Khuduksk Series (Baisinsk deposits), Lower Cretaceous ("Neocomian").



Text-Fig. 33. *Gobiaeshna occulta* PRITYKINA, 1977. Holotype PIN 3145 / 672. - forewing (drawing after PRITYKINA 1977: text-fig. 4).

Diagnosis: The differences from *Progobiaeshna liaoningensis* gen. et sp. nov. are listed in the diagnosis of the latter species. The total length of the forewing was probably 43.5 mm, thus, of similar size as in the new species. The area of the Mspl is not preserved in the holotype (the single known specimen), but due to the phylogenetic position of this taxon it probably did not have a Mspl as well.

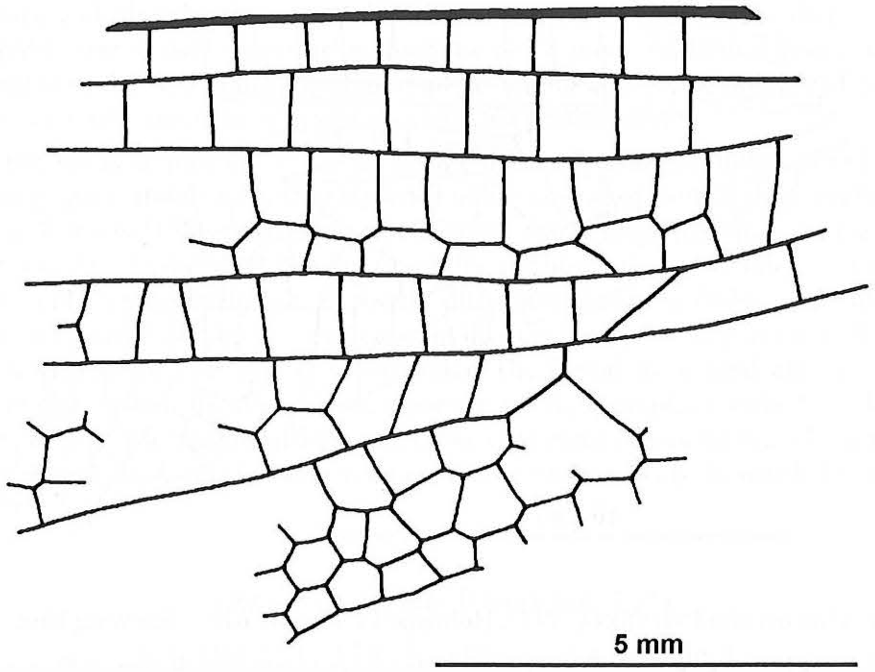
The drawing in the original description shows only a single oblique vein eight cells distal of the subnodus, but this very distal location clearly indicates that there was a second oblique vein 'O' which was probably close to the subnodus (not figured in the drawing of PRITYKINA, since the concerning area is not preserved but "reconstructed"). The lack of crossveins in the distal half of the antesubnodal area probably is an artifact of this "reconstruction", too, and therefore no valid derived similarity with Gomphaeschnidae. A very unusual feature would be the single crossvein in the median space, but this seems to be another drawing error of PRITYKINA (see below).



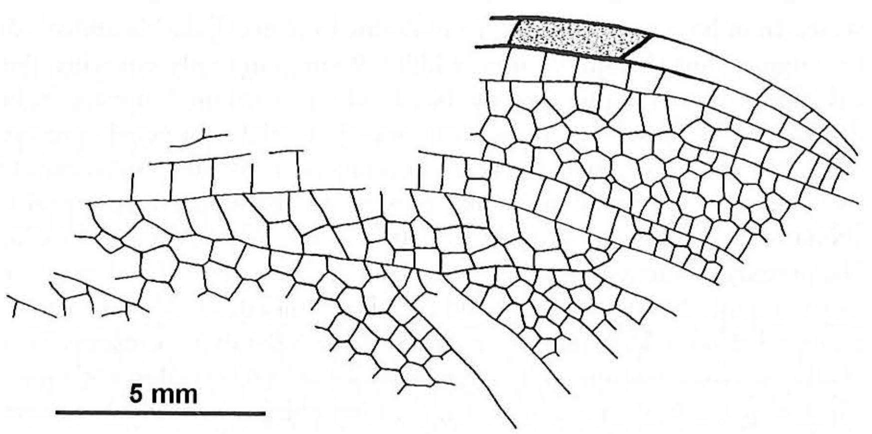
Text-Fig. 34. *Gobiaeshna occulta* PRITYKINA, 1977. Holotype PIN 3145 / 672. - forewing base.

Redescription: The original drawing of PRITYKINA (1968) is partly "reconstructed", especially in the nodal area. The lack of crossveins in the distal half of the antesubnodal area, and the absence of the basal oblique vein 'O', therefore have to be regarded as myths.

Forewing: Total length 43-44 mm, thus, of similar size as in *Progobiaeshna liaoningensis* gen. et sp. nov.; width at nodus, distance from base to nodus, and from nodus to pterostigma, unknown; distance from base to arculus 6.8 mm. Pterostigma short (length 3.0 mm; width 0.9 mm), and only covering about three cells; distal side of pterostigma distinctly more oblique than the basal side; pterostigmal brace vein indistinct and perpendicular, but still aligned with the basal side of pterostigma. Postnodal area poorly preserved, only eight postnodal crossveins are visible, not aligned with the corresponding postsubnodal crossveins. Only the basal half of the antenodal area is preserved with nine antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. The primary antenodal crossveins Ax1 and Ax2 are aligned and stronger than the other antenodal crossveins. Ax1 is 1.4 mm basal of arculus, and Ax2 is 4.9 mm distal of Ax1. Three secondary antenodal crossveins of the first row between Ax1 and Ax2, not aligned with the two corresponding antenodal crossveins of the second row. Only the two basal antesubnodal crossveins are preserved in the space between the arculus and the subnodus. Bridge-space (Bqs-area) not preserved. First oblique vein 'O' not preserved, but it was probably present because the second oblique crossvein 'O' is present in a very distal position, just basal of the base of Rspl (it is also more strongly oblique than the primary oblique vein 'O'). Rspl is strongly defined and somewhat curved with up to three rows of cells between it and IR2. Four convex secondary veins originating on Rspl. RP2 and IR2 closely parallel with only a single row of cells in-between up to the level of pterostigma (distally two rows of cells). RP2 is very weakly undulated. No primary IR1, pseudo-IR1 strongly reduced and originating two cells distal of the pterostigma; only one or two rows of cells between pseudo-IR1 and RP1. RP1 and RP2 are closely parallel for a long distance with only a single row of cells in-between up to the level of the second oblique vein 'O', but distally there are two rows of cells in-between (thus, there are two rows of cells basal of the pterostigma). The distal parts of RP3/4 and MA are not preserved. Three rows of cells in the basal part of the postdiscoidal area, but the distal part of this area is not preserved, so that the presence of a Mspl cannot be determined. The hypertriangle (length 5.3 mm; max. width 0.5 mm) is divided by two cross-veins. The discoidal triangle is longitudinally elongated and divided into six cells; length of anterior side 4.4 mm; of basal side 2.4 mm; of distal side MAb 4.2 mm; the distal side MAb is straight. Median space free of crossveins. One accessory cubito-anal crossvein in submedian space between CuP-crossing and PsA. CuP-crossing is 1.5 mm basal of arculus. Subdiscoidal triangle rather well-defined, max. 2.2 mm long and basally 1.8 mm wide (= length of PsA), and divided into two cells by a crossvein. PsA is stronger than the other cubito-anal crossveins and ends at the basal angle of discoidal triangle. A single row of cells in the basal part of the area between MP and CuA. Width of cubito-anal area unknown. Anal area max. 1.6 mm wide (below PsA) with two rows of cells between AA and posterior wing margin.



Text-Fig. 35. *Gobiaeshna occulta* PRITYKINA, 1977. Holotype PIN 3145 / 672. - forewing, median part.



Text-Fig. 36. *Gobiaeshna occulta* PRITYKINA, 1977. Holotype PIN 3145 / 672. - forewing apex.

Aeshnida BECHLY, 1996

Included groups: Cymatophlebioidea stat. nov. and Euaeshnida taxon nov.

Wing venational autapomorphies: Presence of a Mspl (still weakly developed in the groundplan).

Other autapomorphies: Compound eyes enlarged and medially contiguous; presence of a very distinct dorso-longitudinal carina on the abdominal terga 3-8 of adults (convergent to Tarsophlebiidae and Laterocarinida; reduced in *Gomphaeschna*, *contra* LOHMANN 1996a); adult anal appendages elongated (especially the cerci).

The non wing venational characters are unknown in Progobiaeshnidae fam. nov., and therefore could as well represent autapomorphies of Panaeshnida taxon nov.

Superfamily Cymatophlebioidea HANDLIRSCH, 1906 stat. nov.

Type genus: *Cymatophlebia* DEICHMÜLLER, 1886.

Included groups: Cymatophlebiidae HANDLIRSCH, 1906 and Rudiaeschnidae fam. nov.

Wing venational autapomorphies: Rspl distinctly curved and separated by at least three rows of cells from IR2; one to three convex oblique and undulated secondary veins anastomosing between IR2 and RP3/4 immediately basal of the origin of Rspl, at least in the hindwings (somewhat reduced in *Valdaeshna*; apparently present by convergence in *Aktassia*, but different); hindwing subdiscoidal triangle divided into two or three cells. A further putative autapomorphy could be the lateral expansions (genital lobes) along the third segment of the male abdomen that are present in Cymatophlebiinae and Rudiaeschnidae, but which are not visible (mot present or not preserved) in the male holotype of *Valdaeshna surreyensis*, while the concerning character state is unknown for all other Valdaeshninae subfam. nov.

Discussion: The well-defined oblique secondary veins between IR2 and RP3/4 basal of Rspl represent a strong synapomorphy of Cymatophlebiinae, Valdaeshninae subfam. nov. and Rudiaeschnidae fam. nov. This character is currently known from *Cymatophlebia longialata*, *C. herrlenae* sp. nov., *C. zdrzaleki* comb. nov., *C. kuempeli* sp. nov., *C. pumilio* sp. nov., *Prohoyaeshna milleri* gen. et sp. nov., *Hoyaeshna cretacica*, *Valdaeshna surreyensis* (somewhat reduced), and *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. It is quite unique within Odonata, since a superficially similar structure is otherwise only known from the genus *Aktassia* which is certainly unrelated to Aeshnoptera (anal loop absent, Rspl and Mspl absent, RP1 and RP2 basally not parallel, IR2 and RP2 not undulated), and most likely is a close relative of the genus *Aeschnogomphus* within Petalurida (NEL *et al.* 1998).

Family Cymatophlebiidae HANDLIRSCH, 1906

1996a Cymatophlebiidae HANDLIRSCH 1909 [sic]; LOHMANN, p. 231 (incorrectly indicated as "n. *sensu*", but without new content; invalid elevation in rank, since not indicated as "stat. nov.").
1998 Cymatophlebiidae stat. nov., NEL *et al.* (but already cited in BECHLY 1996, 1999a, b).

Type genus: *Cymatophlebia* DEICHMÜLLER, 1886.

Included groups: Cymatophlebiinae HANDLIRSCH, 1906 and Valdaeshninae subfam. nov.

Wing venational autapomorphies: IR2 distinctly undulated (apomorphy) and parallel to RP2 which is also undulated (plesiomorphy); the anastomosing secondary veins between IR2 and RP3/4, immediately basal of Rspl, are more distinctly developed; Rspl is more strongly curved; RP3/4 and MA more strongly undulated; the distal primary antenodal crossvein Ax2 is shifted distinctly basal of the level of the distal angle of the discoidal triangle in the forewings (convergent to Neoaeshnida); the second (more distal) oblique vein between RP2 and IR2 is much more oblique and longer than the basal one (maybe rather a plesiomorphy, since also present in Progobiaeshnidae fam. nov.).

Historical considerations: HANDLIRSCH (1906) erected the fossil subfamily Cymatophlebiina within Gomphidae. COWLEY (1942) and PONOMARENKO (1985) also considered Cymatophlebiinae as Gomphidae. CARPENTER (1932) transferred this subfamily to Aeshnidae. NEEDHAM (1907) and COCKERELL (1924) already regarded the genus *Cymatophlebia* as an Aeshninae, while COCKERELL (1913) advocated the exclusion of this genus from the latter subfamily, although he apparently regarded it as related. However, most authors included them in the Petaluridae, e.g. TILLYARD & FRASER (1940), FRASER (1957), PRITYKINA (1968), SCHLÜTER

(1981), CARPENTER (1992), BRIDGES (1994) and JARZEMBOWSKI (1994). HENNIG (1969, 1981) and NEL & PAICHELER (1992) regarded their affinities as uncertain, but also considered that they could be related to Petaluridae. BECHLY (1995) and LOHMANN (1995, 1996a) attributed the genus to a separate family as sistergroup of Austropetaliidae. Recently BECHLY (1996, 1999a, b) and NEL *et al.* (1998) have demonstrated that this genus is certainly not related to Petaluridae but belongs to the aeshnid stemgroup. Furthermore, they suggested an elevation to family rank and a new subfamily for the genera *Valdaeshna* and *Hoyaeshna* that were previously regarded as Aeshnidae, while they included all species of *Cymatophlebia* in the subfamily Cymatophlebiinae.

Stratigraphy and palaeobiogeography: All known Cymatophlebiidae are from the Upper Jurassic and Lower Cretaceous. These dragonflies have been found in Germany (Upper Jurassic laminated limestones of Solnhofen and Nusplingen, and "Bankkalke" of the Swabian Alb), England (Lower Cretaceous Weald Clay), and Spain (Lower Cretaceous laminated limestones of Las Hoyas). Doubtful cymatophlebiids have been described from Mongolia and Kazakhstan. After MEYEN (1987: 319-321, fig. 90) these areas were in the "European-Sinian area", a palaeofloristic province of the Upper Jurassic - Lower Cretaceous with warm, rather dry climates characterized by alternations of dry and wet seasons. Cymatophlebiidae could have been an euro-asiatic endemic faunal element.

Subfamily Cymatophlebiinae HANDLIRSCH, 1906 sensu nov.

1906 Cymatophlebiina HANDLIRSCH, p. 591.
1932 Cymatophlebiinae; CARPENTER, p. 110.

Type genus: *Cymatophlebia* DEICHMÜLLER, 1886.

Included genera: Currently only including the type genus *Cymatophlebia*, thus, preliminarily a redundant taxon. All other genera that were previously considered as Cymatophlebiinae (= Cymatophlebiidae auct.) have to be excluded from this subfamily, including *Libellulium* WESTWOOD, 1854 which is a nomen dubium, thus, not a synonym of *Cymatophlebia*, but a possible Cymatophlebiidae - Valdaeshninae subfam. nov. (see below).

Wing venational autapomorphies: Undulation of RP2 more strongly developed (convergent to Eumorbaeschnidae fam. nov. and some Gomphaeschnidae); anal loop reduced, not distinctly posteriorly closed (but somewhat variable in *C. longialata*); Mspl usually better developed (thus, distinctly concave although often still zigzagged, and therefore apparently indistinct if the corrugation is disregarded), and strongly curved.

Other autapomorphies: Superior anal appendages (cerci) foliate (convergent to Mesuropetalidae, Polycanthagynini including *"Aeschna" petalura*, and Petalurinae). The unique ventro-lateral expansions (genital lobes) of the male abdominal tergum 3 are also present in Rudiaeschnidae fam. nov. (see below) and therefore do not seem to be an autapomorphy of Cymatophlebiinae.

New diagnosis: The diagnosis of the Cymatophlebiinae proposed by HANDLIRSCH (1906: 591) was based on the following characters: 1) several rows of cells between RP2 and IR2; 2) a well-defined Rspl; 3) the anal loop is weakly developed or absent; 4) several rows of cells in the area between MP and CuA (*sensu* HANDLIRSCH); 5) the compound eyes are distinctly separated; 6) the male abdomen is widened in segment four; 7) the male cerci are basally narrow and foliate. Characters "1" and "2" are rather homoplastic (e.g. a Rspl also occurs in Aeschnidiidae and Eurypalpida) and furthermore certainly symplesiomorphies on a level with Cymatophlebiinae. Character "3" is rather homoplastic, too, and also shows some variability in *Cymatophlebia longialata*. Character "5" is incorrect (see below). Character "6" is not known from all species. Character "7" is present by convergence also in Mesuropetalidae, Petalurinae and Polycanthagynini. Consequently, this diagnosis has to be regarded as insufficient.

CARPENTER (1932) characterized the Cymatophlebiinae by an aeshnid-like appearance («In general structure of the wing and especially in the undulation of R3 [RP2] *Cymatophlebia* is close to the Aeschninae [sic]; ...»), but he added that they differ from the extant Aeshnidae (auct.) by the alleged absence of the anal loop («...but the anal loop, characteristic of this extant subfamily, is entirely absent. For this reason, a separate subfamily for *Cymatophlebia* is justified.»).

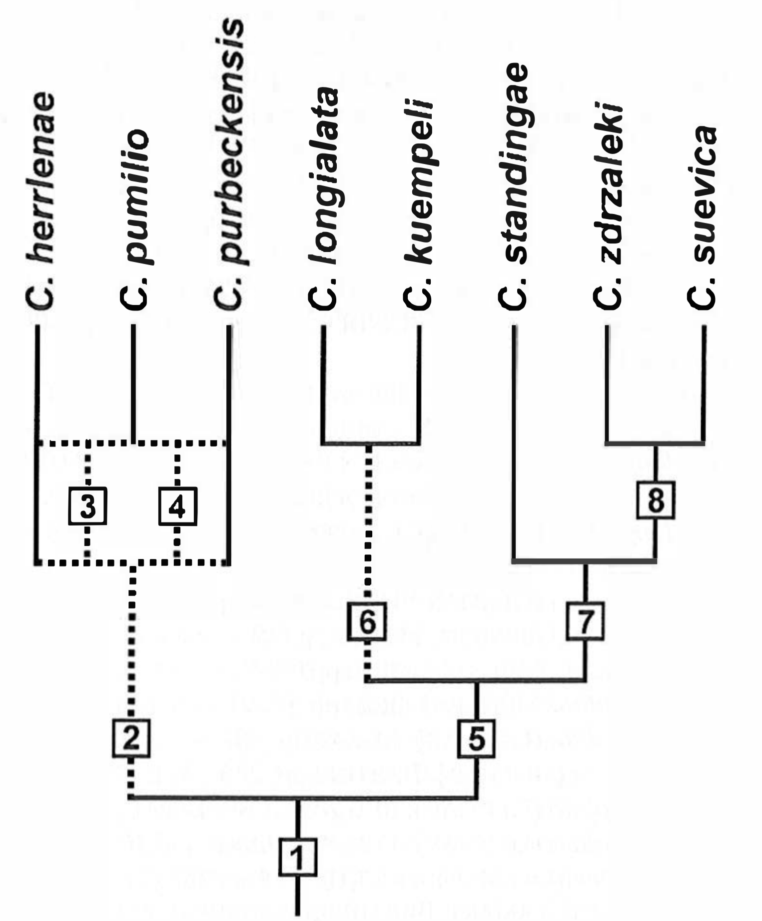
Our new diagnosis is based on the present study of numerous specimens, and includes the following wing venational characters: Dense wing venation with numerous cells; the two rows of secondary antenodal crossveins are not aligned; postnodal crossveins and postsubnodal crossveins not aligned; pterostigma elongated and braced; apparent furcation of AA into an anterior secondary branch PsA and a posterior main branch AAa; Rspl always well-defined and curved with several rows of cells between it and IR2; Mspl indistinct or distinct, but mostly present in at least one of the pairs of wings and always curved; MA, RP3/4, IR2 and RP2 strongly undulated; there are several rows of cells in the areas between MA and RP3/4, and between IR2 and RP2 along the posterior wing margin; MA and RP3/4 reach the posterior wing margin at right angles; RP2 and IR2 reach the posterior wing margin at a very oblique angle; there are two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl in both pairs of wings; two oblique veins 'O'; discoidal triangles are divided into several cells; anal and cubito-anal areas very wide in the hindwings; CuAa with numerous posterior branches; the anal loop is reduced or absent; The body structures are not known from all species, but probably include the following characters, based on the evidence from some species: Compound eyes medio-dorsally approximated or even broadly confluent; terga of all abdominal segments with a medio-dorsal longitudinal carina; abdomen at least in the male sex (but also in one female specimen) with latero-ventral expansions (genital lobes) at least on the abdominal tergum 3; male and female cerci are well-developed and foliate; the ovipositor is not hypertrophied.

Genus *Cymatophlebia* DEICHMÜLLER, 1886 stat. restor.

Type species: *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839), by original designation.

Other species: *C. zdrzaleki* (JARZEMBOWSKI, 1994) comb. nov., *C. standingae* (JARZEMBOWSKI, 1994) comb. nov., *C. suevica* sp. nov., *C. herrlenae* sp. nov., *C. kuempeli* sp. nov., *C. pumilio* sp. nov., and probably also including *C. purbeckensis* sp. nov. (Text-Fig. 37). *"Cymatophlebia" jurassica* CARPENTER, 1932 had to be removed from this genus, since it is conspecific with *"Morbaeschna muensteri"* (*sensu* NEEDHAM 1907) that is here redescribed in a new genus as *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov., since *Morbaeschna* NEEDHAM, 1907 has to be regarded as a junior subjective synonym of *Mesuropetala* HANDLIRSCH, 1906 (see above), due to a misidentification of the type species. *"Cymatophlebia" mongolica* COCKERELL, 1924 has to be regarded as an Anisoptera of uncertain position (see below).

Autapomorphies and diagnosis: Same as for subfamily.



Text-Fig. 37. Phylogenetic tree of the *Cymatophlebia* DEICHMÜLLER, 1886 stat. rest. species.

Synapomorphies: (1) see text; (2) monophyly unclear, no synapomorphies known yet, but large phenetic similarity; (3) no accessory cubito-antenodal crossveins between CuP-crossing and PsA, postdiscoidal area hardly widened distally; (4) only few secondary antenodal crossveins between Ax1 and Ax2, subdiscoidal triangle two-celled; (5) more than three rows of cells in the basal postdiscoidal area of the hindwing; (6) monophyly unclear, no synapomorphies known yet, but large phenetic similarity and same age and locality; (7) wings longer than 70 mm, very dense venation with numerous cells; (8) well-defined and curved Mspl, convex pseudo-veins in the postdiscoidal area (also between Mspl and MA).

Cymatophlebia longialata (MÜNSTER in GERMAR, 1839)

Text-Figs 38-61, 73, Plate 13: Figs 3-4, Plates 14-25

*v 1839 *Libellula longialata* MÜNST., MÜNSTER in GERMAR, pp. 216-217, pl. 23, fig. 15.
v. 1842 *Aeschna longialata* GERMAR, pp. 79-81, pl. 9, fig. 1, pl. 13, fig. 6 a, b.
1846 *Aeschna longialata* (GERMAR); GEINITZ, pp. 186-187, pl. 8, fig. 5.
1848 *Gynacantha longialata* (GERMAR); HAGEN, pp. 9-10.
1848 *Anax*? *longialatus* MUENSTER; HAGEN, p. 11 (description of the specimens figured in GERMAR 1842).
1850 *Gynacantha longialata* (GERMAR); HAGEN in SELYS, p. 361.
1856 *Aeschna longialata* (GERMAR); GIEBEL, p. 279.
1856 *Aeschna Bavarica* GIEBEL, p. 280.
1857 *Aeschna multicellulosa* GIEBEL, pp. 374-380, pl. 6, fig. 2 (description).
1860 *Aeschna multicellulosa* GIEBEL, p. 131.
1856 *Aeschna Bavarica* GIEBEL, p. 280.
1862 *Aeschna longialata* (GERMAR); GIEBEL, p. 639.
1862 *Aeschna Bavarica* GIEBEL, p. 639.
1862 *Petalia*? *longialata* GERM.; HAGEN, pp. 127-133, pl. 13, figs 1-2 (description, and synonymy of *A. multicellulosa* and *A. Bavarica* with *Petalia longialata*).
1869 *Petalia longialiata* (GERMAR); WEYENBERGH, p. 251.
1885 *Petalia longialata* MÜNST.; SCUDDER in ZITTEL, p. 775.
1886 *Cymatophlebia longialata* (GERMAR); DEICHMÜLLER, pp. 48-52, pl. 3, figs 5-8 (description).
1890 *Cymatophlebia longialata* (GERMAR); KIRBY, p. 171.
1897 *Cymatophlebia longialata* HAGEN; MEUNIER, pp. 8-11, pl. 3, fig. 3, pl. 6, fig. 7.
v. 1898 *Cymatophlebia longiolata* DEICHMÜLLER; MEUNIER, pp. 121-122, pl. 11, fig. 23. (incorrect subsequent spelling).
1900 *Petalia longialata* MÜNST.; SCUDDER in ZITTEL, p. 685, fig. 1451.
1906 *Cymatophlebia longialata* GERMAR; HANDLIRSCH, pp. 591-592, pl. 47, figs 13-15 (description and synonymy; one new figure).
v? 1907 *Cymatophlebia longiolata* MUENST.; NEEDHAM, p. 141, fig. 1 (new figure).
v. 1910 *Cymatophlebia longialata* MÜNST.; SCUDDER in ZITTEL, p. 585, fig. 1403.
v. 1915 *Cymatophlebia longialata* MÜNST.; SCUDDER in ZITTEL, pp. 662-663, fig. 1446.
v. 1924 *Cymatophlebia longialata* MÜNST.; SCUDDER in ZITTEL, pp. 698-699, fig. 1454.
1932 *Cymatophlebia longialata* (GERMAR); CARPENTER, pp. 110-111, fig. 5 (redescription, new figure).
1939 *Cymatophlebia longialata* (GERMAR); HANDLIRSCH, p. 165.
1957 *Libellulium longialatum* (GERMAR); FRASER, p. 95.
1968 *Cymatophlebia longialata* MÜNST.; LEICH, pp. 92-93.
1972 *Cymatophlebia longialata* MÜNST.; LEICH, pp. 92-93.
v. 1976 *Cymatophlebia longialata* (GERMAR); MALZ, fig. 49.
v. 1978 *Libellulium longialatum* [GERMAR]; BARTHEL, p. 236, pl. 15, fig. 1.
v. 1979 *Cymatophlebia longialata* (GERMAR); MALZ & SCHRÖDER, fig. 2.
1985 *Cymatophlebia longialata* (GERMAR); PONOMARENKO, p. 136.
n 1985 *Libellulium longialatum* (GERMAR); FRICKHINGER, p. 262 (fig.).
v. 1990 *Libellulium longilatum* (GERMAR); BARTHEL, SWINBURNE & CONWAY MORRIS, p. 144, fig. 7.38 (incorrect subsequent spelling).
1992 *Libellulium longialatum* (GERMAR); CARPENTER, p. 83.

1992 *Libellulium longialatum* (GERMAR); NEL & PAICHELER, pp. 316-317.
1994 *Libellulium longiolata* (MÜNSTER); BRIDGES, pp. VII.137, VIII.38 (incorrect subsequent spelling).
1994 *Libellulium longialatum* (GERMAR); JARZEMBOWSKI, p. 71.
n 1994 *Libellulium longialatum* (GERMAR); FRICKHINGER, p. 135, fig. 252.
v. 1996 *Libellulium longialatum* (GERMAR); SCHWEIGERT *et al.*, pp. 4-5, figs 2-3 (description of the first specimen from the Upper Kimmeridgian laminated limestones of Nusplingen in Baden-Württemberg, Germany).
v. 1996 *Cymatophlebia longialata*; TISCHLINGER, p. 292, 296-297, figs 2, 4, 14, 17-18.
1998 *Cymatophlebia*; RÖPER & ROTHGAENGER, p. 54, 2 figs without number on p. 55.
1998 *Cymatophlebia longialata* (GERMAR); NEL *et al.*, pp. 5, 55.
1999 *Cymatophlebia longialata* (GERMAR); FRICKHINGER, p. 50, figs 82-83.

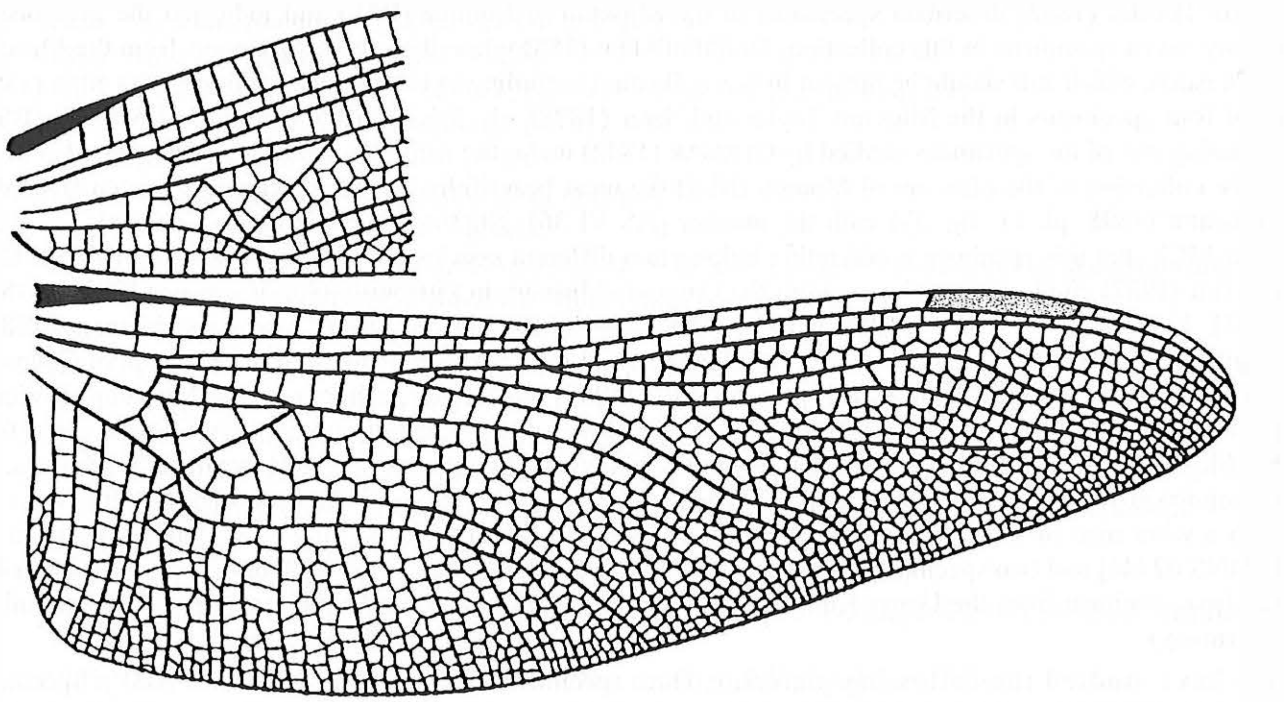
Holotype: Specimen no. [AS VII 792], BSP, Munich.

Paratype (?): Specimen no. [AS VII 796], BSP, Munich.

Additional material: GERMAR (1839) indicated that the type is located in coll. MÜNSTER and that there is another specimen in coll. MURCHISON. HAGEN (1848) studied some specimens of coll. MÜNSTER. GIEBEL (1857) figured and described a forewing in coll. BISCHOF (coll. University of Heidelberg; DEICHMÜLLER 1886). HAGEN (1862) described specimens in the Museum of Munich (BSP) and indicated the presence of twenty-seven specimens in this collection. DEICHMÜLLER (1886) described some specimens from the Museum of Dresden, which still should be present in this collection according to LÖSER (pers. comm.). MEUNIER (1897) cited four specimens in the Museum Teyler and, later (1898), six fossils in the Museum of Munich (BSP), including one of the specimens studied by GERMAR (1842) under the name *Aeschna longialata*. We also found in the collection of the Museum of Munich (BSP) the most beautifully preserved female specimen figured in MEUNIER (1898: pl. 11, fig. 23) with the number [AS VI 36]. NEEDHAM (1907) figured a female specimen from MCZ, but this specimen could rather belong to a different species of *Cymatophlebia* (see below). CARPENTER (1932) cited nine specimens from the Carnegie Museum in Pittsburgh (specimens nos [3823], [3824-5103], [3825-3826], [5104], [5105], [5106], [5107], and [5108] in coll. BAYET, and specimen no. [3827] acquired from the Museum of Munich) (Text-Fig. 38), and fourteen specimens from the Museum of Comparative Zoology in Cambridge (MZC). PONOMARENKO (1985) cited five specimens in the Museum of Vienna (NHV). MALZ (1976) and MALZ & SCHRÖDER (1979: fig. 2 and 24) have figured a very fine specimen from the Maxberg-Museum (also studied by us) and a specimen from the Senckenberg Museum in Frankfurt a. M. (specimen no. VI 200). LEICH (1972: pp. 92-93) mentions and figures a specimen from Eichstätt in coll. LEICH with a wing span of 125 mm. TISCHLINGER (1996: 292, 296-297, figs. 2, 4, 14, 17-18) figured specimen no. [SMNS 62744] and two specimens from coll. TISCHLINGER. SCHWEIGERT *et al.* (1996: 4-5, figs 2-3) described the first specimen from the Upper Kimmeridgian laminated limestones of Nusplingen in Baden-Württemberg (Germany).

We have studied the following material: Three specimens in the Museum of Munich (BSP): Specimens nos [AS VII 792] (holotype), [AS VII 796] (paratype ?), and [AS VI 36]. Twenty specimens in the Jura-Museum in Eichstätt (JME): Specimens nos [SOS 1713], [SOS 1714 Wh.-1960.], [SOS 1715], [SOS 1718], [52.-1959.-30,5.-Bl.], [1957-14-ak-Bl.], [SOS 3610], [SOS 3975], [SOS 2041], [SOS 2042], [SOS 3608], [SOS 1703], [SOS 1696], [SOS 1679], [SOS 1675], [SOS 1721], [1982 / 73], [SOS 3614 / So-1957-92.], [W.h.O. 1935 a, b], and one further specimen without number. Thirteen specimens from the Solnhofen Limestone in the museum in Stuttgart (SMNS): Specimens nos [SMNS GB 3, Slg. W. LUDWIG 1992], [SMNS GB 5, Slg. W. LUDWIG 1992], [SMNS 64347 (old number GB 9), Slg. W. LUDWIG 1992; male with genital lobes; see Plate 23: Fig. 5], [SMNS GB 10, Slg. W. LUDWIG 1992; male with genital lobes], [SMNS GB 16, Slg. W. LUDWIG 1992], [SMNS GB 20, Slg. W. LUDWIG 1992], [SMNS GB 23], [SMNS GB 33, Slg. Dr BERTSCH 1921], [SMNS GB 40 a, b, v. WUNDERLICH 1938], [SMNS GB 42, v. SÜSSKIND 1940], [SMNS 64348 (old number GB 55), Slg. W. LUDWIG 1992, fine preserved head with large confluent eyes; see Plate 23: Fig. 4], [SMNS GB 60, Slg. W. LUDWIG 1992], [SMNS 62744, Slg. W. LUDWIG 1992]). In the same museum there is one specimen no. [SMNS 62662] from the somewhat older laminated limestones of Nusplingen. Thirteen specimens in the Museum für Naturkunde in Berlin (MB): Specimens nos [MB. J. 1699], [MB. J. 1700], [MB. J. 1725], [MB. J. 1726], [MB. J. 1727], [MB. J. 1728], [MB. J. 1729], [MB. J. 1731], [MB. J. 1738], [MB. J. 1740], [MB. J. 1749 = MB. 1969.54.90], [MB. J. 1751 = MB. 1973.17.14], and [MB. J. 1754]. Two specimens in the Senckenberg Museum in Frankfurt (SMF): A complete and well-preserved female specimen labelled [VI

200, *Cymatophlebia longialata*, Wintershof (Solenhofener AV), J. Schmitt, v. 23.6.1969] and a specimen labelled [*Cymatophlebia longialata*, det. Malz, J. Schmitt, v. 1966]. Two specimens, a complete male specimen and an isolated forewing (both unlabelled), in the Museum Bergér in Eichstätt. One specimen (without number) in public exhibition of coll. LEICH (Bochum). Fourteen specimens in the Museum of Comparative Zoology in Cambridge (represented by 18 pieces, since four specimens include part and counterpart): Specimens nos [MCZ 5898], [MCZ 6248], [MCZ 6249], [MCZ 6250-6251], [MCZ 6252], [MCZ 6254-6255], [MCZ 6256-6257], [MCZ 6258], and six further specimens without number. Of the just mentioned specimens, specimen no. [MCZ 6248] has the best preserved wing venation, while specimens nos [MCZ 5898], [MCZ 6249], and [MCZ 6254-6255] show a well-preserved head with broadly confluent eyes (Plate 23: Fig. 2, Plate 25: Fig. 3). A single female specimen (MNHN-LP-R. 10409) in the museum in Paris (MNHN, Lab. Paleont.). We also studied four specimens in coll. TISCHLINGER (Stammham) (specimens nos [82/262], [84 / 259], [89/76], and one specimen without number), four specimens without number in coll. KÜMPEL (Wuppertal), including one complete male specimen with genital lobes on the third abdominal segment (Plate 22: Fig. 1), one specimen (no. 16D) with a posteriorly closed and four- or five-celled anal loop in the right hindwing, and one relatively small specimen with a wing span of only 125 mm (forewing length 59.5 mm; hindwing length 58.8 mm; width of hindwing at nodus 16.0 mm). Finally there was a complete and well-preserved specimen in the commercial coll. SCHÄFER (Kiel) (Plate 22: Fig. 2).



Text-Fig. 38. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). CMNH 3823-3824 - female, right pair of wings (drawing after CARPENTER 1932: fig. 5; without scale).

Although all above mentioned specimens could clearly be identified as members of the genus *Cymatophlebia*, many of them are not well enough preserved to be certain if they indeed belong to the type species *Cymatophlebia longialata*, or maybe to the closely related new species *C. kuempeli* sp. nov. which is the only *Cymatophlebia* sp. of similar size from the Solnhofen Limestone.

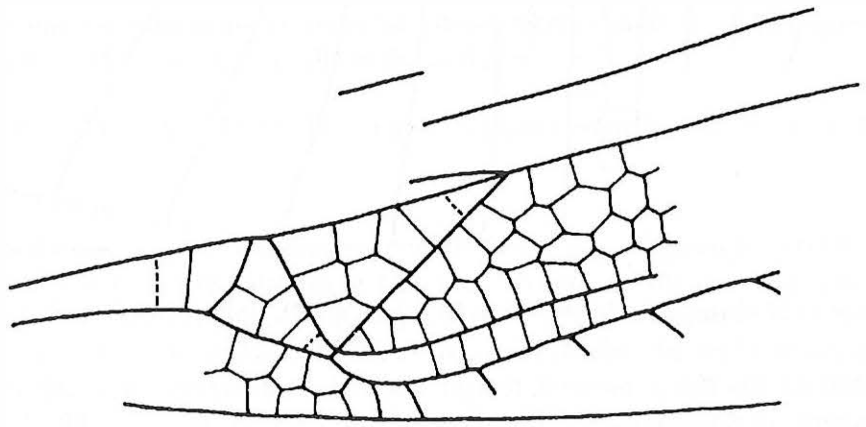
The figure of the holotype in GERMAR (1839) is incomplete and rather unsuitable to characterize this species. The later studies are based on material from the same outcrops, but not on the fossils described by GERMAR (1839, 1842). The holotype of GERMAR is a very poorly preserved fossil, but it shows the main venation characters of *Cymatophlebia longialata*. Although only its main veins are visible, it shares at least one character with other specimens that have been attributed to *C. longialata*, unlike the closely related species *Cymatophlebia kuempeli* sp. nov., viz the number of cells in the fore- and hindwing discoidal triangle. Thus, it is possible to distinguish the two species, even if it would be impossible to redescribe *Cymatophlebia longialata* on the basis of its holotype. The present redescription is mainly based on several other well-preserved specimens, e.g. specimen no. [SOS 1713] in the Jura-Museum in Eichstätt.

Locus typicus: Eichstätt, Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Diagnosis: *C. longialata* is distinguished from other *Cymatophlebia* spp. as follows: Length of wings 58-70 mm instead of 42-50 mm in *Cymatophlebia pumilio* sp. nov.; *C. longialata* has usually only two rows of cells between RP2 and IR2 instead of three rows in *C. zdrzaleki* comb. nov., *C. standingae* comb. nov. and *C. kuempeli* sp. nov. It differs from *C. zdrzaleki* comb. nov. and *C. standingae* comb. nov. by the presence of max. four rows of cells between Rspl and IR2 and in the basal part of the postdiscoidal area. Furthermore, *C. longialata* differs from *C. kuempeli* sp. nov. as follows: It has a less indented hind margin (vein AP + AA'') of the male hindwing anal triangle; the male hindwing has four rows of cells (instead of only two) between the anal margin and the first posterior branch of AA, below the anal triangle; it has only seven cells instead of nine in forewing discoidal triangle, and only five cells in the hindwing discoidal triangle, instead of seven; there is often a third enforced and aligned antenodal crossvein in the forewing between Ax1 and Ax2; its pseudo-anal veins PsA are distincly angled, especially in the hindwings (as in Rudiaeschnidae fam. nov.); a curved Mspl is usually present in all wings, but zigzagged; only three or four rows of cells between pseudo-IR1 and RP2, instead of five or six rows; its lateral lobes on male abdominal segment III are expanded only along the basal two-thirds instead of being expanded along the whole segment; its male abdominal segment IV seems to lack the latero-ventral lobes (maybe an artifact of preservation, since the single visible pair of lobes could be situated on different segments in different specimens of *C. longialata*); the shape of its male cerci is different from that of *C. kuempeli* sp. nov., although both are foliate; the epiproct is not apically bifid and distinctly longer (nearly as long as the cerci) and more narrow than in *C. kuempeli* sp. nov.

Description: The holotype of GERMAR is too poorly preserved for the purpose of a detailed redescription. It seems to be a female specimen, since its hindwings do not show an anal angle. Several much better preserved specimens are described below.



Text-Fig. 39. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Holotype BSP AS VII 792 - forewing discoidal triangle.

Material from Bayerische Staatssammlung für Paläontologie und historische Geologie (BSP), Munich:

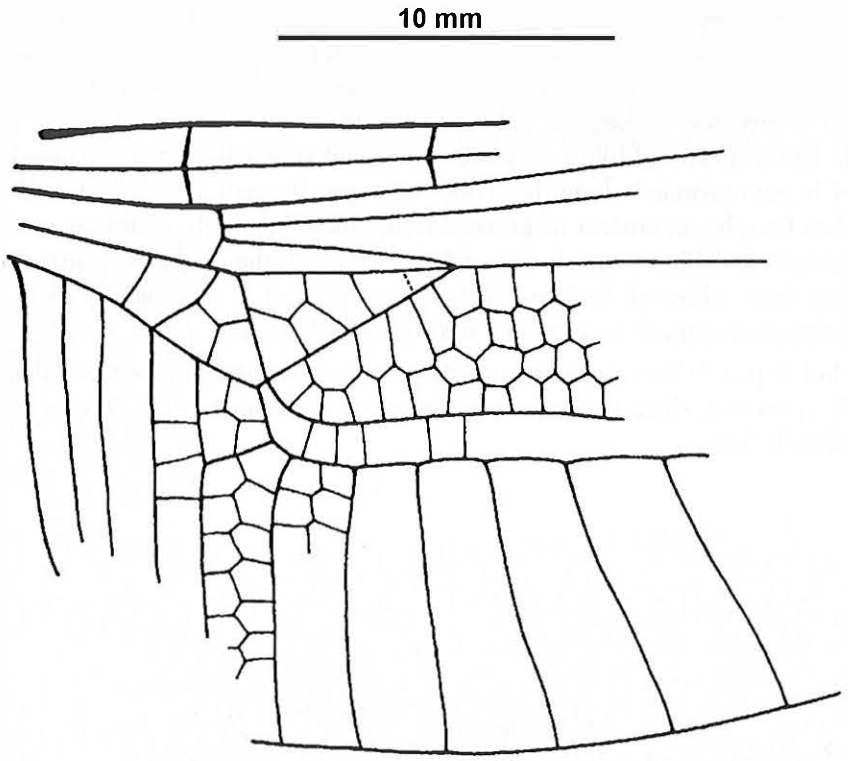
- Specimen no. BSP AS VII 792; holotype; female; labelled «*Petalia* (*Cymatophlebia*) *longialata* GERM. ♀ (= *Aeschna bavarica* GIEB.), Orig. z. GERMAR 1839, Tf. 23, Fig. 15, Lithograph. Schiefer, Eichstätt»

Text-Figs 39-40

A complete adult female with body and all four wings present, but very poorly preserved. The body length from head up to the tip of the abdomen is 92 mm. The venation is rather faint, but it is clearly a *Cymatophlebia*.

Forewing: Length 67 mm. The discoidal triangle is longitudinally elongated and divided into seven or eight cells; length of anterior side 6.8 mm; of basal side 3.6 mm; of distal side MAb 6.6 mm; the distal side MAb of the discoidal triangle is straight. Subdiscoidal triangle divided into four cells. PsA angled. Four rows of cells in the postdiscoidal area immediately distal of the discoidal triangle.

Hindwing: Length 64 mm; distance from base to nodus 27.5 mm. The discoidal triangle is longitudinally elongated and divided into five or six cells; length of anterior side 6.4 mm; of basal side 3.3 mm; of distal side MAb 6.5 mm; the distal side of the discoidal triangle MAb is straight. Subdiscoidal triangle divided into three cells. PsA angled. Four rows of cells in the postdiscoidal area, immediately distal of the discoidal triangle. Ax1 is 0.9 mm basal of the arculus. Ax2 is 7.3 mm distal of Ax1. The arculus is angled and the bases of RP and MA are distinctly separated at arculus. CuP-crossing is 1.8 mm basal of the arculus. Anal loop small, divided into four cells, and posteriorly rather well-closed. The anal margin of the hindwing is rounded, thus, it is a female specimen.



Text-Fig. 40. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Holotype BSP AS VII 792 - hindwing base.

♦ Specimen no. BSP AS VII 796; paratype ?; female; labelled «*Petalia* (*Cymatophlebia*) *longialata* GERM. ♀ (= *Aeschna bavarica* GIEB.), Original z. MÜNSTER 1842, Beitr. V, S. 79, Taf. 9, Fig. 1, Lithograph. Schiefer, Eichstätt»

Plate 13: Figs 3-4, Plate 14: Fig. 1

A nearly completely preserved adult female with three wings, body, head and three legs. Only the right hindwing is missing. The wing venation is excellently preserved, since it is traced by iron-oxide dendrites. The length of the body from head to the tip of the abdomen is 94 mm. A dorso-longitudinal abdominal carina is clearly visible. The wing venation is very similar to specimen no. [SOS 1713].

Forewing: Length 64.7 mm; width at nodus 13.5 mm; distance from base to nodus 33.3 mm; distance from nodus to pterostigma 18.6 mm. There are about twenty-four antenodal crossveins, including the two aligned and enforced primary antenodal crossveins Ax1 and Ax2. Eleven postnodal crossveins between nodus and pterostigma. Pterostigma braced and 6.1 mm long. RP1 and RP2 run parallel up to the pterostigma with two rows of cells in-between except for the four or five most basal cells. Vein pseudo-IR1 originates on RP1 beneath distal side of pterostigma. Two or three rows of cells between pseudo-IR1 and RP1 and four rows between pseudo-IR1 and RP2. Two rows of cells between the undulated parts of RP2 and IR2 in the right forewing, but up to three rows in the left forewing. Three or four rows of cells between IR2 and the curved Rspl. Two oblique veins 'O' between RP2 and IR2, two cells and six cells distal of the subnodus, the distal one is more strongly oblique than the basal one. Two oblique secondary veins between IR2 and RP3/4, immediately basal of the origin of Rspl. RP3/4 and MA are distincly undulated, basally closely parallel, but divergent near the wing margin. A distinct Mspl present, but zigzagged, and curved with up to three rows of cells between Mspl and MA. Four rows of cells in the basal part of the postdiscoidal area (width near discoidal triangle 3.8 mm; width at wing margin 5.8 mm). The discoidal triangle is divided into seven cells; length of anterior side 6.7 mm; of basal side 3.7 mm; of its straight distal side MAb 6.4 mm. Hypertriangle divided by two crossveins (length 8.2 mm). Subdiscoidal triangle divided into four cells. Submedian space divided by a single cubito-anal crossvein between CuP-crossing and PsA. Eight or nine posterior branches of CuA. Two rows of cells in the anal area.

Hindwing: Length 61.5 mm; width at nodus 18.0 mm; distance from base to nodus 26.3 mm; distance from nodus to pterostigma 21.8 mm. Ax2 is slightly distal of the level of the discoidal triangle. About fifteen postnodal crossveins between nodus and pterostigma. Pterostigma braced and 6.3 mm long. RP1 and RP2 run parallel up to the pterostigma with two rows of cells in-between except for the six most basal cells. Pseudo-IR1 is originating on RP1 beneath distal side of pterostigma. Two or three rows of cells between pseudo-IR1 and RP1 and four rows between pseudo-IR1 and RP2. Up to three rows of cells between the undulated parts of RP2 and IR2. Four rows of cells between IR2 and the curved Rspl. Three (!) oblique veins 'O' between RP2 and IR2, one cell, four cells and seven cells distal of the subnodus. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP3/4 and MA are distincly undulated, basally closely parallel, but divergent near the wing margin. A distinct Mspl is present, but zigzagged, and curved with up to three rows of cells between Mspl and MA. Four rows of cells in the basal part of the postdiscoidal area (width near discoidal triangle 4.3 mm; width at wing margin 7.1 mm). The discoidal triangle is divided into five cells; length of anterior side 6.2 mm; of basal side 3.3 mm; of the straight distal side MAb 6.3 mm. Hypertriangle divided by two crossveins (length 7.1 mm). Subdiscoidal triangles divided into three cells. No cubito-anal crossvein in the submedian space between CuP-crossing and PsA. Nine posterior branches of CuA (including CuAb ?). Up to ten or eleven rows of cells in the cubito-anal area between CuAa and the posterior wing margin. PsA is angled. The anal loop is small, divided into five cells, and posteriorly rather well-closed (by a composite crossvein between CuAb and AA1b, or by a fusion of CuAb with AA1b ?). Four posterior branches of AA between CuA and the anal margin. The anal margin is rounded without an anal angle or anal triangle, thus, it is a female specimen. About twelve or thirteen rows of cells in the anal area.

♦ Specimen no. BSP AS VI 36; female; labelled «*Cymatophlebia longialata* in MEUNIER, 1898, pl. 11, fig. 23»

Plate 14: Fig. 2, Plate 15: Figs 2-3

A nearly complete and exceptionally well-preserved adult female (also figured by ZITTEL 1910, 1915, 1924, BARTHEL 1978, and BARTHEL & SWINBURNE & CONWAY MORRIS 1990) with the wing venation strongly traced by iron-oxide dendrites. The venation of this specimen agrees with that of [SOS 1713]. Complete length of body, 103 mm, from the head up to the tip of the abdomen, excluding the anal appendages that are not preserved. The abdomen is distally somewhat expanded (length 77.0 mm; basal width 3.0 mm; max. distal width 5.8 mm); width of thorax 8.0 mm. There is only one leg visible. Length of head 13.0 mm; width 12.0 mm.

Forewing: Length 67.3 mm: width at nodus 13.8 mm; distance from base to nodus 34.0 mm; distance from nodus to pterostigma 19.9 mm. Twenty-four antenodal crossveins, including the two aligned and enforced primary antenodal crossveins Ax1 and Ax2. There seems to be one aligned and enforced secondary antenodal crossvein between Ax1 and Ax2, on a level with the basal side of the discoidal triangle. About thirteen postnodal crossveins between nodus and pterostigma. Pterostigma braced, 6.0 mm long, and covering fiive cells in the right forewing and four cells in the left forewing. RP1 and RP2 run parallel up to the pterostigma with two rows of cells in-between except for the five most basal cells. Vein pseudo-IR1 originates on RP1 beneath distal side of pterostigma (left forewing) or slightly distal of it (right forewing). Three rows of cells between pseudo-IR1 and RP1 and four rows between pseudo-IR1 and RP2. Two rows of cells between the undulated parts of RP2 and IR2. Three or four rows of cells between IR2 and the curved Rspl. Two oblique veins 'O' between RP2 and IR2, two cells and six cells distal of the subnodus, the distal one is more strongly oblique than the basal one. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP3/4 and MA are distincly undulated, basally closely parallel, but divergent near the wing margin. An indistinct Mspl is present, but zigzagged, and curved with up to three rows of cells between Mspl and MA. Four rows of cells in the basal part of the postdiscoidal area (width near discoidal triangle 4.0 mm; width at wing margin 9.0 mm). The discoidal triangle is divided into seven cells; length of anterior side 6.7 mm; of basal side 3.8 mm; of the straight distal side MAb 6.4 mm. Hypertriangle divided by two crossveins (length 8.2 mm).

Subdiscoidal triangles divided into four cells. Submedian space divided by a single cubito-anal crossvein between CuP-crossing and PsA. Eight or nine posterior branches of CuA. Two rows of cells in the anal area.

Hindwing: Length 65.0 mm; width at nodus 18.7 mm; distance from base to nodus 27.3 mm; distance from nodus to pterostigma 23.0 mm. Sixteen antenodal crossveins, including the two aligned and enforced primary antenodal crossveins Ax1 and Ax2. There are about fifteen postnodal crossveins between nodus and pterostigma. Pterostigma braced, 6.7 mm long and covering five cells (left hindwing). RP1 and RP2 run parallel up to the pterostigma with two rows of cells in-between except for the five most basal cells. The area of pseudo-IR1 is not preserved. There are two rows of cells between the undulated parts of RP2 and IR2. Four rows of cells between IR2 and the curved Rspl. Two oblique veins 'O' between RP2 and IR2, two cells and six cells distal of the subnodus in the left hindwing, but four and six cells distal of the subnodus in the right hindwing, the distal one is more strongly oblique than the basal one. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl in the left hindwing, but three such veins in the right hindwing. RP3/4 and MA are distincly undulated, basally closely parallel, but divergent near the wing margin. An indistinct Mspl is present, but zigzagged, and curved with up to three rows of cells between Mspl and MA. Four rows of cells in the basal part of the postdiscoidal area (width near discoidal triangle 4.8 mm; width at wing margin 8.4 mm). The discoidal triangle is divided into four cells; length of anterior side 6.1 mm; of basal side 3.3 mm; of the straight distal side MAb 6.4 mm. Hypertriangle divided by two crossveins (length 7.7 mm). Subdiscoidal triangles divided into three cells. No cubito-anal crossvein in the submedian space between CuP-crossing and PsA. Seven posterior branches of CuAa (plus CuAb). Up to ten rows of cells in the cubito-anal area between CuAa and the posterior wing margin. Anal loop posteriorly well-closed and four-celled in both hindwings. Four posterior branches of AA between CuAb and the anal margin. Anal margin rounded without an anal angle or anal triangle, thus, it is a female specimen. About twelve rows of cells in the anal area.

Material from Jura-Museum (JME), Eichstätt:

♦ Specimen no. SOS 1675, JME; male; labelled «*Anax buchi* HAGEN, Eichstaett»

A complete, but poorly preserved male. The visible wing venation agrees with that of specimen no. [SOS 1713]. Abdomen 72.1 mm long and 3.8 mm wide. The two cerci are foliate and 4.2 mm long. The inferior appendage (epiproct) is triangular.

Forewing: Length 64.5 mm (?); width 13.0 mm; distance from base to nodus 33.5 mm.

Hindwing: Length 67.5 mm; width 18.5 mm; distance from base to nodus 31.0 mm.

♦ Specimen no. SOS 1679, JME; male ?

A complete, but poorly preserved dragonfly. The wing venation is very poorly preserved, including the region of the anal angle, so that it is not certain that it is indeed a male specimen. Distance between the forewing base and the head 14.5 mm; width of thorax 11.0 mm. The head is relatively well-preserved. The eyes seem to be approximated, but still separated, apparently 2.3 mm apart (?). Length of head 8.5 mm; width 13.4 mm. Diameter of the compound eye 5.5 mm; diameter of an ocellus 0.7 mm. The three ocelli seem to be nearly aligned in front of the compound eyes.

Forewing: Length 67.0 mm; width 16.5 mm.

Hindwing: Length 65.0 mm; width 19.5 mm.

♦ Specimen no. SOS 1696, JME

Plate 16: Fig. 1

An incomplete left pair of wings. The apices and wing bases are missing, but the venation is beautifully preserved and traced by iron-oxide dendrites. The venation agrees with specimen no. [SOS 1713].

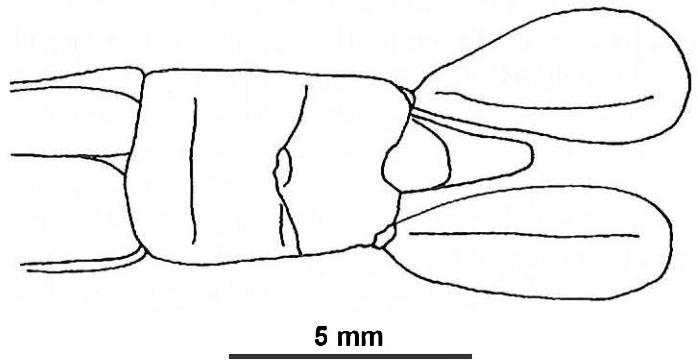
♦ Specimen no. SOS 1703, JME; male; 1953 BL, counterpart

Text-Fig. 41, Plate 15: Fig. 3

A complete, but poorly preserved male. Distance between forewing base and head 14.0 mm; width of thorax 8.0 mm; length of abdomen 73.0 mm; minimal width 2.0 mm; maximal width 4.0 mm. The genital lobes are faintly visible. The superior appendages or cerci (= cercoïdes *sensu* AGUESSE 1968) are foliate, 6.0 mm long and 2.8 mm wide, rounded with a submedian longitudinal dorsal crest. The inferior appendage or epiproct (= lame supra-anale *sensu* AGUESSE 1968) is triangular and apically not bifid. Expanded lobes are visible on abdominal segment III.

Forewing: Length 61.0 mm; width 12.0 mm; distance from base to nodus 31.0 mm.

Hindwing: Length 58.0 mm; width 18.0 mm; distance from base to nodus 30.5 mm.

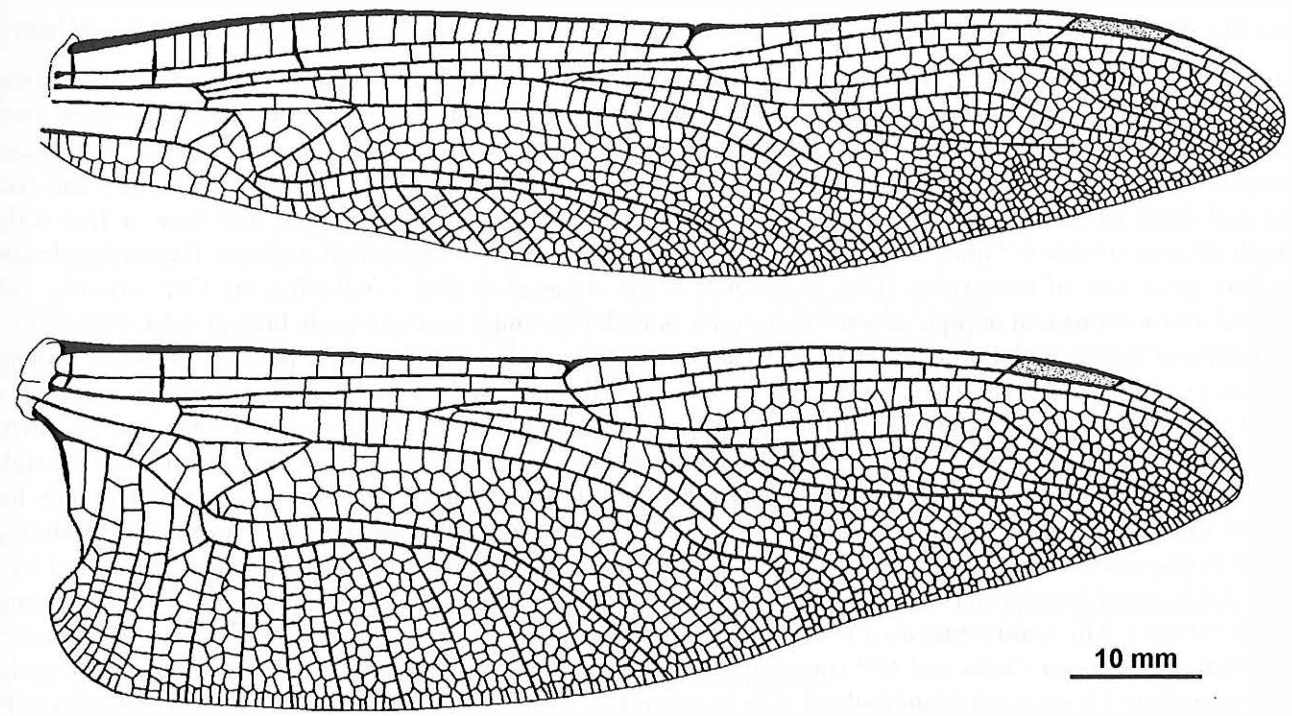


Text-Fig. 41. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1703 - male, anal appendages.

♦ Specimen no. SOS 1713, JME; male; Wintershof quarry; labelled «*Cymatophlebia longialata*»

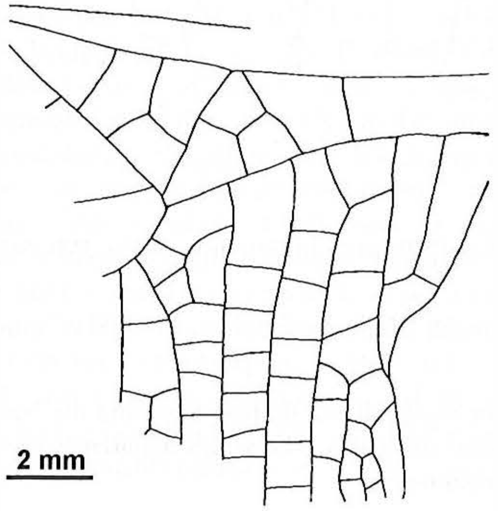
Text-Figs 42-45, Plate 16: Fig. 2

A well-preserved male with all four wings, head, thorax, legs, and the basal third of the abdomen. The wing venation is partly traced by iron-oxide dendrites. The wings apparently have been hyaline. The presence of an anal angle shows that it is a male specimen.



Text-Fig. 42. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1713 - male, right pair of wings.

Forewing: Length 63.5 mm; width 12.0 mm; distance from base to nodus 31.3 mm. Pterostigma 5.5 mm long and max. 1.0 mm wide, covering three (left wing) or four cells (right wing), and braced. Eleven postnodal crossveins between nodus and pterostigma. Twenty-six antenodal crossveins (six secondary antenodal crossveins between the two primary antenodal crossveins Ax1 and Ax2). Three antenodal crossveins are aligned and stronger than the others: Ax1 is 2.2 mm basal of the arculus, one secondary antenodal crossvein 1.5 mm distal of the arculus (definitely not bracket-like enforced like the two primary antenodal crossveins), and Ax2 is 5.0 mm distal of the arculus and two cells basal of the distal angle of the discoidal triangle. The discoidal triangle is divided into seven cells; length of anterior side 6.0 mm; of basal side 4.0 mm; of its straight distal side MAb 6.4 mm. One crossvein in the hypertriangle. Median space free of crossveins. Submedian space traversed by three crossveins, including the CuP-crossing. AA divided into a secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into five cells. Four rows of cells in the postdiscoidal area distal of the discoidal triangle. A weakly developed Mspl (better defined than in the hindwing), but a strongly defined Rspl with up to four rows of cells in the area between Rspl and IR2 (width of this area 2.5 mm). The courses of veins RP3/4, MA, IR2, and RP2 are identical to those of hindwing, thus, distinctly undulated, and pseudo-IR1 is identical as well. Somewhat unusual is the strongly widened area between the undulated parts of RP2 and IR2 with three rows of cells in all four wings.

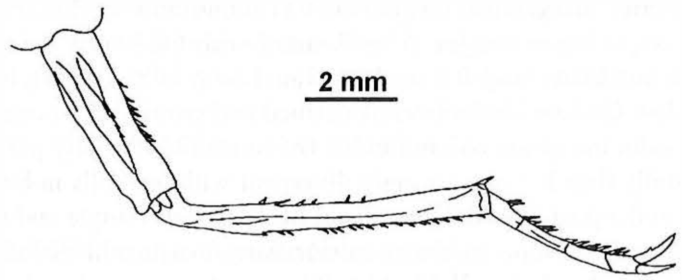


Text-Fig. 43. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1713 - male, left hindwing base.

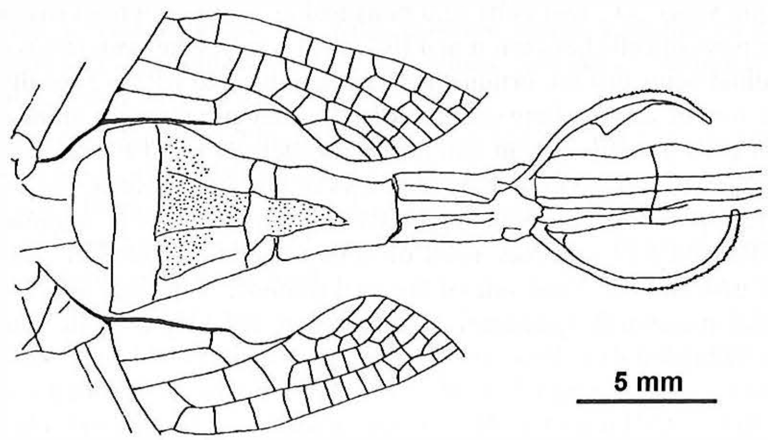
Hindwing: Length 62.5 mm; width 18.0 mm; distance from base to nodus 27.0 mm. Pterostigma 6.0 mm long and max. 1.0 mm wide, covering three (on right wing) or four cells (on left wing) and braced. Thirteen postnodal crossveins between nodus and pterostigma. Thirteen or fourteen antenodal crossveins. The two primary antenodal crossveins are stronger than the secondary antenodal crossveins. Ax1 is basal of the arculus and Ax2 one cell distal of distal angle of discoidal triangle. The discoidal triangle is divided into four or five cells; length of anterior side 6.2 mm; of basal side 3.5 mm; of its straight distal side MAb 6.7 mm. Hypertriangle and median space free of crossveins. Two crossveins in the submedian space, including the CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into three cells. AA has two parallel posterior convex branches reaching the posterior wing margin in anal area, distal of the branch AA2b that closes the anal triangle. The anal area is 11.5 mm wide with twelve rows of cells between AA and the posterior margin. Vein AAa reaches CuA near the posterior angle of the discoidal triangle. Length of free part of CuA 0.4 mm. In the right hindwing, CuAb is directed towards the branch of AA (anal loop incompletely closed posteriorly) and only has a weak posterior branch that is perpendicularly directed towards the wing margin, while in the left hindwing, CuAb is perpendicularly directed towards the posterior margin of the wing and thus not closing the anal loop with AA1b (anal loop posteriorly open). The "anal loop" is divided into three or four cells (length 3.0 mm; width 2.0 mm). The cubito-anal area is wide. CuAa is divided into seven or eight parallel posterior branches. The distance between CuAa and MP smoothly increases distally with eight rows of cells along the posterior wing margin and a secondary longitudinal vein between CuAa and MP. Four rows of cells in the postdiscoidal area distal of the discoidal triangle and this area is progressively widened with finally thirteen cells along the posterior wing margin. No well-defined Mspl, but two or three secondary longitudinal veins that originate on a level with nodus, reach the posterior wing margin in the postdiscoidal area. MA and RP3/4 parallel and strongly undulated below the base of Rspl. MA and RP3/4 are basally converging, but become distinctly divergent near the posterior margin with six cells along the margin. Four bridge-crossveins Bqs. RP2 is aligned with subnodus. Two oblique veins 'O', 1.1 mm and 6.5 mm distal of the subnodus. A strong Rspl with four rows of cells between it and IR2. Rspl distally reaches IR2 (as in *C. kuempeli* sp. nov. and *C. pumilio* sp. nov.). The area between the undulated parts of IR2 and RP2 is distinctly widened (with three rows of cells), then more narrow (two rows of cells), and finally widened again near the posterior wing margin (four rows of cells). IR2 and RP2, as well as MA and RP3/4, are strongly undulated. A very distinct pseudo-IR1 originates distal of the pterostigma. A strong anal angle (male). Anal triangle (male) divided into three cells (length 6.1 mm; width

2.5 mm). Four rows of cells between the anal angle (male) and the posterior convex branch AA1c, below PsA. Three posterior branches of AA between CuAb and the anal triangle, the most basal one originating on the distal side of the anal triangle, while the two basal ones originate on the main branch of AA (similar in both hindwings).

Body: Thorax 14.0 mm long and 7.5 mm wide. The male secondary genital apparatus of second abdominal segment is not visible, since the specimen is preserved in dorsal aspect. Length of first abdominal segment 5.0 mm; of the second 10.0 mm; of the third 10.8 mm. Along the third abdominal segment (at least in the male sex), there are two expanded rounded lobes along two-thirds of the length of this segment, thus, 8.5 mm long and 0.4 mm wide. The exterior side of each lobe bears a row of small spines along its distal third. These lobes seem to be more or less mobile relative to segment III because they do not lie in symmetrical positions (Text-Fig. 45). All the abdominal segments clearly have a medio-dorsal longitudinal carina on the terga. Prothoracic legs: Femora 4.2 mm long and 1.3 mm wide; tibiae 7.5 mm long and 0.6 mm wide; tarsi 4.5 mm long and 0.5 mm wide (Text-Fig. 44). The other legs are poorly preserved.



Text-Fig. 44. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1713 - male, foreleg.



Text-Fig. 45. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1713 - male, genital lobes.

♦ Specimen no. SOS 1714 Wh.-1960, JME; female; Wintershof quarry

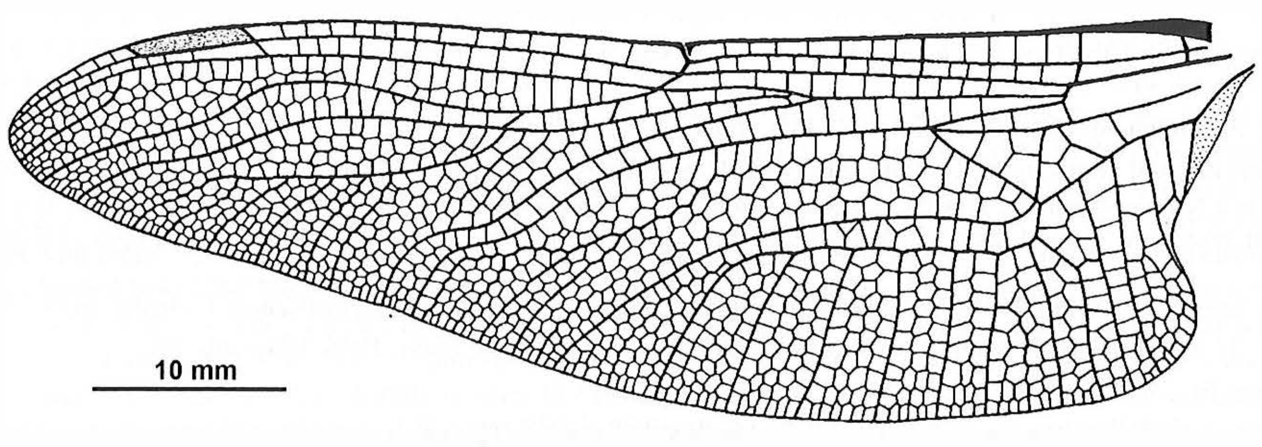
This isolated hindwing agrees with [SOS 1713], except for the absence of an anal angle and anal triangle, thus, it is a female specimen. It is 63 mm long. The anal loop is apparently not posteriorly closed. Mspl is present, but zigzagged. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl.

♦ Specimen no. SOS 1715, JME; male; labelled «Sammlung der Phil.-theol. Hochschule Eichstätt, SOS 1715, 37-8, Malm ζ2b, *Cymatophlebia longialata* (GERMAR 1839), leg. Mayr, 1936, Blumenberg»

Text-Fig. 46, Plate 17: Fig. 1

A remarkably well-preserved isolated right hindwing of a male. The veins are traced by iron-oxide dendrites, but there is no visible coloration of the wing membrane, thus, the wing seems to have been hyaline.

Hindwing: Length 63.9 mm; width 19.0 mm; distance from base to nodus 28.9 mm. Pterostigma 5.7 mm long and max. 0.9 mm wide, covering three cells (the first one very long, maybe subdivided by a very faintly preserved crossvein) and distinctly braced. The basal brace Ax0 is visible near the wing base. Fourteen postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Thirteen antenodal crossveins in the first row, and fifteen in the second row. The two primary antenodal crossveins are stronger than the secondary antenodal crossveins. Ax1 is more or less aligned with the arculus (aberration ?), Ax2 is situated on a level with distal angle of the discoidal triangle, 8.0 mm distal of Ax1. Between the two primary antenodal crossveins there are four secondary antenodal crossveins in the first row, and five in the second row, not precisely aligned. Eleven antesubnodal crossveins between subnodus and arculus without a distinct gap near the subnodus, but with a distinct gap near the arculus. Distance between wing base and arculus 9.2 mm. The arculus is angled and the bases of RP and MA are distinctly separated at arculus. The hypertriangle is traversed by two crossveins. The discoidal triangle is longitudinally elongated and divided into four cells; length of anterior side 5.9 mm; of basal side 3.6 mm; of distal side MAb 6.7 mm; its distal side MAb is straight. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.0 mm basal of the arculus. AA divided into a secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into three cells. PsA angled. AA with three parallel posterior branches that reach the posterior margin. The anal area is 11.6 mm wide (below PsA) with about eleven rows of cells between AA and the posterior margin. AAa is fused with CuA near the posterior angle of discoidal triangle. Length of free part of CuA, only 0.2 mm. The anal loop is posteriorly indistinctly closed and six-celled. CuAb is distinctly bent. CuAa with seven well-defined and parallel posterior branches. Cubito-anal area broad, max. 8.8 mm wide with nine or ten rows of cells. CuAa and MP basally parallel with only a single row of cells in-between, but distally they become strongly divergent with ten cells in-between at the posterior wing margin. Four rows of cells in the postdiscoidal area distal of discoidal triangle and this area is widened distally with seventeen cells between these veins at the posterior wing margin. Mspl rather distinct, but zigzagged, basally curved, but distally very closely parallel to MA. Three or four secondary longitudinal veins, originating on Mspl. MA and RP3/4 are strongly undulated below the base of Rspl. MA and RP3/4 are mostly closely parallel, but they clearly diverge near the posterior wing margin with three rows of cells along the wing margin. Four crossveins basal of the first oblique vein, including three bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', two cells (2.0 mm) and six cells (6.9 mm) distal of the subnodus. A strong Rspl with max. four rows of cells between it and IR2. Rspl reaches the posterior wing margin, as do five convex secondary longitudinal veins that are originating on Rspl. IR2 and RP2 are basally closely parallel and straight with only a single row of cells in-between, but distally they are strongly undulated and more widely separated with two rows of cells in-between, but still rather parallel. RP1 and RP2 are basally closely parallel and even converge near the pterostigma with one or two rows of cells in-between, but below the pterostigmal brace they begin to diverge. A pseudo-IR1 originating on RP1 slightly distal of pterostigma. Two or three rows of cells between pseudo-IR1 and RP1 and four rows of cells between pseudo-IR1 and RP2. Two posterior branches of AA between CuAb and the distal side of the anal triangle. A distinct anal angle and anal triangle, divided into three cells, thus, it is a male specimen. A membranule reaching from the wing base to the middle of the basal side of the anal triangle.



Text-Fig. 46. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1715 - male, left hindwing.

♦ Specimen no. SOS 1718, JME

Four outspread wings in connection with the pterothorax. The venation is poorly preserved, but agrees with specimen no. [SOS 1713]. The forewings are 67.5 mm long, and the hindwings are 65.0 mm long.

♦ Specimen no. SOS 1721, JME; female

A female with body and three wings. The right forewing and the distal parts of both hindwings are missing. The venation is not well-preserved, but the main veins and the corrugation are visible and agree with specimen no. [SOS 1713]. The forewing is 67.5 mm long, and the total body length is 96 mm.

♦ Specimen no. SOS 2041, JME; male; Bl 1963

Plate 17: Fig. 4

A fragment of a male hindwing with the apical third missing. The wing veins are traced by iron-oxide dendrites, but still rather poorly preserved, especially in the costal region. Length from base to nodus 25.4 mm; width at nodus 17.0 mm. Discoidal triangle four-celled; length of anterior side 5.7 mm; of basal side 3.1 mm; of its straight distal side MAb 6.2 mm. Four rows of cells in basal part of postdiscoidal area. There seems to be no distinct Mspl. CuAa with nine parallel posterior branches. Anal loop indistinctly closed and five-celled. A distinct anal angle, thus, it is a male specimen. Four rows of cells between the anal margin and the first branch of AA below the anal triangle. A distinct three-celled anal triangle. Two posterior branches of AA between the anal triangle and CuAb.

♦ Specimen no. SOS 2042, JME; female; Eichstätt, Schwertschlager quarry; labelled «*Cymatophlebia longialata*»

Plate 18: Fig. 1

A nearly complete adult female. The head and legs are missing, and the wing venation is not very well visible, although traced by mangan-oxide dendrites (the apex of the right forewing by iron-oxide dendrites), because of numerous dendrites and several damages. The wing venation agrees with that of [SOS 1713], except for the absence of an anal angle and anal triangle, thus, it is a female specimen. Abdomen 63.5 mm long and 2.5 mm wide; thorax 12.0 mm long and 6.5 mm wide.

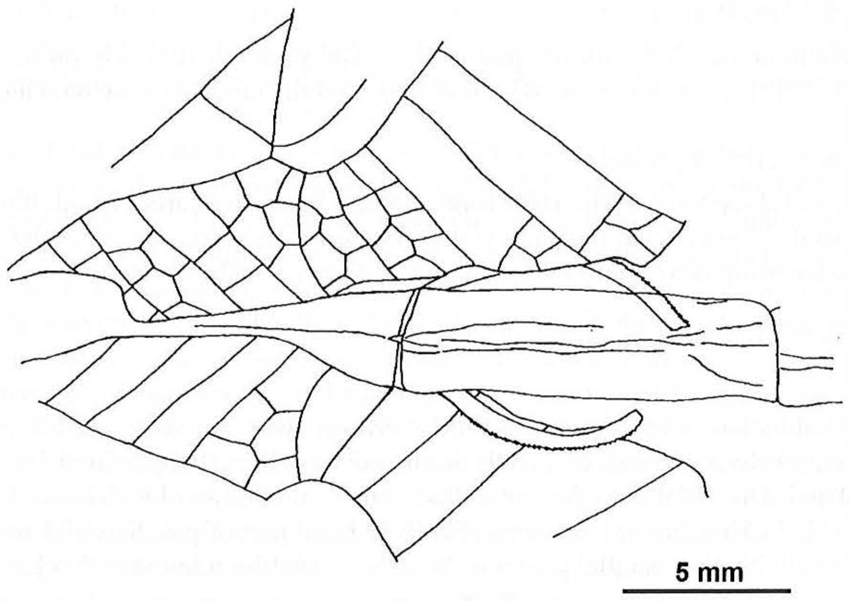
Forewing: Length 68.5 mm; width 12.7 mm; distance from base to nodus 35.3 mm. Pterostigma 5.6 mm long and max. 1.0 mm wide, and braced. There seems to be no third enforced antenodal in the forewing (the enforced antenodal on a level with the middle of the discoidal triangle in the left forewing definitely is Ax2). Four rows of cells in the postdiscoidal area distal of the discoidal triangle. Two rows of cells between RP2 and IR2. Up to three rows of cells between IR2 and Rspl.

Hindwing: Length 66.5 mm; width 20.5 mm; distance from base to nodus 29.5 mm. Pterostigma 6.6 mm long, max. 1.0 mm wide, and braced. Discoidal triangle five-celled (left hindwing); length of anterior side 6.6 mm; of basal side 5.0 mm; of its straight distal side MAb 7.1 mm. Four rows of cells in the postdiscoidal area distal of the discoidal triangle. Two or three rows of cells between RP2 and IR2. Up to four rows of cells between IR2 and Rspl. Anal loop posteriorly open. Five posterior branches of AA between CuAb and the basal wing margin.

♦ Specimen no. SOS 3608, JME; male; labelled «*Isophlebia helle*»

Text-Fig. 47

A male with fore- and hindwings superimposed. The head and the distal part of the abdomen are missing. The wing venation agrees with that of [SOS 1713] and there seems to be a third enforced antenodal as well. This specimen has the same abdominal structures on segment III as [SOS 1713] with the same dimensions and ornamentation (small spines along the exterior margin). In this specimen one of these structures partly covers the anal area of the left hindwing, but is partly covered itself by the anal area of the right hindwing. Furthermore, it partly covers the right side of segment III, while, on the left side, it is removed from the segment III. The dorsal aspect is visible, so that these structures are hidden under the segment III. This evidence clearly confirms that these structures are not artifacts, and that they have been rather flexible.

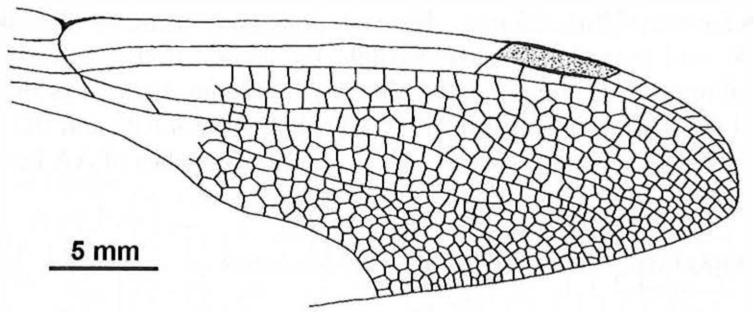


Text-Fig. 47. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 3608 - male, genital lobes.

♦ Specimen no. SOS 3610, JME; Horstbruch 1934, b. Mörnsheim quarry

Text-Fig. 48

Two poorly preserved forewings preserved in connection with the thorax. Length 65.0 mm; width 14.0 mm; distance from base to nodus 35.0 mm. Pterostigma 5.4 mm long and max. 1.0 mm wide, and braced. Twenty-four antenodal and eleven or twelve postnodal crossveins between nodus and pterostigma. The primary antenodal crossveins are difficult to distinguish from secondary antenodal crossveins. Main veins and areas agree with those of specimen no. [SOS 1713]. MA and RP3/4 are undulated with six rows of cells along the posterior margin. Length of anterior side of the discoidal triangle 7.0 mm; of basal side 3.5 mm; of the straight distal side MAb 6.4 mm. Discoidal triangle divided into seven cells. Subdiscoidal triangle divided into four cells. Base of pseudo-IR1 beneath the distal side of the pterostigma. Four rows of cells in the postdiscoidal area distal of the discoidal triangle. Two or three rows of cells between the undulated parts of RP2 and IR2. Up to three rows of cells between IR2 and Rspl. Three rows of cells in the anal area.



Text-Fig. 48. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 3610 - forewing, distal half.

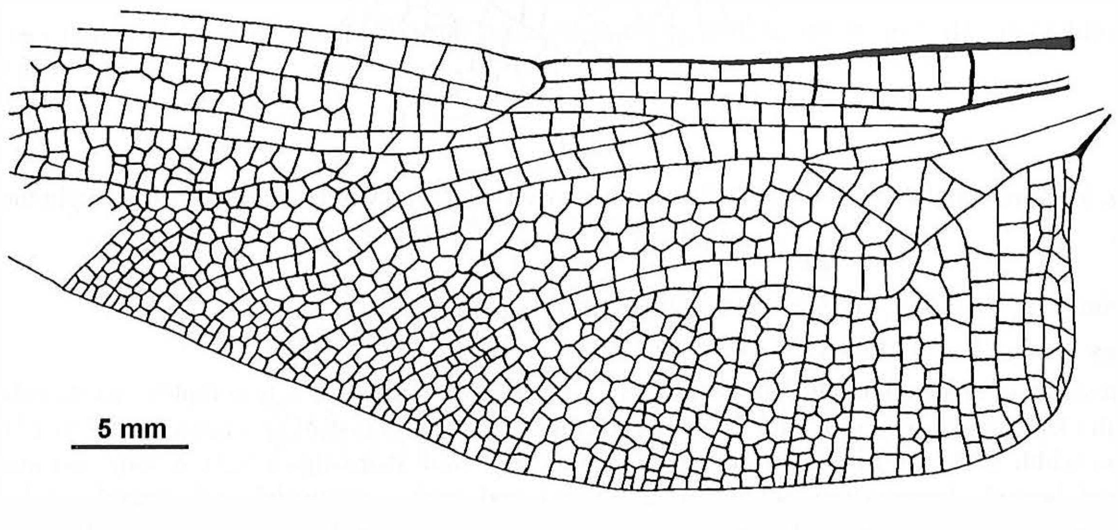
♦ Specimen no. SOS 3614 / So-1957-92., JME; female

Text-Fig. 49, Plate 18: Fig. 2, Plate 19: Figs 1-2

Adult female with all four wings outspread and in connection with the pterothorax. The wing venation and especially the corrugation are well-preserved, and agree with specimen no. [SOS 1713], except for the absence of anal angle and anal triangle, thus, it is a female specimen. The apices of all four wings are still covered by sediment.

Forewing: Length 60.0 mm; width at nodus 11.7 mm; distance from base to nodus 31.0 mm. Ax2 is distinctly basal of the level of distal angle of discoidal triangle. The discoidal triangle is divided into seven cells; length of anterior side 5.8 mm; of basal side 3.5 mm; of its straight distal side MAb 6.4 mm. Two rows of cells between the undulated parts of RP2 and IR2. Mspl distinct and curved. Subdiscoidal triangle four-celled. A single accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA.

Hindwing: Length 58.0 mm; width at nodus 16.8 mm; distance from base to nodus 23 mm. Ax2 is slightly basal of the level of distal angle of discoidal triangle. The discoidal triangle is divided into five cells in the right hindwing and into four cells in the left one; length of anterior side 5.3 mm; of basal side 3.5 mm; of its straight distal side MAb 6.0 mm. Two rows of cells between the undulated parts of RP2 and IR2. Mspl distinct and curved, but somewhat zigzagged especially in the right hindwing. Hypertriangle much broader than in the forewing. Subdiscoidal triangle three-celled. No cubito-anal crossvein in the submedian space between CuP-crossing and PsA. Anal loop posteriorly open. Eight posterior branches of CuAa (plus CuAb) and four posterior branches of AA. Anal margin rounded.



Text-Fig. 49. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME SOS 3614 / So-1957-92. - female, left hindwing.

♦ Specimen no. SOS 3975, JME; Schernfeld

A poorly preserved dragonfly. Only the distal halves of the right pairs of wings show the details of the wing venation that agrees with specimen no. [SOS 1713]. The preservation is quite curious, since the plate is orange, while the fossil (including the wing venation) is whitish yellow. The fossil is flattened without any trace of the original corrugation of the wings. The forewing is 63 mm long and the hindwing 60 mm long.

♦ Specimen no. W.h.O. 1935 a, b, JME; female; WintershofOst

The part and counterpart of the basal half of an isolated hindwing of a female. Width on a level with discoidal triangle (max. width) 19.0 mm. Four rows of cells in the basal part of the postdiscoidal area. Discoidal triangle five-celled. Subdiscoidal triangle three-celled. No cubito-anal crossvein in the submedian space between CuP-crossing and PsA. Anal loop posteriorly open. Four posterior branches of AA between CuAb and the anal margin. Anal margin rounded without an anal angle or anal triangle, thus, it is a female specimen.

♦ Specimen no. 1957-14-ak-Bl., JME; female; labelled «*Cymatophlebia longialata*»

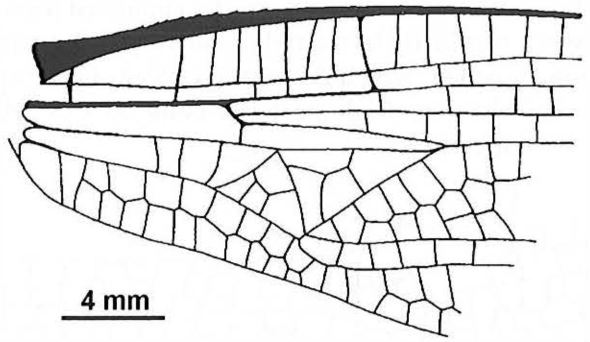
Plate 17: Fig. 2

A complete adult female, but only the distal half of the left forewing shows all details of the wing venation. The base of the hindwing is rounded and lacks any anal angle or anal triangle, thus, it is a female specimen. However, the abdomen also clearly shows expanded lobes on the third segment, and consequently represents the first evidence for the existence of these structures in the female sex of *Cymatophlebia* (maybe an aberrant specimen or an intersex / gynandromorph ?).

Left forewing 65 mm long. Four cells beneath the pterostigma that is distinctly braced. Vein pseudo-IR1 begins beneath the distal side of the pterostigma. Two rows of cells between RP1 and RP2 basal of the pterostigma. Two rows of cells between the undulated parts of RP2 and IR2. Three or four rows of cells between IR2 and Rspl. Four secondary veins originate on Rspl. One oblique secondary vein between IR2 and RP3/4 basal of

Rspl. Mspl is very distinct and curved with up to three or four rows of cells between it and MA. Three secondary veins originate on Mspl. Postdiscoidal area with four rows of cells distal of the discoidal triangle. Anal area with two rows of cells.

Left hindwing: Mspl seems to be less distinct than in the forewing. Four posterior branches of AA between CuAb and the basal margin that is rounded. Neither an anal angle, nor an anal triangle.

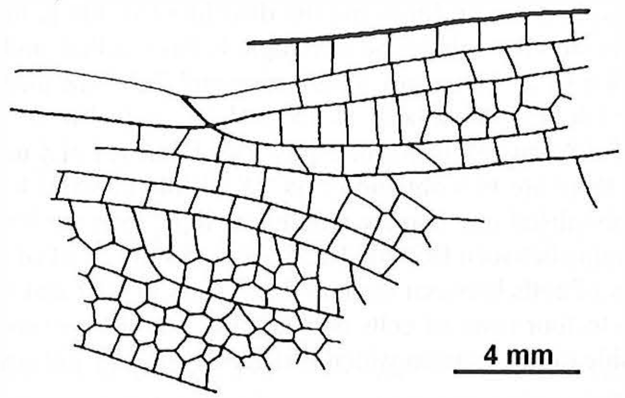


Text-Fig. 50. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME 52.-1959.-30,5.-Bl. - right forewing base.

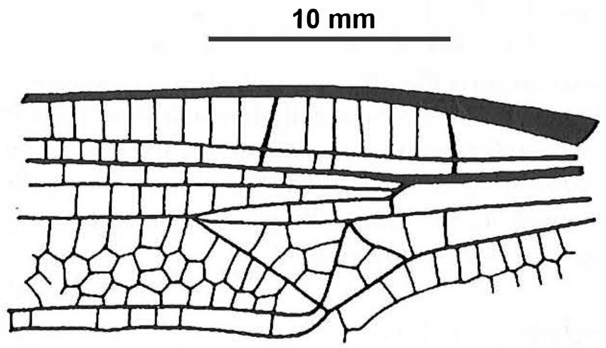
♦ Specimen no. 52.-1959.-30,5.-Bl., JME; Blumenberg quarry

Text-Figs 50-52, Plate 20: Figs 1-2

Two forewings in connection with the pterothorax. The right forewing is nearly complete, while only the basal half of the left one is preserved. The forewing venation agrees with that of specimen no. [SOS 1713]; length 65.6 mm; width 13.3 mm; distance from base to nodus 35.6 mm. Pterostigma 5.2 mm long and max. 1.0 mm wide, and braced. Twenty-four antenodal crossveins and twelve postnodal and postsubnodal crossveins between nodus and pterostigma. Three antenodal crossveins are aligned and stronger than the others: Ax1 is 2.0 mm basal of arculus, one secondary antenodal crossvein on a level with basal angle of discoidal triangle (but definitely not bracket-like enforced like the two primary antenodal crossveins), and Ax2 that is 8.0 mm distal of Ax1 and two cells basal of the distal angle of the discoidal triangle. Five secondary antenodal crossveins in the first row between the two primary antenodal crossveins Ax1 and Ax2 in the right forewing, but six in the left one. The basal brace vein Ax0 is visible near the wing base. A distinct gap of antesubnodal crossveins immediately distal of the arculus. The arculus is angled and the bases of MA and RP are separated at arculus. Two oblique veins 'O' (two and a half cells and five and a half cells distal of the subnodus in the right forewing, one cell distal of the subnodus in the left forewing, in which the second oblique vein is not preserved). There are two rows of cells between RP1 and RP2, except for the first six cells. Two rows of cells between the undulated parts of RP2 and IR2. Up to three rows of cells between IR2 and Rspl. Four rows of cells in the postdiscoidal area distal of the discoidal triangle, but there are six cells adjacent to MAb in the right forewing, but only five in the left one. Rspl is very strong. Mspl is rather well-defined, too (concave, strong, and not very zigzagged) and curved with up to three rows of cells between Mspl and MA. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. The discoidal triangle is longitudinally elongated and divided into six cells; length of anterior side 6.5 mm; of basal side 3.6 mm; of its straight distal side MAb 6.5 mm. Hypertriangle divided by two or three crossveins. Subdiscoidal triangle divided into four cells in the right forewing, and into three cells in the left one. Submedian space divided by a single accessory cubito-anal crossvein between CuP-crossing (2.0 mm basal of the arculus) and PsA. PsA is distinct, but slightly undulated. Two rows of cells in the anal area.



Text-Fig. 51. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME 52.-1959.-30,5.-Bl. - right forewing, median part.



Text-Fig. 52. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). JME 52.-1959.-30,5.-Bl. - left forewing base.

♦ Specimen no. 1982 / 73, JME; male ?; labelled «*Cymatophlebia* sp., K. GOTH, März 1982, Schernfeld»

Plate 20: Fig. 3

Rather poorly preserved thorax and abdomen, including three legs. The expanded genital lobes of the third abdominal segment are clearly visible, as well as the foliate cerci (length 6.5 mm). The abdomen is somewhat expanded distally (basal width 2.9 mm; max. distal width 4.5 mm).

♦ Specimen without number, JME

A very poorly preserved specimen which either represents a single specimen that has been imprinted, then postmortally lifted and displaced, and finally embedded again, 17 mm away from the first imprint, or it represents two parallelly embedded specimens (mating wheel ?). Only one pair of wings is preserved (length of forewing 69 mm; length of hindwing 65 mm).

Material from the Maxberg-Museum (near Solnhofen):

♦ Specimen without number, in exhibition of the Maxberg-Museum; female; labelled «*Cymatophlebia longialata* (GERMAR 1839)»

Plate 21: Figs 1-2

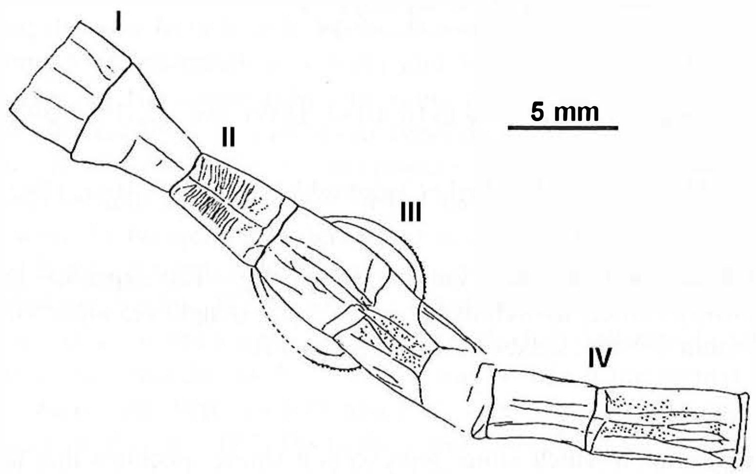
A perfectly preserved and complete female that was figured in MALZ (1976: fig. 49) and MALZ & SCHRÖDER (1979: fig. 2). Only the legs are missing and the basal part of the right forewing is destroyed. The distal part of the abdomen seems to be somewhat expanded. The wing venation is beautifully preserved and traced by iron-oxide dendrites in the right pair of wings. The venation generally agrees with that of specimen no. [SOS 1713], except for the absence of an anal angle and anal triangle, thus, it is a female specimen. The most significant difference is that the Mspl is rather well-defined in all four wings, especially in the left forewing; the basal part of Mspl is curved with up to three rows of cells between it and MA, while the distal part of Mspl is closely parallel to MA with only a single row of cells in-between. There are four rows of cells in the basal part of the postdiscoidal area in all wings. In the right hindwing the discoidal triangle is four-celled, the hypertriangle is traversed by a single crossvein, and the subdiscoidal triangle is three-celled, and there is no accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA. The anal loop seems to be posteriorly open in the right hindwing, while it is indistinctly closed and four-celled in the left hindwing. There are four parallel posterior branches of AA, and eight parallel posterior branches of CuAa (plus CuAb) in both hindwings. In the right hindwing there are two oblique veins 'O' visible between RP2 and IR2, two cells and six cells distal of the subnodus, the distal one is more strongly oblique than the basal one. In all wings there are two long oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. In the right hindwing there are three rows of cells between the undulated parts of RP2 and IR2 (apparently only two rows in the left hindwing), and up to four rows of cells between IR2 and the curved Rspl. Vein pseudo-IR1 originates on RP1 beneath distal side of pterostigma which is distinctly braced and covers three and a half cells.

Material from the Museum Bergér, Eichstätt:

♦ Specimen no. 3, unlabelled; male

Text-Fig. 53, Plate 23: Fig. 1

A nearly complete male; only the distal end of the abdomen and the legs are missing. The wing venation is rather well-preserved and very similar to that of [SOS 1713], but in the right hindwing there are three parallel posterior branches of AA between the anal triangle and CuAb (as in *C. kuempeli* sp. nov.). The discoidal triangle is four-celled and the subdiscoidal triangle three-celled in both hindwings. The hypertriangle is apparently only traversed by a single crossvein. CuAa has seven parallel posterior branches (plus CuAb) in both hindwings. The dorsal side of the abdomen is well-preserved. The median longitudinal dorsal carina is clearly visible on every segment. The expanded lateral lobes of segment III are clearly lying on the ventral side of the segment with small spines along their posterior margin.



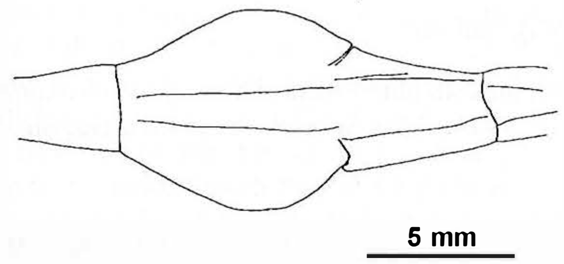
Text-Fig. 53. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Coll. BERGER no. 3 - male, genital lobes.

Material from coll. TISCHLINGER (Stammham):

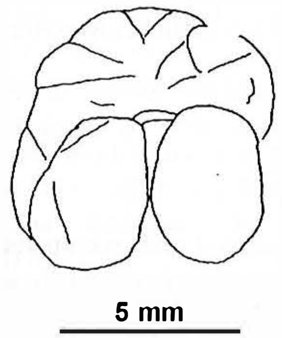
♦ Specimen no. 82/262; male

Text-Fig. 54, Plate 19: Fig. 3

A complete male (figured in TISCHLINGER 1996: fig. 4 and 17-18). The wing venation which is traced by iron-oxide dendrites, but somewhat distorted, is very similar to that of [SOS 1713]. The abdominal segment III of this fossil is well-preserved with its ventral side visible, and clearly shows several features that are less distinct on other specimens. The expanded lateral lobes of segment III are completely visible, and these structures are clearly located on the ventral side of the segment. They are 8.2 mm long and 2.2 mm wide, arriving at 63 % of the whole length of segment from the anterior end. They seem to have been rather flexible relative to the segment, also because a furrow is clearly visible at their base distally.



Text-Fig. 54. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Coll. TISCHLINGER 82/262 - male, genital lobes.



Text-Fig. 55. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Coll. TISCHLINGER 89/76 - female, head.

♦ Specimen no. 89/76; female; labelled «*Cymatophlebia* sp.»

Text-Fig. 55

A nearly complete, but poorly preserved adult female (figured as «? *Protolindenia* sp.» in TISCHLINGER 1996: fig. 15). Only one of the legs is faintly visible. The distal part of the left hindwing is detached and embedded some centimetres distal of body, while the concerning wing base is still connected with the thorax. Although the wing venation is very poorly preserved it shows the typical characters of *Cymatophlebia*, and since the base of the hindwing lacks an anal angle and anal triangle it must be female specimen. The head is well-preserved and the large compound eyes are broadly meeting dorsally (Text-Fig. 55, Plate 17: Fig. 3).

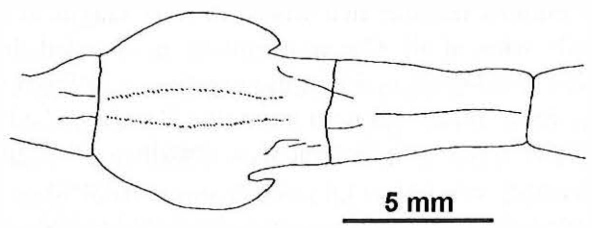
♦ Specimen no. 84/259; female ?

A rather distorted dragonfly (figured in TISCHLINGER 1996: fig. 14), of which only one hindwing is well-preserved. Its venation is traced by iron-oxide dendrites and is very similar to specimen no. [SOS 1713].

♦ Specimen without number; male

Text-Fig. 56, Plate 23: Fig. 3

A rather complete male. Only a part of the head and the distal part of the right forewing, as well as the legs are missing. The wing venation is poorly preserved, but is very similar to that of [SOS 1713]. The dorsal side of the abdomen is visible and all the segments clearly have a dorsal median longitudinal carina. The genital segment III is well-preserved including the expanded lateral lobes of segment III that clearly extend below the abdomen. The foliate cerci are faintly visible as well.



Text-Fig. 56. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). Coll. TISCHLINGER without number - male, genital lobes.

Material from the Staatliches Museum für Naturkunde (SMNS), Stuttgart:

- Specimen no. 62744, SMNS; male; labelled «Libelle: Noch unbestimmte Libelle, *Cymatophlebia longialata* ♂ (det. G. BECHLY, 7/96), Malm zeta, Untertithonium, *Hybonotum*-Zone, Wegscheid bei Eichstätt, Slg. W. LUDWIG 1992»

Plate 24: Fig. 1

A very fine preserved male with parts of the body and all four wings (figured in TISCHLINGER 1996: 290, fig. 2). The wing venation is traced by iron-oxide dendrites and very similar to specimen no. [SOS 1713]. The forewing discoidal triangle is divided into seven cells and that of the hindwing into four cells; the forewing subdiscoidal triangle is four-celled, that of the hindwings is three-celled. A single cubito-anal crossvein in the submedian space between CuP-crossing and PsA in the forewings, but none in the hindwings. Four rows of cells in the basal part of the postdiscoidal area in all wings. Mspl is indistinct in all wings. Anal loop posteriorly open. An anal angle and a three-celled anal triangle in the hindwings, thus, it is a male specimen. Two posterior branches of AA between CuAb and the anal triangle. A dorso-longitudinal carina is visible on the abdomen.

- Specimen no. SMNS 62662; labelled «SMNS Typ. Kat.-Nr. 62662, Arb.-Nr. 884/a, *Libellulium longialatum* (GERMAR), Oberkimmeridgium, Nusplinger Plattenkalke, Nusplinger Steinbruch, Orig. SCHWEIGERT *et al.* (1996), S. 4, Abb. 2, 3»

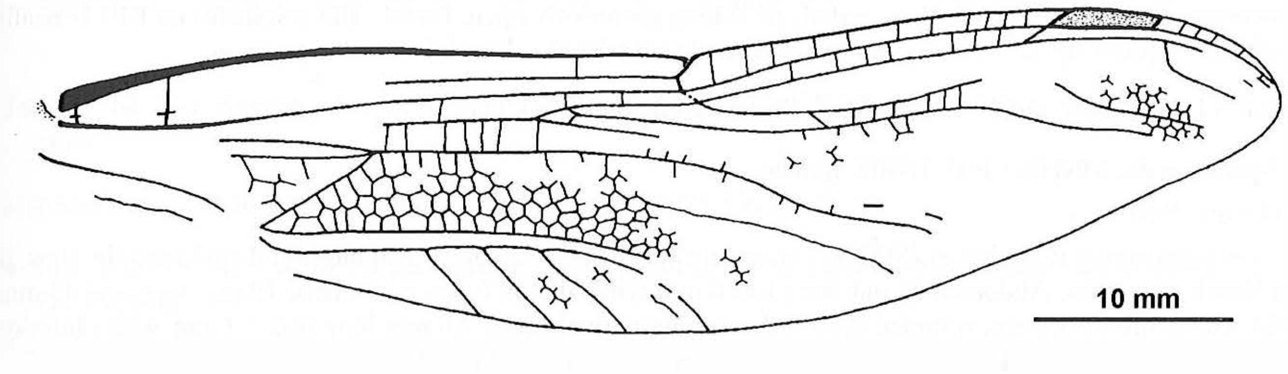
Text-Figs 57-58, Plate 24: Fig. 2

Two isolated forewings that are still connected with each other and are partly overlapping. They are preserved in organic substance, so that even the tiny spines on the main wing veins are clearly visible, but the wing is completely flattened so that its original pleating is not preserved. All visible characters of the wing venation agree with specimen no. [1703]. The fewer number of cells in the discoidal triangle (seven) and the fewer number of postnodal crossveins between nodus and pterostigma (about thirteen) indicates that this specimen belongs to *C. longialata* and not to *C. kuempeli* sp. nov.

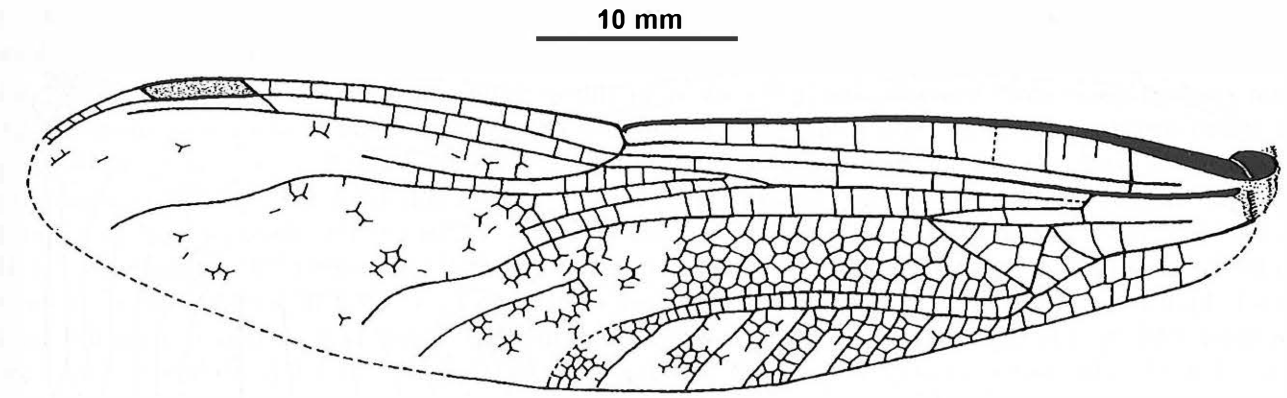
The present specimen and meanwhile four other dragonflies (three specimens of *Aeschnidium densum* and the holotype of *Urogomphus nusplingensis*) and a recently discovered bittacid wing (SMNS 64215) are the only insect remains known from the Upper Jurassic laminated limestones of Nusplingen (Baden-Württemberg, Germany). The bittacid wing and two specimens of *Aeschnidium* were found in the bituminous layer 'G', while the other three dragonflies were found in the kerogene rich layer 'D'. Being of Upper Kimmeridgian age, this *Cymatophlebia* specimen is some hundred-thousand (max. one million) years older than the lithographic limestones of Solnhofen (Bavaria, Germany) and thus represents the second oldest fossil record of Cymatophlebiidae (the oldest are *C. suevica* sp. nov. and *C. herrlenae* sp. nov. from the Lower Kimmeridgian of the Swabian Alb; see below). The single previously published figure of the wing venation of this specimen (SCHWEIGERT *et al.* 1996: fig. 3) shows several curious features that would be very untypical for Cymatophlebiidae, and even rather impossible for a dragonfly wing at all. Our re-examination revealed that the specimen has the normal wing venation of *Cymatophlebia longialata*, and that the mentioned differences are based on some inaccuracies in the concerning drawing. Since the description in SCHWEIGERT *et al.* (1996) is rather brief and preliminary anyway, we decided to provide a redescription and new drawing of this important fossil.

Forewing: Length 62.7 mm; width at nodus 13.6 mm; distance from base to nodus 32.3 mm. Pterostigma elongated (length 5.3 mm; width 1.0 mm), and distinctly braced. The visible postnodal crossveins (total number probably about thirteen) are not aligned with the corresponding postsubnodal crossveins. The antenodal crossveins are very incompletely preserved, but they were numerous, and both rows are not aligned. Ax1 is distinctly stronger than the others (Ax2 is not preserved) and 2.0 mm basal of the arculus. The arculus is 7.4 mm distal of the wing base. The arculus is angled and the bases of RP and MA are separated at arculus. The hypertriangle (length 8.1 mm; max. width 0.9 mm) is divided by at least one crossvein. The discoidal triangle is longitudinal elongated, divided into seven cells, and the distal side MAb is straight; length of anterior side 6.6 mm; of basal side 3.4 mm; of distal side MAb 6.6 mm. RP1 and RP2 are basally closely parallel with one or two rows of cells in-between. Pseudo-IR1 well-defined and originates on RP1 slightly distal of distal side of pterostigma. RP2 and IR2 are more or less parallel and distinctly undulated (the area in-between is widened in the undulated part). An oblique vein 'O' is only preserved in the right forewing, 5.7 mm distal of the subnodus (this distal position indicates that there probably was a second oblique vein closer to the subnodus). Several bridge-crossveins. Area of the Rspl poorly preserved. RP3/4 and MA parallel and undulated. Mspl

relatively well-defined with three rows of cells between it and MA. Four rows of cells in the postdiscoidal area distal of the discoidal triangle. MP and CuA closely parallel with only a single row of cells in-between, but distally they are divergent with four or five cells in-between at the posterior wing margin. CuAa has about ten parallel posterior branches. Cubito-anal area max. 3.9 mm wide. Anal area max. 2.4 mm wide (below PsA) with two rows of cells between AA and the posterior wing margin. AA is divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a distinct subdiscoidal triangle that is divided into four cells. Vein PsA is angled or undulated. Submedian space divided by one accessory cubito-anal crossvein between CuP-crossing (1.9 mm basal of the arculus) and PsA.



Text-Fig. 57. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). SMNS 62662 (Nusplingen). - right forewing.



Text-Fig. 58. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). SMNS 62662 (Nusplingen). - left forewing.

Material from the Museum für Naturkunde (MB), Berlin:
Since only one of the thirteen specimens of this species in this collection is so well-preserved that it is worth a closer description (MB. J. 1727, description see below), we only give a short enumeration of the other specimens with some data about sex and wing length: [MB. J. 1699] male; [MB. J. 1700] female; [MB. J. 1725] Slg. HÄBERLEIN, wing length 60 mm; [MB. J. 1726] REDENBACHER'sche Sammlung, forewing length 65 mm, hindwing length 60 mm; [MB. J. 1728] Slg. HÄBERLEIN 1880, male, hindwing length 63 mm; [MB. J. 1729 a, b] REDENBACHER'sche Sammlung, part and counterpart, forewing length 63 mm; [MB. J. 1731] REDENBACHER'sche Sammlung, a poorly preserved hindwing; [MB. J. 1738] labelled «Anisoptera inc. sed. (vermutl. *Cymatophlebia longialata*), Slg. HÄBERLEIN 1880, Solnhofen»; [MB. J. 1740] poorly preserved specimen of a *Cymatophlebia* sp.; [MB. J. 1749 = MB. 1969.54.90] labelled «Odonata indet., Oberer Jura Solnhofen, coll. RÜHLE V. LILIENSTERN»; [MB. J. 1751 = MB. 1973.17.14] labelled «Odonata indet., Ob. Jura, Solnhofener Plattenkalk, Slg. SCHLUTTER», body fragment with a pair of forewings of a *Cymatophlebia* sp., forewing length 60-61 mm; [MB. J. 1754 a, b] labelled «Anisoptera inc. sed. (vermutl. *Cymatophlebia* sp.), Slg. KAUFMANN», part and counterpart of a poorly preserved dragonfly that probably belongs to *Cymatophlebia*.

- Specimen no. MB. J. 1727, MB

A well-preserved male that has a wing venation that completely agrees with the other described specimens of *Cymatophlebia longialata*, but with the following noteworthy characters:

Forewing: 63.0 mm long. Discoidal triangle divided into seven cells in the left forewing and into eight cells in the right forewing. Hypertriangle divided by two crossveins in the left forewing and by one crossvein in the right forewing. Subdiscoidal triangle divided into three cells in the left forewing and into four cells in the right forewing. Submedian space divided by an accessory cubito-anal crossvein between CuP-crossing and PsA. Pseudo-IR1 originates on RP1 beneath distal side of pterostigma. There seems to be no enforced secondary antenodal crossvein between the two primary antenodal crossveins Ax1 and Ax2.

Hindwing: 62.0 mm long. Discoidal triangle divided into five cells in both hindwings. Hypertriangle divided by only a single crossvein in both hindwings. Subdiscoidal triangle divided into three cells in both hindwings. Between the anal triangle and CuAb, there are two posterior branches of AA in the left hindwing, but the branches in the right hindwing. PsA angled. Anal loop posteriorly open. Pseudo-IR1 originates on RP1 beneath distal side of pterostigma. There is an anal angle and anal triangle, thus, it is a male specimen.

Material from the Museum National d'Histoire Naturelle (MNHN), Paris:

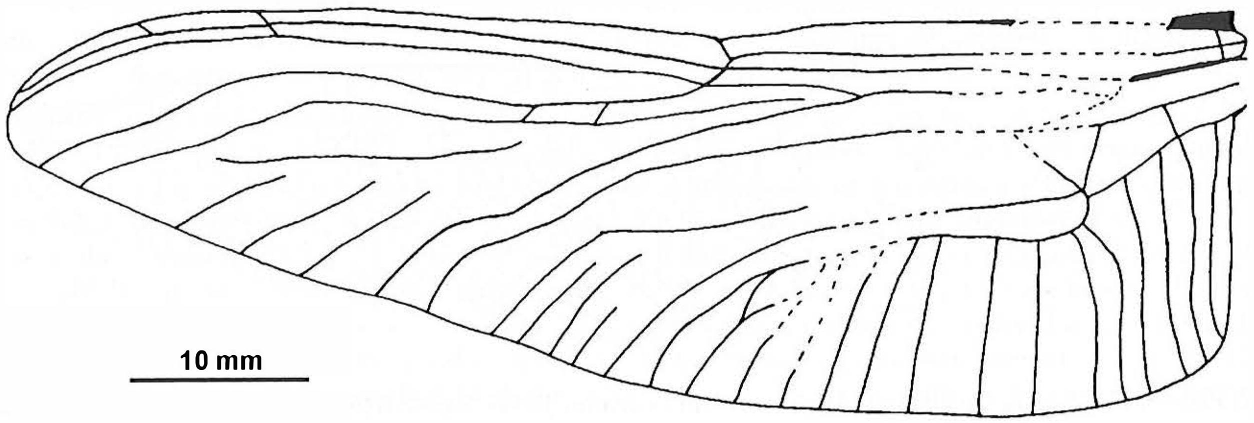
♦ Specimen no. MNHN-LP-R. 10409; female

Text-Figs 59-61

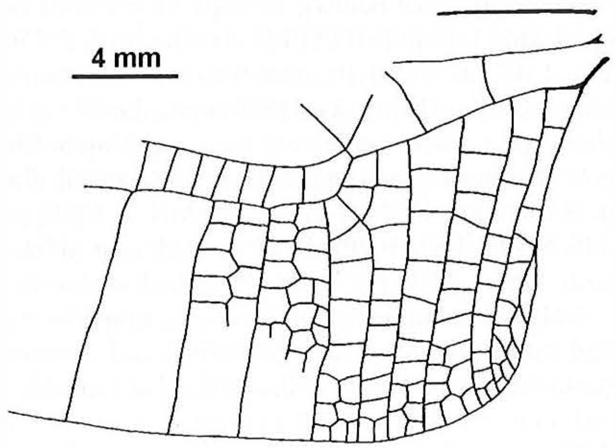
The venation agrees with that of [SOS 1713], except for the absence of an anal angle and anal triangle, thus, it is a female specimen. Abdomen 72 mm long and 6 mm wide; thorax 6 mm wide; head 10 mm long and 13 mm wide. The cerci are foliate, rounded with a dorso-longitudinal crest, 7.6 mm long and 3.3 mm wide. Inferior appendage reduced (female), but there is no visible ovipositor (Text-Fig. 61).

Forewing: Length 69.0 mm; width 14.5 mm; distance from base to nodus 35.0 mm.

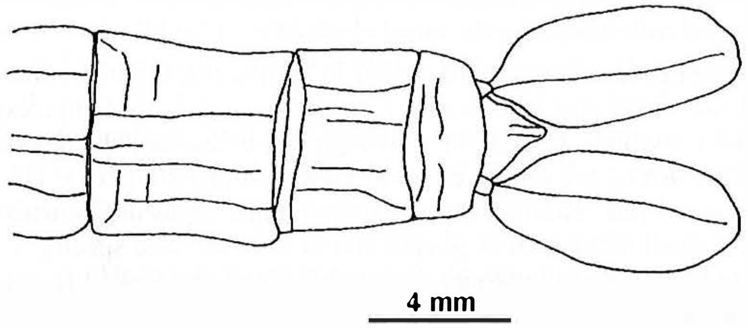
Hindwing: Length 67.0 mm; width 21.0 mm; distance from base to nodus 30.0 mm.



Text-Fig. 59. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). MNHN-LP-R.10409 - female, left hindwing.



Text-Fig. 60. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). MNHN-LP-R.10409 - female, hindwing base.



Text-Fig. 61. *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839). MNHN-LP-R.10409 - female, anal appendages.

Material from the Museum of Comparative Zoology (MCZ), Cambridge:

♦ Specimen no. MCZ 6248; female; labelled «coll. CARPENTER, *Pitalia* (sic) *longialata* GERM., Solenhofen, Dr. KRANTZ; 59»

Plate 25: Figs 1-2

A female with head, thorax, and four wings in outspread position. The posterior and distal parts of the hindwings are missing. The legs are not visible and head and thorax are only poorly preserved, but the wing venation is well-preserved and partly traced by iron-oxide dendrites. Even the spines on the wing veins and the nodal bracket are visible. The venation agrees with that of [SOS 1713], but there seems to be no anal angle and anal triangle, thus, it is a female specimen.

Forewing: Length 62.8 mm (right wing); width at nodus 13.1 mm; distance from wing base to nodus 32.4 mm; distance from nodus to pterostigma 19.6 mm. Thirteen postnodal crossveins between nodus and pterostigma. Pterostigma 5.0 mm long, distinctly braced and covering three and a half cells. The pseudo-IR1 originates on RP1 beneath distal side of pterostigma. Three rows of cells between pseudo-IR1 and RP1, and four rows between pseudo-IR1 and RP2. Two rows of cells in the area between the undulated parts of RP2 and IR2. Two oblique veins 'O' between RP2 and IR2, two cells and six cells distal of the subnodus, the distal one is more strongly oblique than the basal one. Up to three or four rows of cells between IR2 and Rspl. Two or three oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP3/4 and MA are distinctly undulated, basally parallel, but divergent near the wing margin. Four rows of cells in the basal part of the postdiscoidal area. A distinct, but zigzagged Mspl. Basal part of Mspl is curved with up to three rows of cells between it and MA, while the distal part is closely parallel to MA with only a single row of cells in-between. The number of cells in the discoidal triangle is not visible.

Hindwing: Length 60.8 mm (left). The discoidal triangle is four-celled (five-celled in the right hindwing). The hypertriangle is traversed by at least one crossvein. Subdiscoidal triangle divided into three cells by two crossveins. Two rows of cells between the undulated parts of RP2 and IR2, and up to four rows of cells between Rspl and IR2. Two oblique veins 'O' between RP2 and IR2, two cells and eight cells distal of the subnodus, the distal one is more strongly oblique than the basal one.

List of the known characters of *Cymatophlebia longialata*

Head: The compound eyes seem to be widely separated in some specimens, but they clearly meet dorsally in other ones (Text-Fig. 55, Plate 17: Fig. 3, Plate 23: Figs 2 and 4). Since these apparently very different character states certainly cannot be attributed to infra-specific variability, they must be caused by artifacts of preservation. This is quite possible, since the head is generally rather poorly preserved. The most likely explanation is that those heads that show the eyes separated are just preserved in ventral aspect, in which even an extant aeshnid would have apparently separated eyes as well. Those specimens which show the eyes clearly confluent are preserved in dorsal aspect, and thus show the "correct" state. Consequently, *Cymatophlebia* definitely had medio-dorsally broadly confluent eyes just like extant aeshnoid and libelluloid dragonflies. The three ocelli are very rarely visible, but seem to have been more or less aligned on the vertex.

Thorax: Mostly only poorly preserved, but noteworthy for its large size. The legs are strong and spiny, and the tarsi are three-segmented with a hook on the tarsal claws (Text-Fig. 44).

Abdomen: The superior appendages (cerci) are similar in both sexes, foliate, rounded with a distinct longitudinal crest on the dorsal side (Text-Figs 41 and 61). The inferior appendage (epiproct) of the male is triangular (not bifid) and rather long (Text-Figs 41 and 61). No ovipositor extending the apex of the abdomen that would be visible in female specimens that are preserved in dorsal aspect (Text-Fig. 61). The abdomen is only slightly widened distally in both sexes (no "club-tail"); second abdominal segment distinctly narrowed. No expanded latero-ventral lobes at the distal abdominal segments, but at least all male specimens have a pair of expanded lobes along the latero-ventral edge of the tergite of the abdominal segment III (maybe also on segment IV ?). Only one female specimen with such lobes is known (Plate 17: Fig. 2). These abdominal lobes have a row of small spines along their exterior margin. They extend along 60-70 % of the length of concerning segment. Along the medio-dorsal surface of the abdominal terga runs a distinct longitudinal carina. No lateral auricles visible on the male segment II, but this may rather be due to artifacts of preservation.

Wings: The forewing length varies between 60 and 69 mm (not related to sexual dimorphism). The forewing width varies between 11 and 17 mm. The hindwing length varies between 58 and 67.5 mm (not related to sexual dimorphism). The hindwing width varies between 18 and 21 mm. The forewing nodus is in a more basal position relative to the middle of the hindwing. The nodus is nearly midway in the forewing. The pterostigmata are braced. The pterostigma is in a "normal" position relative to the apex of the wings, thus, not basally recessed towards the nodus. The pterostigmata cover three or four cells and are 5.5 to 6.0 mm long, thus, 10 % of the whole length of wing. The forewing discoidal triangle is divided into six to eight cells (mostly seven). The hindwing discoidal triangle is divided into four to six cells (mostly seven). The discoidal triangles are longitudinally elongated in all wings. The discoidal triangles are somewhat broader in the forewings than in the hindwings. The distal sides MAb of the discoidal triangles are straight without angle, and without any convex secondary longitudinal vein (trigonal planate) in the basal postdiscoidal area originating on MAb. There are several antenodal crossveins (about twenty-five in the forewing and fifteen in the hindwing) between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Ax1 of the hindwing is just basal of the arculus, but the forewing Ax1 is definitely in a more basal position. In the forewing, three antenodal crossveins are aligned and stronger than the others: Ax1 and Ax2, and a secondary antenodal crossvein between Ax1 and Ax2 (but less strong than the primary antenodal crossveins, since not bracket-like). In the hindwing, only Ax1 and Ax2 are stronger than the secondary antenodal crossveins. There are numerous secondary antenodal crossveins between the two primary antenodal crossveins of both pairs of wings. ScP reaches the costal margin at the nodus. Eleven to thirteen postnodal crossveins between nodus and pterostigma in the forewing, and about thirteen to fifteen in the hindwing. The postnodal crossveins are not aligned with the corresponding postsubnodal crossveins between RA and RP1. The median spaces are free of crossveins. The submedian spaces and the hypertriangles are either free (artifact or aberration ?), or traversed by one to four crossveins. The hindwing hypertriangle is distinctly broader than that of the forewing. The subdiscoidal triangles are well-defined by the division of AA into PsA and AAa in both wings. The subdiscoidal triangles are divided into three cells in the hindwing and into four or five cells in the forewings. Four rows of cells in the postdiscoidal areas just distal of the discoidal triangles in both pairs of wings. The bases of RP and MA are distinctly separated at arculus. Mspl may be rather well-defined, weakly developed (zigzagged) or even completely absent. Rspl is well-defined in both pairs of wings. There are up to three or four rows of cells between Rspl and IR2. Rspl is strongly curved and usually reaches the posterior wing margin (only rarely ending on IR2). MA and RP3/4 strongly undulated near the posterior wing margin, but they remain parallel. RP2 and IR2 distally strongly undulated, but they remain parallel with two or three rows of cells in-between in this distal area. IR2 and RP2 reach the posterior wing margin very obliquely. There are two rows of cells between IR2 and RP2 below the pterostigma. There are two oblique veins 'O' between IR2 and RP2, more or less distal of the subnodus (the distal one distinctly more oblique than the basal one). RP2 is aligned with the subnodus. There is a short pseudo-IR1, originating beneath distal side of pterostigma or more often even slightly distal of the pterostigma. In the hindwings, the area between MA and RP3/4 is distinctly widened near the posterior wing margin with three or four rows of cells. MA and RP3/4 reach the posterior wing margin at a rectangular angles. AA has four parallel posterior branches reaching the posterior wing margin. In the hindwings, the anal area is broad with about twelve rows of cells between AA and the posterior wing margin. In the hindwings, the anal loop is absent or only rather indistinctly posteriorly closed by CuAb and AA1b and divided into three to five cells. In the hindwings, the cubito-anal area is wide. CuAa has seven or eight parallel posterior branches. The area between CuAa and MP is progressively widened in the hindwing with seven rows of cells along the posterior margin and a secondary longitudinal vein; there are four or five bridge-crossveins Bqs. There is an anal angle in the male hindwings, while the posterior margin is rounded in females. In the male hindwings there is a long and wide anal triangle, divided into three cells. The basal margin of the male anal triangle is distinctly curved at the distal end (but not as strong as in *Cymatophlebia kuempeli* sp. nov.) (Text-Fig. 73). There is a long membranule in the male hindwing. In the male hindwing, AA has two posterior convex branches in the anal area, excluding the branch AA2b that closes the anal triangle and the branch AA2c that crosses through the anal triangle. In the male hindwing, four rows of cells between the anal angle and the posterior convex branch AA1c that is below PsA. In the female hindwing, there are four (or rarely five) posterior branches of AA between CuAb and the basal margin which seem to be homologous with the four posterior branches of AA (including the branches of the anal triangle) in the male sex.

"*Cymatophlebia*" *mongolica* COCKERELL, 1924

(nomen dubium in Anisoptera *incertae sedis* pos. nov.)

* 1924 *Cymatophlebia* (?) *mongolica* COCKERELL, p. 140, pl. 2, figs 3-5.
1939 *Cymatophlebia mongolica*; HANDLIRSCH, p. 166.
1977 *Cymatophlebia* (?) *mongolica* COCKERELL; PRITYKINA, p. 81.
1992 *Libellulium*? *mongolicus* (COCKERELL, 1924); NEL & PAICHELER, p. 318.
1998 *Cymatophlebia mongolica* COCKERELL; NEL *et al.*, p. 5.

Holotype: Specimen no. [64], coll. BERKEY & MORRIS, AMNH, New York.

Locus typicus: Ondai Sair, Gobi Desert, Mongolia.

Stratum typicum: Ondai Sair Formation (paper shales), Lower Cretaceous (?).

Systematic position: *C. mongolica* COCKERELL, 1924 is known by three small wing fragments which belong to different specimens. According to PRITYKINA (1977: 81) only the holotypical specimen clearly represents a dragonfly (COCKERELL 1924: pl. 2, fig. 5), while the other two specimens (COCKERELL 1924: pl. 2, figs 3-4) could rather belong to Ephemeroptera. COCKERELL (1924) did not give any dimensions for *C. mongolica*. The holotype shares no potential synapomorphies with the other species of *Cymatophlebia*. A redescription is necessary to determine the status and position of this species. HANDLIRSCH (1939: 166) already had some doubts about the placement of *C. mongolica* in the genus *Cymatophlebia*, considering that it is too poorly preserved for a definite attribution. For the moment being, *C. mongolica* has to be regarded as a nomen dubium in Anisoptera *incertae sedis*.

Cymatophlebia standingae (JARZEMBOWSKI, 1994) comb. nov.

Text-Fig. 62

*v 1994 *Libellulium standingae* JARZEMBOWSKI, pp. 73-75, figs 4-5.
1998 *Cymatophlebia standingae* (JARZEMBOWSKI 1994); NEL *et al.*, p. 5.

Holotype: Specimen no. [1987.728], Horsham Museum, Horsham; part and counterpart of an isolated and fragmentary female hindwing (wing base and costo-apical area).

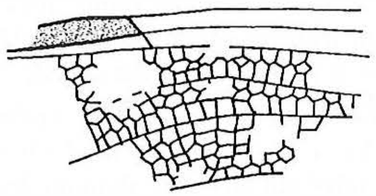
Locus typicus: Rudgwick Brickworks, near Horsham, West Sussex, England.

Stratum typicum: Upper Weald Clay, Lower Cretaceous, Barremian.

Systematic position: *Cymatophlebia standingae* (JARZEMBOWSKI, 1994) comb. nov. shares all important autapomorphies with Cymatophlebioidea stat. nov. - Cymatophlebiidae - Cymatophlebiinae. It differs from *Libellulium agrias* in its RP2 and IR2 are clearly less curved (JARZEMBOWSKI 1994) and in the presence of a supplementary row of cells between these veins. The main distinctions from the other *Cymatophlebia* spp. are the following: *C. standingae* comb. nov. has distinctly longer wings (length of preserved part of hindwing 77.0 mm; width 21.0 mm) than any other species of the genus (except *C. suevica* sp. nov.), especially compared to *C. pumilio* sp. nov.; it has three rows of cells in the broadest area between RP2 and IR2, like *C. kuempeli* sp. nov., but unlike the four to six rows in *C. zdrzaleki* comb. nov., and only two rows in *C. longialata*; it has max. three rows of cells between RP2 and RP1, basal of the pterostigma instead of max. four in *C. zdrzaleki* comb. nov., and only two in the other known species of the genus; it has max. five rows of cells between IR2 and Rspl instead of max. four in *C. longialata* and *C. kuempeli* sp. nov., and max. five to six in *C. zdrzaleki* comb. nov.; PsA of the hindwing is straight, shorter and distinctly less oblique than that of the other species of the genus; the hindwing subdiscoidal triangle only two-celled; there is one accessory cubito-anal cross-vein in the submedian space between CuP-crossing and PsA; the hindwing discoidal triangle is five-celled; the hypertriangle is divided by three crossveins.

The wing venation of *C. standingae* comb. nov. is very similar to *C. zdrzaleki* comb. nov., and the general increase of cell rows, mainly between RP1 and RP2, RP2 and IR2, and IR2 and Rspl, could even be a synapomorphy of these two species and *C. suevica* sp. nov.

Although poorly preserved, the holotype of *C. standingae* comb. nov. probably is a female, since an anal triangle seems to be absent. Like in most other *Cymatophlebia* species and specimens the Mspl is weakly defined and the anal loop is completely absent in *C. standingae* comb. nov. as well.



Text-Fig. 62. *Cymatophlebia standingae* (JARZEMBOWSKI, 1994) comb. nov. Holotype Horsham Mus. 1987.728 - hindwing apex (drawing after JARZEMBOWSKI 1994: fig. 5; without scale).

Cymatophlebia zdrzaleki (JARZEMBOWSKI, 1994) comb. nov.

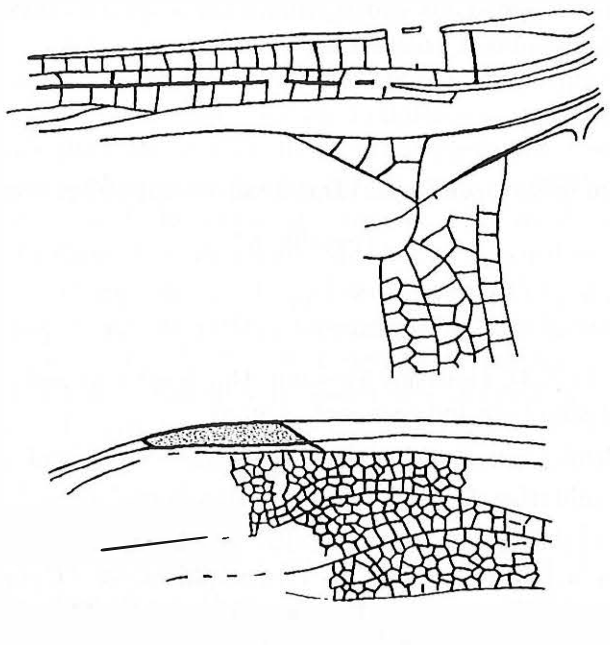
Text-Fig. 63, Plate 26: Fig. 1

*v 1994 *Libellulium zdrzaleki* JARZEMBOWSKI, pp. 71-73, figs 2-3.
1998 *Cymatophlebia zdrzaleki* (JARZEMBOWSKI 1994); NEL *et al.*, p. 5.

Holotype: Specimen no. [1987.727], Horsham Museum, Horsham; part and counterpart of an isolated but nearly complete and well-preserved male hindwing.

Locus typicus: Rudgwick Brickworks, near Horsham, West Sussex, England.

Stratum typicum: Upper Weald Clay, Lower Cretaceous, Barremian.



Text-Fig. 63. *Cymatophlebia zdrzaleki* (JARZEMBOWSKI, 1994) comb. nov. Holotype Horsham Mus. 1987.727 - hindwing base and apex (drawing after JARZEMBOWSKI 1994: fig. 3; without scale).

Systematic position: *Cymatophlebia zdrzaleki* comb. nov. shares all important autapomorphies of Cymatophlebioidea stat. nov. - Cymatophlebiidae - Cymatophlebiinae. It differs from *Libellulium agrias* in its RP2 and IR2 are less strongly curved (JARZEMBOWSKI 1994) and in the presence of supplementary rows of cells between these veins. The wing venation of *C. zdrzaleki* comb. nov. is rather similar to that of the other species of the genus. It also shows the characteristic secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl (autapomorphy of Cymatophlebioidea stat. nov.). The main differences are: Mspl of *C. zdrzaleki*

comb. nov. is strongly defined in the hindwing, contrary to *C. longialata*, *C. kuempeli* sp. nov., or *C. standingae* comb. nov.; it has max. six rows of cells in the broadest area between RP2 and IR2 instead of max. three rows in *C. standingae* comb. nov. and *C. kuempeli* sp. nov., and max. two rows in *C. longialata*; it has four rows of cells in the area between RP2 and RP1, basal of the pterostigma, compared to only two rows in *C. longialata* and *C. kuempeli* sp. nov., and three rows in *C. standingae* comb. nov.; it has max. five to six rows of cells between IR2 and Rspl instead of max. four in *C. longialata* and *C. kuempeli* sp. nov., and max. five in *C. standingae* comb. nov. It also differs from *C. pumilio* sp. nov. by its much larger size (hindwing 70.0 mm long and 20.5 mm wide); the three-celled hindwing subdiscoidal triangle; one accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA; the five-celled hindwing discoidal triangle; and the hypertriangle divided by two crossveins. As in most other Cymatophlebiinae the anal loop is absent (synapomorphy ?).

Cymatophlebia suevica sp. nov.

Text-Fig. 64, Plate 26: Fig. 2

Holotype: Specimen no. [1807 / 1], GPIT, Tübingen; collected and donated by Peter PATZ (Albstadt). This specimen represents the first fossil insect ever discovered in the Malm beta of the Swabian Alb in southern Germany (locality 1 in Text-Fig. 65).

Derivatio nominis: Latinized expression for the region Swabia in southern Germany where the holotype specimen was found.

Locus typicus: Schalksburg-Schule, Neubaugebiet, Albstadt-Ebingen, Swabian Alb, Baden-Württemberg, Germany.

Stratum typicum: "Wohlgeschichtete Kalke", *Planula*-Zone, *Planula*-Subzone, Upper Jurassic (Weißer Jura, Malm beta), Lower Kimmeridgian (not Upper Oxfordian, according to SCHWEIGERT & CALLOMON 1997).

Diagnosis: The holotypical forewing fragment looks rather similar to the corresponding area of the other *Cymatophlebia* species, but differs from all other species by the following autapomorphies: Extremely large size (forewing length 110 mm); much more dense wing venation with five or six rows of cells already at the distal angle of the discoidal triangle; postdiscoidal area between discoidal triangle and the origin of Mspl divided into about ten curious parallel transverse fields by composite convex and zigzagged pseudo-veins (formed by enforced adjacent crossveins); CuA of forewing very elongated with more than ten posterior branches; very narrow and elongated bridge-space (convergent to Petalurida); very well-defined and strongly curved Mspl with several rows of cells between it and MA, and also several secondary veins between it and MA (also present in *C. zdrzaleki* comb. nov., perhaps as a synapomorphy, and in Aeshnidae, certainly as convergence).

Description: The holotype is a well-preserved part and counterpart of a forewing fragment, from the distal half of the discoidal triangle to the nodal area. The wing veins are strongly traced by mangan-oxide dendrites.

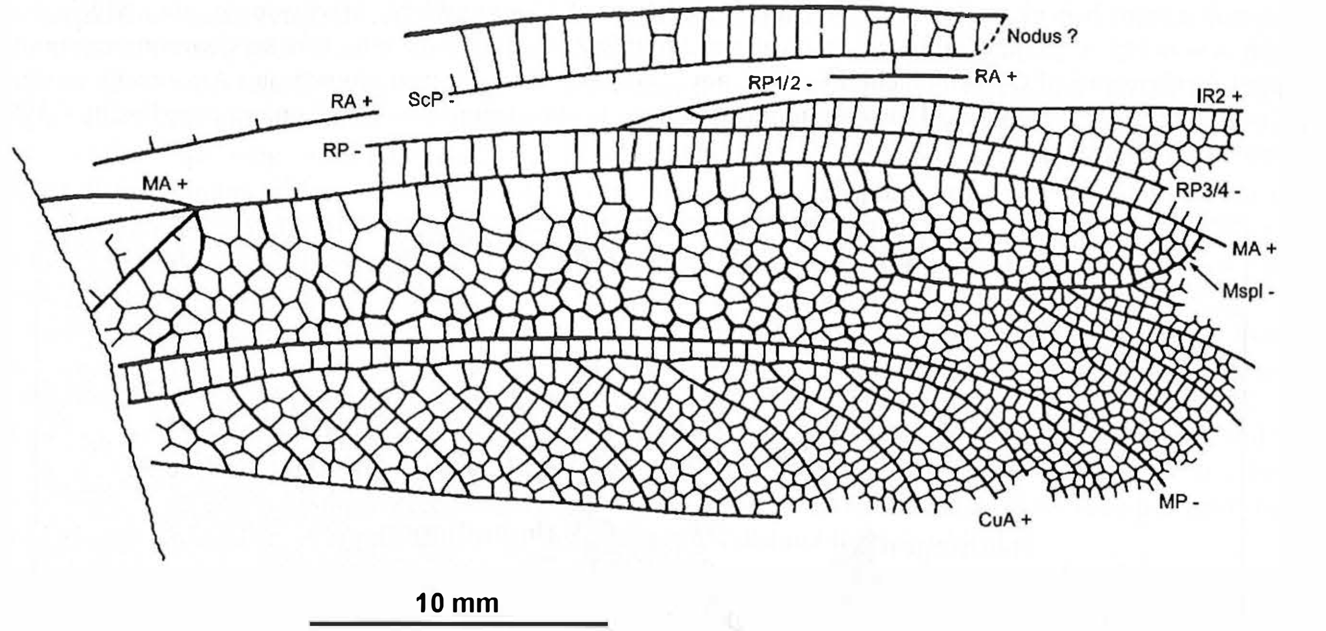
Forewing: Max. length of the fragment 41.1 mm (total length probably 105-113 mm; see below); max. width 17.1 mm. The postnodal area and the area of the pterostigma are not preserved. There are numerous secondary antenodal crossveins visible between costal margin and ScP, but the second row of antenodal crossveins between ScP and RA and the area of the primary antenodal crossveins Ax1 and Ax2 is not preserved. The area of the arculus is not preserved. MA and RP3/4 are closely parallel, but their distal parts are not preserved. The bridge-space is long and narrow, but there are no bridge-crossveins Bqs preserved. The area of the oblique vein 'O' is not preserved. The distal radial area and the area of the potential Rspl are not preserved. Distance from the distal end of the discoidal triangle to the midfork 14.6 mm. Only the distal half of the discoidal triangle is preserved and shows that it was longitudinally elongated and divided into several cells; its distal side MAb is straight. There are no crossveins preserved in the visible part of the hypertriangle. There are five to six rows of cells in the postdiscoidal area immediately distal of the discoidal triangle; the postdiscoidal area is distally widened (min. width near the discoidal triangle 4.8 mm). There is a distinct but short and curved Mspl with up to six rows of cells between MA and Mspl; three convex secondary veins (intercalaries) originate on Mspl in the distal part of the postdiscoidal area. The postdiscoidal area basal of Mspl, and the area between MA and Mspl, is separated into curious distinct transverse fields by parallel enforced composite veins. MP is probably ending somewhat distal of the level of the nodus. MP and CuA are basally closely parallel with only a single row of cells in-between, but they become strongly divergent near the wing margin with more than ten cells in-between along the posterior wing margin. CuA has eleven visible posterior branches and ends basal of the level of the nodus. Max. width of cubito-anal area 5.3 mm. The median space, submedian space, and subdiscoidal triangle are not preserved. The wing base, including the complete anal area, is not preserved either.

Probable total size of the forewing: The total length of this forewing probably was 109-117 mm, resulting in an approximate wing span of at least 225 mm! Within crowngroup Odonata this size is not even matched by *Aeschnogomphus* or *Urogomphus*, and only reached by a few specimens of the "anisozygoptere" *Isophlebia aspasia* (max. forewing length 110 mm) from the Upper Jurassic Solnhofen Limestone. The size of this specimen was estimated from the relative distance from the distal angle of the discoidal triangle to the midfork (14.6 mm) compared to the other *Cymatophlebia* species where this distance represents 12.5-13.4 % of the total wing length. An estimation using the distance from the discoidal triangle to the potential position of the nodus gives about the same result. However, using the max. width as value (17.1 mm), the estimated length would probably "only" be 77-83 mm, since the max. forewing width makes 20.6-22.2 % of the wing length in the other *Cymatophlebia* species (except *C. herrlenae* sp. nov.). The rather different estimated values are due to distinct allometric differences in the wing proportions; especially the basal half of the wing seems to be unusually slender (the distance from discoidal triangle to midfork divided by the width at the midfork gives a quotient of 0.86, compared to 0.59-0.63 in the other species, except *Cymatophlebia herrlenae* sp. nov. which even has a quotient of 0.93-1.03). The CuA is much more elongated and has much more branches than in the other *Cymatophlebia* species. This evidence for a very slender and elongated wing also suggests that the higher estimates of total length are more likely correct than the smaller ones, since bigger odonates generally tend to have more slender wings than their smaller close relatives. Also the very dense wing venation with many intercalary veins strongly suggests a wing of very large size. Although the estimation based on the distance from the discoidal triangle to the midfork can be potentially misleading, as is demonstrated below by the example of *Cymatophlebia herrlenae* sp. nov., in this case all other evidence suggests that the estimation of a total wing length of about 110 mm is indeed most probable. Consequently, this new species represents the largest known Anisoptera and even the largest known crowngroup Odonata at all, only exceeded in length by some of the giant Palaeozoic "protodonates" and maybe *Prohoyaeshna milleri* gen. et sp. nov.

Systematic position: None of the potential synapomorphies with Aeshnoptera, Aeshnida, Cymatophlebioidea stat. nov., and Cymatophlebiidae is preserved. Furthermore, only a single synapomorphy with Aeshnomorpha taxon nov. is visible (forewing with longitudinally elongated discoidal triangle), and likewise only one synapomorphy with Panaeshnida taxon nov. is visible (discoidal triangle divided into more than two cells). Nevertheless, this forewing shows a combination of characters that is only known within Cymatophlebiinae: CuA ends distal of the level of the nodus and has numerous posterior branches (symplesiomorphy); more than three rows of cells in the postdiscoidal area; distinct and curved Mspl (synapomorphy, convergent to Aeshnidae), similar to the hindwing of *C. zdrzaleki* comb. nov.; discoidal triangle longitudinally elongated (synapomorphy with Aeshnomorpha taxon nov.), but with straight distal side MAb (symplesiomorphy). This combination of characters clearly excludes all other taxa that do posses a curved Mspl by convergence, viz Aeschnidiidae, Aeshnidae, and some Libellulidae, since Aeschnidiidae and Libellulidae do possess a transverse discoidal triangle in the forewing (at least partly plesiomorphic), while Aeshnida do possess an angled MAb (groundplan apomorphy of Euaeshnida, which is plesiomorphic absent in *Cymatophlebia suevica* sp. nov.). The forewing fragment looks rather similar to the corresponding area of the forewing of the other *Cymatophlebia* species. Nevertheless, this new species has several distinct autapomorphies: Extremely large wings; five to six rows of cells in the postdiscoidal area already at the distal angle of the discoidal triangle; postdiscoidal area between discoidal triangle and the origin of Mspl divided into about ten curious vertical fields by transverse and zigzagged convex pseudo-veins (formed by enforced adjacent crossveins); CuA of forewing very long with eleven visible branches (plus at least one or two unpreserved branches). Four derived similarities (putative synapomorphies) suggest that this species could be most closely related to *C. zdrzaleki* comb. nov.: Very long wings (◊70 mm); numerous rows of cells between the main veins; very well-defined and strongly curved Mspl (also present in *C. purbeckensis* sp. nov.); transverse and convex pseudo-veins between MA and Mspl, formed by enforced adjacent crossveins (convergent to many higher Aeshnidae). Because of the distinctly larger size of this wing, it does almost certainly not represent the forewing of *C. zdrzaleki* comb. nov. which is only known by the holotypical isolated hindwing.

There are no visible synapomorphies with Valdaeshninae subfam. nov., since the concerning wing areas are not preserved. There is a distinct similarity with the paratype of *Prohoyaeshna milleri* gen. et sp. nov. from the Weald of England. However, this similarity is mostly due to the circumstance that both taxa are very large Cymatophlebiidae (*Prohoyaeshna milleri* gen. et sp. nov. even could have been bigger the *Cymatophlebia*

suevica sp. nov.), including a very dense cross-venation (e.g. six rows of cells in the postdiscoidal area) which is obviously a rather weak and size-related character. Furthermore, a well-defined and curved Mspl is unknown in Valdaeshninae subfam. nov., but occurs in Cymatophlebiinae. Unfortunately the area of the potential Mspl is not preserved in *Prohoyaeshna milleri* gen. et sp. nov., so that it cannot be totally excluded that it is conspecific with *Cymatophlebia suevica* sp. nov.



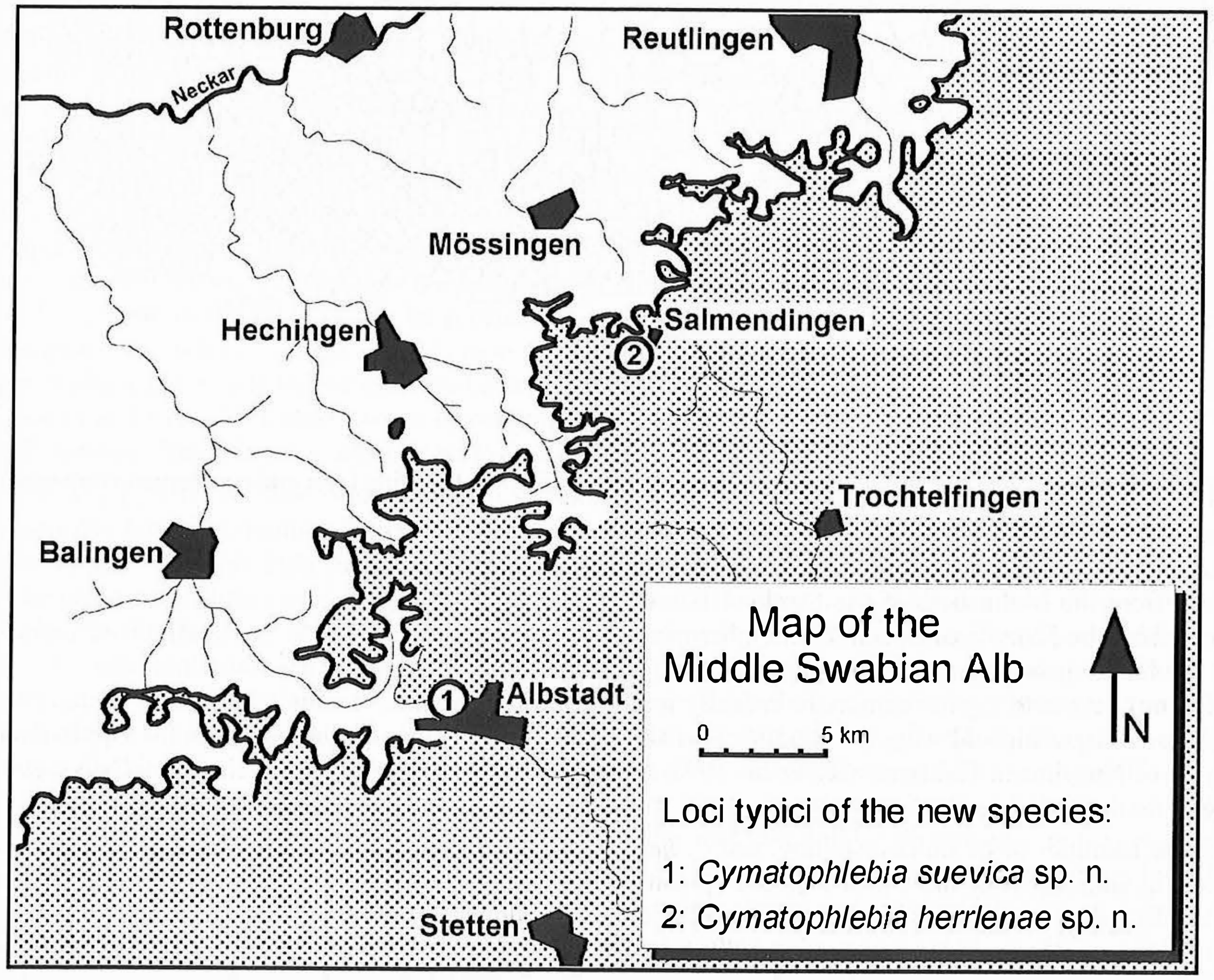
Text-Fig. 64. *Cymatophlebia suevica* sp. nov. Holotype GPIT 1807/1 - forewing (part and counterpart combined).

Discussion: This specimen, and the holotype of *Cymatophlebia herrlenae* sp. nov. described below, are of particular relevance for the local palaeontology of southern Germany, since they represent the first fossil insects from the Malm beta of the Swabian Alb (Text-Fig. 65), while only seven other insect remains, are known from the Jurassic of Baden-Württemberg at all (all in collection of SMNS, Stuttgart): One *Heterophlebia buckmani* from the Lower Toarcian (Lias epsilon) Posidonia Shale of Holzmaden (ANSORGE 1999; according to ANSORGE pers. comm., he recently found several further insect remains from the "Unterer Stein" of Holzmaden), a bittacid wing (BECHLY & SCHWEIGERT 2000) and five dragonflies from the Upper Kimmeridgian of Nusplingen (SCHWEIGERT *et al.* 1996 and pers. comm.), including a specimen of *Cymatophlebia longialata* that is redescribed above.

The type localities of *C. suevica* sp. nov. and *C. herrlenae* sp. nov. are located within the Swabian Marl Basin (Text-Fig. 65), a part of the Upper Jurassic epicontinental sea. The nearest emergent lands were the Rhenish Massif located to the north-west at a distance of at least 150 kilometres and the Bohemian Island located to the north-east at a distance of approximately 200 kilometres (MEYER & SCHMIDT-KALER 1989, 1990; ZIEGLER 1990). A reasonable explanation for the great distance of the two fossil dragonflies to the next emergent land is that dragonflies are very good fliers. This also explains the circumstance, that all but one of the fossil insects known from the Jurassic of Baden-Württemberg are dragonflies, since all concerning localities were quite remote from emergent land. The second explanation is that during the Upper Jurassic the main current direction was from the north to the north-west (RICKEN 1985; MEYER & SCHMIDT-KALER 1989, 1990). As recently demonstrated by TISCHLINGER (1996) a dead dragonflies may drift on the water surface for a relatively long time before they start to sink, and can thus be transported over long distances. Another possibility would be a transport of the dragonfly wings through turbidity currents which are partly seen as the origin of the limestone banks in which they have been found (RICKEN 1985).

Like the holotype of *C. herrlenae* sp. nov., the holotype of *C. suevica* sp. nov. was found in limestone banks, thus, not in laminated limestones. Preservation of fossil insects in such bioturbated beds is very unusual and explains the extreme rarity of fossil insects in the Malm beta of the Swabian Alb. Furthermore, such fossils can only be discovered by random in case of the lucky circumstance that the stone cracks at the right place. Generally the "Wohlgeschichtete Kalke" Formation of the Swabian Alb is poor in terms of recorded macrofossils anyway (nearly exclusively ammonites, with exception of few "Steinkerne" of bivalves and gastropods, and very few crustacean fragments and plant remains). Therefore, it is quite surprising that this formation yielded two random founds of fossil dragonflies in short time, while just fiive fossil dragonflies have been discovered in the laminated limestones of Nusplingen, in spite of a generally very diverse record of macrofossils and quite intensive palaeontological excavations.

The horizon of the holotype of *Cymatophlebia suevica* sp. nov. is at least five million years older than the laminated limestones of Nusplingen, and at least six million years older than the lithographic limestones of the Solnhofen area. It is also slightly older than the holotype of *Cymatophlebia herrlenae* sp. nov. which stems from a younger subzone (*Galar*-Subzone) of the *Planula*-Zone. Consequently, this specimen represents the oldest fossil record of Cymatophlebioidea stat. nov., Aeshnoptera, and even crowngroup Anisoptera, since all Liassic dragonflies (including Liassogomphidae) belong to the stemgroup of Anisoptera (see BECHLY 1996, 1999a, b).



Text-Fig. 65. Map of the type localities of *Cymatophlebia suevica* sp. nov. and *C. herrlenae* sp. nov., the first fossil insects from the Malm beta of the Swabian Alb.

Cymatophlebia herrlenae sp. nov.

Text-Figs 66-67, Plate 26: Figs 3-4

Holotype: Specimen no. [1807 / 2], GPIT, Tübingen; collected and donated on permanent loan to GPIT by L. HERRLEN (Tübingen). This specimen is the second fossil insect that was ever discovered in the Malm beta of the Swabian Alb in southern Germany (locality 2 in Text-Fig. 65).

Derivatio nominis: Named in honour of Mrs Lotte HERRLEN (Tübingen), who collected the specimen, and who happens to be a grand-daughter of the famous German palaeontologist Oskar FRAAS.

Locus typicus: Road works near the Salmendinger Kapelle, Salmendingen, Swabian Alb, Baden-Württemberg, Germany.

Stratum typicum: "Wohlgeschichtete Kalke", *Planula*-Zone, probably *Galar*-Subzone, Upper Jurassic (Weißer Jura, Malm beta), Lower Kimmeridgian (not Upper Oxfordian, according to SCHWEIGERT & CALLOMON 1997).

Diagnosis: The holotypical forewing fragment looks rather similar to the corresponding area of the other *Cymatophlebia* species (e.g. there are two or three oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl, as an important synapomorphy with Cymatophlebioidea stat. nov.), but differs from all other *Cymatophlebia* species by the following autapomorphies: IR2 originating on RP3/4 (quite unique within Anisoptera); the discoidal triangle is distinctly broader and less elongated; the forewing is much more slender, especially in its basal half, and the nodus is in a more distal position (at 54 % of the wing length). It furthermore differs from the forewing of *Cymatophlebia longialata* by the number of cells in the discoidal triangle (only fiive instead of six to eight), the presence of only three rows of cells in the basal part of the postdiscoidal area, and the absence of any cubito-anal crossveins in the submedian space between CuP-crossing and PsA. It differs from the new species *C. suevica* sp. nov., and from *C. zdrzaleki* comb. nov. and *C. standingae* comb. nov. (hindwings), by the smaller size (less than 70 mm wing length) and the presence of only three rows of cells in the basal part of the postdiscoidal area. It differs from the new species *C. suevica* sp. nov. by the shorter forewing CuA with less numerous branches, and the less distinct Mspl. It differs from the forewing of *C. kuempeli* sp. nov. by the number of cells in the discoidal triangle (only five instead of nine), and by the absence of any cubito-anal crossveins in the submedian space between CuP-crossing and PsA. It differs from *C. pumilio* sp. nov. by the bigger size (wings longer than 60 mm) and the five-celled forewing subdiscoidal triangle. It differs from *C. purbeckensis* sp. nov. by the less distinct forewing Mspl.

Description: The holotype represents two well-preserved forewings that are still connected with a small fragment of the pterothorax, but their apical parts are missing. There is no counterpart, and the wing veins are not traced by dendrites. The left forewing of the holotype shows a teratological feature, since RP2 is most unusually fused to IR2 shortly after its origin, resulting in a strongly aberrant radial area.

Right forewing: Length of the fragment 45.3 mm; width at nodus 11.3 mm (max. width 11.5 mm); distance from base to arculus 7.9 mm; distance from base to nodus 34.1 mm. The distal part of the wing, including the area of the pterostigma, is not preserved, and the distal end of the fragment is somewhat distorted. There are fiive postnodal crossveins preserved in the basal part of the postnodal area, not aligned with the eight visible corresponding postsubnodal crossveins between RA and RP1. There are twelve antenodal crossveins visible between costal margin and ScP, but the second row of antenodal crossveins between ScP and RA is not preserved; the primary antenodal crossveins Ax1 and Ax2 are not preserved or cannot be distinguished (artifact of preservation); nevertheless, there are obviously several secondary antenodal crossveins between the probable positions of Ax1 and Ax2. The basal brace Ax0 is not preserved. The bases of RP and MA are distinctly separated at arculus, but the posterior portion of the arculus is not preserved. MA and RP3/4 are more or less parallel (RP is "waving" due to artifacts of preservation) with only a single row of cells between their visible parts; RP3/4 and MA distally distinctly undulated, but their most distal parts are not preserved. There are three bridge-crossveins Bqs preserved (total number probably higher). There are no oblique veins 'O' visible, but this area of the wing is not only distorted but also highly teratological. The same applies to the area of the potential Rspl. IR2 seems to originate on RP3/4 rather than RP1/2 (as in the left forewing). Contrary to the left forewing there are no oblique secondary veins anastomosing between IR2 and RP3/4 (teratological aberration). The base of RP2 is not preserved, but shortly after its origin it is fused to IR2 (teratological aberration). There are two or three rows of cells below RP1 due to the teratological development of RP2. Distance from the distal end of the discoidal triangle to the midfork 11.5 mm. The discoidal triangle is somewhat elongated but rather wide, and divided into five cells; its distal side MAb is straight; length of anterior side of the discoidal triangle 5.1 mm; of basal side 4.4 mm; of distal side MAb 5.4 mm. There is no crossvein visible in the hypertriangle which is very narrow (length 8.2 mm; max. width 0.6 mm). There are three rows of cells in the postdiscoidal area immediately distal of the discoidal triangle. The postdiscoidal area is smoothly widened distally (basal width near the discoidal triangle 3.3 mm; distal width at the undulation of RP3/4 and MA 4.0 mm). There is a distinct but irregular Mspl. MP is ending far distal of the level of the nodus. MP and CuA are basally parallel with only a single row of cells in-between, but they become divergent with numerous cells in-between along the wing margin. CuA has ten or eleven posterior branches; CuA ends slightly distal of the level of the nodus. Max. width of cubito-anal area 3.9 mm. The median space is free of crossveins, as is the submedian space that was probably only traversed by the CuP-crossing, although the latter is not preserved. AA divided into a secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined and elongated subdiscoidal triangle that is divided into several cells (at least three are visible, but probably there were one or two more). Max. width of anal area (below PsA) 3.1 mm with two rows of cells between AA and the posterior margin. A distinct membranule is preserved along the most basal part of the anal margin.

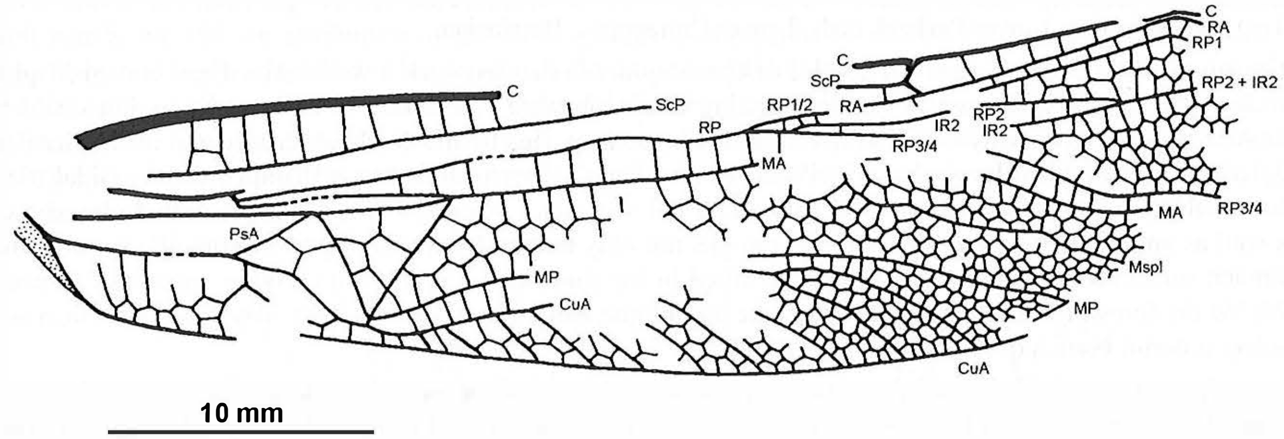
Left forewing: Length of the fragment 47.6 mm; width at nodus 12.5 mm (max. width 12.8 mm); distance from base to arculus 8.9 mm; distance from base to nodus 36.1 mm. The distal part of the wing, including the area of the pterostigma, is not preserved. There are seven postnodal crossveins preserved in the basal part of the postnodal area, not aligned with the four visible corresponding postsubnodal crossveins between RA and RP1. There are about eighteen secondary antenodal crossveins visible between costal margin and ScP (total number probably about twenty), not aligned with the second row of antenodal crossveins between ScP and RA; Ax2 can not be clearly distinguished (artifact of preservation), but Ax1 is distinctly enforced and aligned, situated 2.0 mm basal of the arculus; there are several secondary antenodal crossveins between Ax1 and Ax2. The basal brace Ax0 is visible. The bases of RP and MA are distinctly separated at arculus which is angled. MA and RP3/4 are closely parallel with only a single row of cells in-between. RP3/4 and MA distinctly undulated on a level with the second oblique vein 'O', but their most distal parts are not preserved. There are three bridge-crossveins Bqs preserved (total number probably four or five). There are two oblique veins 'O', two cells (2.2 mm) and six cells (7.2 mm) distal of the subnodus, the distal one is slightly more oblique than the basal one. The area of the potential Rspl is not preserved. IR2 is originating on RP3/4 (instead of RP1/2). There are two or three oblique secondary veins anastomosing between IR2 and RP3/4 immediately basal of the potential origin of Rspl. RP2 is aligned with the subnodus and seems to be closely parallel to RP1 with only one or two rows of cells in-between. Distance from the distal end of the discoidal triangle to the midfork 11.9 mm. The discoidal triangle is somewhat elongated but rather wide, and divided into five cells; its distal side MAb is straight; length of anterior side of discoidal triangle 5.9 mm; of basal side 4.7 mm; of distal side MAb 6.1 mm. There is no crossvein visible in the hypertriangle which is rather narrow (length 8.5 mm; max. width 0.7 mm). There are three rows of cells in the postdiscoidal area immediately distal of the discoidal triangle. MA and MP are more or less parallel, so that only the most distal part of the postdiscoidal area seems to be widened (basal width near the discoidal triangle 3.7 mm; distal width at the undulation of RP3/4 and MA 4.3 mm). There is a distinct but irregular Mspl with about three rows of cells between Mspl and MA. MP is ending far distal of the level of the nodus. MP and CuA are basally parallel with only a single row of cells in-between, but they become divergent with numerous (about ten) cells in-between along the wing margin. CuA has ten or eleven posterior branches, of which the most distal one is secondarily branching on CuA; CuA ends somewhat distal of the level of the nodus. Max. width of cubito-anal area 3.8 mm. The median space is free of crossveins, and the submedian space is only traversed by the CuP-crossing, 1.6 mm basal of the arculus (thus, no accessory cubito-anal crossvein between CuP-crossing and PsA). AA divided into a secondary anterior branch PsA (very distinct and not angled) and a posterior main branch AAa, delimiting a well-defined and elongated subdiscoidal triangle that is divided into five cells. Max. width of anal area (below PsA) 2.9 mm with two rows of cells between AA and the posterior margin. The membranule is not preserved.

Probable total length of the forewings: As in *C. suevica* sp. nov. (see above), the estimations of the total length of the forewing differ significantly depending on the used reference values. The estimations for the right forewing would be: 86-92 mm based on distance from discoidal triangle to midfork (12.5-13.4 % of the wing length in the other species); 52-56 mm based on max. width (20.6-22.2 % of the wing length in the other species); 66-70 mm based on distance base to nodus (48.5-51.5 % of the wing length in the other species). The same estimations for the left forewing would be: 89-95 mm based on distance from discoidal triangle to midfork; 57-62 mm based on max. width; 70-74 mm based on distance base to nodus. The average values would thus be 90.5 mm based on the distance from discoidal triangle to midfork; 56.8 mm based on the max. width; and 70 mm based on the distance base to nodus. The arithmetical mean value of all estimations would be 72.4 mm. Fortunately there is a further criterion to decide which of the estimations is most likely to be close to the truth. This criterion is wing shape, which can easily be applied by an adequate zooming of the drawing of the fragment to fit the corresponding area of the drawing of a complete wing of the other species of *Cymatophlebia*. The result suggests a total forewing length of 60-67 mm, which is nearest to the lower limit of the estimations based on the distance from base to nodus and the upper limit of the estimations based on max. width. As result we assume a forewing length of about 65 mm. Of course the best way to estimate the total wing length from fragments can be quite different in different taxa. Only careful comparisons with the complete wings of the closest available relatives and a good knowledge of the group in question can avoid very inaccurate estimations.

From the above considerations it is quite clear that *Cymatophlebia herrlenae* sp. nov. significantly differs in its wing proportions from the other known species in the following two points: The forewing nodus is in a more distal position (at 54 % of the wing length); and especially the basal half of the wing is much more slender (the distance from base to nodus divided by the max. width near the nodus gives a quotient of 2.8, compared to 2.3-2.4 in the other species). Maybe the wing was even more slender than the wing of *Cymatophlebia suevica* sp. nov. (see above).

Systematic position: This species shares undulated veins RP3/4 and MA as synapomorphy with Aeshnoptera (*sensu* BECHLY 1996), but none of the potential synapomorphies with Aeshnomorpha taxon nov. is preserved, with exception of the discoidal triangle, although the latter is not much longitudinally elongated. The single preserved synapomorphy with Panaeshnida taxon nov. is the division ofthe discoidal triangle into more than two cells. There is no visible synapomorphy with Aeshnida, with the possible exception of the more or less distinct Mspl, although the polarity and homology of the latter character is somewhat unsafe. A very distinct and unique synapomorphy with Cymatophlebioidea stat. nov. is the presence of two or three oblique secondary veins that are anastomosing between the basal parts of IR2 and RP3/4. Consequently, there is no doubt about the cymatophlebioid affinities of this new species. A putative synapomorphy with Cymatophlebiidae is the more pronounced obliquity of the second distal oblique vein 'O' relative to the basal one. As in *Cymatophlebia suevica* sp. nov. the combination of characters suggests a position in Cymatophlebiinae, although this is not based on synapomorphies but rather on symplesiomorphies and general phenetic similarity. Anyhow, this new species does not share any synapomorphies with the other cymatophlebiid subfamily Valdaeshninae subfam. nov., especially not the presence of a pseudo-ScP distal of the nodus.

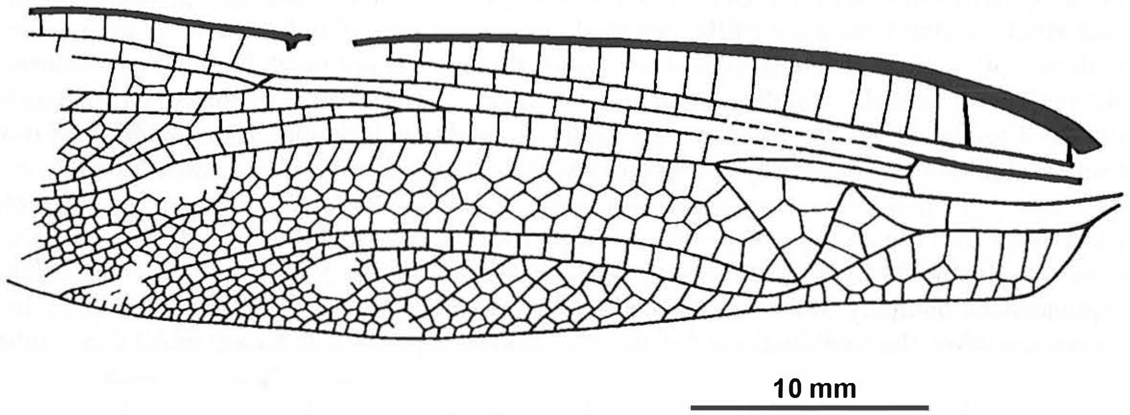
The presence of only three rows of cells in the basal part of the postdiscoidal area is a similarity with the new species *C. pumilio* sp. nov. and *C. purbeckensis* sp. nov. However, the polarity of this character is not yet clear; it could either be a symplesiomorphy or a synapomorphic reversal. Further similarities with *C. pumilio* sp. nov. are the parallel course of MA and MP in the forewing, resulting in a postdiscoidal area that is distally hardly widened, and the absence of any cubito-anal crossveins between CuP-crossing and PsA, which is quite probably a reversal and thus a potential synapomorphy. Therefore, this new species seems to be most closely related to *C. pumilio* sp. nov. from the Upper Jurassic Solnhofen Limestone.



Text-Fig. 66. *Cymatophlebia herrlenae* sp. nov. Holotype GPIT 1807/2 - right forewing.

Discussion: From the taphonomical point of view this specimen is very curiously preserved within a limestone bank: The wing articulation area lies directly on a sharp ridge with the two wings being "flapped" downwards into the calcite matrix, thus, not preserved on the same level. Since it is quite unlikely that this ridge was already present at the time of deposition, and it is even more unlikely that the fossil fragment just happened to be deposited on such a ridge with its articulation area, it is most likely due to diagenetic distortion, that is also suggested by the very different proportions of the two connected forewings.

The holotype of *Cymatophlebia herrlenae* sp. nov. was found in the "Wohlgeschichtete Kalke" Formation (Malm beta, Lower Kimmeridgian), just like the holotype of *Cymatophlebia suevica* sp. nov. (see above). However, it stems from a younger subzone (*Galar*-Subzone) of the *Planula*-Zone, while *C. suevica* sp. nov. stems from the *Planula*-Subzone. The two horizons are lithologically nearly identical. They consist of an interlayered bedding of 10-40 cm thick limestone banks and 0.5-5 cm thick marly interlayers. Both dragonflies were found within the limestone banks, thus, not in laminated limestones like the dragonflies from Nusplingen and the Solnhofen area. The present large differences in carbonate content (90-95 % in the limestone banks, and 60-75 % in the marly interlayers) have been reinforced by burial diagenesis and originally have not been that significant. Burial diagenesis is also partly responsible for the compaction of the limestone banks by 20 % and the marly interlayers by 80 % (RICKEN 1985). The above mentioned distortion of the holotype of *C. herrlenae* sp. nov. was probably caused by this diagenetic compaction. Such distortions are also common in ammonites from the same locality and bed (SCHWEIGERT pers. comm.).



Text-Fig. 67. *Cymatophlebia herrlenae* sp. nov. Holotype GPIT 1807/2 - left forewing.

Cymatophlebia purbeckensis sp. nov.

Text-Fig. 68, Plate 27: Fig. 1

Holotype: Specimen no. [57630], coll. British Geological Survey, Keyworth, U.K.

Derivatio nominis: After the "Isle of Purbeck" where this specimen was found.

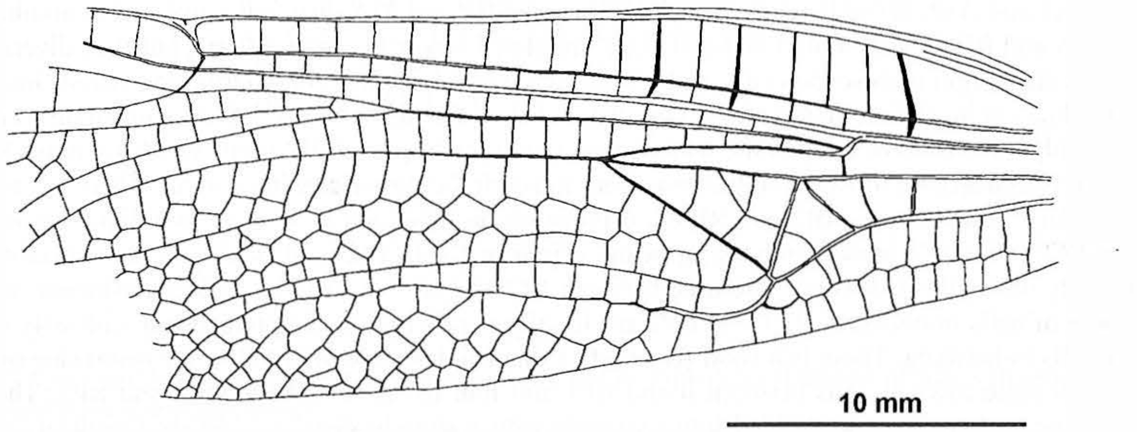
Locus typicus: Isle of Purbeck, Durlston Bay, Dorset, England.

Stratum typicum: Lower Purbeck beds, Lower Cretaceous, Berriasian.

Diagnosis: The only other known species of *Cymatophlebia* that has such a well-defined and curved Mspl in the forewing is *C. suevica* sp. nov. (the forewing of *C. zdrzaleki* comb. nov. is still unknown, but could be similar) which can be easily distinguished from the present species by the much larger size and the higher density of cells (more than three rows of cells in the postdiscoidal area immediately distal of the discoidal triangle). Within the genus the small number (only three) of secondary antenodal crossveins between Ax1 and Ax2, as well as an only two-celled subdiscoidal triangle, are only known from *Cymatophlebia pumilio* sp. nov. that is much smaller in size and lacks any distinct Mspl in the forewings. Contrary to all other species of *Cymatophlebia* the forewing PsA is rather looking like an oblique and enforced cubito-anal crossvein than like a secondary anterior branch of AA.

Description: A relatively well-preserved imprint of the basal half of an isolated forewing in a micritic limestone. The wing seems to have been hyaline. Length of fragment 35.1 mm (probable total length of wing, 55 mm); maximal width 12.8 mm; distance from base to nodus 29.2 mm; distance from base to arculus 6.8 mm. Arculus located between the two primary antenodal crossveins Ax1 and Ax2. Ax1 is 1.7 mm basal of the arculus, and Ax2 is 5.9 mm distal of Ax1. Three secondary antenodal crossveins between the two primary antenodal crossveins Ax1 and Ax2 in the first row, but only two secondary antenodal crossveins in the second row. There seems to be a third enforced and aligned antenodal crossvein two cells distal of Ax2 (similar to *C. longialata*). Thirteen secondary antenodal crossveins in the first row between Ax2 and nodus, not aligned with the eleven secondary antenodal crossveins between ScP and RA. Numerous (eleven preserved) antesubnodal crossveins in the area between RA and RP, basal of the subnodus. Eleven crossveins between RP and MA basal of the midfork (base of RP3/4). Only two basal postnodal crossveins are preserved. The arculus is angled. ScP fuses with the costal margin at the nodus. RP2 aligned with subnodus. The origin of RP3/4 is 7.6 mm and the origin of IR2 is 5.4 mm basal of the subnodus. Three bridge-crossveins Bqs in the area between RP and IR2 basal of the subnodus. Only a single visible oblique vein 'O', 1.8 mm distal of the subnodus. Only the basal part of Rspl is visible, 2.7 mm distal of the oblique vein 'O'. There seems to be an oblique secondary vein between IR2 and RP3/4 basal of Rspl. Median space free of crossveins. Submedian space divided by an accessory cubito-anal crossvein between CuP-crossing and PsA. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into two cells (max. length 3.0 mm; max. width 2.4 mm = length of PsA). No crossveins are visible in the hypertriangle, but its surface is obscured by sediment so that this character state is rather uncertain; hypertriangle very long and narrow (length 7.9 mm; max. width 0.8 mm). Discoidal triangle longitudinally elongated and divided into five cells; length of anterior side 6.4 mm; of basal side 3.1 mm; of distal side MAb 6.6 mm; the distal side MAb of the discoidal triangle is straight and there is no secondary convex vein originating at MAb. Three rows of cells in the postdiscoidal area just distal of the discoidal triangle, but this area is distally widened (width near discoidal triangle 3.5 mm). Mspl well-defined and distinctly curved with two rows of cells between it and MA. Basally only a single row of cells in the area between MP and CuA that are closely parallel, but they diverge near the posterior wing margin. CuA reaches the posterior wing margin on a level with nodus. CuA has seven posterior branches, of which the four distal ones are most distinct. Cubito-anal area with max. five rows of cells between CuA and the posterior wing margin. Max. width of cubito-anal area 3.5 mm. Width of anal area (below PsA) 2.9 mm. Two rows of cells in the anal area.

Discussion: Although the two wing venational autapomorphies of Aeshnoptera are not preserved in the holotype, the presence of a Rspl, the longitudinally elongated forewing discoidal triangle indicates a position in Aeshnomorpha taxon nov. within Aeshnoptera. The presence of a Mspl, the discoidal triangle that is divided into more than two cells, and the presence of an accessory cubito-anal crossvein indicate a position in Aeshnida. *Cymatophlebia purbeckensis* sp. nov. differs from all known aeshnid dragonflies in the Lower Cretaceous of the UK, but on the first glance looks somewhat similar to the Progobiaeshnidae fam. nov. and Rudiaeschnidae fam. nov., except for the presence of a distinct Mspl. However, this similarity is based on symplesiomorphies. The apparent presence of an oblique secondary vein between IR2 and RP2 basal of Rspl suggests a position in Cymatophlebioidea stat. nov. The straight distal side MAb of the discoidal triangle and the absence of a convex secondary vein in the postdiscoidal area exclude a position in Euaeshnida, while the divided subdiscoidal triangles and five-celled discoidal triangles, as well as the basal position of Ax2 in the forewing, represent potential synapomorphies with Cymatophlebiidae. The combination of a longitudinally elongated discoidal triangle with a straight distal side MAb and a well-defined and distinctly curved Mspl is only known from some species of the genus *Cymatophlebia*. Also the presence of three aligned and enforced antenodal crossveins in the forewing is a derived character that is only known in *Cymatophlebia*. All other characters are well consistent with an attribution of this new species to the genus *Cymatophlebia* which therefore can be regarded as strongly supported. The presence of a rather well-defined Mspl is a derived similarity with *C. pumilio* sp. nov., *C. suevica* sp. nov. and *C. zdrzaleki* comb. nov., while the few number of secondary antenodal crossveins between Ax1 and Ax2, as well as the only two-celled subdiscoidal triangle could indicate a sistergroup relationship with *C. pumilio* sp. nov., although the latter species lacks a distinct Mspl in the forewing, contrary to *C. suevica* sp. nov.



Text-Fig. 68. *Cymatophlebia purbeckensis* sp. nov. Holotype coll. British Geological Survey 57630 - left forewing, basal half.

Cymatophlebia pumilio sp. nov.

Text-Figs 69-72, Plate 27: Figs 2-5

Holotype: Specimen no. [6234-6235], coll. CARPENTER, MCZ, Cambridge; labelled «*Aeschna muensteri* GERM., Solenhofen, Dr. KRANTZ».

Paratypes: Specimen without number (labelled «coll. HAEBERLEIN»), coll. CARPENTER, MCZ, Cambridge (even though this specimen has no number, it can easily be recognized after our photograph); specimen no. [SOS 3977 Li], JME, Eichstätt; specimen no. 312 (BMMS 261a) / 313 (BMMS 261b), BMM, Solnhofen; specimen no. [1982 I 39], BSP, Munich.

Derivatio nominis: After the reduced dimensions of this new species.

Locus typicus: Solnhofen, Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Diagnosis: This species is similar to *Cymatophlebia longialata* and *C. kuempeli* sp. nov., but can be easily distinguished by its distinctly smaller dimensions, its small number (about three) of secondary antenodal crossveins between Ax1 and Ax2 (also present in *C. purbeckensis* sp. nov.), its two-celled subdiscoidal triangles in both pairs of wings (also present in *C. purbeckensis* sp. nov.), its better defined Mspl in the hindwing (similar to *C. zdrzaleki* comb. nov. and maybe *C. suevica* sp. nov. and *C. purbeckensis* sp. nov.), and its Rspl that is apparently ending on IR2 instead of the posterior wing margin in both wings (as in *C. kuempeli* sp. nov.).

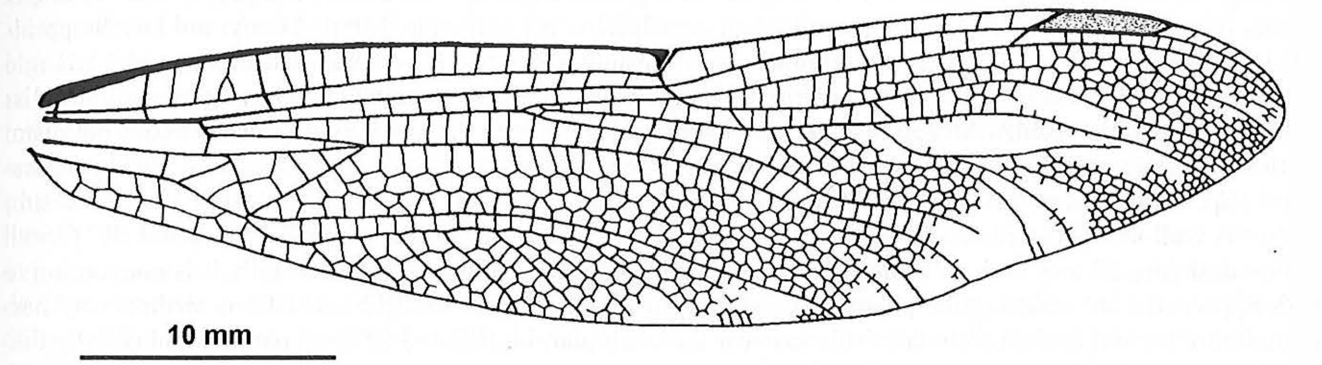
Description

♦ Specimen no. MCZ 6234-6235; holotype

Text-Fig. 69, Plate 27: Figs 2-3

The holotype is a well-preserved part and counterpart of an isolated, but complete forewing.

Forewing: Length 49.5 mm; width at nodus 10.7 mm; distance from base to arculus 6.3 mm; distance from base to nodus 24.8 mm (the nodus is nearly midway between base and apex); distance from nodus to pterostigma 14.7 mm. Pterostigma 4.6 mm long and 0.8 mm wide, and covering at least five cells; it is strongly braced by an oblique crossvein that is aligned with its basal side. The costal and posterior sides of the pterostigma are broadened. Twelve postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. About seventeen secondary antenodal crossveins visible between costal margin and ScP (total number probably nineteen or twenty), not aligned with the second row of antenodal crossveins between ScP and RA. Only the two primary antenodal crossveins are aligned and stronger than the other antenodal crossveins. Ax1 is 2.2 mm basal of the arculus, and Ax2 is 4.8 mm distal of Ax1, on a level with the middle of the discoidal triangle. Three or four secondary antenodal crossveins between Ax1 and Ax2. Basal brace Ax0 visible. Bases of RP and MA distinctly separated at arculus which is angled. MA and RP3/4 are parallel and distinctly undulated below the base of Rspl, but they diverge near the posterior wing margin with several cells in-between along that wing margin. Four bridge-crossveins Bqs; there are two oblique veins 'O', 2.1 mm and 7.7 mm distal of the subnodus. A well-defined and strongly curved Rspl with probably three rows of cells in the widened area between Rspl and IR2 (max. width 1.6 mm). Rspl is distally strongly converging to IR2 and does not seem to reach the posterior wing margin. There are several convex secondary veins between IR2 and RP3/4, originating on Rspl, and there are two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP2 is aligned with the subnodus. IR2 and RP2 distally distinctly undulated. The area between IR2 and RP2 is distally distinctly widened with two or three rows of cells in-between. RP1 and RP2 are basally parallel up to the pterostigma with only one or two rows of cells in-between. There is a short pseudo-IR1 that originates on RP1 below the distal side of the pterostigma with three rows of cells between it and RP1 and four to six rows between it and RP2. The discoidal triangle is very elongated and divided into five cells with a straight distal side MAb; length of anterior side 5.2 mm; of basal side 2.4 mm; of distal side MAb 5.2 mm. Only a single distal crossvein visible in the hypertriangle (length 6.2 mm; width 0.8 mm). Three rows of cells in the postdiscoidal area distal of the discoidal triangle. The postdiscoidal area is distally widened (basal width near the discoidal triangle 2.7 mm; distal width at the wing margin 5.4 mm). No Mspl. MP is ending far distal of the level of the nodus. MP and CuA are basally parallel with only a single row of cells in-between, but they become divergent with several cells in-between along the wing margin. CuA has eight posterior branches and ends somewhat distal of the level of the nodus; max. width of cubito-anal area 3.2 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 mm basal of the arculus. AA divided into a secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into two cells by a single crossvein; max. width of anal area (below PsA) 1.7 mm with two rows of cells between AA and the posterior margin. A very narrow membranule is visible at the basal anal margin.



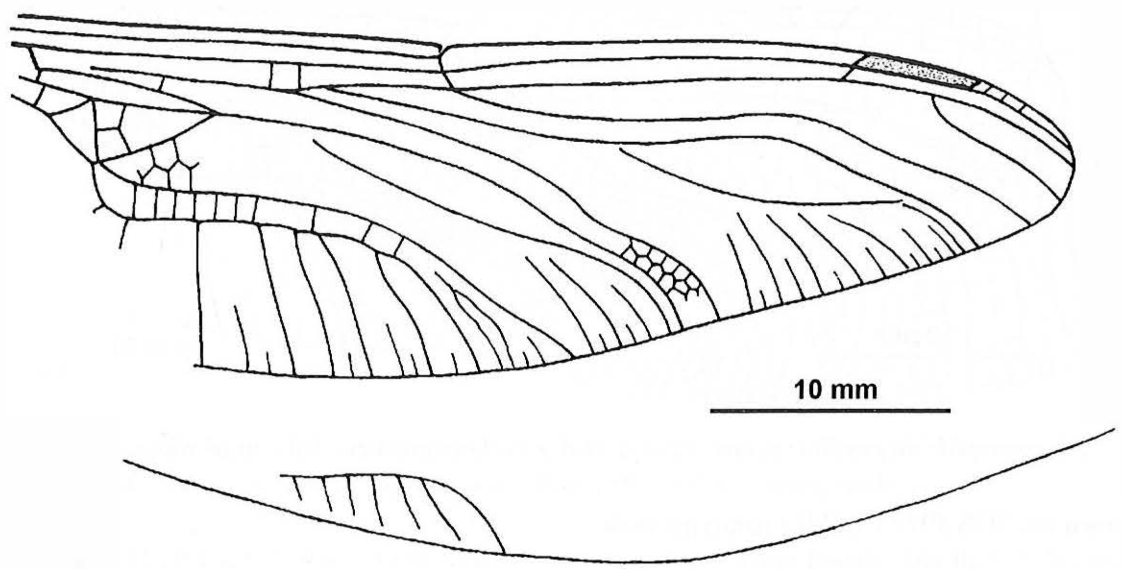
Text-Fig. 69. *Cymatophlebia pumilio* sp. nov. Holotype MCZ 6235 - forewing.

♦ Specimen without number, MCZ; paratype; labelled «coll. HAEBERLEIN, Solenhofen»

Text-Figs 70-71, Plate 27: Figs 4-5

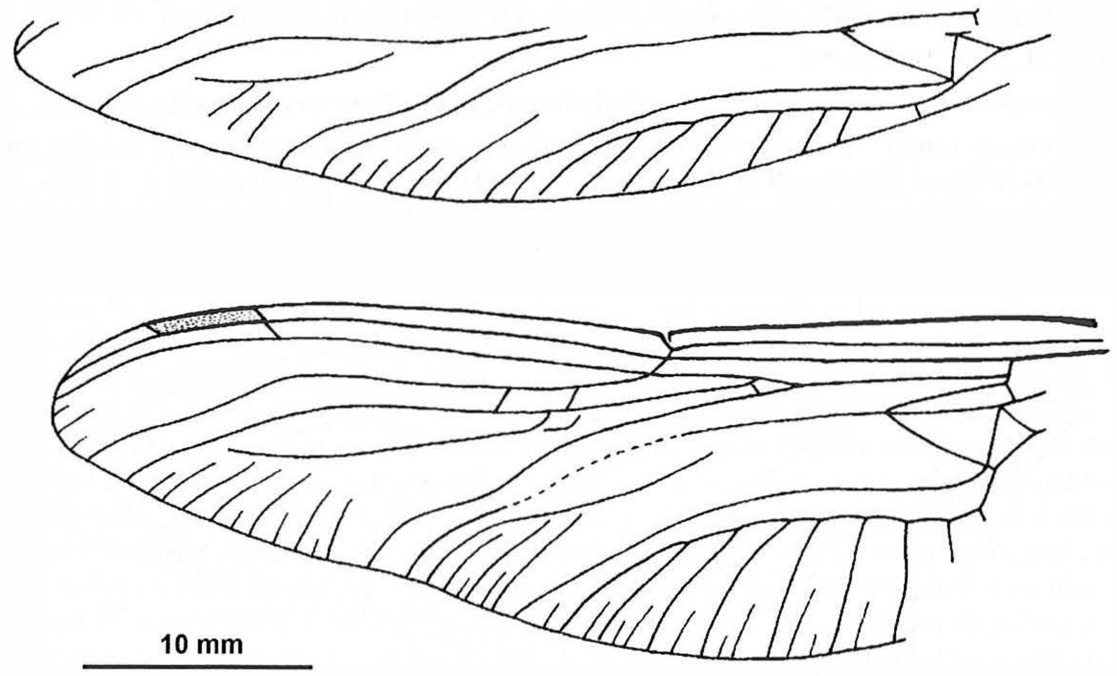
Part and counterpart of two overlapping fore- and hindwings, less well-preserved than the holotype.

Forewings (very poorly preserved): Length 47.0 mm; further visible characters are the parallel, but undulated veins RP2 and IR2 as well as RP3/4 and MA. Rspl curved. CuA with numerous posterior branches. An elongated discoidal triangle with a straight distal side MAb, and a distinct subdiscoidal triangle; apparently no Mspl.



Text-Fig. 70. *Cymatophlebia pumilio* sp. nov. Paratype MCZ without number - right pair of wings (forewing fragment shifted posterior of hindwing).

Hindwings (better preserved): Length 46.2 mm; width at nodus 14.0 mm; distance from base to arculus 4.2 mm; distance from base to nodus 19.2 mm (the nodus is in a rather basal position); distance from nodus to pterostigma 17.7 mm. The pterostigma is distinctly braced (length 4.7 mm; width 0.8 mm). No postnodal, postsubnodal, antenodal or antesubnodal crossveins preserved. The bases of RP and MA are distinctly separated at arculus which is angled. The discoidal triangle is elongated with a straight distal side MAb; length of anterior side 5.0 mm; of basal side 2.6 mm; of distal side MAb 5.0 mm. The hypertriangle is 0.9 mm wide and 5.7 mm long in the left hindwing, but 7.4 mm long in the right hindwing (certainly an aberration). AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle. The median space, submedian space, subdiscoidal triangle and hypertriangle appear to be free, but this is not significant regarding the very poor preservation of the cross-venation. There is an accessory cubito-anal crossvein visible in the submedian space of the right hindwing, on a level with arculus (the CuP-crossing was certainly more basal and is obviously not preserved). The anal area is not preserved. CuAa has about eight posterior branches, and the cubito-anal area is max. 6.1 mm wide. MP and CuAa are basally parallel, but distally divergent. The postdiscoidal area is distally widened (basal width near discoidal triangle 3.2 mm; distal width at posterior wing margin 5.0 mm). A well-defined Mspl which is basally curved and distally closely parallel to MA. MA and RP3/4 parallel and distinctly undulated below the base of Rspl, but distal of this undulation they are divergent with two or three rows of cells in-between. At least three bridge-crossveins Bqs. Two oblique veins 'O', 3.1 mm and 6.2 mm distal of the subnodus. RP2 is aligned with the subnodus. A well-defined Rspl which is basally strongly curved with a rather wide area between it and IR2 (width at broadest part 2.1 mm in the left hindwing and 2.6 mm in the right hindwing), but distally it is converging to IR2, apparently not reaching the posterior wing margin. The area between IR2 and RP2 is without any narrowed portion, and is even distinctly widened near the wing margin. IR2 and RP2 are parallel and distally distinctly undulated. RP1 and RP2 are basally parallel up to the level of pterostigmal brace. A short pseudo-IR1 that originates below the distal half of the pterostigma.



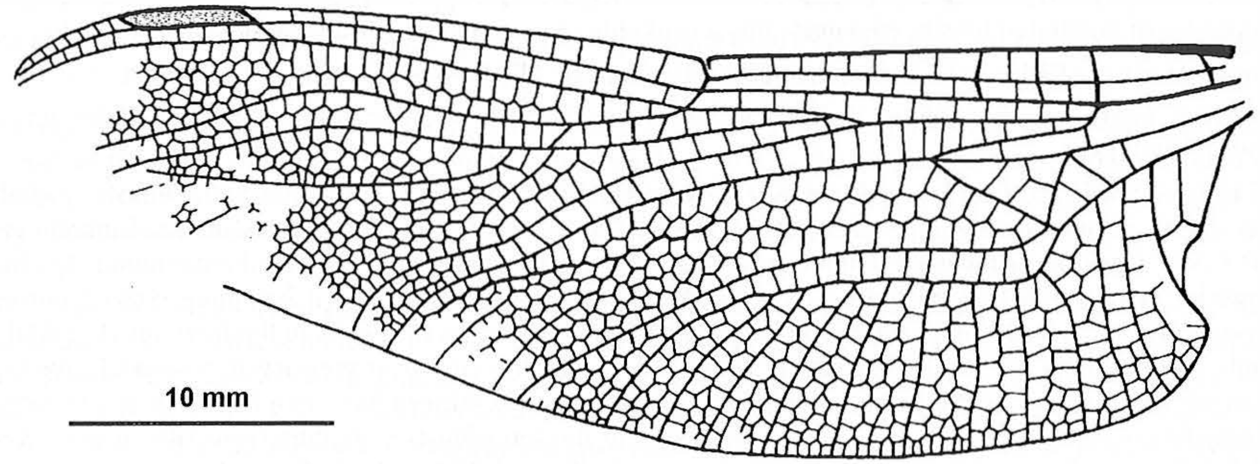
Text-Fig. 71. *Cymatophlebia pumilio* sp. nov. Paratype MCZ without number - left pair of wings.

♦ Specimen no. SOS 3977 Li, JME; paratype; male

Text-Fig. 72

A nearly complete and well-preserved isolated male hindwing; only the posterior part of the apex is destroyed.

Length 47.5 mm; width at nodus 15.1 mm; distance from base to nodus 21.1 mm (the nodus is in a rather basal position); distance from nodus to pterostigma 17.4 mm. The pterostigma is 4.7 mm long and 0.8 mm wide, covers four cells, and is distinctly braced by an oblique crossvein that is aligned with its basal side. Twelve (probably thirteen) antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except the two primary antenodal crossveins Ax1 and Ax2 and one secondary antenodal midway between Ax1 and Ax2. The two primary antenodal crossveins are stronger than secondary antenodal crossveins. Ax1 aligned with arculus (!). Ax2 is 4.7 mm distal of Ax1, distinctly basal of the distal angle of the discoidal triangle. Fifteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. The area of pseudo-IR1 is not preserved, but it obviously must have originated distal of the pterostigma. RP2 is aligned with the subnodus. Two oblique veins 'O' between RP2 and IR2, 0.8 mm and 4.3 mm distal of the subnodus, the basal one is less oblique than the distal one. RP2 and IR2 are distinctly undulated. The area between IR2 and RP2 basally with a single row of cells and distally with two rows of cells, but not distinctly widened. Four bridge-crossveins Bqs. A strong Rspl with up to four rows of cells between it and IR2. Rspl does not seem to reach the posterior wing margin, but apparently ends on IR2. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl, of which the basal one is zigzagged, while the distal one is straight. RP3/4 and MA parallel and strongly undulated below the base of Rspl. Only a single row of cells between RP3/4 and MA up to the level of Rspl, but more distally these two veins diverge and are separated by three or four cells near the wing margin. Three rows of cells in the postdiscoidal area just distal of the discoidal triangle. Width of the postdiscoidal area 3.4 mm near the discoidal triangle and 5.4 mm at the wing margin. A zigzagged Mspl with basally two rows of cells between Mspl and MA, but distally only a single row of small cells between these veins. Two convex secondary veins originate on Mspl in the distal postdiscoidal area. The discoidal triangle is divided into only four cells; length of anterior side 5.3 mm; of basal side 2.8 mm; of distal side MAb 5.2 mm. Only a single crossvein in the hypertriangle (length 6.0 mm; max. width 0.9 mm). Subdiscoidal triangle divided into three cells and basally delimited by a straight PsA (length of PsA 2.1 mm). Median space free of crossveins. Submedian space only traversed by CuP-crossing (1.2 mm basal of the arculus). The area between CuAa and MP is distally widened with about eight rows of cells along the posterior wing margin. CuAa has eight parallel convex posterior branches. The cubito-anal area is max. 6.8 mm wide with nine rows of cells between CuAa and the hind margin. Length of subdiscoidal vein (part of CuA between discoidal triangle and the fusion with AAa) 0.5 mm. AA has three parallel convex posterior branches. The anal area is 8.7 mm wide (below PsA) with ten rows of cells between AA and the posterior margin. Anal loop absent. A distinct anal angle, thus, it is a male specimen. A distinct and very large anal triangle that is divided into three cells. The basal side of the anal triangle is distinctly bulged (like *C. longialata*, but less than *C. kuempeli* sp. nov.). No membranule preserved.



Text-Fig. 72. *Cymatophlebia pumilio* sp. nov. Paratype JME SOS 3977 Li - male, hindwing.

♦ Specimen no. 312 (BMMS 261a) / 313 (BMMS 261b), BMM; paratype; female; labelled «Schernfeld»

Part and counterpart of three connected wings (one forewing and both hindwings) of a female, that are rather poorly preserved, but show the main veins.

Forewing: Length 50.0 mm; the visible characters agree with the other specimens, including the two-celled subdiscoidal triangle.

Hindwings: Length 49.0 mm; the visible characters agree with the other specimens, including the two-celled subdiscoidal triangle; anal loop weakly closed; four posterior branches of AA; the wing is basally rounded without an anal angle or anal triangle, thus, it is a female specimen.

- Specimen no. 1982 I 39, BSP; paratype; male; labelled «cf. *Tarsophlebia eximia* (HAGEN), Eichstätt / Schernfeld»

Thorax and all four wings, of which only the right hindwing is complete. The hindwing is 47.5 mm long and shows a long three-celled anal triangle, thus, it is a male specimen.

Discussion: These specimens can clearly be attributed to the genus *Cymatophlebia* because they share all the main venational characters of this genus: RP2 and IR2 as well as RP3/4 and MA distinctly undulated, but more or less parallel; Rspl well-defined and distinctly curved; the discoidal triangles are elongated, divided into several cells, and with a straight distal side MAb; subdiscoidal triangles well-defined and subdivided; numerous not aligned antenodal and postnodal crossveins; two oblique veins 'O' between RP2 and IR2; two oblique secondary veins between IR2 and RP3/4 immediately basal of the Rspl; pterostigmata elongated and strongly braced; pseudo-IR1 short; the cubito-anal areas are wide with numerous branches of CuA.

All three specimens have distinctly shorter wings than all the other species within the genus *Cymatophlebia*, being only 46-49 mm long, instead of being more than 55 mm long in all other species. They also agree in the two-celled subdiscoidal triangles and the circumstance that Rspl is not reaching the posterior wing margin.

Cymatophlebia kuempeli sp. nov.

Text-Figs 73-75, Plate 28: Figs 1-2

v. 1999 *Cymatophlebia kuempeli* BECHLY *et al.*; FRICKHINGER, p. 50, fig. 84 (nomen nudum).

Holotype: Specimen no. [42], coll. KÜMPEL (now deposited on loan in the Jura-Museum in Eichstätt, and will later be inherited to this museum).

Other specimens: A (maybe lost) specimen without number in coll. CARPENTER (MCZ, Cambridge) could belong to this species. Many of the specimens that have been attributed to *Cymatophlebia longialata* have not preserved the diagnostic characters that are necessary to distinguish these two species, so that at least some of them could belong to this new species as well.

Derivatio nominis: Named in honour of Mr Dieter KÜMPEL (Wuppertal), a dedicated collector and gifted preparator of Solnhofen fossils, who made this remarkable specimen kindly available for scientific study.

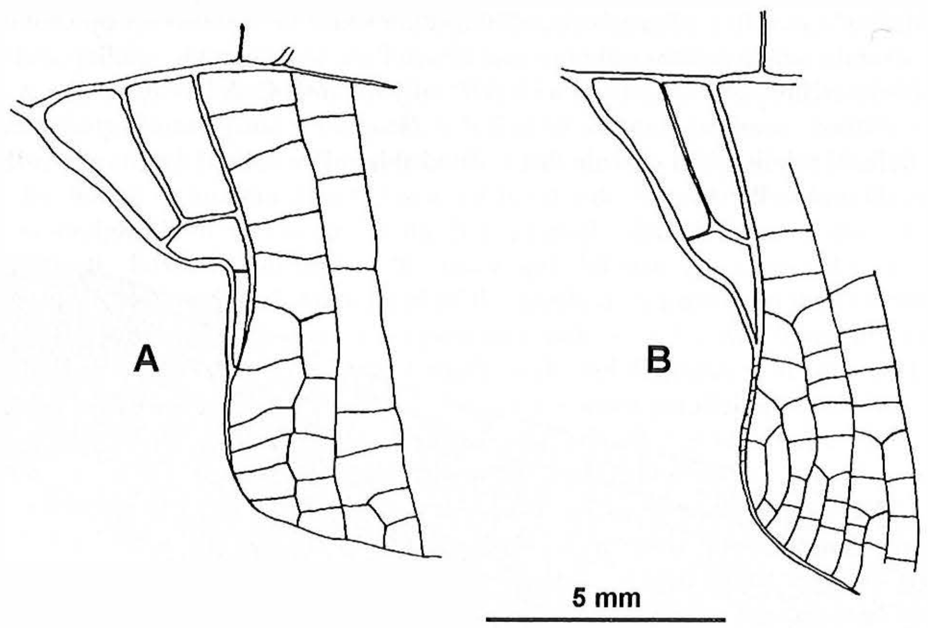
Locus typicus: Eichstätt / Solnhofen, Southern Frankonian Alb, Bavaria, Germany.

Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Diagnosis: This species is very similar to *C. longialata*. The two species only differ in the following characters: In the male hindwing of *C. kuempeli* sp. nov. the anal triangle is four-celled and its hind margin (vein AP + AA'') is strongly indented (unique autapomorphy); it has only two rows of cells between male hindwing posterior margin and first posterior branch of AA, opposite the anal angle; it has three convex posterior branches of AA in male anal area (versus two in *C. longialata*); it has nine cells in the forewing discoidal triangle and seven in the hindwing one (probable autapomorphy); it has twenty-seven postnodal crossveins between nodus and pterostigma in the forewing (versus eleven to thirteen in *C. longialata*); it has twenty-six postnodal crossveins between nodus and pterostigma in the forewing (versus thirteen to fifteen in *C. longialata*); there are five or six rows of cells between pseudo-IR1 and RP2, instead of only three or four rows; the lateral lobes of male abdominal segment III are expanded along the whole segment; the male abdominal segment IV has lateral lobes similar to those of segment III (these could also be present in *C. longialata*, although there is only a single pair of abdominal lobes visible in all known specimens, since these could be situated on different segments in some of these specimens); the shape of the male superior appendages (cerci) is also foliate, but distinctly different from that of *C. longialata*; the epiproct is apically bifid and distinctly shorter (much less than half of the length of the cerci) and broader than in *Cymatophlebia longialata*. A further difference could be the presence of a basal accessory antenodal crossvein in both pairs of wings, if this should not be an individual aberration of the holotype of this new species.

C. kuempeli sp. nov. differs from *C. zdrzaleki* comb. nov. in the following characters: It has only three rows of cells in the area between IR2 and RP2 instead of five; its hindwing discoidal triangle is divided into seven cells instead of five; its veins IR2 and RP2 are less undulated than those of *C. zdrzaleki* comb. nov.; no well-defined Mspl in the hindwing; the hindwing is distinctly shorter (length only 64 mm instead of 70 mm). It differs from *C. standingae* comb. nov. in the following characters: Its hindwing discoidal triangle is divided into seven cells instead of five-celled; the hindwing is distinctly shorter (length only 64 mm instead of 77 mm). It differs from

C. suevica sp. nov. by its smaller dimensions and the much less dense venation with fewer rows of cells, e.g. in the postdiscoidal area. *C. kuempeli* sp. nov. differs from *C. pumilio* sp. nov. by its much larger dimensions (forewing 68 mm long instead of max. 50 mm) and the absence of a well-defined Mspl in the hindwing, as well the presence of more than two cells in the subdiscoidal triangle, but the two species share the Rspl that is apparently ending on IR2 instead of the posterior wing margin. It differs from *C. purbeckensis* sp. nov. in the less distinct Mspl in the forewing and the number of cells in the subdiscoidal triangle. It also differs from *C. herrlenae* sp. nov., *C. purbeckensis* sp. nov., and *C. pumilio* sp. nov. in the presence of four (instead of only three) rows of cells in the basal part of the postdiscoidal area.

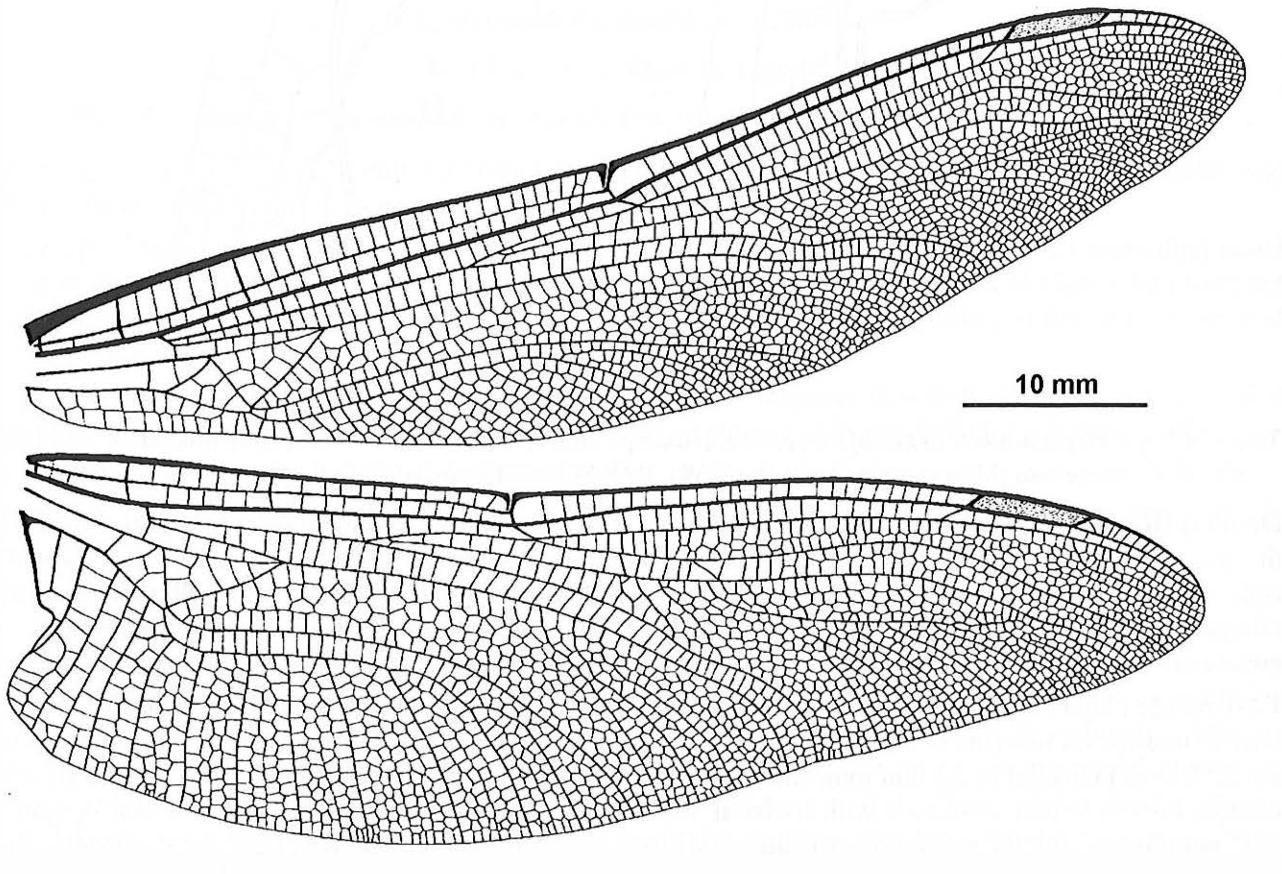


Text-Fig. 73. A: *Cymatophlebia kuempeli* sp. nov. Holotype coll. KÜMPEL no. 42 - male, right hindwing, anal triangle. B: *C. longialata* (MÜNSTER in GERMAR, 1839). JME SOS 1713 - male, right hindwing, anal triangle.

Description: The holotype is a remarkably well-preserved imprint of a complete male in dorsal aspect. Only the apex of the left forewing is missing and has been supplemented by the preparator. The wing venation of the right pair of wings is traced by iron oxide dendrites, therefore the description is mainly based on the right wings. The same could be the case with the abdominal colour pattern, especially of the abdominal lobes. The counterpart only shows a faint outline of the body.

Forewing: Length 68.0 mm (wing span of the forewings, 140 mm); width at nodus 14.1 mm; distance from base to nodus 33.4 mm (the nodus is nearly midway between base and apex); distance from nodus to pterostigma 22.8 mm. Pterostigma 5.1 mm long and 1.2 mm wide, covering seven cells, and distinctly braced by a very oblique crossvein that is aligned with its basal side. Thirty antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Only the two primary antenodal crossveins are aligned and stronger than the others. Ax1 is 2.0 mm basal of the arculus, and Ax2 is 7.1 mm distal of Ax1, on a level with the middle of the discoidal triangle. Between ScP and RA there is a single basal accessory antenodal crossvein between Ax1 and the basal brace Ax0 (aberration ?). Twenty-seven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. RP1 and RP2 are closely parallel up to the pterostigma with two rows of cells in-between from the eighth cell onwards. Below basal side of pterostigma RP1 and RP2 become divergent with three or more rows of cells in-between. Vein pseudo-IR1 has an indistinct basal origin beneath distal side of pterostigma. Three rows of cells between pseudo-IR1 and RP1, and five or six rows between pseudo-IR1 and RP2. RP2 and IR2 are parallel and distinctly undulated. Basally there is only a single row of cells between RP2 and IR2, but in the undulated area there are two or three rows of cells in-between (at the wing margin four rows of cells). Two oblique veins 'O' between RP2 and IR2, 3.1 mm and 8.0 mm distal of the subnodus (the distal one distinctly more oblique than the basal one). RP2 is aligned with the subnodus. A well-defined and curved Rspl that is apparently ending on IR2 with up to four rows of cells in the area between Rspl and IR2 (max. width of this area 2.2 mm). Three oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl (somewhat less distinct than in the hindwing). Four convex secondary veins originating on

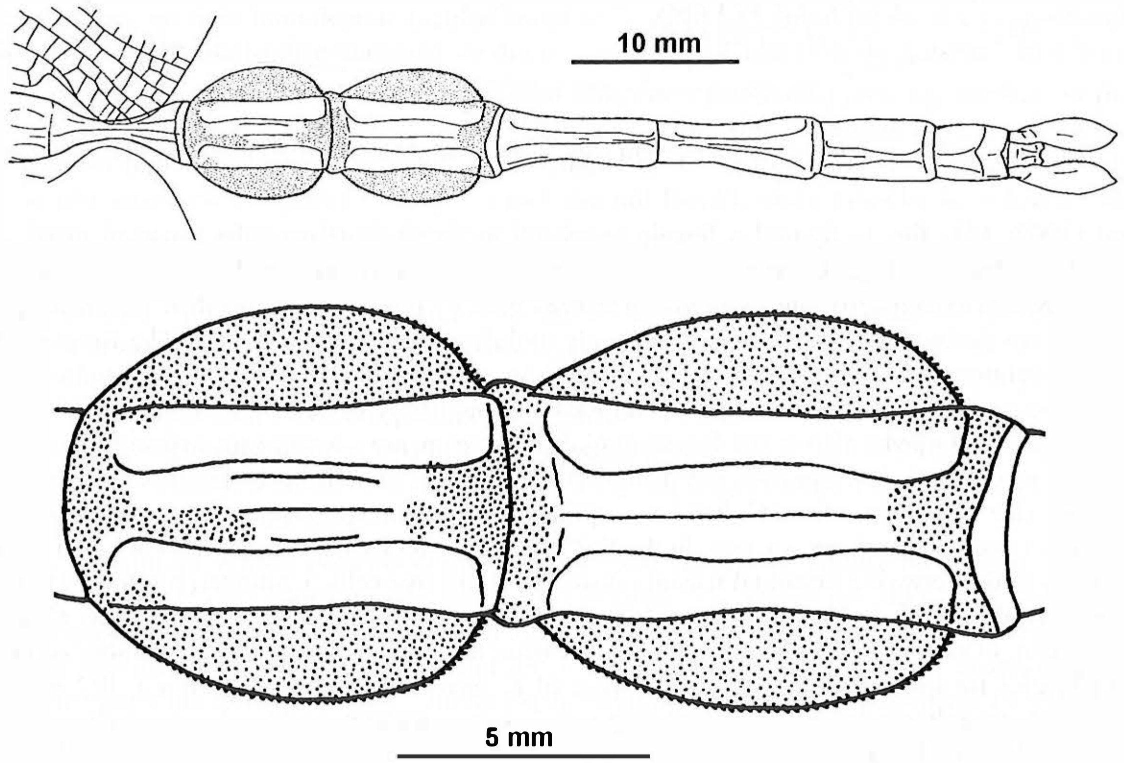
Rspl and reaching the posterior wing margin. RP3/4 and MA are undulated, but parallel with only a single row of cells in-between up to the level of Rspl, but more distally they are divergent and separated by five cells along the wing margin. The arculus is angled and the bases of RP and MA are distinctly separated at arculus. Four rows of cells in the postdiscoidal area immediately distal of the discoidal triangle. The postdiscoidal area is distally widened with nineteen cells between MA and MP at the wing margin (width near discoidal triangle 3.2 mm; width at wing margin 5.3 mm). A weakly developed and zigzagged Mspl. Three convex secondary veins are originating on Mspl in the distal part of the postdiscoidal area, reaching the posterior wing margin. The discoidal triangle is divided into nine cells; length of anterior side 6.5 mm; of basal side 3.6 mm; of distal side MAb 5.9 mm; the distal side MAb is straight. Five crossveins in the hypertriangle (length 8.0 mm; max. width 0.9 mm). Median space free of crossveins. Submedian space only traversed by CuP-crossing (1.5 mm basal of the arculus) and a single cubito-anal crossvein above PsA. Length of the subdiscoidal vein (free part of CuA between discoidal triangle and the fusion with AA) only 0.1 mm. CuA has about nine posterior branches. AA divided into a distinct secondary anterior branch PsA (length 2.9 mm) and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into five cells. Two rows of cells in the anal area which is 2.2 mm wide (below PsA).



Text-Fig. 74. *Cymatophlebia kuempeli* sp. nov. Holotype coll. KÜMPEL no. 42 - male, right pair of wings.

Hindwing: Length 64.0 mm; width at nodus 18.7 mm; distance from base to nodus 26.2 mm (the nodus is in a rather basal position); distance from nodus to pterostigma 24.7 mm. Pterostigma 6.2 mm long and 1.3 mm wide, covering six cells, and distinctly braced by a very oblique crossvein that is aligned with its basal side. Nineteen antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Only the two primary antenodal crossveins are aligned and stronger than secondary antenodal crossveins. Ax1 is 1.1 mm basal of the arculus, and Ax2 is 7.8 mm distal of Ax1, slightly basal of the distal angle of the discoidal triangle. There might be an aligned basal accessory antenodal crossvein near the wing base, between the basal brace Ax0 and Ax1. Twenty-six postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. RP1 and RP2 are closely parallel up to the pterostigma with two rows of cells in-between from the eleventh cell onwards. Below basal side of pterostigma RP1 and RP2 become divergent with three or more rows of cells in-between. A short pseudo-IR1 that originates below the distal side of the pterostigma. Three rows of cells between pseudo-IR1 and RP1, and five or six rows between pseudo-IR1 and RP2. RP2 and IR2 are parallel and

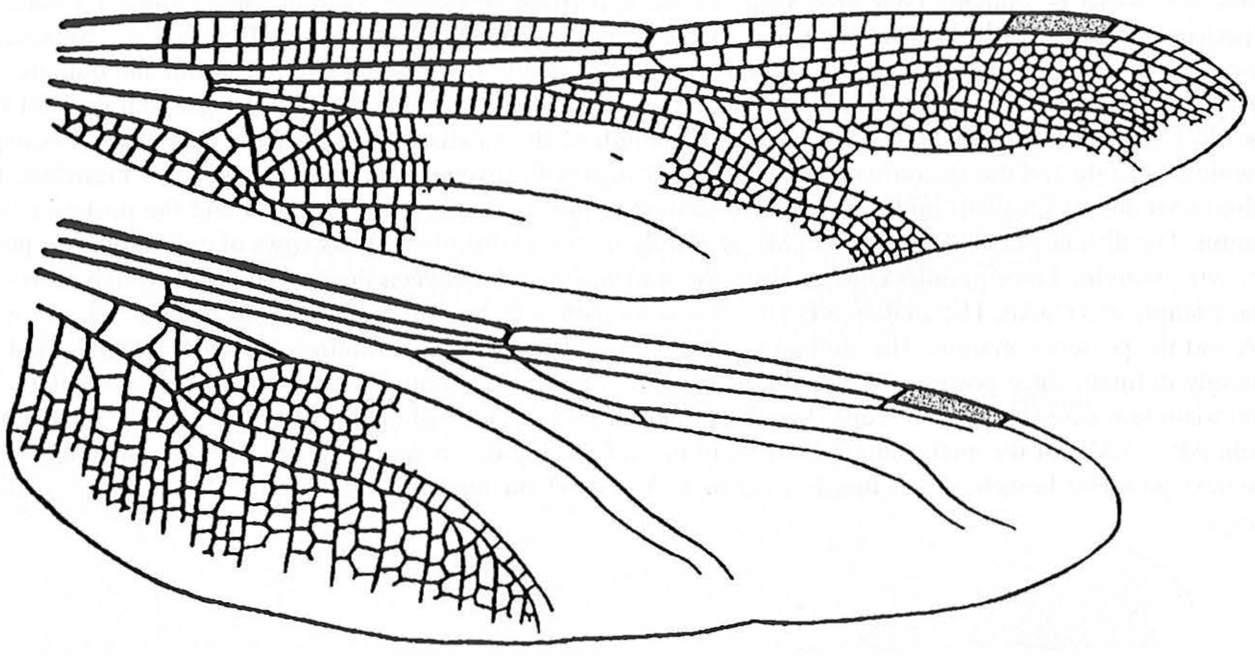
distinctly undulated. Basally there is only a single row of cells between RP2 and IR2, but in the undulated area there are two or three rows of cells in-between (six cells in-between at the wing margin). RP2 is aligned with the subnodus. Two oblique veins 'O', 4.6 mm and 8.5 mm distal of the subnodus (the distal one distinctly more oblique than the basal one). A well-defined and curved Rspl that is apparently ending on IR2 with up to four rows of cells in the area between Rspl and IR2 (max. width of this area 2.5 mm). Three oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. Four convex secondary veins originating on Rspl and reaching the posterior wing margin. Six bridge-crossveins Bqs; MA and RP3/4 strongly undulated below the base of Rspl, although this undulation is less prominent than in *C. longialata*. MA and RP3/4 are mostly parallel, but become clearly divergent near the posterior margin with three rows of cells in-between. The arculus is angled and the bases of RP and MA are rather shortly separated at arculus. Four rows of cells in the postdiscoidal area just distal of the discoidal triangle, but this area is progressively widened and has nineteen rows of cells along the posterior wing margin (width near discoidal triangle 3.7 mm; width at wing margin 8.6 mm). No distinct Mspl, but there are three convex secondary longitudinal veins in the distal postdiscoidal area, originating on a level with nodus and reaching the posterior wing margin. The discoidal triangle is divided into seven cells; length of anterior side 6.5 mm; of basal side 3.3 mm; of distal side MAb 6.7 mm; the distal side MAb is straight. Four crossveins in the hypertriangle (length 7.6 mm; max. width 1.1 mm; the hypertriangle is distinctly broader than that of the forewing). Median space free of crossveins. Submedian space only traversed by CuP-crossing (1.0 mm basal of the arculus). AA divided into a strong and oblique secondary anterior branch PsA (length 2.4 mm) and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into three cells. Length of the subdiscoidal vein (free part of CuA between discoidal triangle and the fusion with AA) 0.2 mm. CuAa with seven parallel convex posterior branches. The cubito-anal area is max. 9.7 mm wide with up to thirteen rows of cells between CuAa and the posterior wing margin. The distance between CuAa and MP gradually increases distally with six rows of cells along the posterior wing margin. Three parallel convex posterior branches of AA between the branch AA2b which closes the anal triangle and CuAb. The anal area is 10.2 mm wide (below PsA) with nine to eleven rows of cells between AA and the posterior margin. The anal loop is transverse (length 2.0 mm; width 3.3 mm), five-celled, but not strongly defined, since posteriorly indistinctly closed. A distinct anal angle, thus, it is a male specimen. The anal triangle is divided into four cells (length of anterior side 3.4 mm; of distal side 6.6 mm). The hind margin (vein AP + AA'') of the anal triangle is strongly indented. Only two rows of cells between the anal angle and the next posterior branch of AA that lies below PsA. The characteristical anal area is identical in both hindwings.



Text-Fig. 75. *Cymatophlebia kuempeli* sp. nov. Holotype coll. KÜMPEL no. 42 - male, abdomen with genital lobes and anal appendages.

Body: Total body length (from head up to end of abdomen, including anal appendages), 97 mm. The head and thorax are very poorly preserved, but have been rather large; the legs are not visible. The male secondary genital apparatus of the second abdominal segment is not visible, since the holotype is preserved in dorsal aspect; Length of first abdominal segment 2.7 mm; of second 8.2 mm; of third 9.2 mm; the second segment is distinctly constricted with a width of 1.2 mm; there are no auricles visible on the second segment. There is a pair of symmetrical expanded and rounded lobes on abdominal segment III that are 7.7 mm long and 1.8 mm wide with a row of small spines along the distal third of the exterior margin of these lobes (Text-Fig. 75); identical lobes are also present on segment IV. All the abdominal segments clearly have a dorsal median longitudinal carina. The cerci are clearly visible and foliate, 5.7 mm long and 1.8 mm wide; they are narrower than those in males of *C. longialata*, less rounded and with a small spine at their apex (Text-Fig. 75); the inferior appendage (epiproct) is short (1.8 mm) and broad (1.4 mm), about rectangular in shape, and apically slightly bifid.

Discussion: The holotype shares all autapomorphies (enumerated above) of the Cymatophlebioidea stat. nov., Cymatophlebiidae and Cymatophlebiinae, while it lacks all autapomorphies of Valdaeshninae subfam. nov. Therefore, *C. kuempeli* sp. nov. can clearly be attributed to the genus *Cymatophlebia* (Cymatophlebiinae).



Text-Fig. 76. *Cymatophlebia* sp. MCZ - female, right pair of wings (drawing after NEEDHAM 1907: fig. 1; without scale).

NEEDHAM (1907: 141, fig. 1) figured a female specimen in the collection of the Museum of Comparative Zoology (Cambridge) that has eleven cells in the forewing discoidal triangle and eight cells in the hindwing discoidal triangle (Text-Fig. 76), but otherwise it agrees with *C. longialata* rather than *C. kuempeli* sp. nov. (e.g. only thirteen postnodal crossveins, more strongly undulated veins RP2 and IR2). The forewing length is 69 mm. The specimen distinctly differs from *C. kuempeli* sp. nov. as well as from *C. longialata* by the presence of three oblique secondary veins between IR2 and RP3/4 immediately basal of Rspl (as in the hindwing of *C. kuempeli* sp. nov., and maybe also in the forewing *C. herrlenae* sp. nov., a more transverse forewing discoidal triangle (also present in *C. herrlenae* sp. nov.), and only three rows of cells in the basal part of the postdiscoidal area (otherwise only known from *C. herrlenae* sp. nov., *C. pumilio* sp. nov., and *C. purbeckensis* sp. nov.). It mainly differs from *C. herrlenae* sp. nov. in the IR2 originating on RP1/2 instead of RP3/4, and the presence of eleven cells in the forewing discoidal triangle instead of only five cells. CARPENTER (1932: 112) supposed this specimen could belong to *"Cymatophlebia" jurassica* CARPENTER, 1932 (here classified as *Eumorbaeschna jurassica* gen. et comb. nov.), but it clearly differs from this species, in its greater number of cells in the discoidal triangles (at least compared to the paratype of *E. jurassica* gen. et comb. nov.), IR2 is much more undulated, Rspl strongly curved, and the anal loop missing. It is without doubt not conspecific with *E. jurassica* gen. et comb. nov., but a true *Cymatophlebia*; probably not a female specimen of *C. kuempeli* sp. nov., but maybe a somewhat aberrant specimen of *C. longialata* or *C. herrlenae* sp. nov. or more probably even a new species. Only a redescription of this specimen could solve this question, since considerable inaccuracies in

NEEDHAM's drawing cannot be excluded, e.g. the number of cells in the discoidal triangles (compare the differences between NEEDHAM's figure of *"Morbaeschna muensteri"* (*sensu* NEEDHAM 1907) and our new drawing of the same specimen in Text-Figs 93-96). Unfortunately, the first author could not find the original specimen during his thorough study of all fossil dragonflies in the CARPENTER collection at MCZ.

With now at least three (maybe four) known species from the lithographic limestones of Bavaria, the genus *Cymatophlebia* is not only one of the most common elements of the odonate fauna of the Upper Jurassic Solnhofen lagoon (together with *Tarsophlebia* and *Stenophlebia*), but also turns out to have been relatively diverse at this locality. A further species will be described by BECHLY (in prep.).

Nature of the expanded lobes on abdominal segments IV and/or III in *Cymatophlebia* species

Text-Figs 45, 47, 53-54, 56, and 75

These structures have been figured without interpretation by DEICHMÜLLER (1886: pl. 3, fig. 6), but HANDLIRSCH (1906: 591, pl. 47, figs 14-15) already considered that they correspond to a widening of the abdomen and that they are a constant character in males of *C. longialata*. They have also been recently briefly mentioned and figured in TISCHLINGER (1996, fig. 2, 4, 17-18).

These structures are visible in nearly all well-preserved male specimens (determined on the basis of the presence of the anal angle and anal triangle of the hindwings), and also preserved in at least one female specimen (no. 1957-14-ak-Bl., JME). However, the latter could of course be an aberrant specimen or an intersex / gynandromorph (compare SIVA-JOTHY 1987).

Each lobe appears to be more or less flexible and located on the latero-ventral side of the concerning segment with a small furrow between its posterior part and the main part of the segment that is formed by the corresponding tergite. These lobes occupy only 70 % of the length of segment in *C. longialata*, but they have the same length as the segment in *C. kuempeli* sp. nov. They generally possess small spines along the posterior parts of their exterior margins.

These unique abdominal lobes of *Cymatophlebia* can of course not be homologous with the lateral auricles of segment II of Anisoptera (BECHLY 1996), or the hypertrophied hamuli of some extant Trichodopalpida (e.g. *Apocordulia macrops* WATSON, 1980), because they are very dissimilar and are even situated on a different segment.

Structures that are certainly homologous (synapomorphic ?) with the genital lobes of Cymatophlebiinae are present in the related family Rudiaeschnidae (see discussion under the latter family and Plate 30: Figs 1-2).

Structures that are somewhat similar to the abdominal lobes of Cymatophlebiinae are present on the genital segment II in *Hypopetalia pestilens* (MCLACHLAN, 1870) (Austropetaliidae), additional to the auricles, and on the same segment in many Trichodopalpida (= Macromiidae & "Corduliidae" & Macrodiplacidae & Libellulidae), e.g. in *Oxygastra curtisii* (DALE, 1834), but they are not flexible and cannot be homologous, since they are located on a different segment than in Cymatophlebiinae.

However, some extant Gomphides - Lindeniinae and - Phyllogomphinae have quite similar lobes on the distal abdominal segments which correspond to movable lateral expansions of the tergites. These structures are always present in males, but sometimes also in females, e.g. in *Phyllogomphus aethiops* SELYS, 1854. In *Lindenia tetraphylla* (VAN DER LINDEN, 1825), there is a lateral lobe on each side of segments 7 and 8, while in *Phyllogomphus aethiops* such lobes are present on segment VIII and IX. Very similar lateral lobes are also present on segment VIII of male specimens of *Phyllopetalia apicalis* SELYS, 1857 (Aeshnoptera - Austropetaliidae). Since being located on different segments, too, these structures cannot be homologous with the abdominal lobes of Cymatophlebiinae either.

Nevertheless, the similar ventral position of these lobes, their relative flexibility and similar ornamentation strongly suggest that the corresponding structures of *Cymatophlebia longialata* and *Cymatophlebia kuempeli* sp. nov. are expanded lobes of the abdominal tergites of segment III (plus segment IV in *C. kuempeli* sp. nov.). The single visible difference between the lateral lobes of *Cymatophlebia* spp. is the absence of any small spines along the outer margin of these lobes in the extant Gomphides and Austropetaliidae. Even if they have a similar origin in extant Gomphides, Austropetaliidae and fossil Cymatophlebiinae, these structures are not homologous because they occur on segments 7-9 in the former and on segments 4 and/or 3 in Cymatophlebiinae. The great variability in dimensions and ornamentation of these lobes in different species of the same extant genus of Gomphides (e.g. Lindeniinae) suggests that a similar situation occurred in Mesozoic Cymatophlebiinae. Furthermore, the always single visible pair of "abdominal lobes" in *C. longialata* seems to be situated on different segments (3, 4, or even 5) in some specimens. Thus, this structure alone would not justify the creation of a separate genus and species for the specimen in coll. KÜMPEL (*C. kuempeli* sp. nov.).

The function of these structures remains unknown, but it could be possible that these abdominal lobes were distinctly coloured (as indicated by the kind of preservation of the holotype of *C. kuempeli* sp. nov.) and involved in a kind of courtship behaviour with expansion of the lobes by contraction of the dorso-ventral muscles of the concerning abdominal segments. On the other hand, this function could hardly explain the presence of spines along the margin of the lobes. The apparently obvious hypothesis of a correlation of the position of these lobes with that of the male secondary genital apparatus would be contradicted by the presence in the female sex (see above).

The presence of paired lobes on basal abdominal segments of *Cymatophlebia longialata* and *Cymatophlebia kuempeli* sp. nov. suggests that similar structures could be expected in other *Cymatophlebia* spp. and Cymatophlebiidae as well (phylogenetic inference of an unknown character; compare BRYANT & RUSSELL 1992, and NEL 1997).

Subfamily Valdaeshninae subfam. nov.

1996 Valdaeshninae; BECHLY, p. 383. (nomen nudum).

Type genus: *Valdaeshna* JARZEMBOWSKI, 1988.

Further included genera: *Hoyaeshna* NEL & MARTÍNEZ-DELCLÒS, 1993 and *Prohoyaeshna* gen. nov., and maybe *Libellulium* WESTWOOD, 1854 (see below).

Wing venational autapomorphies: Presence of a pseudo-ScP, derived from postnodal crossveins (only known from *Valdaeshna* and *Hoyaeshna*, not preserved in *Prohoyaeshna* gen. nov., but probably present, since *Prohoyaeshna* gen. nov. shares with *Hoyaeshna* the basal position of the pterostigmal brace as synapomorphy that is not shared by *Valdaeshna*); primary IR1 is secondarily much elongated and straight (convergent to Petalurida, Austropetaliida taxon nov. and a few aeshnids, like *Boyeria*); RP1 and RP2 secondarily divergent; RP3/4 and MA closely parallel up to the wing margin in both pairs of wings; PsA straight and short and much less oblique than in Cymatophlebiinae, correlated with longitudinally elongated discoidal triangles (unknown for *Prohoyaeshna* gen. nov., and transformed in ?*Valdaeshna andressi* sp. nov.).

Systematic position: *Valdaeshna surreyensis* JARZEMBOWSKI, 1988 and *Hoyaeshna cretacica* NEL & MARTÍNEZ-DELCLÒS, 1993 have been previously assigned to Aeshnidae (auct.) (JARZEMBOWSKI 1988, NEL *et al.* 1994), but several characters in their venation reveal that they are indeed members of the Cymatophlebiidae (BECHLY 1996):

(1) Dorso-longitudinal abdominal carina: *Valdaeshna* clearly has a dorsal longitudinal carina on the abdominal segments. Among extant Anisoptera such a structure is only found in Euaeshnida (except in *Gomphaeschna*) and in Eurypalpida, almost certainly by convergence. A dorsal abdominal carina is present in *Cymatophlebia*, too (see above). Since this carina is absent in the Heterophlebioptera (sistergroup of the Anisoptera, *Paraheterophlebia marcusi* NEL & HENROTAY in NEL *et al.*, 1993) and other Anisoptera, and since *Valdaeshna* and *Cymatophlebia* are without doubt unrelated to Eurypalpida, this character probably represents a synapomorphy with Euaeshnida. Unfortunately, the character state in *Prohoyaeshna* gen. nov. and *Hoyaeshna* is unknown, since the abdomen is not preserved in the concerning holotypes.

(2) Mspl: All Euaeshnida, including *Eumorbaeschna jurassica* gen. et comb. nov., and all basal extant aeshnids, do possess a very distinct Mspl, convergent to some Cymatophlebiinae, Aeschnidiidae and some Eurypalpida. The Mspl in *Valdaeshna* and *Hoyaeshna* is rather indistinct (unknown in *Prohoyaeshna* gen. nov.) and thus excludes a position of these two genera in Euaeshnida, since this would imply a unique reversal.

(3) Radial area: RP1 and RP2 are diverging from their origins in *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna*, while they are basally parallel in most other Aeshnoptera. Thus, within Aeshnoptera, the character state of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* has to be regarded as apomorphic reversals which represents a further potential synapomorphy for these three genera. It could only be interpreted as symplesiomorphy if these three genera would be regarded as most basal Aeshnoptera, even more basal than *Mesuropetala*, which would be in strong conflict with numerous other mentioned characters.

(4) Pseudo-anal vein PsA: *Valdaeshna* and *Hoyaeshna* share with Aeshnodea the apomorphic reduction of PsA to a "normal" cubito-anal crossvein (reversal). Nevertheless, this character is of rather low phylogenetic significance, since it is convergently present in many other unrelated Anisoptera, too, e.g. in the hindwing of some Petalurida, Lindeniinae and all Eurypalpida, and in both wings of Hageniidae and Cordulegastrida. This character is correlated with a secondary longitudinally elongated shape of the discoidal triangles which can easily evolve by convergence. The strongly longitudinally elongated discoidal triangles in *Valdaeshna* (and maybe in *Prohoyaeshna* gen. nov. and *Hoyaeshna*) indeed seem to be a convergence with Aeshnodea, since Gomphaeschnidae still have less elongated discoidal triangles at least in the hindwings.

(5) RP3/4 and MA distinctly parallel and distally undulated: This character is an autapomorphy of Aeshnoptera. It is shared by *Prohoyaeshna* gen. nov. and *Hoyaeshna*, but secondarily absent in *Valdaeshna*. Since the close relationship of *Hoyaeshna* and *Valdaeshna* is strongly supported, the reduction of the undulation in *Valdaeshna* and Aeshnodea must be due to convergence, just like in *Aeschnopsis* (except the type species) and *Archipetalia*.

(6) IR2-fork: The plesiomorphic absence of a dichotomic furcation of IR2 would exclude a position of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* within Aeshnodea, although a few Aeshnodea have secondarily lost this furcation (e.g. *Oplonaeschna* and *Boyeria*).

(7) Presence of two oblique veins 'O': This state is a shared similarity of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* with *Mesuropetala* and *Cymatophlebia*, but almost certainly represents a symplesiomorphy. Nevertheless, this symplesiomorphy excludes any position within Neoaeshnida which have the distal oblique vein 'O' reduced in the groundplan, while all Austropetaliida taxon nov. have the basal oblique vein 'O' reduced.

(8) Number of posterior branches of CuA in hindwings: *Valdaeshna* has seven branches of CuA, *Hoyaeshna* has nine branches of CuA, and *Cymatophlebia* generally has seven to nine branches of CuA as well. On the other hand, *Mesuropetala* has only six branches, the Austropetaliida taxon nov. have only four to six branches and Euaeshnida only four to seven branches. The more numerous branches seem to represent a symplesiomorphy that does not suggest a position within Austropetaliida taxon nov. or Euaeshnida. The lower number of branches cannot be considered as probable synapomorphy of Austropetaliida taxon nov. and Euaeshnida, because it is of too low phylogenetic significance, since it is present by convergence in most other extant Anisoptera as well.

(9) Rspl: The Aeshnidae (including *Epiaeschna* and *Oplonaeschna*) have a Rspl that is curved and separated by several rows of cells from IR2. Nevertheless, the character state in the basal Euaeshnida (Eumorbaeschnidae fam. nov., Gomphaeschnidae, Brachytronidae, and Telephlebiidae stat. nov., clearly demonstrates that this curved shape is a derived condition (synapomorphy of *Epiaeschna*, *Oplonaeschna*, and other Aeshnidae) which is definitely absent in the groundplan of Euaeshnida. A similarity of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* with *Oplonaeschna* in this character is irrelevant, since several other characters mentioned above exclude a position within Euaeshnida, therefore this similarity can only be due to convergence. A curved Rspl is a derived groundplan character (autapomorphy) of Cymatophlebioidea stat. nov., and at least in some Cymatophlebiidae a curved Mspl occurs as well (e.g. *C. zdrzaleki* comb. nov.). Therefore, the character state in *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* can be interpreted as a synapomorphy with Cymatophlebiidae.

(10) Pseudo-ScP: The presence of a pseudo-ScP in the aeshnid genus *Aeschnophlebia* is irrelevant, just like the presence in *Phenes* and Aeschnidiidae, since *Valdaeshna* and *Hoyaeshna* can clearly be excluded from crowngroup Euaeshnida, Petalurida and Aeschnidiidae, of which a pseudo-ScP is not representing a groundplan character. Therefore, this pseudo-ScP cannot be interpreted as homologous, but it can well be interpreted as a putative synapomorphy of *Valdaeshna* and *Hoyaeshna* (unknown in *Prohoyaeshna* gen. nov.).

(11) Long primary IR1: The same argument applies to the IR1. The long primary IR1 in *Boyeria*, *Allopetalia*, *Petaliaeschna* and *Cephalaeschna* represents an apomorphic state which does not belong to the groundplan of Euaeshnida. Since *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* cannot be regarded as ingroup Aeshnodea, this similarity is irrelevant, just like the long primary IR1 in Petalurida and Neopetaliidae. There is no conflicting evidence to the interpretation that the long primary IR1 is homologous in *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna*. It could be regarded as synapomorphy of these three genera, or as potential synapomorphy with Austropetaliida taxon nov., which is less likely.

(12) IR2 and RP2 parallel and undulated: In *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna*, these veins are well parallel and strongly undulated, just like in *Cymatophlebia*. This character state is absent in Austropetaliida taxon nov. and all Euaeshnida, and furthermore quite unique within Anisoptera (only present in very few "derived" genera, e.g. the libellulid *Pantala*). This character is a strong synapomorphy of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* with Cymatophlebiidae.

(13) Presence of a multicellular anal loop: A posteriorly closed anal loop with four to six cells is a groundplan character of Anisoptera. Furthermore, this is character is highly homoplastic and thus no strong conflicting evidence anyway. The anal loop was convergently reduced in several cases within Anisoptera (e.g. in Cymatophlebiinae) and also convergently enlarged several times (e.g. in *Hoyaeshna*).

(14) Well-defined convex oblique and undulated secondary veins anastomosing between IR2 and RP3/4, immediately basal of the origin of Rspl: This character is clearly present in *Prohoyaeshna* gen. nov. and *Hoyaeshna*, and weakly present in the hindwings of *Valdaeshna*, and represents a strong synapomorphy with Cymatophlebioidea stat. nov., especially Cymatophlebiinae.

(15) MAb and trigonal planate: MAb is straight in *Prohoyaeshna* gen. nov., unknown in *Hoyaeshna*, and angled in *Valdaeshna*. A convex secondary vein (trigonal planate) that is originating on MAb in the basal postdiscoidal area is well-developed in *Valdaeshna*, but absent in the other two genera. The angled MAb and trigonal planate of *Valdaeshna* therefore has to be regarded as a convergence to Liupanshaniidae fam. nov. (hindwing) and Euaeshnida / Neoaeshnida. Obviously, both states have been plesiomorphic in the groundplan of Valdaeshninae subfam. nov.

Conclusion: Character 13 is a common plesiomorphic state within Anisoptera and thus no valid phylogenetic evidence. Several characters strongly contradict a position of *Valdaeshna*, *Prohoyaeshna* gen. nov. and *Hoyaeshna* within Euaeshnida or even Aeshnodea (characters 2, 5, 6, 7, 8, 15). Therefore, any similarities with certain derived taxa within Aeshnodea are irrelevant, since they have to be interpreted as convergences that at best represent autapomorphies of Valdaeshninae subfam. nov. (characters 3, 4, 10, 11). Some of the derived similarities with Euaeshnida are also present in Cymatophlebiidae and therefore seem to belong to the groundplan of Aeshnida (characters 1). At least three characters have to be interpreted as strong evidence for a closer relationship with Cymatophlebiinae rather that Euaeshnida (characters 9, 12, and 14). Since there are no convincing synapomorphies known between Valdaeshninae subfam. nov. and any other families of Anisoptera or Aeshnoptera, there are no reasonable alternatives to a position in Cymatophlebiidae.

Genus *Valdaeshna* JARZEMBOWSKI, 1988

Type species: *Valdaeshna surreyensis* JARZEMBOWSKI, 1988, by original designation.

Other species: ?*Valdaeshna andressi* sp. nov.

New diagnosis: Within Valdaeshninae subfam. nov. this genus is characterized by the following features (hindwing): Discoidal triangle very elongated and narrow (autapomorphy), and divided into at least five cells; distal side MAb of the discoidal triangle bent (autapomorphy), and a well-defined convex secondary vein (trigonal planate) originates at the angle of MAb in the basal postdiscoidal area (autapomorphy); hypertriangle at least four-celled; one basal accessory antenodal crossvein between ScP and RA basal of Ax1 (probably an autapomorphy, but unknown in *Prohoyaeshna* gen. nov. and *Hoyaeshna*); most distal posterior branch of CuAa is distinctly secondarily branched from CuAa (autapomorphy, but weakly present in *Hoyaeshna*, too, and unknown in *Prohoyaeshna* gen. nov.).

Systematic position: *Valdaeshna surreyensis* was regarded as a "comparatively specialized" member of Aeshnidae - Brachytroninae by JARZEMBOWSKI (1988), but was transferred to Cymatophlebiidae by BECHLY (1996, 1999a, b) since it shares all autapomorphies of the Cymatophlebiidae, e.g. the parallel, but undulated course of RP2 and IR2 (synapomorphy); Rspl distinct with several rows of cells between it and IR2 (synapomorphy). Contrary to the original description there is no distinct Mspl (symplesiomorphy that excludes a position in Euaeshnida), and two oblique veins 'O' present in all three preserved wings (symplesiomorphy that excludes a position in Neoaeshnida). The distinct four- or five-celled anal loop that is posteriorly well-closed excludes a position in Cymatophlebiinae. *Valdaeshna* shares all autapomorphies of the Valdaeshninae subfam. nov. as enumerated above. Probable autapomorphies of *Valdaeshna* are the secondarily not undulated and distally not divergent veins RP3/4 and MA, the very elongated and narrow triangles in both wings, the unicellular subdiscoidal triangles in both pairs of wings (reversal), and the weak development of the secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. The holotype of *V. surreyensis* is very interesting also because of the surprisingly well-preserved thoracic and abdominal colour pattern (aeshnoid-like), indicating that this character state belongs to the groundplan of Aeshnida.

Valdaeshna surreyensis JARZEMBOWSKI, 1988

Text-Fig. 77

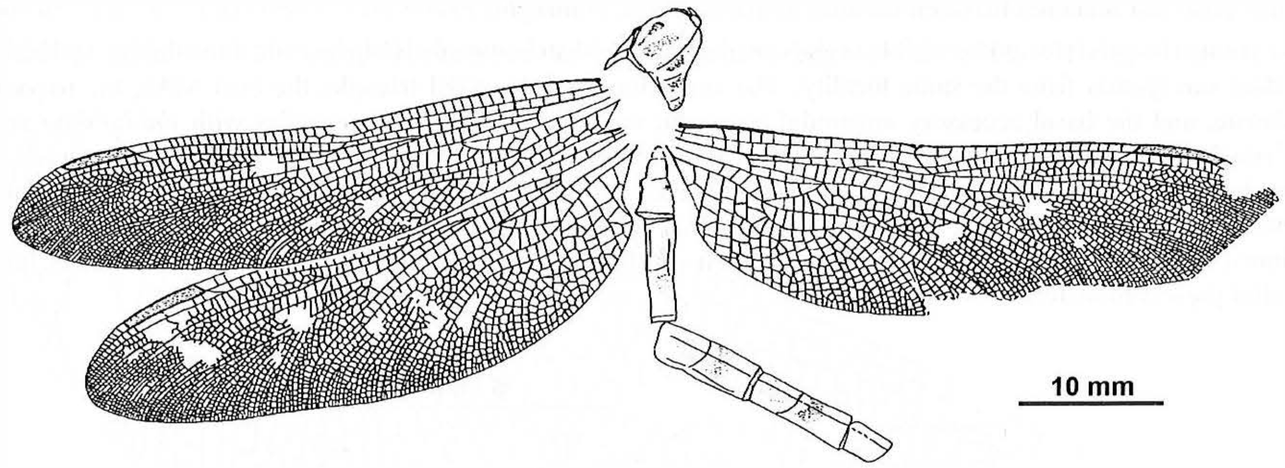
v. 1987 «the Surrey dragonfly», JARZEMBOWSKI, pp. 12-13.
*v 1988 *Valdaeshna surreyensis* JARZEMBOWSKI, pp. 763-767, text-figs 1-4 (in Aeshnidae).
1993b *Valdaeshna surreyensis* JARZEMBOWSKI; NEL & MARTÍNEZ-DELCLÒS, pp. 357-358.
1994 *Valdaeshna surreyensis* JARZEMBOWSKI 1988; NEL *et al.*, pp. 176-177.

Holotype: Specimen no. [In. 64632 a, b], BMNH, London; part and counterpart of an excellently preserved male, of which only head, end of abdomen, and the right forewing are missing.

Locus typicus: Auclaye Brickworks pit, near Capel, Surrey, England.

Stratum typicum: Upper Weald Clay, Lower Cretaceous, Barremian (not Hauterivian and Lower Weald Clay as previously stated by JARZEMBOWSKI 1988, and NEL *et al.* 1994).

New diagnosis: The only known distinctions from ?*Valdaeshna andressi* sp. nov. are the straight and short PsA, the two-celled submedian space and subdiscoidal cell, and the smaller anal loop which is only four- or five-celled.



Text-Fig. 77. *Valdaeshna surreyensis* JARZEMBOWSKI, 1988. Holotype BMNH In. 64632 a, b - male (combined drawing after JARZEMBOWSKI 1988: text-figs 1-3).

?*Valdaeshna andressi* sp. nov.

Text-Fig. 78

v. 1984 «aeshnid dragonfly», JARZEMBOWSKI, p. 74, fig. 3.
v. 1996b «Unnamed hindwing base»; JARZEMBOWSKI & NEL, p. 9, pl. 3, fig. 9.

Holotype: Specimen no. [1996. 222] (old. no. CH775), coll. E. JARZEMBOWSKI, MNEMG, Maidstone.

Derivatio nominis: Named in honour of Mr Raymond ANDRESS (London), a dedicated researcher and painter of Anisoptera, especially Petaluridae and Austropetaliidae.

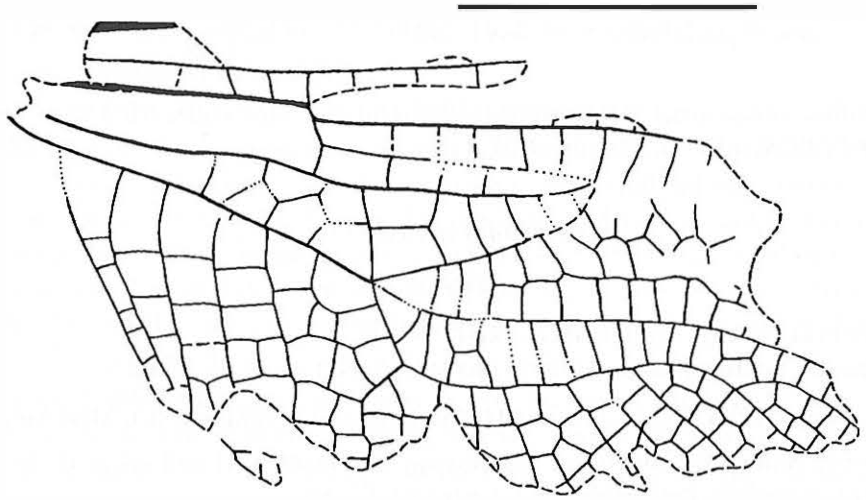
Locus typicus: Clockhouse Brickworks, near Capel, Surrey, England.

Stratum typicum: Lower Weald Clay, Lower Cretaceous, Hauterivian.

Diagnosis: Differing from the type species *Valdaeshna surreyensis* in the following hindwing characters: Anal loop relatively large, transverse pentagonal-shaped, and divided into eight cells; submedian space between CuP-crossing and PsA divided into three cells by a Y-shaped crossvein; PsA strongly zigzagged; subdiscoidal triangle divided into three cells; three posterior branches of AA basal of the anal loop in the female hindwing.

Description: Imprint of the basal part of a female hindwing. Except the dark veins there is no trace of coloration preserved, thus, the membrane has probably been hyaline. Length of fragment 15.6 mm; width 8.1 mm; distance from base to arculus 5.1 mm. Nodus and pterostigma not preserved. The antenodal crossveins between costal margin and ScP are poorly preserved, and only some of the antenodal crossveins between ScP and RA are visible, too, although according to their pattern, there probably have been numerous antenodal crossveins in both rows; there seems to be a basal accessory antenodal crossvein between ScP and RA basal of Ax1. Median space free of crossveins. Submedian space between the CuP-crossing (1.5 mm basal of the arculus) and PsA is divided into three cells. PsA strongly zigzagged and relatively weak. Subdiscoidal triangle only weakly defined and divided into three cells. Discoidal triangle very elongated, rather narrow and divided into six or seven cells; length of anterior side 4.0 mm; of basal side 1.5 mm; of distal side MAb, probably 4.3 mm; the distal side MAb of the discoidal triangle is curved or bent, but not really angled. Hypertriangle rather narrow (length 4.7 mm; max. width 0.5 mm), and at least four-celled. The bases of RP and MA are distinctly separated at arculus. Area between RP and MA traversed by numerous crossveins. Three rows of cells in the postdiscoidal area distal of the discoidal triangle. A distinct convex secondary vein (trigonal planate) in the postdiscoidal area, parallel to MA and MP, and originating on MAb. Width of the postdiscoidal area near the discoidal triangle 2.3 mm. CuAa has six strong posterior branches, the most distal one is secondarily branched from CuAa. The cubito-anal area seems to have been wide with probably more about six rows of cells between CuAa and the posterior wing margin. The anal area is broad with more than seven rows of cells between AA and the posterior wing margin. Anal loop large and transverse (length 2.4 mm; width 1.7 mm), of pentagonal shape, posteriorly well-closed, and divided into eight cells. No anal triangle, thus, it is a female specimen. AA has three posterior branches between the anal loop and the basal margin.

Systematic position: The visible wing venation of ?*Valdaeshna andressi* sp. nov. is very similar to *Valdaeshna surreyensis* from the same locality. The very elongated discoidal triangle, the bent MAb, the trigonal planate, and the basal accessory antenodal crossvein are all putative synapomorphies with *Valdaeshna surreyensis*. Unfortunately none of the autapomorphies of Cymatophlebiidae and Valdaeshninae is preserved in the fragmentary holotype. The very peculiar zigzagged and weak PsA in the hindwing could also represent a putative synapomorphy with *Rudiaeschna limnobia*, although this would be in conflict with the other mentioned characters. Anyway, the generic attribution of this new species has to be regarded as preliminary until better preserved material becomes available.



Text-Fig. 78. ?*Valdaeshna andressi* sp. nov. Holotype MNEMG 1996. 222 - female, right hindwing base.

Genus *Hoyaeshna* NEL & MARTÍNEZ-DELCLÒS, 1993b

Type species: *Hoyaeshna cretacica* NEL & MARTÍNEZ-DELCLÒS, 1993b, by original designation.

Systematic position: *Hoyaeshna* was regarded by NEL & MARTÍNEZ-DELCLÒS (1993b) and NEL *et al.* (1994) as an Aeshnidae - Gomphaeschninae, closely related to *Valdaeshna*. Nevertheless, *Hoyaeshna* shares all autapomorphies of Cymatophlebiidae, e.g. the parallel, but undulated course of RP2 and IR2 (synapomorphy), as well as RP3/4 and MA (symplesiomorphy); Rspl distinct with several rows of cells between it and IR2 (synapomorphy). The presence of two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl is a strong synapomorphy with the other Cymatophlebioidea stat. nov., while the absence of a well-defined Mspl is a symplesiomorphy that excludes a position in Euaeshnida. The plesiomorphic distinct anal loop that is posteriorly better closed than in *Cymatophlebia* excludes a position within Cymatophlebiinae. *Hoyaeshna* shares all autapomorphies of the Valdaeshninae subfam. nov. as enumerated above. A probable autapomorphy of *Hoyaeshna* seems to be the enlarged anal loop with thirteen cells. Potential synapomorphies of *Hoyaeshna* and *Prohoyaeshna* gen. nov. are discussed under the latter genus.

Hoyaeshna cretacica NEL & MARTÍNEZ-DELCLÒS, 1993b

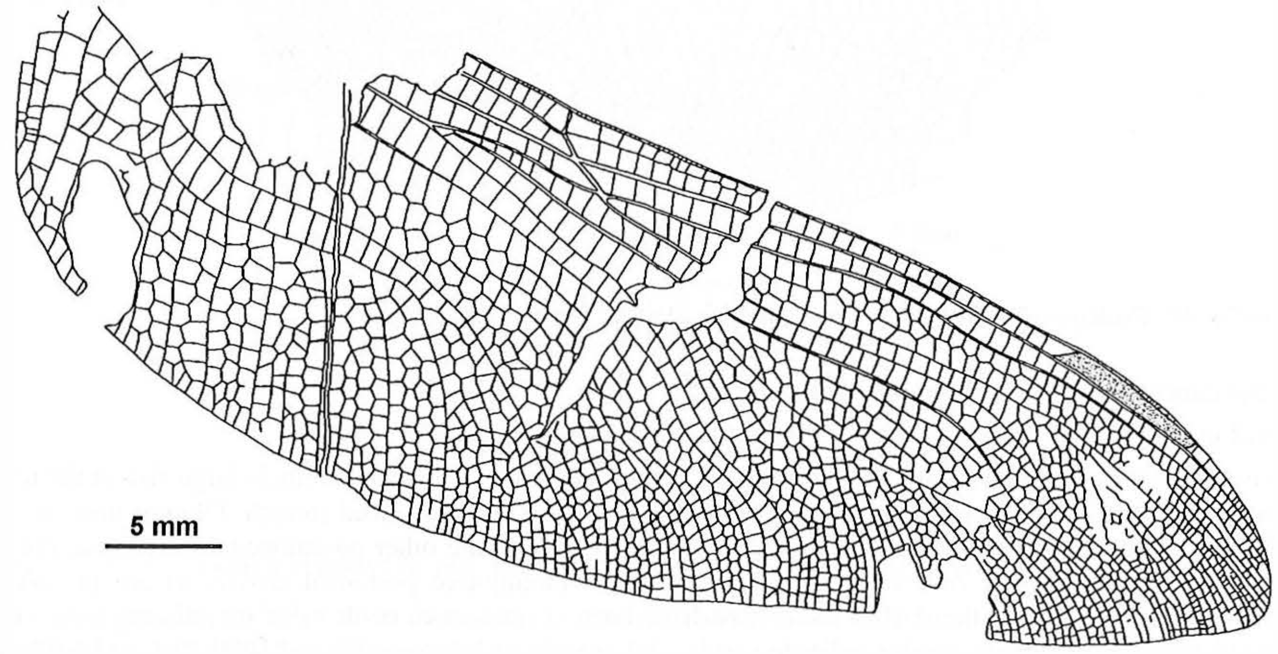
Text-Fig. 79

1988 «Aeshnidae (?) LEACH, 1815» SANZ *et al.*
*v 1993b *Hoyaeshna cretacica* NEL & MARTÍNEZ-DELCLÒS, pp. 354-358 (in Aeshnidae).
1994 *Hoyaeschna cretacica* NEL & MARTÍNEZ-DELCLÒS 1993b; NEL *et al.*, p. 177. (incorrect subsequent spelling of *Hoyaeshna* as *Hoyaeschna*).

Holotype: Specimen no. [ADR-0033-I], coll. Armado DIAZ-ROMERAL, Museo de Cuenca, Spain; an isolated female hindwing.

Locus typicus: Las Hoyas, 4 km NE of La Cierva, Cuenca Province, Spain.

Stratum typicum: Calizas de la Huérguina Formation (episodio 2), Lower Cretaceous, Barremian.



Text-Fig. 79. *Hoyaeshna cretacica* NEL & MARTÍNEZ-DELCLÒS, 1993b. Holotype Mus. Cuenca ADR-0033-I - female, right hindwing (drawing after NEL & MARTÍNEZ-DELCLÒS 1993b: fig. 3).

Genus *Prohoyaeshna* gen. nov.

Type species: *Prohoyaeshna milleri* sp. nov.

Derivatio nominis: After the genus *Hoyaeshna* due to its similarities.

Diagnosis: This genus and species is characterized as follows: Extremely large wings (maybe even the biggest crowngroup odonate at all) with very dense cross-venation; primary IR1 is secondarily very long (synapomorphy with other Valdaeshninae subfam. nov.); there are more than four rows of cells in the area between RP1 and RP2, basal of the pterostigma (synapomorphy with *Hoyaeshna*), viz three rows anterior of primary IR1 and one row posterior of it; the pterostigmal brace is basally recessed, four cells basal of the pterostigma (synapomorphy with *Hoyaeshna*); four rows of cells between RP2 and IR2 below the pterostigma (autapomorphy); max. seven rows of cells in the area between Rspl and IR2 (autapomorphy); two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl (synapomorphy with Cymatophlebioidea stat. nov.) that are very distinct and long (synapomorphy with *Hoyaeshna*); RP3/4 and MA undulated (symplesiomorphy with *Hoyaeshna*); about five rows of cells in the basal part of the postdiscoidal area (autapomorphy).

Prohoyaeshna milleri sp. nov.

Text-Figs 80-81

Holotype: Specimen no. [1996. 220], coll. R. CORAM, MNEMG, Maidstone.

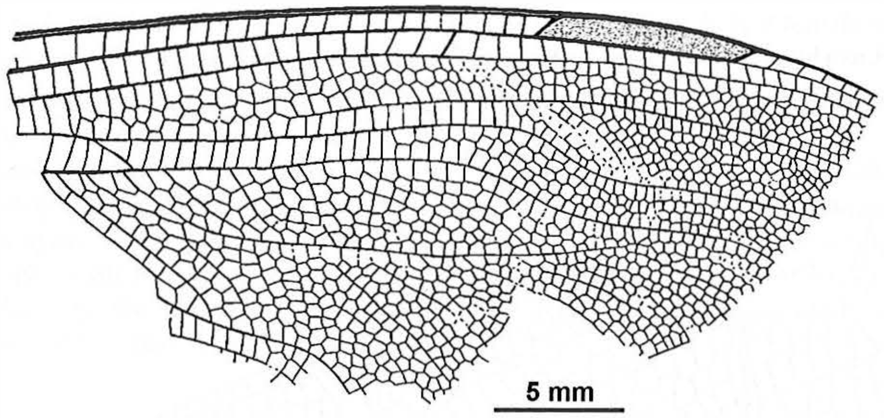
Paratype: Specimen no. [1996. 221], coll. R. CORAM, MNEMG, Maidstone.

Derivatio nominis: Named in honour of the late Dr Peter Lamont MILLER, in recognition of his important contributions to odonatology.

Locus typicus: Durlston Bay, Dorset, England.

Stratum typicum: Middle Purbeck beds, Lower Cretaceous, Berriasian.

Description



Text-Fig. 80. *Prohoyaeshna milleri* sp. nov. Holotype MNEMG 1996. 220 - wing apex.

♦ Specimen no. MNEMG 1996. 220; holotype

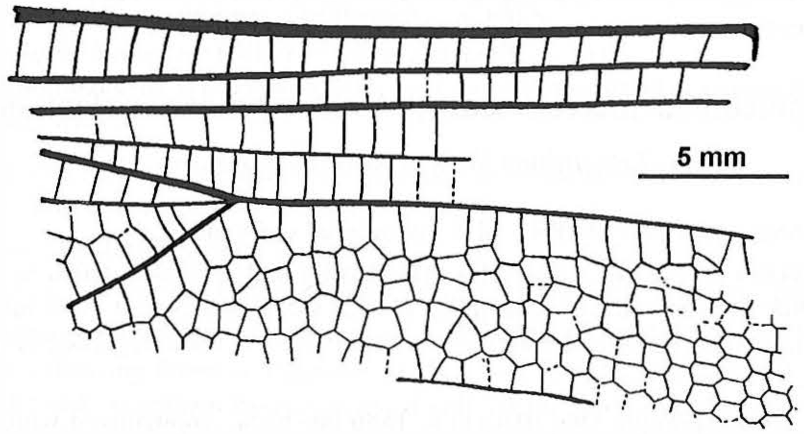
Text-Fig. 80

A costo-apical fragment of a wing. Length of fragment 33.8 mm, indicating an extremely large size of the total wing. Pterostigma very elongated, covering ten and a half cells, and unbraced (length 7.9 mm; max. width 1.2 mm); the pterostigmal brace vein is oblique and stronger than the other postsubnodal crossveins, but is recessed three and a half cells basal of the pterostigma. Twenty-five postnodal crossveins are preserved between nodus and pterostigma (but there must have been several more of them in the missing area), not aligned with the numerous corresponding postsubnodal crossveins between RA and RP1. RP1 and RP2 are sub-parallel up to the pterostigma, but there are up to four rows of cells between these veins basal of the pterostigma; RP1 and RP2 become strongly divergent beneath the pterostigma with numerous rows of cells in-between. There is a well-defined, straight and very long primary IR1 originating 9.4 mm basal of the pterostigma with three rows of cells between its basal part and RP1, and with only a single row of cells between its basal part and RP2; pseudo-IR1 seems to be fused with the primary IR1, but the base of pseudo-IR1 is still clearly visible as an oblique long vein between RP1 and IR1 below the distal half of the pterostigma. RP2 and IR2 are long and more or less parallel, but strongly undulated below the pterostigma; basally only a single row of cells between RP2 and IR2, but four rows of cells between the undulated parts of IR2 and RP2, and five or more rows of cells in the widened distal part of the area between these two veins. A very oblique vein 'O' is clearly visible in a relatively distal position between RP2 and IR2 which strongly suggests that there was another basal oblique vein 'O' near the subnodus. There is a well-defined vein and curved Rspl with six to eight rows of cells between it and IR2; Rspl and IR2 are distally converging. Two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. About five convex secondary veins (intercalaries) originate on Rspl and reach the posterior wing margin. RP3/4 and MA, although only partly preserved, are clearly undulated near the posterior wing margin; the distal parts of RP3/4 and MA first converge with only a single row of cells in-between, but diverge near the wing margin with two or more rows of cells in-between. The distinctly thickened costal margin is clearly developed as a double-barrel structure (the anterior "barrel" is formed by a fusion of CA + ScA, and the posterior "barrel" represents ScP).

♦ Specimen no. MNEMG 1996. 221; paratype

Text-Fig. 81

An antero-basal fragment of a forewing. Length of fragment 26.8 mm; compared to *Cymatophlebia kuempeli* sp. nov. the estimated total length of the hindwing is 91.3 mm, and that of the forewing 97.0 mm, based on the distance from discoidal triangle to nodus, but the estimated total length of the wings is 106.7 mm (forewing) and 100.4 mm (hindwing) when the width of the postdiscoidal area is used as reference value. Distance from distal angle of discoidal triangle to nodus 18.5 mm (this relatively "short" distance from discoidal triangle to nodus indicates that it is a fragment of a hindwing). There are numerous antenodal crossveins, twenty three are visible between costal margin and ScP, not aligned with the corresponding antenodal crossveins between ScP and RA. The second primary antenodal crossvein Ax2 is aligned and stronger than the secondary antenodal crossveins, and Ax2 is on a level with distal angle of discoidal triangle; seven secondary antenodal crossveins preserved basal of Ax2. Numerous antesubnodal crossveins in the area between RA and RP basal of subnodus. Numerous antefurcal crossveins visible between RP and MA basal of midfork. Arculus not preserved. Hypertriangle long and divided into many cells by more than four crossveins. The discoidal triangle is elongated and divided into at least eleven cells; its distal side MAb is straight without angle. Postdiscoidal area (width near discoidal triangle 6.0 mm) with five rows of cells directly of discoidal triangle. No Mspl visible in the preserved part of the postdiscoidal area.



Text-Fig. 81. *Prohoyaeshna milleri* sp. nov. Paratype MNEMG 1996. 221 - wing, discoidal area.

Discussion: Although these two fragments are very different parts of the wings, they probably belong to the same taxon, since both fragments come from the same locality and stratum, both can be attributed to Cymatophlebiidae, both are compatible in their large size, and both do not agree with any known species. The attribution of the holotype to Cymatophlebiidae is based on the following characters: RP2 and IR2 are strongly undulated and parallel, MA and RP3/4 are also strongly undulated and parallel, and Rspl is well-defined and strongly curved. The attribution of the paratype to Cymatophlebiidae is based on the following characters: There are numerous antenodal crossveins, the discoidal triangle is elongated and divided into many cells, the postdiscoidal area is very wide without distinct Mspl. Furthermore, all these characters occur together in the other Cymatophlebiidae, even if the paratype only shares symplesiomorphies and weak synapomorphies with this family. The holotype has a secondarily elongated primary IR1 and its pterostigmal brace is recessed basally; these characters are not present in Cymatophlebiinae, but only in Valdaeshninae subfam. nov., as convergence to Petalurida. Considering the synapomorphies shared by the holotype with Cymatophlebiidae, the most parsimonious solution is that this species belongs to the Cymatophlebiidae - Valdaeshninae subfam. nov. rather than to the Petalurida. Besides, some extant Aeshnodea like *Allopetalia*, *Boyeria*, *Petaliaeschna* and *Cephalaeschna*, also have a secondarily elongated primary IR1, similar to that of *Prohoyaeshna* gen. nov., while *Anax* also has a basally recessed pterostigmal brace (although in this case the pterostigma is recessed, too), thus, some homoplasy concerning these structures is even present within Aeshnoptera.

Prohoyaeshna milleri gen. et sp. nov. and *Libellulium agrias* (both from the Purbeck Limestone Group) share some characters, viz there are numerous rows of cells between a well-defined Rspl and IR2, and IR2 and RP2 both have a strong curvature. Nevertheless, the original figure of the holotype of *L. agrias* does not show the main autapomorphic characters of Valdaeshninae subfam. nov. and *Prohoyaeshna milleri* gen. et sp. nov., viz the secondarily elongated and straight primary IR1; the basally recessed pterostigmal brace; and it also shows significantly fewer of rows of cells between the main veins. Thus, a synonymy of these two taxa can be certainly excluded and there is also no sufficient evidence for a sistergroup relationship of *Prohoyaeshna milleri* gen. et sp. nov. and *L. agrias*. However, *Prohoyaeshna* gen. nov. shares with *Hoyaeshna* several highly derived characters, viz the basally recessed pterostigmal brace; the secondarily elongated and straight primary IR1; the very broad areas between Rspl and IR2 and between IR2 and RP2; and the very numerous postnodal crossveins between nodus and pterostigma. The only differences are as follows: There are many more rows of cells between Rspl and IR2, between IR2 and RP2, and between RP1 and RP2 in *Prohoyaeshna* gen. nov. compared to *Hoyaeshna*. Furthermore, within the Cymatophlebiidae, *Prohoyaeshna* gen. nov. has all the apomorphic characters of the Valdaeshninae subfam. nov. as listed above, although the presence of a pseudo-ScP distal of the nodus and the reduction of PsA, cannot be verified, since the concerning areas are not preserved in *Prohoyaeshna* gen. nov. Nevertheless, there is sufficient evidence for an attribution of *Prohoyaeshna* gen. nov. to Valdaeshninae subfam. nov. Since the pterostigmal brace is not recessed in *Valdaeshna*, the derived recession in *Prohoyaeshna* gen. nov. and *Hoyaeshna* most likely represents a synapomorphy of these two genera.

The postdiscoidal area is even wider than in *Cymatophlebia suevica* sp. nov. which is strikingly similar in the visible venation (the single reason why it was not synonymized with the present species is the well-defined Mspl which is not known in Valdaeshninae subfam. nov., although the concerning area is not preserved in *Prohoyaeshna milleri* gen. et sp. nov.). Therefore, the total length of the wing of *Prohoyaeshna milleri* gen. et sp. nov. even might have been bigger than in *Cymatophlebia suevica* sp. nov., and could thus represent the biggest known crowngroup Anisoptera at all.

Cymatophlebiidae incertae sedis (? Valdaeshninae subfam. nov.)

Genus *Libellulium* WESTWOOD, 1854 pos. nov.

Type species: *Libellulium agrias* WESTWOOD, 1854, by original designation.

Other species: WESTWOOD (1854: 387, pl. 17, fig. 21) also figured an insect which he named *Libellulium kaupii*. HANDLIRSCH (1908: 655) and NEL & PAICHELER (1992: 318) considered it as an Insecta *incertae sedis*, but we concur with HANDLIRSCH (1939) and JARZEMBOWSKI (1993: 177) who regarded the holotype specimen as an orthopteroid insect.

Systematic position: *Cymatophlebia* DEICHMÜLLER, 1886 has been synonymized with *Libellulium* WESTWOOD, 1854 by COWLEY (1934b), mainly based on the preliminary inclusion of *Libellulium agrias* in *Cymatophlebia* by HANDLIRSCH (1906). TILLYARD & FRASER (1940: 374), FRASER (1957: 95), CARPENTER (1992), NEL & PAICHELER (1992), JARZEMBOWSKI (1994), and BRIDGES (1994), like many others, followed this opinion. Obviously based on HANDLIRSCH (1906), LOHMANN (1996a) recently also classified *Libellulium agrias* in the genus *Cymatophlebia* which is of course at odds with the rules of nomenclature, since the generic name *Libellulium* is older than *Cymatophlebia*. WESTWOOD (1854) based the genus *Libellulium* on a poorly preserved and very incomplete fragment of the costo-apical part of a wing (Text-Fig. 82) from the Lower Cretaceous of England (JARZEMBOWSKI 1993, 1994). WESTWOOD (1854) only gave the following information: «pl. xv fig. 4 represents a portion (near the extremity) of one of the wings of a *Libellula* of very large size», and he named this fossil "*Libellulium agrias* W." without giving its dimensions. WESTWOOD's figure does not show any scale, but it was probably drawn to the scale 1:1. HANDLIRSCH (1906: 592) indicated that it is the apical part of a wing, of 70-75 mm total length with a similarly (compared to *C. longialata*) curved second branch of RP2 (called by him Medialis). HANDLIRSCH (1906) did not give any new figure and synonymized *Libellulium* with *Cymatophlebia* with some doubt. This doubt became pretended certitude with FRASER (1957) who synonymized these two genera without revision of the concerning types. The figure of WESTWOOD (the single available evidence, since the holotype is lost) shows Rspl, IR2, RP2, RP1, RA and the costal margin. The pterostigma is not clearly figured. The area between Rspl and IR2 seems to be very broad (six rows of cells), IR2 and RP2 make strong curves, stronger than that of *Cymatophlebia longialata*, but they are figured

reaching the posterior wing margin at right angles and not obliquely as in *C. longialata*. This figure of the fossil does not give any certain information. *Libellulium* shares with *Cymatophlebia* the strongly curved Rspl, IR2 and RP2, but this is only indicating its relationship with Cymatophlebiidae, but is not sufficient to for a generic identity of the two taxa because *L. agrias* has only two rows of cells between IR2 and RP2, unlike the very wide corresponding area in *Cymatophlebia*. A generic synonymy of *Libellulium* and *Cymatophlebia* could only be postulated if new well-preserved specimens of *Libellulium* would be discovered, and it would be demonstrated that the genus *Cymatophlebia* is paraphyletic to *Libellulium*. The wing venation of *Libellulium*, as far as it is known, is much more similar to *Hoyaeshna* or *Prohoyaeshna* gen. nov. than to *Cymatophlebia*, indicating that *Libellulium* could rather belong to the cymatophlebiid subfamily Valdaeshninae subfam. nov. than Cymatophlebiinae. Consequently, it is necessary to re-establish the distinction between the two valid genera *Libellulium* and *Cymatophlebia*, and to restore *Cymatophlebia longialata* in its original generic combination. Since the holotype is lost and the existing figures are insufficient for a diagnosis, *Libellulium agrias* WESTWOOD, 1954 has to be regarded as a nomen dubium which represents a Cymatophlebiidae *incertae sedis* (probably Valdaeshninae subfam. nov.).

Libellulium agrias WESTWOOD, 1854 nomen dubium

Text-Fig. 82

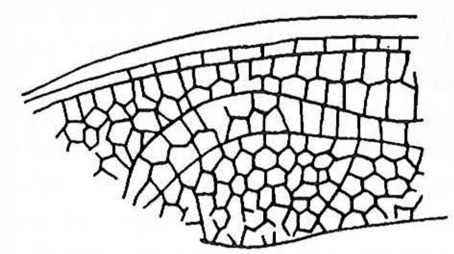
* 1854 *Libellulium agrias* WESTWOOD, pp. 387, 393-394, pl. 15, fig. 4.
1856 *Libellulium agrias*; GIEBEL, p. 286.
1906 ?*Cymatophlebia agrias* WESTWOOD; HANDLIRSCH, p. 592.
1934b *Libellulium agrias* WESTW.; COWLEY, p. 276.
1992 *Libellulium agrias* WESTWOOD; CARPENTER, p. 83.
1992 *Libellulium agrias* (WESTWOOD); NEL & PAICHELER, pp. 316-317.
1994 *Libellulium agrias* WESTWOOD; JARZEMBOWSKI, p. 71.
1994 *Libellulium agrias* WESTWOOD; BRIDGES, p. VII.5.
1996a *Cymatophlebia agrias* (WESTWOOD); LOHMANN, p. 231.
1998 *Libellulium agrias* WESTWOOD; NEL *et al.*, p.64 (considered as nomen dubium in Anisoptera *incertae sedis*).

Holotype: Current deposition unknown. The holotype has to be regarded as lost, and a neotype cannot be designated, since the holotype is the only known specimen.

Locus typicus: Durlston Bay, Dorset, England.

Stratum typicum: Lower Purbeck beds, Lulworth Formation, Lower Cretaceous, Berriasian.

Diagnosis: Not sufficiently known to allow a well-founded differential diagnosis, but this species could be characterized by the following features: Presence of two rows of cells between RP1 and RP2 basal of pterostigma; RP1 and RP2 only separated by two rows of cells at the strongest curvature of RP2 (beneath pterostigma); RP2 and IR2 relatively closely parallel, and very strongly undulated, but only separated by two rows of cells in the undulated area; Rspl very well-defined and strongly curved with up to six rows of cells between Rspl and IR2. The wings probably were very large, if the figure of WESTWOOD (1854) should indeed be in scale 1:1 (see above).



Text-Fig. 82. *Libellulium agrias* WESTWOOD, 1854. Holotype (lost) - apical wing fragment (drawing after WESTWOOD 1854: pl. 15, fig. 4; without scale).

Family Rudiaeschnidae fam. nov.

Type genus: *Rudiaeschna* DONG & ZI-GUANG, 1996.

Included genera: Currently only including the type genus *Rudiaeschna* DONG & ZI-GUANG, 1996, thus, preliminarily a redundant taxon.

Wing venational autapomorphies: PsA of the hindwing is more strongly zigzagged and distinctly weaker than that of the forewing (convergent *?Valdaeshna andressi* sp. nov. and some specimens of *Cymatophlebia longialata*); anal loop enlarged and gaff prolonged; RP1 and RP2 secondarily divergent; RP2 and IR2 distally distinctly diverging.

Diagnosis: As for type genus.

Systematic position: Rudiaeschnidae fam. nov. shares the following characters with Cymatophlebiidae: PsA well-defined (symplesiomorphy), but more or less angled (synapomorphy with Cymatophlebiidae ?); discoidal triangle elongated in both pairs of wings (autapomorphy of Aeshnomorpha); a strong Rspl (autapomorphy of Panaeshnida) which is distinctly curved and separated by several rows of cells from IR2 (synapomorphy with Cymatophlebiidae); two oblique veins 'O' (symplesiomorphy); more than two rows of cells in the postdiscoidal area (symplesiomorphy); an at least weakly defined Mspl (autapomorphy of Aeshnida ?); relatively broad and posteriorly well-closed anal loop (symplesiomorphy with Valdaeshninae subfam. nov. and Euaeshnida); about two oblique secondary veins are anastomosing between IR2 and RP3/4 basal of Rspl (this unique character state is a strong synapomorphy with Cymatophlebiidae). Consequently, the relationship of Rudiaeschnidae fam. nov. with Cymatophlebiidae is based on one strong and a few weak synapomorphies, and the absence of substantial conflicting evidence. The slightly enlarged anal loop with an elongated gaff is a derived similarity with Progobiaeshnidae fam. nov. and Euaeshnida, but is a very homoplastic character without phylogenetic significance. Therefore, we classify *Rudiaeschna* in a new family that is considered as sistergroup of Cymatophlebiidae, and distinguished from the latter by the presence of a more strongly zigzagged PsA in the hindwing (autapomorphy), and the plesiomorphic absence of the autapomorphies of Cymatophlebiidae (see above).

However, it must be noted that the photos of the *Rudiaeschna* specimen in coll. ROCKERS (Plate 30: Figs 1-2) show a male which clearly has lateral expansions on the third abdominal segment just like *Cymatophlebia*. Such expansions are not visible on the abdomen of the male holotype of *Valdaeshna surreyensis* JARZEMBOWSKI, 1988 (Text-Fig. 77), but this character state is unknown for all other Valdaeshninae subfam. nov. It cannot be excluded that these genital lobes represent a synapomorphy of the genera *Rudiaeschna* and *Cymatophlebia*, but it is as well possible that such lobes are also present in Valdaeshninae and are only invisible in the holotype of *Valdaeshna surreyensis* since they are flexed beneath the abdomen.

(+ Tunuiaeschna Lin et al. 2004. 1619A)

Genus *Rudiaeschna* DONG & ZI-GUANG, 1996

Type species: *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996, by original designation.

Diagnosis: DONG & ZI-GUANG (1996) gave a brief diagnosis of this genus that is not sufficient to compare it with other Aeshnoptera. The following new diagnosis is mainly based on the new specimens of *R. limnobia* described below: Pterostigmata elongated and distinctly braced; secondary antenodal crossveins not aligned; Ax2 on a level with distal angle of discoidal triangle; IR2 and RP2 smoothly undulated (less than Cymatophlebiidae) and distally divergent with about three rows of cells in-between; two oblique veins 'O'; RP1 and RP2 basally slightly diverging with two or three rows of cells in-between basal of pterostigma; only a short pseudo-IR1 present between RP1 and RP2; anal loop much more distinct and broader than in *Cymatophlebia*; more or less pentagonal, posteriorly rather well-closed, and divided into five to eleven cells; Rspl well-defined and slightly curved with two or three rows of cells between it and IR2; two oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl (at least distinct in the hindwing); MA and RP3/4 are smoothly undulated (less than Cymatophlebiidae) and divergent near the wing margin; a short and weakly developed Mspl with two or three rows of cells between it and MA; distal side MAb of discoidal triangle straight; discoidal triangles elongated and divided into six or seven small cells in forewing and four to six cells in hindwing; hypertriangles divided by one to three crossveins; at least one accessory cubito-anal crossvein in the submedian space between CuP-crossing and PsA; subdiscoidal triangles divided into three or four small cells in both pairs of wings; PsA weaker in hindwing than in forewing and distinctly zigzagged; basal part of area between MP and CuAa just distal of discoidal triangle broadened in hindwing (correlated with the elongation of the gaff), and both veins are distally strongly divergent; maybe there was a gap of antesubnodal crossveins between RA and RP close to arculus, especially in hindwings.

Rudiaeschna differs from *Cymatophlebia* in veins RP2 and IR2 being less distinctly undulated, in the presence of three rows of cells between RP1 and RP2 basal of the pterostigma, and in the broader and better-defined anal loop. It differs from the species of Valdaeshninae subfam. nov. in the following characters: Absence of a

secondarily elongated and straight primary IR1; presence of only three rows of cells between Rspl and IR2; presence of a well-defined PsA; pterostigmal brace not basally recessed (unlike in *Hoyaeshna* and *Prohoyaeshna* gen. nov.).

Rudiaeschna limnobia differs from *?Valdaeshna andressi* sp. nov., the only other species with a strongly zigzagged PsA, in the following hindwing characters: Discoidal triangle shorter and broader; distal side MAb of discoidal triangle straight; no convex secondary vein (trigonal planate) originating on MAb in the basal postdiscoidal area; submedian space divided into two cells by a single cubito-anal crossvein between CuP-crossing and PsA (instead of three cells); only two posterior branches of AA in female hindwing, basal of anal loop (instead of three branches).

Discussion: All the specimens that we attribute to *R. limnobia* only differ in minor features of infra-specific value and they also share the same shape and organisation of the main veins and areas. The very different shape and dimensions of the right and the left anal loop of specimen R. 55183 (male paratype) might suggest that the wing venation is more variable in this taxon than for example in extant Aeshnidae. Specimen R. 55183 (also male paratype) has distinctly longer wings than the other specimens, but these differences remain acceptable within the range of infra-specific variation. Since there are no important differences between any of these specimens that could not be interpreted as infra-specific variability or even artifacts of preservation, we attribute all of them to the same species *R. limnobia*.

Rudiaeschna limnobia DONG & ZI-GUANG, 1996

Text-Figs 83-89, Plate 29: Figs 1-2, Plate 30: Figs 1-2

* 1996 *Rudiaeschna limnobia*; DONG & ZI-GUANG, pp. 96-97, figs 1-4.

Holotype: Specimen no. [LB 94010], Geological Museum of China, Beijing; a female with head, thorax, two legs, basal three segments of abdomen, and complete fore- and hindwings.

Paratype: Specimen no. [LB 94011], Geological Museum of China, Beijing; a female with thorax, one leg, basal four segments of abdomen, complete hindwings and nearly complete forewings (only the apices are missing).

Additional material: Specimens nos [MNHN-LP-R. 55182] (imprint of left fore- and hindwings, connected to part of thorax), [MNHN-LP-R. 55183] (male hindwing and fragments of forewing), and [MNHN-LP-R. 55184] (female hindwing), MNHN, Paris; specimen no. [1995 I 39], coll. KIRSCH, BSP, Munich. There is also a rather poorly preserved isolated forewing in coll. BONNOT in Aubagne (France), and a well-preserved complete male specimen in the collection of the fossil trader Mr Glenn ROCKERS (PaleoSearch Inc.) in Hays (Kansas) who kindly supplied photographs of this specimen to the first author (Plate 30: Figs 1-2).

Locus typicus: Near Chaomidian Village, 25 km SE of Beipiao City, western Liaoning Province, P.R. China.

Stratum typicum: Yixian Formation, Lower Cretaceous (not Upper Jurassic as stated by DONG & ZI-GUANG 1996), Aptian (SMITH *et al.* 1995, WELLNHOFER 1997).

Diagnosis: Same as for genus, since monotypic.

Redescription: The original description by DONG & ZI-GUANG (1996) is very short and does not mention all important characters available and necessary for comparison with other Aeshnoptera, but the provided figures are excellent and allow an attribution of new material to this species. We therefore provide a "redescription" that is mainly based on such new material from the museums in Paris (MNHN) and Munich (BSP). Specimen no. [BSP 1995 I 39] represents the first record of this taxon from the Jiufutang-Formation (lower Aptian, 121.0 mybp), which is slightly younger than the Yixian Formation (Barremian - Aptian boundary, 121.1-122.9 mybp) (SMITH *et al.* 1995, WELLNHOFER 1997).

♦ Specimen no. MNHN-LP-R. 55182

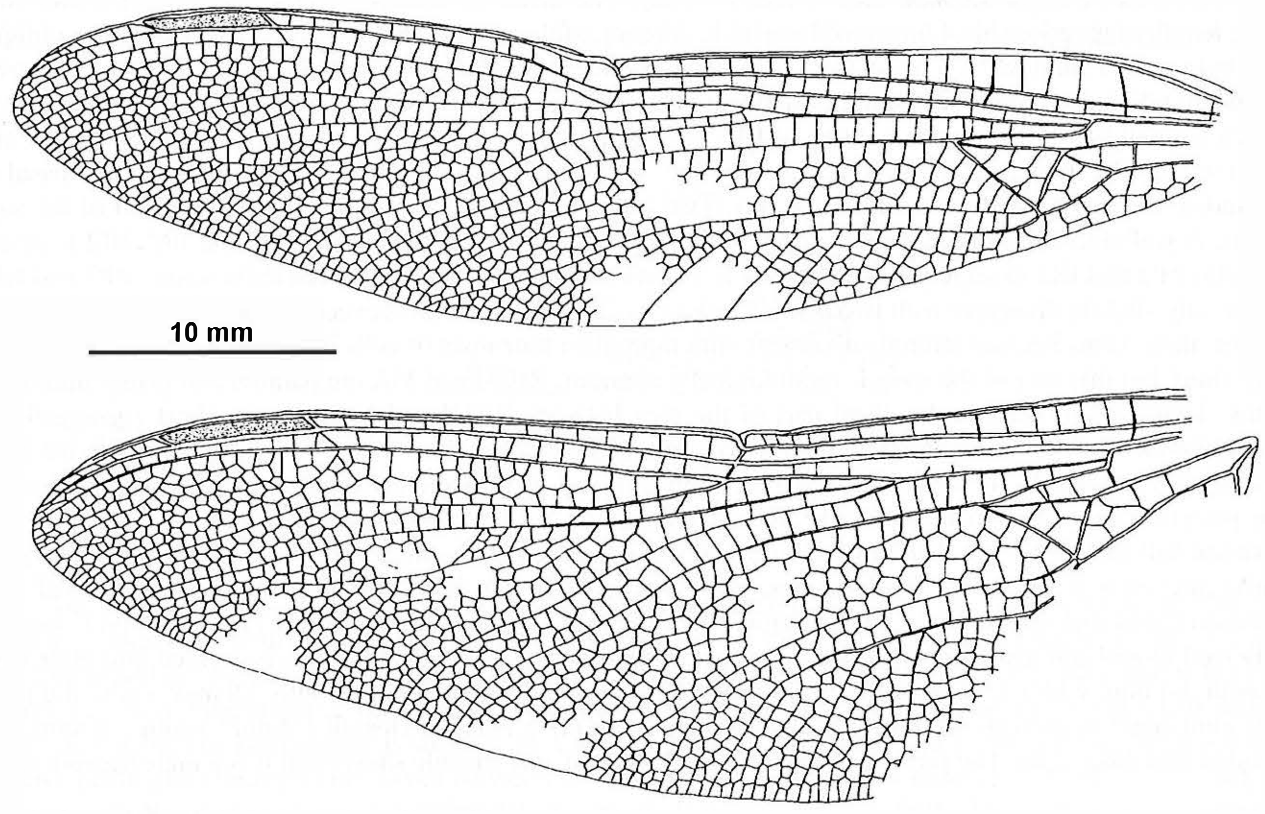
Text-Fig. 83

Imprint of the left fore- and hindwings, connected to part of the thorax. there is no preserved coloration, thus, the wings probably were hyaline.

Forewing: Length 50.0 mm; width 11.0 mm; distance from base to arculus 5.7 mm; distance from base to nodus 25.7 mm (the nodus is nearly midway between base and apex); distance from nodus to pterostigma

13.8 mm. Pterostigma elongated (length 5.0 mm; width 0.9 mm), covering four and a half cells, and strongly braced by a very oblique crossvein that is aligned with its basal side. Fourteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. Two primary antenodal crossveins aligned and stronger than the not aligned nineteen secondary antenodal crossveins; three secondary antenodal crossveins between Ax1 and Ax2; Ax1 is 1.4 mm basal of arculus, and Ax2 is 5.6 mm distal of Ax1, somewhat basal of distal angle of discoidal triangle. ScP fused with costal margin at nodus. Thirteen antesubnodal crossveins in area between RA and RP, basal of subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing and one distal cubito-anal crossvein. Hypertriangle traversed by two small crossveins (length 5.4 mm; max. width 0.6 mm). Distance from arculus to discoidal triangle 1.0 mm. Discoidal triangle elongated, divided into seven smaller cells; length of anterior side 4.3 mm; of basal side 2.4 mm; of distal side MAb 4.3 mm; MAb is straight. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle divided into four cells, (length 3.0 mm; max. width at PsA 2.1 mm). Base of IR2 5.1 mm basal of nodus that of RP3/4 7.1 mm basal of nodus. Bases of RP and MA distinctly separated at angled arculus. Area between RP and MA traversed by numerous crossveins. Five crossveins Bqs in space between RA, IR2 and basal of oblique vein 'O', including four bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', 0.8 mm and 4.5 mm distal of subnodus. A well-defined, long and slightly curved Rspl with three rows of cells between it and IR2. Three convex secondary veins originating on Rspl. RP2 and IR2 gently diverging, both smoothly undulated. Two to four rows of cells between distal parts of RP2 and IR2 (four cells in-between at wing margin). RP2 and RP1 basally divergent with two or three rows of cells in-between up to pterostigma, but below basal side of pterostigma, these veins become more strongly divergent with four or more rows of cells in-between. Pseudo-IR1 very short, originating on RP1 slightly distal of distal side of pterostigma. RP3/4 and MA parallel, gently undulated, but diverging near the wing margin with five cells along wing margin. Three or four rows of cells in postdiscoidal area distal of discoidal triangle, the width of this area distal of discoidal triangle is 2.7 mm and 3.3 mm. One convex secondary vein in distal postdiscoidal area originating on Mspl. MP and MA more or less parallel. MP and CuA distally strongly divergent, separated by probably nineteen cells at wing margin. CuAa with five distal long posterior branches. Cubito-anal area max. 3.4 mm wide with five or six rows of cells between CuA and posterior margin. Two rows of cells in anal area which is 1.7 mm wide (below PsA).

Hindwing: Length 50.1 mm; width at nodus 14.9 mm; distance from base to arculus 6.0 mm; distance from base to nodus 21.2 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 17.1 mm. Pterostigma elongated (length 6.2 mm; width 1.0 mm), covering six cells of irregular length, and strongly braced by a very oblique crossvein that is aligned with its basal side. Sixteen postnodal crossveins between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins. Two primary antenodal crossveins aligned and stronger than the not aligned fourteen secondary antenodal crossveins; five secondary antenodal crossveins between Ax1 and Ax2; Ax1 is 1.0 mm basal of arculus, and Ax2 is 6.3 mm distal of Ax1, nearly on a level with distal angle of discoidal triangle. ScP fused with costal margin at nodus. Only five antesubnodal crossveins preserved between RA and RP, basal of subnodus, but they are not preserved (or have been absent) in the basal part of this area. Median space free of crossveins. Submedian space only traversed by CuP-crossing (2.1 mm basal of arculus) and one distal cubito-anal crossvein above PsA. Hypertriangle traversed by three small crossveins (length 5.2 mm; max. width 1.0 mm). Distance from arculus to discoidal triangle 1.0 mm. Discoidal triangle elongated, divided into four small cells; length of anterior side 4.4 mm; of basal side 2.3 mm; of distal side MAb 4.3 mm; MAb is straight. Oblique PsA between AA and MP + CuA distinctly weaker than in forewing and strongly zigzagged. A well-defiined three-celled subdiscoidal triangle (length 3.0 mm; max. width at PsA 2.1 mm). Base of IR2 5.7 mm basal of nodus; that of RP3/4 6.6 mm basal of nodus. Bases of RP and MA distinctly separated at arculus. Arculus angled. Area between RP and MA traversed by numerous antefurcal crossveins. Six crossveins between RP and IR2 basal of 'O', including five bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.6 mm and 5.7 mm distal of subnodus. Rspl well-defined and slightly curved with up to three rows of cells between it and IR2. Two or three convex secondary veins originating on Rspl. One or two oblique secondary veins between IR2 and RP3/4 immediately basal of origin of Rspl, but they are somewhat indistinct and distally zigzagged. RP2 and IR2 gently diverging, both smoothly undulated with three rows of cells between distal parts of these veins (four cells in-between at wing margin). RP2 and RP1 basally slightly divergent with two or three rows of cells in the area in-between, but below the pterostigma, these veins become strongly divergent with more than four rows of cells in-between. Pseudo-IR1 very short, originating on RP1 below distal side of pterostigma. RP3/4 and MA parallel and gently undulated, diverging near wing margin. Two to four rows of cells in distal area between RP3/4 and MA (six cells in-between at wing margin). A short and zigzagged Mspl with two or three rows of cells between it and MA. Two convex secondary veins originating on Mspl in distal part of postdiscoidal area. Four to five rows of cells in postdiscoidal area distal of discoidal triangle, MP and MA are more or less parallel, so that postdiscoidal area only smoothly widened distally (width near discoidal triangle 3.4 mm; width at wing margin 6.3 mm). One or two rows of cells in the basal area between MP and CuA, but distally MP and CuAa strongly divergent, separated by eleven cells at wing margin. CuAa with five posterior branches. Cubito-anal area max. 6.6 mm wide with ten or eleven rows of cells between CuAa and posterior wing margin. Basal part of cubito-anal area and complete anal area not preserved, so that it is hardly possible to determine the sex of this specimen, although the preserved base of the anal vein suggests the presence of a membranule and an anal triangle, so that it could rather be a male specimen.



Text-Fig. 83. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. MNHN-LP-R. 55182 - left pair of wings.

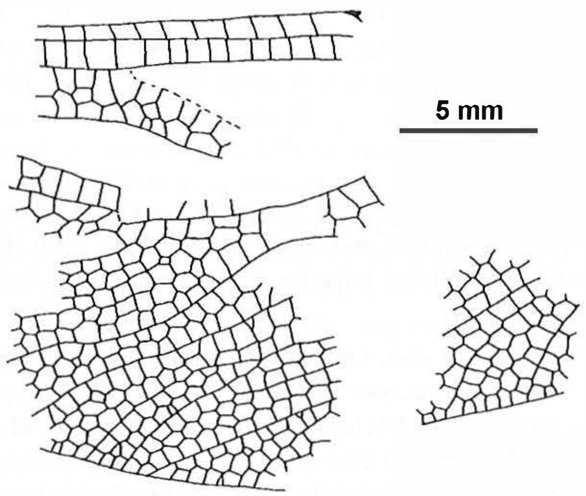
♦ Specimen no. MNHN-LP-R. 55183; male

Text-Figs 84-86

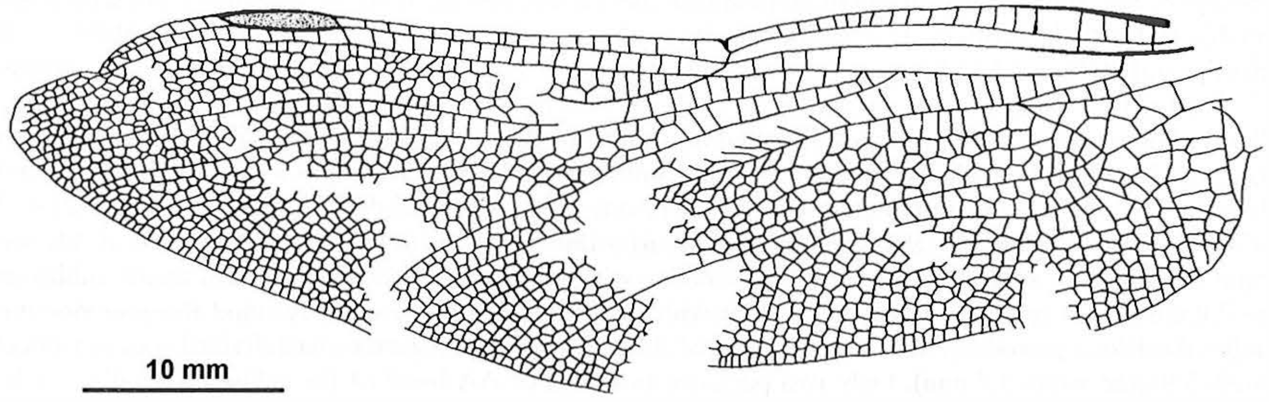
Imprint of a nearly complete left hindwing, the anal area of the right hindwing, and fragments of the left forewing. Only the median part of this forewing is preserved. The left hindwing shows a teratological deformation in the costo-apical region. The wings probably have been hyaline. An anal angle and anal triangle is visible in the hindwings, thus, it is a male specimen.

Forewing: Length unknown; width 14.6 mm. Only a small part of nodus preserved. Eleven postnodal crossveins visible between nodus and pterostigma, not aligned with corresponding postsubnodal crossveins between RA and RP1. Three rows of cells between RP1 and RP2. Only the distal oblique vein 'O' is preserved. Rspl strong with two or three rows of cells between it and IR2. RP3/4 gently undulated. Two rows of cells between RP3/4 and MA 6.2 mm basal of Rspl. The area between RP3/4 and MA is widened near the posterior wing margin. Mspl is rather well-defined, 6.0 mm long with two rows of cells between it and MA. The area between MA and MP is not distinctly widened near the posterior wing margin (width of postdiscoidal area at posterior wing margin 5.2 mm).

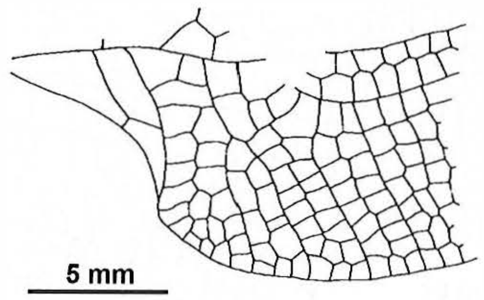
Hindwing: Length 65.0 mm; width 17.5 mm; distance from base to arculus 7.5 mm; distance from base to nodus 27.5 mm. The nodus is in a basal position; distance from nodus to pterostigma 19.3 mm. Pterostigma 5.5 mm long and 1.1 mm wide, covering four and a half cells, and strongly braced by an oblique crossvein that is aligned with its basal side. More than eighteen postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are aligned and stronger than the seventeen preserved secondary antenodal crossveins between costal margin and ScP, while the second row of antenodal crossveins between ScP and RA is not preserved; only two secondary crossveins visible between Ax1 and Ax2; Ax1 is 1.6 mm basal of the arculus, and Ax2 is 6.0 mm distal of Ax1, nearly on a level with distal angle of the discoidal triangle. ScP fuses with the costal margin at the nodus. Four antesubnodal crossveins preserved in the area between RA and RP basal of the subnodus, but these crossveins are not preserved (or have been absent) in the basal part of this area. Median space free of crossveins. Submedian space apparently only traversed by the CuP-crossing. Hypertriangle divided by three crossveins (length 5.6 mm; max. width 1.0 mm). The discoidal triangle is elongated, divided into four cells; length of anterior side 4.6 mm; of basal side 2.8 mm; of the straight distal side MAb 4.5 mm. The oblique PsA between AA and MP + CuA is weakly defined (distinctly weaker and more zigzagged than in the known forewings). Subdiscoidal triangle well-defined and three-celled. Base of IR2 6.8 mm basal of the nodus; that of RP3/4 8.5 mm basal of the nodus. Bases of RP and MA distinctly separated at arculus. Area between RP and MA traversed by numerous crossveins. Seven bridge-crossveins Bqs in the space between RP and IR2 basal of subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 4.0 mm and 9.3 mm distal of the subnodus. A well-defined, rather straight and long Rspl with three rows of cells between it and IR2. IR2 is nearly straight. RP2 and IR2 diverge gently. Three to five rows of cells in the area between these veins. RP2 and RP1 are basally slightly divergent with two or three rows of cells in the area in-between, but nearly below the pterostigma, these veins become strongly divergent with more than four rows of cells in-between. The pseudo-IR1 is very short, but this part of the wing is teratologically aberrant. RP3/4 and MA are parallel and gently undulated veins. Two rows of cells in the distal part of the area between RP3/4 and MA. A very short zigzagged and poorly defined Mspl, 4.0 mm long with three rows of cells between it and MA. Four rows of cells in the postdiscoidal area distal of the discoidal triangle; width of this area near the discoidal triangle 4.0 mm and along the posterior wing margin 6.5 mm. MP and MA are more or less parallel. Two rows of cells in the area between MP and CuAa just distal of the discoidal triangle, but distally these veins become strongly divergent. CuAa has seven or eight posterior branches. The cubito-anal area is 6.5 mm wide with about ten rows of cells between CuAa and the posterior wing margin. The anal area is broad, 8.7 mm wide. The anal loop is posteriorly well-closed and nearly as broad as in the female paratype R. 55184, the left one is divided into eight cells (length 4.4 mm; width 3.2 mm) while the right one is divided into nine cells (length 3.8 mm; width 4.0 mm). The anal angle is present, but not very acute. The anal triangle is broad (length 6.2 mm; width 5.8 mm), and divided into three cells. The presence of an anal angle and an anal triangle shows that it is a male specimen.



Text-Fig. 84. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. MNHN-LP-R. 55183 - male, left forewing, median part.



Text-Fig. 85. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. MNHN-LP-R. 55183 - male, left hindwing.

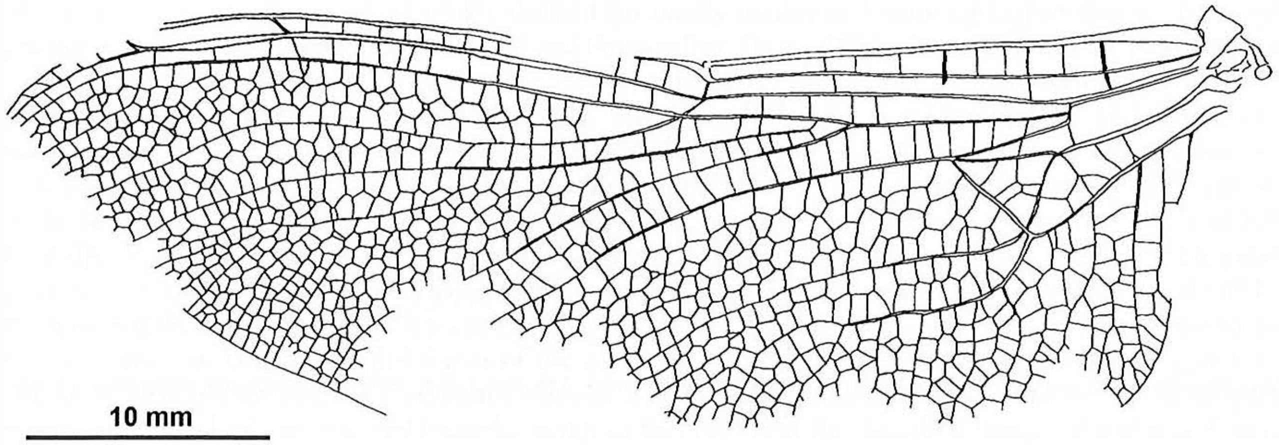


Text-Fig. 86. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. MNHN-LP-R. 55183 - male, right hindwing base.

♦ Specimen no. MNHN-LP-R. 55184; female

Text-Fig. 87

This specimen is representing the imprint of a nearly complete female hindwing. The wing apparently was hyaline. Hindwing length 51.6 mm; estimated width at nodus 17.3 mm; distance from base to arculus 5.6 mm; distance from base to nodus 21.0 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 17.8 mm. Pterostigma elongated (length 6.4 mm; width 1.3 mm), and covering three and a half cells of irregular length. The pterostigma is strongly braced by an oblique crossvein that is aligned with its basal side. Twelve postnodal crossveins preserved between nodus and pterostigma (total number probably seventeen), not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are aligned and stronger than the seven preserved secondary antenodal crossveins; four secondary crossveins between Ax1 and Ax2; Ax1 is 1.7 mm basal of the arculus, and Ax2 is 6.7 mm distal of Ax1 on a level with distal angle of discoidal triangle. ScP fuses with the costal margin at the nodus. Four antesubnodal crossveins preserved in the area between RA and RP, basal of the subnodus, but these crossveins are not preserved (or have been absent) in the basal part of this area. Median space free of crossveins. Submedian space only traversed by CuP-crossing (2.0 mm basal of the arculus) and one distal cubito-anal crossvein between CuP-crossing and PsA. Hypertriangle only divided by one crossvein (length 5.0 mm; max. width 1.0 mm). Discoidal triangle is elongated, divided into six cells, and is distinctly broader and shorter than that of the hindwing of the holotype; length of anterior side 4.3 mm; of basal side 3.3 mm; of the distal side MAb 4.2 mm; MAb is straight. PsA is relatively weak and distinctly angled, similar to that in the other specimens. Subdiscoidal triangle well-defined and divided into four cells (length 3.1 mm; max. width at PsA 2.3 mm). The base of IR2 is 5.6 mm basal of the subnodus; that of RP3/4 is 7.0 mm basal of the subnodus. Bases of RP and MA distinctly separated at arculus. The arculus is angled. The area between RP and MA is traversed by numerous antefurcal crossveins. Four bridge-crossveins Bqs in the space between RP and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 3.1 mm and 8.7 mm distal of the subnodus. A well-defined Rspl which is long and slightly curved with two or three rows of cells between it and IR2. Three oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP2 and IR2 are distally divergent and gently undulated veins (RP2 more distinctly so) with three or four rows of cells between their distal parts. RP2 and RP1 are basally more or less parallel with three rows of cells in-between up to the pterostigma, but below the basal side of pterostigma, these veins become more strongly divergent with four or more rows of cells in-between. The pseudo-IR1 is very short, originating on RP1 below the distal side of the pterostigma. RP3/4 and MA are parallel and gently undulated veins with at least two rows of cells between their distal parts. A very short, zigzagged and poorly defined Mspl with two or three rows of cells between it and MA. Four rows of cells in the postdiscoidal area distal of the discoidal triangle. MP and MA are more or less parallel, so that the postdiscoidal area is only smoothly widened distally (width near discoidal triangle 4.1 mm; width near wing margin probably 6.3 mm). Two rows of cells in the basal area between MP and CuAa just distal of the discoidal triangle. CuAa has six posterior branches. Cubito-anal area wide with probably up to eleven rows of cells between CuAa and the posterior wing margin; estimated max. width of the cubito-anal area 7.0 mm. Anal area broad (width 9.1 mm) with ten rows of cells between AA and the posterior wing margin. Anal loop posteriorly less distinctly closed than in the other specimens, and divided into eleven cells (length 3.9 mm; width 3.4 mm). Only two posterior branches of AA basal of the anal loop. Neither an anal angle, nor an anal triangle, thus, it is a female specimen. A membranule is not preserved.



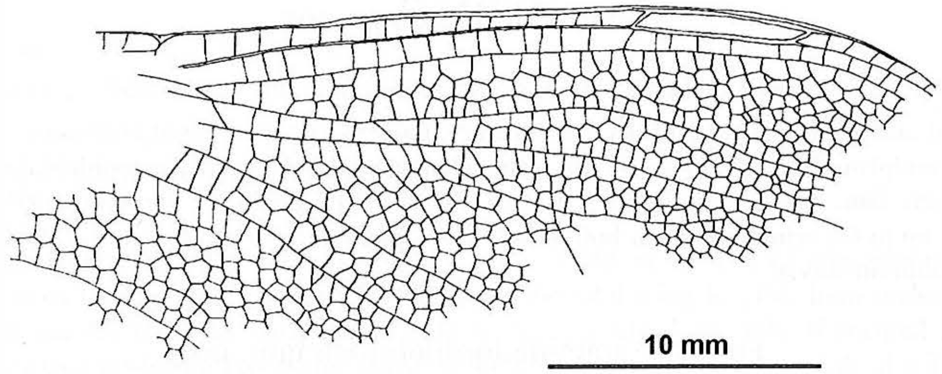
Text-Fig. 87. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. MNHN-LP-R. 55184 - female, left hindwing.

♦ Specimen no. BSP 1995 I 39; labelled «*Gobiaeschna* sp. (det. Ernst-Gerhard BURMEISTER Zool. Staatssammlung München), Unterkreide, Jiufutang-Formation, Provinz Liaoning, China»

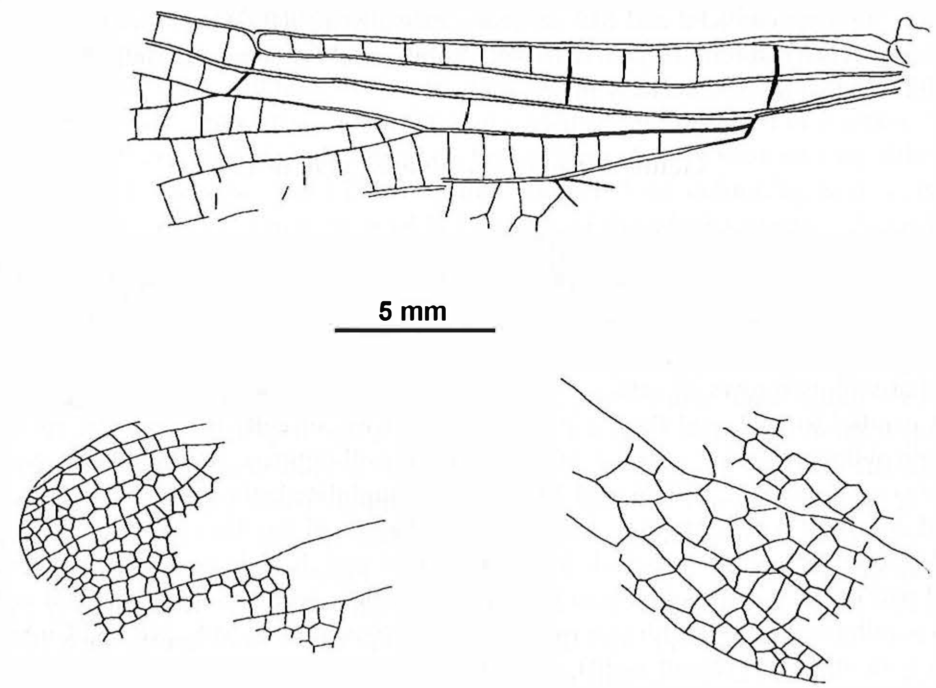
Text-Figs 88-89, Plate 29: Figs 1-2

This specimen is representing the imprint of two hindwings that were originally attached to the thorax, but unfortunately the thorax and wing bases have been destroyed by the Chinese preparator who faked a very curious and large wasp-like body with long antennae and a petiolus between thorax and abdomen. Several potentially important characters have been destroyed by this incredible procedure. Hindwing length 52.5 mm; distance from base to arculus 5.0 mm; distance from base to nodus 21.2 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 18.5 mm. Pterostigma elongated (length 6.7 mm; width 1.0 mm), covering nearly five and a half cells of irregular length, and strongly braced by an oblique crossvein that is aligned with its basal side. Seventeen postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are aligned and stronger than the ten secondary antenodal crossveins (no antenodal crossveins visible between ScP and RA, but this is certainly due to an artifact of preservation); three secondary antenodal crossveins visible between Ax1 and Ax2; Ax1 is 0.5 mm basal of the arculus, and Ax2 is 6.8 mm distal of Ax1, nearly on a level with distal angle of the discoidal triangle. ScP fuses with the costal margin at the nodus. There are less than three antesubnodal crossveins visible in the area between RA and RP, basal of the subnodus, but they are not preserved (or have not been present) in the basal part of this area. Median space probably free of crossveins. Submedian space not preserved. AA divided into a weak and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into three cells. The discoidal triangle is only partly preserved, but it was probably elongated. The hypertriangle is also only poorly preserved. The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Two or three preserved bridge-crossveins Bqs in the space between RP and IR2 basal of the subnodus, but they were probably more numerous (about six). Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.4 mm and 7.5 mm distal of the subnodus. A well-defined, long and slightly curved

Rspl with three rows of cells between it and IR2. IR2 is nearly straight. Two distinct oblique secondary veins between IR2 and RP3/4 immediately basal of the origin of Rspl. RP2 and IR2 distally divergent with three rows of cells in the area between their distal parts. RP2 and RP1 basally slightly divergent with two or three rows of cells in-between up to the pterostigma, but below the pterostigma, these veins become more strongly divergent with four or more rows of cells in-between. The pseudo-IR1 is very short, originating on RP1 below the distal side of the pterostigma. RP3/4 and MA parallel and gently undulated with two or three rows of cells between their distal parts. No distinct Mspl visible in the preserved parts of the postdiscoidal area. More than three rows of cells in the postdiscoidal area distal of the discoidal triangle, the width of this area is 3.5 mm near the discoidal triangle. MP and MA are more or less parallel. CuAa is not preserved. The anal area is poorly preserved, but it is broad with about eight or nine rows of cells between AA and the posterior wing margin; width of anal area 8.7 mm. Anal loop relatively small (length 3.1 mm; width 2.5 mm), posteriorly well-closed, and divided into six cells.



Text-Fig. 88. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. BSP 1995 I 39 - right hindwing, distal half.



Text-Fig. 89. *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996. BSP 1995 I 39 - left hindwing, nodal area, base, and apex.

♦ Specimen without number, coll. ROCKERS; male

Plate 30: Figs 1-2

A complete and well-preserved specimen. The wing venation totally agrees with the other known specimens, so that their specific identity is almost certain: Pterostigma elongated; IR1 originating beneath distal end of pterostigma; area between RP2 and IR2 distally widened; Rspl; no Mspl; discoidal triangles four-celled and subdiscoidal triangles three-celled in both pairs of wings; anal loop well-defined and five-celled; five rows of cells between MA and MP directly distal of the discoidal triangles; anal angle and three-celled anal triangle, thus it is a male specimen. The body is rather well-preserved, too, and shows strongly approximated or even touching compound eyes and a very well-defined genital lobe (certainly no artifact!) on the left side of the third abdominal segment. The latter character is very important, since the genital lobe looks exactly like that of *Cymatophlebia*, and the circumstance that the right lobe is not visible even suggests that these lobes have been flexible as in *Cymatophlebia*.

Paneuaeshnida taxon nov.

Included groups: Paracymatophlebiidae fam. nov. and Euaeshnida BECHLY, 1996.

Wing venational autapomorphies: Mspl is rather distinct, long and rather straight, and more or less parallel to MA in the groundplan (but its course is still somewhat irregular in Paracymatophlebiidae fam. nov. and Eumorbaeschnidae fam. nov.); RP2 and IR2 not parallel (?); RP2 distinctly undulated; RP3/4 and MA run closely parallel up to the wing margin in both pairs of wings (convergent to Mesuropetaloidea stat. nov. and Valdaeshninae subfam. nov.).

Family Paracymatophlebiidae fam. nov.

Type genus: *Paracymatophlebia* gen. nov.

Included genera: Currently only including the type species *Paracymatophlebia splendida* gen. et sp. nov., thus, preliminarily a redundant taxon.

Wing venational autapomorphies: Two rows of cells in the basal area between RP1 and RP2; the distal second oblique vein 'O' between RP2 and IR2 is secondarily absent; RP3/4 and MA more strongly undulated; hypertriangles free (reversal); secondarily no accessory cubito-anal crossveins in the submedian space between CuP-crossing and PsA; anal loop posteriorly poorly closed.

Genus *Paracymatophlebia* gen. nov.

Type species: *Paracymatophlebia splendida* sp. nov.

Derivatio nominis: After the genus *Cymatophlebia* in reference to the similarities between the two genera.

Diagnosis: This new genus can be recognized by the following combination of hindwing characters: Pterostigma elongated and braced; pseudo-IR1 originates on RP1 somewhat distal of pterostigma; RP1 and RP2 basally parallel, but with two rows of cells between these veins basal of pterostigma; RP2 is smoothly undulated; IR2 is not parallel to RP2, and there are two to three rows of cells between the median parts of these veins; only a single oblique vein 'O' near the subnodus; Rspl well-defined, parallel to IR2, and with one to two rows of cells between it and IR2; RP3/4 and MA strongly undulated; three secondary antenodal crossveins between Ax1 and Ax2, and Ax2 is on a level with the distal angle of the discoidal triangle; hypertriangle free; discoidal triangle elongated and three-celled; MAb is straight and there is no trigonal planate; three rows of cells in the basal part of the postdiscoidal area that is only slightly widened distally; Mspl rather well-defined and more or less parallel to MA, but with two rows of cells between it and MA; MP and CuAa distally strongly divergent; CuAa with numerous (about eight) well-defined posterior branches; subdiscoidal triangle unicellular; anal loop weakly defined, about equilateral, and five-celled.

Systematic position: *Paracymatophlebia* gen. nov. resembles *Cymatophlebia* in several characters, such as the strongly undulated MA, RP3/4 and RP2, the rather weakly defined anal loop, and the presence of two rows of cells between RP1 and RP2 basal of the pterostigma. However, all these characters are rather homoplastic and for example also occur in Euaeshnida. *Paracymatophlebia* gen. nov. differs from all Cymatophlebiidae in several important characters, e.g. the Rspl is more or less parallel to IR2 with max. two rows of cells between these two veins. The obvious similarities with Progobiaeshnidae fam. nov. and Rudiaeschnidae fam. nov. are all based on symplesiomorphies, and therefore indicate a similar common ancestor of Aeshnida.

Paracymatophlebia gen. nov. shares several putative synapomorphies with Euaeshnida: RP2 undulated (in the groundplan) with IR2 not strictly parallel to RP2; Mspl more distinct, long and more or less parallel to MA. Furthermore, it shares with the Neoaeshnida the reduction of the second distal oblique vein 'O', but this character is very homoplastic within Anisoptera. Nevertheless, *Paracymatophlebia* gen. nov. does not share the other autapomorphies of the Euaeshnida, viz it has no angled distal side MAb of the discoidal triangle, and it has no strong convex secondary longitudinal vein (trigonal planate) in the postdiscoidal area originating on MAb. Its MP and CuA are strongly diverging up to the wing margin, contrary to Neoaeshnida.

Consequently, we preliminarily consider the Paracymatophlebiidae fam. nov. as the sistergroup of Euaeshnida.

Paracymatophlebia splendida sp. nov.

Text-Fig. 90

Holotype: Specimen no. [2997 / 7], PIN, Moscow.

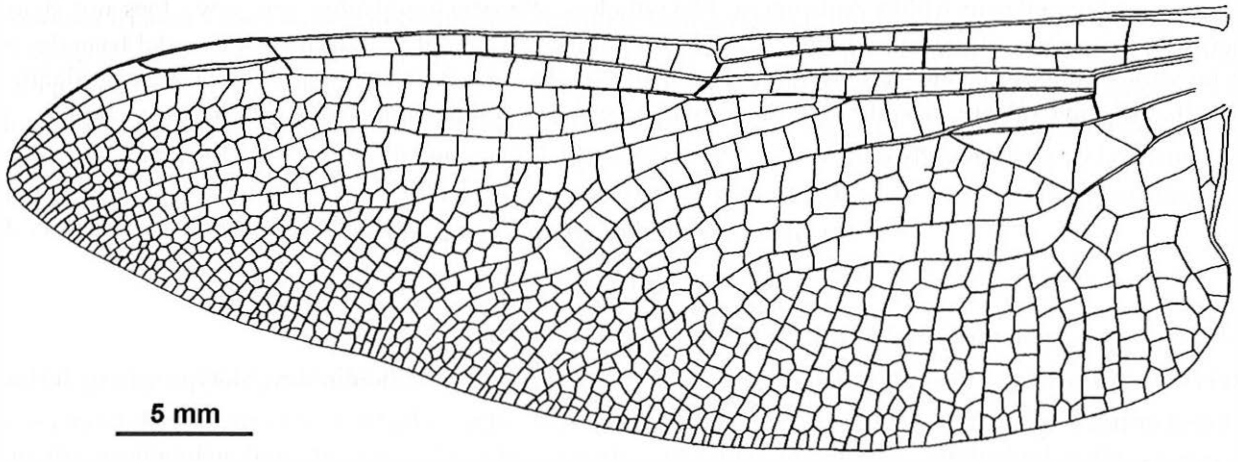
Derivatio nominis: After the "splendid" preservation of the wing venation in the holotype.

Locus typicus: Karatau, Kazakhstan, ex USSR.

Geological age: Upper Jurassic.

Diagnosis: Same as for the genus.

Description: An isolated male hindwing. Length 46.3 mm; width at nodus 15.2 mm; distance from base to arculus 5.0 mm; from base to nodus 19.3 mm (at 42 % of the total wing length); from nodus to pterostigma 16.7 mm. Pterostigma 4.8 mm long and max. 1.1 mm wide, covering three cells of unequal length, and distinctly braced. Thirteen postnodal crossveins between nodus and pterostigma, not aligned with the ten corresponding postsubnodal crossveins. Ten antenodal crossveins in the first row between costal margin and ScP, and seven in the second row between ScP and RA. Only the two primary antenodal crossveins are aligned and stronger than the secondary antenodal crossveins; Ax1 is 1.0 mm basal of the arculus, and Ax2 is 7.6 mm distal of Ax1 (slightly distal of distal angle of discoidal triangle); between Ax1 and Ax2 there are three secondary antenodal crossveins in the first row, and two in the second row, not aligned with each other. There are eight antesubnodal crossveins between RA and RP basal of the subnodus. The arculus is angled, and the bases or RP and MA are somewhat separated at arculus. The discoidal triangle is longitudinally elongated and divided into three cells; length of anterior side 5.0 mm; of basal side 2.5 mm; of its straight distal side MAb 5.2 mm. The hypertriangle is free (length 5.7 mm; max. width 0.9 mm). Median space free of crossveins. Submedian space only traversed by the CuP-crossing, 1.7 mm basal of the arculus. AA divided into an oblique, but not very strong, secondary anterior branch PsA and a posterior main branch AAa, delimiting an unicellular subdiscoidal triangle; PsA ends on MP + CuA 0.5 mm basal of basal angle of discoidal triangle. AA has only two parallel posterior branches reaching the posterior wing margin (AA1b forming the basal side of the anal loop, and AA2b forming the distal side of the anal triangle). The anal area is max. 8.5 mm wide with up to eight rows of cells between AA and the posterior margin. The subdiscoidal veinlet is short (0.2 mm), but distinctly present. CuAb is basally directed towards the wing base, forming the basal side of the anal loop. The anal loop is indistinctly closed posteriorly, and divided into five cells (max. length 3.1 mm; max. width 3.1 mm). The cubito-anal area is max. 7.0 mm wide with up to ten rows of cells. CuAa has eight well-defined posterior branches. The area between CuAa and MP is distally strongly widened with fourteen rows of cells along the posterior wing margin and a secondary longitudinal vein between CuAa and MP. The postdiscoidal area is more or less equilateral (width near discoidal triangle 3.1 mm; width at posterior wing margin 4.4 mm) with three rows of cells immediately distal of the discoidal triangle and eleven cells along the posterior wing margin. A relatively well-defined Mspl, parallel with MA and with two rows of cells between its median part and MA. MA and RP3/4 more or less parallel and strongly undulated below the base of Rspl; MA and RP3/4 are somewhat divergent near the posterior wing margin with four cells in-between at the posterior wing margin. Three bridge-crossveins Bqs basal of subnodus. RP2 is aligned with subnodus. Only a single oblique vein 'O', one and a half cells (1.6 mm) distal of the subnodus. Rspl well-defined and more or less parallel to IR2 with one to two rows of cells between it and IR2; Rspl distally reaches IR2. Several convex secondary veins originate on Rspl and reach the posterior wing margin. The area between the undulated parts of IR2 and RP2 is distinctly widened with three rows of cells, then more narrow with two rows of cells, and finally widened again near the posterior wing margin with three to six rows of cells. IR2 is not strongly undulated, unlike RP2, MA and RP3/4. RP1 and RP2 are basally parallel with two rows of cells in-between basal of the pterostigma (except for the three most basal cells); near the pterostigma RP1 and RP2 become divergent with three or more rows of cells in-between. A short pseudo-IR1 originates on RP1 somewhat distal of the pterostigma. Wing base with a strong anal angle and a three-celled anal triangle, thus, it is a male specimen.



Text-Fig. 90. *Paracymatophlebia splendida* sp. nov. Holotype PIN 2997 / 7 - male, left hindwing.

Euaeshnida BECHLY, 1996

1996a Palanisoptera; LOHMANN, pp. 222-224 (nec Palanisoptera PFAU, 1991).

Included groups: Eumorbaeschnidae fam. nov. and Neoaeshnida BECHLY, 1996.

Wing venational autapomorphies: RP2 and IR2 more distinctly not parallel; forewing discoidal triangle more elongated than that of the hindwing (convergent to *Valdaeshna*; but unknown in Paracymatophlebiidae fam. nov.); forewing subdiscoidal triangle free; distal side MAb of the discoidal triangles at least somewhat bent, or angled, or sigmoidally curved (BECHLY 1995); anal loop more or less transversely enlarged and gaff prolonged.

Discussion: The name Palanisoptera (*sensu* LOHMANN 1995, 1996a) for this monophylum is rejected by us, because it is not only a younger synonym, but could lead to considerable confusion because of the previous use of this name (Palanisoptera PFAU, 1991) for a very different monophylum (Aeshnomorpha taxon nov.).

Family Eumorbaeschnidae fam. nov.

1996 Eumorbaeschnidae; BECHLY, p. 383 (nomen nudum).

Type genus: *Eumorbaeschna* gen. nov.

Included genera: Currently only including the type genus *Eumorbaeschna* gen. nov., thus, preliminarily a redundant taxon.

Wing venational autapomorphies: In the forewing MA is distally converging to MP, so that the postdiscoidal area is distally not widened, but narrowed; in the forewing a primary antenodal crossvein (probably Ax2) is on a level with the basal angle of the discoidal triangle (convergent to Gomphaeschnaoidinae subfam. nov. and Telephlebiidae stat. nov.); RP2 more strongly undulated; RP3/4 and MA are more strongly undulated, and strictly parallel up to the posterior wing margin; hindwing subdiscoidal triangle two-celled (see discussion below).

Discussion: As somewhat less parsimonious alternative, the strongly undulated RP2 could also be regarded as a derived groundplan character of Aeshnida that has been preserved in Cymatophlebiinae, Eumorbaeschnidae fam. nov. and some Gomphaeschnidae, while it was more or less reduced in Progobiaeshnidae fam. nov., Valdaeshninae subfam. nov., Rudiaeschnidae fam. nov., Paracymatophlebiidae fam. nov., some Gomphaeschnidae, and all Aeshnodea. A free hypertriangle could be a further autapomorphy of Eumorbaeschnidae fam. nov., although in one specimen the hypertriangle is apparently divided by several crossveins, so that this character is ambiguous. Furthermore, the hypertriangle is also free in some Neoaeshnida. The two-celled subdiscoidal triangle of the hindwings cannot be regarded as a very convincing autapomorphy of this taxon, since it is somewhat variable in *Eumorbaeschna jurassica* gen. et comb. nov. and also very homoplastic (convergently present in *Cymatophlebiella euryptera*, *Progobiaeshna liaoningensis* gen. et sp. nov., *Hypopetalia pestilens*, and Cymatophlebioidea stat. nov., except *Valdaeshna surreyensis*).

Genus *Eumorbaeschna* gen. nov.

Type species: *Eumorbaeschna jurassica* (CARPENTER, 1932).

Derivatio nominis: Referring to the "true" genus "*Morbaeschna*" intended by NEEDHAM (1907).

Autapomorphies: Same as for family.

Diagnosis: This genus is characterized by the following features: RP2 strongly curved; usually two oblique veins 'O', rarely only one; pterostigma distinctly braced and covering two to four cells; few antesubnodal crossveins between RA and RP (distal of the arculus and basal of the subnodus); anal loop relatively small, as long as broad, and divided into four or five cells; CuAa with six or seven secondary branches; Rspl rather straight and parallel to IR2 with only a single row of cells between it and IR2; IR2 relatively straight, not parallel to RP2, and with three rows of cells between it and RP2; RP3/4 and MA distinctly undulated and more or less parallel; Mspl more or less parallel to MA, rather straight in the forewing with only a single row of cells between it and MA, but somewhat irregular in the hindwing with one to three rows of cells between it and MA; hindwing discoidal triangles usually three-celled, and forewing discoidal triangles usually four-celled (rarely five-celled); forewing subdiscoidal triangle free, while the hindwing subdiscoidal triangle is mostly divided into two cells by one crossvein; no accessory cubito-anal crossveins in the submedian space, at least of the forewings. The (male) cerci are very elongated and the epiproct is strongly bifid (Text-Fig. 99)

It is uncertain if Eumorbaeschnidae fam. nov. did retain the divided hypertriangles and accessory cubito-anal-crossveins of the groundplan of Aeshnida, since these two character states were only found in the hindwings of one specimen, while they seem to be absent in all others (see below). If this is due to infra-specific variation, individual aberration (atavism) or even artifacts of preservation cannot be decided, unless further well-preserved specimens become available.

Discussion: "*Aeschna*" *muensteri* was described by GERMAR (1839: 215, pl. 23, fig. 12) on the basis of two very poorly preserved specimens in coll. MÜNSTER. One of them is housed in the Museum of Munich (BSP), and the other one in the Museum of Cambridge University (U.K.). Later, HANDLIRSCH (1906: 589) renamed it "?*Mesuropetala muensteri*". HAGEN (1862: pl. 13, fig. 3) figured a specimen under the name "*Petalura muensteri*", but named it "*Petalura*? *wittei*" in the text (p. 133). HAGEN (1862: 107, 137-138) also synonymized "*Aeschna*" *muensteri* GERMAR, 1839 (= *Cordulegaster muensteri* (GERMAR), HAGEN 1848: 8-9; = *Diastatomma muensteri* (GERMAR) GIEBEL 1856) with his "*Petalura*? *wittei*". WEYENBERGH (1869), DEICHMÜLLER (1886: 37) and HANDLIRSCH (1906) considered that the figured specimen in HAGEN (1862) was actually *Protolindenia wittei* (GIEBEL, 1860). Later, CARPENTER (1932: 113) commented that the type of "*Aeschna*" *muensteri* GERMAR is a very poorly preserved specimen and added that «*muensteri* and *schmiedeli* should be dropped from the literature as unrecognisable insects». CARPENTER probably meant with this statement that these two taxa have to be considered as nomina dubia. Even if CARPENTER should be right, some problems would remain: NEEDHAM (1907) described a specimen, labelled «MCZ 6241, *Aeschna Muensteri* GERM., Solenhofen, Dr. KRANTZ» that he considered to be the type of his new genus "*Morbaeschna*" in the HAGEN collection at the Museum of Comparative Zoology (Cambridge) and named it "*Morbaeschna*" *muensteri* (GERMAR). Since a genus cannot have a type specimen, but only a type species, NEEDHAM obviously believed that his specimen was the type of "*Aeschna*" *muensteri* GERMAR, 1839, and so it is self evident that the latter species has to be regarded as type species of "*Morbaeschna*" NEEDHAM, 1907, either by original designation (assumed in BRIDGES 1991, 1994, and CARPENTER 1992), or at least by original indication by monotypy (Art. 68.3 IRZN).

We recently had the opportunity to re-examine the type material of "*Aeschna*" *muensteri* GERMAR, 1839. One specimen is located in the collection of the Museum of Munich (BSP), and is labelled «AS VII 794, Syntyp. Origin. GERMAR, 1839, Taf. 23, fig. 12, Malm Zeta, Solnhofen, NO. 45, *Aeshna Munsteri*, Origin. Ex., *Aeshna grandis* ? KÖHL.». The other one is located in Sedgwick Museum (Cambridge, U.K.) and is labelled «F1 1469, Sedgwick Mus. Cambridge; *Aeschna munsteri* GERM., Eichstadt, lithographic slate; figured GERMAR, Nov. Act. Acad. Caes. Leop. Carol., XIX, I, (1839), p. 215, pl. XXIII, fig. 12; MÜNSTER Collection». Thus, these two specimens are supposed to correspond to the same plate and figure in GERMAR's work and thus both could be the potential type of *A. muensteri*. Fortunately GERMAR (1839) indicated that one of the specimens was smaller than the other. The specimen in the Cambridge Museum is smaller (forewing length, about 40 mm) than the specimen in the Museum of Munich (forewing length, about 50 mm), so that the latter specimen must be regarded as the true type. Consequently, the specimen labelled «MCZ 6241, "*Aeschna*" *muensteri* GERMAR, Solenhofen, Dr. KRANTZ» in the HAGEN collection of fossil Odonata in the Museum of Comparative Zoology (Cambridge), has been erroneously considered by NEEDHAM (1907: 141) and subsequent authors (CARPENTER 1932, 1992, NEL *et al.* 1994), as the type of the species "*Aeschna*" *muensteri* and the genus "*Morbaeschna*" NEEDHAM, 1907.

The genuine type of "*Aeschna*" *muensteri* GERMAR and the specimen no. [MCZ 6241] clearly belong to different genera, species, and even families. Thus, the specimen described by NEEDHAM under the name "*Morbaeschna muensteri* (GERMAR)" does not belong to "*Aeschna*" *muensteri* GERMAR, 1839, the type species of "*Morbaeschna*" NEEDHAM, 1907. According to Art. 67.9 and Art. 70.3 we here decide to fix this case of "misidentified type species" by confirming the status of "*Aeschna*" *muensteri* GERMAR, 1839 as the type species of *Morbaeschna* NEEDHAM, 1907, regardless of the misidentification by NEEDHAM.

The exact position of "*Aeschna*" *muensteri* GERMAR was previously very uncertain due to the very poor preservation of the holotype. Only a careful re-examination revealed that this specimen is conspecific with *Mesuropetala koehleri* (HAGEN), so that the latter species has to be regarded as a junior subjective synonym of the former, and *Morbaeschna* NEEDHAM, 1907 consequently now has to be regarded as a junior subjective synonym of *Mesuropetala* HANDLIRSCH, 1906 (see above).

Furthermore, the specimen no. [MCZ 6241] and alleged "type" of "*Morbaeschna*" *muensteri* (*sensu* NEEDHAM 1907) is not the specimen figured in HAGEN (1862: pl. 13, fig. 3) because it has a wider area between IR2 and RP2, whereas the specimen figured in HAGEN (1862) has a narrow area. NEL *et al.* (1998) revised *Protolindenia wittei* and demonstrated that the specimen figured by HAGEN (1862: pl. 13, fig. 3) (labelled in his text *Protolindenia wittei*) remains of uncertain systematic position.

As the type species of "*Morbaeschna*" NEEDHAM, 1907 is "*Aeschna*" *muensteri* GERMAR, the specimen described and figured by NEEDHAM (1907) remained generically and specifically unnamed and needed a redescription which is provided in this publication. As is demonstrated below "*Cymatophlebia*" *jurassica* CARPENTER, 1932 is conspecific with NEEDHAM's aeshnid and thus representing the valid specific name. Nevertheless, it was still necessary to create a new genus for it, since it is of course no *Cymatophlebia*.

We have found two new undescribed specimens in the Jura-Museum (Eichstätt) that are very similar to the specimen of "*Morbaeschna muensteri*" (*sensu* NEEDHAM 1907) figured by NEEDHAM (1907: fig. 2). We also had the opportunity to re-examine the specimen no. [MCZ 6240-6241], the alleged "type" of "*Morbaeschna*" *muensteri* (*sensu* NEEDHAM 1907) and the specimen no. [MCZ 6193-6275], the paratype of *Cymatophlebia jurassica* CARPENTER, 1932. All these specimens are very similar and definitely seem to belong to the same species.

Systematic position: "*Morbaeschna muensteri*" (*sensu* NEEDHAM 1907) of the Upper Jurassic lithographic limestones of Solnhofen was described in Aeshninae. COCKERELL (1913) advocated its exclusion from Aeshninae. CARPENTER (1932: 110, foot note, 113) erroneously regarded NEEDHAM's specimen from MCZ as a "*Cymatophlebia* (*longialata*)" and consequently synonymized these two taxa. However, this specimen is very different from a *Cymatophlebia*, as already pointed out by NEEDHAM (1907 and COCKERELL (1907), and certainly is not even a Cymatophlebiidae (see below). WIGHTON & WILSON (1986) considered "*Morbaeschna*" as Aeshnidae - Gomphaeschninae without reference to CARPENTER (1932). CARPENTER (1992: 82-83) agreed with this last opinion, including "*Morbaeschna*" in the Aeshnidae and *Cymatophlebia* in the Petaluridae; thus, he implicitly considered the two genera as distinct.

WIGHTON & WILSON (1986) made the first attempt towards a phylogenetic analysis of the "lower" aeshnids based only on 15 wing venation characters for 16 taxa. Thus, this attempt was rather preliminary and insufficient. Nevertheless, "*Morbaeschna*" (*sensu* NEEDHAM 1907) was considered to be the most basal aeshnid of the "gomphaeschnine" grade. This opinion was followed and supported by NEL *et al.* (1994), BECHLY (1996, 1999a, b), and NEL *et al.* (1998).

LOHMANN (1995: 57, 1996a: 227) recently considered «*Morbaeschna muensteri* (GERMAR 1839)» as «an example for a typical representative of crowngroup Aeshnata LOHMANN, 1996a (= Aeshnoidea *sensu* LOHMANN 1995; = Aeshnodea in the present publication) from the Jurassic» without mentioning any evidence. This hypothesis is strongly contradicted by our phylogenetic analysis which suggests that this species is more basal than Gomphaeschnidae (= Gomphaeschnata LOHMANN, 1996a), instead of more derived.

We here demonstrate that the genus "*Morbaeschna*" NEEDHAM, 1907 is a synonym of *Mesuropetala* HANDLIRSCH, 1906, and that the specimen described and figured by NEEDHAM (1907) is not conspecific with "*Aeschna*" *muensteri* GERMAR, the type species of "*Morbaeschna*" NEEDHAM, 1907. Consequently, NEEDHAM's aeshnid had to be regarded as unnamed and therefore is here redescribed by us as *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov. This new genus clearly differs from *Cymatophlebia* in the following important characters: Anal loop well-defined, broad and posteriorly closed; Mspl well-defined and parallel to MA; Rspl parallel to IR2 with only a single row of cells between these two veins; IR2 not strongly undulated and not parallel to RP2.

The long parallel veins RP1 and RP2 in *Eumorbaeschna* gen. nov. represents an autapomorphy of the Aeshnoptera (BECHLY 1996, 1999a, b, NEL *et al.* 1998). This character has evolved convergently in few Gomphides - Lindeniidae (*sensu* BECHLY 1996), Cordulegastrida and Chlorogomphoidea, but these taxa do not share with *Eumorbaeschna* gen. nov. the elongated discoidal triangles and RP2 undulated (or curving) below the pterostigma. The distinct prolongation of the gaff is a synapomorphy with Aeshnomorpha taxon nov. The somewhat enlarged anal loop (at least five-celled) and the presence of a strongly defined Rspl are autapomorphies of Aeshnida (= Cymatophlebiidae + Rudiaeschnidae fam. nov. + Euaeshnida BECHLY, 1996). *Eumorbaeschna* gen. nov. shares with the Euaeshnida all above listed synapomorphies, including a distinct Mspl, elongated discoidal triangles, and an angled distal side MAb of the discoidal triangle; number of CuA branches reduced in hindwings (although variable in *Eumorbaeschna* gen. nov.). On the other hand, it has no strong putative synapomorphies with the Cymatophlebiidae, such as IR2 undulated and parallel to RP2, and Rspl curved and separated by several rows of cells from IR2 (convergent to *Oplonaeschna* and higher aeshnids), although it shares two derived characters with this family, viz the distinctly undulated RP2, RP3/4 and MA (probably acquired convergently). Because of several plesiomorphies, e.g. the basal oblique vein 'O' is not constant and the second distal oblique vein is not generally suppressed, Eumorbaeschnidae fam. nov. is herein considered as the most basal group of Euaeshnida (sistergroup of Neoaeshnida).

Eumorbaeschna gen. nov. has very few autapomorphic characters that could characterize it clearly within the Euaeshnida (see above). One of the more obvious characters, the more strongly undulated RP2 is also present by convergence in Cymatophlebiinae and some genera of Gomphaeschnidae (e.g. *Paramorbaeschna* gen. nov. and *Linaeschna* MARTIN, 1908). This character probably evolved by convergence within Cymatophlebiidae, since it is absent in their sistergroup Rudiaeschnidae fam. nov.

Eumorbaeschna jurassica (CARPENTER, 1932) comb. nov.

Text-Figs 91-104, Plate 31: Figs 1-6, Plate 32: Figs 1-2, Plate 33: Fig. 2

1907 *Morbaeschna*; COCKERELL, pp. 134-136 (nomen nudum).

v. 1907 *Morbaeschna muensteri* (GERMAR, 1839); NEEDHAM, pp. 141-142, fig. 2. (NEEDHAM misidentified his specimen as "*Aeschna*" *muensteri* GERMAR which is indeed represents a senior subjective synonym of *Gomphus koehleri* HAGEN that was later classified as *Mesuropetala koehleri* by HANDLIRSCH; consequently *Morbaeschna* NEEDHAM is a synonym of *Mesuropetala* HANDLIRSCH).

1932 *Morbaeschna muensteri* (GERMAR, 1839) [obviously *sensu* NEEDHAM]; CARPENTER, p. 110.

*v 1932 *Cymatophlebia jurassica* CARPENTER, pp. 111-112, fig. 6. (first valid description of this species, even though CARPENTER erroneously believed that his new species is conspecific with the *Cymatophlebia*-specimen figured by NEEDHAM (1907), and not with the *Morbaeschna*-specimen which he regarded as a *Cymatophlebia longialata*).

1986 *Morbaeschna muensteri* (GERMAR, 1839) [obviously *sensu* NEEDHAM]; WIGHTON & WILSON, p. 507.

1992 *Morbaeschna muensteri* (GERMAR, 1839) [obviously *sensu* NEEDHAM]; CARPENTER, p. 82 (listed).

1992 *Libellulium? jurassicum* (CARPENTER, 1932); NEL & PAICHELER, pp. 317-318.

1994 *Morbaeschna muensteri* (GERMAR, 1839) [obviously *sensu* NEEDHAM]; NEL *et al.*, p. 176.

1996a *Morbaeschna muensteri* (GERMAR, 1839) [obviously *sensu* NEEDHAM]; LOHMANN, p. 227.

1998 *Morbaeschna muensteri* (GERMAR, 1839) [*sensu* NEEDHAM]; NEL *et al.*, p. 6, 16.

1998 *Cymatophlebia jurassica* CARPENTER; NEL *et al.* , p. 5.

Holotype: Specimen no. [3815], coll. Gordon THOMSON (secured by Baron de BAYET), Carnegie Museum, Pittsburgh; a dragonfly with all four wings outspread, but faintly preserved wing venation.

Paratype: Specimen no. [6193-6275], coll. CARPENTER, MCZ, Cambridge; fore- and hindwing of a female. Our study of this paratype clearly demonstrated that it is conspecific with the specimen no. [MCZ 6240-6241], figured by NEEDHAM (1907: fig. 2). Contrary to the statements in several publications, e.g. CARPENTER (1992: 82) and NEL *et al.* (1994: 176), the latter specimen has never been a valid type of any taxon at all!

Other specimens: Specimens nos [SOS 3714], [SOS 1697]; [1983 / 2633, Sln. 240 a, b], JME, Eichstätt; specimen [59746], BSP, Munich; specimen no. [MB. J. 1734 a, b], MB, Berlin; specimen no. [64342], coll. LUDWIG, SMNS, Stuttgart; a specimen without number, and specimen no. [MCZ 6231], labelled «*Tarsophlebia eximia* HAGEN ?, Solenhofen, Dr. KRANTZ», coll. CARPENTER, MCZ, Cambridge; specimen [No. 1] and three further specimens without number in coll. KÜMPEL (Wuppertal); one specimen in coll. LEICH (Bochum), but currently not in public exhibition. Finally, there are two specimens without number in coll. BÜRGER (Bad Hersfeld, Germany), of which one is very curiously preserved with a abnormal elongated abdomen (forewing 41 mm long, hindwing 40 mm long, body 83 mm long, abdomen incl. appendices 57 mm long).

Locus typicus: Solnhofen, Southern Frankonian Alb, Bavaria, Germany.

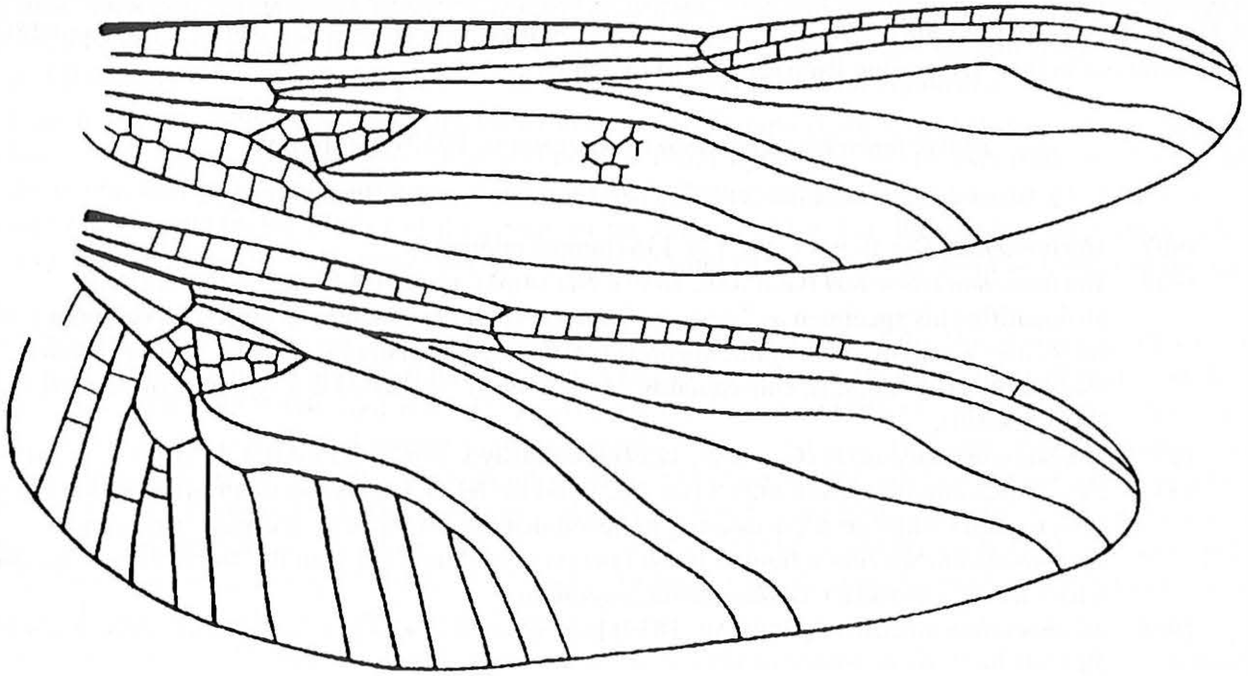
Stratum typicum: Solnhofen Lithographic Limestone, *Hybonotum*-Zone, Upper Jurassic, Malm zeta 2b, Lower Tithonian.

Autapomorphies: Same as for family.

Diagnosis: Same as for the genus.

Discussion: All these specimens have very similar wing venation. Although there is a remarkable variability in size (wing length from 37 mm to 47 mm), the few differences can be attributed to infra-specific variability, aberrations, or artifacts of preservation. Consequently, we preliminarily assign all described specimens to the same species.

Description



Text-Fig. 91. *Eumorbaeschna jurassica* (CARPENTER, 1932). CARPENTER's combined drawing from holotype CMNH 3815 and paratype MCZ 6193-6275 - female, right pair of wings (drawing after CARPENTER 1932: fig. 6; without scale).

♦ Specimen no. CMNH 3815; holotype of *Cymatophlebia jurassica* CARPENTER, 1932

Text-Fig. 91

Unfortunately, we did not yet have the possibility to study the holotype of *Cymatophlebia jurassica* CARPENTER, 1932, but only the paratype at MCZ (see below). Nevertheless, the original description and figure given by CARPENTER (1932) clearly shows that it is an *Eumorbaeschna* gen. nov. and not a *Cymatophlebia*: Much smaller size (forewing length 43.0 mm; hindwing length 42.0 mm); IR2 not undulated and not parallel to RP2 which is strongly undulated; distinct anal loop present and posteriorly well-closed, correlated with a distinctly elongated gaff. There are no cells featured between the main veins, so that the apparent absence of the veins Rspl and Mspl almost certainly represents an artifact of the drawing. Like other "unusual characters" in the same publication, e.g. the absence of primary antenodal crossveins in the figures of *Cymatophlebia longialata* and "*Protolindenia*" *koehleri*, or the incorrect venation of the forewing discoidal triangle and subdiscoidal triangle of *Urogomphus giganteus* (CARPENTER 1932: figs 4-7), the apparently multicellular discoidal triangles and subdiscoidal triangles in "*Cymatophlebia*" *jurassica* are most likely due to misinterpretations and drawing errors, too, regarding the fact that all other characters are identical with the other specimens described below. A scientific curiosity is CARPENTER's erroneous statement that the *Cymatophlebia longialata* specimen figured by NEEDHAM (1907: fig. 1) shall be conspecific with his "*Cymatophlebia*" *jurassica*, while the "*Morbaeschna muensteri*" (*sensu* NEEDHAM 1907) specimen figured by NEEDHAM (1907: fig. 2) should be a *Cymatophlebia longialata*, although a comparison of the concerning figures in both publications clearly shows that it is vice versa (compare CARPENTER 1932: figs 5 and 6). The correct affinities of the corresponding figures are so obvious that a confusion of the figures or a lapsus by CARPENTER (1932) seems to be the most likely explanation.

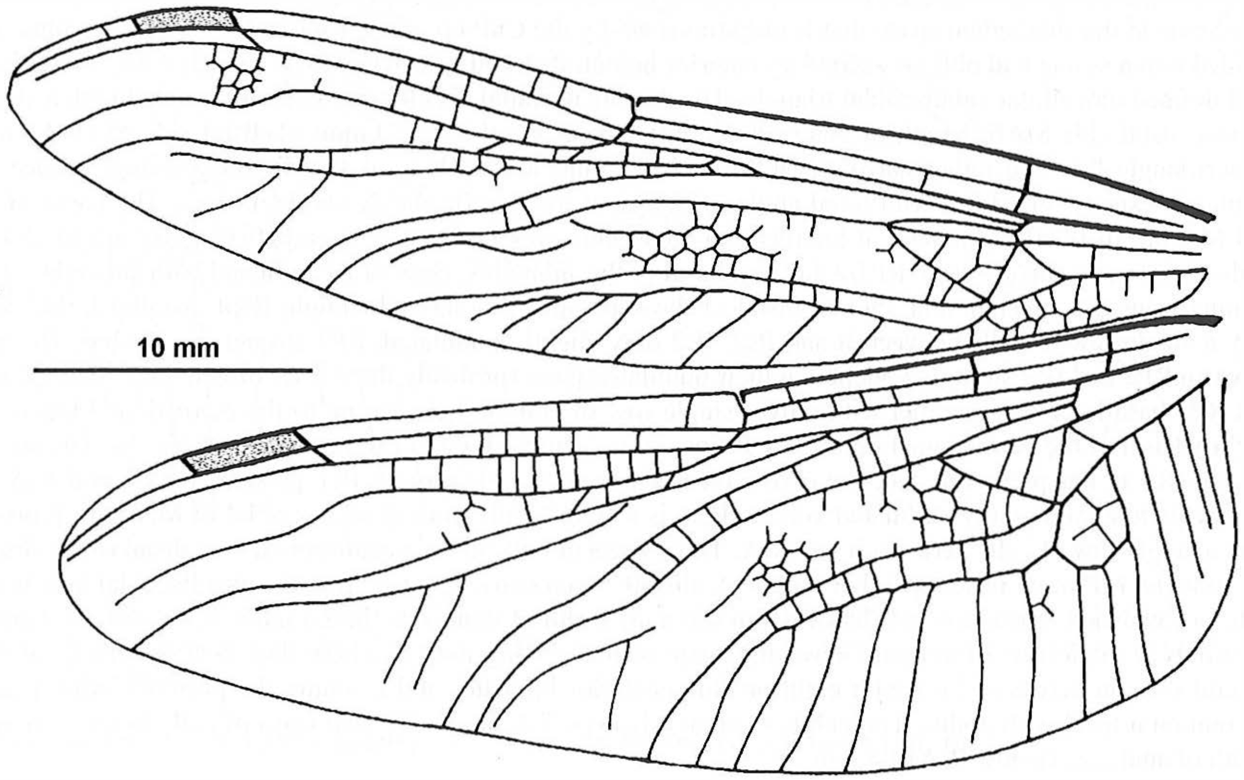
♦ Specimen no. MCZ 6193-6275; paratype of *Cymatophlebia jurassica* CARPENTER, 1932; female

Text-Fig. 92, Plate 31: Figs 1-3

Part (6193) and counterpart (6275) of a relatively well-preserved left pair of wings of a female. There is no trace of coloration preserved, thus, the wings were probably hyaline.

Forewing: Length 44.2 mm; width at nodus 9.5 mm; distance from base to arculus 7.0 mm; distance from base to nodus 21.8 mm; distance from nodus to pterostigma 14.9 mm. Pterostigma 3.5 mm long and 0.8 mm wide. The number of cells covered by the pterostigma is unknown, but the latter is strongly braced by an oblique crossvein that is aligned with its basal side. The precise number of antenodal and postnodal crossveins is unknown. The postnodal crossveins are not aligned with the corresponding postsubnodal crossveins. The antenodal area is rather poorly preserved. One of the two primary antenodal crossveins is just distal of the arculus, on a level with basal angle of discoidal triangle. ScP fuses with the costal margin at the nodus which is in a rather distal position. No antesubnodal crossvein preserved in the area between RA and RP, basal of the subnodus (probably an artifact). Median space free of crossveins. There seem to be no accessory cubito-anal crossveins in the submedian space that is only traversed by the CuP-crossing, 2.6 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is elongated and four-celled with a slightly bent distal side MAb; length of anterior side 4.9 mm; of basal side 2.3 mm; of distal side MAb 4.6 mm. Hypertriangle free and rather narrow (width, max. 0.5 mm) and as long as the discoidal triangle, since the arculus is exactly on a level with basal angle of discoidal triangle (probably an aberration). The bases of RP and MA are distinctly separated at arculus. No crossveins preserved in the area between RP and MA. Two bridge-crossveins Bqs between RP1/2 and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.0 mm and 3.9 mm distal of the subnodus. A long and straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 only slightly undulated. RP2 strongly undulated. The area between RP2 and IR2 strongly widened in their undulated parts (probably three rows of cells in-between). RP2 and RP1 basally closely parallel with only a single row of cells in-between up to the pterostigmal brace, but slightly basal of the pterostigmal brace they become divergent with three rows of cells in-between. The area of pseudo-IR1 is not preserved, but there was clearly no elongated primary IR1 present. RP3/4 and MA are closely parallel and gently undulated veins. There is a long Mspl, more or less parallel to MA with probably only a single row of cells between it and MA. Three rows of cells in the postdiscoidal area distal of the discoidal triangle. MP more or less parallel with MA, distally even converging, so that the postdiscoidal area is distally not widened, but narrowed (basal width 2.6 mm; width at wing margin 2.4 mm). MP and CuA parallel with only a single row of cells in-between, except near the wing margin where they become divergent with several cells in-between. CuA with eight or nine posterior branches and reaching the posterior wing margin beyond on a level with nodus. The cubito-anal area is max. 2.8 mm wide. Two rows of cells in the anal area; width of anal area (below PsA) 1.8 mm.

Hindwing: Length 43.4 mm; width at nodus 13.6 mm; distance from base to arculus 5.5 mm; distance from base to nodus 18.0 mm; distance from nodus to pterostigma 15.7 mm. Pterostigma 4.2 mm long and 0.9 mm wide, and strongly braced by an oblique crossvein that is aligned with its basal side. The number of postnodal crossveins is unknown, but the postnodal crossveins are not aligned with the corresponding postsubnodal crossveins. The antenodal area rather poorly preserved as well, but some of the distal secondary antenodal crossveins, as well as the two primary antenodal crossveins are visible. Ax1 is 1.2 mm basal of the arculus and Ax2 is 5.0 mm distal of Ax1. ScP fuses with the costal margin at the nodus which is in a rather basal position. No antesubnodal crossvein preserved in the area between RA and RP basal of the subnodus (probably an artifact). Median space free of crossveins. The submedian space seems to be free of crossveins, too, but the CuP-crossing that was certainly present is not preserved either. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is less elongated than that of the forewing, divided into three cells by two parallel crossveins, and with a slightly bent distal side MAb; length of anterior side 4.8 mm; of basal side 2.8 mm; of distal side MAb 4.6 mm. Hypertriangle free (length 5.3 mm; max. width 0.7 mm wide). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. No preserved bridge-crossveins Bqs in the space between RP1/2 and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 2.0 mm and 5.1 mm distal of the subnodus. A long and straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 only slightly undulated. RP2 strongly undulated. The area between RP2 and IR2 is strongly widened at their undulated parts (with probably three rows of cells in-between). RP2 and RP1 are basally closely parallel with only a single row of cells in-between up to the pterostigmal brace, but beneath the latter they become distinctly divergent. Area of IR1 not preserved. RP3/4 and MA closely parallel and gently undulated veins. There is a long Mspl, more or less parallel to MA (course not straight, but somewhat irregular) with probably one or two rows of cells between it and MA. There are three rows of cells in the postdiscoidal area distal of the discoidal triangle. The postdiscoidal area is distally widened (basal width near the discoidal triangle 4.2 mm; distal width at the posterior wing margin 6.4 mm). MP and CuA basally parallel with only a single row of cells in-between, but distally they become divergent with more than one row of cells in-between. CuA with seven posterior branches and reaching the posterior wing margin somewhat distal of the level of the nodus. Cubito-anal area max. 6.5 mm wide. Anal area broad, width of anal area (below PsA) 8.4 mm. Four parallel posterior branches of AA between the anal loop and the wing base. Anal loop relatively small and rather transverse (max. length 2.7 mm; max. width 3.9 mm), divided in four cells, and posteriorly well-closed. Anal margin rounded without anal angle or anal triangle, thus, it is a female specimen.

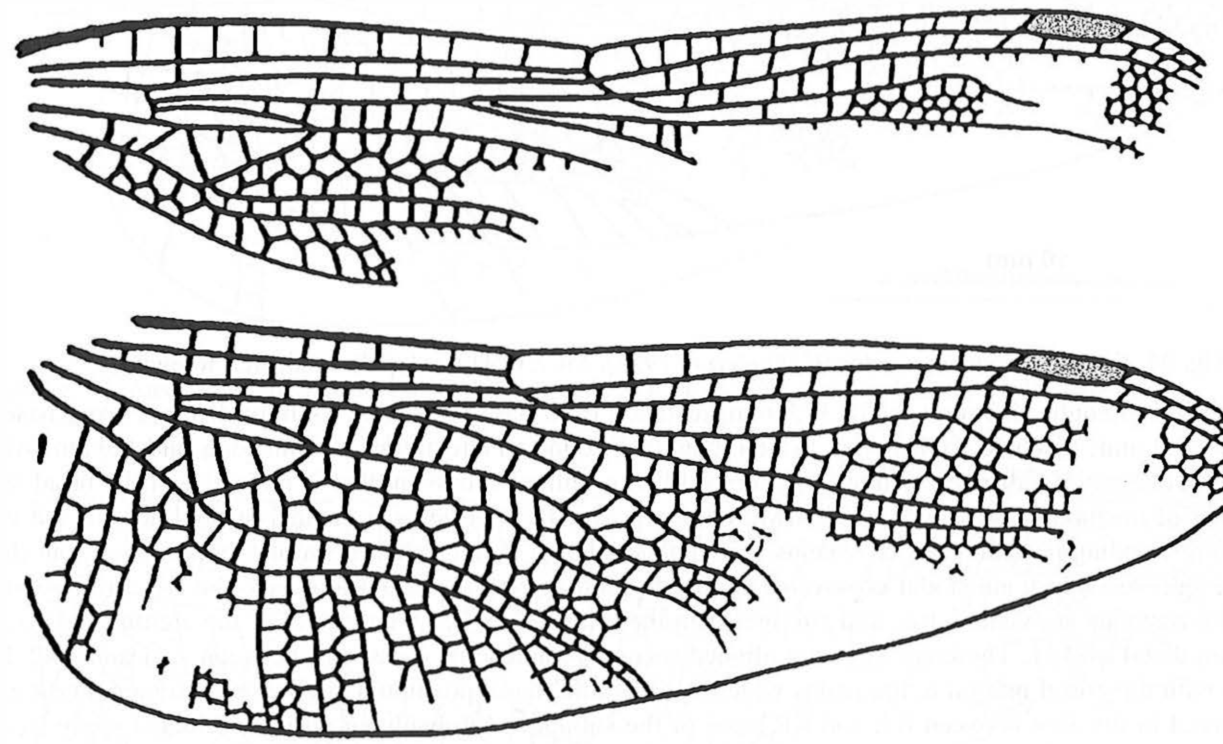


Text-Fig. 92. *Eumorbaeschna jurassica* (CARPENTER, 1932). Paratype MCZ 6193-6275 - left pair of wings.

♦ Specimen no. MCZ 6241; original of NEEDHAM 1907; male; labelled «coll. CARPENTER, *Aeschna Muensteri* GERM., Solenhofen, Dr. KRANTZ, *Cymatophlebia longialata*»

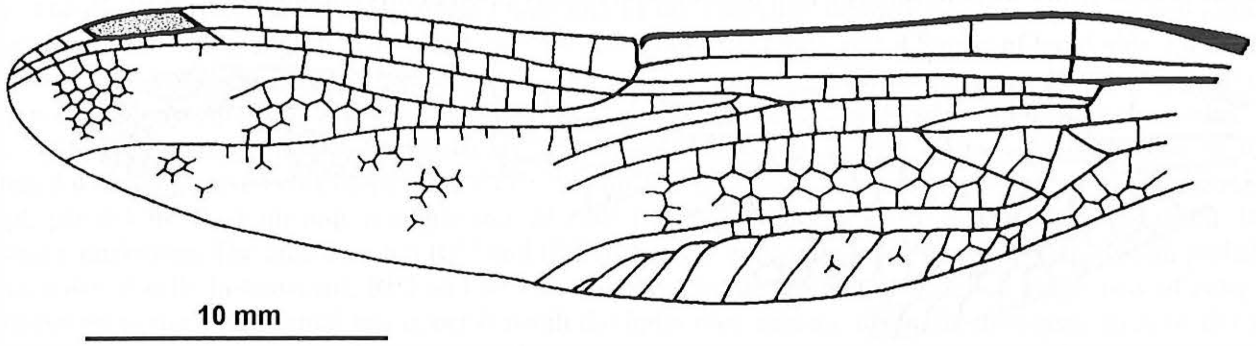
Text-Figs 93-96, Plate 31: Figs 5-6, Plate 32: Fig. 1

A male with the wings comparatively well-preserved. The right forewing is missing and the left hindwing is partly overlapped by the left forewing and twisted so that the specimen apparently has two "right hindwings". A counterpart is also housed in the same collection and has the number [MCZ 6240]. The wing venation is generally very similar to that of specimen no. [MCZ 6193-6275]; Since the drawing of NEEDHAM (1907: fig. 2) contains several errors we here supply a new drawing and redescription of this important specimen.



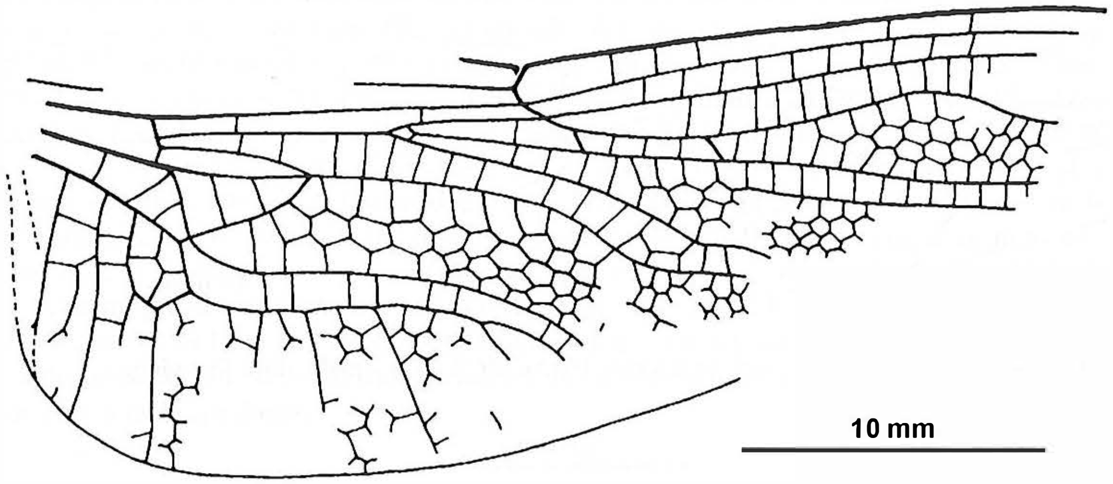
Text-Fig. 93. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6241 (no type!) - male, right pair of wings (drawing after NEEDHAM 1907: fig. 2; without scale).

Forewing: Length 41.7 mm; width at nodus 8.6 mm; distance from base to arculus 5.0 mm; distance from base to nodus 20.6 mm; distance from nodus to pterostigma 15.0 mm. Pterostigma 3.3 mm long and max. 0.8 mm wide, covering nearly four cells, and strongly braced by an oblique crossvein that is aligned with its basal side. Eleven visible postnodal crossveins, not aligned with the corresponding postsubnodal crossveins. Antenodal area rather poorly preserved with only some distal secondary antenodal crossveins preserved, and one primary antenodal crossvein on a level with basal angle of discoidal triangle, 1.0 mm distal of the arculus. ScP fuses with the costal margin at the nodus which is in a rather distal position. Ten antesubnodal crossvein preserved in the area between RA and RP basal of the subnodus, but there were probably some more. Median space free of crossveins. There seem to be no accessory cubito-anal crossveins in the submedian space that is only traversed by the CuP-crossing, 1.4 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is elongated and four-celled with an angled distal side MAb; length of anterior side 4.8 mm; of basal side 2.3 mm; of distal side MAb 4.7 mm. Hypertriangle free and rather narrow (length 5.8 mm; max. width 0.8 mm). Bases of RP and MA are distinctly separated at arculus that is distinctly angled. Only a single bridge-crossvein Bq preserved between RP1/2 and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. No oblique vein 'O' preserved (artifact). The area of the Rspl is poorly preserved. IR2 only slightly undulated. RP2 strongly undulated. The area between RP2 and IR2 strongly widened in their undulated parts with three rows of cells in-between. RP2 and RP1 are basally closely parallel with only a single row of cells in-between, but somewhat basal of the pterostigmal brace they become divergent with several rows of cells in-between. Vein pseudo-IR1 is not preserved, but apparently was rather vestigial, and there was clearly no elongated primary IR1 present. RP3/4 and MA closely parallel (distal parts not preserved). The area of Mspl is poorly preserved, but it was present and more or less parallel to MA with only a single row of cells between it and MA. Three rows of cells in the postdiscoidal area distal of the discoidal triangle. MP more or less parallel with MA, distally even converging, so that the postdiscoidal area is distally not widened, but narrowed (basal width 2.5 mm). MP and CuA parallel with only a single row of cells in-between, except near the wing margin where they become divergent. CuA with eight or nine posterior branches and reaches the posterior wing margin on a level with nodus; max. width of cubito-anal area 2.2 mm; there are two rows of cells in the anal area; width of anal area (below PsA) 1.8 mm.

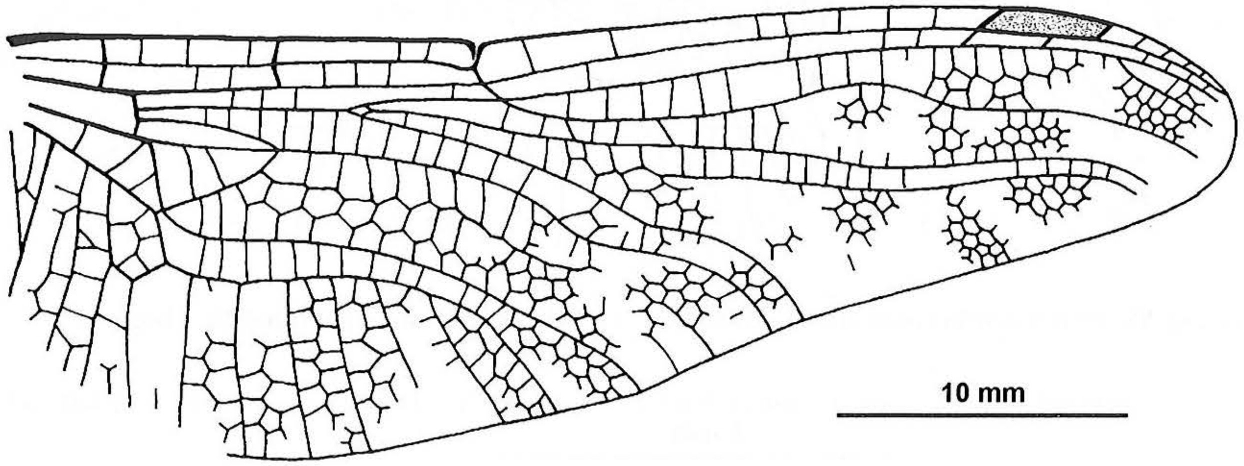


Text-Fig. 94. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6241 (no type!) - male, left forewing.

Hindwing: Length 42.7 mm; width 12.9 mm; distance from base to arculus 4.4 mm; distance from base to nodus 16.2 mm; distance from nodus to pterostigma 17.6 mm. Pterostigma 3.8 mm long and 0.9 mm wide, covering one and a half cells, and strongly braced by an oblique crossvein that is aligned with its basal side. Number of postnodal crossveins is unknown, but the postnodal crossveins are numerous and not aligned with the corresponding postsubnodal crossveins. The antenodal area is somewhat incompletely preserved, but there are several secondary antenodal crossveins visible in both rows that are not aligned. The two primary antenodal crossveins are visible, too, and stronger than the others. Ax1 is 1.0 mm basal of the arculus and Ax2 is 6.0 mm distal of Ax1. There are three not aligned secondary antenodal crossveins between Ax1 and Ax2. ScP fuses with the costal margin at the nodus which is in a rather basal position. Only few antesubnodal crossvein preserved in the area between RA and RP basal of the subnodus (probably an artifact). Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.3 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined subdiscoidal triangle that is divided into two cells by a single crossvein (in both hindwings). The discoidal triangle is less elongated than that of the forewing, divided into three cells by two parallel crossveins (in both hindwings), and with a distinctly bent or angled distal side MAb; length of anterior side 4.3 mm; of basal side 2.4 mm; of distal side MAb 4.3 mm. Hypertriangle free (length 4.9 mm; max. width 0.8 mm). The bases of RP and MA are distinctly separated at arculus that is angled. The area between RP or RP3/4 and MA is traversed by numerous crossveins (basally only a single row of cells in-between; distally two rows of cells). Only a single preserved bridge-crossvein Bq in the space between RP1/2 and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 2.1 mm and 5.2 mm distal of the subnodus in the right hindwing, and 1.2 mm and 5.7 mm distal of the subnodus in the left hindwing. A long and straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 is only slightly undulated. RP2 is strongly undulated. The area between RP2 and IR2 is strongly widened at their undulated parts (with four rows of cells in-between in the broadest part). RP2 and RP1 basally closely parallel with only a single row of cells in-between, but somewhat basal of the pterostigmal brace they become distinctly divergent with three rows of cells in-between. Pseudo-IR1 well-defined, but very short, originating on RP1 slightly distal of the pterostigma with one or two rows of cells between it and RP1 and three rows of cells between it and RP2. RP3/4 and MA closely parallel and gently undulated veins. A long Mspl, more or less parallel to MA (course not straight, but somewhat irregular) with one to three rows of cells between it and MA in both hindwings. Three rows of cells in the postdiscoidal area distal of the discoidal triangle. Postdiscoidal area distally widened (basal width near the discoidal triangle 3.1 mm; distal width at the posterior wing margin 5.0 mm). MP and CuA basally parallel with only a single row of cells in-between, but distally they become divergent with several rows of cells in-between. CuA with seven posterior branches and reaching the posterior wing margin somewhat distal of the level of the nodus. The cubito-anal area is max. 5.5 mm (left hindwing) or 6.1 mm (right hindwing) wide. Anal area broad, below PsA 7.6 mm wide. Only a single posterior branch of AA between the anal loop and the anal triangle (male). Anal loop relatively small and rather transverse (max. length 1.9 mm; max. width 3.2 mm), divided into four cells in the left hindwing and into five cells in the right hindwing, and posteriorly well-closed. Anal margin with an anal angle and a three-celled anal triangle, thus, it is a male specimen.



Text-Fig. 95. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6241 (no type!) - male, left hindwing.

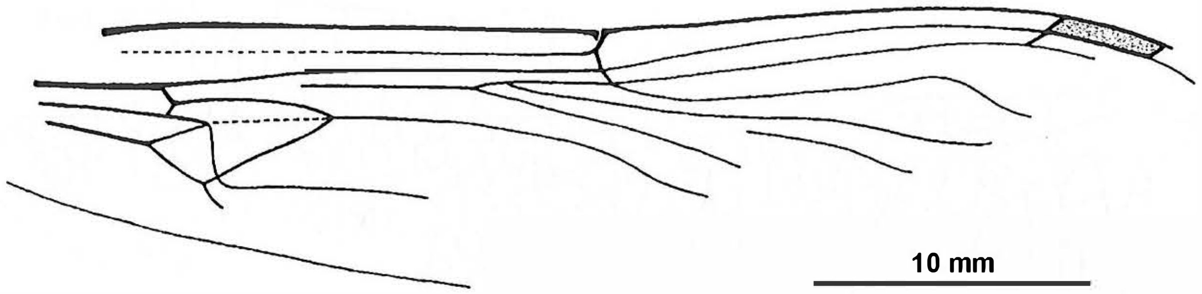


Text-Fig. 96. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6241 (no type!) - male, right hindwing.

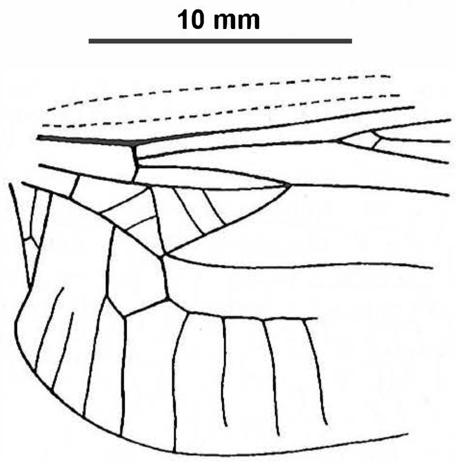
♦ Specimen no. MCZ 6231; male; labelled «coll. CARPENTER, *Tarsophlebia eximia* HAGEN ?, Solenhofen, Dr. KRANTZ, 48»

Text-Figs 97-99

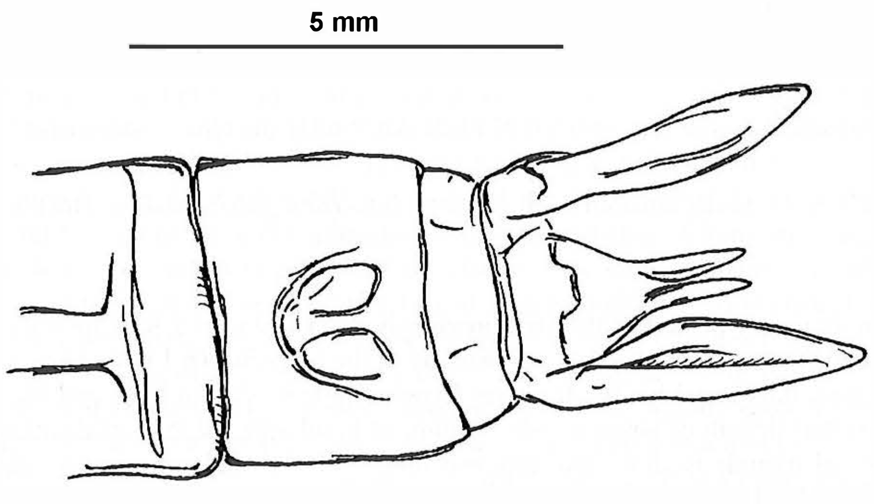
This adult male is more poorly preserved than the previously described ones with which it agrees in all visible venational characters. Distance from nodus to pterostigma in the forewing 16.1 mm. The forewing pterostigma is 3.9 mm long and max. 0.8 mm wide. The forewing hypertriangle is 5.9 mm long, and the forewing discoidal triangle is very elongated (length of anterior side 4.5 mm; of basal side 1.9 mm; of distal side MAb 4.7 mm). The hindwing discoidal triangle is elongated, too, and three-celled (length of anterior side 5.3 mm; of basal side 2.6 mm; of distal side MAb 5.3 mm); the hindwing subdiscoidal triangle seems to be two-celled, but there are no accessory cubito-anal crossveins visible in the submedian space, except the CuP-crossing (2.0 mm basal of the arculus). The anal loop is max. 2.4 mm long and 3.4 mm wide, and there seem to be two posterior branches of AA between the anal loop and the anal triangle. The presence of an anal angle and a three-celled anal triangle shows that it is a male specimen. The genital valvulae of segment nine and the terminal appendages are preserved and very similar to extant "primitive" aeshnids: The cerci are 0.42 mm long and relatively slender (lanceolate), and the epiproct is 0.28 mm long and deeply bifurcate. The detailed drawing of these appendages (Text-Fig. 99), although very carefully made with a camera lucida under large magnification and extreme sidelight, still has some uncertainties and is rather a reconstruction than a purely documentary drawing of the fossil, since the concerning area is not that well-preserved.



Text-Fig. 97. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6231 - male, right forewing.



Text-Fig. 98. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6231 - male, right hindwing base.



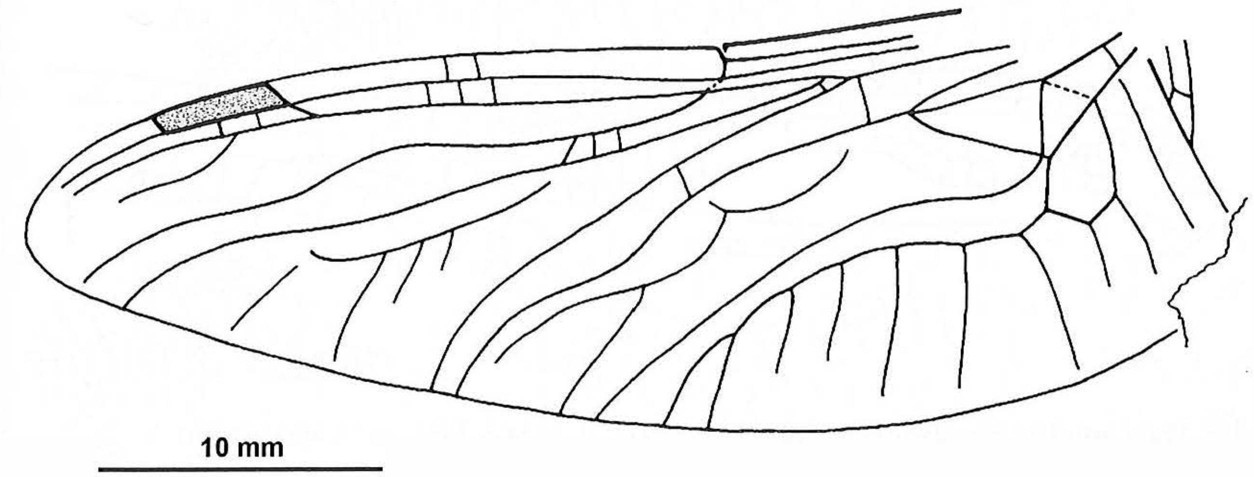
Text-Fig. 99. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ 6231 - male, anal appendages.

♦ Specimen without number, MCZ; male; labelled «coll. CARPENTER, coll. HAEBERLEIN, Solenhofen

Text-Fig. 100

A rather poorly preserved male with body and hindwings, but without the forewings.

Hindwing: Length 41.7 mm; width at nodus 13.5 mm; distance from base to nodus 16.2 mm; distance from nodus to pterostigma 16.0 mm. Pterostigma 4.0 mm long and 0.9 mm wide, covering at least three cells, and strongly braced by an oblique crossvein. RP2 is somewhat less strongly undulated than in the other specimens, but distinctly more than IR2 which is rather straight. Only a single oblique vein 'O' is visible 4.8 mm distal of the subnodus, but there was probably a second one closer to the subnodus. Rspl is parallel to IR2. Three or four convex secondary veins between IR2 and RP3/4, originating on Rspl. Mspl is more or less parallel to MA, but somewhat irregular. At least one convex secondary vein between MA and MP, originating on Mspl. Discoidal triangle elongated with a relatively straight distal side MAb; length of anterior side 4.9 mm; of basal side 2.6 mm; of distal side MAb 5.0 mm. Although hypertriangle and subdiscoidal triangle seem to be free, this cannot be regarded as significant, since the crossveins that were certainly present in the discoidal triangle and the anal loop are not preserved either. Anal loop rather transverse (max. length 2.6 mm; max. width 4.2 mm). CuAa with seven posterior branches; max. width of cubito-anal area 6.1 mm. Only a single posterior branch of AA between the anal loop and the anal triangle (male). Anal margin with an anal angle and a three-celled anal triangle, thus, it is a male specimen.

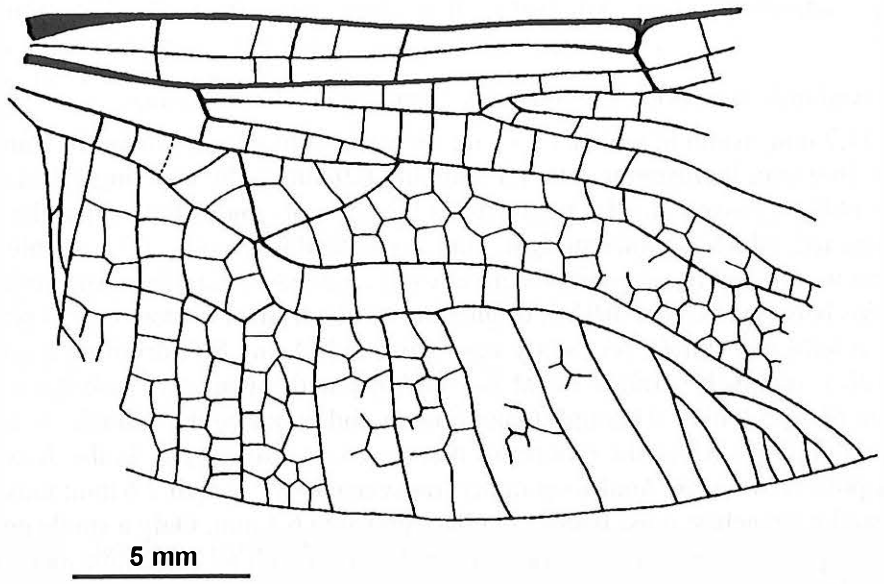


Text-Fig. 100. *Eumorbaeschna jurassica* (CARPENTER, 1932). MCZ without number - male, left hindwing.

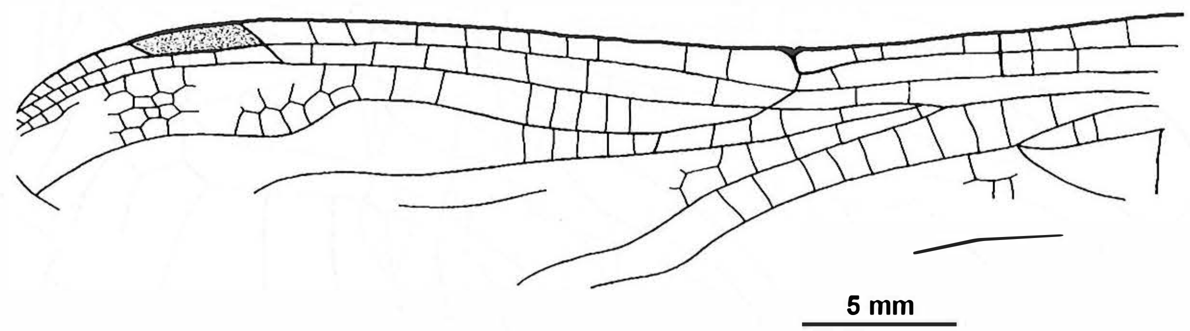
♦ Specimen no. SOS 1697, JME; male

Text-Figs 101-102

Only the two hindwings are partly preserved. There is no trace of coloration, thus, the wings were probably hyaline. The hindwings are very similar to those of specimen no. [MCZ 6193-6275], the main differences are as follows: Length 44.5 mm; width 14.0 mm; distance from base to arculus 5.2 mm; anal loop is divided into four cells, instead of fiive; posterior branches of CuA better defiined; pterostigma apparently covers only two and a half cells; two accessory cubito-anal crossveins between CuP-crossing and PsA; subdiscoidal triangle divided into two cells by a crossvein; one or two rows of cells between Mspl and MA. This specimen is the only one in which accessory cubito-anal crossveins and divided hypertriangles are visible. These character states would be in agreement with the groundplan of Aeshnida, but regarding their apparent absence in the other specimens it cannot be excluded that they are either aberrations, or even artifacts. The following characters, not preserved in specimen no. [MCZ 6193-6275], are visible: The two primary antenodal crossveins are clearly visible and 7.0 mm apart. Vein Ax1 is 3.8 mm distal of the base of the wing. The arculus is located between the primary antenodal crossveins, nearer Ax1 than Ax2, 1.1 mm distal of Ax1. The anal triangle is narrow and three-celled. The anal area is 8.5 mm wide with six or eight rows of cells between AA and the posterior wing margin.



Text-Fig. 101. *Eumorbaeschna jurassica* (CARPENTER, 1932). JME SOS 1697 - male, right hindwing, basal half.



Text-Fig. 102. *Eumorbaeschna jurassica* (CARPENTER, 1932). JME SOS 1697 - male, left hindwing.

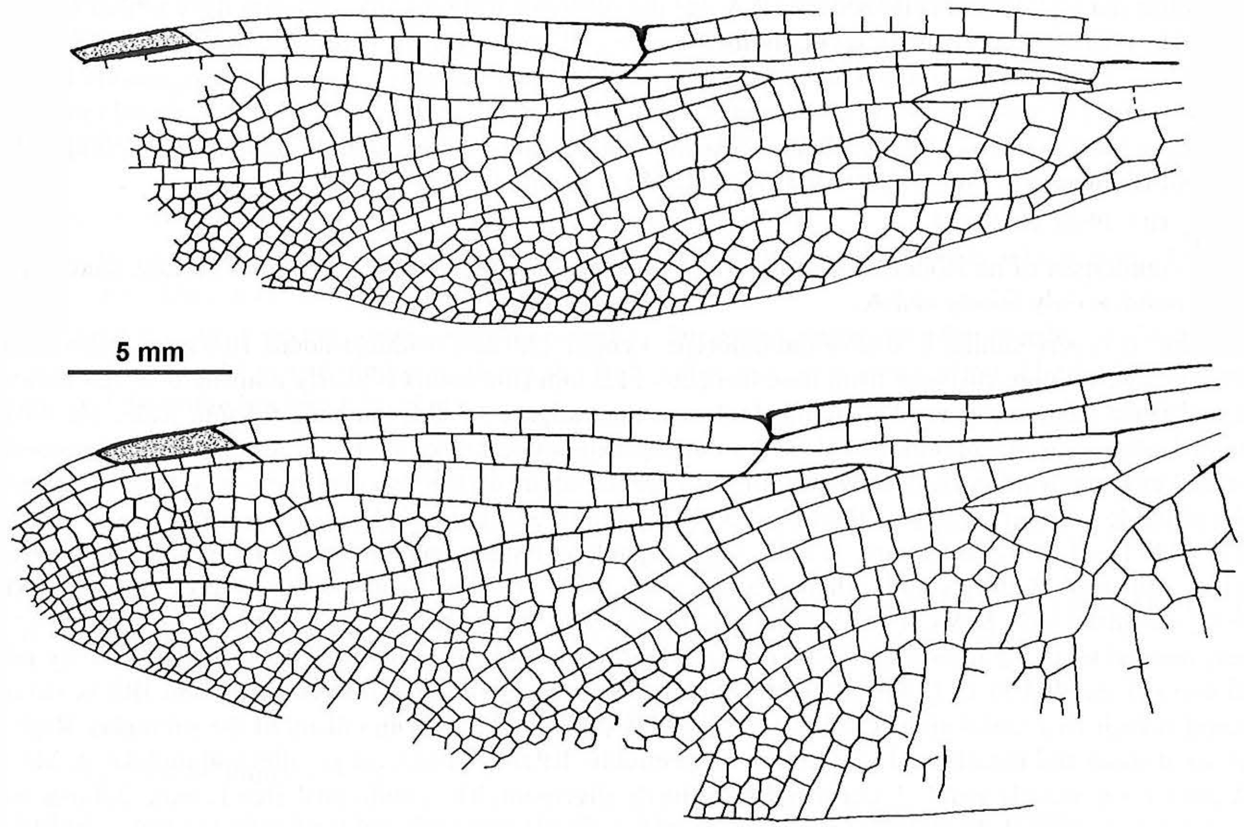
♦ Specimen no. SOS 3714, JME (erroneously labelled «*Heterophlebia aequalis*»)

Text-Fig. 103, Plate 32: Fig. 2

The left fore- and hindwings are preserved except for the hindwing anal area which is partly missing. There is no trace of coloration, thus, the wings were probably hyaline. There is also a faint imprint of the body, but it is too poorly preserved to be of any value.

Forewing: Length 37.0 mm; width 9.5 mm; distance from base to arculus 3.8 mm; distance from base to nodus 18.0 mm; distance from nodus to pterostigma 14.0 mm. Pterostigma 3.8 mm long and 0.7 mm wide, covering three cells, and strongly braced by an oblique crossvein that is aligned with its basal side. Eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1, except one. The antenodal area is rather poorly preserved, the primary antenodal crossveins are not visible. Eleven secondary antenodal crossveins preserved between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. ScP fuses with the costal margin at the nodus. There were probably few antesubnodal crossveins in the area between RA and RP, basal of the subnodus (only one of them is visible). Median space free of crossveins. Only the distal part of the submedian space is preserved, but the CuP-crossing is just visible, 1.2 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is elongated and five-celled with an angled distal side MAb; length of anterior side 4.8 mm; of basal side 2.2 mm; of distal side MAb 4.9 mm. Hypertriangle rather narrow (length 5.7 mm; max. width 0.6 mm). There is one crossvein visible in the hypertriangle. The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Three bridge-crossveins Bqs in the space between RP and IR2 basal of the subnodus. Base of RP2

aligned with subnodus. Only a single oblique vein 'O', rather distant from subnodus, 3.6 mm away. A long, nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 is nearly straight. RP2 and IR2 diverge strongly. RP2 is very undulated. Three rows of cells in the area between these veins. RP2 and RP1 are closely parallel basally with a single row of cells in the area in-between, but 2.4 mm basal of the pterostigma, these veins strongly diverge with three rows of cells in-between. Area of IR1 is not preserved, but it was clearly not in a basal position; it probably began below the middle part of the pterostigma (pseudo-IR1), if at all present. RP3/4 and MA are closely parallel and gently undulated veins. A long and straight Mspl, parallel to MA with only a single row of cells between it and MA. Three rows of cells in the postdiscoidal area distal of the discoidal triangle; width of this area distal of the discoidal triangle 2.4 mm and along the posterior wing margin 3.2 mm. MP is more or less parallel with MA. CuA has four or five poorly defined posterior branches and reaches the posterior wing margin on a level with nodus. The cubito-anal area is 2.5 mm wide with four or five rows of cells between CuA and the posterior wing margin. Two rows of cells in the anal area; width of anal area 1.9 mm.



Text-Fig. 103. *Eumorbaeschna jurassica* (CARPENTER, 1932). JME SOS 3714 - left pair of wings.

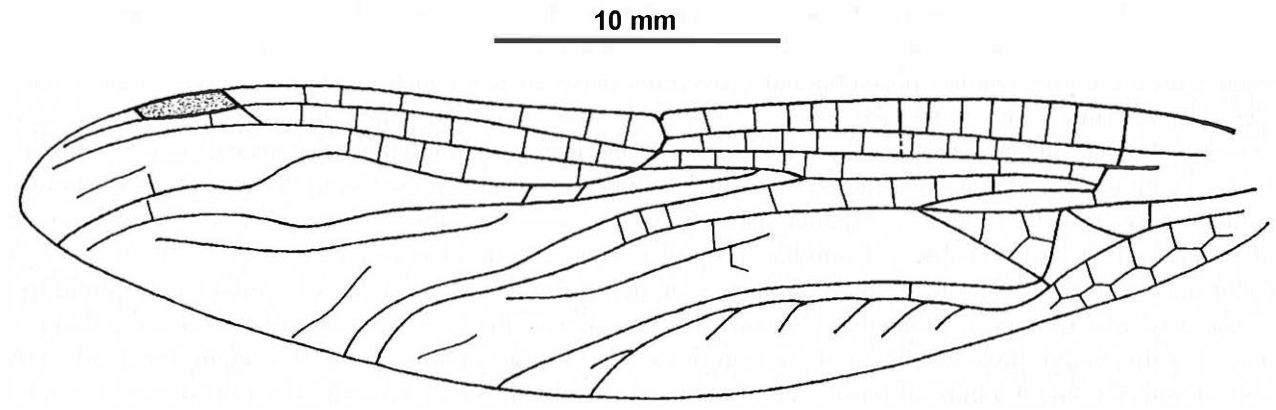
Hindwing: Length 38.5 mm; width 13.0 mm; distance from base to arculus 3.3 mm; distance from base to nodus 14.0 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 16.5 mm. Pterostigma 4.4 mm long and 0.8 mm wide, covering four cells, and strongly braced by an oblique crossvein that is nearly aligned with its basal side. Eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The antenodal area is poorly preserved, the primary antenodal crossveins are not visible. Six secondary antenodal crossveins are preserved between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. ScP fuses with the costal margin at the nodus. Only a single antesubnodal crossvein visible in the area between RA and RP basal of the subnodus. Median space free of crossveins. Submedian space free of crossveins, but the CuP-crossing is partly visible, 2.1 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is elongated (but broader and shorter than the forewing one) and six-celled (very unusual for this taxon, thus, maybe an aberration or even an artifact) with an almost straight distal side MAb; length of anterior side 4.3 mm; of basal side 2.5 mm; of distal side MAb 4.3 mm. The hypertriangle seems to be free of crossveins and is rather narrow (length 5.0 mm; max. width 0.8 mm). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Two bridge-crossveins Bqs in the space between RP and IR2 basal of the subnodus. Base of RP2 aligned with subnodus. Two oblique veins 'O', 1.6 mm and 3.0 mm distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 is nearly straight. RP2 and IR2 diverge strongly. RP2 is strongly undulated, there are three rows of cells in the area between these veins. RP2 and RP1 are closely parallel basally with a single row of cells in the area in-between, but 3.0 mm basal of the pterostigma, these veins diverge strongly with two rows of cells in-between. Vein IR1 is vestigial. RP3/4 and MA are closely parallel and gently undulated veins. MA vanishes distally near the posterior wing margin (clearly a teratological aberration). A long and straight Mspl, more or less parallel to MA (course not straight, but somewhat irregular) with one to three rows of cells between it and MA. Three rows of cells in the postdiscoidal area distal of the discoidal triangle; width of this area distal of the discoidal triangle 3.2 mm and along the posterior wing margin 7.5 mm. MP is more or less parallel with MA. CuA has four or five poorly defined posterior branches and reaches the posterior wing margin on a level with nodus. The cubito-anal area is 5.5 mm wide with six or seven rows of cells between CuA and the posterior wing margin. The anal area is poorly preserved, but it is broad with about six rows of cells between AA and the posterior wing margin (estimation); width of anal area 8.5 mm. The anal loop is relatively small, divided in five cells and nearly as wide as long, but posteriorly well-closed.

♦ Specimen no. 1983 / 2633, JME; labelled «Naam: Vleugel van Libelle, Ouderd: Malm zeta 2b, Vindpl.: ~~Harthof~~ Blumenberg, aank. HERZNER 1975, Sln. 240 a, b, coll. DE BUISONJÉ»

Text-Fig. 104, Plate 31: Fig. 4

Part and counterpart of an isolated forewing. The venation is not traced by iron-oxide dendrites, therefore the cross-venation is only faintly visible.

Forewing: It is very similar to that of the holotype. Length 43.9 mm; width at nodus 10.0 mm; distance from base to arculus 5.3 mm; distance from base to nodus 21.3 mm (the nodus is nearly midway between base and apex); distance from nodus to pterostigma 15.1 mm. Pterostigma 3.2 mm long and 0.8 mm wide. The visible postnodal crossveins are not aligned with the corresponding postsubnodal crossveins. The visible secondary antenodal crossveins (about a dozen) of both rows are not aligned. The two primary antenodal crossveins are not identifiable (artifact), but one might be slightly basal of the arculus (?). No gap of antesubnodal crossveins immediately basal of the subnodus. The discoidal triangle is longitudinally elongated and apparently divided into four cells (only faintly visible); length of anterior side 5.2 mm; of basal side 2.5 mm; of distal side MAb 5.2 mm; the distal side MAb of the discoidal triangle seems to be straight (aberration ?). RP1 and RP2 are closely parallel up to the pterostigma with only a single row of cells in-between. RP2 is distally strongly undulated and not parallel to IR2 that is slightly undulated as well. The area between RP2 and IR2 is strongly widened at their first undulation. Two oblique veins 'O', 2.0 mm and 3.8 mm distal of the subnodus. Rspl and Mspl are distinct and parallel to IR2 and MA, respectively. RP3/4 and MA are parallel and undulated. MP and CuA are basally closely parallel, but distally distinctly divergent. The cubito-anal area is max. 2.9 mm wide. The anal area is max. 1.9 mm wide (below PsA). AA is divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a distinct subdiscoidal triangle. There seem to be no accessory cubito-anal crossveins in the submedian space between CuP-crossing (1.9 mm basal of arculus) and PsA. The arculus is angled and 5.3 mm distal of the wing base. The bases of RP and MA are distinctly separated at arculus.



Text-Fig. 104. *Eumorbaeschna jurassica* (CARPENTER, 1932). JME 1983 / 2633 - left forewing.

♦ Specimen no. 59746, BSP

Thorax and right pair of wings of a female (in ventral aspect, thus, a counterpart). The forewing is 44.8 mm long and the hindwing is 43.4 mm long. The postero-basal margin of the hindwing is rounded.

♦ Specimen no. 64342, SMNS; Wegscheid b. Eichstätt

Plate 33: Fig. 2

An isolated forewing (counterpart missing). The wing venation is well-preserved and traced by iron-oxide dendrites in the basal part, but is only faintly visible in the distal part. Length 43 mm; width at nodus 9.6 mm; hypertriangle clearly free of crossveins; the elongated discoidal triangle is divided into five cells (length of anterior side 4.6 mm; of basal side 4.8 mm; of straight distal side MAb 4.3 mm); the subdiscoidal triangle is clearly divided into two cells; six secondary antenodal crossveins in the first row between Ax1 and Ax2; no accessory cubito-anal crossveins; anal area with two rows of cells.

♦ Specimen no. MB. J. 1734 a, b, MB; labelled «MB.J. 1734, ? *Aeschnidium densum* HAGEN, REDENBACHER'sche Slg., Solnhofen»

Part and counterpart of a poorly preserved dragonfly. It can be identified as a member of this species by the following characters: Hindwing length 43-44 mm; discoidal triangle longitudinally elongated; relatively large anal loop that is posteriorly well-closed; elongated gaff; veins RP2, RP3/4 and MA are undulated.

♦ Specimens in coll. KÜMPEL

There are four specimens of this species in the important coll. KÜMPEL (Wuppertal), which shall all be inherited to the Jura-Museum in Eichstätt (JME).

Specimen [No. 1]: Part and counterpart of a complete, but poorly preserved adult female, of which only the legs are not visible. Only one hindwing shows the main veins, but no cross-venation. The forewing length is 46 mm, and the hindwing length is 45 mm.

Specimen [without number, A]: A very poorly preserved dragonfly with thorax, abdomen, four legs and one pair of wings. The end of the abdomen seems to be somewhat expanded. The hindwing length is 46 mm.

Specimen [without number, B]: Part and counterpart of a nearly complete (only the legs are not visible), but poorly preserved dragonfly. The hindwing length is 45.5 mm.

Specimen [without number, C]: A complete, but relatively poorly preserved adult male. The forewing length is 42.5 mm, and that of the hindwing 42.0 mm. The anal triangle is long and narrow.

Neoaeshnida BECHLY, 1996

1996 Neoaeshnida; BECHLY, p. 384.

Included groups: Gomphaeschnidae (*sensu* BECHLY 1996) and Aeshnodea BECHLY, 1996.

Wing venational autapomorphies: Mspl better defined (not zigzagged) and strictly parallel to MA in the groundplan (but curved in Aeshnidae); both pairs of wings with a strong convex secondary longitudinal vein (trigonal planate) in the postdiscoidal area, correlated with a distinctly angled or sigmoidally curved distal side MAb of the discoidal triangles (BECHLY 1995); in both pairs of wings MP and CuA are closely parallel with only a single row of cells in-between up to the wing margin (MP and CuA not diverging near the posterior wing margin); the distal second oblique vein 'O' between RP2 and IR2 is secondarily absent (two oblique veins are retained in most known wings of Eumorbaeschnidae fam. nov., and can occasionally reappear as atavisms in certain large Aeshnidae like *Neuraeschna*, *Gynacantha*, and *Staurophlebia*, according to PETERS pers. comm.), so that only the basal lestine oblique vein 'O' is retained and shifted basally, close to the subnodus (this basal position is constant in Neoaeshnida, but rather variable in the other Aeshnida); the distal primary antenodal crossvein Ax2 is shifted distinctly basal of the level of distal angle of discoidal triangle in the forewings (convergent to Cymatophlebiidae, Gomphaeschnaoidinae subfam. nov., Telephlebiidae stat. nov., and probably also Eumorbaeschnidae fam. nov.); in the groundplan only two rows of cells in the basal part of the postdiscoidal area between the level of the distal angle of the discoidal triangle and the level of the midfork (retained in Gomphaeschnidae, Brachytronidae and Telephlebiidae stat. nov., but reversed in Aeshnidae); tendency towards the formation of a longitudinal accessory anal loop between CuAb and the most basal posterior branch of CuAa (homology and polarity somewhat unsafe, since within Gomphaeschnidae only known from

Paramorbaeschna araripensis gen. et sp. nov. and *Alloaeschna paskapooensis*, while it is present in most Aeshnodea, except a few taxa, e.g. *Brachytron*).

Other autapomorphies: Larval rectal gills of the derived implicate or foliate duplex type (TILLYARD 1917); larval anal pyramid hyperattenuate with a long epiproctal process and long paraprocts (CARLE 1995, 1996, LOHMANN 1996a); larval prementum more widened distally (CARLE 1996); intraocellar lobe more strongly developed; terminal segment of male vesicula spermalis swab-like with reduced "penile prepuce" (CARLE 1995, 1996); abdominal tergites with distinct lateral carinae (CARLE 1995, 1996).

Discussion: The non wing venational characters are mostly unknown in all fossil Panaeshnida taxon nov., and could therefore represent autapomorphies for more inclusive monophyla.

Family Gomphaeschnidae TILLYARD & FRASER, 1940 nomen correctum

1936 Jagorinae FRASER, p. 55 (from FRASER's wording "No attempt has been made *here* to divide the family Aeshnidae into subfamilies... *might* usefully form the basis for three subfamilies ..." it is clear that the author did not intend to create new family group taxa; thus, Jagoridae FRASER, 1936 has to be regarded as a nomen nullum).

1940 Gomphaeshninae TILLYARD & FRASER, p. 376 (nomen imperfectum).

1957 Gomphaeshninae; FRASER, p. 97.

1981 Gomphaeschnini; DAVIES, p. 28 (stat. nov., and an incorrect subsequent spelling according to Art. 33 IRZN, since the change is not demonstrably intentional).

1986 Gomphaeschninae; WIGHTON & WILSON, pp. 505-506.

1996 Gomphaeschnidae; BECHLY, p. 384 (stat. et sensu nov.).

1996a Gomphaeschnata; LOHMANN, p. 224. (rejected by us as redundant taxon, since only including the family Gomphaeschnidae).

Type genus: *Gomphaeschna* SELYS, 1871 (= *Gomphaeshna* TILLYARD & FRASER, 1940 jun. obj. syn. nov.; see discussion below under the genus *Gomphaeschna*).

Included groups: Gomphaeschnaoidinae subfam. nov. and Gomphaeschninae sensu nov.

Wing venational autapomorphies: The most distal part of the antesubnodal area between RA and RP is free of antesubnodal crossveins (LOHMANN 1996a), but such a "cordulegastrid gap" is not present in *Alloaeschna quadrata*, while it is present as a convergence in *Araripeliupanshania* gen. nov.; no accessory cubito-anal crossveins in the submedian space between CuP-crossing and PsA (reversal); discoidal triangles only divided into two cells by a single crossvein (reversal; not yet present in the most basal genus *Oligoaeschna* and some specimens of *Gomphaeschna furcillata*); hypertriangles secondarily undivided by crossveins (apparently also present in "*Oligoaeschna*" *oligocenica*, but not in the recent species of the most basal genus *Oligoaeschna*).

Other autapomorphies: Derived type of male vesicula spermalis (LOHMANN 1996a) with a pair of long processes on the incus of the first segment, secondarily absent ligula hooks on the second segment, and a pair of posteriorly directed style-like processes and a pair of lateral incisions on the third segment which is strongly curved, and characteristically curved ram-horn-like flagellae on the terminal segment (maybe only an autapomorphy of *Gomphaeschna*); median lobes of the terminal segment of the male vesicula spermalis are secondarily unfused (a reversal that could be explained with an ontogenetic phenomenon, e.g. paedomorphosis, *contra* LOHMANN 1996a).

Discussion: LOHMANN (1995: 54) called this clade Gomphaeschnoidea and indicated this taxon as stat. nov., but this elevation in rank is not available, since the work is unpublished according to Art. 8 IRZN.

LOHMANN (1996a) suggested that the absence of a dorso-longitudinal abdominal carina is a unique symplesiomorphy of his Gomphaeschnata. Since such a carina is indicated in Mesuropetalidae and known to be well-developed in many Austropetaliida taxon nov., all Cymatophlebiidae, some Gomphaeschnidae (e.g. *Oligoaeschna* and the fossil genus *Sinojagoria* gen. nov.) and all Aeshnodea, BECHLY (1996) regarded its absence as an autapomorphic reversal in *Gomphaeschna*. Furthermore, such a carina is even present in many specimens of type species *Gomphaeschna furcillata* (SAY, 1839), so that its suppression might only represent a derived trend within the genus *Gomphaeschna*. Since several of the mentioned putative autapomorphies of Gomphaeschnidae seem to be rather homoplastic or insufficiently known (body characters), only the reduction in the number of antesubnodal crossveins between RA and RP (distal of the arculus and basal of the subnodus) could be regarded as relatively strong autapomorphy, even though it evolved at least one further time by convergence as an autapomorphy of Cavilabiata.

The two-celled male anal triangle of *Gomphaeschna* seems to be an autapomorphy of this genus (convergent to some Aeshnodea, e.g. *Brachytron*, *Basiaeschna*, and some Aeshnini, and all Eurypalpida) since the anal triangle is three-celled in *Linaeschna*, *Oligoaeschna* and *Gomphaeschnaoides* (still unknown in the other fossil taxa).

Subfamily Gomphaeschnaoidinae subfam. nov.

1998 Gomphaeschnaoidinae; BECHLY, p. 62 (nomen nudum).

Type genus: *Gomphaeschnaoides* CARLE & WIGHTON, 1990.

Included groups: The two sister-tribes Sinojagorini trib. nov. and Gomphaeschnaoidini trib. nov., and *Anomalaeschna berndschusteri* gen. et sp. nov. in tribus *incertae sedis*.

Wing venational autapomorphies: In the forewing there is only a single secondary antenodal crossvein between Ax1 and Ax2 which is aligned like a primary antenodal crossvein (unknown in *Plesigomphaeschnaoides* gen. nov.); in the forewing Ax2 is shifted basally on a level with the basal angle of the discoidal triangle (convergent to Telephlebiidae stat. nov. and probably also Eumorbaeschnidae fam. nov.; unknown in *Plesigomphaeschnaoides* gen. nov.); pterostigmal brace vein very oblique.

Tribus incertae sedis

Genus *Anomalaeschna* gen. nov.

Type species: *Anomalaeschna berndschusteri* sp. nov.

Derivatio nominis: After the generic name *Aeschna* and the anomalous position of RP2 distal of the subnodus.

Diagnosis: This new genus is distinguished by the following characters: Wing length 27 mm; only a single secondary antenodal crossvein between Ax1 and Ax2; hypertriangles, discoidal triangles, and subdiscoidal triangles free; anal loop five-celled; only two rows of cells between CuA and wing margin in the forewing, and only three rows in the hindwing; Rspl and Mspl parallel to IR2 and MA, respectively, with only a single row of cells in-between; only a single row of cells between RP3/4 and MA; RP2 originates distinctly distal of the subnodus (unique autapomorphy within Anisoptera); RP1 and RP2 basally divergent (autapomorphic reversal); area between RP2 and IR2 distally strongly widened with two to four rows of cells in-between; pseudo-IR1 zigzagged with only a single row of cells between its basal half and RP1; pterostigma very short, only covering a single cell (autapomorphy); only three cells in the short area between RA and anterior wing margin distal of pterostigma.

Systematic position: The presence of only a single secondary antenodal crossvein between Ax1 and Ax2, and the basal position of Ax2 on a level with the basal side of the discoidal triangle, indicate a close relationship with Gomphaeschnaoidinae subfam. nov. The less oblique and straight pterostigmal brace vein could represent a unique plesiomorphic condition within this group, which would suggest a more basal position of this new genus. On the other hand, the general character pattern (e.g. antenodal and antesubnodal area) is very similar to *Progomphaeschnaoides* gen. nov., so that a close relationship would be possible, if the pterostigmal brace vein should represent a reversal. Because of this uncertainty, we preliminarily place this genus in Gomphaeschnaoidinae tribus *incertae sedis*.

Anomalaeschna berndschusteri sp. nov.

Text-Figs 134-137, Plate 34: Fig. 1

Holotype: Specimen no. [515], coll. MURATA, Kyoto (old number G 22).

Derivatio nominis: Named in honour of Mr Bernd SCHUSTER (Hünstetten, Germany), who generously provided numerous of his excellent photos of fossil insects to the first author.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

Diagnosis: Same as for the genus.

Description: Pterothorax with four legs and all wings, with well-preserved venation, but the wings are partly superimposed. Forewing: Length of preserved part 26.5 mm (total length probably 28.4 mm); width at nodus 6.6 mm; distance from nodus to pterostigma 12.0-12.1 mm. Pterostigma very short (1.5-1.6 mm long and max. 0.8 mm wide), covering only a single cell, and braced by an oblique crossvein (brace vein is not curved or undulated). About six postnodal crossveins between nodus and pterostigma, not aligned with the five to seven corresponding postsubnodal crossveins. Only three cells in the short area between RA and anterior wing margin distal of pterostigma. Seven antenodal crossveins visible between costal margin and ScP, not aligned with the antenodal crossveins of the second row between ScP and RA, except for the two primary antenodal crossveins Ax1 and Ax2 that are also stronger than the secondary antenodal crossveins. Ax1 is 1.8 mm basal of the arculus, and Ax2 is 3.1 mm distal of Ax1, on a level with basal angle of discoidal triangle. Only a single secondary antenodal of the first row between the two primary antenodal crossveins, not precisely aligned with the corresponding antenodal of the second row. Only three antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus and immediately distal of the arculus. Only a single bridge-crossvein Bq. Base of RP2 not aligned with subnodus, but originating 0.6-0.8 mm distal (!) of it. Only a single oblique vein 'O', close to the origin of RP2. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2; Rspl originates 4.2 mm distal of subnodus in the left forewing, and 5.0 mm in the right forewing. Three indistinct convex secondary veins originate on Rspl and reach the posterior wing margin. RP2 and IR2 strongly diverge distally with two to four rows of cells in-between. Pseudo-IR1 zigzagged and originating on RP1 beneath the pterostigma. RP1 and RP2 are basally divergent with only a single row of cells in-between, and below the pterostigma, they diverge more strongly with two or more rows of cells in-between. There is no oblique crossvein between RP1 and RP2 that is slanted towards the pterostigma. RP3/4 and MA are more or less parallel, but MA is gently undulated with a single row of cells in-between. Mspl is well-defined, originating 1.5 mm (left forewing) or 2.4 mm (right forewing) distal of discoidal triangle, and running parallel to MA with only a single row of cells in-between. No distinct convex secondary veins originate on Mspl and reach the posterior wing margin. The postdiscoidal area is distally widened (width near discoidal triangle 1.4-1.5 mm; width at posterior wing margin 5.1-5.2 mm) with only a single row of cells immediately distal of the discoidal triangle, so that there is no secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle elongated and free of crossveins (length 3.2-3.3 mm; max. width 0.4 mm). The elongated discoidal triangle is free of crossveins, and it is distinctly more narrow than that of the hindwing; length of anterior side 2.3-2.5 mm; of basal side 1.2-1.3 mm; of angled distal side MAb 2.4-2.5 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.2 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 but short unicellular subdiscoidal triangle, max. 1.3-1.4 mm long and basally 1.1-1.2 mm wide (= length of PsA); the posterior margin of the subdiscoidal triangle is distinctly angled. PsA ends on MP + CuA at or slightly below basal angle of discoidal triangle. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin far distal of the level of the nodus, and CuA reaches the posterior wing margin slightly distal of the level of nodus as well. There are no well-defined posterior branches of CuA. Only two rows of cells between CuA and posterior wing margin; max. width of cubito-anal area only 1.2 mm. Anal area max. 1.1 mm wide (below origin of PsA) with one or two rows of cells between AA and the posterior wing margin (the area is not well-preserved, but there could be an elongated paranal cell).

Hindwing: Length 27.4 mm; width at nodus 9.4 mm; distance from base to arculus 4.6 mm; distance from base to nodus 10.8 mm, thus, the nodus is in a rather basal position at 39-40 % of the total wing length; distance from nodus to pterostigma 12.8 mm. Pterostigma very short (1.7 mm long and max. 0.7-0.8 mm wide), covering only a single cell, and braced by an oblique crossvein (brace vein is not curved or undulated). There are ten postnodal crossveins between nodus and pterostigma, not aligned with the six corresponding postsubnodal crossveins. Only three cells in the short area between RA and anterior wing margin distal of pterostigma. There are only five antenodal crossveins between costal margin and ScP, aligned with the five antenodal crossveins of the second row between ScP and RA, except for the most distal one; the two primary antenodal crossveins Ax1 and Ax2 are also stronger than the others; Ax1 is 2.2 mm basal of the arculus, and Ax2 is 3.4 mm distal of Ax1, with only a single aligned secondary antenodal crossvein in-between. Ax1 is slightly slanted towards the wing base. There are only two antesubnodal crossveins in the space between arculus and subnodus with a distinct gap immediately basal of the subnodus and immediately distal of the arculus. Only a single bridge-crossvein Bq. Base of RP2 not aligned with subnodus, but originating 0.6 mm distal (!) of it. Only a single oblique vein 'O', close to the origin of RP2. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2; Rspl originates 4.0 mm distal of subnodus in the left hindwing, but only 2.8 mm distal of subnodus in the right hindwing. Two convex secondary veins originate on Rspl and reach the posterior wing margin. RP2 and IR2 strongly diverge distally with two to four rows of cells in-between. Pseudo-IR1 is zigzagged and originates beneath the middle of the pterostigma; only a single row of cells between the basal parts of pseudo-IR1 and RP1 (separated by three to four cells at the posterior wing margin), and only three rows of cells between pseudo-IR1 and RP2. In both hindwings RP1 and RP2 are basally divergent with only a single row of cells in-between, but they become more strongly divergent near the pterostigmal brace with two or more rows of cells in-between. There is no oblique crossvein between RP1 and RP2 that is slanted towards the pterostigma. RP3/4 and MA are more or less parallel, but MA is distinctly undulated; there is only a single row of cells between RP3/4 and MA. Mspl is well-defined, running parallel to MA with only a single row of cells between it and MA. No well-defined convex secondary veins originate on Mspl. The postdiscoidal area is distally widened (width near discoidal triangle 2.2 mm; width at wing margin 4.6-4.8 mm); there is no zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. The hypertriangle is free of crossveins (length 3.1 mm; max. width 0.5-0.6 mm). The discoidal triangle is free of crossveins, and it is very stout, thus much less elongated than that of the forewing; length of anterior side 2.4-2.5 mm; of basal side 1.8-2.0 mm; of (rather straight) distal side MAb 2.7 mm in the left hindwing, and 2.4 mm in the right hindwing. Median space poorly preserved, but apparently free of crossveins. Submedian space poorly preserved, the CuP-crossing is not visible. AA divided into an (faintly preserved) oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle, max. 2.3 mm long and basally 1.5 mm wide (= length of PsA). PsA ends on MP + CuA at basal angle of discoidal triangle in both hindwings. A single row of cells in the area between MP and CuA in the left hindwing, but there are distally two to three rows of cells in the right hindwing. MP reaches the posterior wing margin distinctly distal of the level of nodus, and CuA reaches the posterior wing margin about the level of nodus. There are four distal posterior branches of CuA. Only three rows of cells between CuA and the posterior wing margin, max. width of cubito-anal area 2.9-3.0 mm. Anal area poorly preserved, but apparently not very wide with only about four to five rows of cells between AA and the posterior wing margin. Anal loop broad (max. length 2.5 mm; max. width 2.7 mm), posteriorly well-closed, and divided into five cells. Basal of the anal loop, there is a slightly elongated paranal cell. Even though there are no well-defined posterior branches of AA visible, the presence of at least three to four transverse rows of cells between anal loop and basal wing margin suggests that it could be a female specimen.

Tribus Sinojagorini trib. nov.

Type genus: *Sinojagoria* gen. nov.

Included groups: Currently only including the type species *Sinojagoria imperfecta* gen. et sp. nov., thus, preliminarily a redundant taxon.

Autapomorphies: No strong autapomorphies are yet known (see diagnosis of type genus).

Genus *Sinojagoria* gen. nov.

Type species: *Sinojagoria imperfecta* sp. nov.

Derivatio nominis: After "sino-" (China) and "*Jagoria*" in reference to its resemblance to the genus *Oligoaeschna* whose junior subjective synonym is *Jagoria*.

Diagnosis: This new genus is distinguished by the following characters: Forewing discoidal triangle longitudinally elongated and two-celled; hindwing discoidal triangle four-celled and rather stout; anal loop large, six- or seven-celled, nearly as wide as long (possible autapomorphy); Ax2 on a level with the basal side of the discoidal triangle in the forewing; one secondary antenodal crossvein between Ax1 and Ax2 in the forewing, and two in the hindwing; RP2 is weakly undulated; pterostigma covering two cells; only four antesubnodal crossveins between RA and RP basal of the subnodus in the forewing; Rspl and Mspl more or less straight with a single row of cells between Rspl and IR2 and between Mspl and MA; IR2 straight; RP3/4 and MA more or less parallel and gently undulated veins; MA distally more undulated than RP3/4, resulting in a short widened area with two rows of cells in-between; MP diverging strongly from MA in the hindwing.

Systematic position: *Sinojagoria* gen. nov. shares with the Gomphaeschnidae the following synapomorphies: The distal part of the antesubnodal area between RA and RP is free of antesubnodal crossveins; the submedian space, between CuP-crossing and PsA, is free of crossveins; forewing discoidal triangles only divided into two cells by a single crossvein; hypertriangles secondarily undivided by crossveins. It shares with *Oligoaeschna* the hindwing discoidal triangle divided in more than two cells. Some specimens of modern *Oligoaeschna* have their hindwing discoidal triangle divided into four cells, just like *Sinojagoria* gen. nov. Nevertheless, it differs from *Oligoaeschna* in its forewing primary antenodal crossvein Ax2 lying on a level with the basal side of the discoidal triangle. This character is an autapomorphy of the Gomphaeschnaoidinae subfam. nov. (convergent to Telephlebiidae stat. nov.). *Sinojagoria* gen. nov. shares with this group the following other synapomorphies: In the forewing there is only a single secondary antenodal crossvein between Ax1 and Ax2; the pterostigmal brace is very oblique. Nevertheless, it differs from this group in the following points: Absence of a characteristic elongated distal paranal cell in the hindwing, immediately basal of the anal loop; its pterostigmal brace is not undulated. Both character states have to be regarded as plesiomorphies. Unfortunately, two of the known autapomorphies of Gomphaeschnaoidini trib. nov. (the basally widened cell below the pterostigma, and the weakly defined posterior branches of hindwing CuAa) are currently unknown in *Sinojagoria* gen. nov. Nevertheless, the hypothesis of a sistergroup relationship between *Sinojagoria* gen. nov. and the remaining Gomphaeschnaoidinae subfam. nov. is reasonably supported, and there is also no conflicting evidence against this hypothesis.

Sinojagoria imperfecta sp. nov.

Text-Figs 105-108

Holotype: Specimen no. [MNHN-LP-R. 55193], coll. A. NEL, MNHN, Paris.

Derivatio nominis: After the rather poor preservation of the holotype.

Locus typicus: Near Chaomidian Village, 25 km SE of Beipiao City, western Liaoning Province, P.R. China.

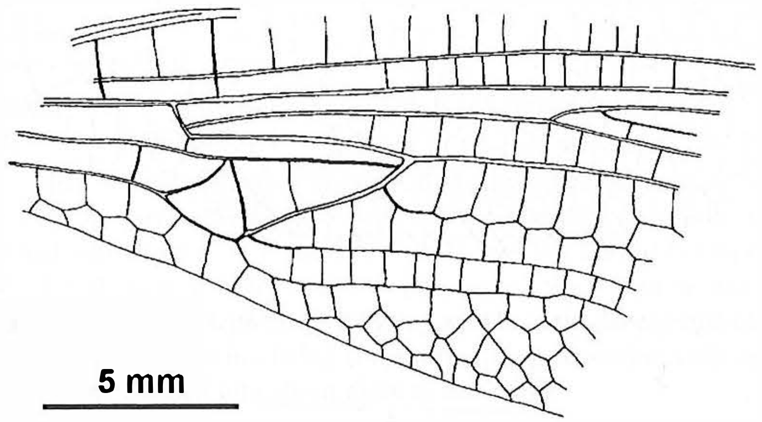
Stratum typicum: Yixian Formation, Lower Cretaceous, Aptian (SMITH *et al.* 1995, WELLNHOFER 1997).

Diagnosis: Same as for the genus.

Description: Part and counterpart of a female. The wings are only partly preserved, but still attached to the thorax. Fragments of the abdomen and head are present, too, but poorly preserved. The four wings were probably hyaline, since no trace of coloration is visible.

Forewing: Length 39.7 mm; width at nodus 10.7 mm; distance from base to arculus 5.8 mm; from base to nodus 19.7 mm; from nodus to pterostigma 14.3 mm. Pterostigma 2.9 mm long and 0.9 mm wide, covering two cells, and strongly braced by a very oblique (but straight) crossvein that is aligned with its basal side. Nine postnodal crossveins between nodus and pterostigma, not aligned with the ten corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the twelve secondary antenodal crossveins between costal margin and ScP that are not aligned with the second row of antenodal crossveins between ScP and RA. Between Ax1 and Ax2 there is only a single secondary antenodal crossvein in the first row, and apparently none in the second row; Ax1 is 1.8-2.1 mm basal of the arculus, and Ax2 is 3.0 mm distal of Ax1 (on a level with basal angle of discoidal triangle). ScP fuses with the costal margin at the nodus that is of the normal Anisoptera-type. Four antesubnodal crossveins visible in the median part of the area between RA and RP basal of the subnodus with a distinct gap immediately basal of the subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.2 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The two-celled discoidal triangle is very elongated with a slightly bent distal side MAb; length of anterior side 4.3 mm; of basal side 2.0 mm; of distal side MAb 4.1 mm. At least in the right forewing the basal side of the hypertriangle ends on MAb, so that the hypertriangle is somewhat quadrangular (unknown in the left forewing); hypertriangle free of crossveins and rather narrow (length 5.5 mm; max. width 0.5 mm). The arculus is angled and the bases of RP and MA are distinctly separated at arculus. The basal area between RP and MA is traversed by very numerous antefurcal crossveins. Three bridge-crossveins Bqs basal of the subnodus. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2; at least one convex secondary vein is visible in the area between Rspl and RP3/4.

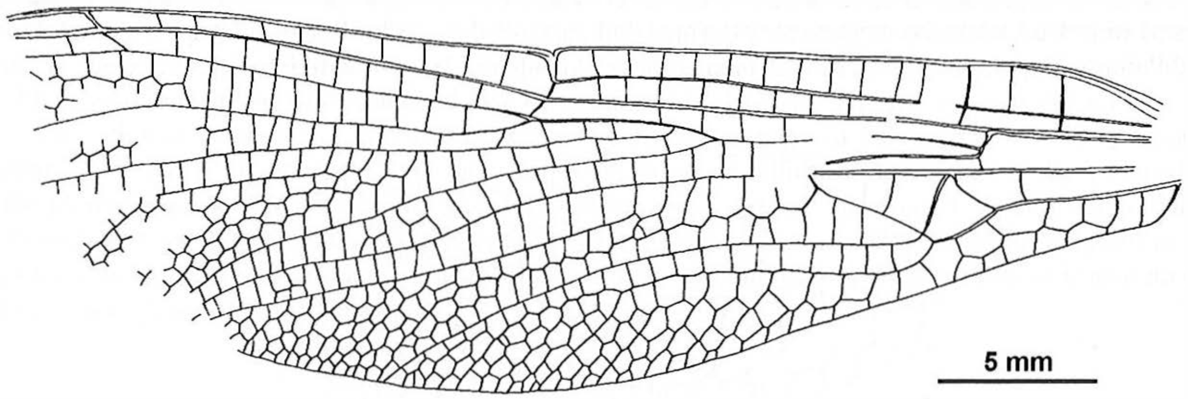
IR2 is nearly straight. RP2 and IR2 begin to diverge somewhat basal of the pterostigma with three rows of cells in the widened area between these two veins. RP2 slightly undulated. RP2 and RP1 are basally closely parallel with only a single row of cells in the area in-between, but somewhat basal of the pterostigma they become divergent with two or more rows of cells in-between. Pseudo-IR1 not preserved. RP3/4 and MA parallel and gently undulated (MA distally more undulated than RP3/4) with only a single row of cells in-between, except for a short area with two rows of cells below the base of Rspl. Mspl is long and parallel to MA with a single row of cells between it and MA. The postdiscoidal area is distally strongly widened (width near discoidal triangle 2.1 mm; width at wing margin 6.8 mm); two rows of cells in the postdiscoidal area immediately distal of the discoidal triangle; MP ends far distal of the level of nodus, and CuA ends somewhat distal of the level of nodus as well. CuA with about six weakly defined and zigzagged posterior branches; max. width of cubito-anal area 2.9 mm with up to five rows of cells; max. width of anal area 1.7 mm with two rows of cells.



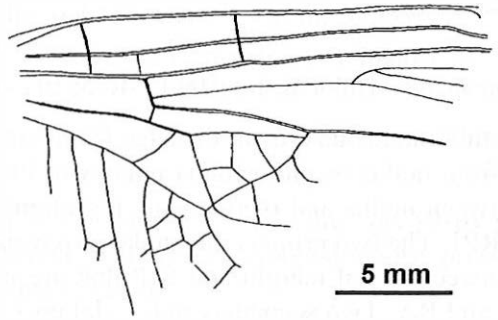
Text-Fig. 105. *Sinojagoria imperfecta* sp. nov. Holotype MNHN-LP-R. 55193 - female, right forewing base.

Hindwing: Length unknown, width at nodus unknown; distance from base to arculus 5.8 mm; distance from base to nodus 20.0 mm; distance from nodus to pterostigma unknown. Pterostigma not preserved. Ten postnodal crossveins are preserved between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are aligned and stronger than the secondary antenodal crossveins between costal margin and ScP that are not aligned with the second row of antenodal crossveins between ScP and RA. Two secondary antenodal crossveins between Ax1 and Ax2 in the first row, but only one visible in the second row. Ax1 is 2.3-2.4 mm basal of the arculus, and Ax2 is 6.4-6.5 mm distal of Ax1. Ax2 is situated distinctly basal of the distal end of the discoidal triangle. The antesubnodal crossveins are not preserved in the area between RA and RP basal of the subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.9 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle; PsA ends on MP + CuA somewhat basal of the discoidal triangle. The four-celled discoidal triangle is rather broad and stout with smoothly bent distal side MAb; length of anterior side 4.8-5.1 mm; of basal side 3.0-3.1 mm; of distal side MAb 5.0-5.1 mm. At least in the right hindwing the basal side of the hypertriangle distinctly ends on MAb, so that the hypertriangle is somewhat quadrangular (less distinct in the left hindwing); hypertriangle free (length 6.6-6.8 mm; max. width 1.0 mm). The bases of RP and MA are distinctly separated at arculus which is angled. The basal area between RP and MA is traversed by several antefurcal crossveins. No preserved bridge-crossveins Bqs. Base of RP2 aligned with subnodus. The basal oblique vein 'O' is not preserved, but there might be a second weakly defined distal oblique vein 'O' (?). Rspl is not well-preserved, but apparently it is parallel to IR2 with only a single row of cells between these two veins. IR2 nearly straight. RP2 apparently smoothly undulated. RP2 and RP1 are basally closely parallel with only a single row of cells in the basal part of the area in-between. Pseudo-IR1 not preserved. RP3/4 and MA run parallel, but MA is distally gently undulated, while RP3/4 is relatively straight. There are two rows of cells in the distal part of the area between RP3/4 and MA. Mspl is hardly preserved. Two rows of cells in the postdiscoidal area immediately distal of the discoidal triangle (width of postdiscoidal area near the discoidal triangle 3.8 mm). MP and MA diverge strongly. Only the basal part of CuAa is preserved, including the bases of three posterior branches. The width of the cubito-anal area is unknown. The area between MP and CuA is basally distinctly widened, apparently with two rows of cells. The anal area is poorly preserved, but it is broad with more than five rows of cells between AA and the posterior wing margin. The six- or seven-celled anal loop is rather transverse (max. length 3.7 mm; max. width 4.6 mm), and posteriorly well-closed. No elongated distal paranal cell in the hindwing, immediately basal of the anal loop. The area of the potential anal angle and anal triangle is not preserved, thus, it is not possible to recognize if it is a male or a female specimen; however, the presence of three posterior branches of AA basal of the anal loop strongly suggests that it is a female specimen.

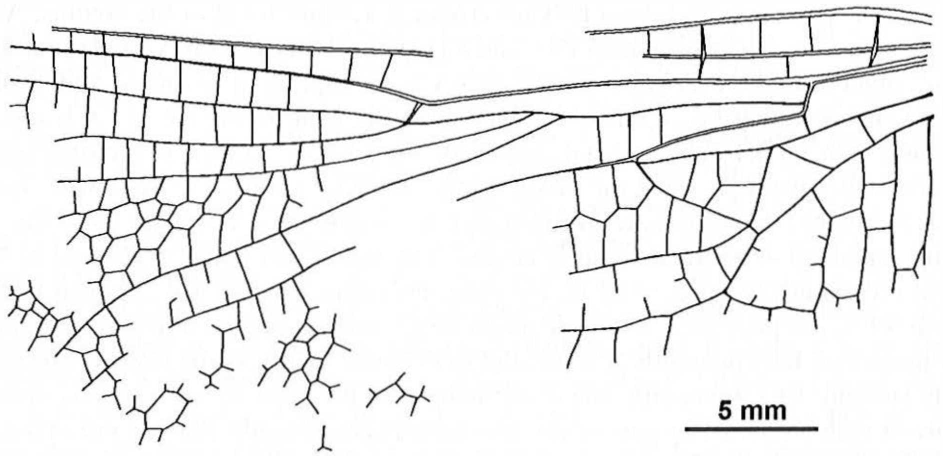
Abdomen with a median carina that is most clearly visible on segments III and IV.



Text-Fig. 106. *Sinojagoria imperfecta* sp. nov. Holotype MNHN-LP-R. 55193 - female, left forewing.



Text-Fig. 107. *Sinojagoria imperfecta* sp. nov. Holotype MNHN-LP-R. 55193 - female, right hindwing base.



Text-Fig. 108. *Sinojagoria imperfecta* sp. nov. Holotype MNHN-LP-R. 55193 - female, left hindwing (part and counterpart combined).

Tribus Gomphaeschnaoidini trib. nov.

Type genus: *Gomphaeschnaoides* CARLE & WIGHTON, 1990.

Included groups: The genera *Paramorbaeschna* gen. nov., *Progomphaeschnaoides* gen. nov., *Plesigomphaeschnaoides* gen. nov., and *Gomphaeschnaoides* CARLE & WIGHTON, 1990.

Wing venational autapomorphies: Presence of a characteristic elongated distal paranal cell in the hindwing, immediately basal of the anal loop (convergent to Cordulagomphinae *contra* CARLE & WIGHTON 1990); pterostigmal brace vein slightly undulated; basally widened cell below the pterostigma, caused by a curvature of RP1 at the pterostigmal brace (but unknown in *Sinojagoria* gen. nov.); posterior branches of CuAa are relatively weakly defined in the hindwing (but unknown in *Sinojagoria* gen. nov.).

Genus *Paramorbaeschna* gen. nov.

Type species: *Paramorbaeschna araripensis* sp. nov.

Derivatio nominis: After "para-" and "*Morbaeschna*" in reference to its resemblance to *Eumorbaeschna* gen. nov. (= "*Morbaeschna*" *sensu* NEEDHAM 1907).

Diagnosis: This genus differs from the other described Aeshnoptera from the same outcrops which are belonging to the genera *Gomphaeschnaoides* and *Progomphaeschnaoides* gen. nov. in the following characters: RP2 strongly undulated with three to four rows of cells between it and IR2; Mspl gently curved with two rows of cells between the basal parts of Mspl and MA (autapomorphy); area between MP and CuA basally distinctly widened in the hindwing (autapomorphy); CuAa with only five poorly defined distal posterior branches reaching the wing margin in the hindwing (autapomorphy); hindwing with accessory anal loop present between CuAb and CuAa and divided into about eight to nine cells.

More generally this genus is characterized as follows: Wing length 40.0-41.7 mm (forewing) and 37.0-40.6 mm (hindwing); only a single oblique vein 'O', one cell distal of the subnodus; pterostigma covering less than two cells with only a single crossvein beneath it; pterostigmal brace vein strongly oblique and undulated; anal loop wider than long, divided into five or six cells, and posteriorly well-closed; pseudo-IR1 relatively short, originating beneath the distal side of the pterostigma; Rspl more or less straight with a single row of cells between Rspl and IR2; RP3/4 and MA more or less parallel and gently undulated veins, with distally two rows of cells in-between; MP diverging strongly from MA in the hindwing; forewing discoidal triangle longitudinally elongated and divided into two or three cells, while hindwing discoidal triangle is always only two-celled and stout; hypertriangles and subdiscoidal triangles free of crossveins.

Systematic position: This new genus shares all important synapomorphies with Aeshnoptera, Aeshnida, Euaeshnida, and Neoaeshnida. Its attribution to the Neoaeshnida, rather than Eumorbaeschnidae fam. nov., is only based on the suppression of the distal oblique vein, the shifting of the basal oblique vein close to the subnodus, and the enlargement of the anal loop. All other characters also agree with this attribution: RP1 and RP2 long and parallel basally; discoidal triangles elongated, forewing discoidal triangle distinctly longer than that of the hindwing; RP2 undulated basal of the pterostigma; a well-defined Rspl; distal oblique crossvein absent and the basal one shifted basally close to the subnodus; a distinct (not zigzagged) Mspl; distal side MAb of the discoidal triangle angled; number of CuA branches reduced in hindwings; anal loop transversely broadened and posteriorly well-closed; RP3/4 and MA only gently undulated.

Paramorbaeschna gen. nov. shares with the Gomphaeschnidae the following two synapomorphies: Only a few antesubnodal crossveins between RA and RP (distal of the arculus and basal of the subnodus); no accessory cubito-anal crossveins in the submedian space between CuP-crossing and PsA. Furthermore, *Paramorbaeschna* gen. nov. shares with the Gomphaeschnidae several plesiomorphic characters within the Neoaeshnida: Anal loop still smaller than in Aeshnodea; AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle; only a single row of cells between Rspl and IR2 and two rows between Mspl and MA. *Paramorbaeschna* gen. nov. shares with *Cymatophlebia*, *Eumorbaeschna* gen. nov., *Linaeschna*, and *Progomphaeschnaoides* gen. nov. the presence of a strongly undulated RP2 with three rows of cells between it and IR2 (polarity and homology uncertain). *Paramorbaeschna* gen. nov. shows several more advanced features than *Eumorbaeschna* gen. nov.: It has only a single oblique vein 'O' (not constant in *Eumorbaeschna* gen. nov.); its MP is strongly curved and not parallel with MA; its CuAa is shorter than that of *Eumorbaeschna* gen. nov. with fewer and relatively poorly defined posterior branches; there are two rows of cells anteriorly between its Mspl and MA, instead of one. *Paramor-*

baeschna gen. nov. also differs from *Eumorbaeschna* gen. nov. in the following features of uncertain polarity: Its discoidal triangle is divided into two cells instead of three or more and it has fewer bridge-crossveins Bqs. The hindwing discoidal triangle of *Eumorbaeschna* gen. nov. is somewhat more elongated than that of *Paramorbaeschna* gen. nov. which could be an autapomorphic state.

Therefore we preliminarily refer *Paramorbaeschna* gen. nov. to the Gomphaeschnidae, although this conclusion is only based on two (rather weak) putative synapomorphies, and the absence of any substantial conflicting evidence.

This genus is most likely closely related to the genera *Gomphaeschnaoides* and *Progomphaeschnaoides* gen. nov., as is indicated by four putative synapomorphies with Gomphaeschnaoidinae subfam. nov. and Gomphaeschnaoidini trib. nov. (unfortunately mostly unknown for the probably related genus *Plesigomphaeschnaoides* gen. nov.): In the forewing there is only a single secondary antenodal crossvein between Ax1 and Ax2 which is aligned like a primary antenodal crossvein; in the forewing Ax2 is shifted basally on a level with basal angle of discoidal triangle; the very oblique and undulated pterostigmal brace vein; and the basally widened cell below the pterostigma, caused by a curvature of RP1 at the pterostigmal brace. A further similarity are the weakly defined posterior branches of CuAa in the hindwing. On the other hand, the gap of antesubnodal crossveins basal of the subnodus which is an important autapomorphy of Gomphaeschnidae, is not very distinct in some specimens of *Paramorbaeschna* gen. nov., and the presence of a much longitudinally elongated forewing discoidal triangle and an accessory anal loop in *Paramorbaeschna araripensis* gen. et sp. nov. could well be interpreted as potential synapomorphies with Aeshnodea or even Aeshnoidea (*sensu* BECHLY 1996, 1999a, b). Nevertheless, we preferred a placement in Gomphaeschnidae, as most basal genus of Gomphaeschnaoidini trib. nov., mainly because it is more parsimonious regarding the mentioned synapomorphies with Gomphaeschnaoidinae subfam. nov. and Gomphaeschnaoidini trib. nov., the absence of several autapomorphies of Aeshnodea, and the unsafe polarity of the mentioned similarities with Aeshnodea (see below). An accessory anal loop is e.g. also present in *Alloaeschna paskapooensis*, and consequently seems to be a derived groundplan character of Neoaeshnida rather than Aeshnoidea (*contra* BECHLY 1996, 1999a, b).

Paramorbaeschna araripensis sp. nov.

Text-Figs 109-110, Plate 35: Figs 1-2, Plate 36: Figs 1-3, Plate 37: Figs 1-2

? *1993* «Aeshnidae undescribed» [?]; MARTILL *et al.*, p. 143.
1998 *Paramorbaeschna araripensis*; BECHLY, p. 63 (nomen nudum).

Holotype: Specimen no. [63068 a, b] (old number B 7 a, b), SMNS, Stuttgart.

Paratypes: Specimen no. [MNHN-LP-R. 55180], coll. D. MARTILL, MNHN, Paris; specimen no. [29], NSM, Tokyo; specimen no. [64218] (ex coll. OBERLI, St. Gallen), SMNS, Stuttgart; specimen no. [518], coll. MURATA, Kyoto.

Derivatio nominis: After the geographic name of the Sierra do Araripe in Brazil.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

Diagnosis: Same as for the genus.

Description

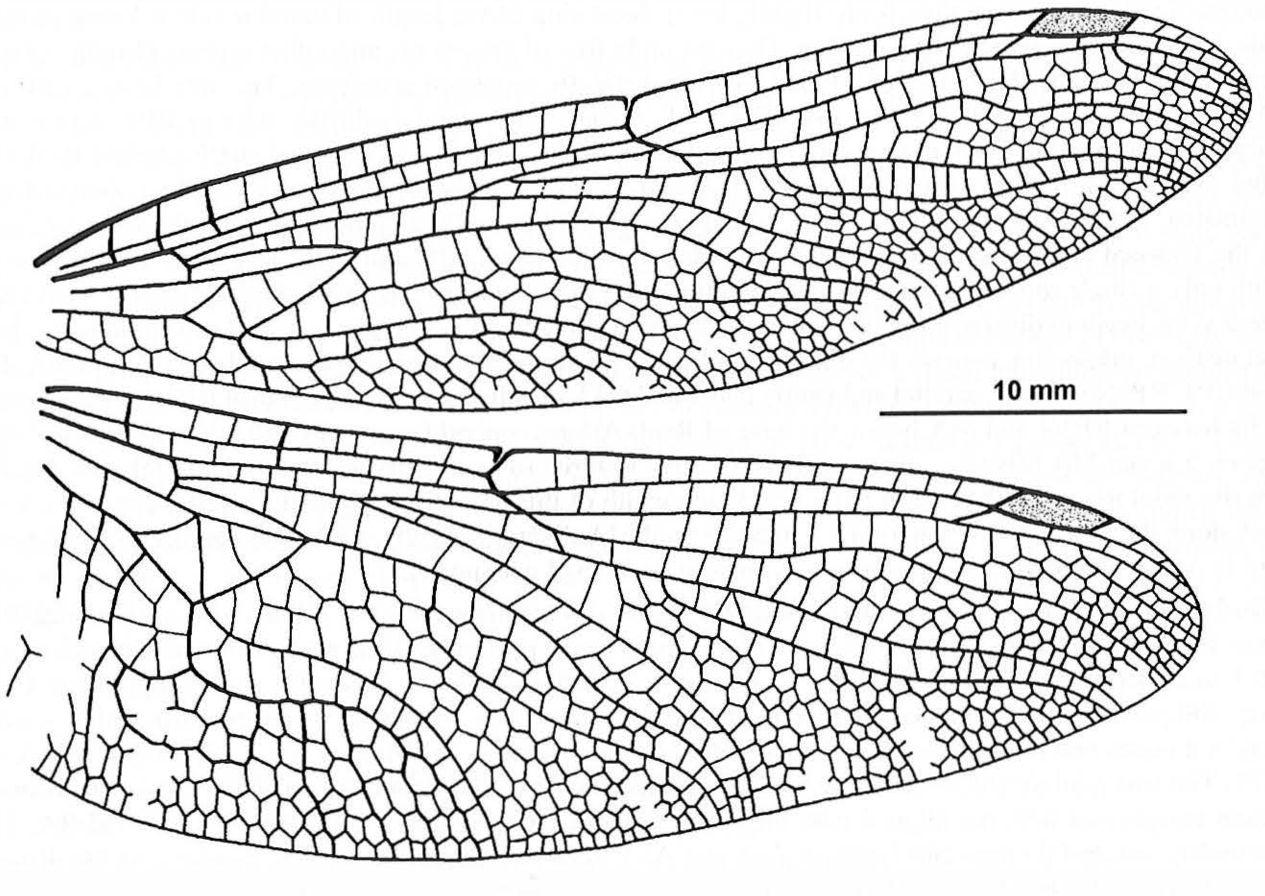
♦ Specimen no. 63068 a, b, SMNS; holotype; female

Text-Fig. 109, Plate 35: Fig. 1, Plate 36: Fig. 3

A well-preserved and complete female.

Forewing: Length 40.0 mm; width at nodus 9.7 mm; distance from base to arculus 5.1 mm; distance from base to nodus 20.6 mm; distance from nodus to pterostigma 13.6 mm. Pterostigma 3.1 mm long and 0.9 mm wide, covering two cells, and strongly braced by a very oblique and slightly undulated crossvein that is aligned with its basal side. Eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the thirteen secondary antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Only a single secondary antenodal crossvein between Ax1 and Ax2 which is aligned and somewhat enforced (but not bracket-like like a primary antenodal crossvein). Ax1 is 2.0 mm basal of the arculus and the distance from Ax1 to Ax2 is 3.4 mm. Ax2 is on a level with basal angle of discoidal triangle. ScP fuses with the costal margin at the nodus. Eight antesubnodal crossveins visible in the area between RA and RP, basal of the subnodus, and there is no distinct gap immediately basal of the subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.3 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The two-celled discoidal triangle is very elongated with a nearly straight (only slightly bent) distal side MAb; length of anterior side 4.4 mm; of basal side 1.8 mm; of distal side MAb 4.6 mm. Hypertriangle free of crossveins and rather narrow (length 5.7 mm; max. width 0.6 mm). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by very numerous crossveins. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2 (distally very narrow). IR2 is only slightly undulated. RP2 and IR2 begin to diverge strongly somewhat basal of the pterostigma with three rows of cells in the widened area between these veins. RP2 strongly undulated. RP2 and RP1 are closely parallel basally with only a single row of cells in the area in-between up to the pterostigma, but below the pterostigmal brace these veins begin to diverge strongly with more than two rows of cells in-between. pseudo-IR1 relatively short, but distinct, originating beneath the distal side of the pterostigma. Only two rows of cells between pseudo-IR1 and RP1. RP3/4 and MA parallel and gently undulated (MA distally more undulated than RP3/4). Two rows of cells between RP3/4 and MA below the base of Rspl. A long, smoothly curved Mspl with two rows of cells between it and MA (distally only a single row). Two to three rows of cells in the postdiscoidal area distal of the discoidal triangle and basal of the midfork; the width of this area distal of the discoidal triangle is 2.6 mm and along the posterior wing margin 7.6 mm. MP and MA diverge strongly. CuAa has seven zigzagged posterior branches and reaches the posterior wing margin on a level with nodus.

Hindwing: Length 39.0 mm; width at nodus 13.1 mm; distance from base to arculus 5.0 mm; distance from base to nodus 15.4 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 16.7 mm. Pterostigma 3.0 mm long and 1.0 mm wide, covering one and a half cells, and strongly braced by a very oblique and slightly undulated crossvein that is aligned with its basal side. Fourteen postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the six secondary antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Two secondary antenodal crossveins between Ax1 and Ax2. Ax1 is 1.6 mm basal of the arculus and the distance from Ax1 to Ax2 is 5.0 mm. ScP fuses with the costal margin at the nodus. Seven antesubnodal crossveins visible in the area between RA and RP, basal of the subnodus, and there is no distinct gap immediately basal of the subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.0 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The two-celled discoidal triangle is rather broad and stout with smoothly bent distal side MAb; length of anterior side 3.7 mm; of basal side 2.7 mm; of distal side MAb 3.9 mm. Hypertriangle 4.7 mm long and max. 0.7 mm wide. The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 nearly straight (only slightly undulated). Six cells distal of the oblique vein 'O', RP2 and IR2 begin to diverge strongly with three rows of cells in the widened area in-between. RP2 strongly undulated. RP2 and RP1 are closely parallel basally with a single row of cells in the area in-between up to the pterostigmal brace, but immediately basal of the pterostigma, these veins begin to diverge strongly with two or more rows of cells in-between. Pseudo-IR1 relatively short, but distinct, originating beneath the distal side of the pterostigma. There are only two rows of cells between pseudo-IR1 and RP1. RP3/4 and MA run parallel, but MA is distally gently undulated, while RP3/4 is rather straight. There are two rows of cells between RP3/4 and MA below the base of Rspl. A long, smoothly curved Mspl with two rows of cells between it and MA (distally only a single row). Three rows of cells in the postdiscoidal area distal of the discoidal triangle, the width of this area distal of the discoidal triangle is 3.7 mm and along the posterior wing margin 7.4 mm. MP and MA diverge strongly. CuAa with only four zigzagged distal posterior branches that reach the posterior wing margin. CuAa reaches the posterior wing margin on a level with nodus; the cubito-anal area is 4.7 mm wide with five rows of cells between CuA and the posterior wing margin. The area between MP and CuA is basally distinctly widened. The anal area is poorly preserved, but it is broad with about seven or eight rows of cells between AA and the posterior wing margin, width of anal area 8.9 mm. The six-celled anal loop is rather transverse (length 2.6 mm; width 3.6 mm), and posteriorly well-closed. A relatively well-defined accessory anal loop between CuAb and the most basal posterior branch of CuAa, enclosing an elongated area of nine cells. Anal area somewhat distorted, including the area of the potential anal angle and anal triangle, but there are clearly two posterior branches of AA visible basal of the anal loop, thus, it is a female specimen.



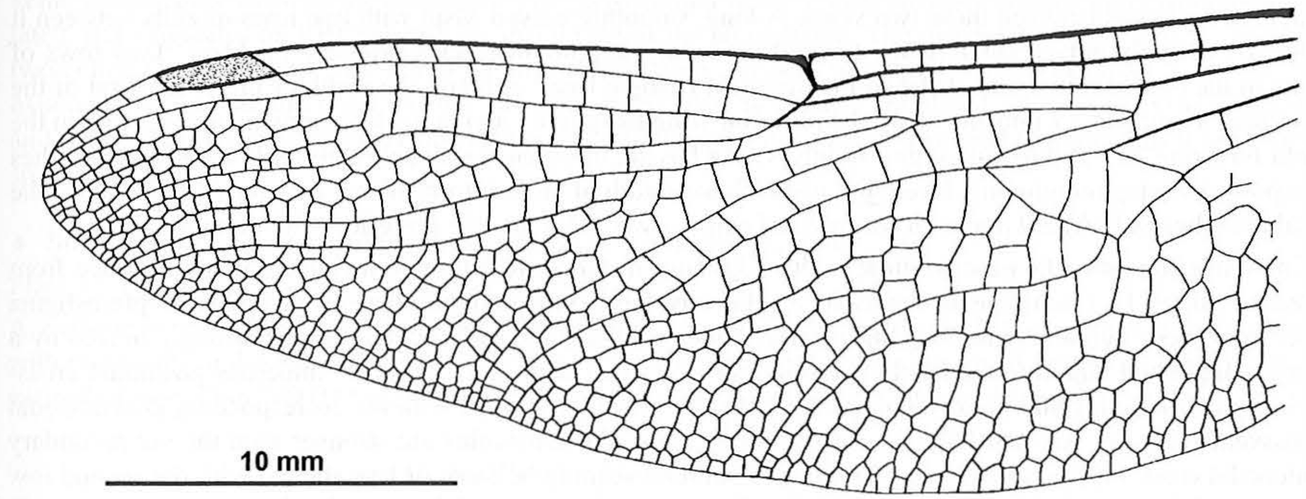
Text-Fig. 109. *Paramorbaeschna araripensis* sp. nov. Holotype SMNS 63068 a, b - female, right pair of wings.

♦ Specimen no. MNHN-LP-R. 55180; paratype

Text-Fig. 110

A nearly complete hindwing, of which only the most basal part is missing. Length 37.8 mm; width 12.9 mm; distance from base to nodus 15.0 mm (the nodus is in a relatively basal position); distance from base to arculus 5.5 mm; distance from nodus to pterostigma 15.0 mm. Pterostigma 3.0 mm long and 0.8 mm wide, covering nearly two cells, and strongly braced by a very oblique and distinctly undulated crossvein that is aligned with its basal side. Eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the seven secondary antenodal crossveins between costal margin and ScP that are not aligned with the second row of antenodal crossveins between ScP and RA. Two secondary antenodal crossveins between Ax1 and Ax2 in the first row, and one in the second row; Ax1 is 1.5 mm basal of the arculus and the distance from Ax1 to Ax2 is 4.5 mm. ScP fuses with the costal margin at the nodus. Only four antesubnodal crossveins visible in the area between RA and RP with a short but distinct gap immediately basal of the subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.5 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The two-celled discoidal triangle is rather broad and stout with an angled distal side MAb; length of anterior side 3.5 mm; of basal side 2.4 mm; of distal side; 3.9 mm. Hypertriangle rather narrow (length 4.5 mm; max. width 0.7 mm). The bases of RP and MA are shortly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly

straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. IR2 nearly straight. RP2 and IR2 diverge strongly with three rows of cells in the widened area between these veins. RP2 strongly undulated. RP2 and RP1 closely parallel basally with a single row of cells in the area in-between, but 3.5 mm basal of the pterostigma, these veins begin to diverge strongly with more than two rows of cells in-between. The pseudo-IR1 seems to be rather vestigial (partly zigzagged; probably an aberration), and originates beneath the middle of the pterostigma. Three rows of cells between pseudo-IR1 and RP1. RP3/4 and MA are closely parallel and gently undulated veins (MA distally more undulated than RP3/4). Two rows of cells between RP3/4 and MA below the base of Rspl. A long, smoothly curved Mspl with two rows of cells between it and MA (distally only a single row). Three rows of cells in the postdiscoidal area distal of the discoidal triangle, the width of this area distal of the discoidal triangle is 3.5 mm and along the posterior wing margin 7.7 mm. MP and MA diverge strongly. CuAa with four poorly defined distal posterior branches that reach the posterior wing margin. CuAa reaches the posterior wing margin on a level with nodus. The cubito-anal area is 4.6 mm wide with five rows of cells between CuA and the posterior wing margin. The area between MP and CuA is basally distinctly widened. The anal area is poorly preserved, but it is broad with about eight rows of cells between AA and the posterior wing margin, width of anal area 7.7 mm. The five-celled anal loop is 2.9 mm long and 2.7 mm wide, and posteriorly well-closed. A weakly defined accessory anal loop between CuAb and the most basal posterior branch of CuAa, enclosing an elongated area of eight cells.



Text-Fig. 110. *Paramorbaeschna araripensis* sp. nov. Paratype MNHN-LP-R. 55180 - left hindwing.

♦ Specimen no. 29, NSM; paratype; female

Plate 35: Fig. 2, Plate 36: Figs 1-2

A well-preserved complete adult female with all four wings in outstretched position. Head, thorax and abdomen (except the anal appendages) are preserved as well. Unfortunately, it was not possible to make a drawing of this specimen before it was sold to Japan, therefore the present description is mainly based on the available photographs. The head is globular with the compound eyes being broadly confluent (max. width of head 7.8 mm). The body length from the head to the tip of the abdomen is 58.8 mm, the width of the abdomen 2.6 mm.

Forewing: Length 41.7 mm; width at nodus 9.5 mm; distance from base to arculus 5.4 mm; distance from base to nodus 21.3 mm; distance from nodus to pterostigma 13.8 mm. Pterostigma 2.9 mm long and 0.9 mm wide, covering one and a half cells, and strongly braced by a very oblique crossvein that is aligned with its basal side. About eleven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the thirteen secondary antenodal crossveins between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Only a single secondary antenodal between Ax1 and Ax2 which is more or less aligned, but not bracket-like enforced like a primary antenodal. Ax1 is 1.8 mm basal of the arculus and the distance from Ax1 to Ax2 is 2.7 mm. Ax2 is on a level with basal angle of discoidal triangle. ScP fuses with the costal margin at the nodus. There seem to be relatively numerous antesubnodal crossveins between arculus and subnodus. Median space free of crossveins. Submedian space only traversed by

CuP-crossing, 1.4 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The discoidal triangle is very elongated, divided into two cells in the left forewing, but into three cells in the right forewing; length of anterior side 4.9 mm; of basal side 2.2 mm; of distal side MAb 5.1 mm; the distal side MAb of the discoidal triangle is smoothly bent rather than angled, but a secondary sector of the postdiscoidal area originates on MAb. Hypertriangle free of crossveins and rather narrow (length 5.9 mm; max. width 0.6 mm). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by very numerous crossveins. There seems to be only a single bridge-crossvein Bq; base of RP2 aligned with subnodus; there is only a single oblique vein 'O', less than one cell distal ofthe subnodus. There is a long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2 (distally very narrow). Several secondary longitudinal veins originate on Rspl. IR2 is only slightly undulated. RP2 and IR2 begin to diverge strongly somewhat basal of the pterostigma with three rows of cells in the widened area between these veins. RP2 is strongly undulated. RP2 and RP1 are basally closely parallel up to the pterostigma with only a single row of cells in the area in-between, but below the pterostigmal brace these veins begin to diverge strongly with more than two rows of cells in-between. Pseudo-IR1 relatively short, but distinct, originating beneath the distal side of the pterostigma. Only two rows of cells between pseudo-IR1 and RP1, and three rows between it and RP2. RP3/4 and MA are parallel and gently undulated veins (MA distally more undulated than RP3/4). Two rows of cells between RP3/4 and MA below the base of Rspl, but before and after this area there is only a single row of cells between these two veins. A long, smoothly curved Mspl with two rows of cells between it and MA (distally only a single row). Several secondary longitudinal veins originate on Mspl. Two rows of cells in the postdiscoidal area distal of the discoidal triangle basal of Mspl; the width of this area distal of the discoidal triangle is 2.7 mm and along the posterior wing margin 6.7 mm in the left forewing and 7.5 mm in the right forewing. MP and MA diverge strongly. CuAa has six or seven zigzagged posterior branches and reaches the posterior wing margin on a level with nodus. Max. width of the cubito-anal area 2.2 mm. Max. width ofthe anal area (below PsA) 2.0 mm withtwo rows of cells between AA and the posterior wing margin.

Hindwing: Length 40.6 mm; width at nodus 13.0 mm; distance from base to arculus 5.6 mm; distance from base to nodus 16.7 mm (the nodus is in a relatively basal position); distance from nodus to pterostigma 16.7 mm. Pterostigma 2.9 mm long and 1.0 mm wide, covering one and a half cells, and strongly braced by a very oblique and slightly undulated crossvein that is aligned with its basal side. Numerous postnodal crossveins between nodus and pterostigma (at least nine or ten), not aligned with the corresponding postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are stronger than the six secondary antenodal crossveins between costal margin and ScP that seem to be more or less aligned with the second row of antenodal crossveins between ScP and RA. Two secondary antenodal crossveins between Ax1 and Ax2. Ax1 is 1.8 mm basal of the arculus and the distance from Ax1 to Ax2 is 5.2 mm. ScP fuses with the costal margin at the nodus. Six or seven antesubnodal crossveins visible in the area between arculus and subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 2.1 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. The two-celled discoidal triangle is rather broad and stout with smoothly bent distal side MAb. A secondary sector in the postdiscoidal area originates on MAb; length of anterior side 3.9 mm; of basal side 2.8 mm; of distal side MAb 4.2 mm. Hypertriangle not divided by crossveins (length 4.9 mm; max. width 0.7 mm). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. Several secondary longitudinal veins originating on Rspl. IR2 is only slightly undulated. Six cells distal of the oblique vein 'O', RP2 and IR2 begin to diverge strongly with three rows of cells in the widened area in-between. RP2 is strongly undulated. RP2 and RP1 are basally closely parallel up to the pterostigmal brace with a single row of cells in the area in-between, but immediately basal of the pterostigma, these veins begin to diverge strongly with two or more rows of cells in-between. Pseudo-IR1 is relatively short, but distinct, originating beneath the distal side of the pterostigma. Only two rows of cells between pseudo-IR1 and RP1, and three rows of cells between it and RP2. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4). Two rows of cells between RP3/4 and MA below the base of Rspl. A long, smoothly curved Mspl with two rows of cells between it and MA (distally only a single row). Several secondary longitudinal veins originating on Mspl. Three or four rows of cells in the postdiscoidal area distal of the discoidal triangle, the width of this area distal of the discoidal triangle is 3.7 mm and along the posterior wing margin 7.8 mm. MP and MA diverge strongly. CuAa has four or five zigzagged distal posterior branches that reach the posterior wing margin. CuAa reaches the posterior wing margin on a level with nodus. The cubito-anal area is max. 5.0 mm wide with five or six rows of cells between CuA and the posterior wing margin. Area between MP and CuA basally distinctly widened. Anal area broad with about seven or eight rows of cells between AA and the posterior wing margin, max. width of anal area (below PsA) 8.9 mm. The five-celled anal loop is rather transverse (length 2.8 mm; width 5.0 mm), and posteriorly well-closed. A relatively well-defined accessory anal loop between CuAb and the most basal posterior branch of CuAa, enclosing an elongated area of about nine cells. Three or four posterior branches of AA basal of the anal loop (female). Anal margin rounded without an anal angle or anal triangle, thus, it is a female specimen.

♦ Specimen no. 64218, SMNS; paratype; female

Plate 37: Fig. 1

A well-preserved isolated hindwing (length, 37.0 mm; width at nodus 6.8 mm). The wing venation is similar to the other specimens, except for the presence of four rows of cells in the widened area between IR2 and the strongly undulated RP2, and the presence of two "doubled" cells in the widened basal area between MP and CuA. A single row of cells between Rspl and IR2, but basally two rows of cells between MA and Mspl, which is curved. There are five or six antesubnodal crossveins, and a short (length 3.0 mm) but distinct gap of crossveins immediately basal of the subnodus. The pterostigmal brace vein is strongly oblique and distinctly undulated. IR1 originates on RP1 beneath the distal side of the pterostigma. The discoidal triangle is very stout and two-celled (length of anterior side 3.6 mm; of basal side 2.6 mm; of curved distal side MAb 3.9 mm). The hypertriangle and subdiscoidal triangle are unicellular. PsA is slightly undulated. The anal loop is six-celled and the accessory anal-loop is divided into eight cells. There is no anal angle or anal triangle, thus it is a female specimen.

♦ Specimen no. 518, old number G 13, coll. MURATA; paratype; female

Plate 37: Fig. 2

A well-preserved female specimen (forewing length 35.5 mm; hindwing length 35.0 mm; anal loop transverse with eight cells in the left hindwing and cells in the right hindwing) that is preserved as part of a large "aggregation" of more than 100 (!) fossil insects, including locusts, bugs, beetles, and cockroaches, etc.

Genus *Progomphaeschnaoides* gen. nov.

Type species: *Progomphaeschnaoides ursulae* sp. nov.

Other species: *Progomphaeschnaoides staniczeki* sp. nov.

Derivatio nominis: After "pro-" and "*Gomphaeschnaoides*", in reference to the close similarity to Gomphaeschnaoides and the plesiomorphic absence of the most important autapomorphy of the latter genus.

Diagnosis and autapomorphies: This new genus is very similar to the four species of *Gomphaeschnaoides*, except for the following differences in the hindwing venation: Wing length less than 30 mm (autapomorphy); two secondary antenodal crossveins between the primary antenodal crossveins Ax1 and Ax2 (plesiomorphy); no oblique crossvein that is slanted towards the pterostigma, between RP1 and RP2 (plesiomorphy); three rows of cells between RP2 and IR2 (plesiomorphy ?); the basal posterior branches or CuA are very weakly defined (autapomorphy ?), being even less defined than in most specimens of *Gomphaeschnaoides obliquus*; the anal loop is distinctly longer than wide (autapomorphy); basal of the anal loop there are no well-defined posterior branches of AA in the female hindwing (autapomorphy).

Systematic position: According to the wing venation this new genus clearly belongs to Gomphaeschnidae - Gomphaeschnaoidinae subfam. nov. However, most similarities with the genus *Gomphaeschnaoides* seem to be symplesiomorphies. The most distinct synapomorphy of the four species of *Gomphaeschnaoides* is absent in *Progomphaeschnaoides* gen. nov., viz the oblique veinlet between RP1 and RP2. The absence of the oblique vein between RP1 and RP2 clearly excludes a subordinate position in the genus *Gomphaeschnaoides*. The secondarily basally divergent veins RP1 and RP2 (reversal in Aeshnoptera) of *Progomphaeschnaoides staniczeki* sp. nov. cannot be regarded as a putative synapomorphy with *Gomphaeschnaoides*, since these veins are closely parallel in the type species *Progomphaeschnaoides ursulae* gen. et sp. nov.

Progomphaeschnaoides ursulae sp. nov.

Text-Figs 111-113, Plate 38: Fig. 1

1998 *Progomphaeschnaoides ursulae*; BECHLY, p. 63 (nomen nudum).

Holotype: Specimen no. [2357 PAL], SMNK, Karlsruhe (collected by Dr Eberhard FREY).

Derivatio nominis: Named in honour of Mrs Ursula BECHLY (Böblingen, Germany), dear mother of the first author who most generously supported his studies.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

Diagnosis: Differing from the closely related species *P. staniczeki* sp. nov. in the following hindwing characters: The basal primary antenodal crossvein Ax1 is slanted towards the wing base (autapomorphy); only seven postnodal crossveins between nodus and pterostigma (plesiomorphy ?); RP1 and RP2 are basally closely parallel; IR1 originates on RP1 below the distal end of the pterostigma (autapomorphy); there are one or two rows of cells between the median parts of pseudo-IR1 and RP1, and three rows of cells between the median parts of pseudo-IR1 and RP2 (plesiomorphy); two rows of cells in the distal half of the area between RP3/4 and MA (autapomorphy); short subdiscoidal triangle. The presence of only two secondary antenodal crossveins distal of Ax2 (instead of three) and the presence of only three antesubnodal crossveins (instead of four) could be further diagnostic characters, but they could also be variable.

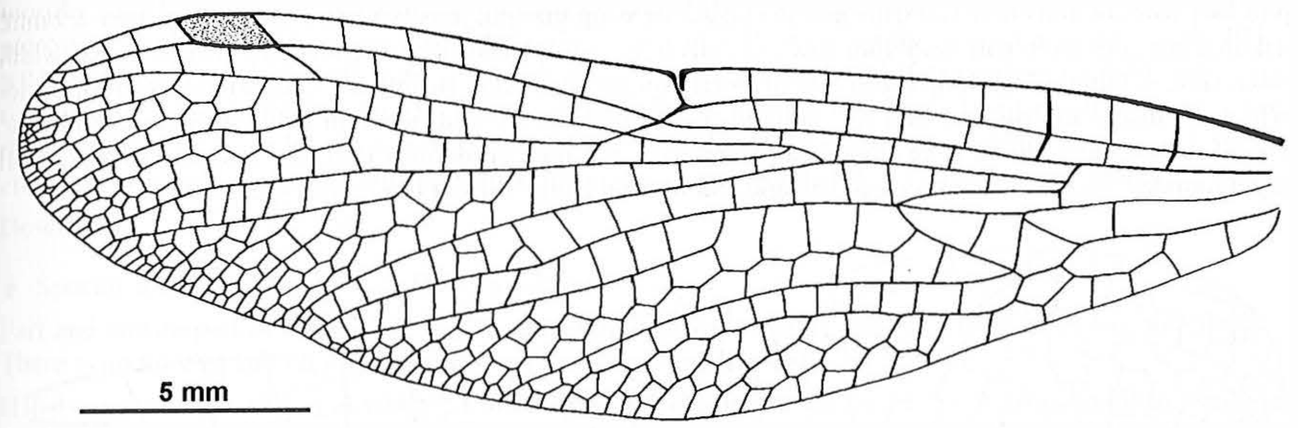
Description

♦ Specimen no. SMNK 2357 PAL, Karlsruhe; holotype; female

A female with poorly preserved body (head and thorax), but with all four wings well-preserved. Abdomen and legs are missing.

Forewing: Length 27.5 mm; width at nodus 7.6 mm; distance from base to arculus 4.3 mm; distance from base to nodus 13.2 mm; from nodus to pterostigma 9.0 mm. Pterostigma short (1.8 mm long and max. 0.8 mm wide), covering one and a half cells, and strongly braced by a very oblique and smoothly curved crossvein. Five postnodal crossveins between nodus and pterostigma, not aligned with the five corresponding postsubnodal crossveins. Seven antenodal crossveins visible between costal margin and ScP, not aligned with the eight antenodal crossveins of the second row between ScP and RA, except for the two primary antenodal crossveins Ax1 and Ax2 that are also stronger than the secondary antenodal crossveins. Ax1 is 1.9 mm basal of the arculus, and Ax2 is 2.8 mm distal of Ax1, on a level with basal angle of discoidal triangle. Only a single secondary antenodal of the first row between the two primary antenodal crossveins, not precisely aligned with the corresponding antenodal of the second row. Four antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus and immediately distal of the arculus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2; Rspl is relatively short, originating 4.7 mm distal of the subnodus. Three convex secondary veins originate on Rspl and reach the posterior wing margin. RP2 and IR2 strongly diverge near the pterostigmal brace with two to four rows of cells in-between. Pseudo-IR1 well-defined and originating on RP1 slightly distal of the pterostigma in both forewings. RP1 and RP2 are basally closely parallel with only a single row of cells in-between, but below the pterostigma, they strongly diverge with two or more rows of cells in-between. There is no oblique crossvein between RP1 and RP2 that is slanted towards the pterostigma. RP3/4 and MA are more or less parallel, but MA is gently undulated with a single row of cells in-between (in both forewings). Mspl is well-defined, parallel to MA with only a single row of cells between it and MA; in both forewings there is a distinctly oblique crossvein in the median part of the area between MA and Mspl. Two convex secondary veins originate on Mspl and reach the posterior wing margin. The postdiscoidal area is distally widened (width near discoidal triangle 1.7 mm; width at posterior wing margin 4.4 mm) with two rows of cells immediately distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins (length 3.4 mm; max. width 0.5 mm). The discoidal triangle is divided into two cells by a basal crossvein, and it is distinctly more narrow than that of the hindwing; length of anterior side 2.7 mm; of basal side 1.3 mm; of distal side MAb 2.8 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.2 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

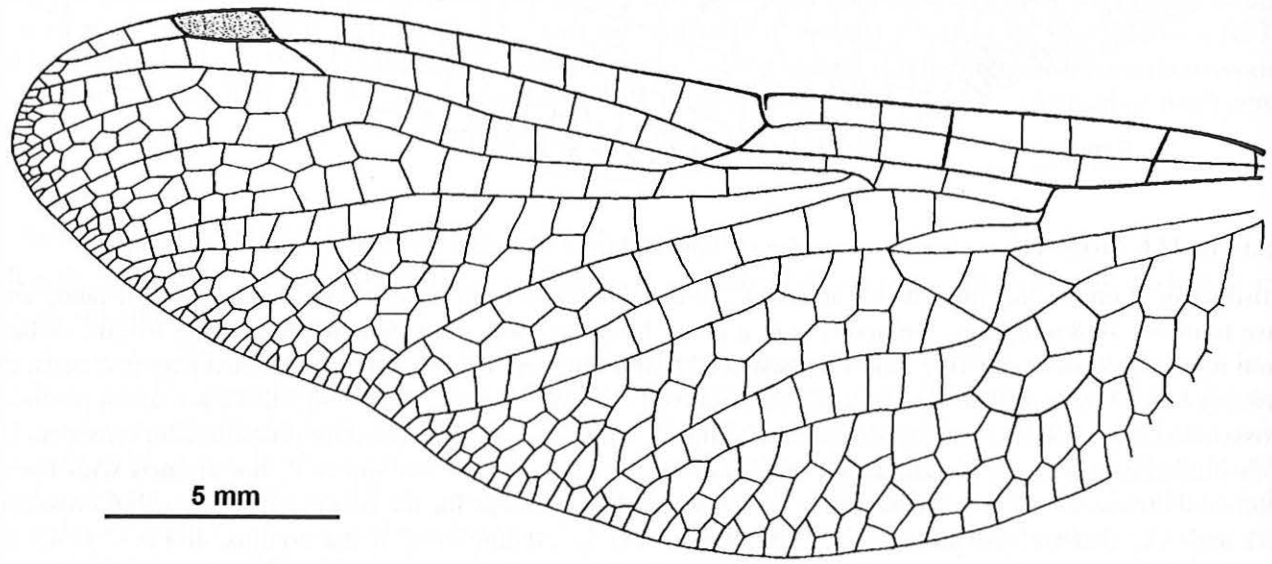
but short unicellular subdiscoidal triangle, max. 1.1 mm long and basally 1.3 mm wide (= length of PsA); the posterior margin of the subdiscoidal triangle is distinctly angled. PsA ends on MP + CuA slightly below basal angle of discoidal triangle. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin far distal of the level of the nodus, and CuA reaches the posterior wing margin somewhat distal of the level of nodus as well. The posterior branches of CuA are zigzagged and relatively weak veins. Up to three rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 1.8 mm. Anal area is max. 1.4 mm wide (below the origin of PsA) with two rows of cells between AA and the posterior wing margin, including an elongated paranal cell.



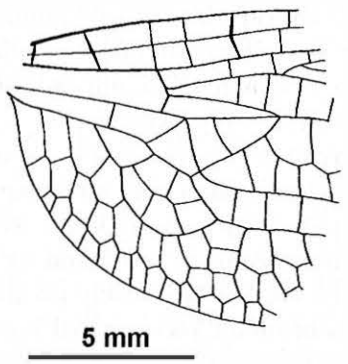
Text-Fig. 111. *Progomphaeschnaoides ursulae* sp. nov. Holotype SMNK 2357 PAL - female, left forewing.

Hindwing: Length 26.9 mm; width at nodus 9.9 mm; distance from base to arculus 4.5 mm; distance from base to nodus 10.8 mm, thus, the nodus is in a rather basal position at 40 % of the total wing length; distance from nodus to pterostigma 10.7 mm. Pterostigma 2.0 mm long and max. 0.7 mm wide, covering two cells, and strongly braced by a very oblique and smoothly curved crossvein. In both hindwings there are seven postnodal crossveins between nodus and pterostigma, not aligned with the five corresponding postsubnodal crossveins. In both hindwings there are six antenodal crossveins between costal margin and ScP, not aligned with the six antenodal crossveins of the second row between ScP and RA, except for the two primary antenodal crossveins Ax1 and Ax2 that are also stronger than the others. Ax1 is 2.0 mm basal of the arculus, and Ax2 is 4.5 mm distal of Ax1. In both hindwings there are two secondary antenodal crossveins in both rows between Ax1 and Ax2, nearly aligned with each other in the right hindwing, but not aligned with each other in the left hindwing. Ax1 is distinctly slanted towards the wing base in both hindwings. In both hindwings there are only three antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus and immediately distal of the arculus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2; Rspl is relatively short, originating 4.5 mm distal of the subnodus. Two convex secondary veins originate on Rspl and reach the posterior wing margin. RP2 and IR2 strongly diverge somewhat basal of the level of pterostigmal brace with two to four rows of cells in-between. Pseudo-IR1 well-defined and originating beneath the distal end of the pterostigma in both hindwings; in both hindwings there are only one to two rows of cells between the basal parts of pseudo-IR1 and RP1 (separated by about eight cells at the wing margin), and only three rows of cells between pseudo-IR1 and RP2, except near the wing margin (six or seven cells). In both hindwings RP1 and RP2 are basally closely parallel with only a single row of cells in-between, but they become strongly divergent beneath the pterostigmal brace with two or more rows of cells in-between. There is no oblique crossvein between RP1 and RP2 that is slanted towards the pterostigma. RP3/4 and MA are more or less parallel, but MA is gently undulated; basally there is only a single row of cells between RP3/4 and MA, but distally there are two rows of cells up to the wing margin (in both hindwings). Mspl is well-defined, parallel to MA with only a single row of cells between it and MA; in both hindwings there is a distinctly oblique crossvein in the median part of the area between MA and Mspl. Two or three convex secondary veins originate on Mspl. The postdiscoidal area is distally widened (width near discoidal triangle 2.2 mm; width at wing margin 4.6 mm) with two to three rows of cells immediately distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. The hypertriangle is free of crossveins (length 3.3-3.6 mm; max. width

0.5-0.6 mm). The discoidal triangle is divided into two cells by a crossvein, and it is less elongated than that of the forewing; length of anterior side 2.6-2.8 mm; of basal side 1.6-1.7 mm; of distal side MAb 2.7-2.9 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 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 unicellular subdiscoidal triangle that is relatively short in both hindwings, max. 1.5 mm long and basally 1.6 mm wide (= length of PsA). PsA ends on MP + CuA at the basal angle of discoidal triangle in both hindwings. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin distinctly distal of the level of nodus, and CuA reaches the posterior wing margin somewhat distal of the level of nodus as well. There are five distal posterior branches of CuA that are rather well-defined veins. Up to four rows of cells between CuA and the posterior wing margin, max. width of cubito-anal area 2.9 mm. Anal area not very wide with only four rows of cells between AA and the posterior wing margin (max. width of anal area. 4.2 mm). Anal loop broad and distinctly longer than wide (length 3.1 mm; width 2.1 mm), posteriorly well-closed, and divided into five cells in the right hindwing and into four cells in the left hindwing. Basal of the anal loop, there is an elongated paranal cell, but no well-defined posterior branches of AA. Anal margin rounded, there is neither an anal triangle, nor an anal angle, thus, it is a female specimen.



Text-Fig. 112. *Progomphaeschnaoides ursulae* sp. nov. Holotype SMNK 2357 PAL - female, left hindwing.



Text-Fig. 113. *Progomphaeschnaoides ursulae* sp. nov. Holotype SMNK 2357 PAL - female, right hindwing base.

Progomphaeschnaoides staniczeki sp. nov.

Text-Fig. 114, Plate 38: Fig. 2, Plate 39: Fig. 1

1998 *Progomphaeschnaoides staniczeki*; BECHLY, p. 63 (nomen nudum).

Holotype: Specimen no. [AP 1997 / 4 a, b] (old number B 48 a, b), JME, Eichstätt.

Other specimen: A second putative representative of this new taxon is specimen no. [F 62], coll. *ms-fossil*, Sulzbachtal.

Derivatio nominis: Named in honour of Dr Arnold STANICZEK (Tübingen, Germany), colleague of the first author and specialist on mayfly morphology and phylogeny.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

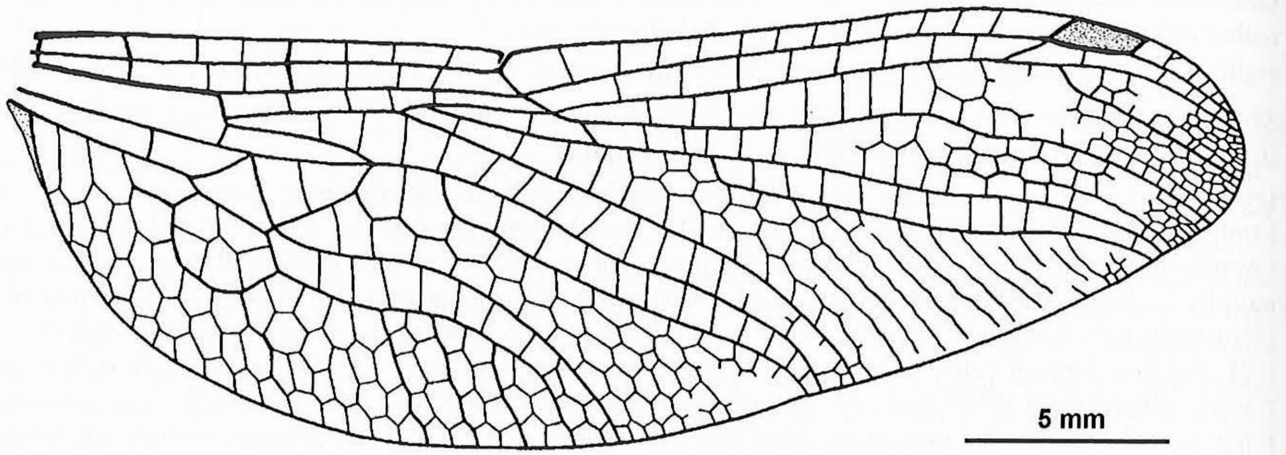
Diagnosis: Differing from the type species *Progomphaeschnaoides ursulae* gen. et sp. nov. from the same locality in the following hindwing characters: The basal primary antenodal crossvein Ax1 is not slanted towards the wing base (plesiomorphy); twelve postnodal crossveins between nodus and pterostigma (autapomorphy ?); RP1 and RP2 are basally somewhat divergent; IR1 originates on RP1 below the basal part of the pterostigma (plesiomorphy); there are three or four rows of cells between the median parts of pseudo-IR1 and RP1, and four rows of cells between the median parts of pseudo-IR1 and RP2 (autapomorphy); only a single row of cells between RP3/4 and MA (plesiomorphy); more elongated subdiscoidal triangle. The presence of three secondary antenodal crossveins distal of Ax2 (instead of two) and the presence of four antesubnodal crossveins (instead of three) could be further diagnostic characters, but they could also be variable.

Description

♦ Specimen no. AP 1997 / 4 a, b, JME; holotype; female

Part and counterpart of a complete hindwing of a female with a body fragment (part of thorax and abdomen). There is no trace of coloration, the wing seems to have been hyaline.

Hindwing: Length 29.3 mm; width 9.3 mm; distance from base to nodus 11.2 mm; from nodus to pterostigma 13.4 mm; distance from base to arculus 4.7 mm. Pterostigma 2.0 mm long, strongly braced by a very oblique and distinctly undulated crossvein and covering one and a half cells. Twelve postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. The first postnodal crossvein and the last antenodal crossvein are distinctly slanted towards the nodus. Seven antenodal crossveins visible between costal margin and ScP, more or less aligned with the second row of antenodal crossveins between ScP and RA. The primary antenodal crossveins are distinctly stronger, and there are two secondary antenodal crossveins in-between. Only four antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. Rspl well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 diverge in their distal half with three rows of cells in-between. RP1 and RP2 are basally slightly divergent, but there is only a single row of cells in-between in their basal half, and below the pterostigmal brace they begin to diverge more strongly with three rows of cells in-between. RP2 is distinctly undulated, but IR2 is rather straight. Pseudo-IR1 relatively long and originating beneath the basal side of pterostigma. RP3/4 and MA are parallel and rather straight (there is a gentle bulge in the median part of MA) with a single row of cells in-between. Mspl begins two cells distal of the discoidal triangle and is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is distally widened with two rows of cells distal of the discoidal triangle and a secondary longitudinal vein, originating at the strongly angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins. The discoidal triangle is rather stout and divided into two cells by a crossvein; length of anterior side 2.9 mm; of basal side 1.8 mm; of distal side MAb 2.8 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.6 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 subdiscoidal triangle that is elongated, but unicellular. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin on a level with the oblique vein 'O'. CuA reaches the posterior wing margin on a level with subnodus. Only four distal posterior branches of CuA are well-defined, the others are zigzagged and very weak veins. Four rows of cells between CuA and the posterior wing margin, width of cubito-anal area 3.1 mm. The anal area is broad with max. five rows of cells between AA and the posterior wing margin. The five-celled anal loop is broad and rather longitudinally elongated (length 2.9 mm; width 1.7 mm), and posteriorly well-closed. No anal angle or anal triangle, thus, it is a female specimen, but there are no well-defined posterior branches of AA basal of the anal loop (contrary to the females of the other species of *Gomphaeschnaoides*). There is a small membranule visible.



Text-Fig. 114. *Progomphaeschnaoides staniczeki* sp. nov. Holotype JME AP 1997 / 4 a, b - female, right hindwing.

♦ Specimen no. F 62, coll. *ms-fossil*; female

Two hindwings of a female (length 25 mm). The wing venation is more or less identical to the holotype, including basally slightly diverging RP1 and RP2; IR1 originating on RP1 below the basal part of the pterostigma; three rows of cells between the median parts of pseudo-IR1 and RP1, and three to four rows of cells between the median parts of pseudo-IR1 and RP2; only a single row of cells between RP3/4 and MA;

Genus *Plesigomphaeschnaoides* gen. nov.

Type species: *Plesigomphaeschnaoides mongolensis* sp. nov.

Other species: *Plesigomphaeschnaoides pindelskii* sp. nov., and maybe also including the two species ?*P. paleocenica* comb. nov. and ?*P. danica* comb. nov. from the Lower Tertiary of Denmark.

Derivatio nominis: After the Greek word "plesi-" and "*Gomphaeschnaoides*", in reference to the probable close relationship to *Gomphaeschnaoides* and the presence of several plesiomorphies.

Diagnosis: This new genus is very similar to the other genera of Gomphaeschnaoidini trib. nov., but can be recognized by the following hindwing characters: Two secondary antenodal crossveins between Ax1 and Ax2 (plesiomorphy; dubious in *P. mongolensis* sp. nov.); relatively numerous (ten or more) postnodal crossveins between nodus and pterostigma (plesiomorphy); two rows of cells between pseudo-IR1 and RP1, and three rows of cells between pseudo-IR1 and RP2 (plesiomorphy; unknown in *P. pindelskii* sp. nov.); RP1 and RP2 basally somewhat divergent (reversal; putative synapomorphy with *Progomphaeschnaoides* gen. nov. and *Gomphaeschnaoides*); no oblique crossvein between RP1 and RP2 that is slanted towards the pterostigma (plesiomorphy); RP2 not strongly undulated (dubious in *P. pindelskii* sp. nov.), and two rows of cells in the widened part of the area between RP2 and IR2 (putative synapomorphy with *Gomphaeschnaoides*); Rspl straight and parallel to IR2 with only a single row of cells between Rspl and IR2 (plesiomorphy); two rows of cells in the postdiscoidal area immediately distal of the discoidal triangle; Mspl straight and parallel to MA with only a single row of cells between Mspl and MA (plesiomorphy); the basal posterior branches or CuA are very weakly-defined (putative synapomorphy with *Progomphaeschnaoides* gen. nov.); PsA undulated (autapomorphy).

Systematic position: This new genus clearly belongs to the Neoaeshnida, since it shares the concerning synapomorphies, as well as all important autapomorphies of Aeshnoptera, Aeshnida, and Euaeshnida, respectively. Also the other (symplesiomorphic) characters agree with this phylogenetic position, e.g. the well-defined subdiscoidal triangle. Furthermore, this genus has the wing venational autapomorphies of the Gomphaeschnidae: Distal part of the area between RA and RP, immediately basal of subnodus, free of antesubnodal crossveins; submedian space, between CuP-crossing and PsA, without accessory cubito-anal crossveins; discoidal triangles only divided into two cells by a single crossvein; hypertriangles secondarily undivided by crossveins. It also shares those autapomorphies of the Gomphaeschnaoidinae subfam. nov. and Gomphaeschnaoidini trib. nov. that are visible in the hindwing: Presence of a characteristical elongated distal paranal cell, immediately basal of the anal loop (convergent to Cordulagomphinae *contra* CARLE & WIGHTON 1990); the very oblique and slightly undulated pterostigmal brace vein; and the basally widened cell below the pterostigma, caused by a curvature of RP1 at the pterostigmal brace; the posterior branches of CuAa are relatively weakly defined. The characters mentioned in the diagnosis suggest that *Plesigomphaeschnaoides* gen. nov. is very closely related to *Progomphaeschnaoides* gen. nov. and *Gomphaeschnaoides*, maybe representing the sistergroup of the latter genus. Unfortunately, several of the above mentioned autapomorphies of Gomphaeschnaoidinae subfam. nov. and Gomphaeschnaoidini trib. nov. are unknown for the *Plesigomphaeschnaoides* gen. nov., since they are only visible in the forewings. Therefore, it can only be assumed that this new genus belongs to Gomphaeschnaoidini trib. nov., because of three weak synapomorphies, the great overall similarity, and the absence of conflicting evidence. A more definite statement about the precise phylogenetic position of *Plesigomphaeschnaoides* gen. nov. can only be made when more complete material (esp. the forewings) will become available.

The close relationship of the type species *Plesigomphaeschnaoides mongolensis* gen. et sp. nov. and *P. pindelskii* sp. nov. is documented by at least one strong synapomorphy (undulated PsA), numerous symplesiomorphies, and again the absence of conflicting evidence.

Plesigomphaeschnaoides mongolensis sp. nov.

Text-Fig. 115, Plate 39: Fig. 3

Holotype: Specimen no. [3559 / 10201] and S/N1, PIN, Moscow.

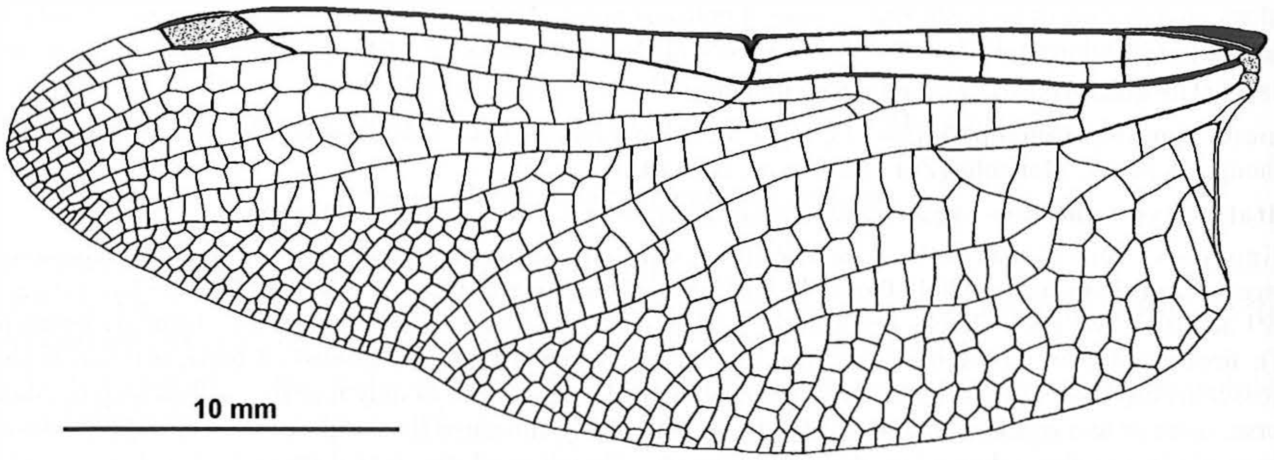
Derivatio nominis: After the country Mongolia.

Locus typicus: Outcrop 88 (site 73, layer 8), 5 km south of Lake Bon-Tsagan-Nur, Bon-Tsagan, Bayan-Khongorsk aimak, Mongolia (ZHERIKHIN pers. comm.).

Stratum typicum: Bon-Tsagan Series (Baisinsk deposits), Lower Cretaceous, Barremian / Aptian (?).

Diagnosis: Very similar to the *P. pindelskii* sp. nov., only differing in the following hindwing characters: Larger size (hindwing length 38.0 mm, instead only 32.5 mm); two rows of cells between the basal parts of RP1 and RP2; two rows of cells between the median parts of RP3/4 and MA; RP2 is less distinctly undulated (?); fewer postnodal crossveins between nodus and pterostigma (only ten instead of fourteen); two bridge-crossveins Bqs; five to six rows of cells in the cubito-anal area (instead of only four rows); anal loop not transverse, more or less equilateral, or even slightly longitudinally elongated (convergence to *Progomphaeschnaoides* gen. nov.).

Description: Part and counterpart of an isolated complete hindwing of a male. It was probably hyaline with no trace of coloration. Length 38.0 mm; width at nodus 12.4 mm; distance from base to nodus 15.2 mm (the nodus is in a relatively basal position); distance from base to arculus 5.1 mm; distance from nodus to pterostigma 14.5 mm. Pterostigma 2.6 mm long and 1.0 mm wide, covering one and a half cells, and strongly braced by a very oblique and slightly undulated crossvein that is aligned with its basal side. Ten postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins between RA and RP1. Ax1 is stronger than the four secondary antenodal crossveins between costal margin and ScP that are not aligned with the second row of antenodal crossveins between ScP and RA, although these crossveins are not well-preserved, Ax2 is not well-preserved. Apparently only a single not aligned secondary antenodal crossvein in both rows between Ax1 and Ax2 (however, these are so widely separated and weakly preserved that this state could rather be an artifact or an individual aberration). Ax1 is 1.1 mm basal of the arculus, and Ax2 is 4.2 mm distal of Ax1. ScP fuses with the costal margin at the nodus. Four antesubnodal crossveins visible in the area between arculus and subnodus. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle; PsA is distinctly undulated and ends at the basal angle of discoidal triangle. The two-celled discoidal triangle is rather broad and stout with smoothly bent distal side MAb; length of anterior side 3.7 mm; of basal side 2.0 mm; of distal side MAb 3.9 mm. A secondary sector in the postdiscoidal area originates on MAb. Hypertriangle not divided by crossveins (length 4.5 mm; max. width 0.7 mm). The bases of RP and MA are distinctly separated at arculus. The area between RP and MA is traversed by numerous crossveins. Two bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell distal of the subnodus. A long and nearly straight Rspl, parallel to IR2 with only a single row of cells between it and IR2. Several secondary longitudinal veins originating on Rspl. IR2 is only slightly undulated. Eight cells distal of the oblique vein 'O', RP2 and IR2 begin to diverge with two rows of cells in the widened area in-between. RP2 is slightly undulated. RP2 and RP1 are basally closely parallel, but, on a level with the base of Rspl, they begin to diverge with two rows of cells in the area in-between. Pseudo-IR1 is relatively short, but distinct, originating beneath the distal side of the pterostigma. Three rows of cells between pseudo-IR1 and RP1, and three rows of cells between it and RP2. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4). Two rows of cells between RP3/4 and MA below the base of Rspl. A long, smoothly curved Mspl with a single row of cells between it and MA. Several secondary longitudinal veins originating on Mspl. Two rows of cells in the postdiscoidal area distal of the discoidal triangle, the width of this area distal of the discoidal triangle is 3.2 mm and along the posterior wing margin 6.6 mm. MP and MA diverge strongly. CuAa has six or seven zigzagged posterior branches that reach the posterior wing margin, but the more basal branches are more weakly defined than the others. CuAa reaches the posterior wing margin distinctly distal of the level of nodus. The cubito-anal area is max. 4.0 mm wide with five rows of cells between CuA and the posterior wing margin. Area between MP and CuA basally distinctly widened. Anal area broad with about six rows of cells between AA and the posterior wing margin, max. width of anal area (below PsA) 6.1 mm. The five-celled anal loop is nearly as long as wide (max. length 3.3 mm; width 2.8 mm), and posteriorly well-closed. An elongated distal paranal cell is well-defined (length 1.4 mm; width 1.0 mm). Anal margin with an anal angle and a three-celled anal triangle, thus, it is a male specimen.



Text-Fig. 115. *Plesigomphaeschnaoides mongolensis* sp. nov. Holotype PIN 3559 / 10201 - male, left hindwing (combined drawing from part and counterpart).

Plesigomphaeschnaoides pindelskii sp. nov.

Text-Fig. 116

Holotype: Specimen no. [1996. 223], coll. PINDELSKI, MNEMG, Maidstone.

Derivatio nominis: Named in honour of the collector Mr M. PINDELSKI (London).

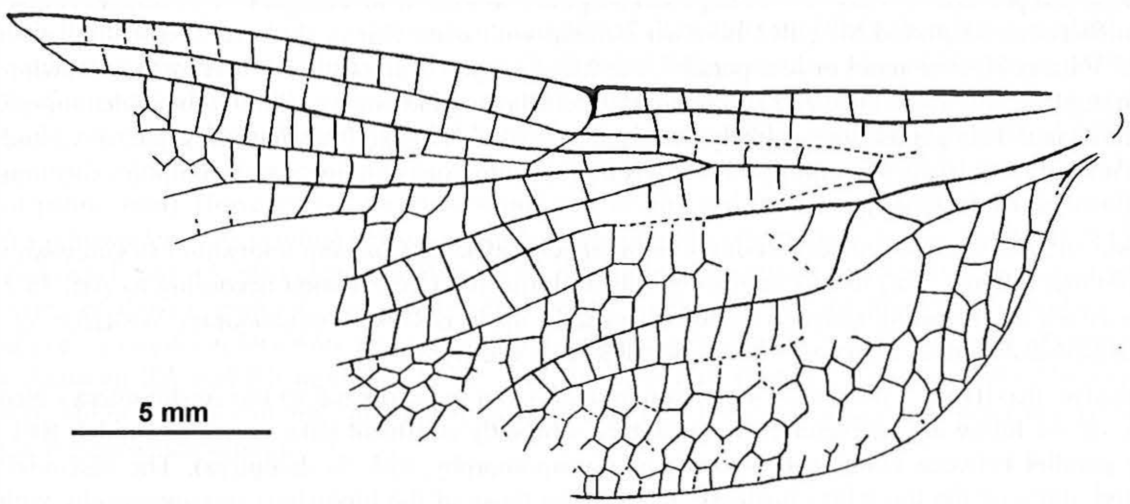
Locus typicus: Clockhouse Brickworks, near Capel, Surrey, England.

Stratum typicum: Lower Weald Clay, Lower Cretaceous, Hauterivian.

Diagnosis: Very similar to the type species *Plesigomphaeschnaoides mongolensis* gen. et sp. nov., only differing in the following hindwing characters: Smaller size (hindwing length only 32.5 mm, instead of 38.0 mm); only a single row of cells between the basal parts of RP1 and RP2; only a single row of cells between RP3/4 and MA, also in the more distal parts; RP2 is more distinctly undulated (?); postnodal crossveins between nodus and pterostigma more numerous (fourteen instead of only ten); only a single bridge-crossvein Bq; only four rows of cells in the cubito-anal area (instead of five to six rows); anal loop more transverse.

Although of similar size, this hindwing clearly does not belong to *Cretalloaeschna cliffordae* JARZEMBOWSKI & NEL, 1996a, the only other possible Gomphaeschnidae from the same locality, since RP1 and RP2 are closely parallel up to the pterostigma in this latter taxon, contrary to the divergent veins in this new species. Furthermore, the pterostigmal brace vein of *Cretalloaeschna* is short and neither very oblique, nor undulated, and thus clearly contradicting any relationship with Gomphaeschnaoidinae subfam. nov. at all. Even though the hindwings are not preserved in the holotype of *Cretalloaeschna*, such a dissimilarity between fore- and hindwing can be generally regarded as most unlikely.

Description: Imprint of a hindwing with the apex and the postero-distal part of the wing missing. There is no preserved coloration. Length of preserved part 27.7 mm, probable total length 32.5 mm; width at nodus 10.5 mm; distance from base to arculus 5.2 mm; distance from base to nodus 12.4 mm; from nodus to pterostigma 14.5 mm. Only the basal side of pterostigma is preserved which is strongly braced by a very oblique crossvein. Fourteen postnodal crossveins between nodus and pterostigma, not aligned with the ten corresponding postsubnodal crossveins. Six antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the distal primary antenodal crossvein Ax2. The basal primary antenodal crossvein Ax1 is not preserved, but Ax2 is visible and situated distinctly basal of the level of the distal angle of discoidal triangle; two not aligned secondary antenodal crossveins in both rows are visible basal of Ax2. Only four antesubnodal crossveins between RA and RP with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell (0.6 mm) distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 diverge strongly 8.3 mm distal of the subnodus with two (or possibly more) rows of cells in this widened area. RP1 and RP2 are basally slightly divergent with a single row of cells in-between, but 3.3 mm basal of the pterostigma, they diverge with two or more rows of cells in-between. RP3/4 and MA are nearly parallel and gently undulated with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is distally widened (width near discoidal triangle 2.3 mm; width at wing margin unknown) with two rows of cells immediately distal of the discoidal triangle. Hypertriangle not well-preserved (length 3.3 mm), but it seems to be free of crossveins. The discoidal triangle is rather stout and divided into two cells by a crossvein; length of anterior side 2.8 mm; of basal side 2.0 mm; of distal side MAb 2.7 mm. Median space seems to be free of crossveins. Submedian space only traversed by CuP-crossing, 1.7 mm basal of arculus. PsA is well-defined and delimits an unicellular subdiscoidal triangle; PsA is slightly undulated and ends on MP + CuA 0.4 mm basal of the discoidal triangle. Only a single row of cells in the area between MP and CuA except near the posterior wing margin. CuA reaches the posterior wing margin somewhat distal of the level of the nodus. The posterior branches of CuA (especially the basal ones) are weak and slightly zigzagged veins. Up to four rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 3.3 mm. Anal area broad (max. width 5.1 mm) with up to six rows of cells between AA and the posterior wing margin. Anal loop broad and rather transverse (probably divided into about five cells), and posteriorly well-closed. Anal margin rounded without anal angle or anal triangle, thus, it is a female specimen.



Text-Fig. 116. *Plesigomphaeschnaoides pindelskii* sp. nov. Holotype MNEMG 1996. 223 - female, left hindwing.

?*Plesigomphaeschnaoides paleocenica* (MADSEN & NEL, 1997) comb. nov. and ?*P. danica* comb. nov. (MADSEN & NEL, 1997)

MADSEN & NEL (1997) described two Gomphaeschnidae from the Danish Palaeocene/Eocene Mo-Clay, and provisionally attributed them to the genus *Gomphaeschna* with the names *G. paleocenica* and ?*G. danica*.

ANDERSEN & ANDERSEN (1996: figs 10-11) figured a further specimen of *G. paleocenica*, which was not mentioned by MADSEN & NEL (1997). RUST (1999: 25-28, text-fig. 8, pl. 2 fig. a) briefly redescribed the two species, especially the body of the holotype of *G. paleocenica*, and mentioned new material. This material will be used for a redescription by RUST & BECHLY (in prep.). The two mentioned species share with the Gomphaeschnaoidinae subfam. nov. the following synapomorphies: Presence of a transverse hindwing paranal cell (more distinct in the male than in the female specimens); the forewing Ax2 is on a level with the basal side of the discoidal triangle; the pterostigmal brace is very oblique and more or less sigmoidal.

Although these two species show more similarity to *Plesigomphaeschnaoides* gen. nov. than to any other genus within this subfamily, their attribution to this genus is very uncertain because they only share symplesiomorphies. The main differences are their variable number of secondary antenodal crossveins between the primary antenodal crossveins Ax1 and Ax2 (one or two depending on the wing), and their distinctly less wide areas between CuA and the posterior wing margin.

A very similar fossil gomphaeschnid (thorax and two forewings) from Eocene Baltic amber could recently be purchased by SMNS (Stuttgart), but still has to be described (BECHLY in prep.).

Genus *Gomphaeschnaoides* CARLE & WIGHTON, 1990

1987 *Gomphaeschna*; WIGHTON, p. 311-314.
1990 *Gomphaeschnaoides* CARLE & WIGHTON, pp. 63-64.
1996a *Gomphaeschnoides* LOHMANN, p. 226 (unjustified emendation, jun. obj. syn. nov.).

Type species: *Gomphaeschnaoides obliquus* (WIGHTON, 1987), by original designation.

Other species: *Gomphaeschnaoides magnus* sp. nov., *Gomphaeschnaoides petersi* sp. nov., and *Gomphaeschnaoides betoreti* sp. nov.

Diagnosis: This genus is characterized as follows: Presence of an obliquely slanted crossvein between the basal parts of RP1 and RP2 (autapomorphy, convergent to Libellulidae); RP1 and RP2 are diverging from their bases (putative synapomorphy with *Progomphaeschnaoides* gen. nov.); RP2 is undulated, but much less than in *Paramorbaeschna* gen. nov.; only a single oblique vein 'O', one cell distal of the subnodus; the pterostigma covers max. two cells, and is strongly braced by a very oblique and slightly undulated crossvein; only a single secondary antenodal crossvein between Ax1 and Ax2 in the hindwing (autapomorphy); in the hindwing, there are only four or five antesubnodal crossveins between RA and RP (distal of the arculus and basal of the subnodus) with a distinct gap immediately basal of the subnodus (synapomorphy with Gomphaeschnidae); max. ten postnodal crossveins between nodus and pterostigma (autapomorphy); the anal loop is divided into four to eight cells, and posteriorly well-closed; Rspl and Mspl are straight with a single row of cells between Rspl and IR2, and between Mspl and MA; IR2 is rather straight with max. two or three rows of cells between it and RP2; RP3/4 and MA are more or less parallel, but MP diverges distinctly from MA in the hindwing; the discoidal triangle is only two-celled and still relatively stout in the hindwing, while it is somewhat more elongated in the forewing. This genus is most likely the sister-genus of *Progomphaeschnaoides* gen. nov., and together closely related to *Paramorbaeschna* gen. nov., as indicated by four putative synapomorphies mentioned above in the diagnosis of the latter genus.

Discussion: The intended correction of the original generic name *Gomphaeschnaoides* to *Gomphaeschnoides* by LOHMANN (1996a: 226) has to be regarded as an unjustified emendation according to Art. 33.2.3 IRZN, since it is not in prevailing usage. The correct generic name is *Gomphaeschnaoides* WIGHTON & WILSON, while *Gomphaeschnoides* LOHMANN is a junior objective synonym.

Systematic position: The genus *Gomphaeschnaoides* can be attributed to the Aeshnoptera - Neoaeshnida because of the following characters: Compound eyes broadly confluent (like recent aeshnids). RP1 and RP2 closely parallel between nodus and pterostigma (synapomorphy with Aeshnoptera). The discoidal triangles elongated, those of the forewings distinctly longer than those of the hindwings (synapomorphy with Euaeshnida). RP2 is undulated beneath the pterostigma (synapomorphy with Aeshnida, secondarily even more pronounced). A well-defined Rspl (synapomorphy with Aeshnida). A well-defined Mspl (synapomorphy with Euaeshnida). The distal side MAb of the discoidal triangle is angled (synapomorphy with Euaeshnida). The number of CuA branches is reduced in the hindwings. Anal loop transversely broadened (synapomorphy with Euaeshnida) and posteriorly well-closed (symplesiomorphy). The distal oblique vein is reduced (synapomorphy with Neoaeshnida); the retained "lestine" oblique vein 'O' is shifted basally close to the subnodus (synapomorphy with Neoaeshnida).

On the basis of some weak alleged synapomorphies with Cordulagomphinae (see below), and considering the fact that convex curvatures of RP2 and Rspl and Mspl have evolved independantly in aeshnid and libelluloid dragonflies, and only knowing the holotype that lacks the forewings, CARLE & WIGHTON (1990: 64) believed that «a similar trend is likely in Gomphidae», so that the presence of these character states in *Gomphaeschnaoides* would not conflict a position within gomphids. Nevertheless, this hypothesis would be extremely unparsimonious regarding the other above mentioned characters, so that it must be regarded as almost certain that the presence of Rspl and Mspl in *Gomphaeschnaoides* are true synapomorphies with the concerning Aeshnoptera-taxa, especially since *Gomphaeschnaoides* shares not even a single exclusive synapomorphy with the groundplan of Gomphides. CARLE & WIGHTON (1990) attributed *Gomphaeschnaoides* to their Gomphidae - Cordulagomphinae CARLE & WIGHTON, 1990 on the basis of the following alleged synapomorphies: 1) both rows of antenodal crossveins distinctly more aligned than in other Aeshnoptera; 2) only a single crossvein beneath the pterostigma; 3) a strongly slanted pterostigmal brace; 4) weak pectination of CuAa (anal vein *sensu* CARLE & WIGHTON 1990); 5) a rounded (rather than elongated) anal loop; 6) a very wide distal paranal cell; 7) bases of RP and MA ("sectors of arculus") distinctly separated at arculus; and 8) subdiscoidal triangle well-defined. Character 1 is incorrect for most specimens of *Gomphaeschnaoides*, and within Cordulagomphinae only distinct in *Cordulagomphus fenestratus* CARLE & WIGHTON, 1990, but not in *Cordulagomphus tuberculatus* CARLE & WIGHTON, 1990 and *Procordulagomphus xavieri* NEL & ESCUILLIÉ, 1994, and also not in a new undescribed species of *Cordulagomphus* (BECHLY 1998); this state also occurs in many Eurypalpida (= Libelluloidea *sensu* FRASER 1957), but is reversed in a few Libellulidae (e.g. *Paleotramea* and *Zenithoptera*), thus, it is highly homoplastic within the Anisoptera. Character 2 is present in many Eurypalpida and in the two Neoaeshnida *Gomphaeschna furcillata* (SAY, 1839) and *Caliaeschna microstigma* SCHNEIDER, 1845, so that this character is homoplastic, too, and maybe rather a synapomorphy of *Gomphaeschnaoides* with some other Gomphaeschnidae. Character 3 is possibly a plesiomorphy of the Anisoptera; it is also present in *Gomphaeschna furcillata*. Character 4 is dubious, since the mentioned new undescribed species of *Cordulagomphus* does still possess a well branched CuAa, just like *Gomphaeschnaoides magnus* sp. nov., too, while numerous other crowngroup Anisoptera indeed have a more or less reduced pectination of CuAa. Character 5 is a symplesiomorphy of the non-libelluloid Anisoptera, also present in numerous Aeshnoptera. Furthermore, the anal loop of *Gomphaeschnaoides* is very dissimilar to the anal loop of Cordulagomphinae while it perfectly agrees with the anal loop of basal Euaeshnida, including the distinctly elongated gaff which is unknown in Gomphides. Characters 7 and 8 are not autapomorphies of the Cordulagomphinae, but symplesiomorphies of the Anisoptera (BECHLY 1996, JARZEMBOWSKI & NEL 1996a). Only character 6 seems to be absent in other Neoaeshnida, but this single derived similarity, is by no means sufficient for the attribution of *Gomphaeschnaoides* to the Cordulagomphinae within Gomphides, especially considering the substantial conflicting evidence mentioned above (e.g. broadly confluent compound eyes and all the other strong synapomorphies with Euaeshnida). For some of the above mentioned reasons NEL & PAICHELER (1994) already rejected the attribution of *Gomphaeschnaoides* to Cordulagomphinae and regarded this genus as a Gomphidae (auct.) or Aeshnoidea (auct) of uncertain familial position. Contrary to LOHMANN (1996a: 226) who attributed *Gomphaeschnaoides* to the stemgroup of his Gomphaeschnata (equivalent to Gomphaeschnidae), LOHMANN (1996c: 362) regarded *Gomphaeschnaoides* as stemgroup representative of his Palanisoptera (equivalent to Euaeshnida in the present publication). However, on the basis of our new results and the presented arguments, the retransfer of *Gomphaeschnaoides* to its original placement in the Neoaeshnida - Gomphaeschnidae by BECHLY (1996) is strongly supported, and it is also clearly confirmed by our finding of several new specimens of *Gomphaeschnaoides*, some of them completely preserved including the forewings and the head with broadly confluent compound eyes. *Gomphaeschnaoides* shares with the Gomphaeschnidae the reduced number of antesubnodal crossveins between RA and RP immediately basal of the subnodus (putative synapomorphy, convergent to Cavilabiata), and the absence of any cubito-anal crossveins in the submedian space between CuP-crossing and PsA (maybe a symplesiomorphy).

Gomphaeschnaoides obliquus (WIGHTON, 1987)

Text-Figs 117-119, Plate 39: Figs 2 and 4-5, Plate 40: Figs 1-3, Plate 41: Fig. 1

* 1987 *Gomphaeschna obliqua* WIGHTON, pp. 311-314, figs 1-2 (in Aeshnidae - Gomphaeschninae).
1990 *Gomphaeschnaoides obliqua* (WIGHTON); CARLE & WIGHTON, pp. 63-64, figs 18-19 (in Gomphidae - Cordulagomphinae).
1993 *Gomphaeschnaoides obliqua* WIGHTON; MARTILL *et al.*, p. 143 (in Gomphidae).

1994 *Gomphaeschnaoides obliqua* (WIGHTON); NEL & PAICHELER, pp. 63-65 (in Gomphidae or Aeshnoidea).
1996 *Gomphaeschnaoides obliqua* WIGHTON; MARTILL & NEL, p. 284 (in Gomphidae).
1996 *Gomphaeschnaoides obliqua* (WIGHTON); BECHLY, p. 378 (in Aeshnoptera - Gomphaeschnidae).
1996a *Gomphaeschnoides obliquus* (WIGHTON); LOHMANN, p. 226 (in Palanisoptera - Gomphaeschnata).
1997 *Gomphaeschnoides obliquus* (WIGHTON); MADSEN & NEL, p. 290 (in Aeshnoidea).
1998 *Gomphaeschnaoides obliquus*; BECHLY, p. 62.

Holotype: Specimen no. [43257], Invertebrate Dept. Coll., AMNH, New York; donated by Dr H.R. AXELROD; two complete hindwings of a male, still in connection with a body fragment.

Other specimens: Specimen no. [54], NSM, Tokyo, adult male with the four wings connected to the thorax; specimen no. [63069] (old number B 22), SMNS, Stuttgart, adult male with all wings and remnants of thorax and abdomen; specimens nos [C 16], [C 17], [C 18], [C 19], [D 11] (see Plate 41: Fig. 1), [E 19], [G 31], [H 9], [K 18], [L 4 = M 70], [L 12], [L 45], [M 59], [M 61], and [M 120], coll. *ms-fossil*, Sulzbachtal. Specimen no. [C 17] (new number 13) was meanwhile sold to the Museum of Munich (BSP), and specimen no. [L 45] (two poorly preserved forewings in connection with thorax fragment) was recently donated to SMNS in Stuttgart (new number SMNS 64346); the complete female specimen no. [L 4 = M 70] and the two male hindwings with nos [M 59] and [M 61] are scheduled to be purchased by SMNS. One specimen without number is present in the palaeontological collection of the Staatliches Museum für Naturkunde, Karlsruhe (SMNK).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

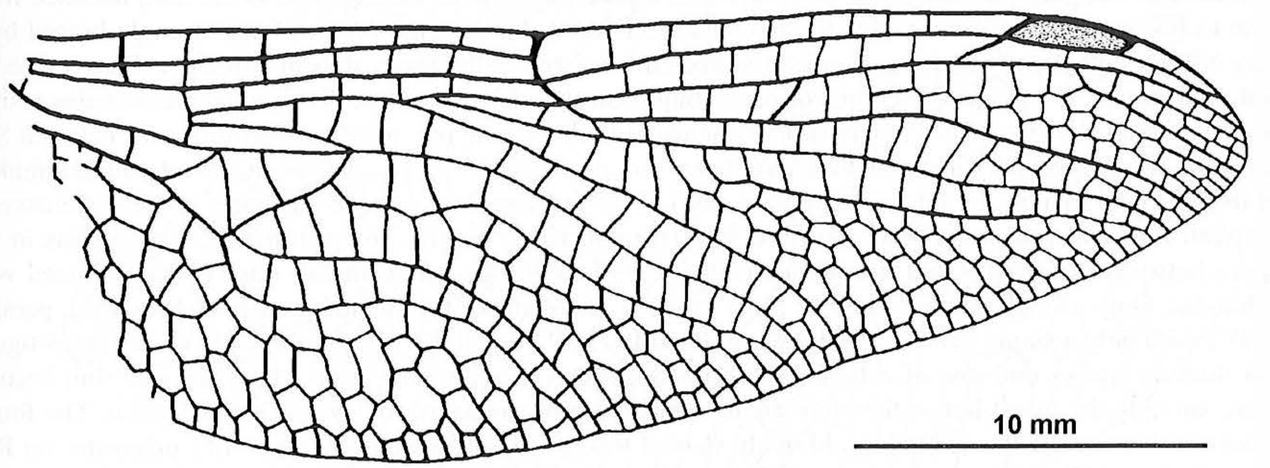
Diagnosis: Differing from *Progomphaeschnaoides* gen. nov. in the following characters: Presence of only a single secondary antenodal between the primary antenodal crossveins Ax1 and Ax2 in the hindwing (putative synapomorphy of the four species of *Gomphaeschnaoides*); presence of a distinct oblique veinlet that is slanted towards the pterostigma, between RP1 and RP2 in both pairs of wings (strong synapomorphy of the four species of *Gomphaeschnaoides*); only one or two rows of cells between RP2 and IR2 (apparently rather variable within this range); less than four rows of cells between the median parts of pseudo-IR1 and RP1 and RP2, respectively (symplesiomorphy with the other species of *Gomphaeschnaoides*); anal loop transverse (symplesiomorphy with the other species of *Gomphaeschnaoides*), contrary to the more longitudinal anal loop of *Progomphaeschnaoides* gen. nov.; presence of several posterior branches of AA basal of the anal loop in the female hindwing (symplesiomorphy with the other species of *Gomphaeschnaoides*). The forewing discoidal triangle is mostly less longitudinally elongated than in *G. magnus* sp. nov. In the hindwing there are only three secondary antenodal crossveins between Ax2 and the nodus (as in *P. staniczeki* sp. nov. and *Plesigomphaeschnaoides* gen. nov.), while there are four of them in *G. magnus* sp. nov. and *G. petersi* sp. nov. The wing length (31-35 mm) is distinctly smaller than in *G. magnus* sp. nov. (wing length 41-45 mm), and at least somewhat bigger than in *G. betoreti* sp. nov. or *Progomphaeschnaoides* gen. nov. (wing length 28-29 mm).

Description: The present redescription is based on the published figures of holotype and on our examination of the other mentioned specimens.

♦ Specimen no. AMNH 43257; holotype; male

Text-Fig. 117

Hindwing: There is no trace of coloration, the wings seem to have been hyaline. Length 34.3 mm; width at nodus 11.5 mm; distance from base to arculus 4.7 mm; distance from base to nodus 14.0 mm; from nodus to pterostigma 13.3 mm. Pterostigma 3.2 mm long, strongly braced by a very oblique and slightly undulated crossvein, and covering one and a half cells. Eight postnodal crossveins between nodus and pterostigma that are not aligned with the corresponding postsubnodal crossveins. Six antenodal crossveins visible between costal margin and ScP, rather well-aligned with the second row of antenodal crossveins between ScP and RA. Only a single secondary antenodal crossvein between the two primary antenodal crossveins, and three between Ax2 and nodus. Ax1 is 1.6 mm basal of the arculus and Ax2 4.0 mm distal of Ax1. Only four antesubnodal crossveins visible in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. Several convex secondary veins originate on Rspl. The space between RP2 and IR2 is distally somewhat widened, but there are only one or two rows of cells in-between in this widened area. Pseudo-IR1 well-defined and originating beneath the basal half of the pterostigma. RP1 and RP2 are basally only slightly divergent, but they begin to diverge more strongly beneath the pterostigmal brace, because of a distinct curvature of RP2. The fourth crossvein between RP1 and RP2 is very obliquely slanted (potential synapomorphy with *G. magnus* sp. nov.; convergent to Libellulidae). RP3/4 and MA are more or less parallel with a single row of cells in-between, but MA is slightly undulated while RP3/4 is rather straight. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. Several convex secondary veins originate on Mspl. The postdiscoidal area is distally widened (width near discoidal triangle 3.0 mm; width at wing margin 6.1 mm) with two rows of cells distal of the discoidal triangle and a secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins (length 4.8 mm; max. width 0.7 mm). The discoidal triangle is divided into two cells by a crossvein; it is rather stout; length of anterior side 3.7 mm; of basal side 2.3 mm; of distal side MAb 4.0 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing 1.6 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. A single row of cells in the area between MP and CuAa. CuAa reaches the posterior wing margin on a level with nodus. The six posterior branches of CuA (including CuAb and five branches of CuAa) are not straight, but zigzagged and weakly defined veins. Four rows of cells between CuAa and the posterior wing margin, width of cubito-anal area 4.4 mm. Anal area broad with six rows of cells between AA and the posterior wing margin. The five-celled anal loop is broad and rather transverse (length 2.4 mm; width 3.3 mm), it is posteriorly well-closed. Anal margin distorted and the extreme base of the wings are not preserved (including the area of the potential anal angle and anal triangle), but since there are no posterior branches of AA visible basal of the anal loop it clearly is a male specimen.



Text-Fig. 117. *Gomphaeschnaoides obliquus* (WIGHTON, 1987). Holotype AMNH 43257 - male, right hindwing (drawing after WIGHTON 1987: fig. 2).

♦ Specimen no. 54, NSM; female

Plate 40: Fig. 1

A well-preserved adult female with all four wings in outstretched position. Thorax and basal third of the abdomen are preserved as well. Unfortunately, it was not possible to make a drawing of this specimen before it was sold to Japan, therefore the present description is mainly based on the available photographs. The thorax is poorly preserved, but the abdomen clearly shows a medio-dorso-longitudinal carina. There is no trace of coloration, the four wings seem to have been hyaline.

Forewing: Length 34.9 mm; width at nodus 8.7 mm; distance from base to arculus 5.4 mm; distance from base to nodus 18.4 mm; from nodus to pterostigma 10.3 mm. Pterostigma 2.9 mm long, strongly braced by an oblique crossvein and covering two cells. Five or six postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Nine antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except the three most basal antenodal crossveins, including Ax1 and Ax2 that are aligned and stronger than the others.

Ax2 is of the level of the basal side of the discoidal triangle. The aligned and enforced secondary antenodal crossvein between Ax1 and Ax2 is somewhat basal of the arculus, while Ax1 is distinctly basal of it. There seems to be a distinct gap of antesubnodal crossveins in the space between the arculus and the subnodus immediately basal of the latter. There is only a single bridge-crossvein Bq visible in the right forewing. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 weakly diverge slightly basal of the level of pterostigma, but there is always one row of cells in-between. RP2 is slightly undulated, while IR2 is more or less straight; pseudo-IR1 originates on RP1 beneath the middle of the pterostigma with one or two rows of cells between it and RP1 and three rows of cells between it and RP2. RP1 and RP2 are basally gently divergent with an oblique crossvein in-between that is slanted towards the pterostigma, but below the pterostigma, they diverge with two or more rows of cells in-between. RP3/4 and MA are parallel and gently undulated with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is not very widened distally with two rows of cells distal of the discoidal triangle and a secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins. The discoidal triangle is divided into two cells by a crossvein, and is distinctly longer than that of the hindwing; length of anterior side 4.3 mm; of basal side 1.8 mm; of distal side MAb 4.5 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin on a level with nodus, and CuA reaches the posterior wing margin somewhat basal of the level of the nodus. The posterior branches of CuA are zigzagged and weak veins. Two rows of cells between CuA and the posterior wing margin, width of cubito-anal area 1.8 mm. The anal area is 1.5 mm wide (below PsA) with two rows of cells between AA and the posterior wing margin.

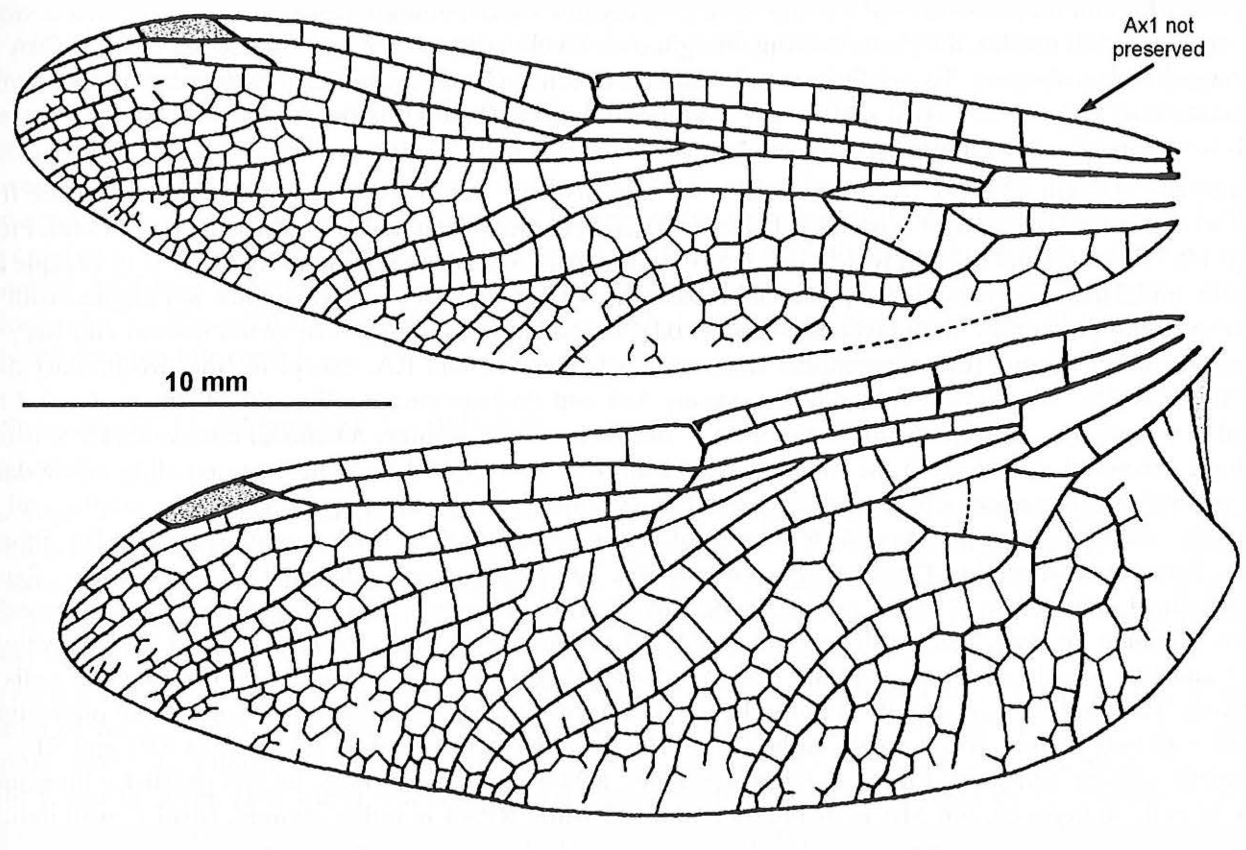
Hindwing: Length 34.6 mm; width at nodus 11.2 mm; distance from base to arculus 5.5 mm; distance from base to nodus 15.5 mm; from nodus to pterostigma 11.9 mm. Pterostigma 2.9 mm long, strongly braced by a very oblique and slightly undulated crossvein, and covering two cells. Six postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Six antenodal crossveins visible between costal margin and ScP, more or less aligned with the second row of antenodal crossveins between ScP and RA. The two primary antenodal crossveins are stronger than the others. Ax2 is on a level with the middle of the discoidal triangle, and Ax1 is distinctly basal of the arculus. Only a single secondary antenodal crossvein between Ax1 and Ax2, on a level with arculus. There seems to be only few antesubnodal crossveins in the space between the arculus and the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 weakly diverge below the pterostigma, but there is always one row of cells in-between. RP1 and RP2 are basally somewhat divergent, but become more strongly divergent below the pterostigmal brace with two or more rows of cells in-between. The fourth crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. Pseudo-IR1 originates on RP1 beneath the middle of the pterostigma. RP3/4 and MA are parallel and gently undulated with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is distally widened, but basal of Mspl there are only two rows of cells distal of the discoidal triangle, separated by a strong convex secondary longitudinal vein (trigonal planate) that is originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins. The discoidal triangle is less elongated than that of the forewing and is divided into two cells by a crossvein; length of anterior side 3.5 mm; of basal side 1.9 mm; of distal side MAb 3.9 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. A single row of cells in the area between MP and CuAa. CuAa reaches the posterior wing margin on a level with nodus. CuAb and the five posterior branches of CuAa are rather weak veins. Four rows of cells between CuAa and the posterior wing margin, width of cubito-anal area 4.2 mm. The anal area is broad, below PsA 6.4 mm wide with five rows of cells between AA and the posterior wing margin. The anal loop is broad and rather transverse (length 2.6 mm; width 3.6 mm), posteriorly well-closed, and divided into five cells in the left hindwing and four cells in the right hindwing. Four posterior branches of AA (female), including the one that is forming the basal margin of the anal loop. The anal margin is somewhat distorted, but clearly rounded without an anal angle or anal triangle, thus, it is a female specimen.

Discussion: The presence of only a single row of cells between RP2 and IR2 in all four wings is a unique character which is neither present in any of the other specimens of *Gomphaeschnaoides obliquus*, nor in any specimen of the other species of *Gomphaeschnaoides* and the closely related genera *Plesigomphaeschnaoides* gen. nov., *Progomphaeschnaoides* gen. nov., and *Paramorbaeschna* gen. nov. Whether this condition is representing infra-specific variability or an individual aberration, or if this specimen even belongs to a new species, can only be decided when further material will be available.

♦ Specimen no. 63069, SMNS; male

Text-Fig. 118, Plate 39: Figs 4-5

A well-preserved adult male with all four wings completely preserved and in connection with the thorax (wing span 66 mm), but the right pair of wings is not so well-preserved as the left pair. Thorax and abdomen are preserved as well, but the head and the apex of the abdomen are missing (length of preserved part of abdomen, 38 mm; basal width 3 mm; distal width 2 mm). There is no trace of coloration, the four wings seem to have been hyaline.



Text-Fig. 118. *Gomphaeschnaoides obliquus* (WIGHTON, 1987). SMNS 63069 - male, left pair of wings.

Forewing: Length 32.0 mm; width at nodus 8.0 mm; distance from base to arculus 5.0 mm; distance from base to nodus 16.1 mm; from nodus to pterostigma 10.1 mm. Pterostigma 2.2 mm long and 0.7 mm wide, covering two cells, and strongly braced by a very oblique and slightly undulated crossvein. Six postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossvein. Ten antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. Two antenodal crossveins are stronger than the others (these are not Ax1 and Ax2, but Ax2 and a secondary antenodal crossvein immediately basal of it, while Ax1 is not preserved or teratologically absent, as is clearly indicated by its presence in specimen B 54 which has three basal antenodal crossveins stronger than the others, of which the distal two are in the same position as the two only ones in this specimen). The secondary antenodal crossvein that is looking like Ax1 (see above) is 0.7 mm basal of the arculus. Ax2 is 1.8 mm distal of this enforced secondary, on a level with basal angle of discoidal triangle. Only a single secondary antenodal crossvein between Ax1 (which is missing, see above) and Ax2 which is aligned and enforced like a primary antenodal crossvein. Six or seven antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 weakly diverge below the pterostigmal brace with two rows of cells in-between. Pseudo-IR1 well-defined, but its origin beneath the pterostigma is not preserved. RP1 and RP2 are basally slightly divergent, but below the pterostigmal brace, they strongly diverge with two or more rows of cells in-between. The fourth crossvein between RP1 and RP2 is distinctly oblique and slanted towards the pterostigma. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4) with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. Several convex secondary veins originate on Mspl. The postdiscoidal area is not very widened distally with two rows of cells distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins. The discoidal triangle is divided into two cells by a crossvein, it is distinctly more narrow than that of the hindwing; length of anterior side 3.4 mm; of basal side 1.7 mm; of distal side MAb 3.6 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle, max. 1.6 mm long and basally 1.6 mm wide (= length of PsA). A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin on a level with nodus. The posterior branches of CuA are zigzagged and weak veins. Two or three rows of cells between CuA and the posterior wing margin. Max. width of cubito-anal area 1.9 mm. The anal area is max. 2.0 mm wide (below the origin of PsA) with two rows of cells between AA and the posterior wing margin.

Hindwing: Length 32.0 mm; width at nodus 10.7 mm; distance from base to arculus 5.1 mm; distance from base to nodus 13.8 mm, thus, the nodus is in a rather basal position; from nodus to pterostigma 11.9 mm. Pterostigma 2.5 mm long and 0.8 mm wide, covering two and a half cells, and strongly braced by a very oblique and slightly undulated crossvein. Seven postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Six antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. The primary antenodal crossveins Ax1 and Ax2 are stronger than the others. Ax1 is 1.3 mm basal of the arculus. Ax2 is 3.6 mm distal of Ax1. Between the two primary antenodal crossveins there is only a single secondary antenodal in the first row that is more or less aligned with the corresponding antenodal of the second row; there are only four antesubnodal crossveins visible in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. Several convex secondary veins originate on Rspl. Pseudo-IR1 well-defined and originating beneath the basal half of the pterostigma. RP2 and IR2 weakly diverge somewhat basal of the level of pterostigmal brace with two rows of cells in-between. RP1 and RP2 are basally slightly divergent, but become strongly divergent beneath the pterostigmal brace with two or more rows of cells in-between. The third and fourth crossveins between RP1 and RP2, are distinctly oblique and slanted towards the pterostigma. RP3/4 and MA are more or less parallel with a single row of cells in-between, but MA is distinctly undulated while RP3/4 is rather straight. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. Several convex secondary veins originate on Mspl. The postdiscoidal area is distally widened with two rows of cells distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins. The discoidal triangle is divided into two cells by a crossvein, it is less elongated than that of the forewing; length of anterior side 3.5 mm; of basal side 2.1 mm; of distal side MAb 3.7 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle, max. 2.0 mm long and basally 1.9 mm wide (= length of PsA). A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin on a level with nodus. The posterior branches of CuA are zigzagged and weak veins (only CuAb and four distal branches of CuAa are distinct). Four or five rows of cells between CuAa and the posterior wing margin, max. width of cubito-anal area 4.1 mm. The anal area is broad, 5.4 mm wide with probably five or six rows of cells between AA and the posterior wing margin. Anal loop broad and rather transverse (length 2.5 mm; width 3.0 mm), it is divided into five cells and posteriorly well-closed. A distinct anal triangle (probably three-celled) and an anal angle, thus, it is a male specimen. No posterior branches of AA between the anal loop and the anal triangle (male). A long, but narrow membranule is visible along the basal side of the anal triangle.

♦ Specimen no. C 16, coll. *ms-fossil*; male

Plate 40: Fig. 2

A well-preserved and rather complete adult male with all four wings in connection with the thorax. However, the body is very poorly preserved. The wing venation is very similar to the other herein described specimens of this species.

Forewings: Length 32.2 mm; width at nodus 7.9 mm; distance from base to nodus 17.0 mm. Only a single imprecisely aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with basal angle of discoidal triangle. Five antesubnodal crossveins with a distinct gap basal of the subnodus. Six not aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. Six not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the distal half of the pterostigma. The third crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. One to two rows of cells in the distal area between RP2 and IR2. The discoidal triangle is elongated and divided by one crossvein. Hypertriangle and subdiscoidal triangle are free.

Hindwings: Length 32.0 mm; width at nodus 10.2 mm; distance from base to nodus 13.6 mm. Only a single aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with the middle of the discoidal triangle. Three hardly aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. Four antesubnodal crossveins with a distinct gap basal of the subnodus. Seven not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the distal half of the pterostigma (right wing) or even beneath the distal side of the pterostigma (left wing). The second crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. One to two rows of cells in the distal area between RP2 and IR2. The discoidal triangle is less elongated than that of the forewing, but also divided by one crossvein. Hypertriangle and subdiscoidal triangle are free. CuAa with four rather poorly defined posterior branches. Anal loop transverse and with five cells. Anal triangle is visible in the right hindwing, thus, it is a male specimen, although the anal angle is relatively rounded. There is no posterior branch of AA between anal loop and anal triangle (male).

♦ Specimen no. 13, old number C 17, BSP; male

Plate 40: Fig. 3

A well-preserved and rather complete adult male with all four wings in connection with the thorax. The basal abdominal segments, two fore legs and the head are preserved as well. The head is well-preserved (length 5.8 mm; width 7.0 mm) and shows the mouth parts, as well as the large globular compound eyes that are broadly confluent as in recent aeshnids. Even the ommatidia of the compound eye are still visible. The wing venation is very similar to the other herein described specimens of this species.

Forewings: Length 33.0 mm; width at nodus 8.0 mm; distance from base to nodus 17.1 mm. Only a single aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with basal angle of discoidal triangle. Seven not aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. Six (right wing) or seven (left wing) antesubnodal crossveins with a distinct gap basal of the subnodus. Seven (right wing) or eight (left wing) not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the basal half of the pterostigma. The third crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. Only a single row of cells in the distal area between RP2 and IR2. The discoidal triangle is elongated and divided by one crossvein. Hypertriangle and subdiscoidal triangle are free.

Hindwings: Length 32.7 mm; width at nodus 11.0 mm; distance from base to nodus 14.0 mm. Only a single aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with the middle of the discoidal triangle. Four imprecisely aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. Four antesubnodal crossveins with a distinct gap basal of the subnodus. Eight not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the basal half of the pterostigma. The fifth (right wing) or third (left wing) crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. One (left wing) or two (right wing) rows of cells in the distal area between RP2 and IR2. The discoidal triangle is less elongated than that of the forewing, but also divided by one crossvein. Hypertriangle and subdiscoidal triangle are free. CuAa with five rather well-defined posterior branches. Anal loop transverse and with five cells. Three-celled anal triangle, thus, it is a male specimen, although the anal angle seems to be relatively rounded. There is no posterior branch of AA between anal loop and anal triangle (male).

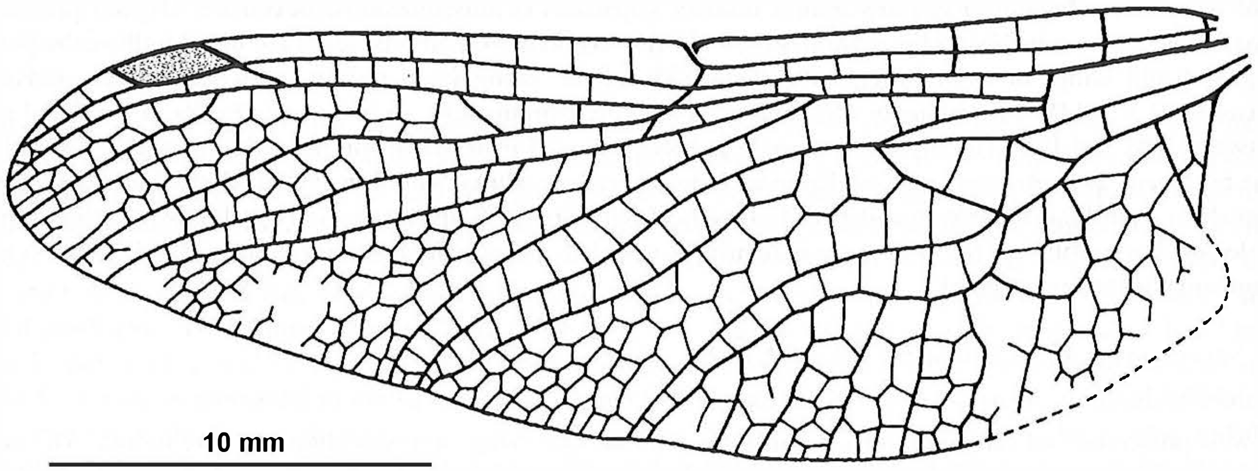
♦ Specimen no. C 18, coll. *ms-fossil*

A pair of completely and relatively well-preserved forewings in connection with the thorax (in frontal aspect) and with all legs. The wing venation is very similar to the other herein described specimens of this species. It is not possible to determine the sex of this specimen, since neither the hindwings, nor the abdomen are preserved.

Forewings: Length 33.9 mm; width at nodus 8.8 mm; distance from base to nodus 18.0 mm. Only a single aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with basal angle of discoidal triangle. Six or seven not aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. Five antesubnodal crossveins with a distinct gap basal of the subnodus. Seven not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath distal side of pterostigma. The third crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. One to two rows of cells in the distal area between RP2 and IR2. The discoidal triangle is elongated and divided by one crossvein. Hypertriangle and subdiscoidal triangle are free.

♦ Specimen no. C 19, coll. *ms-fossil*; male

Text-Fig. 119, Plate 39: Fig. 2



Text-Fig. 119. *Gomphaeschnaoides obliquus* (WIGHTON, 1987). Coll. *ms-fossil* C 19 - male, left hindwing.

Hindwing: No trace of coloration, the wings seem to have been hyaline. Length 33.0 mm; width at nodus 10.6 mm; distance from base to nodus 14.6 mm; from nodus to pterostigma 12.3 mm; distance from base to arculus 5.2 mm. Pterostigma 2.7 mm long and 0.9 mm wide, covering one and a half cells, and strongly braced by a very oblique and slightly undulated crossvein. Seven postnodal crossveins between nodus and pterostigma that are not aligned with the corresponding postsubnodal crossveins. Six antenodal crossveins visible between ScP and RA, but the distal antenodal crossveins between costal margin and ScP are not preserved. Only a single not aligned secondary antenodal crossvein between the two primary antenodal crossveins, and three between Ax2 and nodus. Ax1 is 1.5 mm basal of the arculus, and Ax2 4.0 mm distal of Ax1. Basal brace Ax0 preserved. Only five antesubnodal crossveins visible in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', less than one cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. The space between RP2 and IR2 is distally somewhat widened with two rows of cells in-between in this widened area. Pseudo-IR1 well-defined and originating beneath the basal half of the pterostigma. RP1 and RP2 are basally somewhat divergent, but they begin to diverge more strongly beneath the pterostigmal brace, because of a distinct curvature of RP2. The third crossvein between RP1 and RP2 is very obliquely slanted. RP3/4 and MA are more or less parallel with a single row of cells in-between, but MA is slightly undulated while RP3/4 is rather straight. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is distally widened (width near discoidal triangle 2.8 mm; width at wing margin 5.7 mm) with two rows of cells distal of the discoidal triangle and a secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins, 4.5 mm long and 0.7 mm wide. The discoidal triangle is divided into two cells by a crossvein; it is rather stout; length of anterior side 3.5 mm; of basal side 2.0 mm; of distal side

MAb 3.7 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 mm basal of the arculus. AA divided into a strong and oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a well-defined unicellular subdiscoidal triangle. A single row of cells in the area between MP and CuA. CuA reaches the posterior wing margin slightly distal of the level of the nodus. CuAb and the six posterior branches of CuAa are not straight, but zigzagged and somewhat weakly defined veins. Four rows of cells between CuAa and the posterior wing margin, max. width of cubito-anal area 4.3 mm. Anal area broad with six rows of cells between AA and the posterior wing margin. The four-celled anal loop is broad and quadrate (length 2.7 mm; width 2.7 mm), and posteriorly well-closed. The basal part of the posterior wing margin is only weakly preserved, but there seems to have been an anal angle (male). A three-celled anal triangle and there are no posterior branches of AA visible basal of the anal loop, thus, it is a male specimen.

♦ Specimen without number, SMNK, Karlsruhe; female

The wing venation of this well-preserved isolated right hindwing of a female perfectly agrees with the other specimens of *G. obliquus*, including a five-celled anal loop, free hypertriangle, two-celled discoidal triangle, two rows of cells between the distal parts of RP2 and IR2, gap of antesubnodal crossveins immediately basal of subnodus, and the characteristical oblique crossvein between RP1 and RP2. The single significant difference is the larger size (hindwing length 37.0 mm).

Gomphaeschnaoides magnus sp. nov.

Text-Fig. 120, Plate 42: Figs 1-2, Plate 43: Figs 1-2

? 1993 «Dragonfly»; MARTILL *et al.*, p.59, pl. 8, fig. 2.
1998 *Gomphaeschnaoides magnus*; BECHLY, p. 62 (nomen nudum).

Holotype: Specimen no. [AP 1997 / 2] (old number B 40), JME, Eichstätt.

Paratypes: Specimen no. 64344 (old numbers 71 and H 17), SMNS, Stuttgart; specimen no. [M 62], coll. *ms-fossil* (scheduled to be purchased by SMNS); a potential further specimen of this new species is illustrated in MARTILL *et al.* (1993: pl. 8, fig. 2). This specimen from the collections of the Leicester University Geology Department which is labelled [LEIUG 113603], is a female with all four wings preserved in connection with the pterothorax, but without the rest of the body (predated specimen ?). According to the indicated scale (1:1) of the figure, the forewing length of this specimen would be 45 mm (wing span 93 mm). The venation seems to agree with that of the holotype with the notable exception that there is only a single row of cells between RP2 and IR2. However, the latter character seems to be variable in *Gomphaeschnaoides obliquus* as well.

Derivatio nominis: Latin expression for "large", because of its distinctly larger size than *G. obliquus*.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

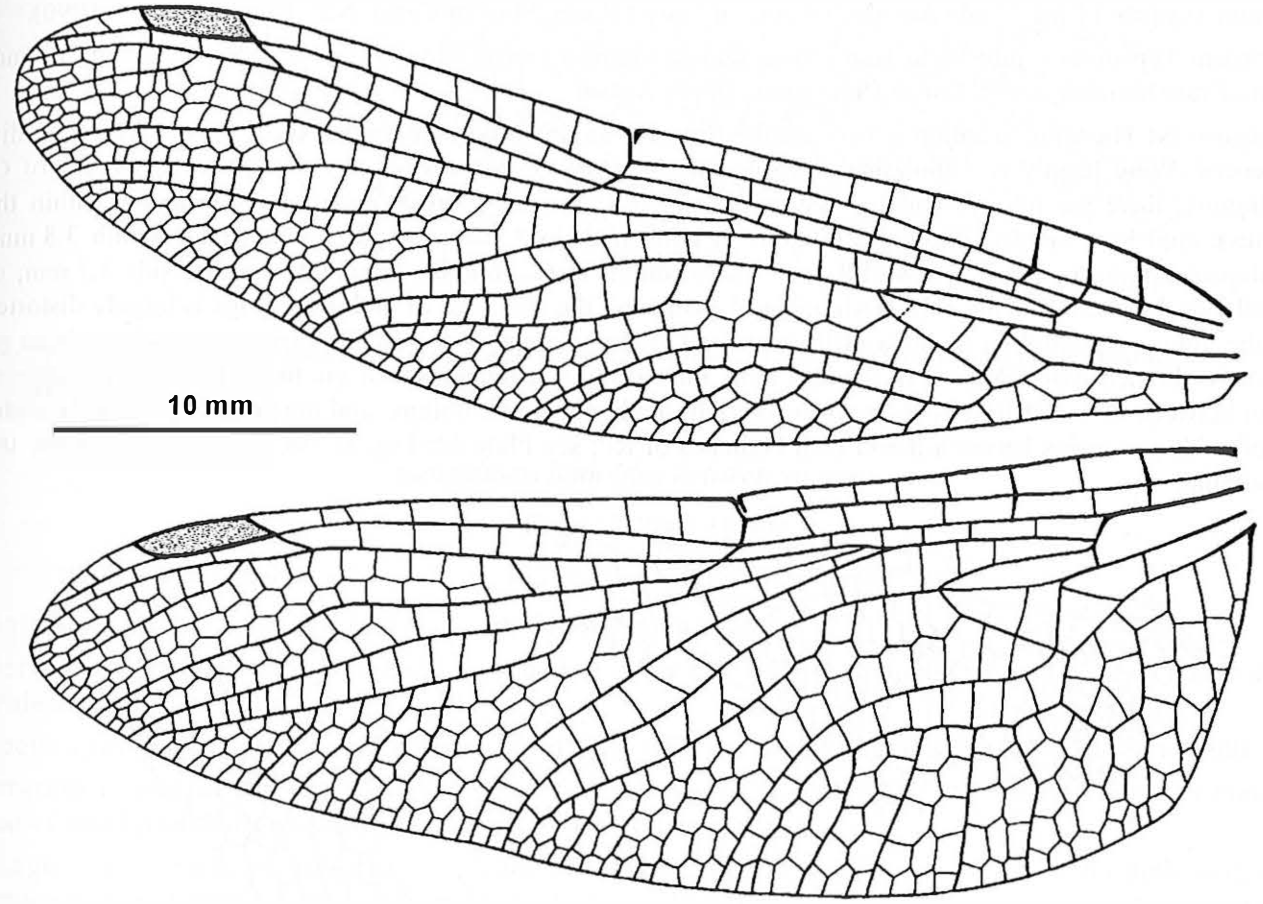
Diagnosis: Nearly identical wing venation as *G. obliquus* and *G. petersi* sp. nov., including the presence of only a single secondary antenodal between the primary antenodal crossveins Ax1 and Ax2 in the hindwing, and the presence of a distinct oblique veinlet that is slanted towards the pterostigma, between RP1 and RP2 in both pairs of wings (important synapomorphy). The single significant difference is the very distinctly larger size with a wing span of 85 mm instead of only 66-68 mm (rarely up to 76 mm) (autapomorphy ?).

Description: The holotype is a complete female with the left pair of wings complete and well-preserved, while the right forewing is overlapping the right hindwing (the apparently missing right forewing was supplemented by painting of the first preparator and has meanwhile been removed by the preparator of the Jura-Museum). The wing span is 85 mm. Pterothorax and base of the abdomen are preserved as well, while the rest of the abdomen is painted like the "right forewing". There is no trace of coloration, the wings seem to have been hyaline.

Forewing: Length 42.1 mm; width at nodus 10.1 mm; distance from base to arculus 5.8 mm; distance from base to nodus 21.7 mm; from nodus to pterostigma 13.3 mm. Pterostigma 3.3 mm long and 1.0 mm wide, covering two cells, and strongly braced by a very oblique and slightly undulated crossvein. Eight postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Eleven antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the three most basal ones including the primary antenodal crossveins. The primary antenodal crossveins Ax1 and Ax2 are stronger than the more distal antenodal crossveins. Ax1 is 2.1 mm basal of the arculus. Ax2 is 3.8 mm distal of Ax1, on a level with basal angle of discoidal triangle. Only a single secondary antenodal of the first row between the two primary antenodal crossveins, well-aligned with the corresponding antenodal of the second row and distinctly enforced like a primary antenodal. Eight antesubnodal crossveins in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. RP2 and IR2 weakly diverge below the pterostigmal brace with two rows of cells in-between. Pseudo-IR1 well-defined and originating on RP1 beneath the middle of the pterostigma. RP1 and RP2 are basally slightly divergent, but below the pterostigmal brace, they strongly diverge with two or more rows of cells in-between. The third crossvein between RP1 and RP2 is distinctly oblique and slanted towards the pterostigma. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4) with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. The postdiscoidal area is not very widened distally (width near discoidal triangle 2.4 mm; width at wing margin 7.7 mm) with two rows of cells immediately distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. Hypertriangle free of crossveins (length 6.0 mm; max. width 0.6 mm). The discoidal triangle is divided into two cells by a crossvein (maybe there is a second crossvein near the distal angle of the discoidal triangle), and it is distinctly more narrow than that of the hindwing; length of anterior side 4.5 mm; of basal side 1.8 mm; of distal side MAb 4.4 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 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 unicellular subdiscoidal triangle, max. 1.8 mm long and basally 1.8 mm wide (= length of PsA). PsA ends on MP + CuA somewhat distal of basal angle of discoidal triangle. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin slightly distal of the level of the nodus, while CuA reaches the posterior wing margin on a level with nodus. The posterior branches of CuA are zigzagged and weak veins. Three rows of cells between CuA and the posterior wing margin; max. width of cubito-anal area 2.6 mm. Anal area is max. 1.8 mm wide (below the origin of PsA) with two rows of cells between AA and the posterior wing margin.

Hindwing: Length 41.0 mm; width at nodus 13.0 mm; distance from base to arculus 4.7 mm; distance from base to nodus 17.1 mm, thus, the nodus is in a rather basal position; from nodus to pterostigma 15.8 mm. Pterostigma 3.9 mm long and 1.0 mm wide, covering one and a half cells, and strongly braced by a very oblique and slightly undulated crossvein. Eight postnodal crossveins between nodus and pterostigma, not aligned with the corresponding postsubnodal crossveins. Seven antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA, except for the two primary antenodal crossveins. The primary antenodal crossveins Ax1 and Ax2 are stronger than the others. Ax1 is 1.4 mm basal of the arculus. Ax2 is 4.5 mm distal of Ax1. Between the two primary antenodal crossveins there is only a single secondary antenodal in the first row that is not aligned with the corresponding antenodal of the second row. Only five antesubnodal crossveins visible in the space between the arculus and the subnodus with a distinct gap immediately basal of the subnodus. Only a single bridge-crossvein Bq. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell distal of the subnodus. Rspl is well-defined, parallel to IR2 with only a single row of cells between it and IR2. Several convex secondary veins originate on Rspl. Pseudo-IR1 well-defined and originating beneath the basal half of the pterostigma. RP2 and IR2 weakly diverge somewhat basal of the level of pterostigmal brace with two rows of cells in-between. RP1 and RP2 are basally slightly divergent, but become strongly divergent beneath the pterostigmal brace with two or more rows of cells in-between. The fourth crossvein between RP1 and RP2, is distinctly oblique and slanted towards the pterostigma. RP3/4 and MA are more or less parallel and gently undulated veins (MA is distinctly more undulated than RP3/4) with a single row of cells in-between. Mspl is well-defined, parallel to MA with only a single row of cells between it and MA. Several convex secondary veins originate on Mspl. The postdiscoidal area is distally widened (width near discoidal triangle 3.2 mm; width at wing margin 7.3 mm) with two rows of cells immediately distal of the discoidal triangle and a zigzagged secondary longitudinal vein, originating at the angled distal side MAb of the discoidal triangle. The hypertriangle is free of crossveins (length 5.3 mm; max. width 0.9 mm). The discoidal triangle is divided into two cells by a crossvein, and it is less elongated than that of the forewing; length of anterior side 4.2 mm; of basal side 2.3 mm; of distal side MAb 4.4 mm. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.6 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 unicellular subdiscoidal triangle, max. 2.3 mm long and basally 2.1 mm wide (= length of PsA). PsA ends on MP + CuA somewhat distal of basal angle of discoidal triangle. A single row of cells in the area between MP and CuA. MP reaches the posterior wing margin on a level with nodus. The posterior branches of CuA are rather well-defined veins. Five rows of cells between CuA and the posterior wing margin, max. width of cubito-anal area 5.4 mm. Anal area broad, 7.4 mm wide with five or six rows of cells between AA and the posterior wing margin. Anal loop broad and rather transverse (length 2.7 mm; width 3.9 mm), posteriorly well-closed, and divided into five cells. Basal of the anal loop, there are two or three posterior branches of AA (female). Anal margin rounded, there is neither an anal triangle, nor an anal angle, thus, it is a female specimen.



Text-Fig. 120. *Gomphaeschnaoides magnus* sp. nov. Holotype JME AP 1997 / 2 - female, left pair of wings.

♦ Specimen no. 64344 (old numbers 71 and H 17), SMNS, Stuttgart; paratype

Plate 43: Fig. 1

Two forewings (length 42 mm) with thorax and four legs. Only the anterior part of the wing venation is preserved.

♦ Specimen no. M 62, coll. *ms-fossil*; paratype; female

Plate 43: Fig. 2

An incomplete hindwing in connection with the pterothorax. Three legs are visible, but the rest of the body is missing. The visible wing venation agrees with the hindwing of the holotype. Distance from base to nodus 17.8 mm, thus even slightly larger than in the holotype. The rounded basal hind margin, without anal angle and anal triangle, shows that it is a further female specimen.

Gomphaeschnaoides petersi sp. nov.

Text-Figs 121-122, Plate 44: Figs 1-3

1998 *Gomphaeschnaoides petersi*; BECHLY, p. 62 (nomen nudum).

Holotype: Specimen no. [AP 1997 / 3] (old number B 41), JME, Eichstätt.

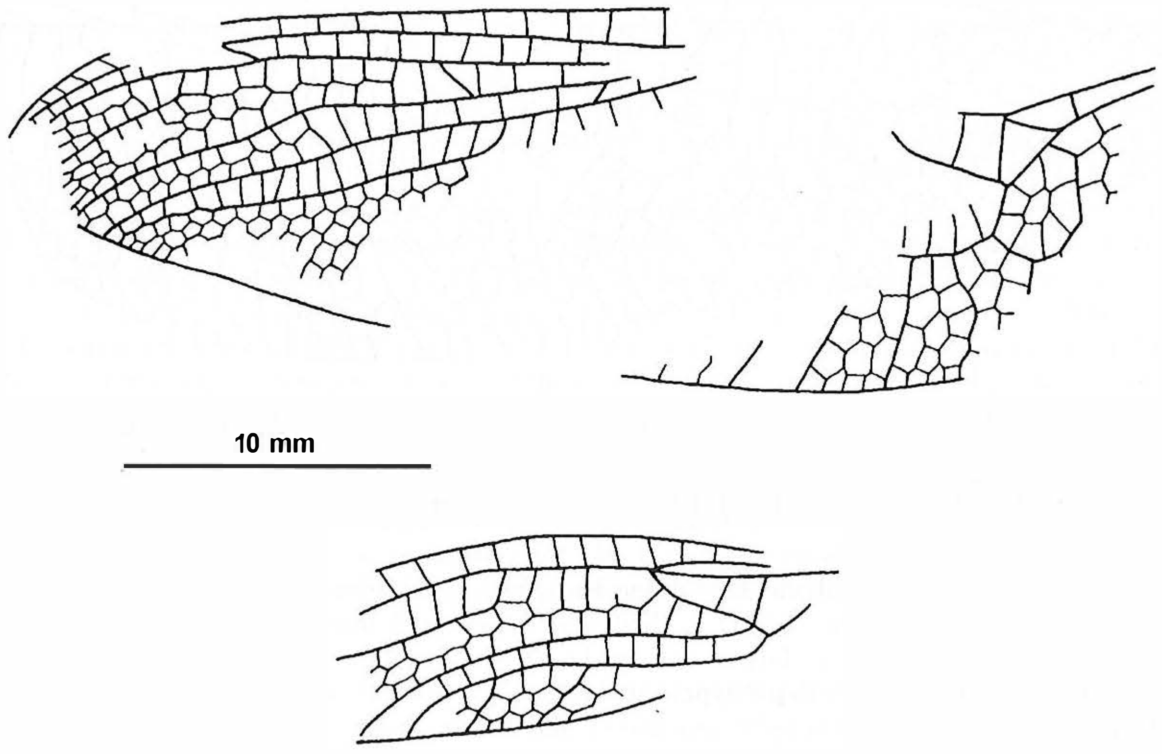
Additional material: Maybe specimen no. [G 9 / G 24], coll. *ms-fossil*, belongs to this species, too, since it has a very similar wing length (hindwing, 38 mm).

Derivatio nominis: Named in honour of Prof. Dr Günther PETERS (Berlin), the pioneer of aeshnid phylogenetic systematics.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

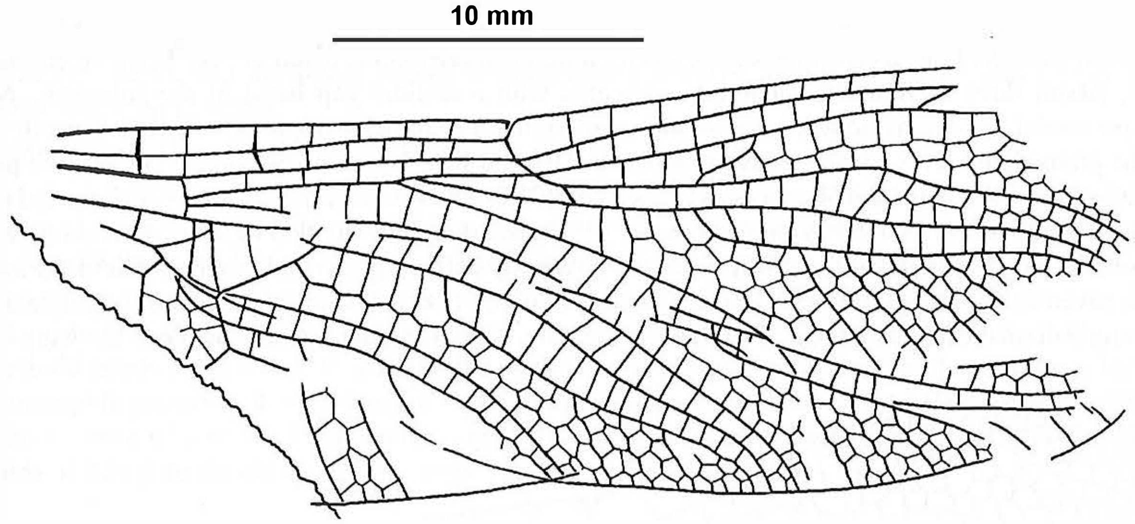
Diagnosis: The wing venation is very similar to *Gomphaeschnaoides obliquus* except for the following differences: Wing length 37.5 mm (thus, intermediate between *G. magnus* sp. nov. and most specimens of *G. obliquus*); there are ten postnodal crossveins between nodus and pterostigma (unique character within the genus); anal loop divided into eight (!) cells in both hindwings (max. length 2.8 mm; max. width 3.8 mm) (autapomorphy); forewing discoidal triangle more similar to *G. obliquus* (length of anterior side 3.7 mm; of basal side 1.6 mm; of distal side MAb 3.9 mm). Although the anal area of both hindwings is largely distorted in the holotype, including the area of the potential anal angle and anal triangle, there seem to have been no posterior branches of AA basal of the anal loop, thus, it must be a male specimen. In the holotype the oblique vein between RP1 and RP2 is aberrant in the right hindwing (more oblique and much longer, strongly undulated with crossveins between it and both branches of RP; see Plate 44: Fig. 3), but it is "normal" in the left hindwing.



Text-Fig. 121. *Gomphaeschnaoides petersi* sp. nov. Holotype JME AP 1997 / 3 - male, left hindwing (above) and left forewing (below).

Description: A complete adult male with all wings present and in connection with the thorax. Although the preservation is fairly good, large parts of the wing venation are obscured, since fore- and hindwings are overlapping. The thorax and two legs are visible, too, but very poorly preserved. There is no trace of coloration, the four wings seem to have been hyaline. The wing venation (Text-Figs 121-122) is more or less identical with that of *G. obliquus* except for the differences mentioned in the diagnosis.

Discussion: The large number of postnodal crossveins and the large number of cells in the anal loop certainly justify the erection of a distinct new species for this specimen, since the only other species of this genus that is similar in these characters (*G. betoreti* sp. nov.) is much smaller and has divided hypertriangles.



Text-Fig. 122. *Gomphaeschnaoides petersi* sp. nov. Holotype JME AP 1997 / 3 - male, right pair of wings (overlapping).

Gomphaeschnaoides betoreti sp. nov.

Text-Fig. 123, Plate 41: Fig. 2

1998 *Gomphaeschnaoides betoreti*; BECHLY, p. 62 (nomen nudum).

Holotype: Specimen no. [11] (old number D 9), BSP, Munich.

Derivatio nominis: Named in honour of the late mother of the odonatologist Dr Carlos BONET BETORET (Valencia, Spain).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, State of Ceará, N.E. Brazil (MAISEY 1990).

Stratum typicum: Crato Formation - Nova Olinda Member (*sensu* MARTILL *et al.* 1993; = Santana Formation - Crato Member auct.), Lower Cretaceous, Upper Aptian.

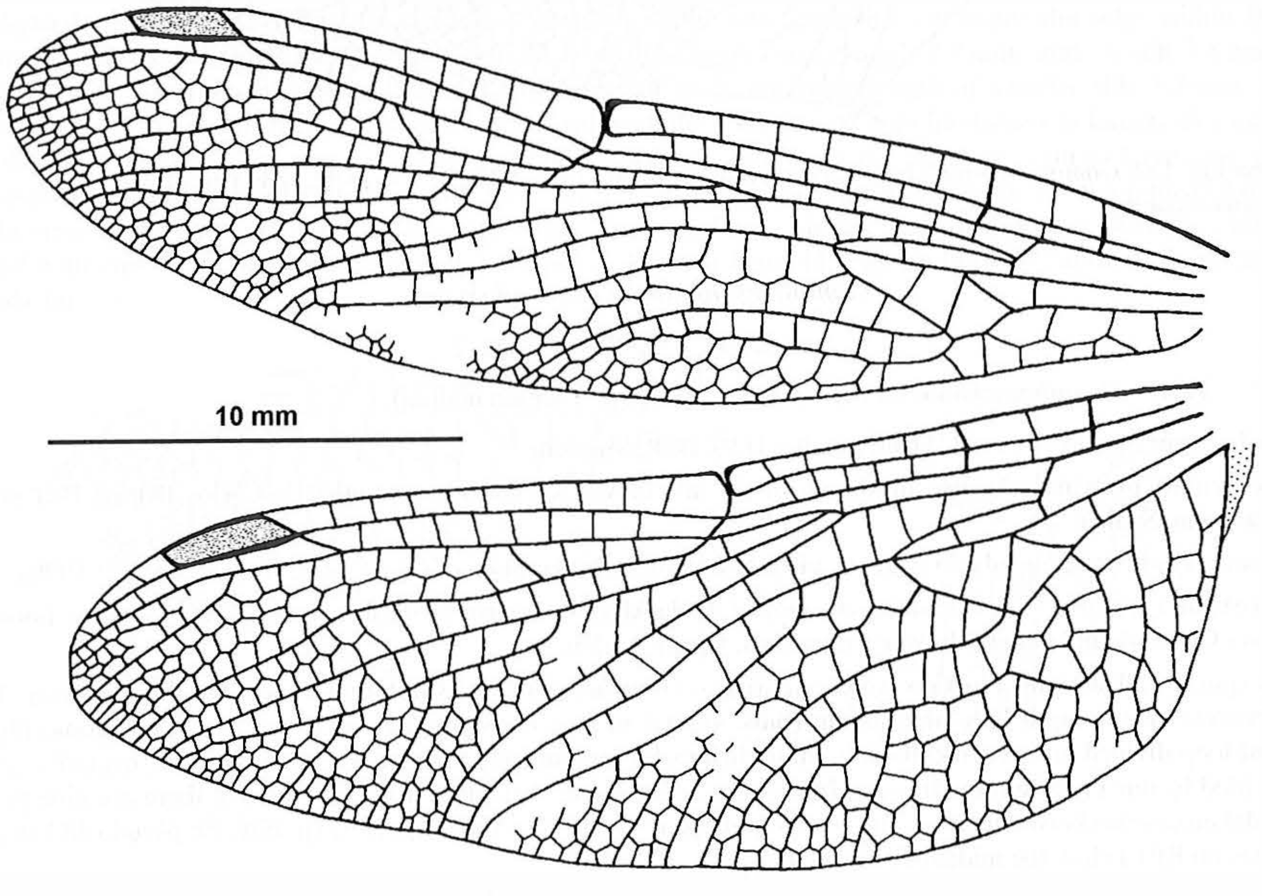
Diagnosis: The wing venation is very similar to *Gomphaeschnaoides obliquus* except for the following differences: Wing length less than 30 mm (thus, similar to *Progomphaeschnaoides* gen. nov.) (autapomorphy); anal loop divided into seven cells in both hindwings (synapomorphy with *G. petersi* sp. nov. ?); hypertriangles divided by one crossvein in all wings (unique autapomorphic character within this genus); there are nine postnodal crossveins between nodus and pterostigma (synapomorphy with *G. petersi* sp. nov. ?); pseudo-IR1 originates on RP1 below the middle of the pterostigma.

Description: A complete and well-preserved adult female with all four wings in connection with the thorax. Only the legs and the apex of the abdomen are missing. The head is well-preserved (length 4.8 mm; width 6.1 mm) and shows large and broadly confluent compound eyes (even the ommatidia of the compound eye are still visible). A longitudinal middorsal carina is faintly visible on the abdomen. There is no trace of coloration, the four wings seem to have been hyaline. Except the above mentioned differences, the wing venation (Text-Fig. 123) is very similar to that of *G. obliquus*, including the presence of the oblique vein between RP1 and RP2 (synapomorphy with *Gomphaeschnaoides*).

Forewings: Length 29.1 mm; width at nodus 6.9 mm; distance from base to nodus 15.0 mm. Only a single hardly aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with basal angle of discoidal triangle. Eight (right wing) or six (left wing) not aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. About six antesubnodal crossveins with a distinct gap basal of the subnodus. Nine (right wing) or eight (left wing) not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the basal half of the pterostigma in the right wing, and beneath its middle in the left wing. The fourth crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma.

Two rows of cells in the distal area between RP2 and IR2. The discoidal triangle is elongated and divided by one crossvein. The hypertriangle is divided by one crossvein as well, at least in the left wing. The subdiscoidal triangle is free.

Hindwings: Length 28.2 mm; width at nodus 9.4 mm; distance from base to nodus 12.0 mm. Only a single imprecisely aligned secondary antenodal crossvein between Ax1 and Ax2. Ax2 is on a level with the middle of the discoidal triangle. Four hardly aligned secondary antenodal crossveins distal of Ax2 between costal margin and ScP. About three or four antesubnodal crossveins with a distinct gap basal of the subnodus. Nine not aligned postnodal crossveins between nodus and pterostigma. Pseudo-IR1 originates on RP1 beneath the middle of the pterostigma. The fourth crossvein between RP1 and RP2 is obliquely slanted towards the pterostigma. Two rows of cells in the distal area between RP2 and IR2. The discoidal triangle is less elongated than that of the forewing, but also divided by one crossvein. The hypertriangle is divided by one crossvein as well. The subdiscoidal triangle is free. CuAa with five relatively weakly defined posterior branches. Anal loop transverse and with seven cells. There are three posterior branches of AA between anal loop and wing base, and there is no anal angle or anal triangle, thus, it is a female specimen. There is a membranule visible at the wing base.



Text-Fig. 123. *Gomphaeschnaoides betoreti* sp. nov. Holotype BSP no. 11 (old number D 9) - female, left pair of wings.

Putative larvae of Gomphaeschnaoidinae subfam. nov.

Plate 48: Figs 2-7

Mesozoic dragonfly larvae that almost certainly belong to Aeshnoptera are known from the Crato Formation of Brazil. They have a typical aeshnid body shape and mask as well as a long anal pyramid. 24 specimens have yet been located by the first author in the collections (e.g. specimens nos [995] and [1016], National Science Museum, Tokyo). This represents 15 % of the 160 known dragonfly larvae from this locality (BECHLY 1998, 1999a, b). Since all adult aeshnids from the same locality and bed belong to the Gomphaeschnidae - Gomphaeschnaoidinae subfam. nov., and constitute a sufficiently similar percentage among the odonate fauna (27 specimens of totally 335 known adult odonates, thus, 8 %), the concerning larvae probably belong to the same taxon.

Subfamily Gomphaeschninae TILLYARD & FRASER, 1940 sensu nov.

(Synonymy see family)

Type genus: *Gomphaeschna* SELYS, 1871 (= *Gomphaeshna* TILLYARD & FRASER, 1940 jun. obj. syn. nov.).

Included groups: Including the type genus *Gomphaeschna* SELYS, 1871, and maybe the extant genus *Oligoaeschna* SELYS, 1889, and the fossil genera *Alloaeschna* WIGHTON & WILSON, 1986 and *Cretalloaeschna* JARZEMBOWSKI & NEL, 1996a.

Autapomorphies: Not yet known.

Discussion: Since no autapomorphies of this taxon are yet known, it could be paraphyletic in its present generic composition. PETERS (pers. comm.) remarked that the position of the nodus 2-4 % distal of the midwing position in the forewings is a derived similarity of extant Gomphaeschninae, but this is most probably due to convergence, since other characters suggest a most basal position of *Oligoaeschna* within Gomphaeschnidae. According to PETERS (pers. comm.) there is no positive evidence for the inclusion of the enigmatic extant aeshnid genus *Linaeschna* MARTIN, 1909 in Gomphaeschnidae or even Gomphaeschninae, because of the plesiomorphic presence of crossveins in the distal part of the antesubnodal area (lack of a "cordulegastrid gap"). The absence of a trigonal supplement could even indicate a more basal position of *Linaeschna* within Euaeshnida, if this state should be a plesiomorphy rather than a reversal.

Genus *Gomphaeschna* SELYS, 1871

(= *Gomphaeshna* TILLYARD & FRASER, 1940 jun. obj. syn. nov.)

1871 *Gomphaeschna*; SELYS, p. 413.
1940 *Gomphaeshna*; TILLYARD & FRASER, p. 380 (unjustified emendation, jun. obj. syn. nov.).

Type species: *Gomphaeschna furcillata* (SAY, 1839), by monotypy.

Discussion: TILLYARD & FRASER (1940) and FRASER (1957) explicitly emended all names that are based on the genus *Aeshna*, only because of their rejection of the emendation of the genus *Aeshna* FABRICIUS, 1775 to *Aeschna* by ILLIGER (1801) and CHARPENTIER (1825: 24), and consequently introduced *Gomphaeshna* SELYS as unjustified emendation of *Gomphaeschna* SELYS, 1871 (TILLYARD & FRASER 1940: 380; FRASER 1957: 97 and 100), so that the former spelling has to be regarded as junior subjective synonym of the latter according to Art. 33.2.3 IRZN, since it is not in prevailing usage.

?*Gomphaeschna inferna* PRITYKINA, 1977

Text-Fig. 124, Plate 45: Figs 1-2

*v 1977 *Gomphaeschna inferna* PRITYKINA, pp. 87-88, text-fig. 5, pl. 2, figs 4-5.
1986 *Gomphaeschna inferna* PRITYKINA, 1980 [sic]; WIGHTON & WILSON, p. 507.
1987 *Gomphaeschna inferna* PRITYKINA, 1980 [sic]; WIGHTON, p. 312.
1994 *Gomphaeschna inferna* PRITYKINA, 1977; NEL *et al.*, p. 177.
1996a *Gomphaeschna inferna* PRITYKINA 1977; LOHMANN, p. 226.

Holotype: Specimen no. [1989 / 1808], PIN, Moscow; a hindwing without base.

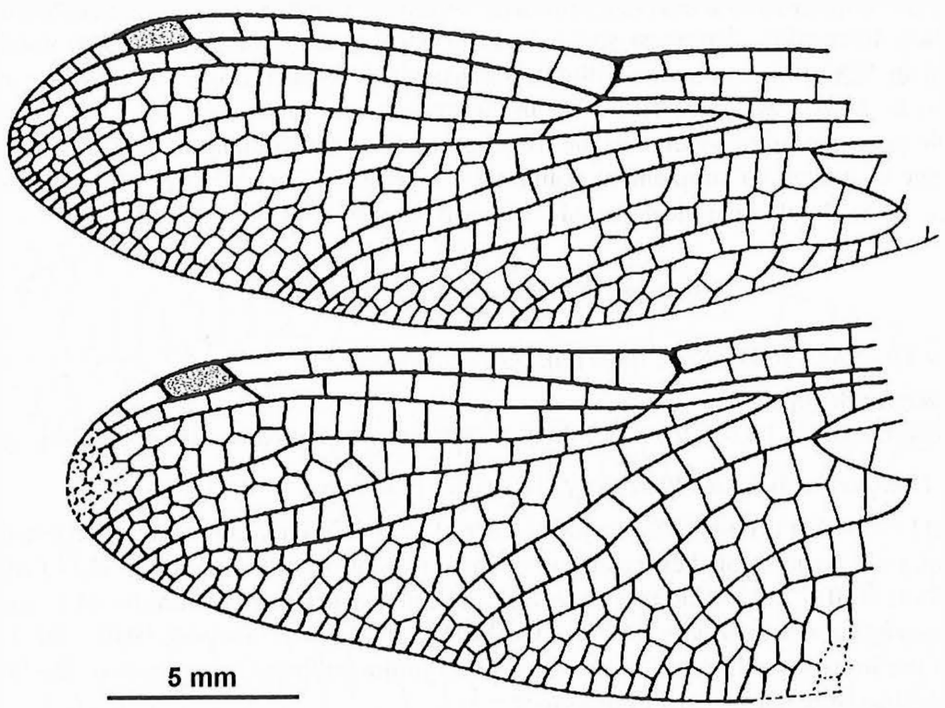
Paratype: Specimen no. [1989 / 1722], PIN, Moscow; a forewing without base, but with well-preserved wing venation.

Locus typicus: Baissa, uppermost course of Vitim River, Transbaikals, Eravninsk region, Buryat Republic (Tyumen'), ex USSR.

Stratum typicum: Zazinsk Series, Lower Cretaceous ("Neocomian").

Systematic position: Because of the very similar wing venation and size, and the origin from the same locality and bed, the attribution of the holotype and paratype to the same species seems to be well justified. This fossil species shows all characters of Gomphaeschnidae (including the lack of distal antesubnodal crossveins as most important synapomorphy). Because of the incomplete state of preservation of its type material, it is impossible to determine if *G. inferna* had or not a hindwing elongated paranal cell, only a single secondary antenodal crossvein between Ax1 and Ax2 in the forewing, a forewing Ax2 basally shifted on a level with basal angle of discoidal triangle and a hindwing CuAa with posterior branches weakly defined. As these characters are the main autapomorphies of the Gomphaeschnaoidinae subfam. nov., the attribution of *G. inferna* to the genus *Gomphaeschna* rather than to the Gomphaeschnaoidinae subfam. nov. cannot be clearly demonstrated.

Nevertheless, it is indeed strikingly similar to the extant species of the genus *Gomphaeschna*. Since this similarity is at least partly based on putative synapomorphies (e.g. the reduced wing venation with fewer rows of cells between the main veins, a short pterostigma with only one or two cells beneath it), the attribution to this genus is quite well supported. Although this fossil species could be considered as the oldest known representative of an extant odonate genus at all, such a statement would be rather meaningless, regarding the artificial nature of the genus category (as rank of the Linnean hierarchy, not as particular monophyletic group of species) and the more or less arbitrary delimitation of genera.



Text-Fig. 124. ?*Gomphaeschna inferna* PRITYKINA, 1977. Paratype PIN 1989 / 1722 (forewing) and holotype PIN 1989 / 1808 (hindwing) - wings (drawing after PRITYKINA 1977: text-fig. 5).

?*Gomphaeschna sibirica* sp. nov.

Text-Figs 125-126, Plate 46: Figs 1-2

Holotype: Specimen no. [4626 / 162], PIN, Moscow.

Paratype: Specimen no. [4626 / 158], PIN, Moscow.

Derivatio nominis: After the region of Siberia.

Locus typicus: Cherovskie Coal mines, near Chita, Chita Region, Siberia, Russia.

Geological age: Lower Cretaceous.

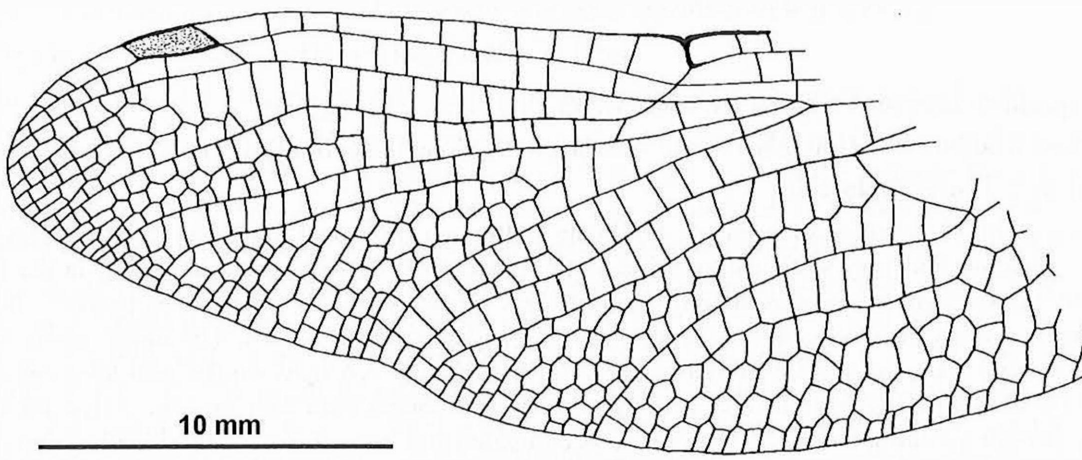
Diagnosis: This species is very similar to *G. inferna*, differing only in the following points: Its hindwing is distinctly longer; its discoidal triangle is free of crossveins; there are two rows of cells in the distal area between RP3/4 and MA; two rows of cells between pseudo-IR1 and RP1; MP reaches the posterior margin distinctly distal of the level of the nodus. ?*Gomphaeschna sibirica* sp. nov. differs from the extant type species *G. furcillata* (SAY, 1839) in its anal loop being not transverse, the free discoidal triangle, and the presence of three rows of cells in the distal part of the area between RP2 and IR2. Thus, its attribution to the genus *Gomphaeschna* can only be preliminary (see discussion below).

Description

♦ Specimen no. PIN 4626 / 162; holotype

Text-Fig. 125, Plate 46: Fig. 1

An isolated hindwing without base. The wing shows no trace of coloration. Length of fragment 31.6 mm (probable total length 34.0 mm); width at nodus 11.7 mm; distance from nodus to pterostigma 13.5 mm. Pterostigma is 2.2 mm long and max. 0.9 mm wide, covering one and a half cells, and strongly braced by an oblique crossvein that is aligned with its basal side. Ten postnodal crossveins between nodus and pterostigma, not aligned with the nine corresponding postsubnodal crossveins visible between RA and RP1. Ax1 and Ax2 are not preserved. The secondary antenodal crossveins between costal margin and ScP are not aligned with the second row of antenodal crossveins between ScP and RA, although these crossveins are not well-preserved. ScP fuses with the costal margin at the nodus which is of the normal Anisoptera-type. Only a single antesubnodal crossvein visible in the area between RA and RP basal of the subnodus with a distinct gap in the distal part of this area. Median space, submedian space, and subdiscoidal triangle not preserved. The discoidal triangle is not completely preserved, but apparently unicellular, rather broad and stout with an angled distal side MAb; length of anterior side 3.6 mm; of basal side 2.1 mm; of distal side MAb 3.6 mm. A secondary sector in the postdiscoidal area originates at the angle of MAb. Hypertriangle only partly preserved, but apparently unicellular. Two antefurcal crossveins preserved between RP and MA. Two bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', a half cell distal of the subnodus. Rspl well-defined, long and nearly straight, parallel to IR2 with only a single row of cells between it and IR2. Several convex secondary longitudinal veins originating on Rspl and reaching the posterior wing margin. IR2 is rather straight. Nine cells distal of the oblique vein 'O', RP2 and IR2 begin to diverge with two to three rows of cells in the widened area in-between. RP2 is slightly undulated. RP2 and RP1 are basally closely parallel with only a single row of cells in-between up to the pterostigma, but one cell basal of the pterostigma, they become divergent with two or more rows of cells in-between. Pseudo-IR1 is rather short, but distinct, originating on RP1 slightly distal of the pterostigma. One to two rows of cells between pseudo-IR1 and RP1, and three to five rows of cells between it and RP2. RP3/4 and MA are parallel and gently undulated (MA more strongly undulated than RP3/4); two rows of cells between the distal parts of RP3/4 and MA. Mspl long and parallel to MA with a single row of cells between it and MA. At least one convex secondary longitudinal vein originating on Mspl and reaching the posterior wing margin. Postdiscoidal area distally widened (width near discoidal triangle 2.7 mm; width at posterior wing margin 5.6 mm) with two rows of cells in the postdiscoidal area immediately distal of the discoidal triangle. CuAa with six poorly defined and zigzagged posterior branches; CuAa reaches the posterior wing margin slightly distal of the level of nodus. The cubito-anal area is max. 3.8 mm wide with up to four rows of cells between CuA and the posterior wing margin. Area between MP and CuA basally distinctly widened, but with only a single row of cells up to the wing margin. Anal area broad with about five rows of cells between AA and the posterior wing margin. The five-celled anal loop is nearly as long as wide, and posteriorly well-closed. The distal paranal cell is not preserved. The anal area basal of the anal loop and the anal margin are not preserved, thus, it is not possible to recognize if it is a male or a female specimen.

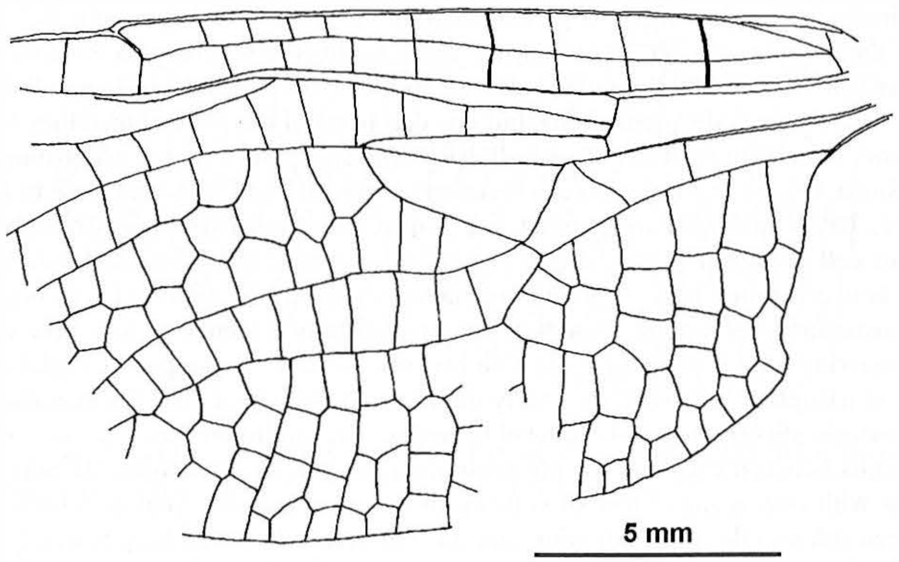


Text-Fig. 125. ?*Gomphaeschna sibirica* sp. nov. Holotype PIN 4626 / 162 - left hindwing.

♦ Specimen no. PIN 4626 / 158; paratype

Text-Fig. 126, Plate 46: Fig. 2

Only the basal half of a female hindwing is preserved (part and counterpart) with no trace of coloration. Length of fragment 17.8 mm (probable total length of wing 35.4 mm); width at nodus 10.2 mm; distance from base to arculus 5.1 mm; distance from base to nodus 15.2 mm. Ax1 is 1.8 mm basal of the arculus, and Ax2 is 4.3 mm distal of Ax1 (on a level with the median part of the discoidal triangle); two aligned secondary antenodal cross-veins in both rows between Ax1 and Ax2; distal of Ax2 there are five secondary antenodal crossveins in the first row, and four of them in the second row, not aligned with each other. Hypertriangle free (length 5.0 mm; max. width 0.6 mm). Discoidal triangle longitudinally elongated and apparently unicellular; length of anterior side 4.0 mm; of basal side 1.8 mm; of distal side MAb 3.8 mm; the distal side MAb is distinctly bent. Two rows of cells in the basal part of the postdiscoidal area with a strong secondary longitudinal vein originating at the angle of MAb. Mspl is parallel to MA with a single row of cells between it an MA. Median space free of crossveins. Submedian space only traversed by CuP-crossing, 1.5 mm basal of arculus. PsA is well-defined, slightly undulated, and delimits a well-defined unicellular subdiscoidal triangle. CuAa with about six posterior branches, the most distal and most basal ones weakly defined and zigzagged. The cubito-anal area is max. 3.4 mm wide with up to four rows of cells. The anal area is max. 5.5 mm wide with up to five rows of cells between AA and the posterior wing margin. The anal loop is as nearly as long as wide (max. length 2.4 mm; max. width 2.6 mm), posteriorly well-closed, and divided into five cells. The distal paranal cell is not transverse. There is no anal triangle, thus, it is a female specimen.



Text-Fig. 126. *?Gomphaeschna sibirica* sp. nov. Paratype PIN 4626 / 158 - female, left hindwing, basal half.

?Gomphaeschna aff. *sibirica* sp. nov.

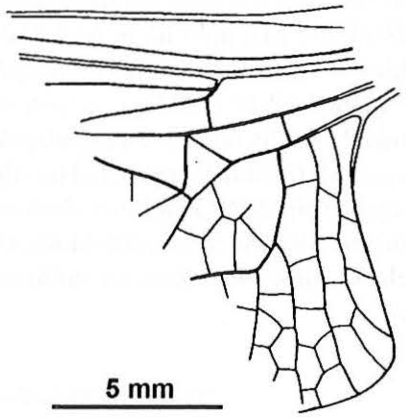
Text-Fig. 127

Material: Specimen no. [3664 / 436], PIN, Moscow, could belong to this species.

Locality: Shin-Khuduk, Mid Gobi aimak, Site 119, layer 39, Mongolia (ZHERIKHIN pers. comm.).

Geological age: Lower Cretaceous.

Description: A basal fragment of a female hindwing. Although this basal hindwing fragment has a rather similar wing venation and very similar dimension as the corresponding part of the hindwing in the holotype and especially the paratype specimens, its attribution to this species has to be regarded as tentative due to the incomplete preservation. It is possible that it represents a new genus and species. The most important difference to the paratype is the presence of only two posterior branches of AA between the anal loop and the wing base. There are six rows of cells in the anal area, the anal loop is longer than wide and six-celled, the hypertriangle is free (length 4.2 mm), the discoidal triangle is elongated and free of crossveins (length of anterior side 3.5 mm; of basal side 1.7 mm; of its angled distal side MAb 3.7 mm), and the subdiscoidal triangle is short (length 1.5 mm) and free as well. The anal margin is rounded and there is no anal triangle, thus, it is a female specimen.



Text-Fig. 127. *?Gomphaeschna* aff. *sibirica* sp. nov. PIN 3664 / 436 - female, left hindwing base.

Discussion: The comparable parts of these three hindwings have a very similar wing venation, and the estimated total size of both wings is very similar, too, thus, we attribute them to the same new species. This species has the wing venational autapomorphies of the Gomphaeschnidae: Distal part of the area between RA and RP (immediately basal of subnodus) free of antesubnodal crossveins; submedian space, between CuP-crossing and PsA, free of crossveins; hypertriangles and discoidal triangles free of crossveins.

Except for the weakly defined posterior branches of CuAa, this new species does not share any of the autapomorphies of Gomphaeschnaoidinae subfam. nov. or Gomphaeschnaoidini trib. nov. that could be visible in the hindwing: No elongated distal paranal cell, immediately basal of the anal loop; pterostigmal brace vein neither very oblique, nor undulated; the cell below the pterostigma is not basally widened, since there is no curvature of RP1 at the pterostigmal brace; the posterior branches of CuAa are weakly defined.

?G. sibirica shares with the recent genus *Gomphaeschna* the same structures as *G. inferna*: A reduced wing venation with fewer rows of cells between the main veins, and a short pterostigma with only one or two cells beneath it. Therefore, we preliminarily attribute this new species to the genus *Gomphaeschna*. The discovery of better preserved material, with the forewing structures, is necessary for the confirmation of this hypothesis.

?Gomphaeschnidae incertae sedis

Genus *Cretalloaeschna* JARZEMBOWSKI & NEL, 1996a

Type species: *Cretalloaeschna cliffordae* JARZEMBOWSKI & NEL, 1996a, by original designation.

Cretalloaeschna cliffordae JARZEMBOWSKI & NEL, 1996a

Text-Fig. 128

*v 1996a *Cretalloaeschna cliffordae* JARZEMBOWSKI & NEL, pp. 97-101, figs 1-2.

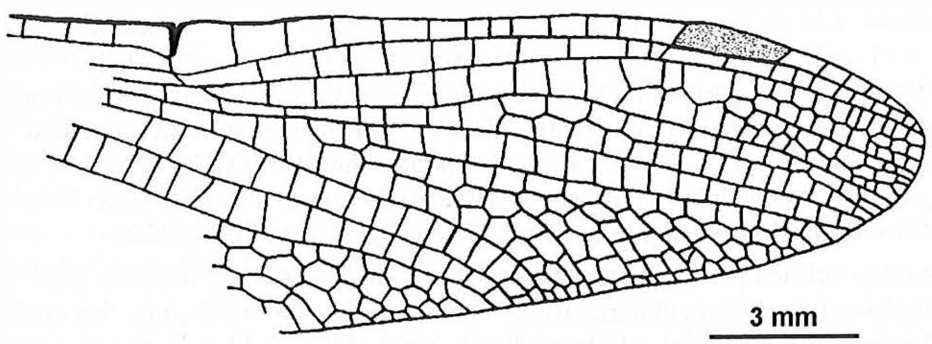
Holotype: Specimen no. [1995. 171 a, b], MNEMG, Maidstone, collector R. CORAM.

Locus typicus: Durlston Bay, Dorset, England.

Stratum typicum: Middle Purbeck beds, Clements' Bed 175, Lower Cretaceous, Berriasian.

Discussion: The total size of the wing was estimated by JARZEMBOWSKI & NEL (1996a: 98) as «about 25 mm». This value is clearly incorrect since the wing is a forewing, and the distance from nodus to apex is 15.8 mm (length of complete fragment 19.6 mm). Since the nodus is at 48-52 % (average 50 %) of the forewing length in all related genera, the total forewing length of *Cretalloaeschna* must be 31.6 mm (± 2 %).

Systematic position: *Cretalloaeschna* shares with other Gomphaeschnidae only symplesiomorphic characters, like an unforked IR2, only a single row of cells between Rspl and IR2 and between Mspl and MA, no aeshnid bulla on MA, and consequently no oblique vein between MA and RP3/4. Its position in Aeshnoptera is demonstrated by the basally parallel course of RP1 and RP2, its position in Aeshnomorpha taxon nov. by the curvature of RP2 and the presence of a Rspl, its position in Aeshnida by the presence of a more distinct Rspl and a Mspl, its position in Euaeshnida by its very distinct and straight (not zigzagged) Mspl and by its secondary parallel course of RP3/4 and MA that are distally not diverging, and its position in Neoaeshnida by the absence of the second oblique vein and the basal position of the single oblique vein close to the subnodus, as well as the not undulated RP3/4 and MA. The presence of only a single row of cells between the distal parts of RP3/4 and MA and the presence of only two rows of cells between RP2 and IR2 could represent synapomorphies with *Gomphaeschna*, *Gomphaeschnaoides*, and *Alloaeschna*, but on the other hand some specimens described as *Alloaeschna* seem to lack the gap of antesubnodal crossveins (WIGHTON & WILSON 1986: fig. 8 and 12) that is an important autapomorphy of Gomphaeschnidae (unfortunately the concerning area is not preserved in *Cretalloaeschna*). The slightly oblique fourth crossvein between RP1 and RP2 could indicate a close relationship with *Gomphaeschnaoides*, but the closely parallel course of RP1 and RP2 basal of the pterostigma, and the short pterostigmal brace vein that is not very oblique and not undulated, strongly contradict such a relationship. Therefore, *Cretalloaeschna* has to be preliminarily regarded as an ?Gomphaeschnidae *incertae sedis*.



Text-Fig. 128. *Cretalloaeschna cliffordae* JARZEMBOWSKI & NEL, 1996a. Holotype MNEMG: 1995. 171 a, b - right forewing, distal half (drawing after JARZEMBOWSKI & NEL 1996a: fig. 2).

Aeshnodea BECHLY, 1996

1996a Aeshnata; LOHMANN, pp. 226-227 (nec Aeshnata BECHLY, 1996).

Included groups: Allopetaliidae stat. et sensu nov. (see below) and Euaeshnodea taxon nov. which includes Brachytronidae (*sensu* BECHLY 1996) and Aeshnoidea (*sensu* BECHLY 1996). The latter are composed of the Telephlebiidae COCKERELL, 1913 (stat. nov.) (= Caliaeschnidae BECHLY, 1996 jun. subj. syn. nov.) and the Aeshnidae (*sensu* BECHLY 1996). According to the new system of extant Aeshnoptera by BECHLY (1999a, b) the Telephlebiidae stat. nov. include the subfamilies Austroaeschninae and Telephlebiinae stat. nov. (= Caliaeschninae BECHLY, 1996 jun. subj. syn. nov.), while the Aeshnidae include the subfamilies Epiaeschninae, Oplonaeschninae, Gynacanthinae and Aeshninae (including the tribes Polycanthagynini, Aeshnini, and Anactini). For a detailed phylogenetic system of extant Aeshnodea see BECHLY (1996, 1999a, b), but also see comment below.

Wing venational autapomorphies: Undulation of RP2 modified to a characteristical curvature beneath the pterostigma; undulation of RP3/4 and MA completely absent (reversal); discoidal triangles more strongly longitudinal elongated, at least in the forewings (a very homoplastic and dubious character which is also present in some Gomphaeschnidae and even in some Cymatophlebiidae); IR2 with a distal dichotomic furcation (secondarily rather indistinctly developed as secondary branch in *Aeshna juncea*, *A. caerulea*, and *Oreaeschna*, while completely suppressed in *Oplonaeschna* and most species of *Boyeria*, except *B. vinosa* and *B. grafiana*; in *Anax* the IR2-fork is present, but much shorter, narrower and shifted distally; maybe plesiomorphic absent in some basal genera like *Baissaeshna*, *Allopetalia* and *Basiaeschna*); PsA reduced to an oblique cubito-anal crossvein (reversal); anal loop enlarged (but still relatively small in *Allopetalia* and *Basiaeschna*), generally more than five-celled.

Other autapomorphies: Adult postclypeus more or less transversely enlarged; imaginal labium without median cleft (LOHMANN 1996a; a dubious groundplan character, since a fissum is retained in some basal aeshnids like *Nasiaeschna* SELYS, 1900 and *Austroaeschna* SELYS, 1883 as indicated by this author in the same publication); epiproct of adult males apically only slightly bifid or even not at all bifid (a bifid epiproct is here regarded as plesiomorphic, *contra* LOHMANN 1996a).

Comment: According to PETERS (pers. comm.) there is strong morphological evidence (male hamuli, wing venation, etc.) for the following modifications of the phylogenetic system of extant aeshnids proposed here and by Bechly (1999a, b): *Linaeschna* MARTIN, 1908 could be more basal than Gomphaeschnidae (see above); *Basiaeschna* SELYS, 1883 is not related to *Allopetalia* SELYS, 1873, but to *Oplonaeschna* SELYS, 1883 within Aeshnidae (curved Rspl and Mspl, bulge in MA, accessory cubito-anal crossveins, shape of anal triangle and membranule, trigonal supplement fusing with Mspl, IR2-fork reduced, structure of the male hamuli); *Epiaeschna* HAGEN, 1875 does not belong to Aeshnidae, but *Epiaeschna* and *Nasiaeschna* SELYS, 1900 are sistergroups and belong to Brachytronidae (males without constriction of the basal abdomen, keel on abdominal tergites VIII and IX, basally prolonged pterostigma except in *Nasiaeschna*); Gynacanthinae could be paraphyletic (e.g. suggested by the different state of the "aeshnid bulla" and the "RP3/4-MA-brace") and appears to be more basal than the other Aeshnidae (Oplonaeschninae + Aeshninae); *Anaciaeschna* SELYS, 1878 may not be the sistergenus of *Anax* LEACH, 1815.

Family Allopetaliidae COCKERELL, 1913 stat. et sensu nov.

1913 Allopetaliini; COCKERELL, p. 582.

Type genus: *Allopetalia* SELYS, 1873.

Included groups: The extant genera *Allopetalia* SELYS, 1873 and *Basiaeschna* SELYS, 1883 (but see comment below), and preliminarily the fossil genus *Baissaeshna* PRITYKINA, 1977.

Wing venational autapomorphies: Two rows of cells between Rspl and IR2, and between Mspl and MA; two rows of cells between RP1 and RP2 basal of the pterostigma (reversal; but not present in *Basiaeschna*).

Comment: According to PETERS (pers. comm.) there is strong morphological evidence that *Basiaeschna* is the sistergenus to *Oplonaeschna* within Aeshnidae - Oplonaeschninae (see above).

Genus *Baissaeshna* PRITYKINA, 1977

Type species: *Baissaeshna prisca* PRITYKINA, 1977, by original designation.

Systematic position: PRITYKINA (1977) regarded the extant genera *Oligoaeschna* and *Oplonaeschna* as closest relatives of *Baissaeshna*. This hypothesis is based on symplesiomorphic and convergent similarities, and rather improbable, since *Baissaeshna* does not seem to belong to Gomphaeschnidae (like *Oligoaeschna*) and certainly not to Aeshnidae (like *Oplonaeschna*, as demonstrated by BECHLY 1996, 1999a, b), but most likely belongs to a basal grade within Aeshnodea, as is indicated by the apomorphic presence of a seven-celled anal loop and an accessory anal loop, the plesiomorphic presence of several crossveins that divide the discoidal triangle and hypertriangle, and the plesiomorphic absence of the oblique RP3/4-MA brace, as well as the plesiomorphic absence of the other autapomorphies of either Aeshnidae, or Telephlebiidae stat. nov. Among extant aeshnids, *Baissaeshna* is most similar and probably most closely related to *Basiaeschna* and *Allopetalia*, because of some putative synapomorphies (two rows of cells between RP1 and RP2 basal of the pterostigma, two rows of cells between Rspl and IR2 and between Mspl and MA) and numerous symplesiomorphies (e.g. Rspl and Mspl not curved, but parallel to IR2 and MA). The unforked IR2 is a potential symplesiomorphy, too, although it cannot be totally excluded that this could be a reversal (as is probably the case in *Boyeria*, and almost certainly in *Oplonaeschna*). As demonstrated by the present phylogenetic analysis, the previous hypothesis of WIGHTON & WILSON (1986) that *Baissaeshna* and *Gobiaeshna* shall be sister-genera or even synonyms, cannot be upheld, since both species belong to different, only remotely related, monophyla within Aeshnoptera. The most parsimonious interpretation is a close relationship of *Baissaeshna* with *Allopetalia* and *Basiaeschna* in a separate basal family Allopetaliidae stat. et sensu nov. within Aeshnodea. A few characters of the latter family (e.g. the unforked IR2, and the smaller anal loop, except in *Baissaeshna prisca*) seem to be more plesiomorphic than in all remaining Aeshnodea that probably form the monophyletic sistergroup of Allopetaliidae stat. et sensu nov., which is here named **Euaeshnodea** taxon nov.

Baissaeshna prisca PRITYKINA, 1977

Text-Fig. 129, Plate 47: Fig. 1

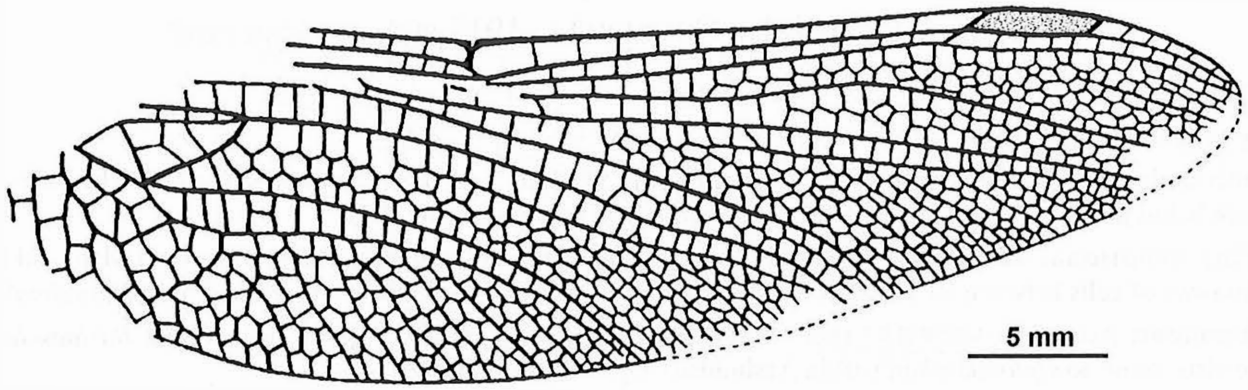
*v 1977 *Baissaeshna prisca* PRITYKINA, pp. 85-86, text-fig. 3, pl. 1, fig. 3.
1986 *Baissaeshna prisca* PRITYKINA, 1980 [sic]; WIGHTON & WILSON, p. 507.
1994 *Baissaeshna prisca* PRITYKINA, 1977; NEL *et al.*, p. 176.

Holotype: Specimen no. [1989 / 1495], PIN, Moscow; a hindwing without base.

Locus typicus: Baissa, course of Bais at upper stream of Vitim River, Eravninsk region, Transbaikals, Buryat Republic, ex USSR.

Stratum typicum: Zazinsk Series, Lower Cretaceous ("Neocomian").

New diagnosis: The hindwing of *B. prisca* differs only slightly from that of *B. zherikhini* sp. nov. in the narrower cubito-anal area, the presence of only a single row of cells between Rspl and IR2 and between Mspl and MA, and in the less numerous postnodal crossveins. The distance from nodus to apex in the hindwing is 27.8 mm, compared to 33.4 mm in the hindwing of *B. zherikhini* sp. nov. Therefore, the total hindwing length of *B. prisca* can be estimated as 47-48 mm.



Text-Fig. 129. *Baissaeshna prisca* PRITYKINA, 1977. Holotype PIN 1989 / 1495 - right hindwing (drawing after PRITYKINA 1977: text-fig. 3).

Baissaeshna zherikhini sp. nov.

Text-Fig. 130, Plate 47: Fig. 2

Holotype: Specimen no. [3064 / 3146], PIN, Moscow.

Derivatio nominis: Named in honour of Dr Vladimir ZHERIKHIN (Moscow), director of the Palaeoentomological Institute (PIN) of the Academy of Science of Russia.

Locus typicus: Zaza, left side of Vitim River downstream / Baissa River mouth, Eravninsk region, Transbaikals, Buryat Republic, ex USSR.

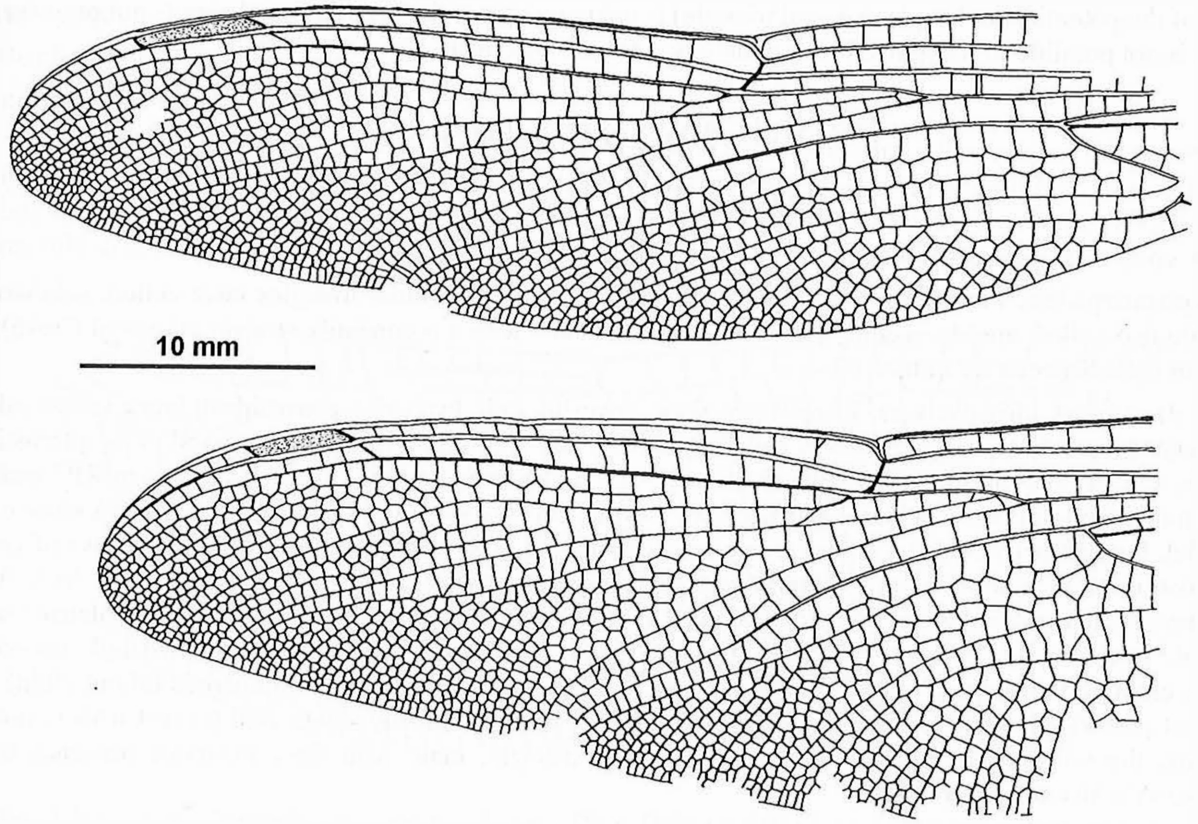
Stratum typicum: Zazinsk Series, Lower Cretaceous ("Neocomian").

Diagnosis: The hindwing of this new species is very similar to that of the type species *B. prisca*, and only differs in the following characters: Cubito-anal area with eight rows of cells (instead of only six rows); up to two rows of cells between Rspl and IR2, and between Mspl and MA (instead of only a single row); fifteen postnodal crossveins (instead of only eleven postnodal crossveins). The hindwing of this new species is also distinctly larger than that of the type species.

Description: Fore- and hindwing without bases, but with well-preserved wing venation. The wings are hyaline without any trace of coloration.

Forewing: Length of fragment 50.5 mm (total length probably 59 mm); width at nodus 12.8 mm; distance from base to nodus unknown; from nodus to pterostigma 21.1 mm. Pterostigma 5.2 mm long and max. 1.0 mm wide, strongly braced by an oblique crossvein aligned with its basal side, and covering five cells. Fourteen postnodal crossveins between nodus and pterostigma, not aligned with the fifteen corresponding postsubnodal crossveins. Ten secondary antenodal crossveins visible between costal margin and ScP, not aligned with the second row of antenodal crossveins between ScP and RA. Ax1 and Ax2 are not preserved. There is no gap of antesubnodal crossveins in the space between the arculus and the subnodus immediately basal of the latter. Four bridge-crossveins Bqs basal of subnodus. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', two cells (2.0 mm) distal of the subnodus. Rspl is well-defined, parallel to IR2 with only one or two rows of cells between these two veins. RP2 and IR2 become strongly divergent distinctly basal of the level of pterostigma with up to four rows of cells in-between. RP2 is somewhat curved, while IR2 is more or less straight.

Pseudo-IR1 strongly defined and originating on RP1 beneath the middle of the pterostigma with three or four rows of cells between it and RP1, and four or more rows of cells between it and RP2. RP1 and RP2 are basally gently divergent with one to two rows of cells in-between basal of pterostigma, but distinctly basal of the pterostigmal brace they become strongly divergent with three or more rows of cells in-between. RP3/4 and MA are more or less parallel and gently undulated with a single row of cells between their basal and distal parts, but with two rows of cells between their median parts. Mspl is well-defined, parallel to MA with two rows of cells between these two veins. The postdiscoidal area is distinctly widened distally (width near discoidal triangle 3.1 mm; width at posterior wing margin 7.9 mm) with three rows of cells immediately distal of the discoidal triangle. An indistinct convex secondary longitudinal vein (trigonal planate) is originating at the angled distal side MAb of the discoidal triangle. Hypertriangle not completely preserved, but apparently free of crossveins (?). The discoidal triangle is divided into six cells, and is apparently somewhat narrower than that of the hindwing; length of anterior side (not completely preserved), probably 5.6 mm; length of basal side (not preserved), probably 2.4 mm; length of distal side MAb 5.6 mm. Median space, submedian space, and subdiscoidal triangle not preserved. A single row of cells in the area between MP and CuA (except near the posterior wing margin). MP and CuA reach the posterior wing margin distinctly distal of the level of nodus. CuA with about nine zigzagged posterior branches. Cubito-anal area max. 4.1 mm wide with up to seven rows of cells between CuAa and the posterior wing margin. Anal area not preserved.



Text-Fig. 130. *Baissaeshna zherikhini* sp. nov. Holotype PIN 3064 / 3146 - left pair of wings.

Hindwing: Length of fragment 45.1 mm (probable total length 57 mm); width at nodus 16.1 mm; distance from base to nodus unknown; from nodus to pterostigma 22.5 mm. Pterostigma 4.2 mm long and max. 1.1 mm wide, strongly braced by a very oblique crossvein aligned with its basal side, and covering nearly four cells. Fifteen postnodal crossveins between nodus and pterostigma, not aligned with the fifteen corresponding postsubnodal crossveins. Seven secondary antenodal crossveins visible between costal margin and ScP, the second row of antenodal crossveins between ScP and RA is not preserved. The two primary antenodal crossveins are not preserved. There are seven visible antesubnodal crossveins without distal gap in the space between the arculus and the subnodus. Six bridge-crossveins Bqs. Base of RP2 aligned with subnodus. Only a single oblique vein 'O', one cell (1.6 mm) distal of subnodus. Rspl well-defined, parallel to IR2 with one or two rows of cells between these two veins. RP2 and IR2 become strongly divergent distinctly basal of the level of pterostigma with up to four rows of cells in-between. RP1 and RP2 are basally parallel with one to two rows of cells in-between basal of pterostigma, but become strongly divergent near the pterostigmal brace with three or more rows of cells in-between. Pseudo-IR1 well-defined and originating on RP1 beneath the distal part of the pterostigma with three rows of cells between pseudo-IR1 and RP1, and with four or more rows of cells between pseudo-IR1 and RP2. RP3/4 and MA are more or less parallel and gently undulated with a single row of cells between their basal parts, but with two rows of cells between their distal parts. Mspl is well-defined, parallel to MA with up to two rows of cells between these two veins. The postdiscoidal area is distally widened (width near discoidal triangle 3.8 mm; width at posterior wing margin 9.7 mm) with three or four rows of cells immediately distal of the discoidal triangle. A short but distinct convex secondary longitudinal vein (trigonal planate) is originating at the angled distal side MAb of the discoidal triangle. The hypertriangle is incompletely preserved, but there is one crossvein visible in the distal part of the hypertriangle. The discoidal triangle appears to be broader than that of the forewing, and a crossvein is visible in its preserved distal part (its basal part is not preserved), thus, it was at least two-celled (more probably four-celled as in *B. prisca*); length of anterior side, basal side, and distal side MAb unknown, since these veins are very incompletely preserved. Median space, submedian space, and subdiscoidal triangle not preserved. A single row of cells in the area between MP and CuAa, except in the distal part (four rows near posterior wing margin). CuAa reaches the posterior wing margin slightly distal of the nodus; six more or less zigzagged posterior branches of CuAa are preserved (total number probably about seven); CuAb is not preserved. Cubito-anal area max. 7.0 mm wide with up to nine rows of cells between CuAa and posterior wing margin. The structure of the anal loop and the anal margin (area of the potential anal angle and anal triangle) is unknown, since the complete anal area is not preserved, so that it is not possible to recognize if it is a male or a female specimen.

Mesozoic Aeshnoptera incertae sedis

Genus *Cymatophlebiella* PRITYKINA, 1968 pos. nov.

Type species: *Cymatophlebiella euryptera* PRITYKINA, 1968, by original designation.

Autapomorphies: Pterostigma very short and weakly braced; discoidal triangles three-celled; subdiscoidal triangle two-celled; anal loop completely reduced (correlated with a secondarily straight course of CuAb); two rows of cells between RP1 and RP2.

New diagnosis (hindwing): Pterostigma short, covering only two cells; pterostigmal brace vein weak and not very oblique; RP1 and RP2 basally parallel, but with two rows of cells in-between basal of the pterostigma; pseudo-IR1 originating on RP1 distinctly distal of pterostigma; two oblique veins 'O' between RP2 and IR2; Rspl rather well-defined, but short, and with two rows of cells between it and IR2; RP3/4 and MA more or less parallel, but distinctly undulated, and with two rows of cells between their distal parts; three rows of cells in the postdiscoidal area; no distinct Mspl; three secondary antenodal crossveins between Ax1 and Ax2; Ax2 is on a level with the distal angle of the discoidal triangle; MAb is straight and there is no trigonal planate; hypertriangle free; discoidal triangle elongated, but rather stout, and three-celled; subdiscoidal triangle two-celled; no accessory cubito-anal crossvein between CuP-crossing and PsA; CuAa with numerous (about eight) well-defined posterior branches; gaff slightly elongated; anal loop completely suppressed (even CuAb is not bent towards the wing base); male with three-celled anal triangle; male with three posterior branches of AA between CuAb and anal triangle.

Systematic position: *Cymatophlebiella* shares with Aeshnoptera the following synapomorphies: RP1 and RP2 basally parallel; Rspl is present; RP3/4 and MA undulated. This genus does not share any significant synapomorphies with Aeshnomorpha taxon nov., and several plesiomorphic characters even indicate a position outside Aeshnomorpha taxon nov.: RP2 not undulated; hypertriangle free of crossveins; anal loop not enlarged (even completely suppressed); Rspl short and not very distinct.

The genus *Cymatophlebiella* has been attributed to Cymatophlebiinae HANDLIRSCH, 1906 by all previous authors until recently (CARPENTER 1992: 83). However, most of the similarities with *Cymatophlebia* are symplesiomorphies (e.g. two oblique veins 'O', no distinct Mspl, etc.), except for three derived characters (anal loop reduced, subdiscoidal triangle divided, and basally two rows of cells between RP1 and RP2) which belong to the most homoplastic wing venational characters known at all, and therefore do not represent compelling evidence for a close relationship. Furthermore, *Cymatophlebiella* does not show any significant synapomorphies with Panaeshnida taxon nov., Aeshnida, Cymatophlebioidea stat. nov., or Cymatophlebiidae. Thus, there is no justification for an attribution of *Cymatophlebiella* to the Cymatophlebiidae.

Cymatophlebiella has been regarded as an Anisoptera of undetermined family by NEL *et al.* (1998), although they considered that it could represent the most basal taxon within Aeshnoptera. The total evidence suggests an unresolved polytomy of *Cymatophlebiella*, Mesuropetaloidea stat. nov., and Panaeshnida taxon nov. within Aeshnoptera. The discoidal triangle that is divided into more than two cells is a derived similarity with Panaeshnida taxon nov., but this character is so homoplastic that it cannot be regarded as sufficient evidence for a closer relationship. Consequently, we preliminarily regard *Cymatophlebiella* as a basal Aeshnoptera *incertae sedis* that could eventually be closer related to Panaeshnida taxon nov.

Cymatophlebiella euryptera PRITYKINA, 1968

Text-Figs 131-133, Plate 48: Fig. 1

*v 1968 *Cymatophlebiella euryptera*, PRITYKINA, pp. 51-52, text-fig. 22, pl. 5, fig. 3.
1992 *Cymatophlebiella euryptera*, CARPENTER, p. 83.
1998 *Cymatophlebiella euryptera*, NEL *et al.*, pp. 5, 65 (considered as Anisoptera *incertae sedis*).

Holotype: Specimen no. [2554 / 211], PIN, Moscow; an isolated male hindwing with the apex missing.

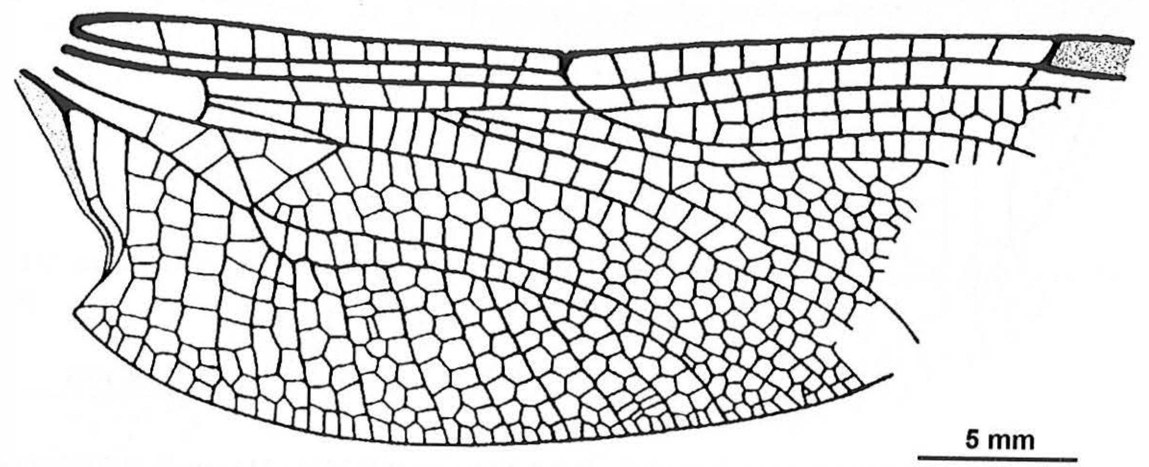
Paratype: Specimen no. [2066 / 28], PIN, Moscow; an isolated hindwing with the base and median part partly destroyed.

Locus typicus: Karatau, Kazakhstan, ex USSR.

Geological age: Upper Jurassic.

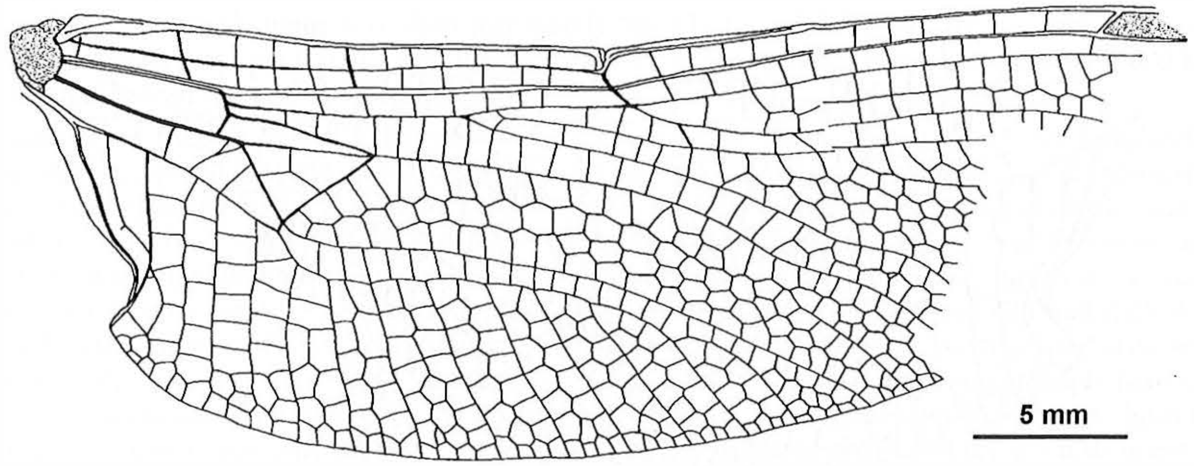
Diagnosis: Same as for the genus.

Redescription: The original description and figure of PRITYKINA (1968) are rather poor. Furthermore, the paratype specimen has never been described or figured. Nevertheless, it adds important information. The two specimens that PRITYKINA attributed to *Cymatophlebiella euryptera* are certainly conspecific because their comparable structures are identical. The following redescription is based on both known specimens.

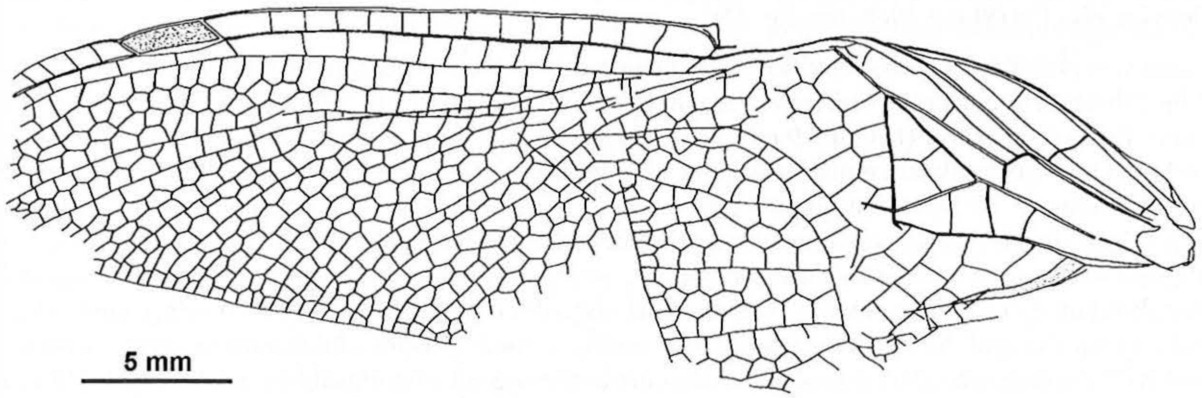


Text-Fig. 131. *Cymatophlebiella euryptera* PRITYKINA, 1968. Holotype PIN 2554 / 211 - male, right hindwing (drawing after PRITYKINA 1968: text-fig. 22).

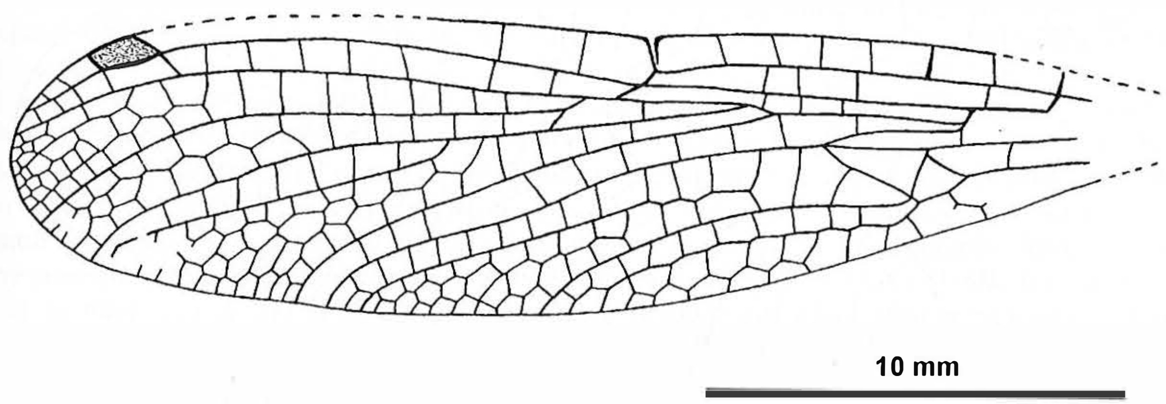
The wing was probably hyaline, since no trace of coloration visible. Hindwing length 42.3 mm; width at nodus 13.1 mm; distance from base to arculus 5.3 mm; from base to nodus 17.8 mm; from nodus to pterostigma 16.3 mm. Pterostigma short (length 2.9 mm; max. width 1.0 mm), and only covering one and a half cells. The pterostigmal brace is weak and not very oblique, but aligned with basal side of pterostigma. Twelve to thirteen postnodal crossveins between nodus and pterostigma (only ten are preserved in the holotype), not aligned with corresponding eleven postsubnodal crossveins between RA and RP1. The two primary antenodal crossveins are aligned and stronger than secondary antenodal crossveins. Ax1 is 0.8-1.1 mm basal of arculus, and Ax2 is 5.5 mm distal of Ax1, on a level with distal angle of discoidal triangle; the aligned secondary antenodal crossveins between Ax1 and Ax2; distal of Ax2 there are six secondary antenodal crossveins in the first row, not aligned with the five secondary antenodal crossveins in the second row. Basal brace Ax0 visible. Seven antesubnodal crossveins between RA and RP with a short gap immediately basal of subnodus and immediately distal of arculus. Two bridge-crossveins Bqs basal of subnodus. Midfork (base of RP3/4) 5.4 mm basal of subnodus, and base of IR2 1.1 mm distal of midfork. Base of RP2 aligned with subnodus. Two oblique veins 'O' visible, two cells (1.7 mm) and five cells (5.4 mm) distal of subnodus; the second oblique vein 'O' is distinctly more oblique than the basal one. Pseudo-IR1 short and originating on RP1 distinctly distal of pterostigma. RP1 and RP2 basally parallel, but with two rows of cells in-between basal of pterostigma; RP1 and RP2 become divergent near the pterostigma with three or more rows of cells in-between. RP2 and IR2 gently curved and closely parallel in their basal preserved part with only a single row of cells in-between; apparently two rows of cells between the distal parts of RP2 and IR2 (only visible in the paratype, even though it has a strongly distorted wing). A rather distinct, but short Rspl present with two rows of cells between it and IR2. At least three convex secondary veins in area between IR2 and RP3/4. RP3/4 and MA parallel and undulated with only a single row of cells in-between up to the level of the distal vein 'O', but distally with two rows of cells in-between. No distinct Mspl, but one convex secondary vein in the distal part of the postdiscoidal area. Postdiscoidal area not distinctly widened near wing margin (width near discoidal triangle 2.9 mm; width at wing margin 3.3 mm). Area between MP and CuAa only widened near the posterior wing margin. Arculus angled, and bases of RP and MA distinctly separated at arculus. Hypertriangle free of crossveins and basally rather broad (length 4.9-5.1 mm; max. width 0.8-0.9 mm). Discoidal triangle longitudinal elongated, but rather stout, and divided into three cells; length of anterior side 4.0-4.1 mm; of basal side 2.8-3.0 mm; of distal side MAb 3.7-3.8 mm; distal side MAb straight. Median space free of crossveins; submedian space only divided by CuP-crossing, 1.3-1.4 mm basal of arculus. Cubito-anal area max. 5.9-6.1 mm wide with up to eight rows of cells; CuAa with eight well-defined posterior branches. CuAb with straight course towards posterior wing margin. Anal loop completely absent. AA divided into a weak oblique secondary anterior branch PsA and a posterior main branch AAa, delimiting a two-celled subdiscoidal triangle. AA with three posterior branches between CuAb and anal triangle (AA2b) (in the male holotype). Anal area max. 7.3 mm wide (below PsA) with up to seven or eight rows of cells. The holotype has a sharp anal angle, a long and broad anal triangle that is divided into three cells, and a long and wide membranule, thus, it is a male specimen. The concerning area of the paratype is not preserved, therefore it is not possible to recognize if it is a male or a female specimen.



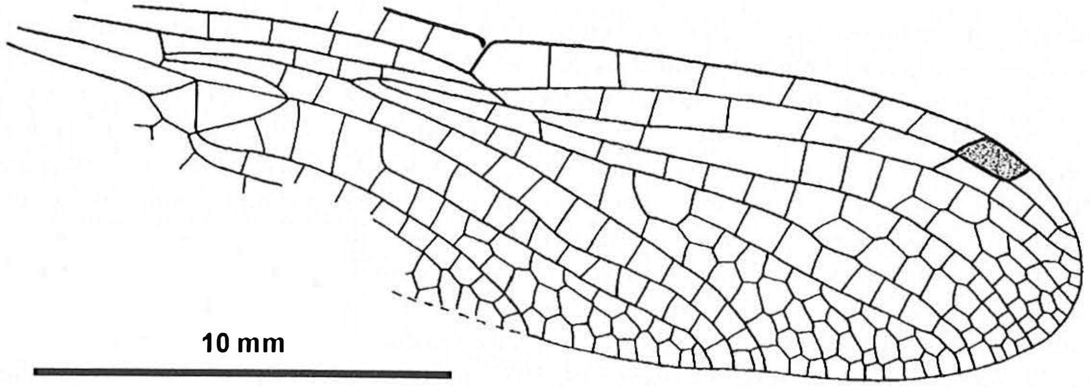
Text-Fig. 132. *Cymatophlebiella euryptera* PRITYKINA, 1968. Holotype PIN 2554 / 211 - male, right hindwing.



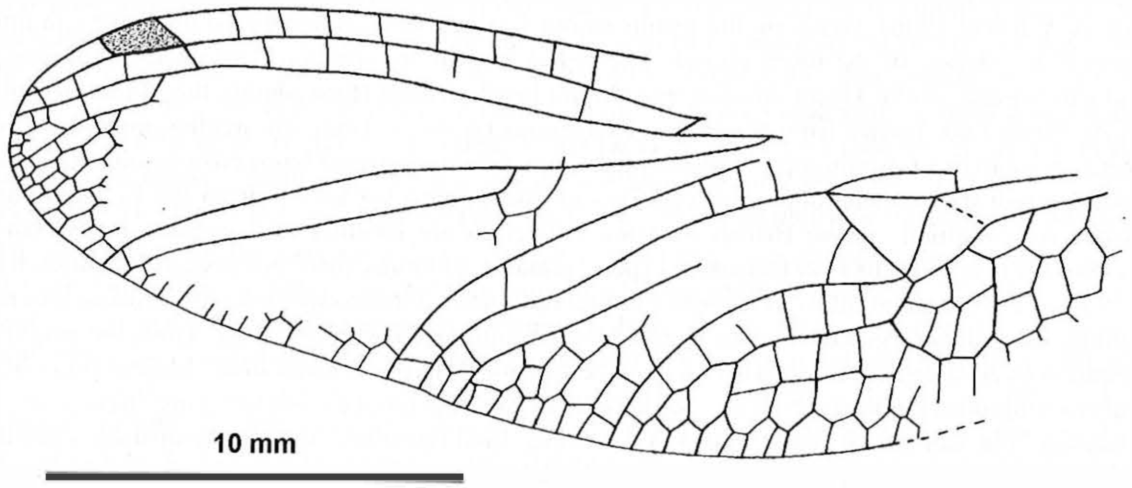
Text-Fig. 133. *Cymatophlebiella euryptera* PRITYKINA, 1968. Paratype PIN 2066 / 28 - left hindwing.



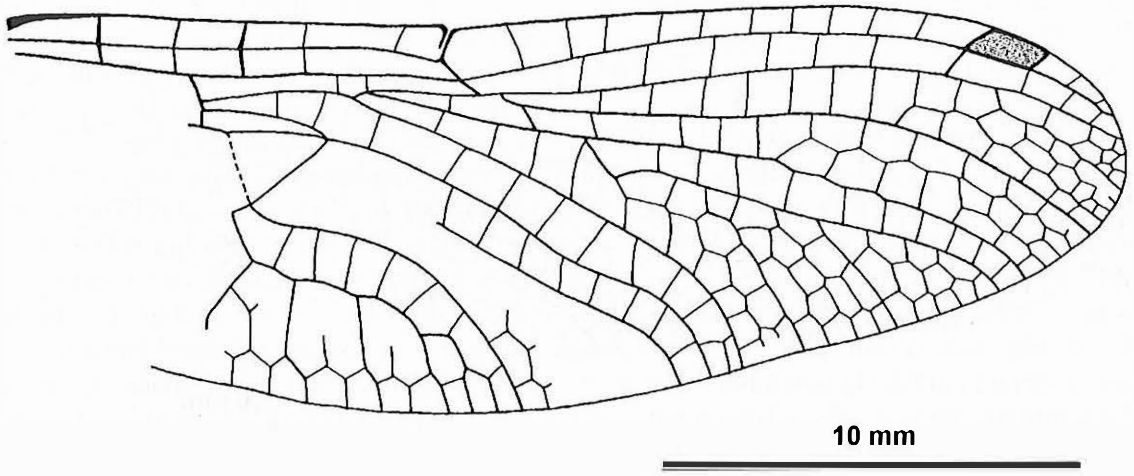
Text-Fig. 134. *Anomalaeschna berndschusteri* gen. et so. nov. Holotype no. 515 / G 22, coll. MURATA - left forewing.



Text-Fig. 135. *Anomalaeschna berndschusteri* gen. et so. nov. Holotype no. 515 / G 22, coll. MURATA - right forewing.



Text-Fig. 136. *Anomalaeschna berndschusteri* gen. et so. nov. Holotype no. 515 / G 22, coll. MURATA - left hindwing.



Text-Fig. 137. *Anomalaeschna berndschusteri* gen. et so. nov. Holotype no. 515 / G 22, coll. MURATA - right hindwing.

Other alleged Mesozoic Aeshnoptera

Some further fossil "aeshnids" have been described from the Mesozoic, but all of these have to be regarded as Anisoptera *incertae sedis*, as already indicated by NEL *et al.* (1994): *Palaeaeschna vidali* MEUNIER, 1914 is based on anisopteroid larvae from the Lower Cretaceous of Montsech in Spain. These larvae have been regarded as Anisoptera *incertae sedis* by WHALLEY & JARZEMBOWSKI (1985) and CARPENTER (1992), but could represent aeshnid larvae indeed (MEUNIER 1914, FERRER 1951, GOMEZ 1986, MARTÍNEZ-DELCLÒS 1987, 1990, 1991), although the concerning conclusions were all based on symplesiomorphies or characters of uncertain polarity. *Palaeaeschna pallerolae* GOMEZ, 1979 was described from an adult dragonfly of the same stratum and locality, but this species was transferred to a new gomphid genus *Ilerdaegomphus* by MARTÍNEZ-DELCLÒS (1989). *Proaeschna* FRITSCH, 1905 is a nomen nudum (no type species) for an odonate larva of the Upper Cretaceous of Bohemia which was already correctly regarded as an Odonata *incertae sedis* by HANDLIRSCH (1908: 667). *Guyuanaeschnidia eximia* LIN, 1982 from the Mesozoic of China is too insufficiently described to allow a phylogenetic analysis.

5. Biostratigraphical and palaeobiogeographical conclusions

Previous statements concerning the oldest known representatives of the aeshnid clade were based on an insufficient knowledge of the phylogenetic relationships of the concerning taxa (ROSS & JARZEMBOWSKI 1993, WIGHTON & WILSON 1996). Based on the results of our analysis (see above; Text-Fig. 2) we can now give a more precise description of the fossil record: The oldest known crowngroup Anisoptera, including Aeshnoptera and Euaeshnida, are of Upper Jurassic age (Malm beta). Within Neoaeshnida the oldest Gomphaeschnidae and Aeshnodea are known from the Lower Cretaceous (Aptian). There are neither any Aeshnoptera, nor Anisoptera - Exophytica (sistergroup of Aeshnoptera), nor Petalurida (most basal crowngroup Anisoptera), nor Aeschnidiidae (advanced stemgroup representatives of Anisoptera) yet known from the Lower Jurassic (two undescribed Aeschnidiidae in the British Museum collection are labelled as Toarcian of UK, but this age remains dubious according to JARZEMBOWSKI (pers. comm.), although there are several localities with a rich fossil record of Liassic dragonflies in Middle Europe, but these contain only stemgroup Anisoptera (e.g. Liassogomphidae and "anisozygopteres", like Isophlebioptera and Heterophlebioptera). Thus, the origin and first diversification of Aeshnoptera most likely has to be estimated to have occurred in the Middle Jurassic, since all Aeshnoptera subgroups basal of the Neoaeshnida (except Austropetaliida taxon nov.) are already present in the Upper Jurassic. The lack of any fossil record of Austropetaliida taxon nov. must be an artifact, since this group must have existed in the Upper Jurassic, too, just like their sistergroup Progobiaeshnidae fam. nov. and Aeshnida ("terminus post quem non" *sensu* HENNIG 1966). Unfortunately, there are no fossil dragonflies yet known from the Middle Jurassic at all, and there are only very few Upper Cretaceous records, such as the aeschnidiid *Tauropteryx krassilovi* PRITYKINA, 1993 from the Cenomanian of Crimes, and the here described new Aeshnoptera taxa *Paraliupanshania torvaldsi* gen. et sp. nov. and *P. rohdendorfi* sp. nov.

The Progobiaeshnidae fam. nov., Rudiaeschnidae fam. nov. and Cymatophlebiidae, Paracymatophlebiidae fam. nov. and Eumorbaeschnidae fam. nov. are all only known from localities of the Palaearctic, while extant Austropetaliida taxon nov. (Archipetaliidae and Austropetaliidae) have a strictly Gondwanian distribution. Mesuropetalidae is strictly Palaearctic, too, while their sistergroup Liupanshaniidae fam. nov. is also represented in the Lower Cretaceous of Brazil. The extant Gomphaeschnidae and Aeshnodea (Brachytronidae, Telephlebiidae stat. nov., and Aeshnidae) which originated from the most basal splitting event in Neoaeshnida are known from the northern, as well as the southern hemisphere. There is no distinct higher percentage of Gondwanian elements among the basal representatives of Gomphaeschnidae or Aeshnodea. Altogether, this geographic pattern does not allow a well-supported reconstruction of the palaeo-biogeographic history of Aeshnoptera by vicariance biogeographical methods, although there is some evidence for a Middle Jurassic Palaearctic origin of Aeshnoptera (see NEL *et al.* 1994; compare CARLE 1995) with a fast subsequent evolution leading to a very diverse Aeshnoptera fauna with world wide distribution already in the Upper Jurassic and Lower Cretaceous, although the main radiation apparently still took place in the Palaearctic. Curiously, there are no Mesozoic Aeshnoptera known at all from North America, northern Africa and Australia, while there are numerous records from the Upper Jurassic and Lower Cretaceous of Brazil, Spain, England, Germany and northern Asia.

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Explanations of Plates

Plate 1

Figures 1-2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov.
1 BSP 1846 a / HAGEN no. 44, neotype of *G. koehleri* HAGEN, 1848, part, female. Scale 10 mm.
2 BSP 1846 b / HAGEN no. 44, neotype of *G. koehleri* HAGEN, 1848, counterpart, female. Scale 10 mm.

Plate 2

Figures 1-2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov.
1 JME 1966 / 64 Ei BI, male. Scale 10 mm.
2 Specimen in private coll. SCHMITT / Frankfurt, female. Photo by K.A. FRICKHINGER. Scale unknown (wing span shall be about 110 mm).

Plate 3

Figures 1-2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov.
1 MCZ 1998, female ?. Scale 10 mm.
2 MCZ 1998, female ?, right wings. Scale 10 mm.

Plate 4

Figures 1-2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov.
1 MCZ 1998, female ?, left wings. Scale 10 mm.
2 MCZ 6203, male. Scale as indicated by the rule.

Plate 5

Figures 1-2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov.
1 MCZ 6203, male, anal appendages. Scale 2 mm.
2 MCZ without number Scale as indicated by the rule.

Figure 3 *Mesuropetala auliensis* PRITYKINA, 1968 - Holotype PIN 2239 / 21, female, right hindwing. Scale as indicated by the rule.

Figure 4 *Mesuropetala costalis* PRITYKINA, 1968 - Holotype PIN 2239 / 20, forewing. Scale 10 mm.

Plate 6

Figures 1-3 *Aeschnopsis perkinsi* sp. nov.
1 Holotype MCZ 6181, part, female, left wings. Scale 10 mm.
2 Holotype MCZ 6180, counterpart, female. Scale 10 mm.
3 Paratype MCZ 6197, male ?. Scale as indicated by the rule.

Figure 4 *Aeschnopsis sp.* - BSP 1964 XXIII x, two forewings. Scale unknown.

Figure 5 Mesuropetalidae indet. - Specimen SMS 358 in coll. RESCH, the single known fossil dragonfly "tandem". Scale 10 mm.

Plate 7

Figures 1-2 *Araripeliupanshania annesusae* gen. et sp. nov.
1 Holotype D 58, MB, male. Photo by B. SCHUSTER. Scale 10 mm.
2 Holotype D 58, MB, male, left wings. Scale 10 mm.

Plate 8

Figures 1-2 *Araripeliupanshania annesusae* gen. et sp. nov.
1 Allotype SMNS 64345 (old number 72), female. Scale 10 mm.
2 Allotype SMNS 64345 (old number 72), female. Without scale.

Plate 9

Figures 1-2 *Araripeliupanshania annesusae* gen. et sp. nov.
1 Paratype SMNS 64343 (old number K 38), male. Scale 10 mm.
2 Paratype no. M 56 in coll. *ms-fossil*, female. Scale 10 mm.

Plate 10

Figures 1-2 *Araripeliupanshania annesusae* gen. et sp. nov.
1 Paratype no. L 75 in coll. SCHWICKERT, male. Scale as indicated by the rule.
2 Paratype no. L 75 in coll. SCHWICKERT, male. Scale as indicated by the rule.

Plate 11

Figure 1 *Araripeliupanshania annesusae* gen. et sp. nov. - Paratype, coll. MURATA, male, left hindwing. Photo by B. SCHUSTER. Scale unknown.

Figures 2-3 *Paraliupanshania torvaldsi* gen. et sp. nov.
1 Holotype PIN 2383 / 14, part, female, hindwing. Scale 10 mm.
2 Holotype PIN 2383 / 14, counterpart, female, hindwing. Scale 10 mm.

Plate 12

Figures 1-2 *Progobiaeshna liaoningensis* gen. et sp. nov.
1 Holotype SMNS 63398, female, thorax and right wings. Scale 10 mm.
2 Holotype SMNS 63398, female, foreleg. Scale 1 mm.

Figures 3-4 *Gobiaeshna occulta* PRITYKINA, 1977
3 Holotype PIN 3145 / 672, forewing base. Scale 10 mm.
4 Holotype PIN 3145 / 672, forewing apex. Scale 10 mm.

Plate 13

Figure 1 *Gobiaeshna occulta* PRITYKINA, 1977 - Holotype PIN 3145 / 672, forewing median part. Scale 10 mm.

Figure 2 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. - Holotype BSP AS VII 794, male ?. Scale unknown.

Figures 3-4 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
3 BSP AS VII 796, paratype ?, female. Scale 10 mm.
4 BSP AS VII 796, paratype ?, female, right forewing. Scale 10 mm.

Plate 14

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 BSP AS VII 796, paratype ?, female, left wings. Scale 10 mm.
2 BSP AS VI 36, female. Scale 10 mm.

Plate 15

Figures 1-3 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 BSP AS VI 36, female, right wings. Scale 10 mm.
2 BSP AS VI 36, female, left wings. Scale 10 mm.
3 JME SOS 1703, male, abdomen with anal appendages. Scale 10 mm.

Plate 16

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 JME SOS 1696, left wings. Scale 10 mm.
2 JME SOS 1713, male, with genital lobes. Scale as indicated by the rule.

Plate 17

Figures 1-4 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 JME SOS 1715, male, left hindwing. Scale 10 mm.
2 JME 1957-14-ak-Bl., female, the single known female specimen with genital lobes. Scale 10 mm.
3 Specimen 89 / 76 in coll. TISCHLINGER, female, with large confluent compound eyes. Scale 10 mm.
4 JME SOS 2041, male, hindwing base. Scale 10 mm.

Plate 18

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 JME SOS 2042, female. Scale 10 mm.
2 JME SOS 3614 / So-1957-92, female. Scale 10 mm.

Plate 19

Figures 1-3 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 JME SOS 3614 / So-1957-92, female, right wings. Scale 10 mm.
2 JME SOS 3614 / So-1957-92, female, left wings. Scale 10 mm.
3 Specimen 82 / 262 in coll. TISCHLINGER, male, with genital lobes. Scale 10 mm.

Plate 20

Figures 1-3 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 JME 52.-1959.-30,5-Bl., thorax with two forewings. Scale 10 mm.
2 JME 52.-1959.-30,5-Bl., right forewing. Scale 10 mm.
3 JME 1982.73, male ?, abdomen with genital lobes and anal appendages. Scale as indicated by the rule.

Plate 21

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 Specimen in exhibition of the Maxberg-Museum, female. Photo by K.A. FRICKHINGER. Scale unknown (body length shall be about 100 mm, and wing span about 130 mm according to FRICKHINGER pers. comm.).
2 Specimen in exhibition of the Maxberg-Museum, female, right hindwing. Scale unknown.

Plate 22

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 Specimen without number in coll. KÜMPEL, male, with genital lobes and anal appendages. Scale 10 mm.
2 Specimen in private coll. SCHÄFER / Kiel, female. Photo by K.A. FRICKHINGER. Scale unknown (wing span shall be about 130 mm according to FRICKHINGER pers. comm.).

Plate 23

Figures 1-5 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 Specimen no. 3 in exhibition of Museum Bergér, male, abdomen with genital lobes. Scale 10 mm.
2 MCZ 5898, head with confluent compound eyes. Scale 10 mm.
3 Specimen without number in coll. TISCHLINGER, male, with genital lobes. Scale 10 mm.
4 SMNS 64348 (old number GB 55), head with large confluent compound eyes. Scale 10 mm.
5 SMNS 64347 (old number GB 9), male, abdomen with genital lobes. Scale as indicated by the rule.

Plate 24

Figures 1-2 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 SMNS 62744, male. Scale 10 mm.
2 SMNS 62662, the single known specimen from Nusplingen, two forewings. Scale as indicated by the rule.

Plate 25

Figures 1-3 *Cymatophlebia longialata* (MÜNSTER in GERMAR, 1839).
1 MCZ 6248, female, right wings. Scale 10 mm.
2 MCZ 6248, female, left wings. Scale 10 mm.
3 MCZ 6249. Scale 10 mm.

Plate 26

Figures 1 *Cymatophlebia zdrzaleki* (JARZEMBOWSKI, 1994) comb. nov. - Holotype 1987.727, Horsham Museum, male, right hindwing. Photo by R. ANDRESS. Scale 10 mm.

Figure 2 *Cymatophlebia suevica* sp. nov. - Holotype GPIT 1807 / 1, part and counterpart, forewing fragment. Scale as indicated by the rule.

Figures 3-4 *Cymatophlebia herrlenae* sp. nov.
3 Holotype GPIT 1807 / 2, two forewings. Scale 10 mm.
4 Holotype GPIT 1807 / 2, left forewing. Scale 10 mm.

Plate 27

Figure 1 *Cymatophlebia purbeckensis* sp. nov. - Holotype BGS 57630, left forewing base. Scale 10 mm.

Figures 2-5 *Cymatophlebia pumilio* sp. nov.
2 Holotype MCZ 6234, counterpart, forewing. Scale 10 mm.
3 Holotype MCZ 6235, part, forewing. Scale 10 mm.
4 Paratype MCZ without number, overlapping right wings. Scale 10 mm.
5 Paratype MCZ without number, overlapping left wings. Scale 10 mm.

Plate 28

Figures 1-2 *Cymatophlebia kuempeli* sp. nov.
1 Holotype no. 42, coll. KÜMPEL, male. Photo by K.A. FRICKHINGER. Scale 10 mm.
2 Holotype no. 42, coll. KÜMPEL, male, right wings and genital lobes. Scale 10 mm.

Plate 29

Figures 1-2 *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996.
1 BSP 1995 I 39, right hindwing and faked body. Scale as indicated by the rule.
2 BSP 1995 I 39, left hindwing. Scale as indicated by the rule.

Plate 30

Figures 1-2 *Rudiaeschna limnobia* DONG & ZI-GUANG, 1996.
1 Specimen without number in coll. ROCKERS, male. Photo by G. ROCKERS. Scale unknown.
2 Specimen without number in coll. ROCKERS, male. Photo by G. ROCKERS. Scale unknown. Please note the presence of genital lobes as in *Cymatophlebia*!

Plate 31

Figures 1-6 *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov.
1 Paratype MCZ 6275, counterpart, female. Scale as indicated by the rule.
2 Paratype MCZ 6193, part, female, right wings. Scale as indicated by the rule.
3 Paratype MCZ 6193, part, female, left wings. Scale as indicated by the rule.
4 JME 1983 / 2633, forewing. Scale 10 mm.

5 MCZ 6241, original of NEEDHAM (1907) (no type!), male. Scale as indicated by the rule.
6 MCZ 6241, original of NEEDHAM (1907) (no type!), male, right hindwing. Scale 10 mm.

Plate 32

Figures 1-2 *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov.
1 MCZ 6241, original of NEEDHAM (1907) (no type!), male, left hindwing. Scale 10 mm.
2 JME SOS 3714, left wings. Scale 10 mm.

Plate 33

Figure 1 *Mesuropetala muensteri* (GERMAR, 1839) comb. nov. - Specimen without number in coll. JUVYNS, male. Photo by R. JUVYNS. Scale unknown.

Figure 2 *Eumorbaeschna jurassica* (CARPENTER, 1932) gen. et comb. nov. - SMNS 64342. Scale 10 mm.

Plate 34

Figure 1 *Anomalaeschna berndschusteri* gen. et sp. nov. - Holotype no. 515 (old number G 22) in coll. MURATA, female ?. Scale as indicated by the rule.

Plate 35

Figures 1-2 *Paramorbaeschna araripensis* gen. et sp. nov.
1 Holotype SMNS 63068 a, part, female, left wings. Scale 10 mm.
2 Paratype NSM no. 29, female. Scale 10 mm.

Plate 36

Figures 1-3 *Paramorbaeschna araripensis* gen. et sp. nov.
1 Paratype NSM no. 29, female, right wings. Scale 10 mm.
2 Paratype NSM no. 29, female, left wings. Scale 10 mm.
3 Holotype SMNS 63068 b, counterpart, female. Scale as indicated by the rule.

Plate 37

Figures 1-2 *Paramorbaeschna araripensis* gen. et sp. nov.
1 Paratype SMNS 64218, female. Scale as indicated by the rule.
2 Paratype no. 518 (old number G 13) in coll. MURATA, female. Scale as indicated by the rule.

Plate 38

Figure 1 *Progomphaeschnaoides ursulae* gen. et sp. nov. - Holotype SMNK 2357 PAL, female. Scale 10 mm.

Figure 2 *Progomphaeschnaoides staniczeki* sp. nov. - Holotype JME AP 1997 / 4 a, part, female, right hindwing. Scale as indicated by the rule.

Plate 39

Figure 1 *Progomphaeschnaoides staniczeki* sp. nov. - Holotype JME AP 1997 b, counterpart, female, hindwing base. Scale 10 mm.

Figure 2 *Gomphaeschnaoides obliquus* (WIGHTON, 1987) - Specimen C 19, coll. *ms-fossil*, male, hindwing. Scale 10 mm.

Figure 3 *Plesigomphaeschnaoides mongolensis* gen. et sp. nov. - Holotype PIN 3559 / 10201 (S/N1), male, hindwing. Scale 10 mm.

Figures 4-5 *Gomphaeschnaoides obliquus* (WIGHTON, 1987)
4 SMNS 63069, male. Scale as indicated by the rule.
5 SMNS 63069, male, pterostigma of left hindwing. Scale 2 mm.

Plate 40

Figures 1-2 *Gomphaeschnaoides obliquus* (WIGHTON, 1987).
1 NSM no. 54, female. Scale 10 mm.
2 Specimen C 16, coll. *ms-fossil*, male. Scale 10 mm.
3 Specimen BSP no. 13 (old number C 17), male. Scale 10 mm.

Plate 41

Figure 1 *Gomphaeschnaoides obliquus* (WIGHTON, 1987) - Specimen D 11, coll. *ms-fossil*. Scale 10 mm.

Figure 2 *Gomphaeschnaoides betoreti* sp. nov. - Holotype BSP no. 11 (old number D 9), female. Scale 10 mm.

Plate 42

Figures 1-2 *Gomphaeschnaoides magnus* sp. nov.
1 Holotype JME AP 1997 / 2, female, with little bonefish *Dastilbe*. Scale as indicated by the rule.
2 Holotype JME AP 1997 / 2, female, left wings. Scale 10 mm.

Plate 43

Figures 1-2 *Gomphaeschnaoides magnus* sp. nov.
1 Paratype SMNS 64344 (old numbers 71 and H 17). Scale as indicated by the rule.
2 Paratype no. M 62 in coll. *ms-fossil*, female. Scale as indicated by the rule.

Plate 44

Figures 1-3 *Gomphaeschnaoides petersi* sp. nov.
1 Holotype JME AP 1997 / 3, male. Scale as indicated by the rule.
2 Holotype JME AP 1997 / 3, male, anal loop of left hindwing. Scale 2 mm.
3 Holotype JME AP 1997 / 3, male, aberrant gomphaeschnaoidine oblique vein of right hindwing. Scale 2 mm.

Plate 45

Figures 1-2 *Gomphaeschna inferna* PRITYKINA, 1977.
1 Paratype PIN 1989 / 1722, left forewing. Scale 10 mm.
2 Holotype PIN 1989 / 1808, left hindwing. Scale as indicated by the rule.

Plate 46

Figures 1-2 *Gomphaeschna sibirica* sp. nov.
1 Holotype PIN 4626 / 162, left hindwing. Scale 10 mm.
2 Paratype PIN 4626 / 158, right hindwing. Scale 2 mm.

Plate 47

Figure 1 *Baissaeshna prisca* PRITYKINA, 1977 - Holotype PIN 1989 / 1495, right hindwing. Scale 10 mm.

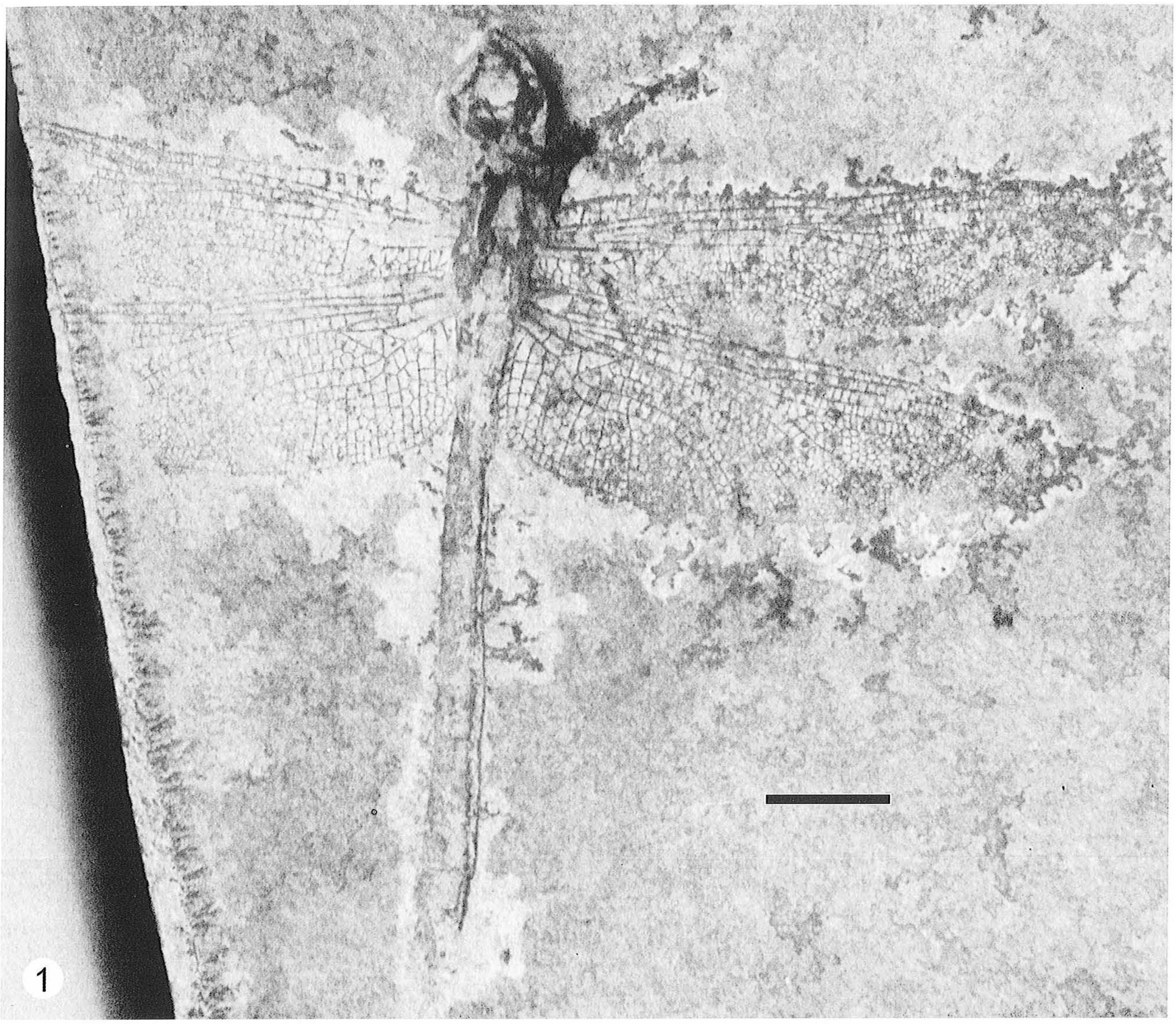
Figure 2 *Baissaeshna zherikhini* sp. nov. - Holotype PIN 3064 / 3146, left wings. Scale as indicated by the rule.

Plate 48

Figure 1 *Cymatophlebiella euryptera* PRITYKINA, 1968 - Holotype PIN 2554 / 211, male, left hindwing. Scale 10 mm.

Figures 2-7 Aeshnid larvae from the Crato-Formation, probably Gomphaeschnaoidinae subfam. nov. Fig. 6 photographed by B. SCHUSTER. Scale 10 mm (scale unknown for Fig. 6).

Plate 1



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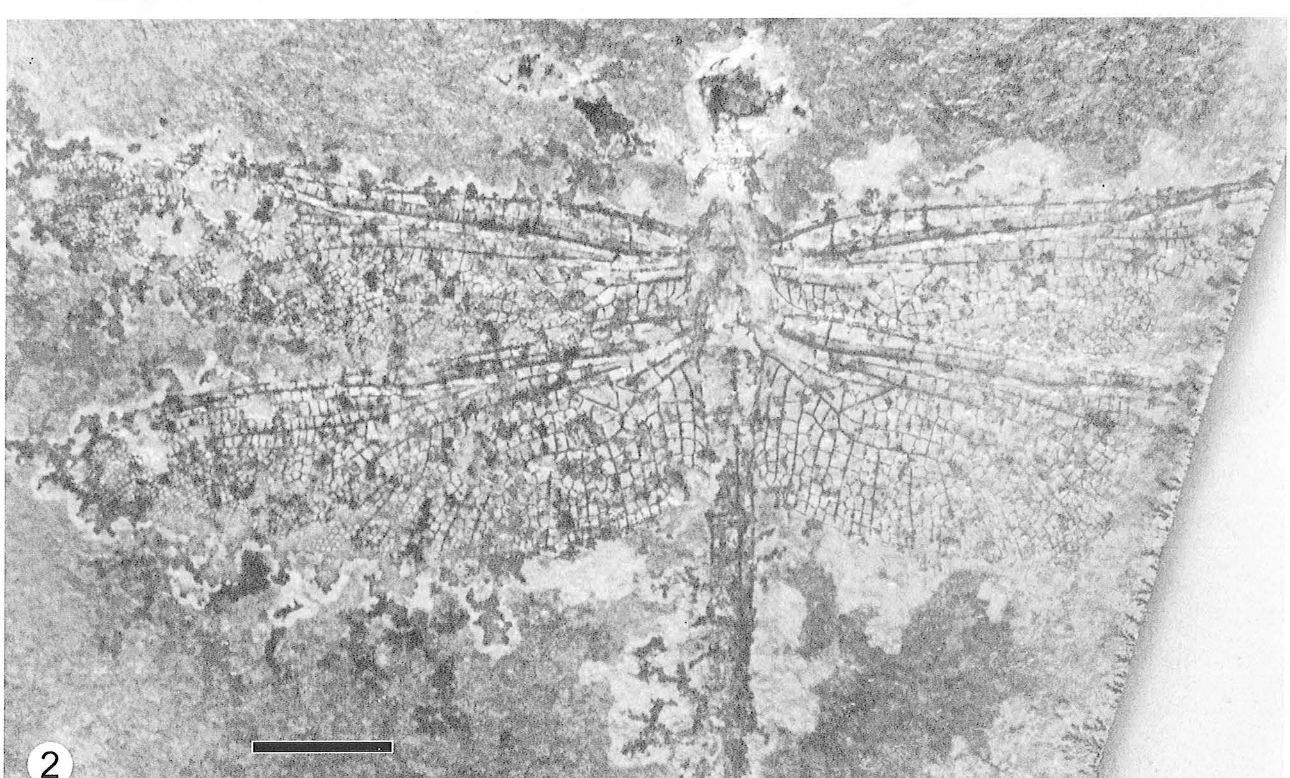
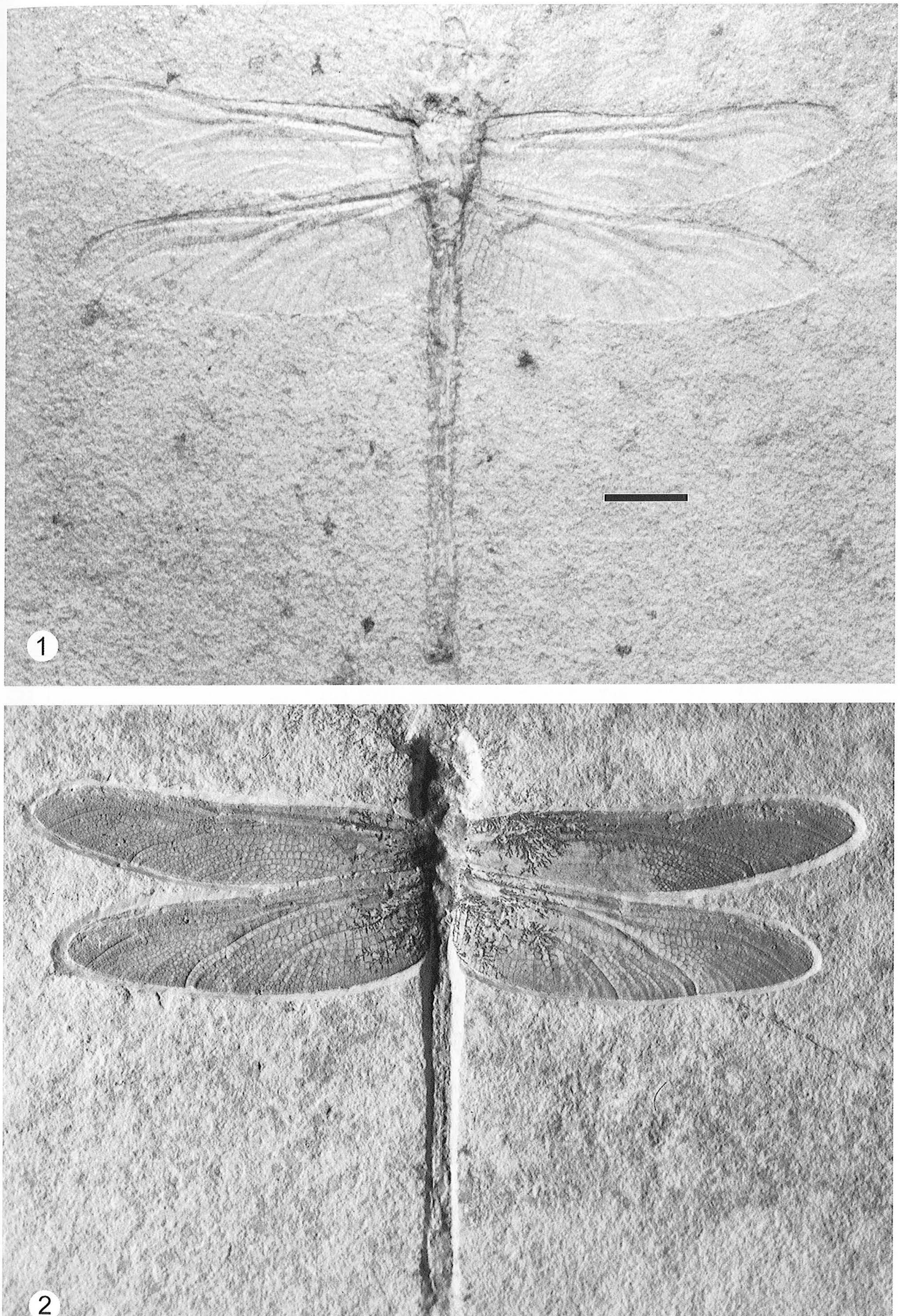


2

Plate 2



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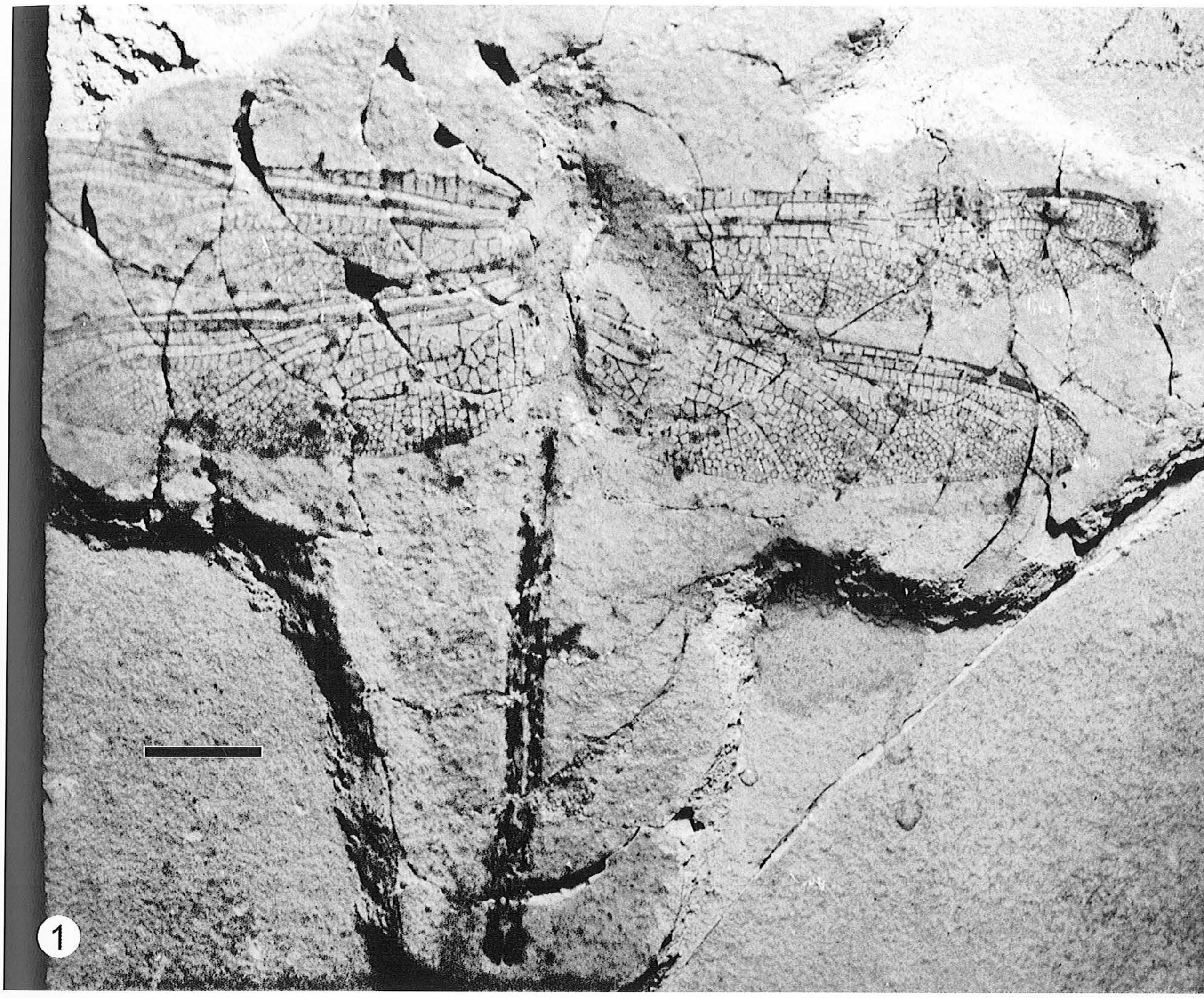

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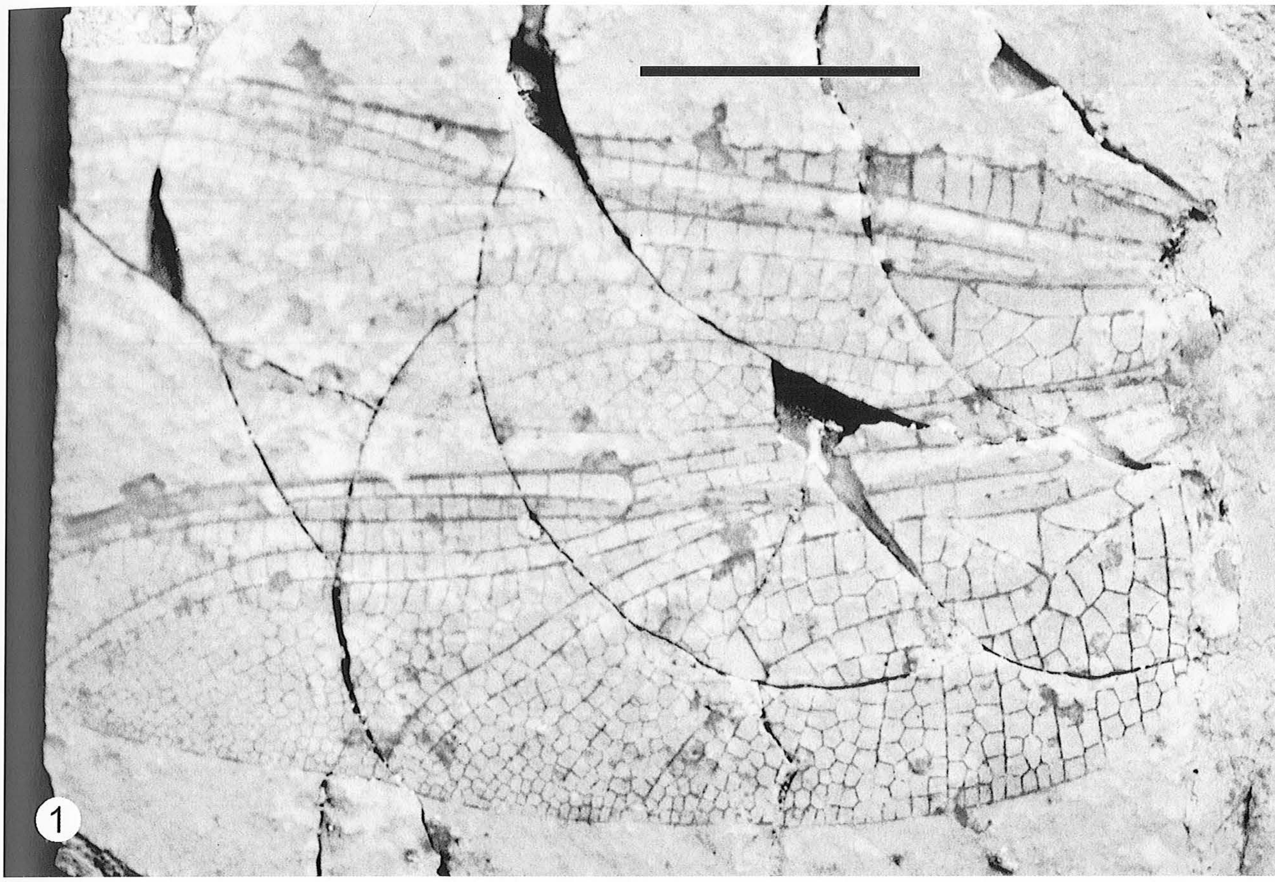

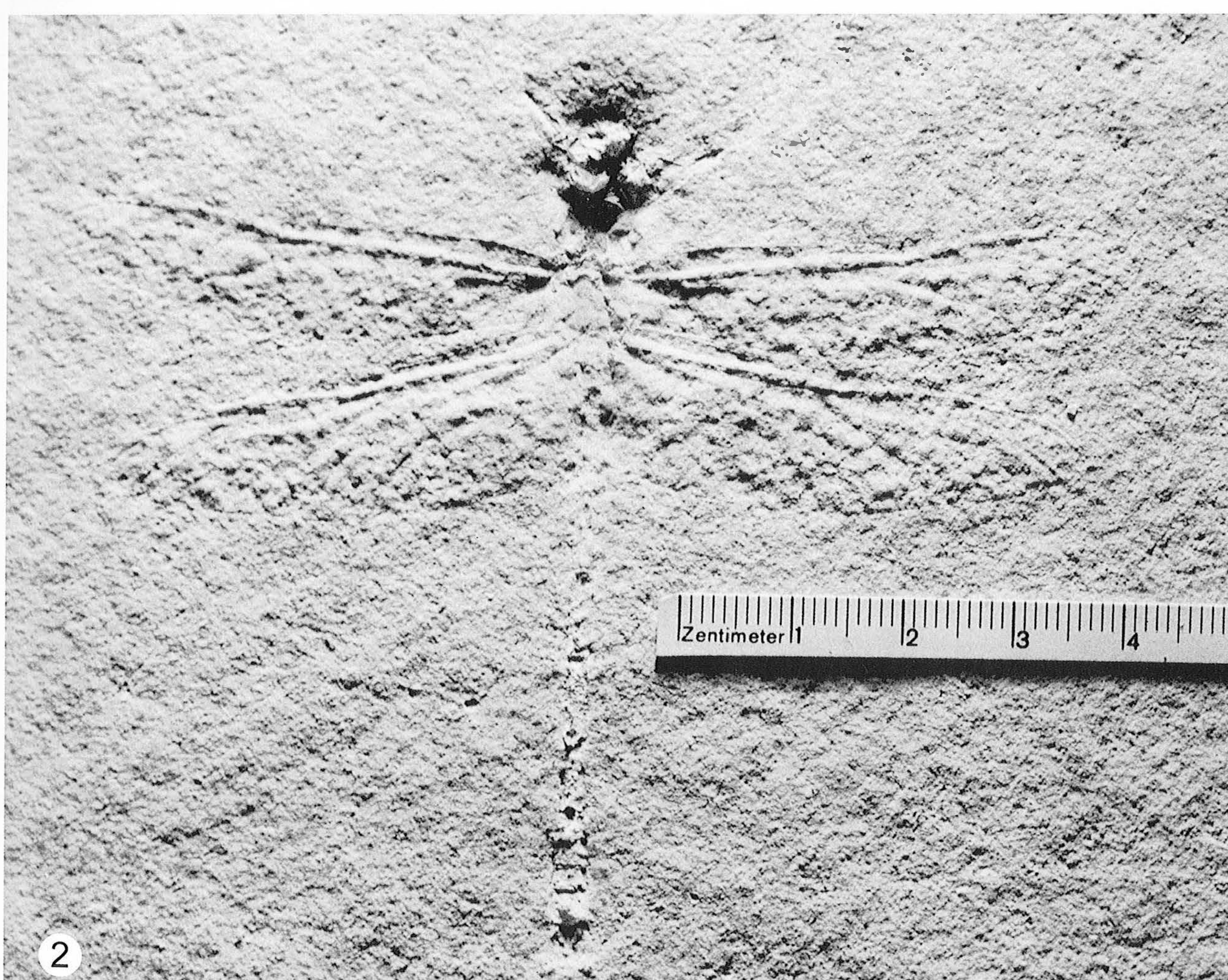

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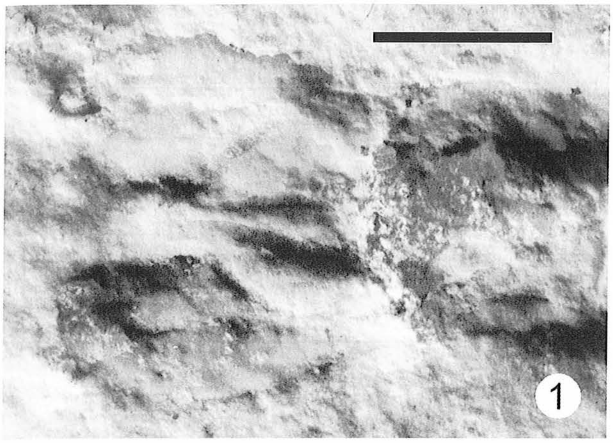
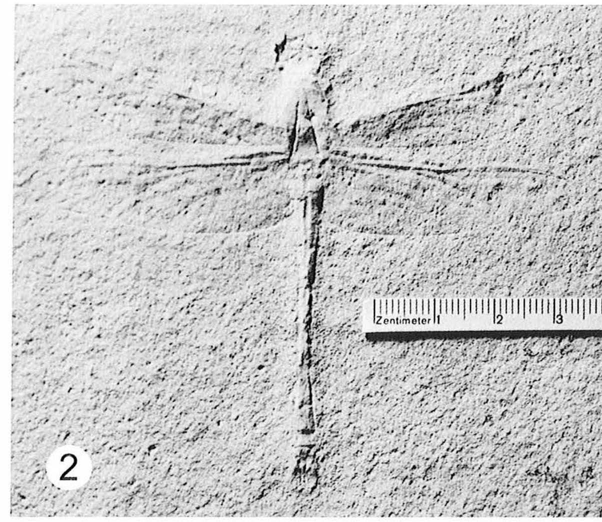
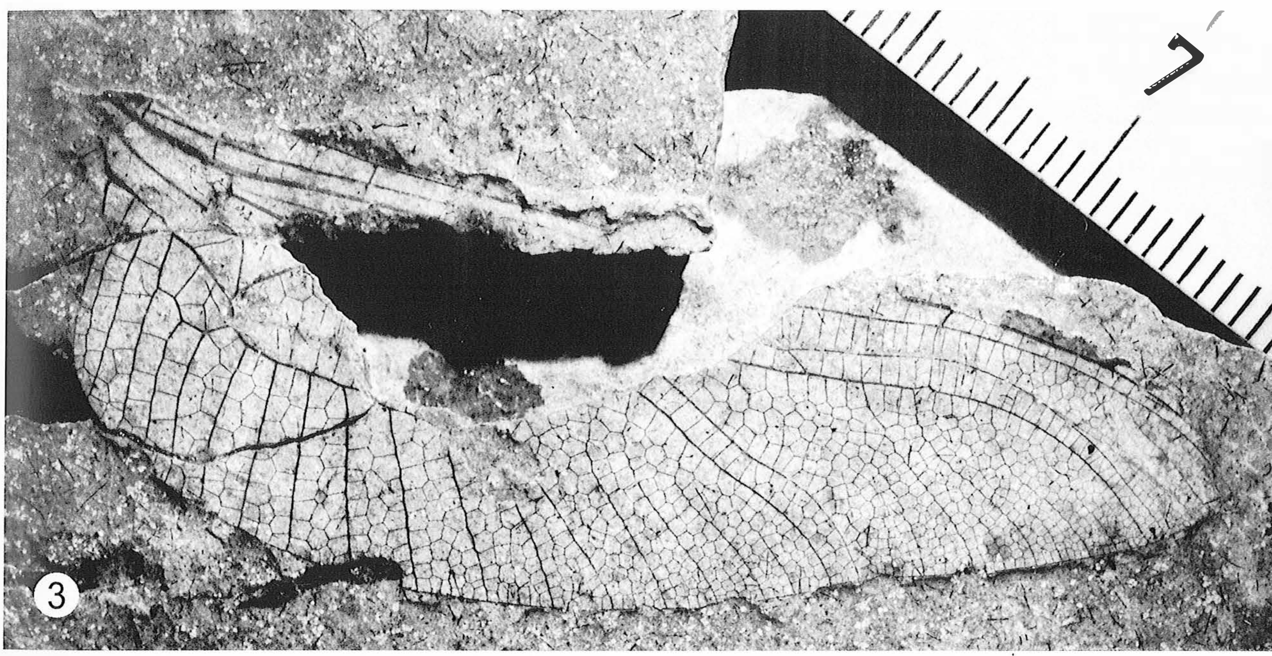






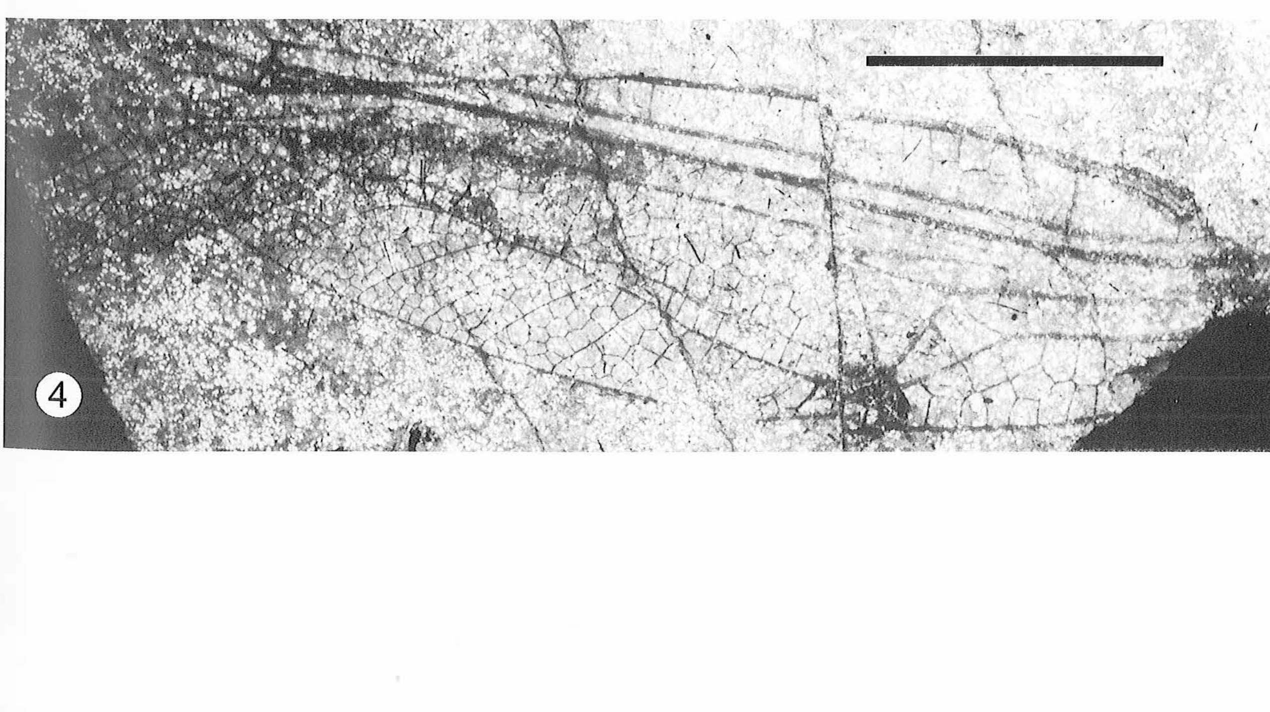


Plate 6

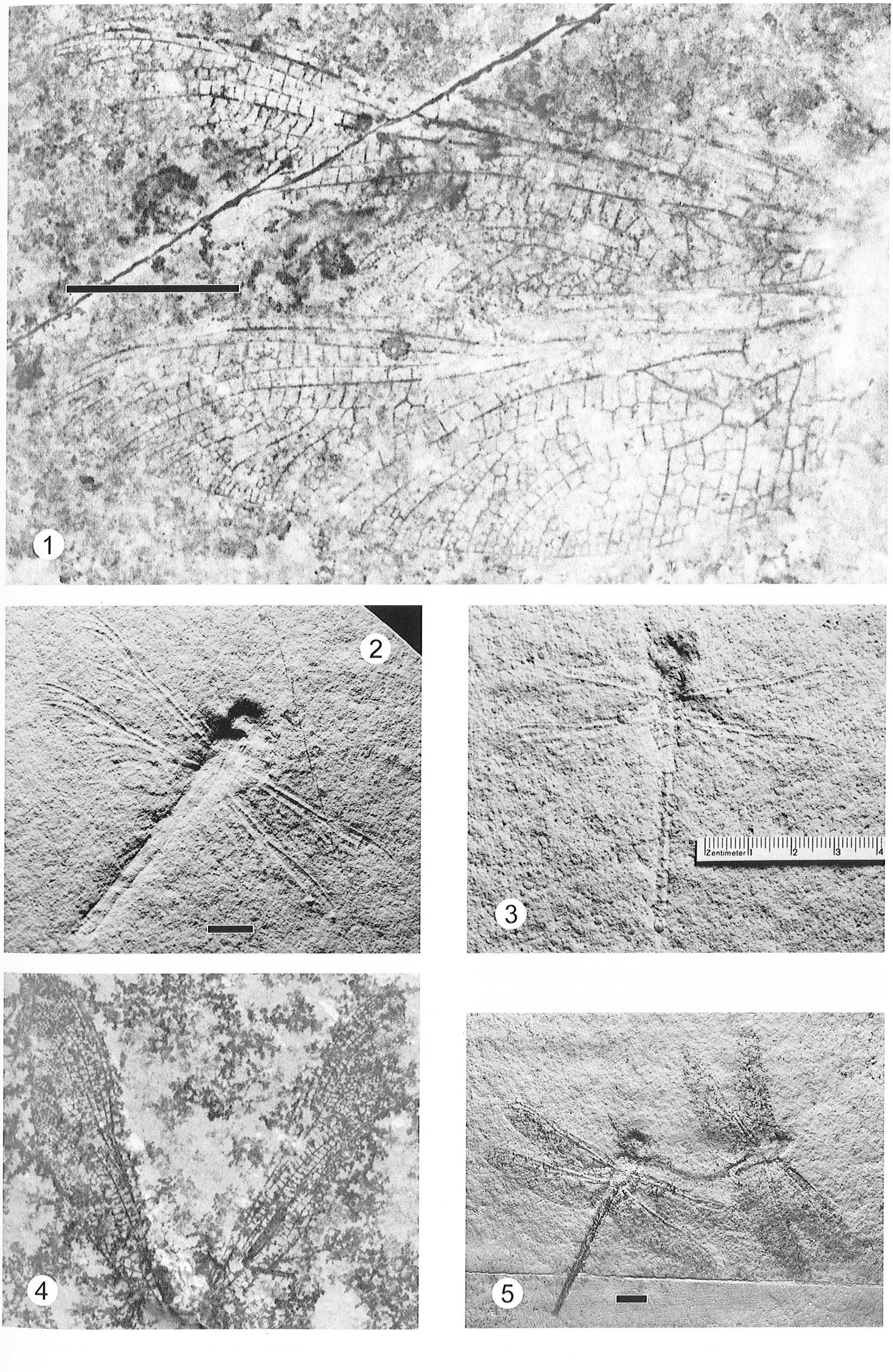
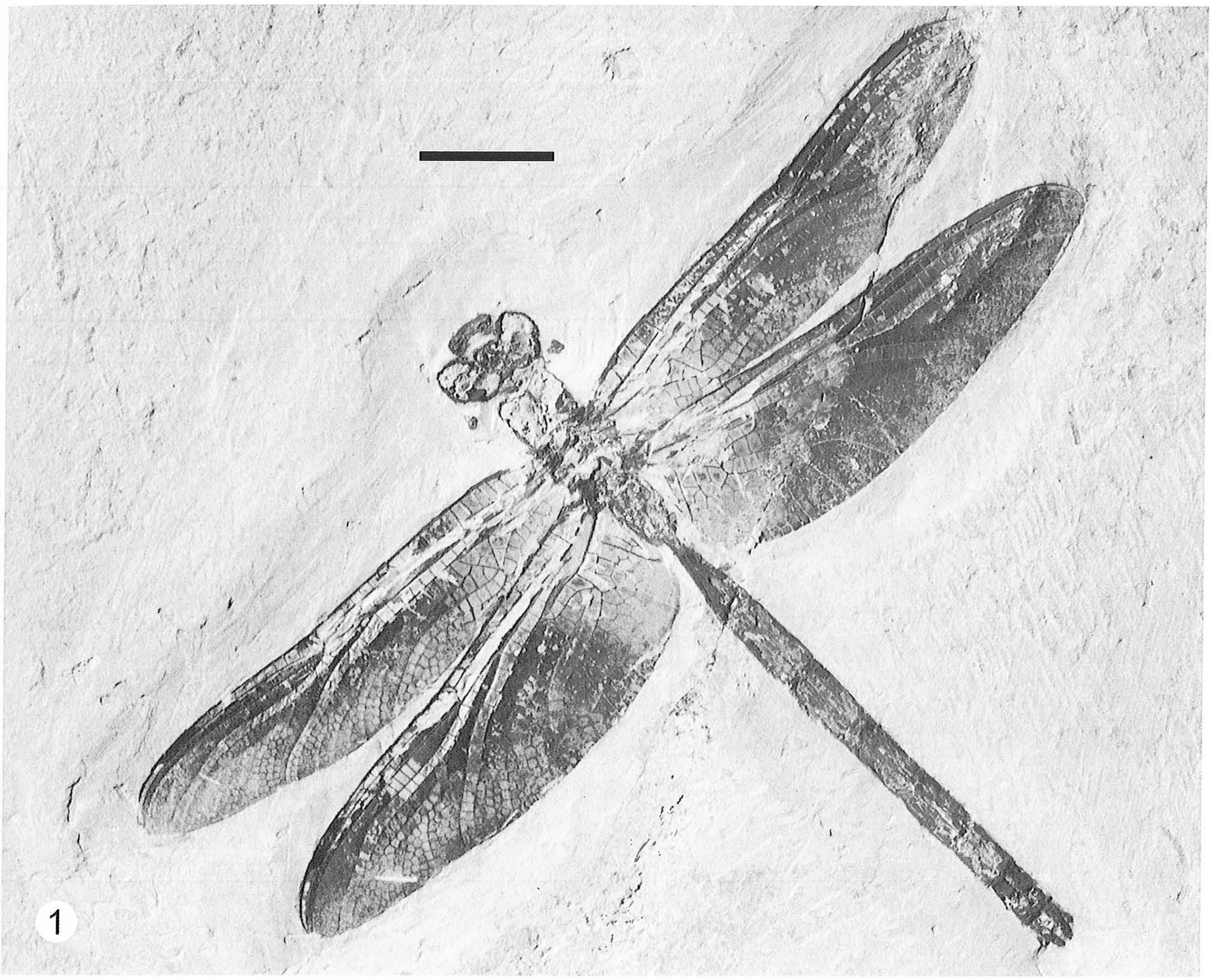
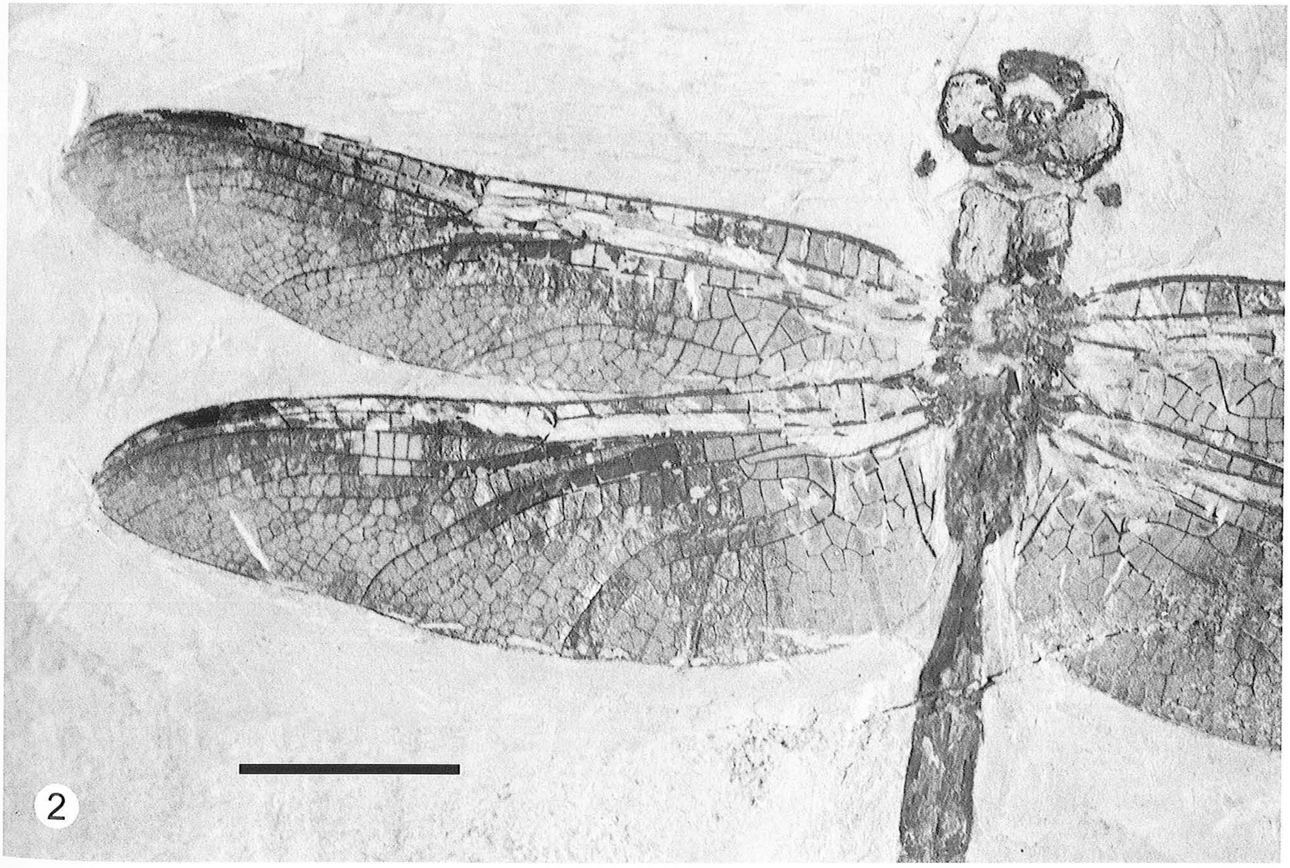


Plate 7





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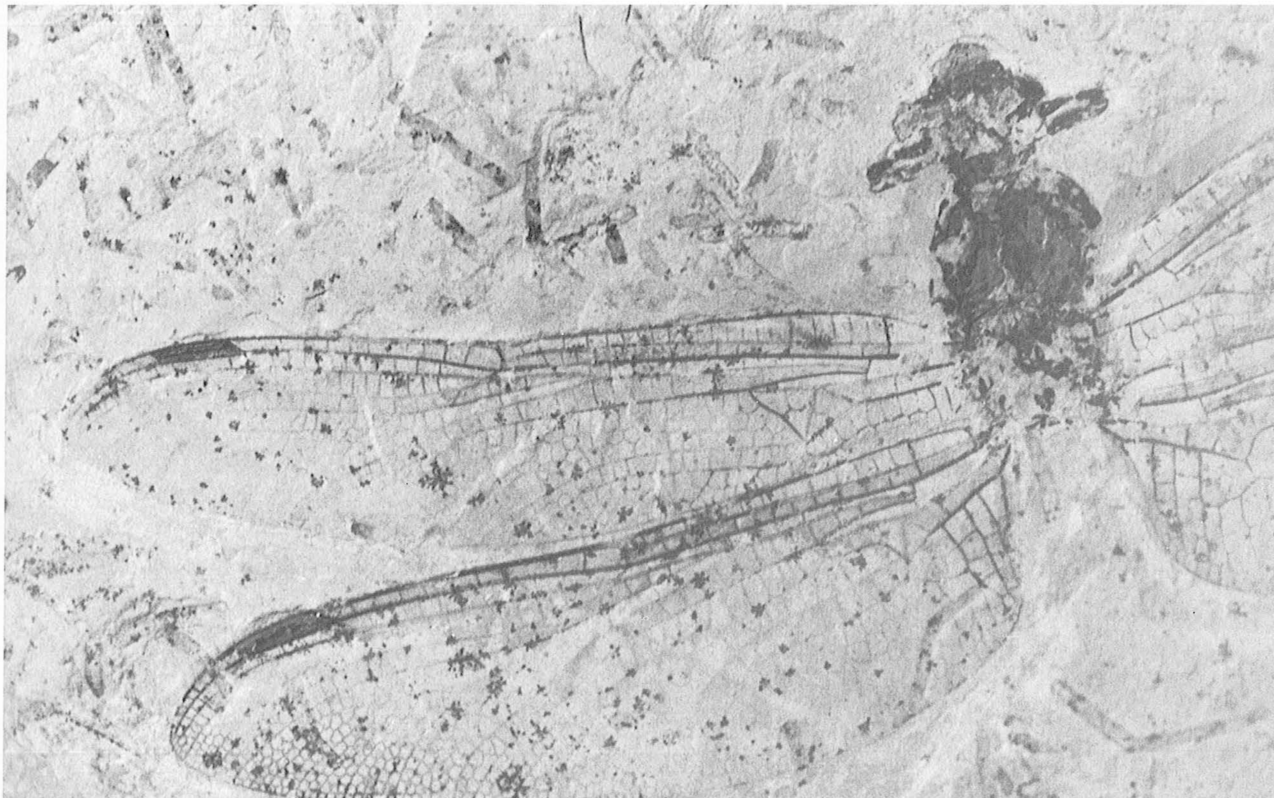

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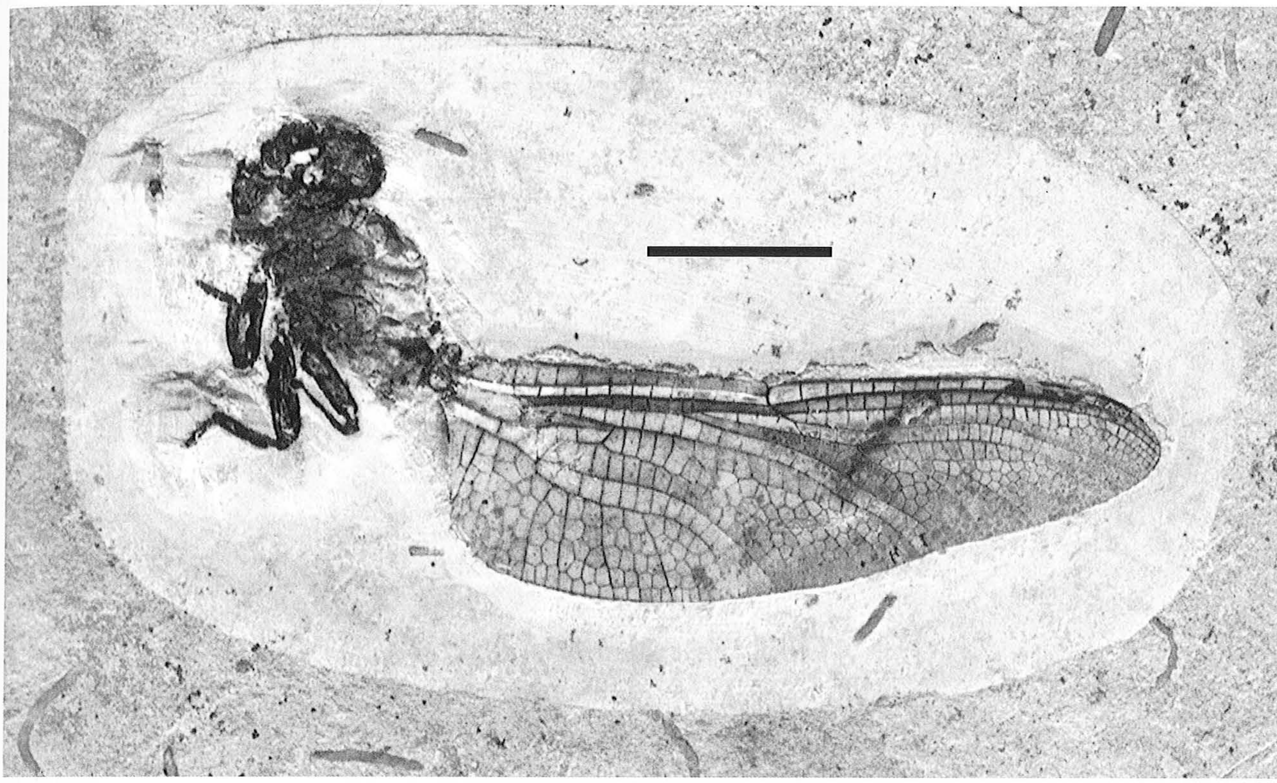

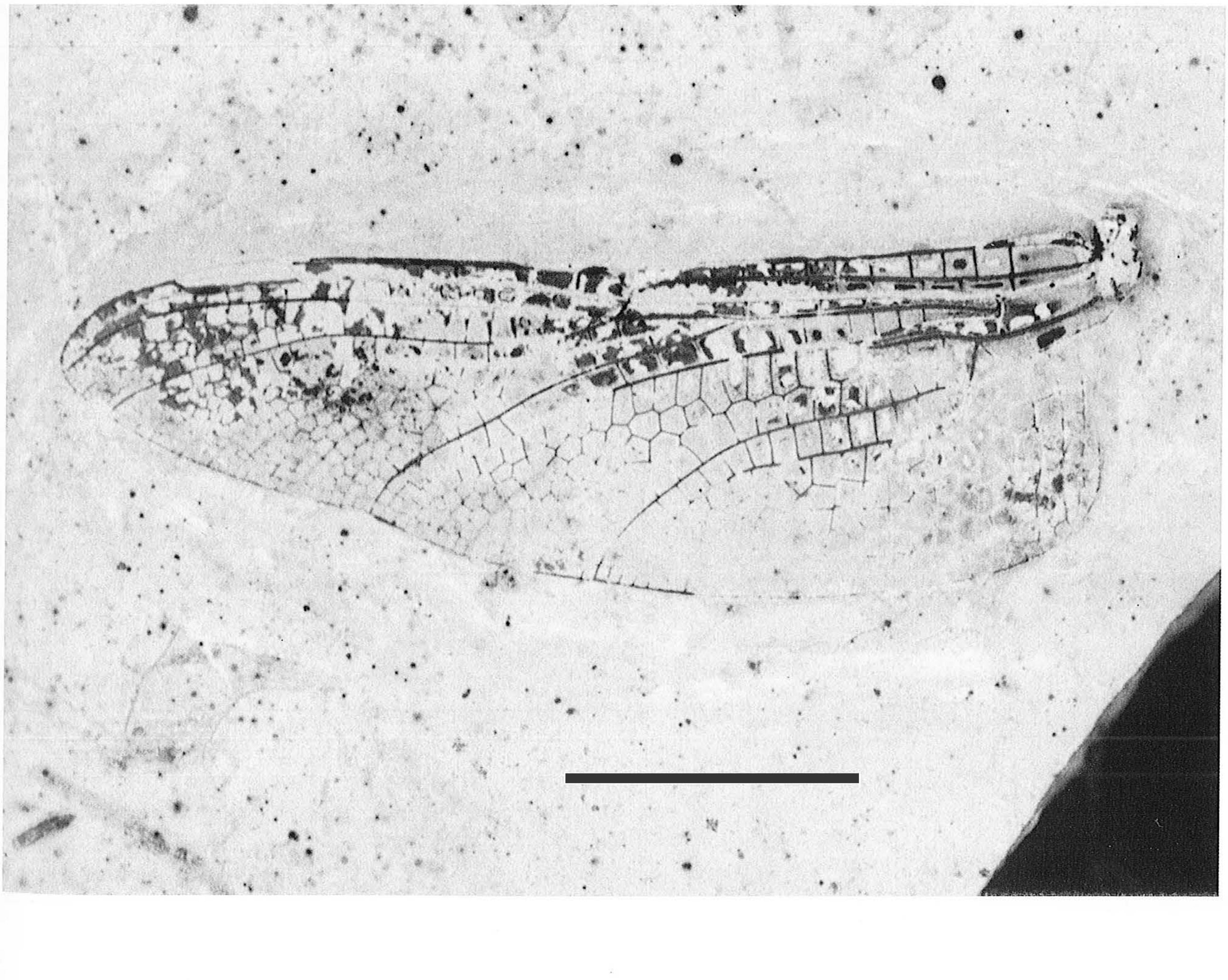

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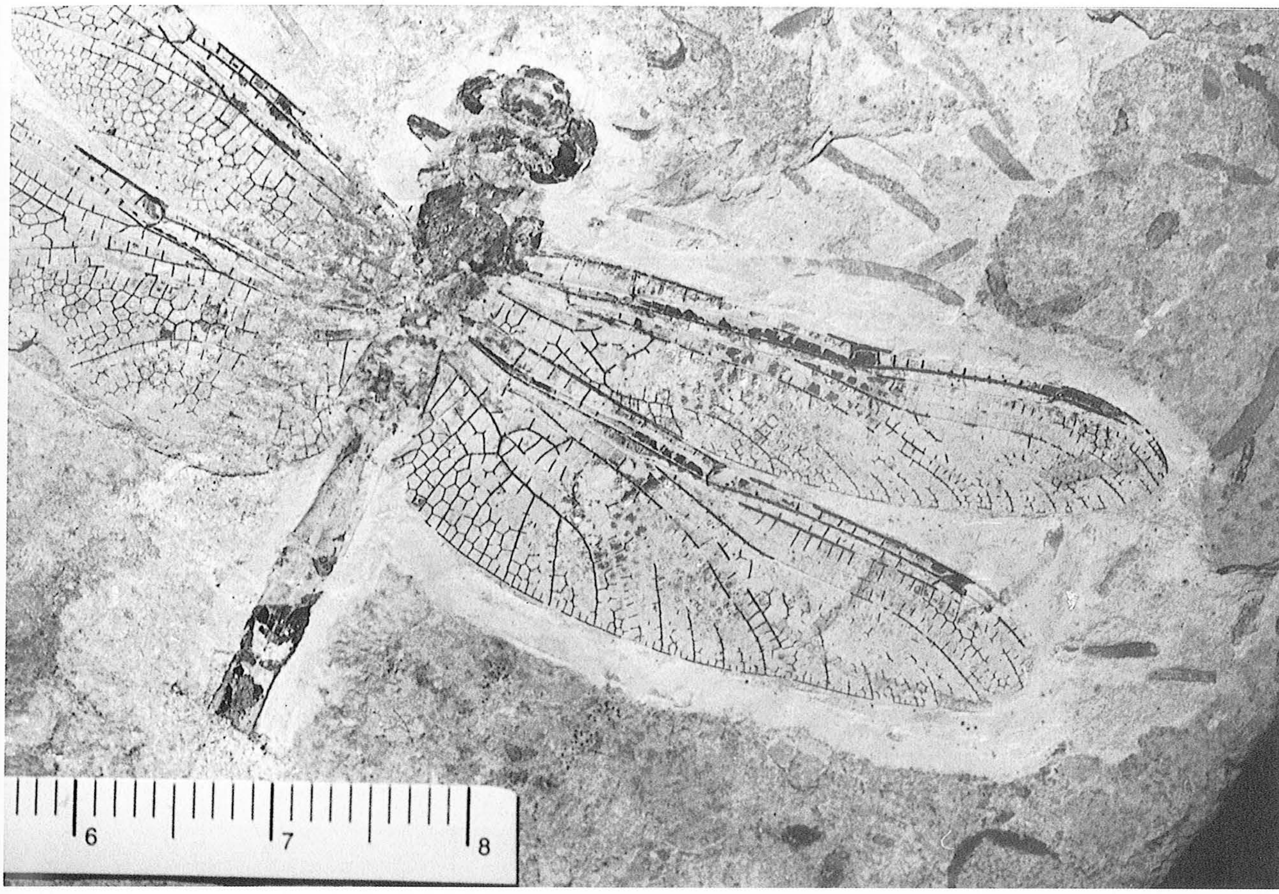

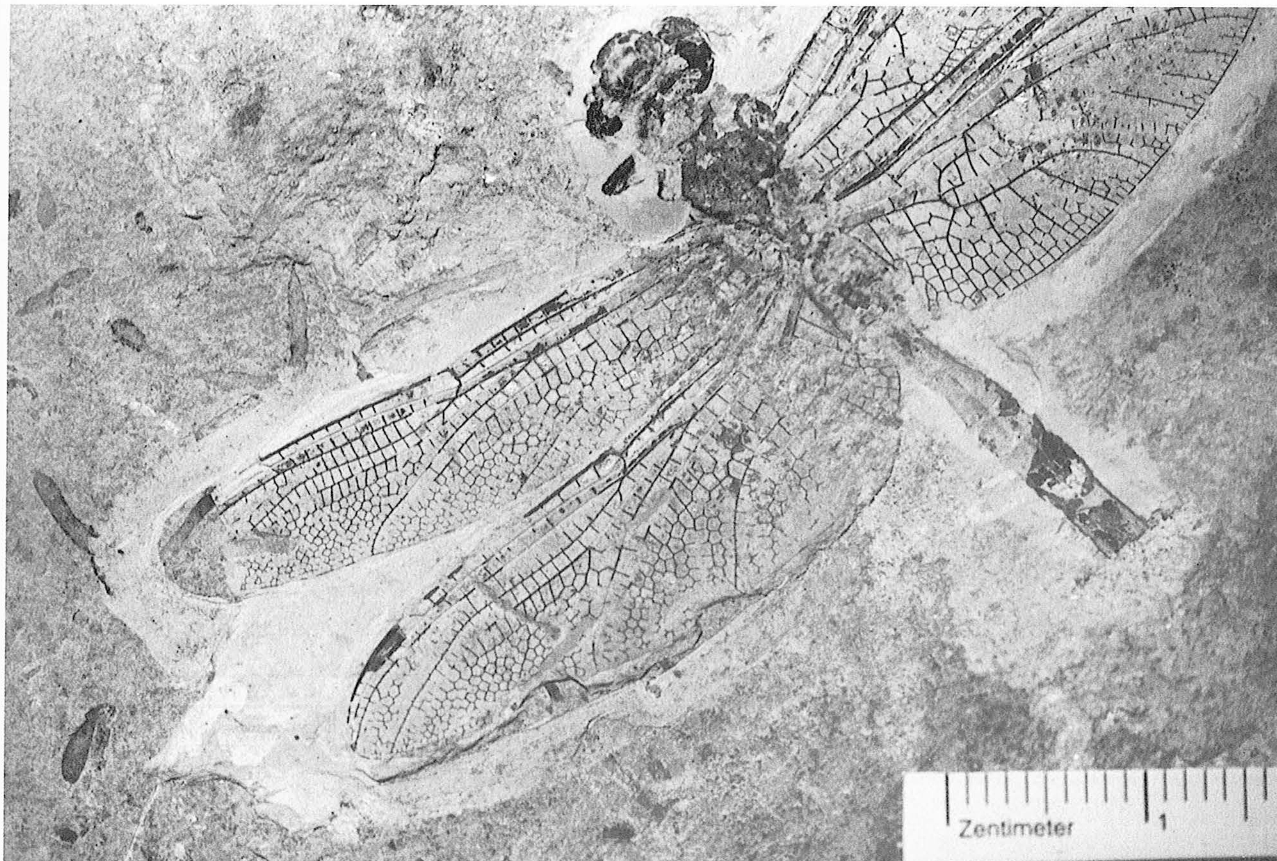

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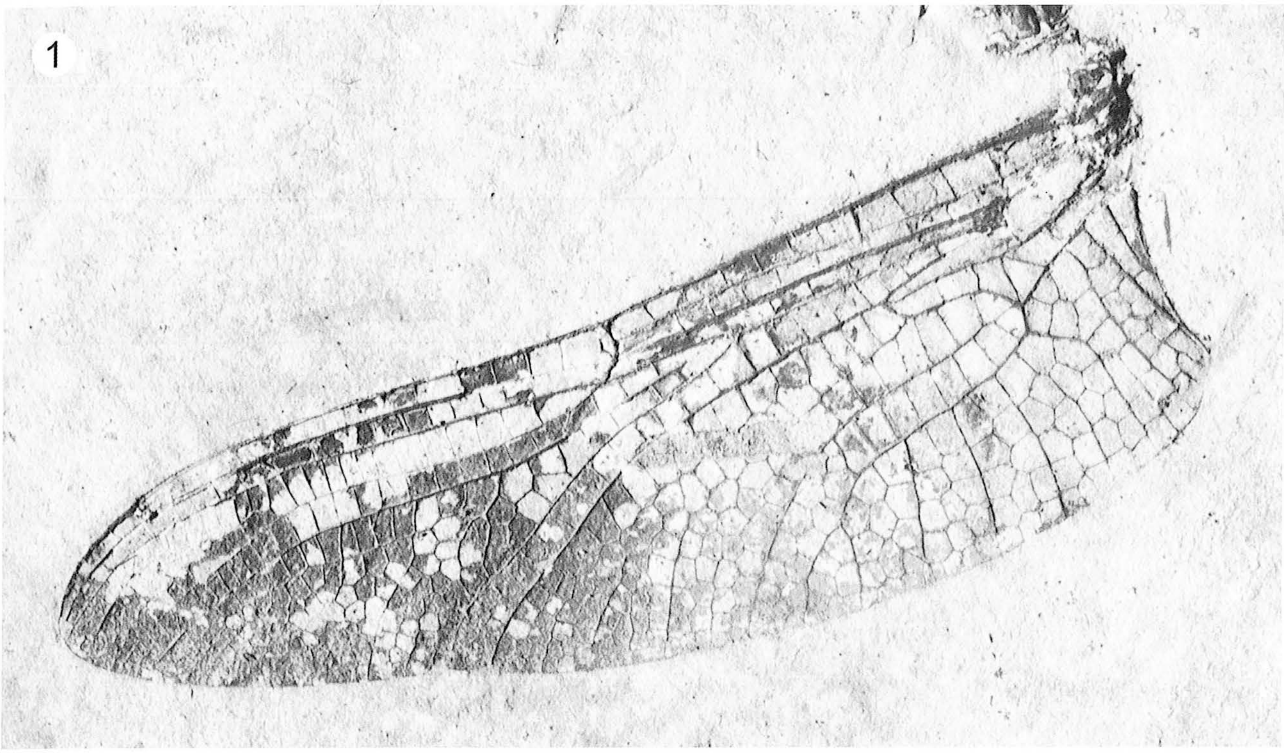

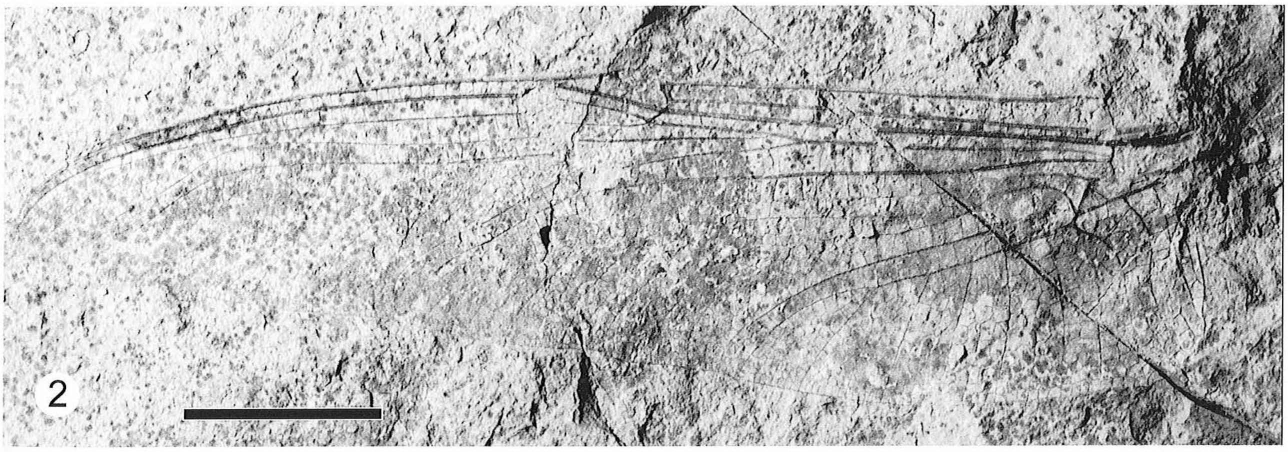

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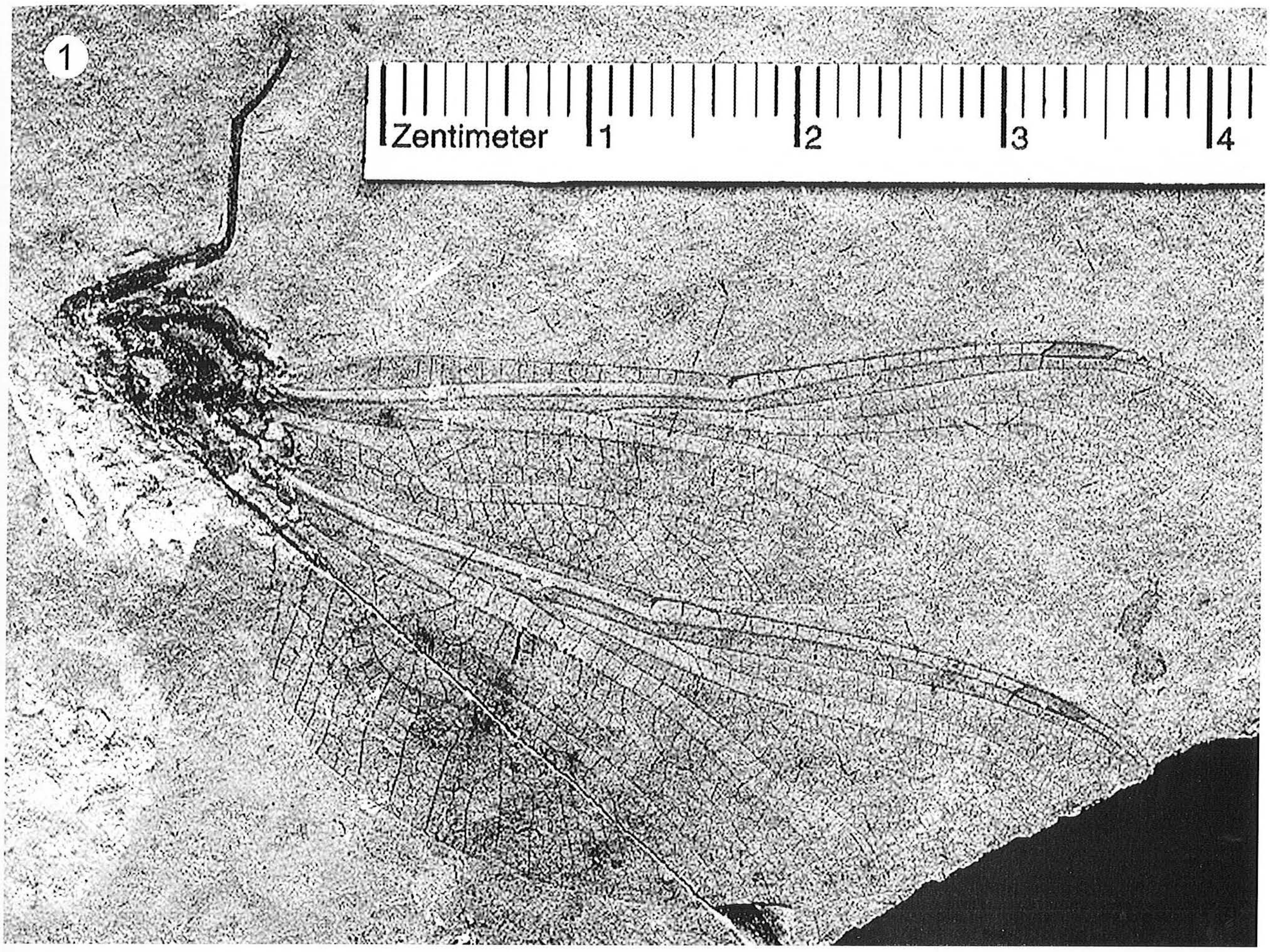

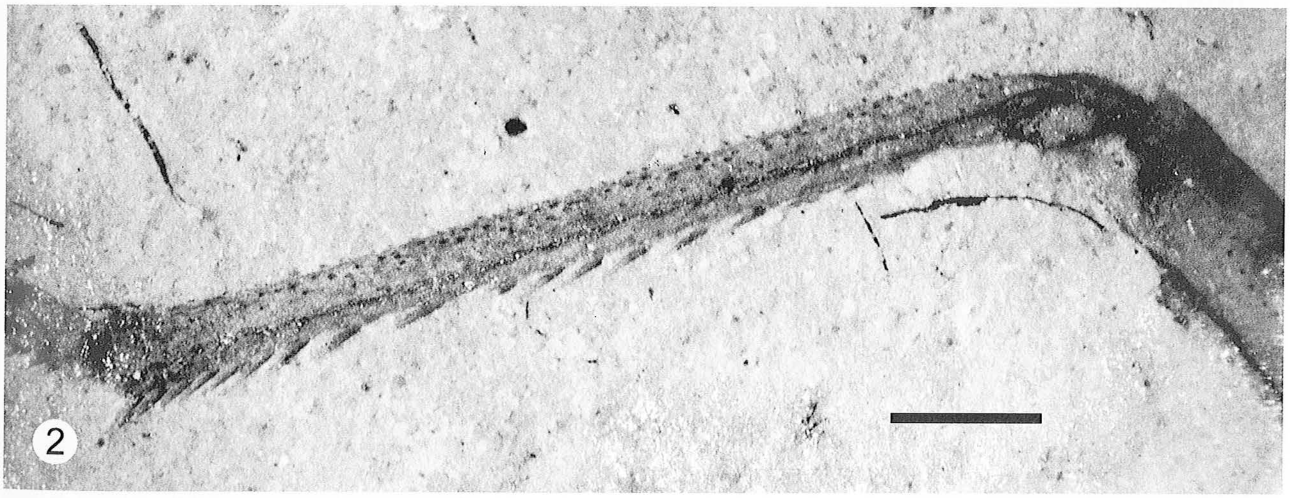

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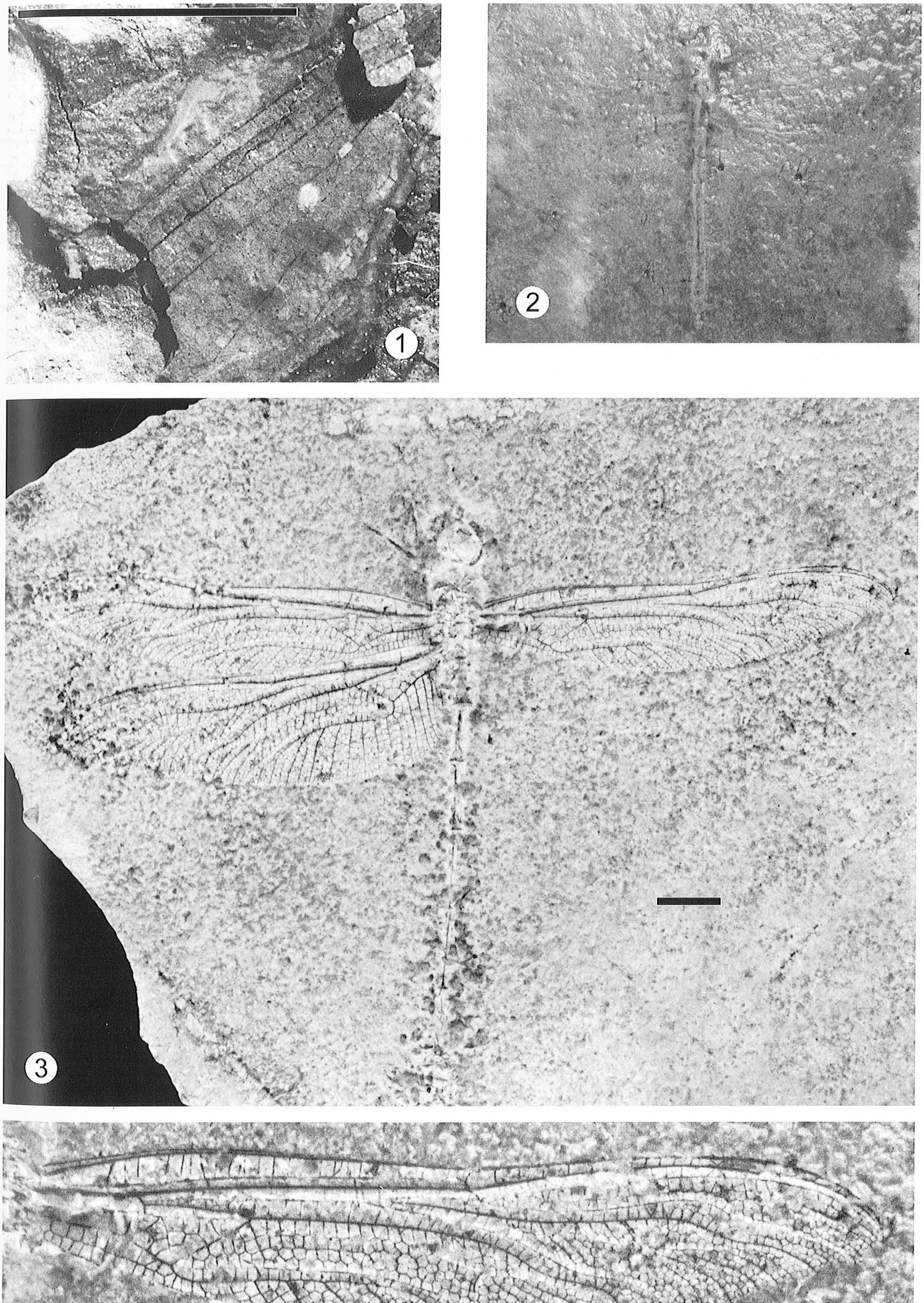

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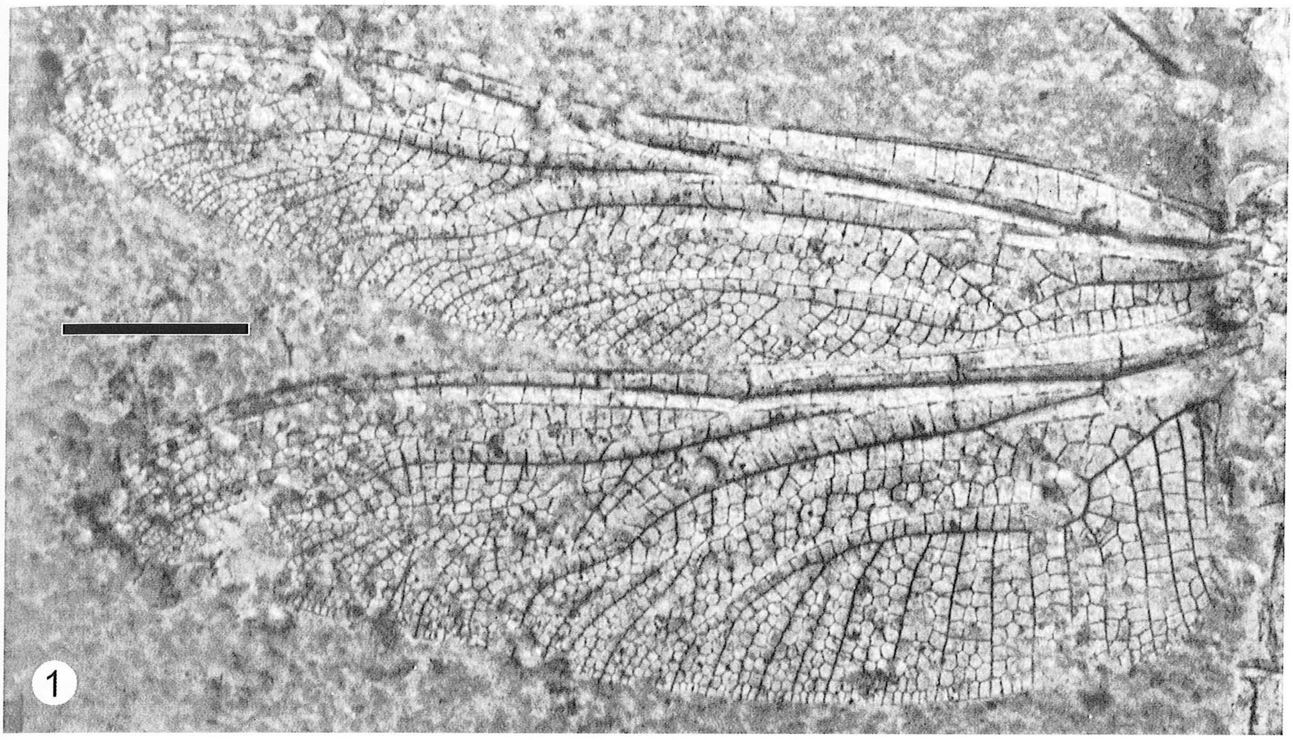

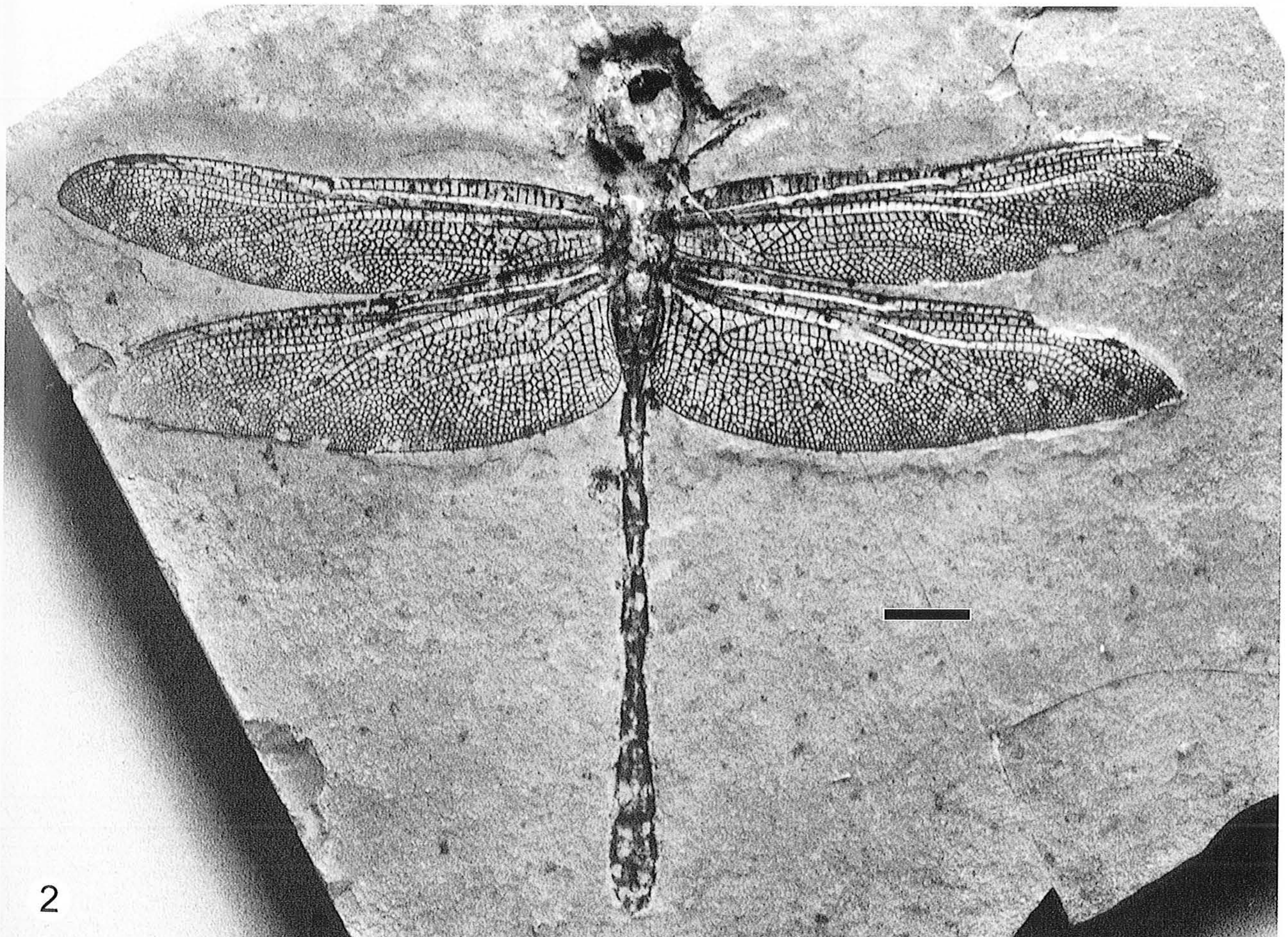

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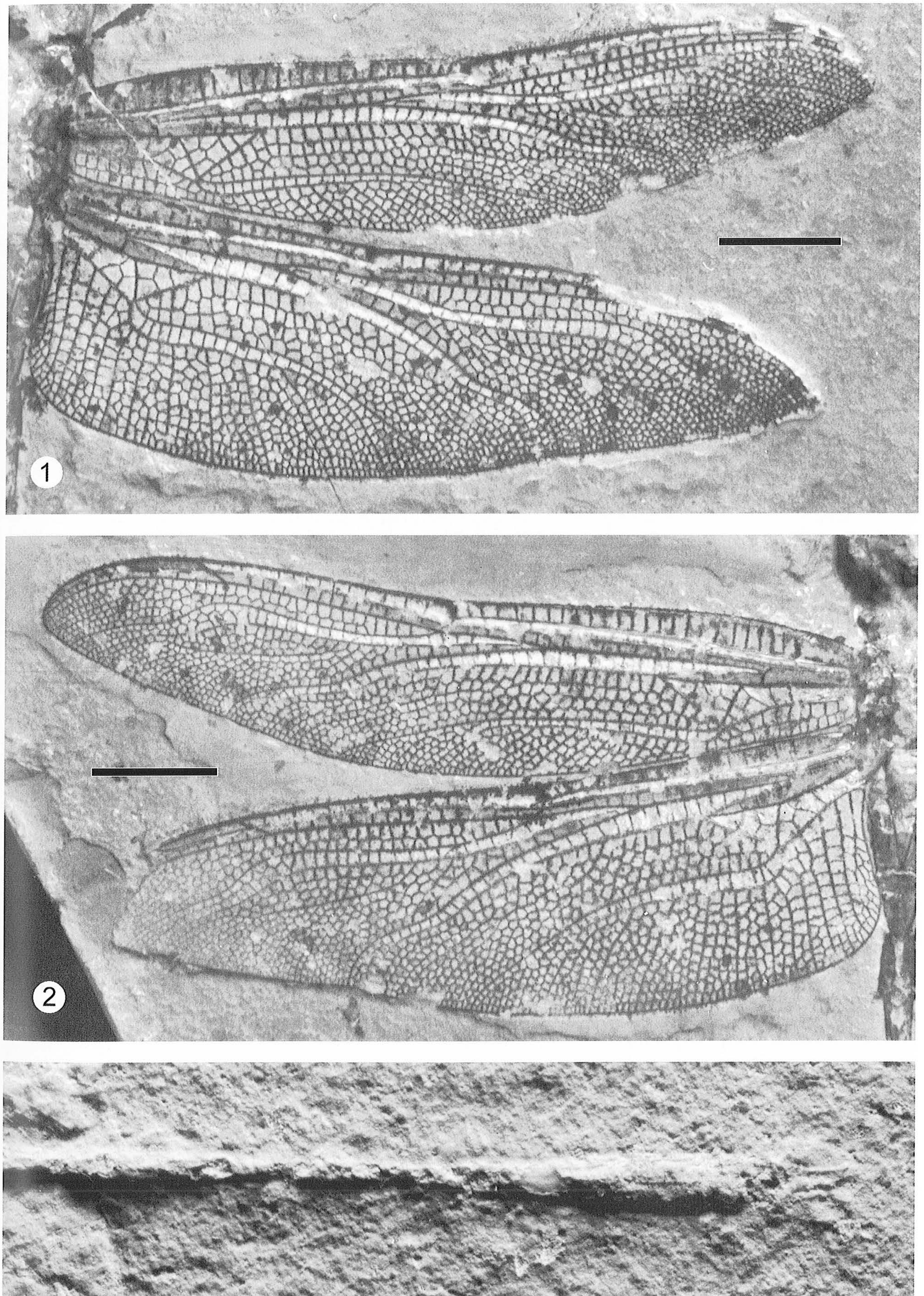

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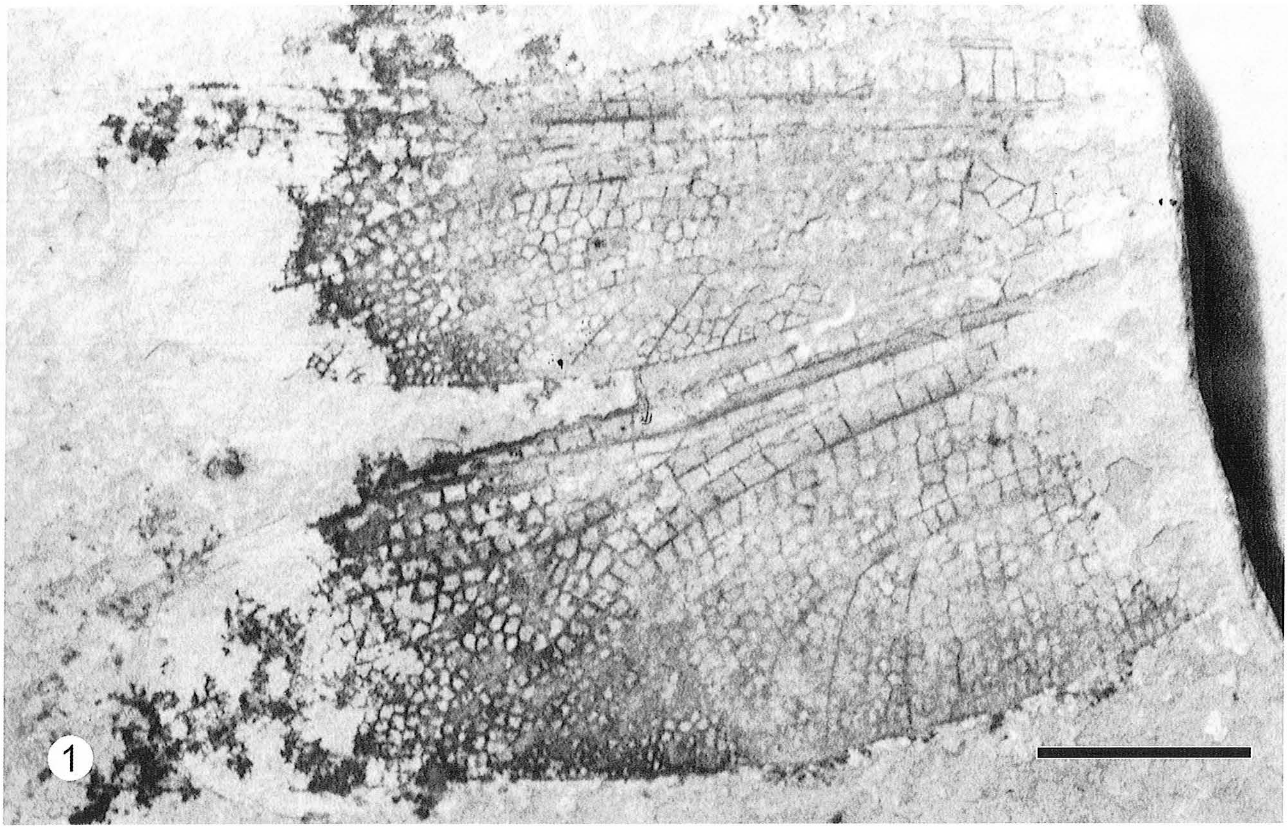

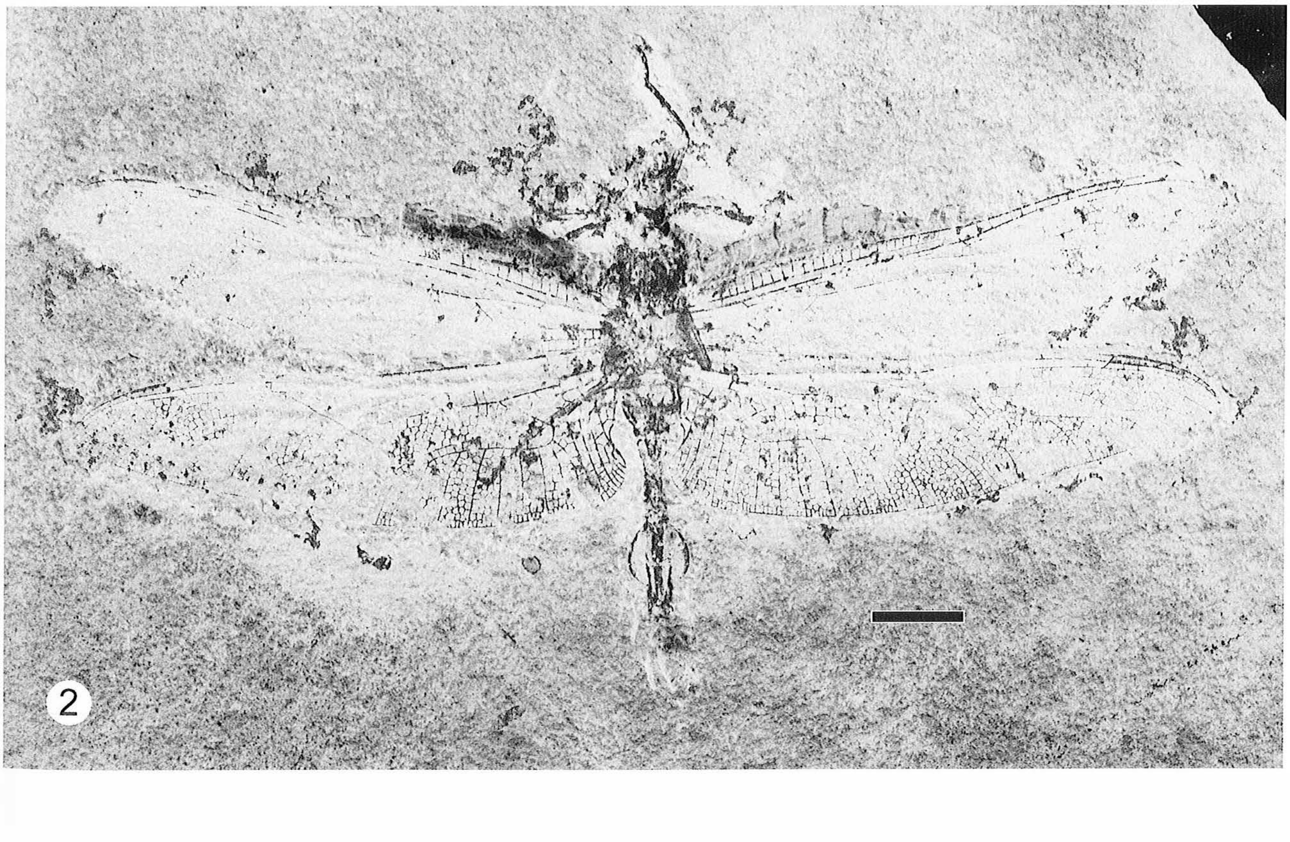

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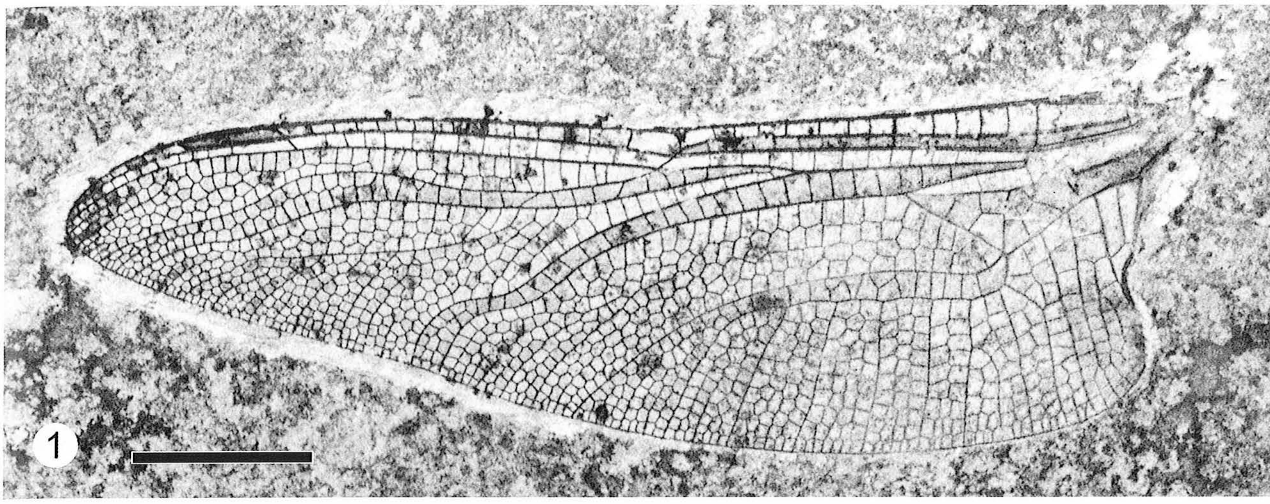

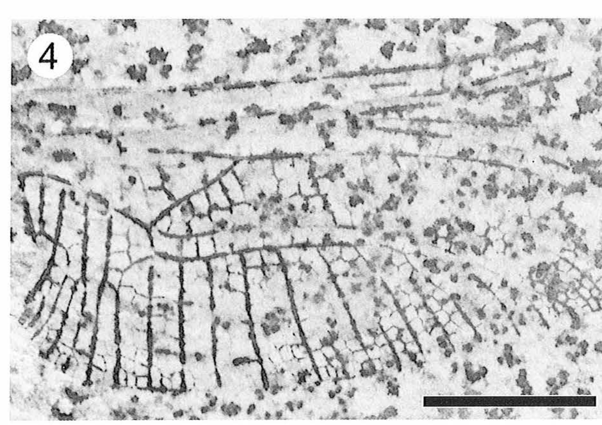

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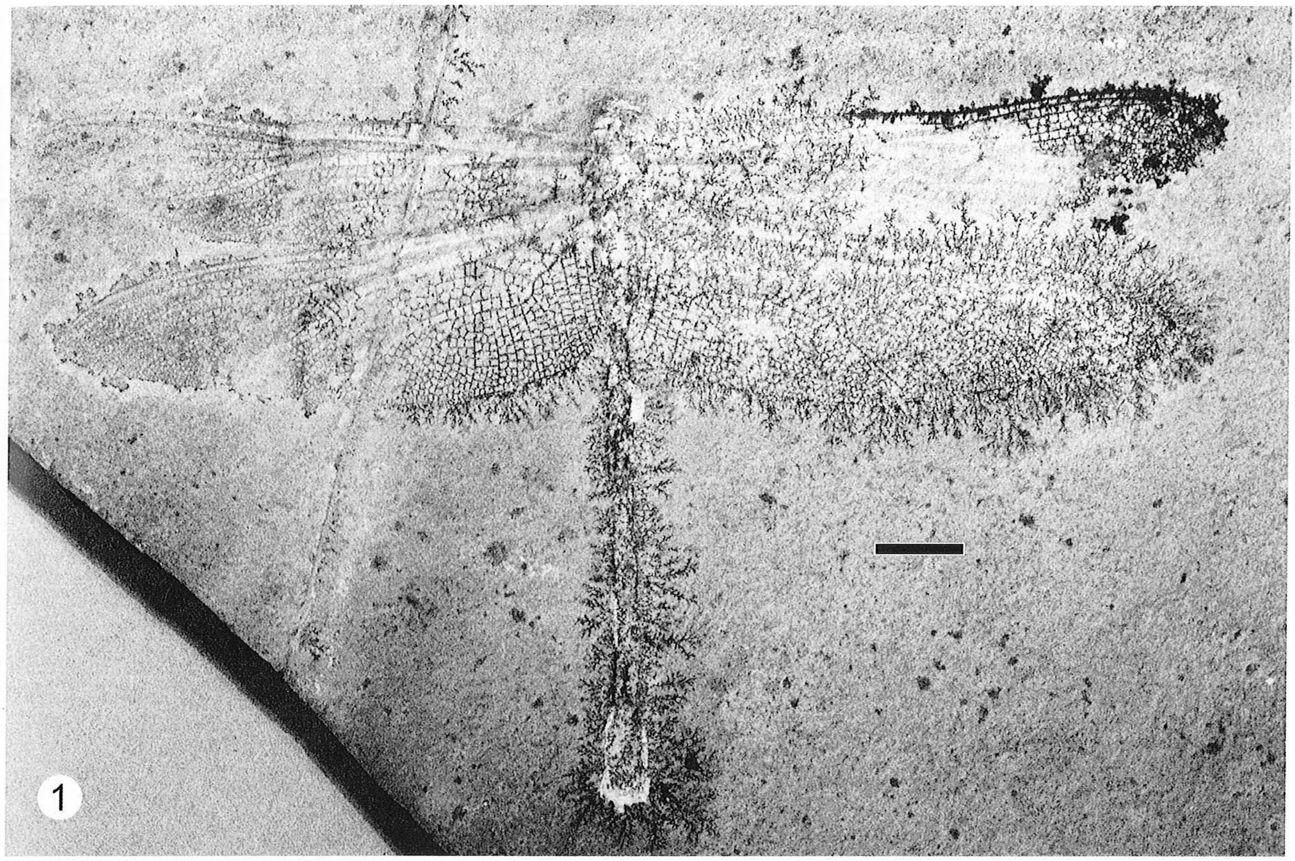

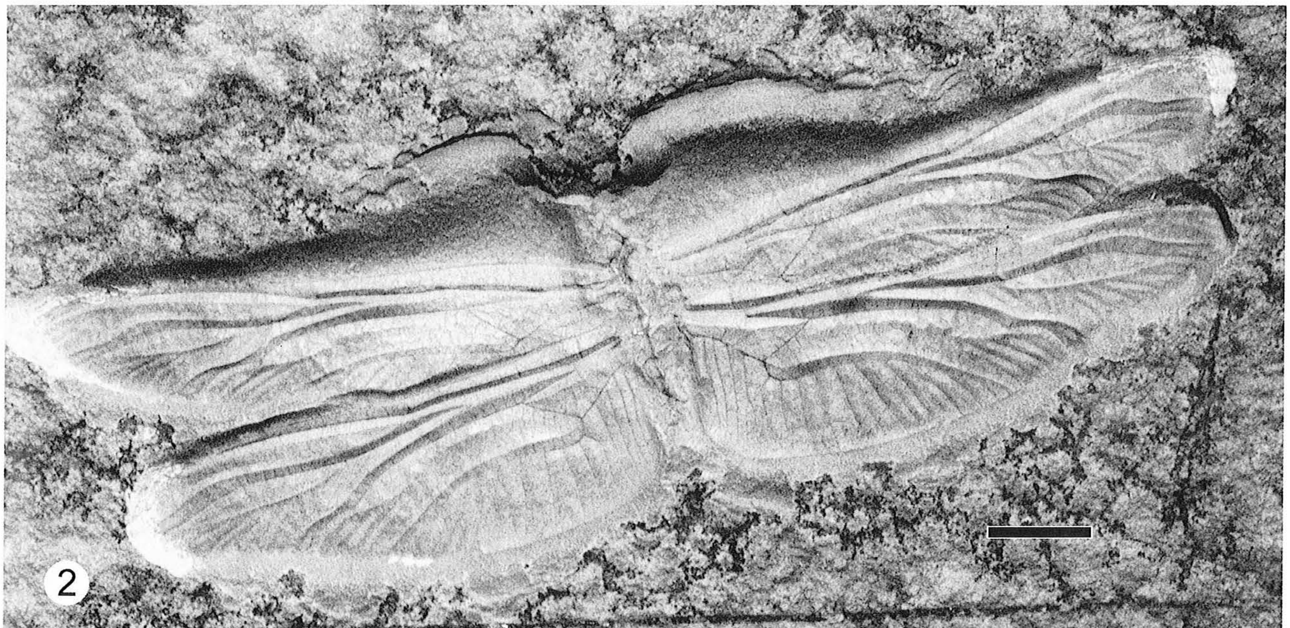

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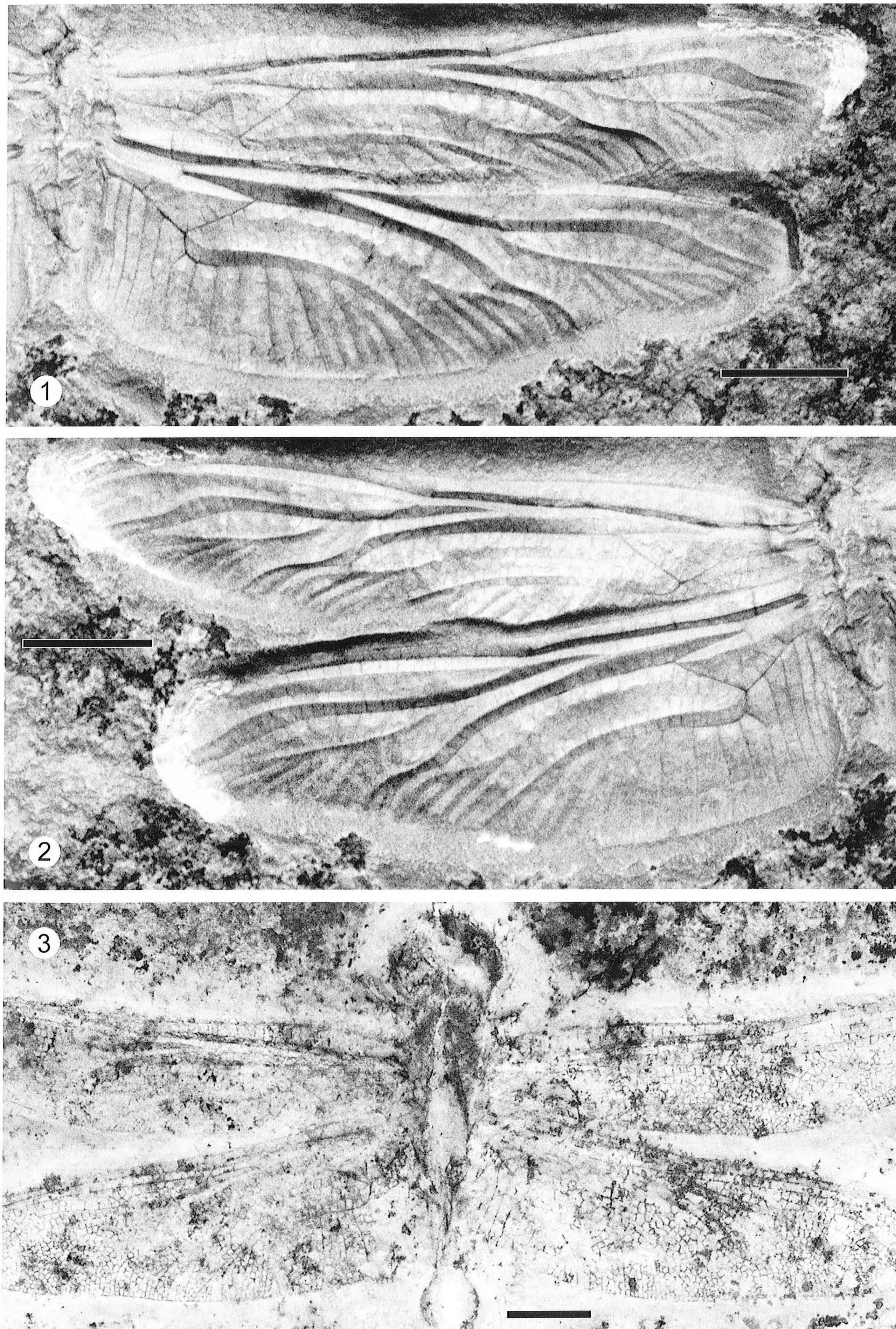

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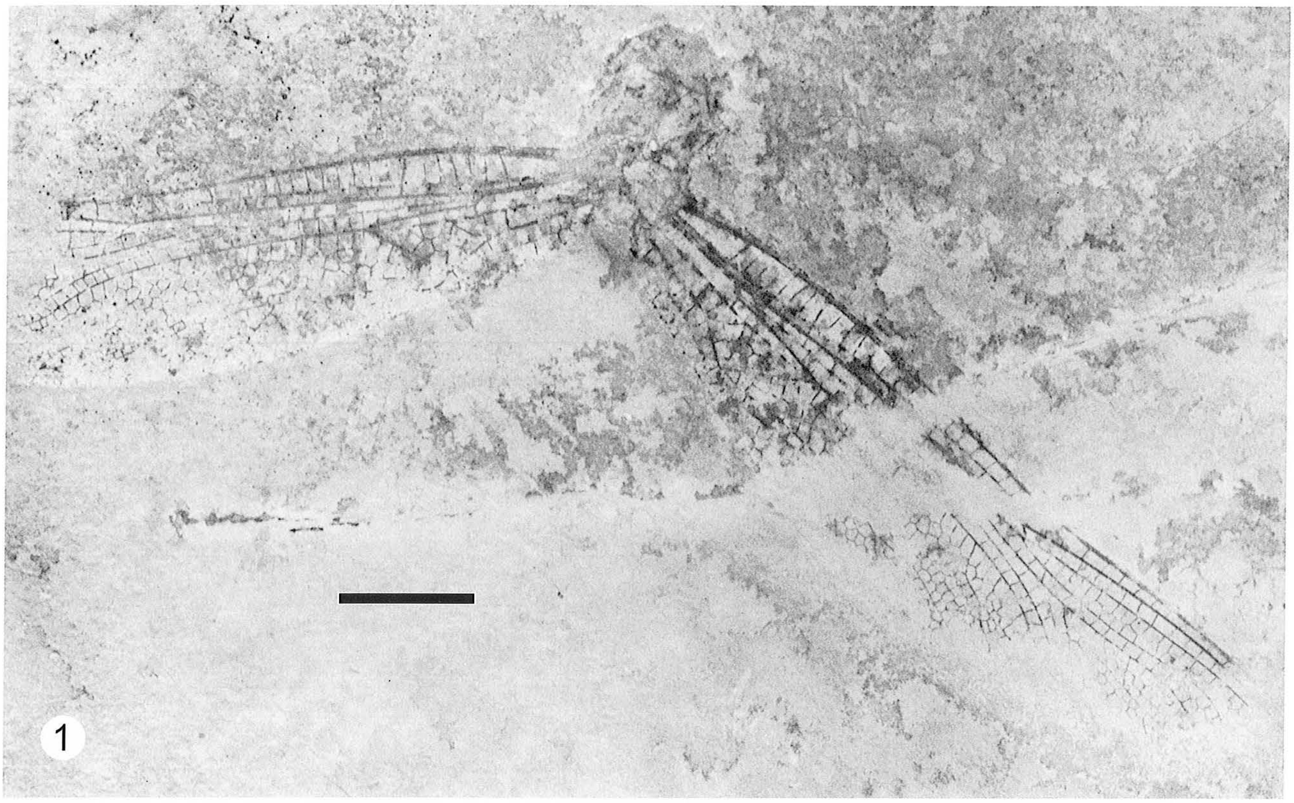

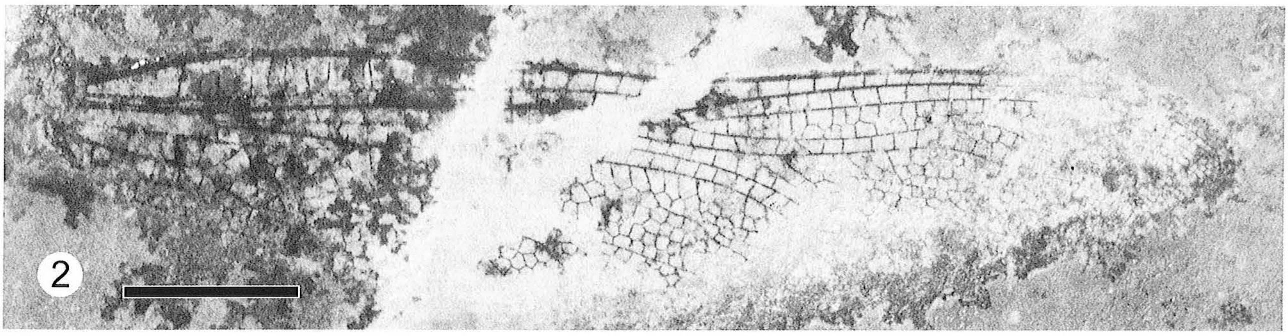

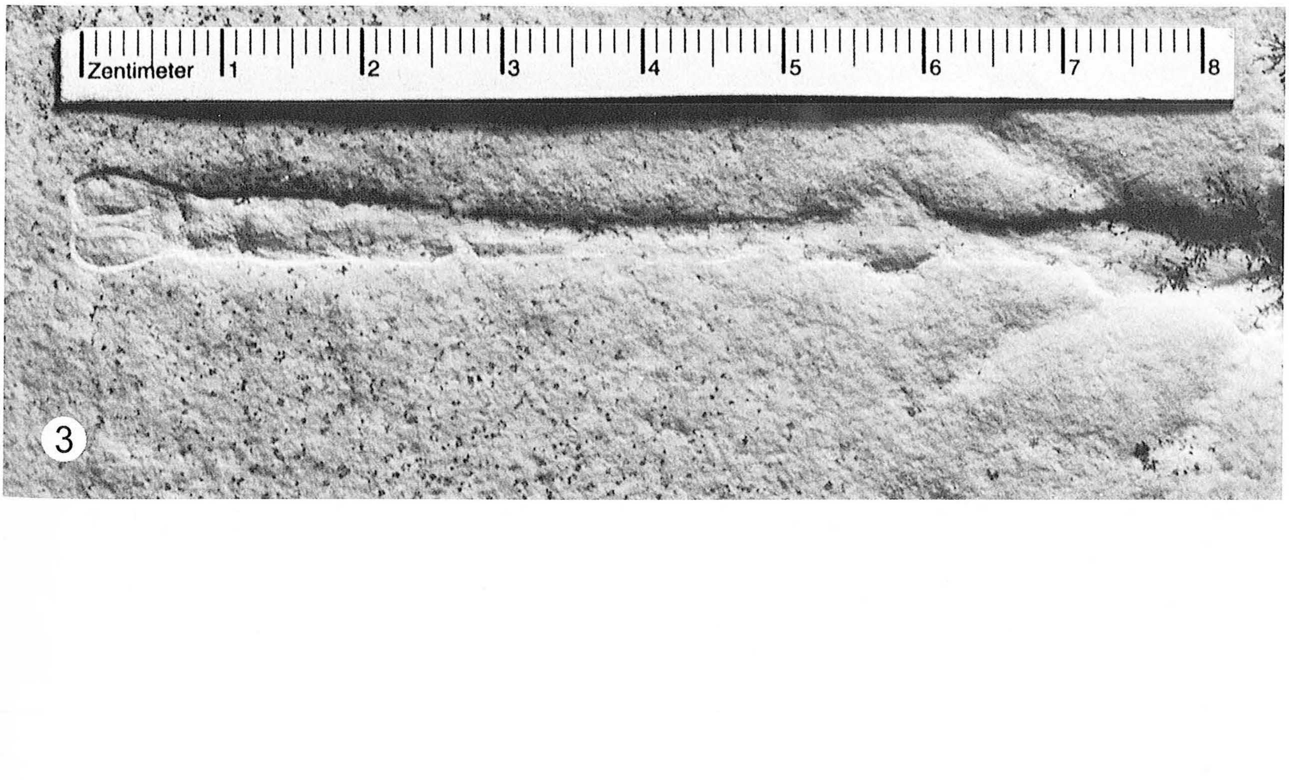

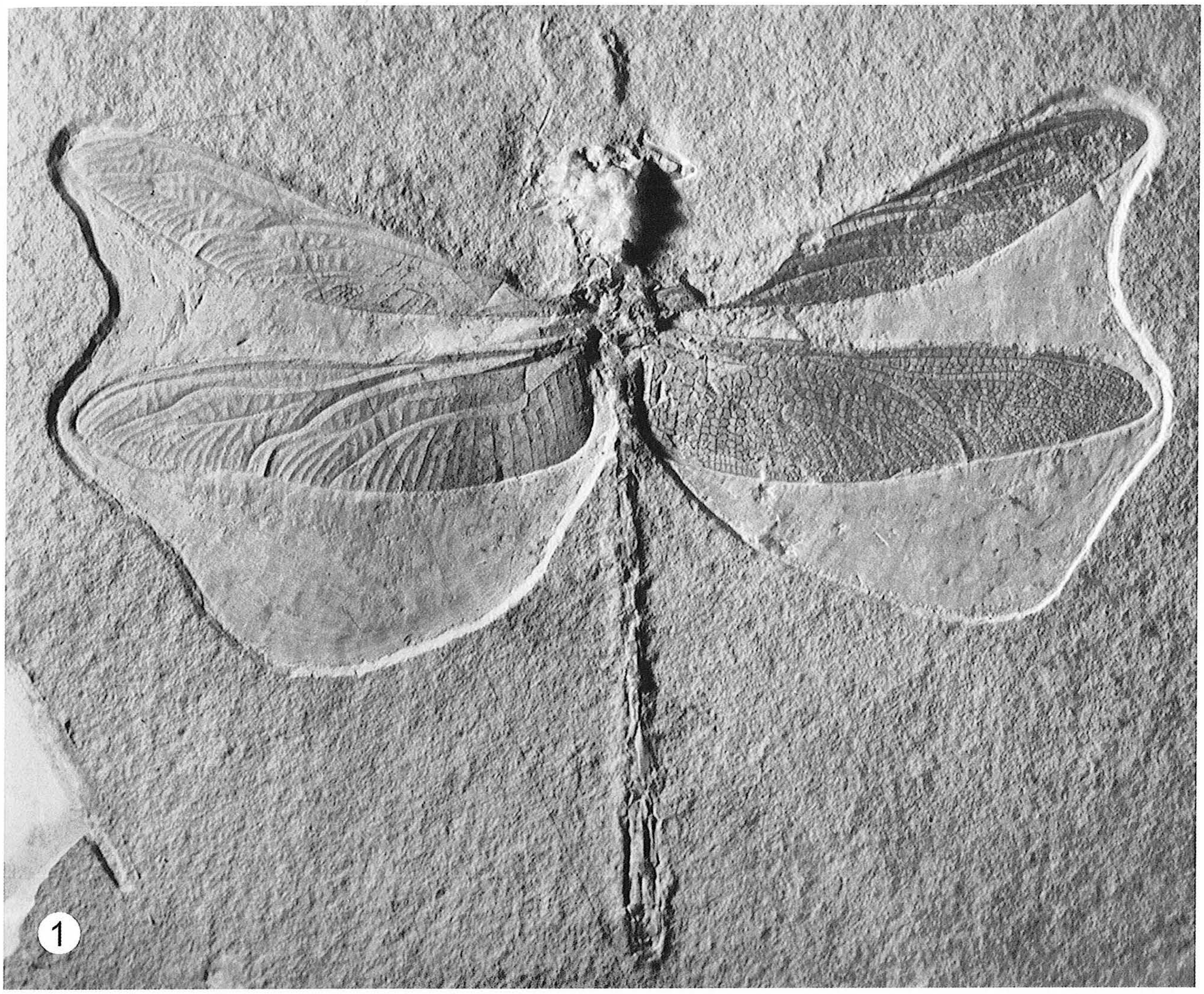
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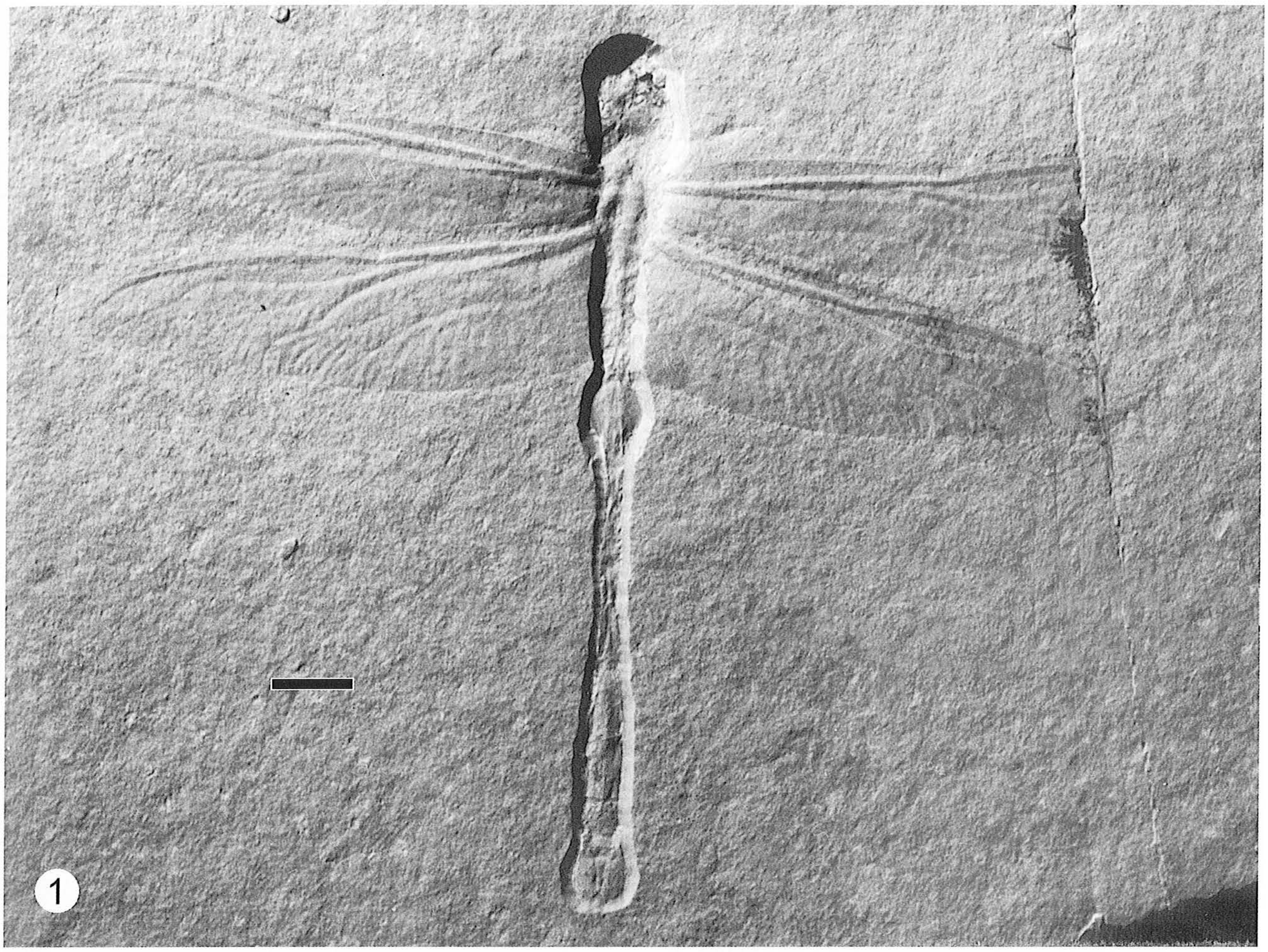

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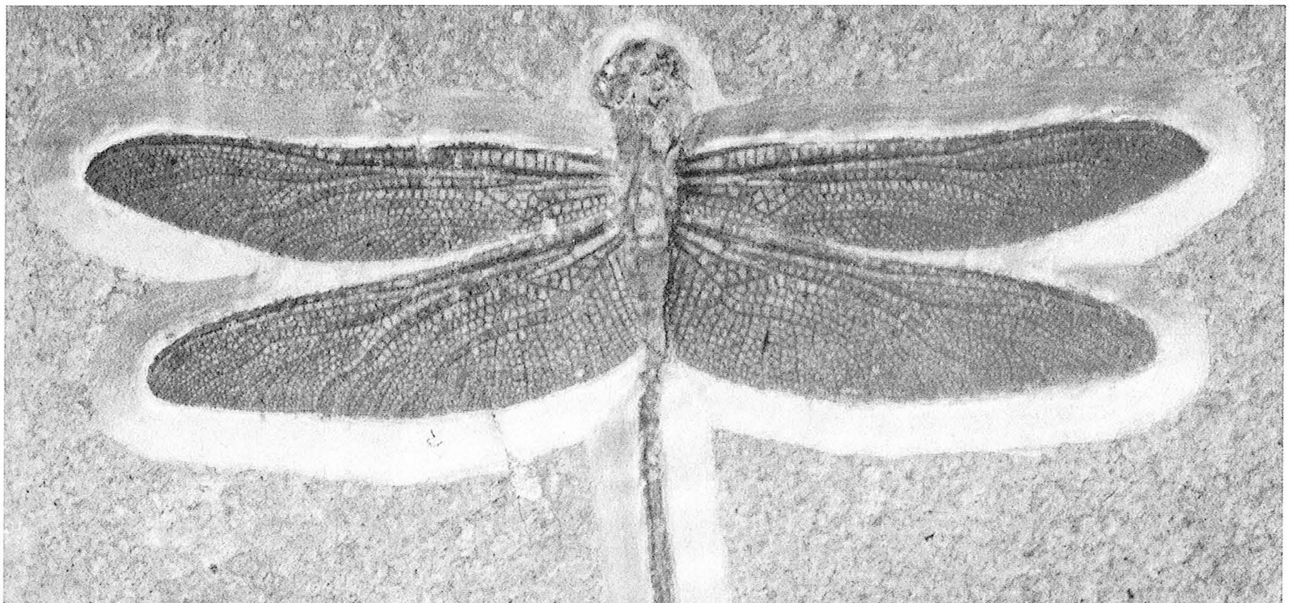

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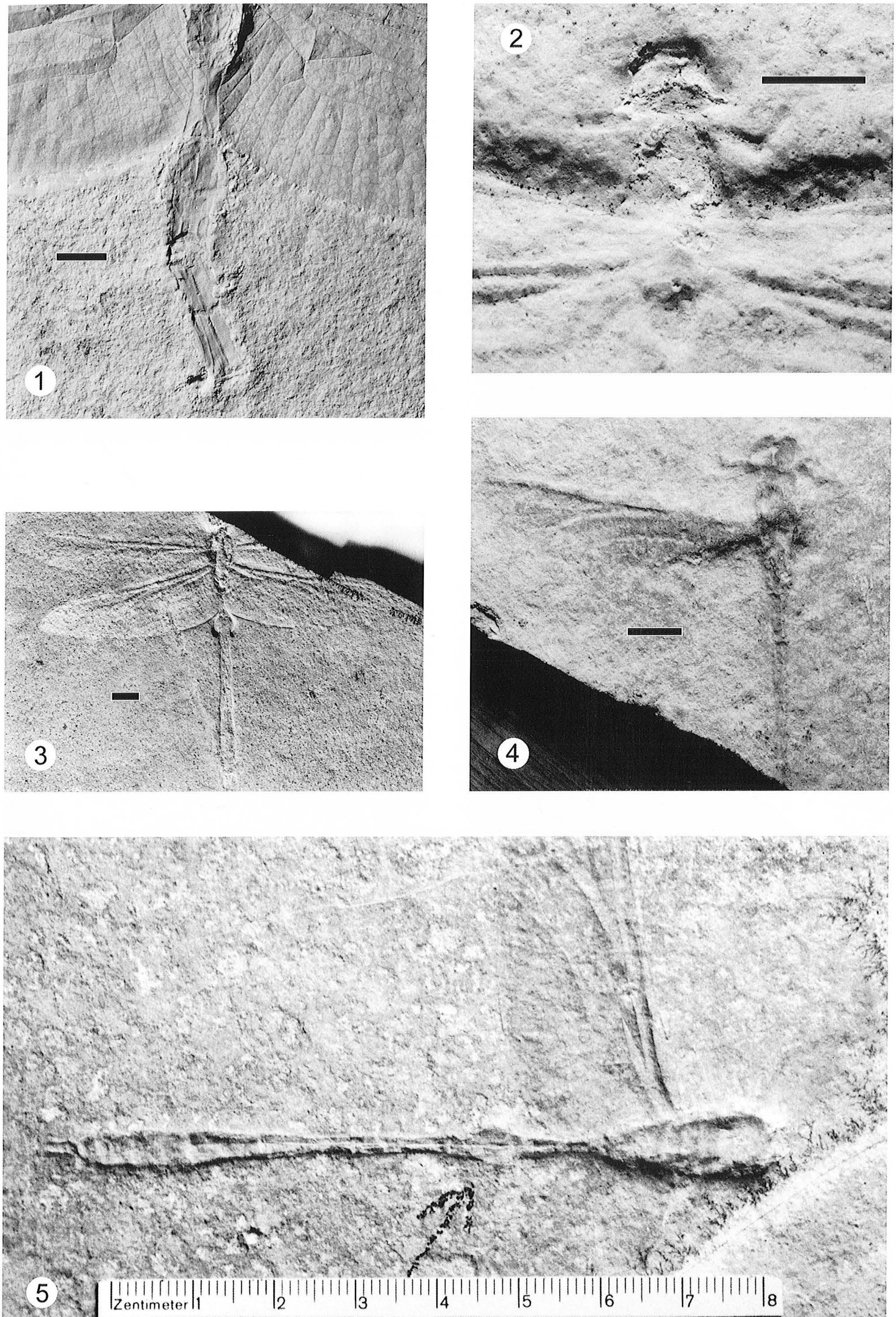

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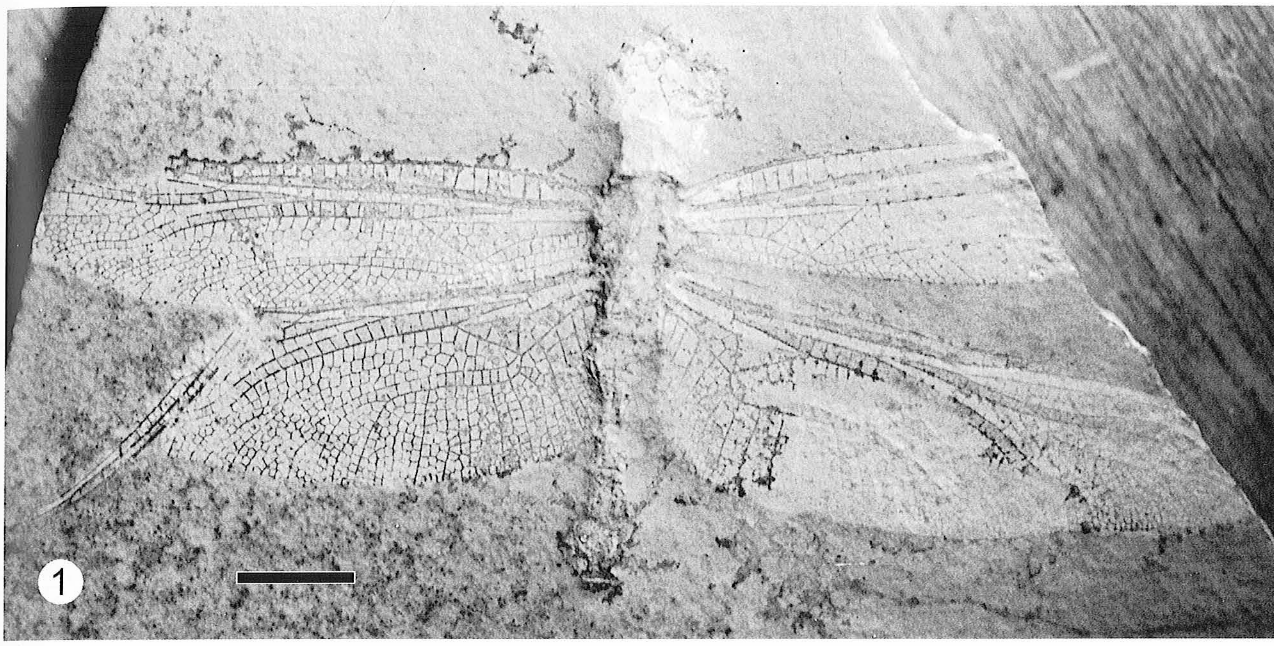

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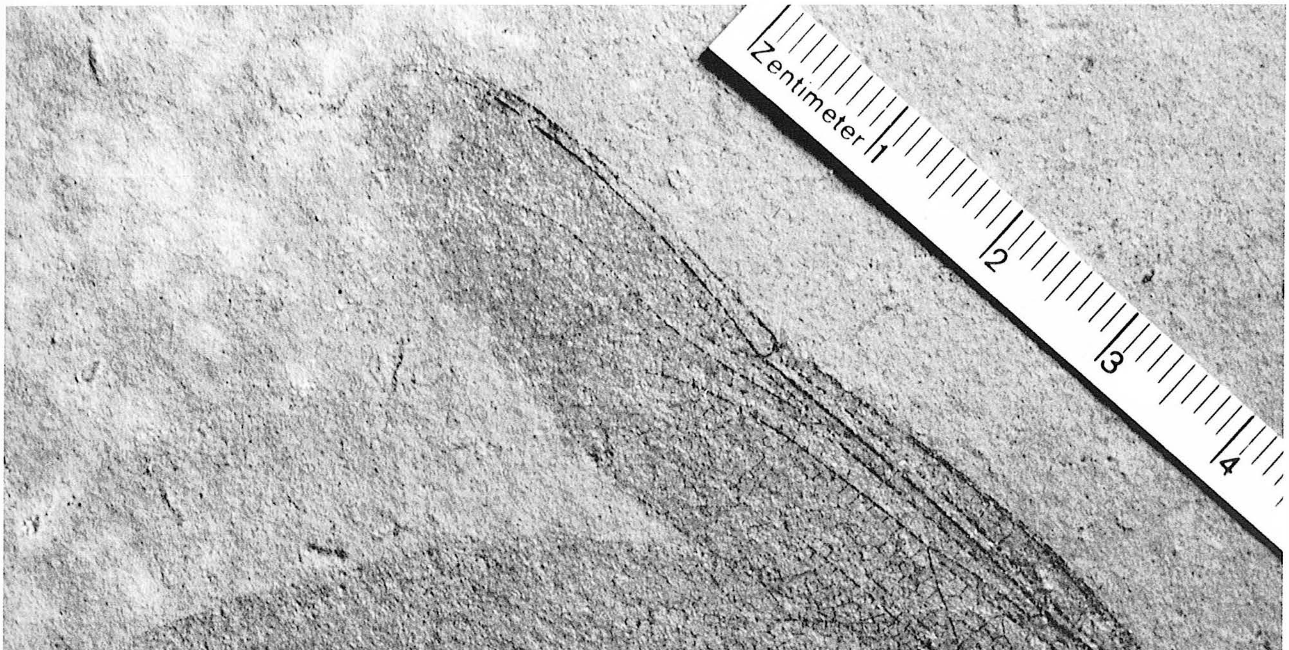

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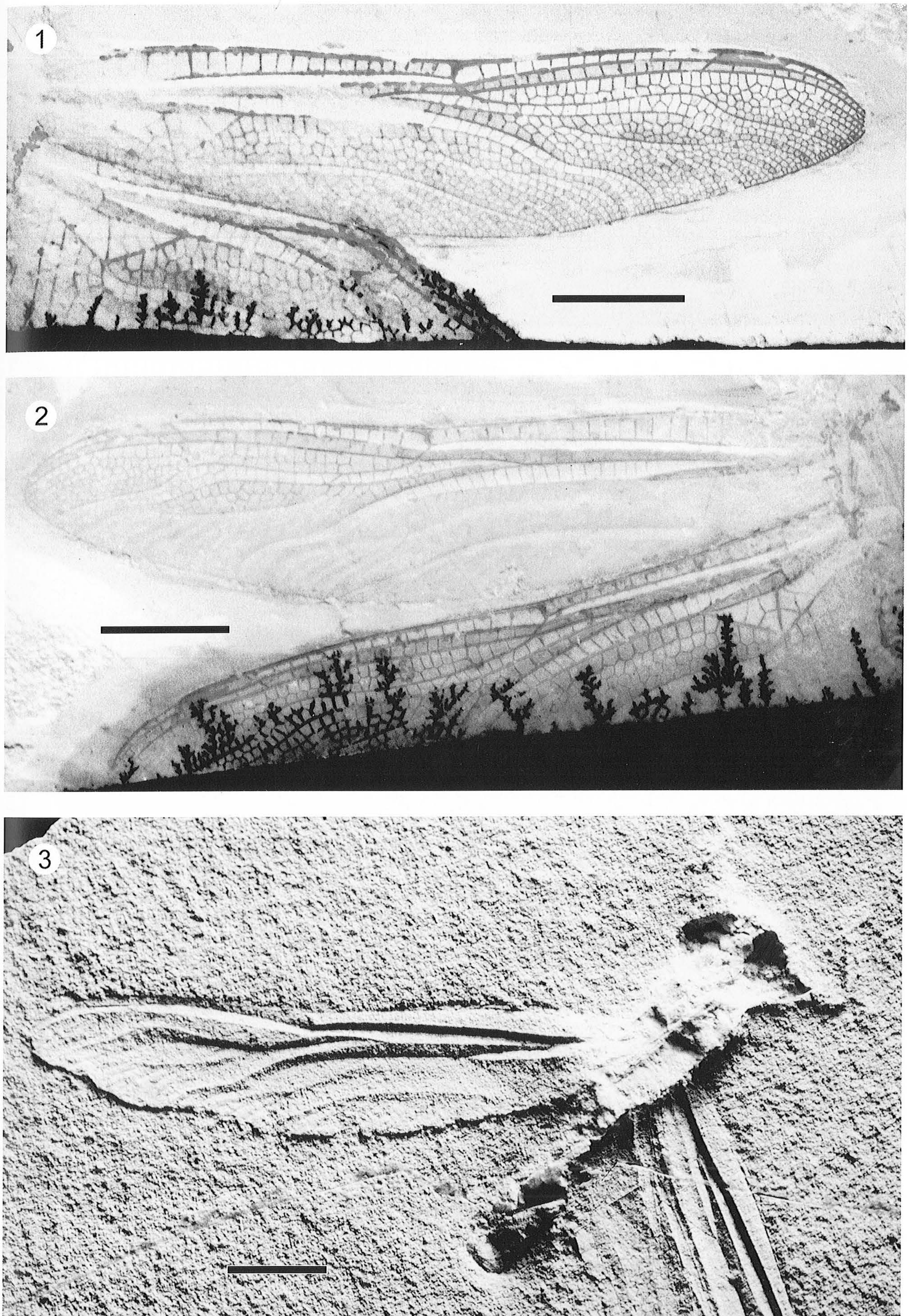

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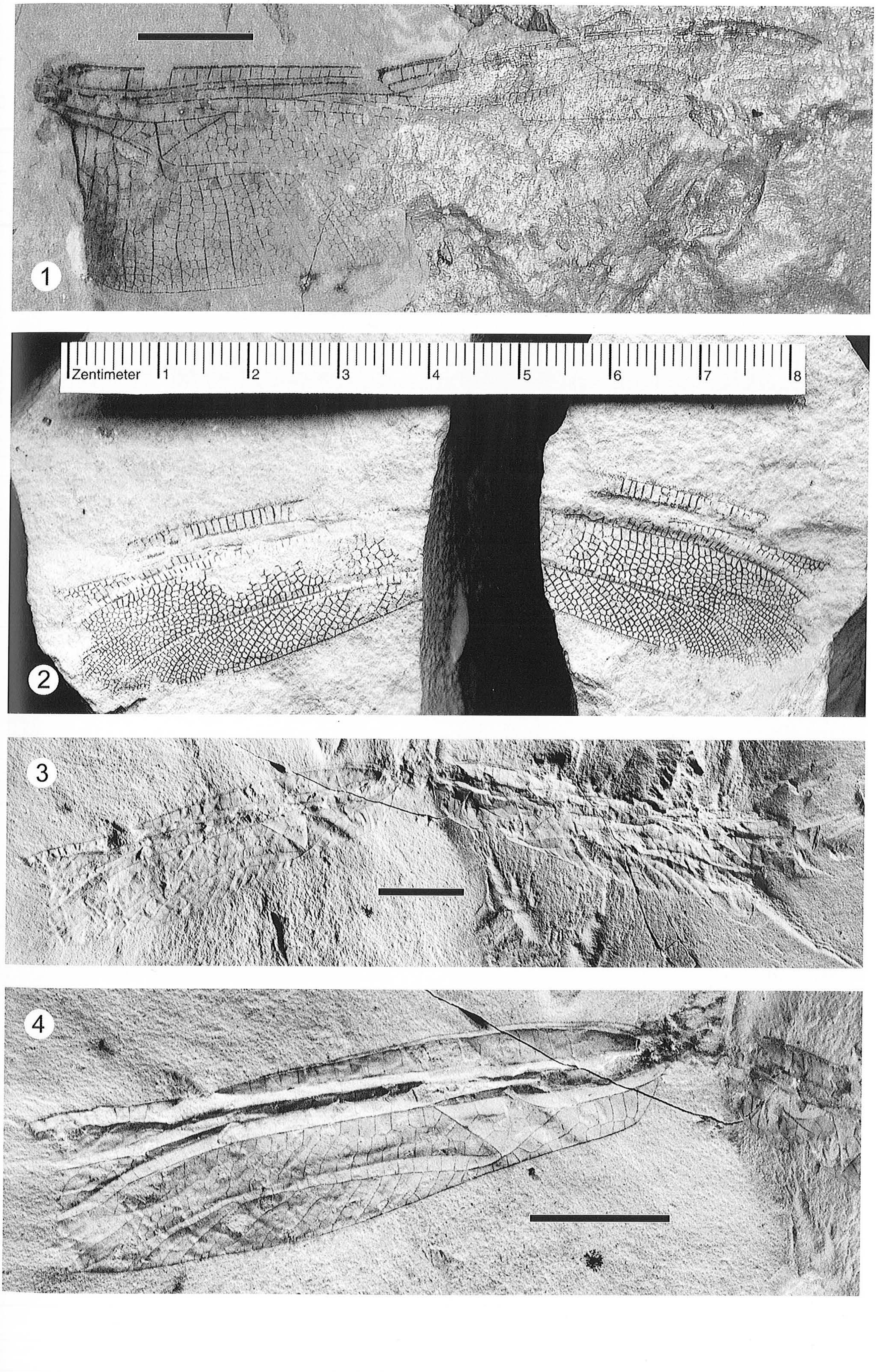

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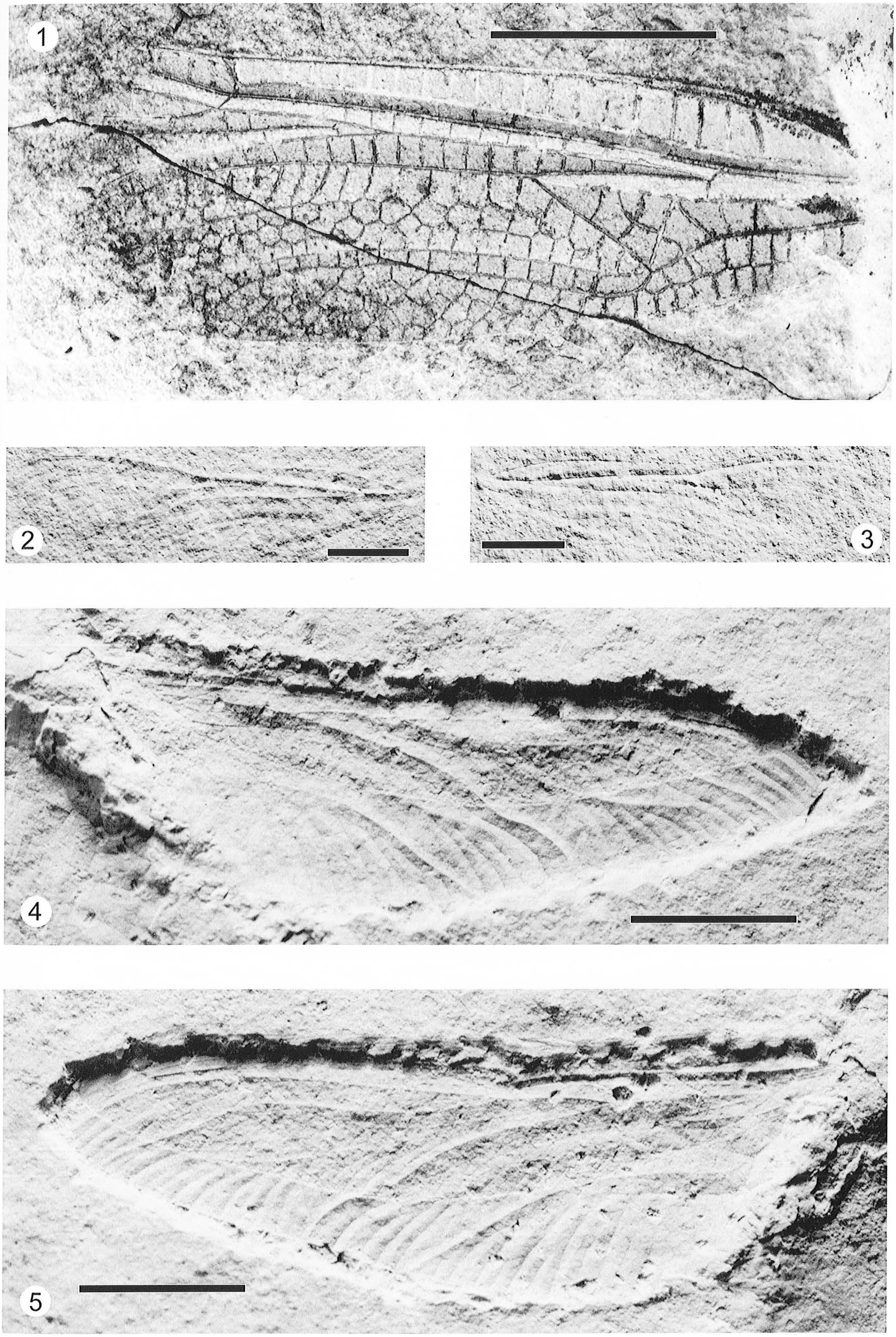

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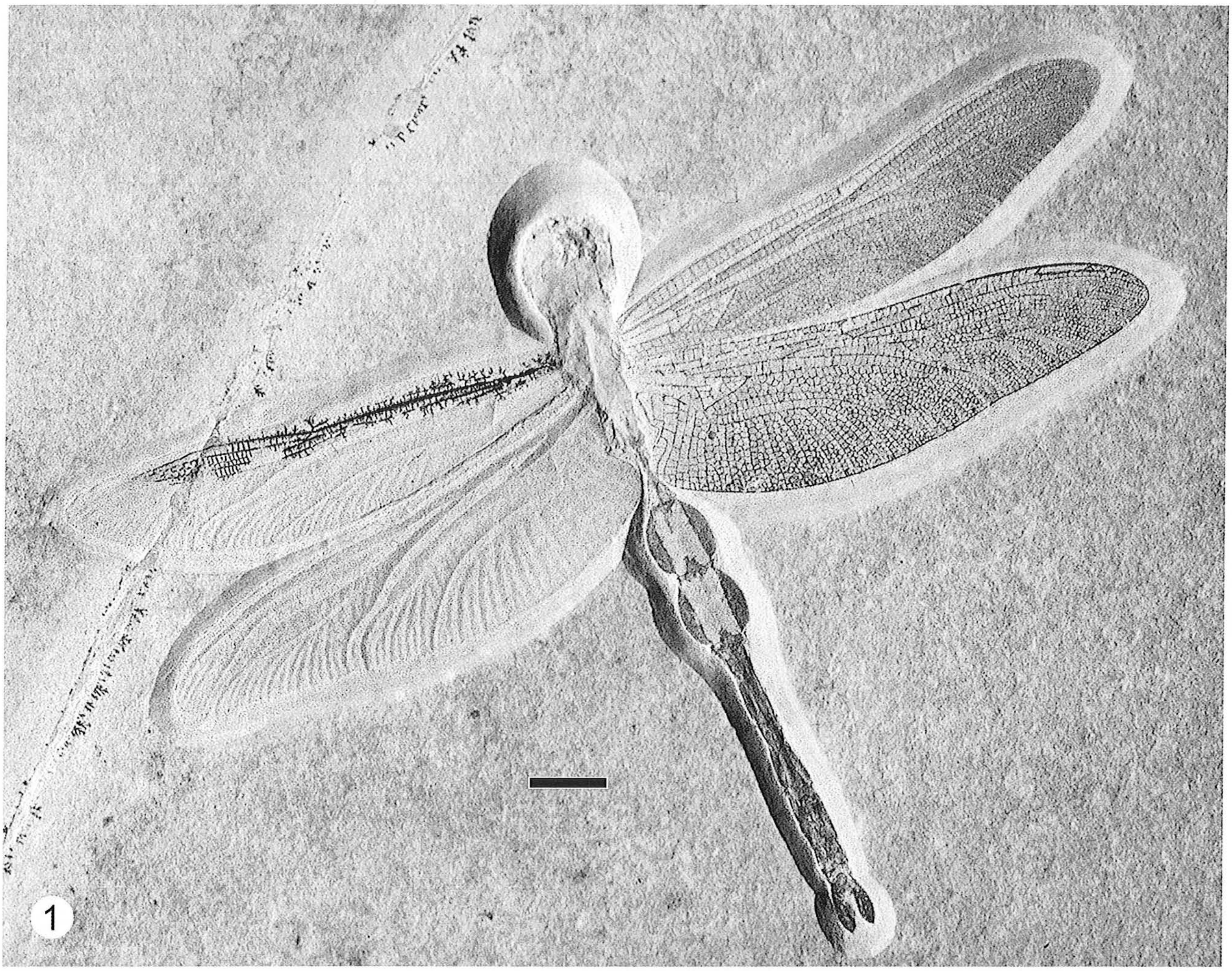

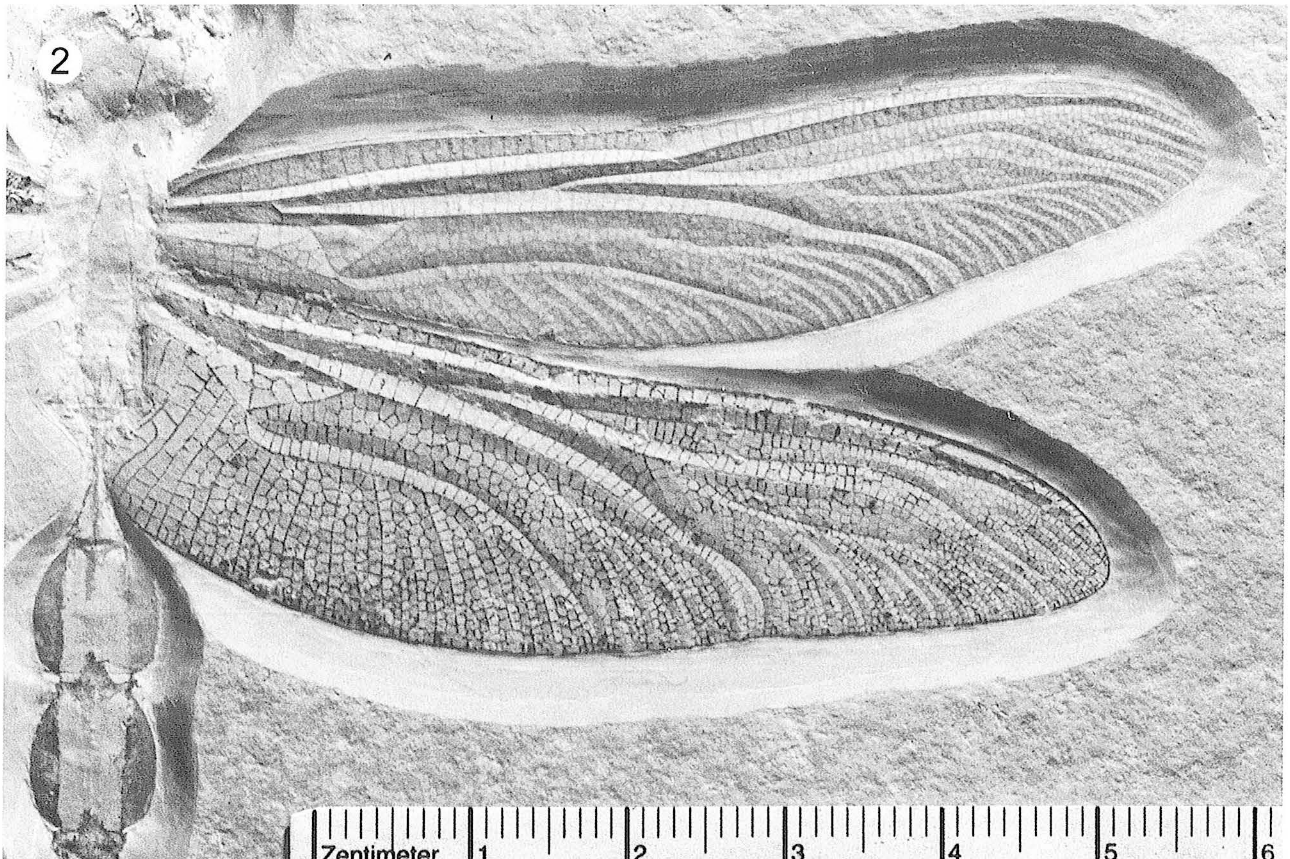

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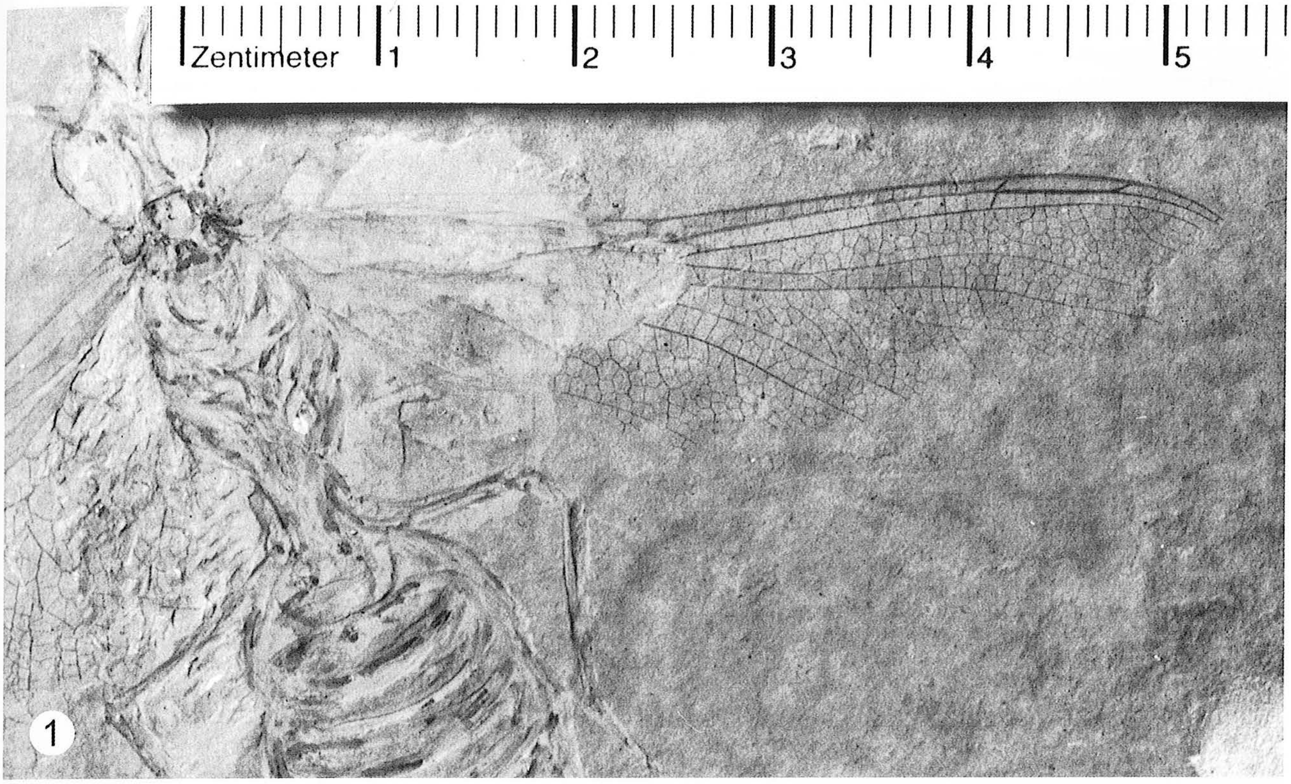

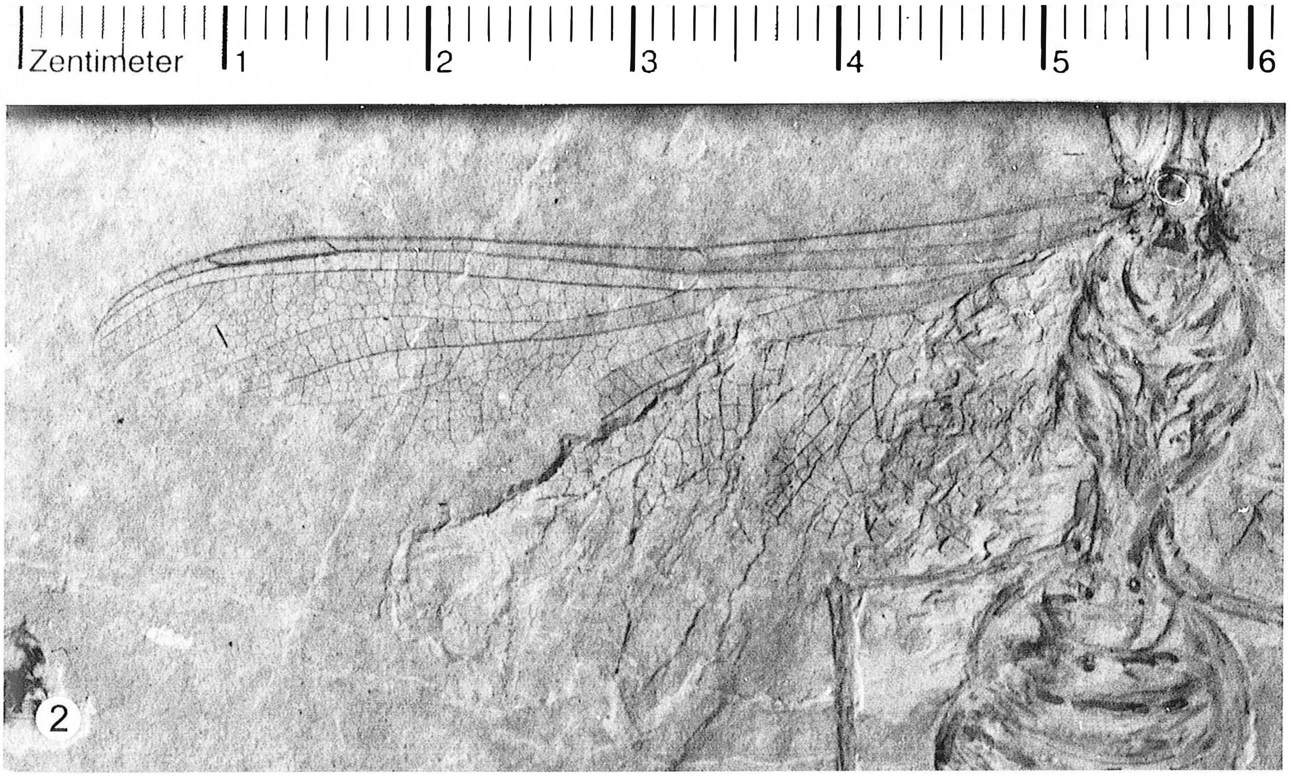

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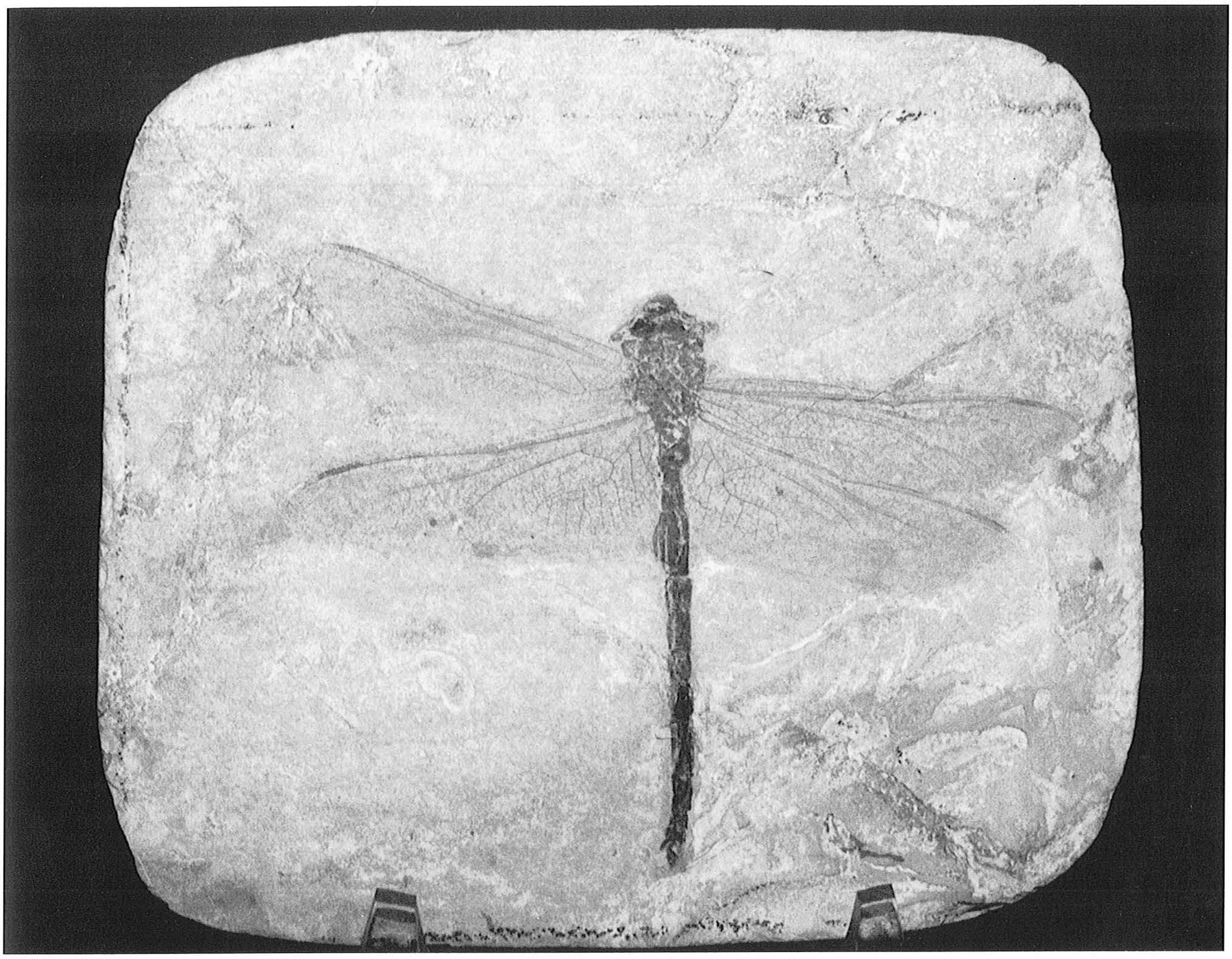

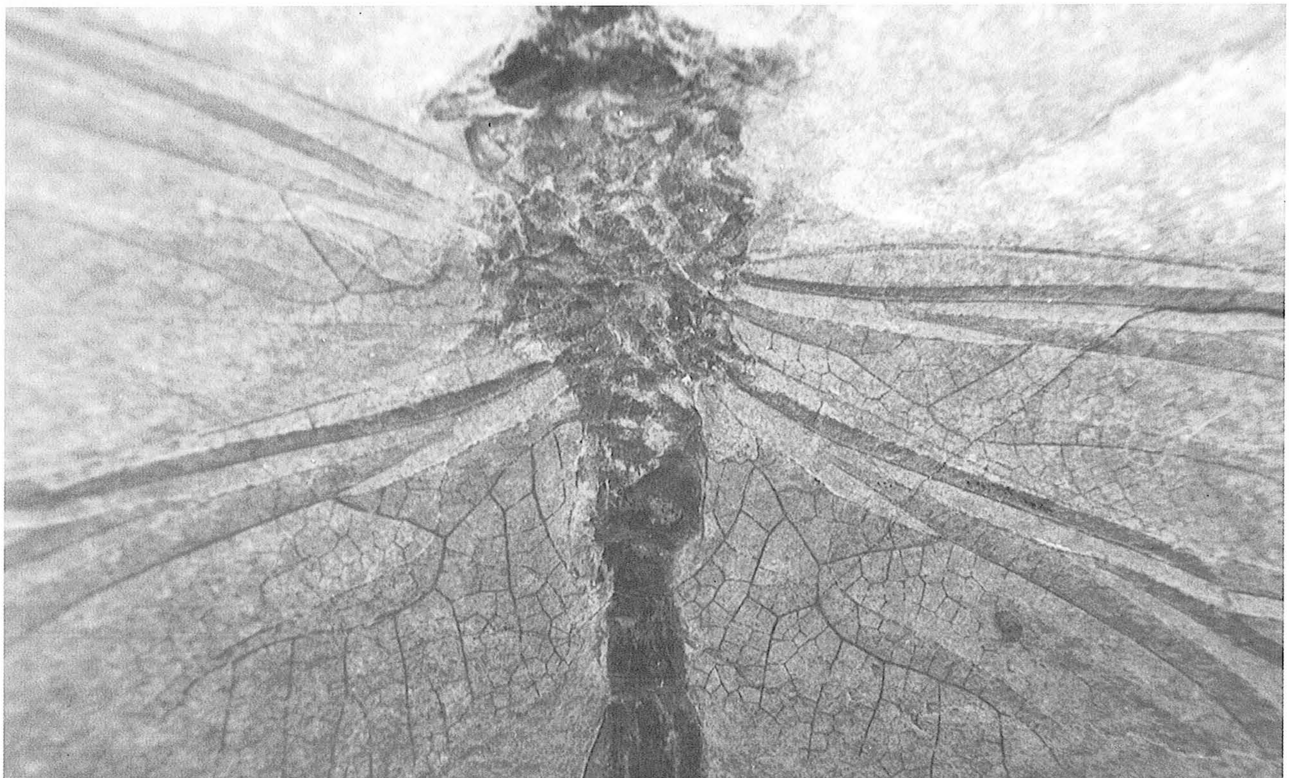

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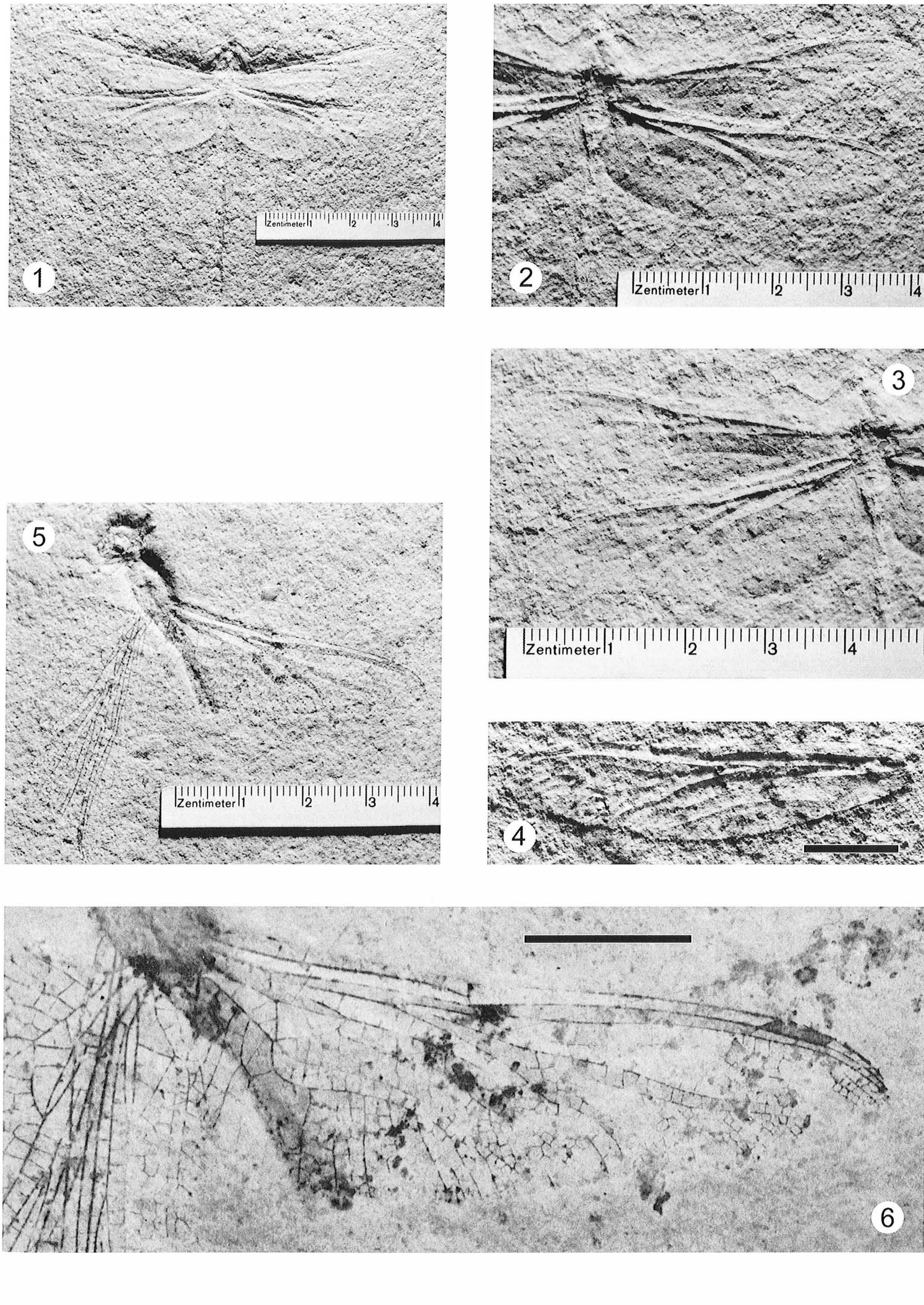
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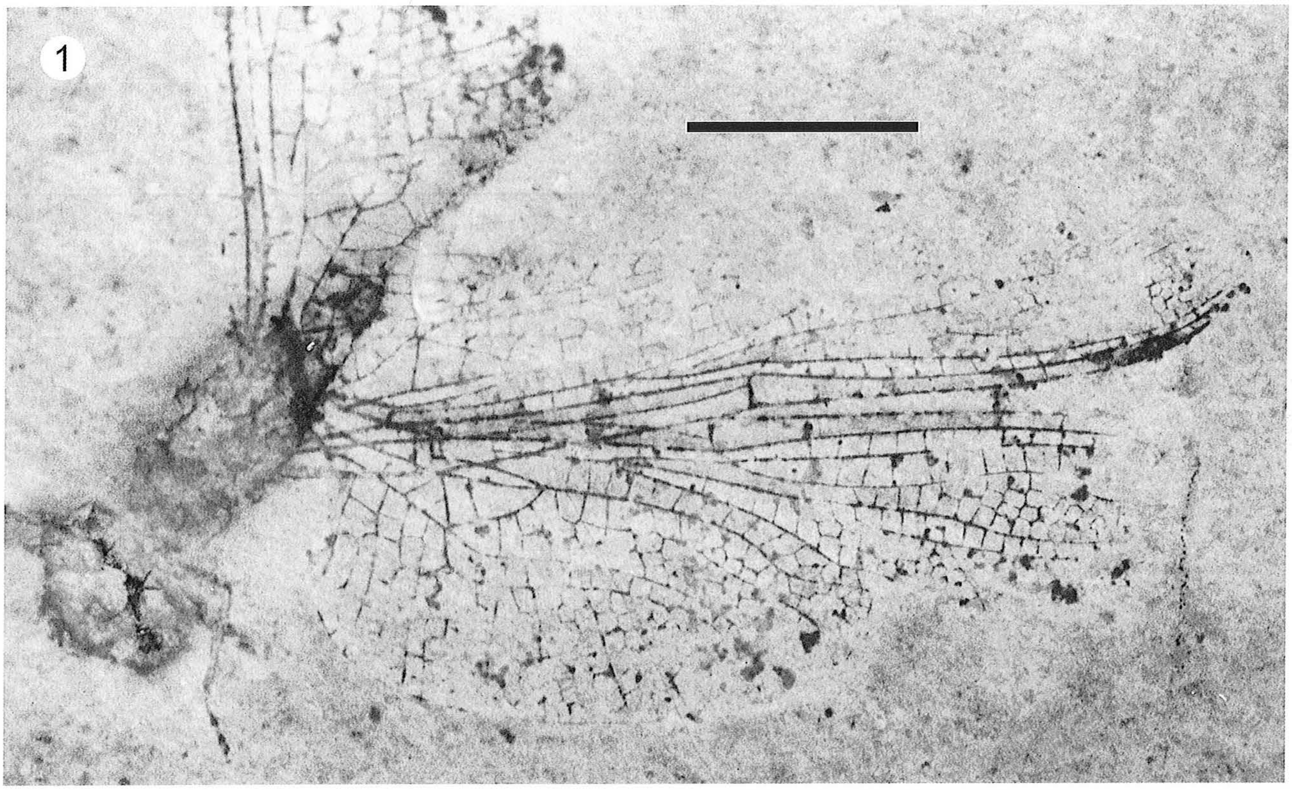

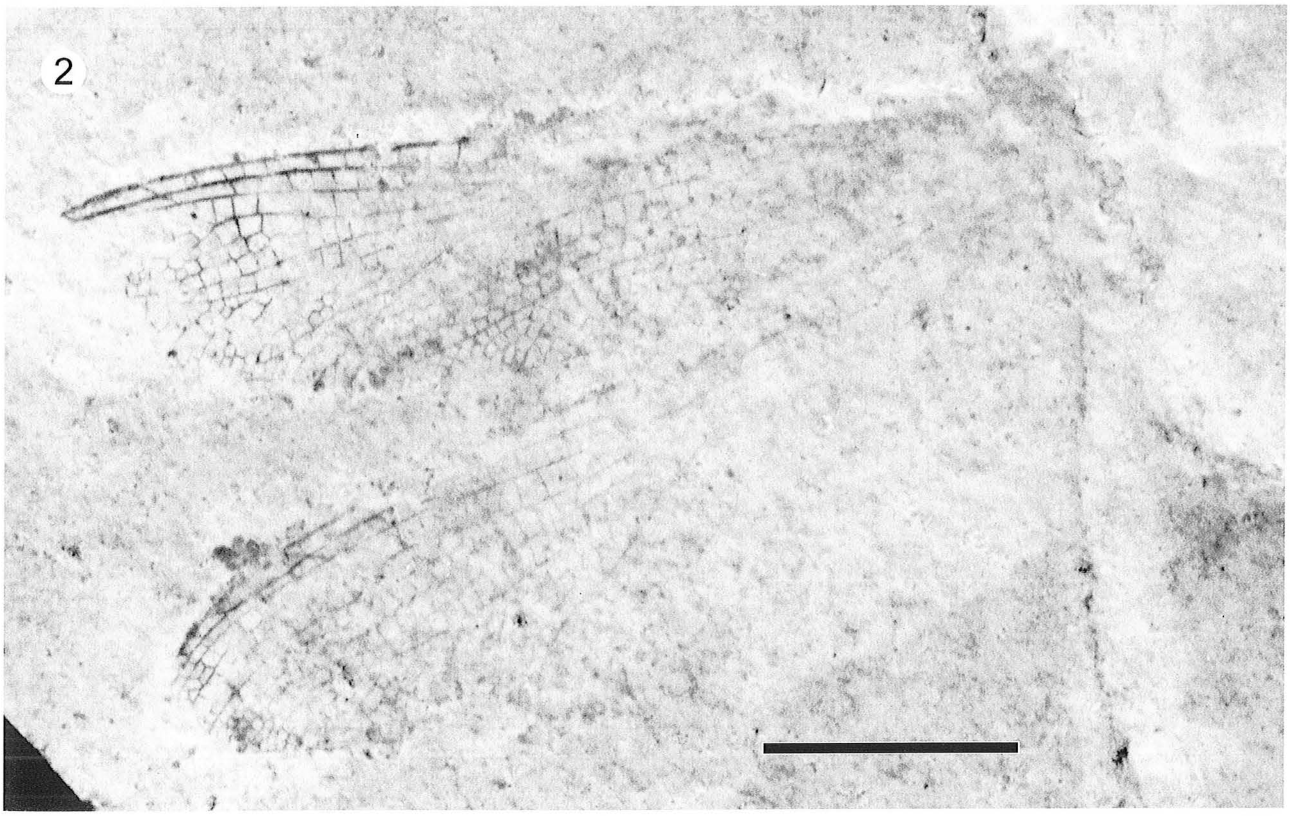

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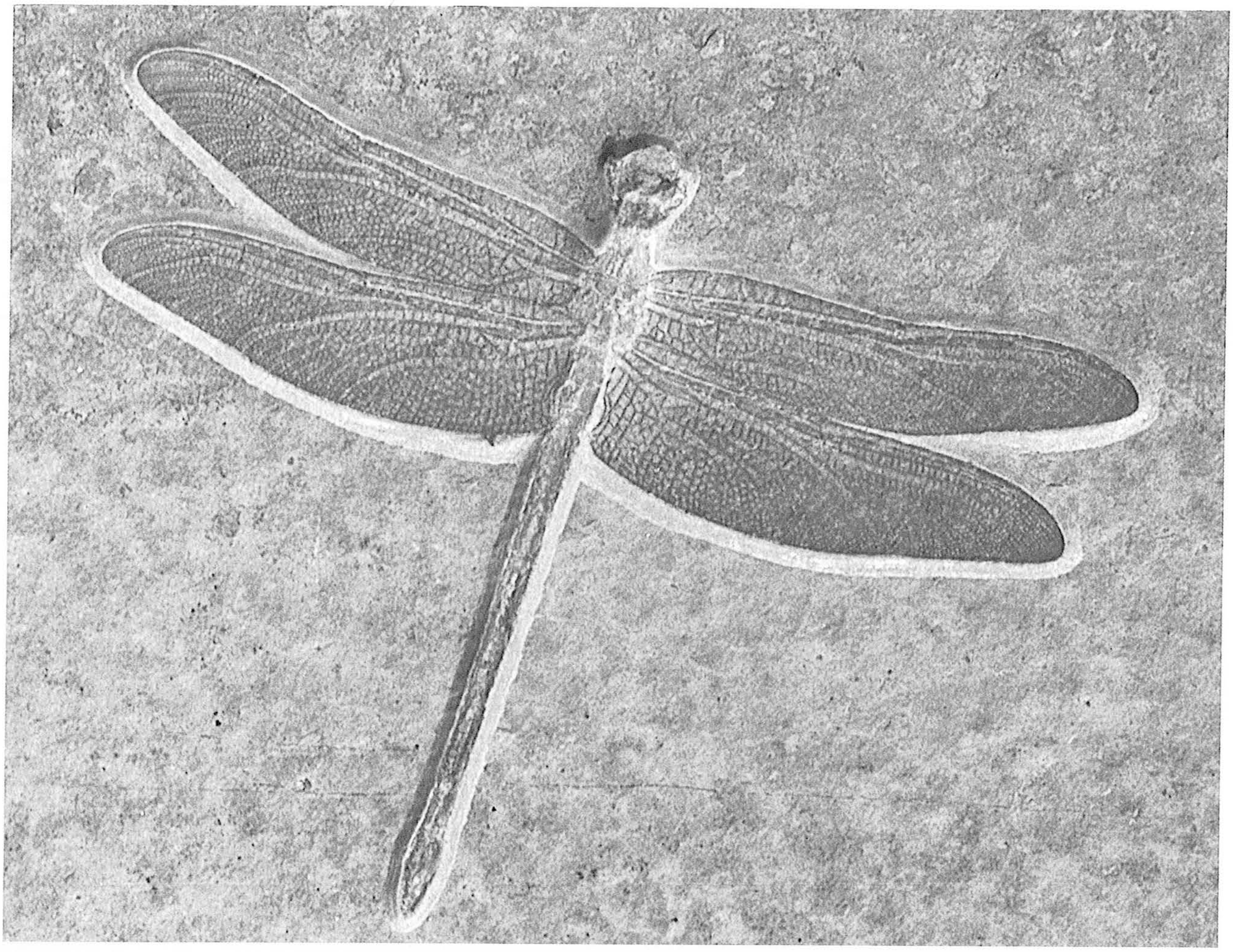

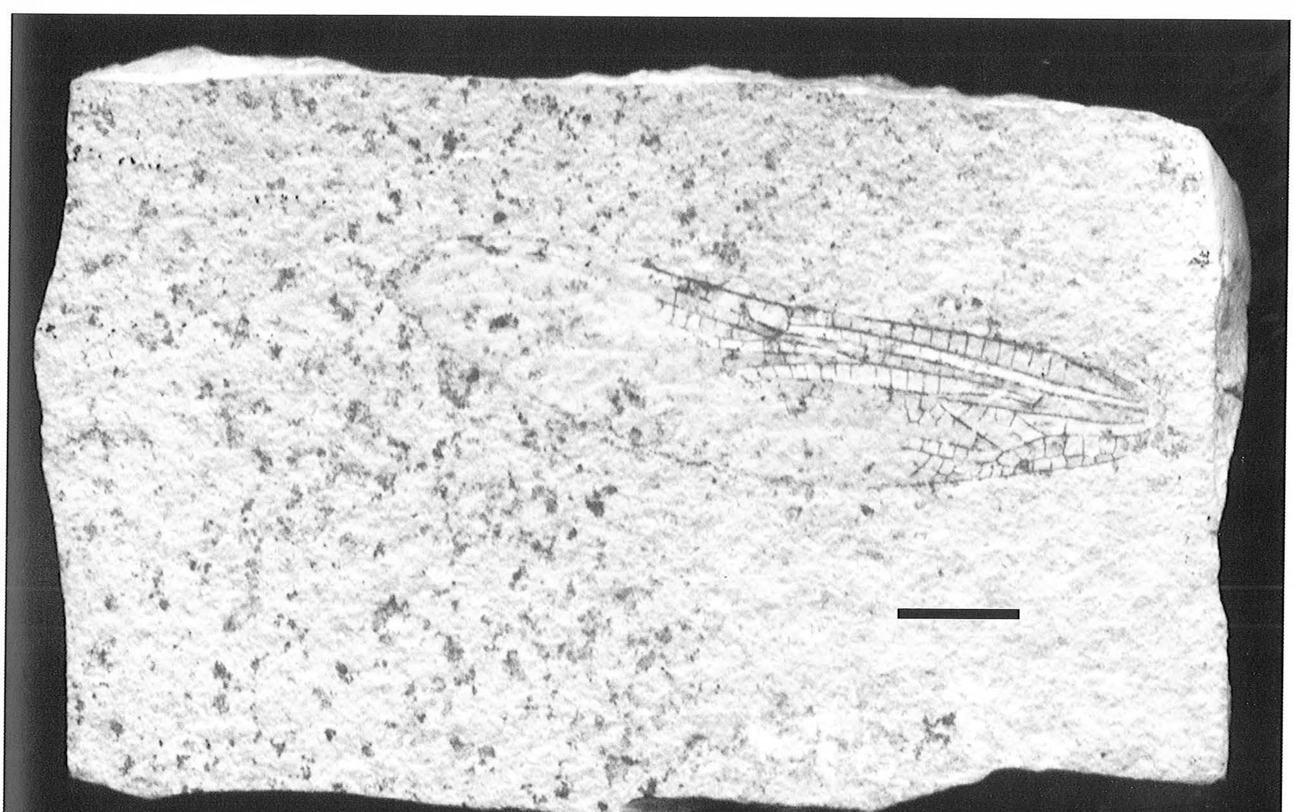


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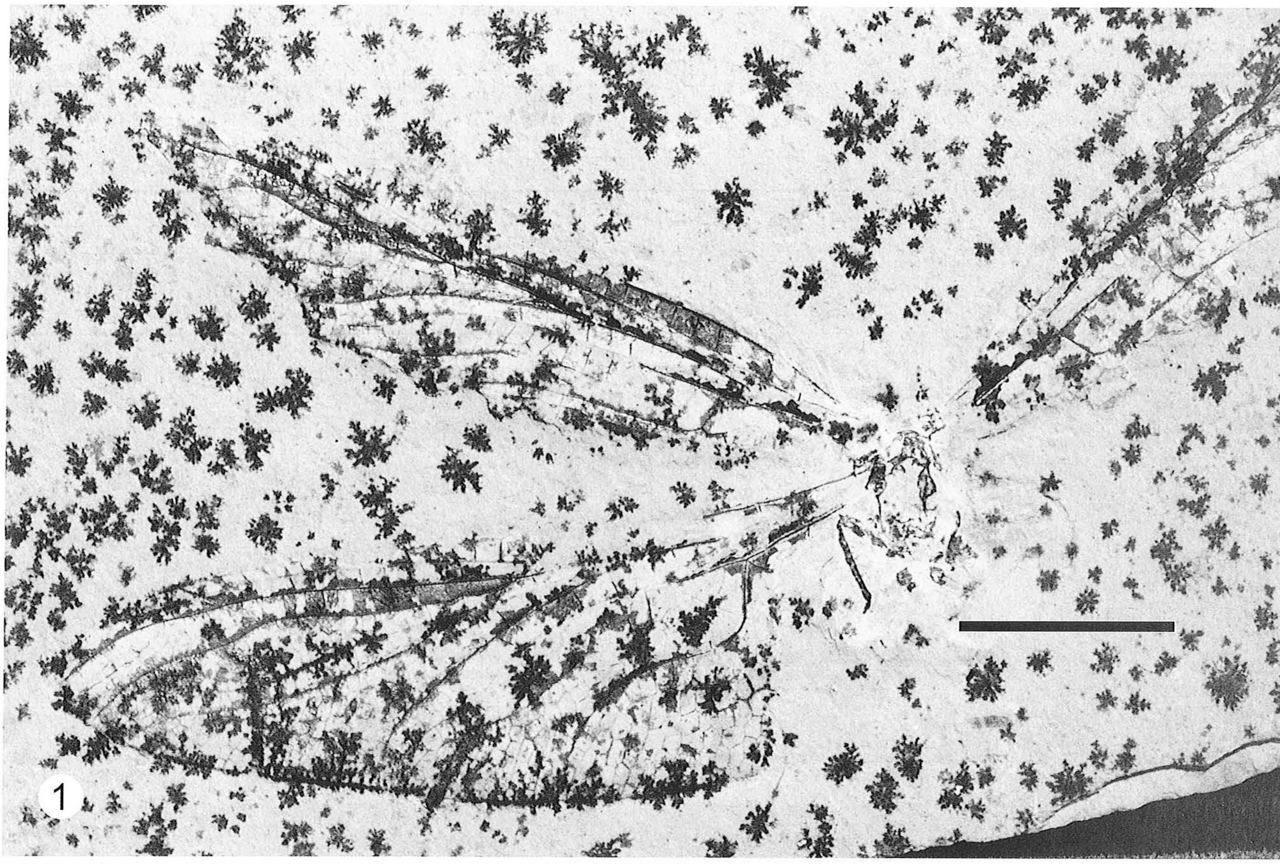

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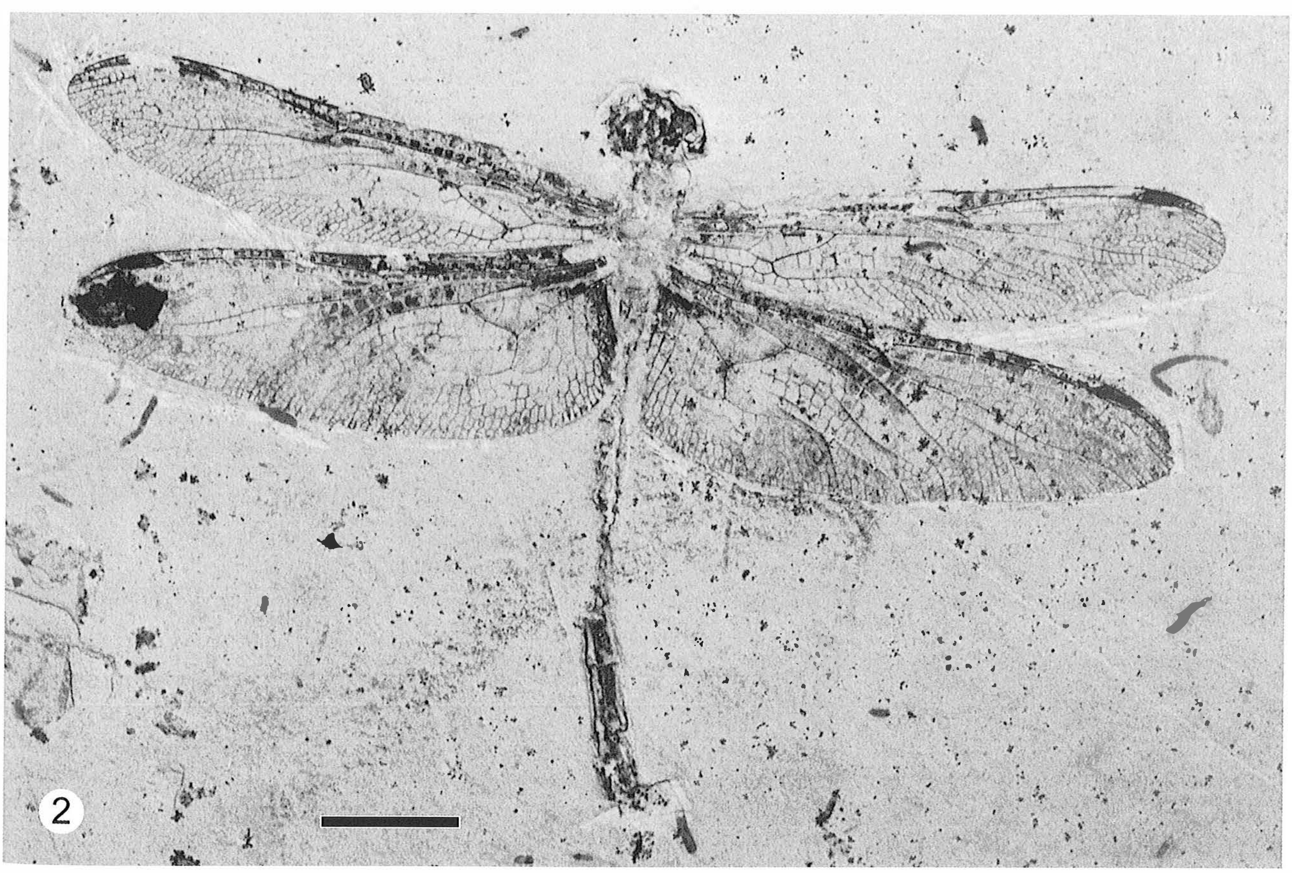

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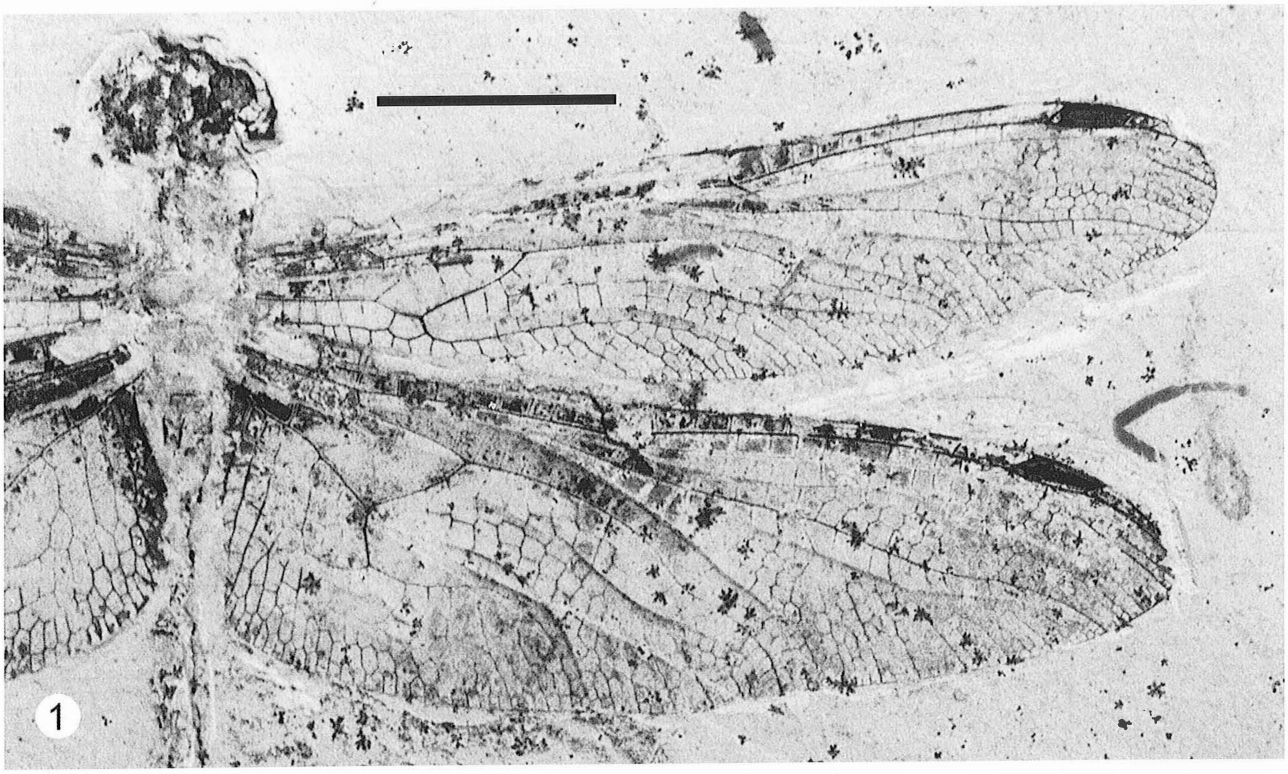

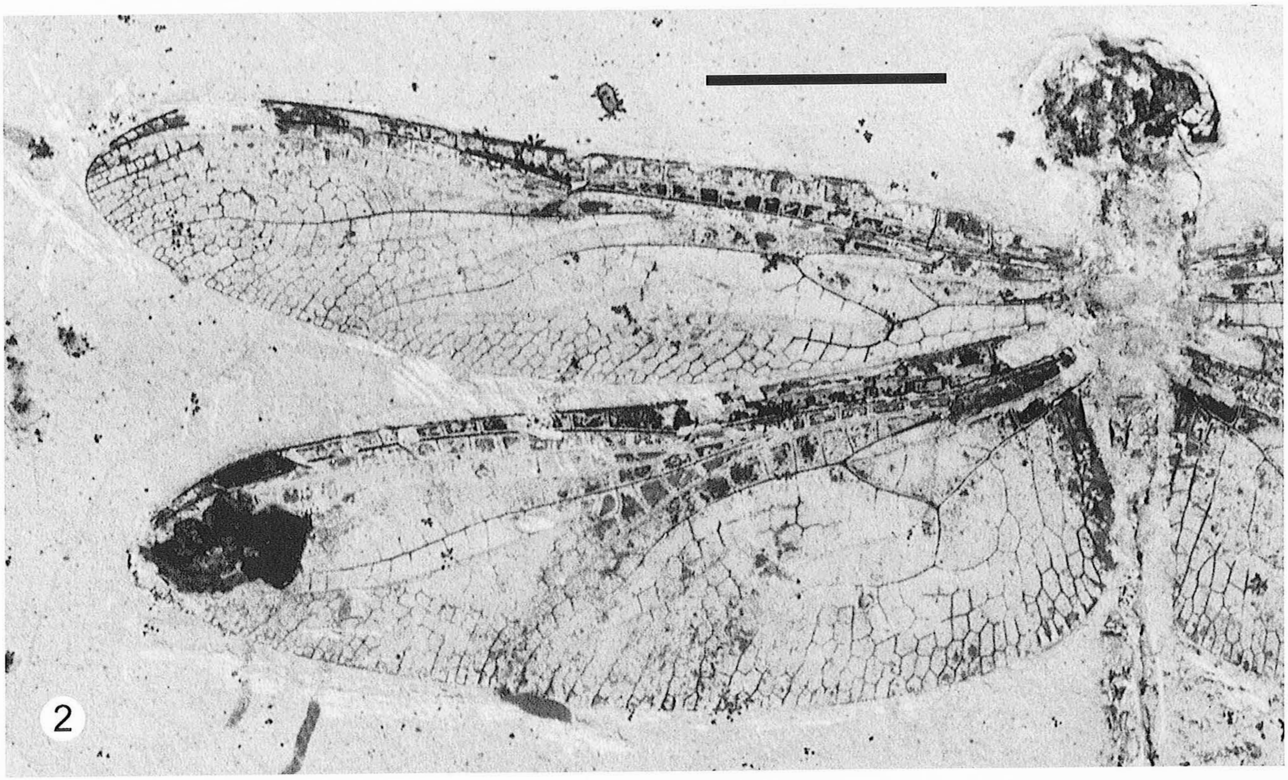

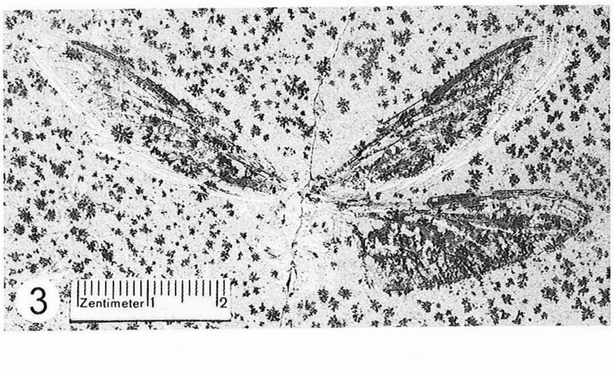

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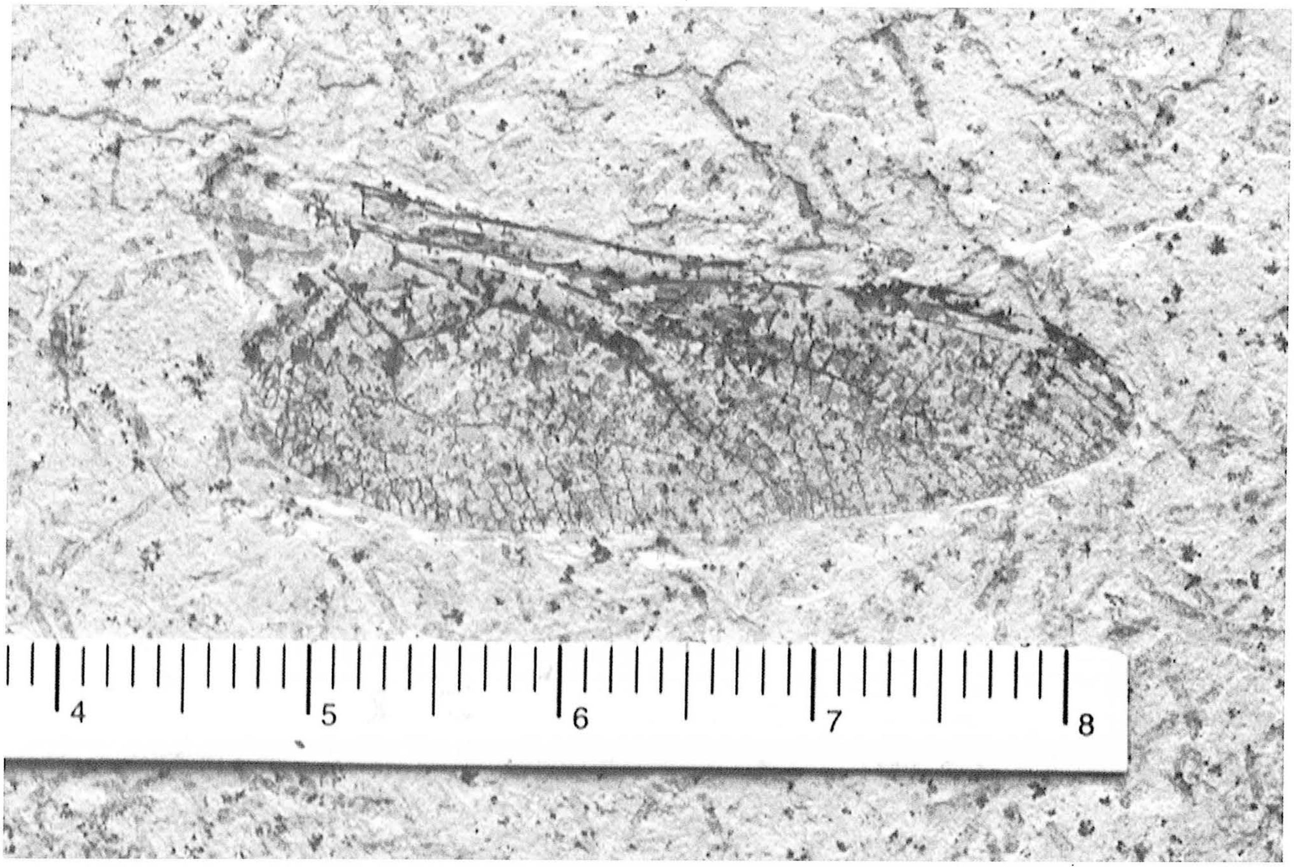

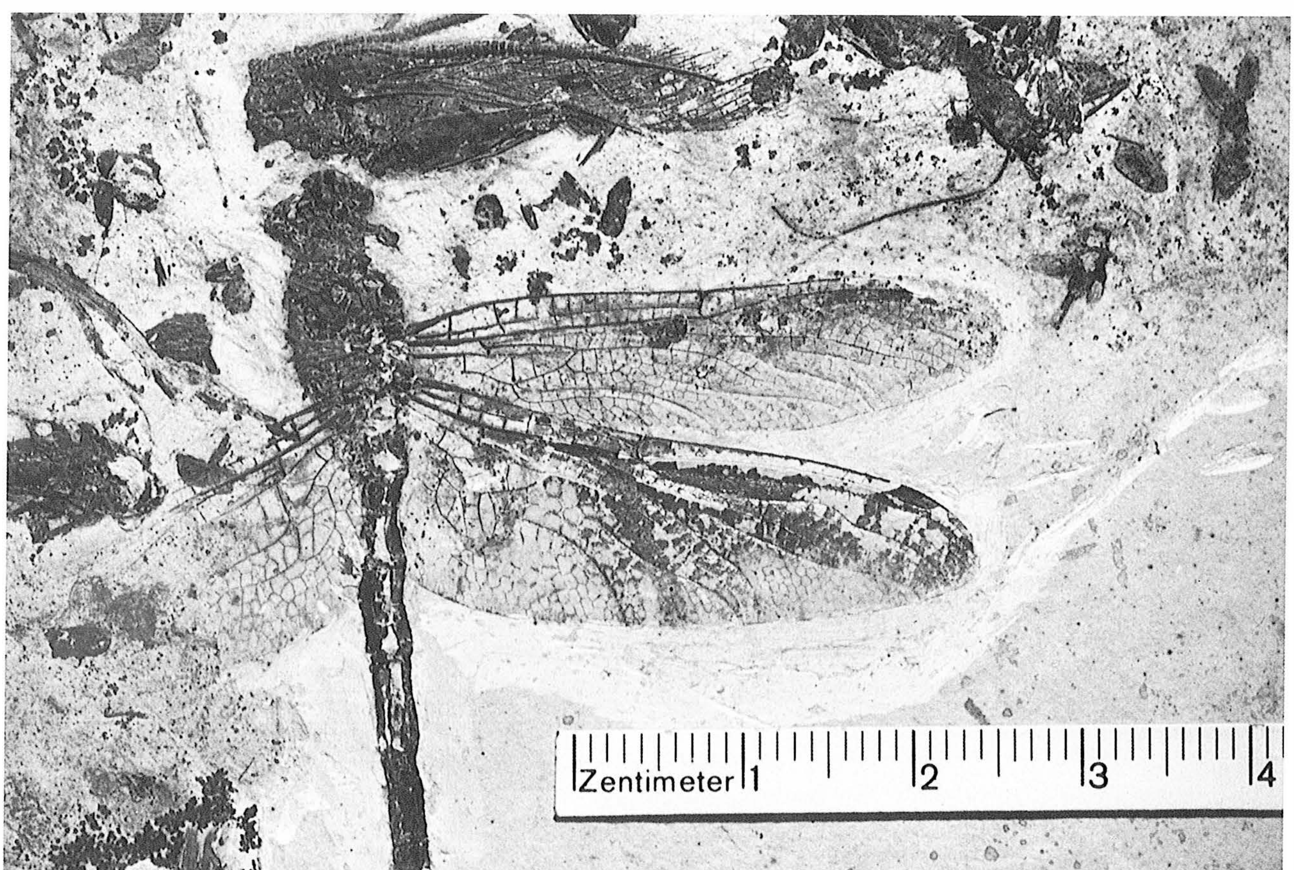

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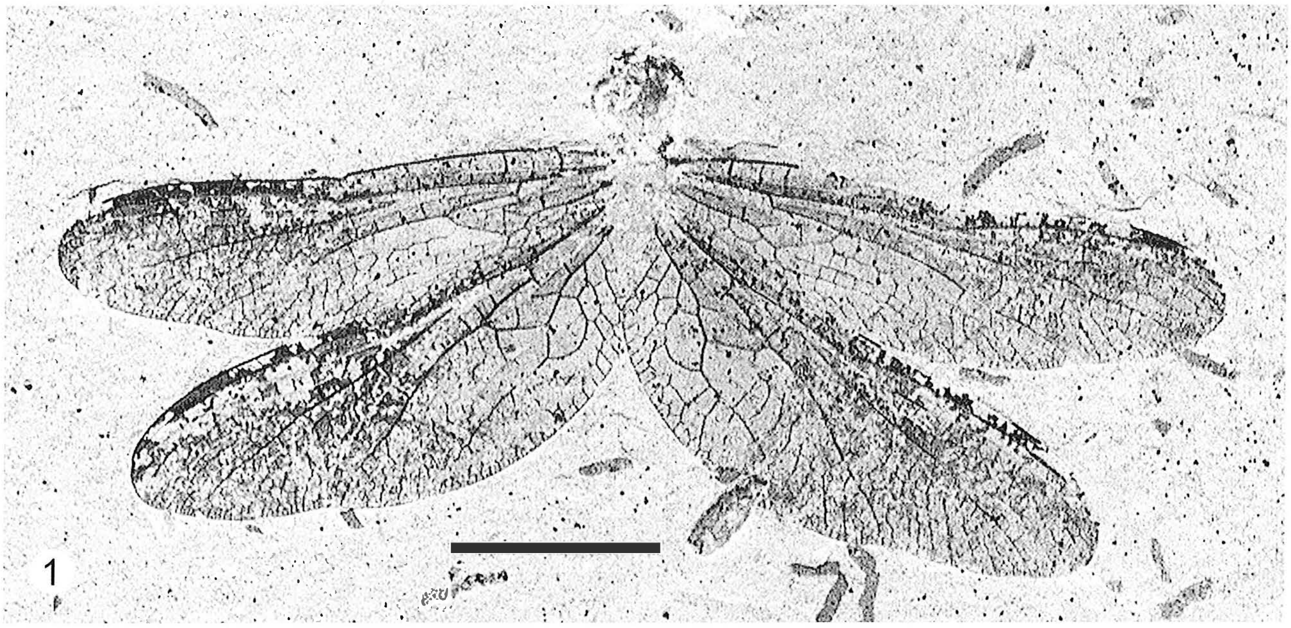

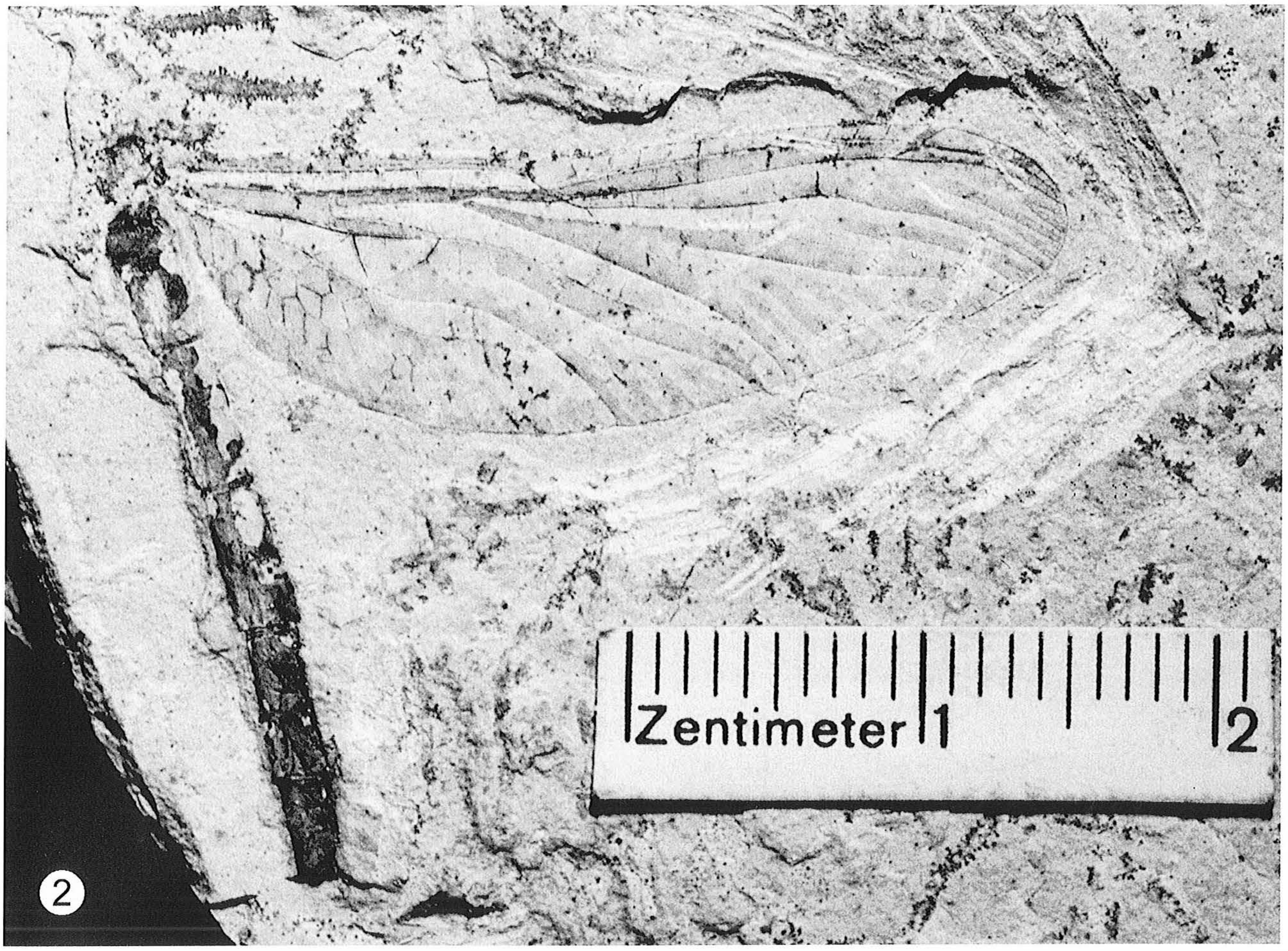

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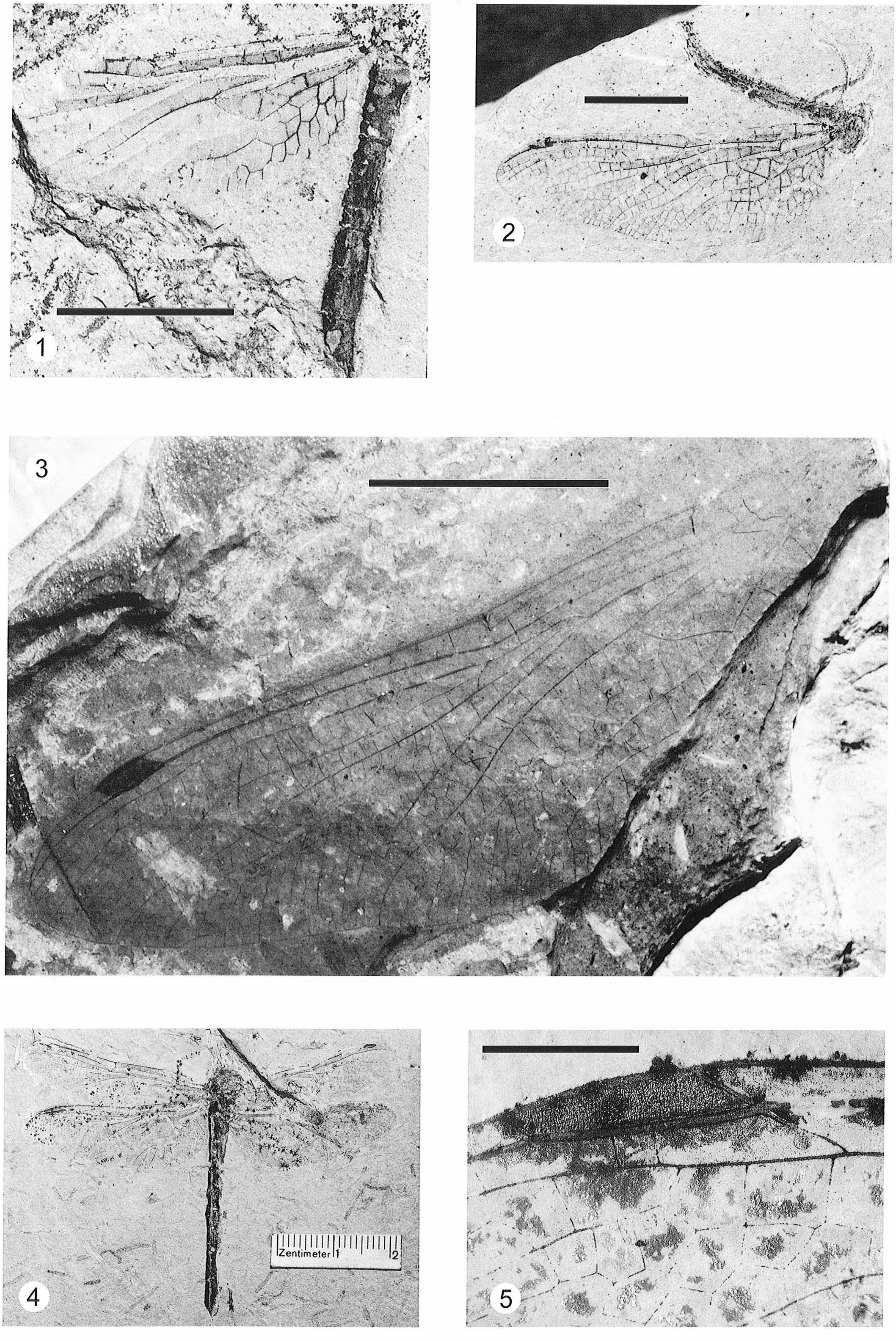

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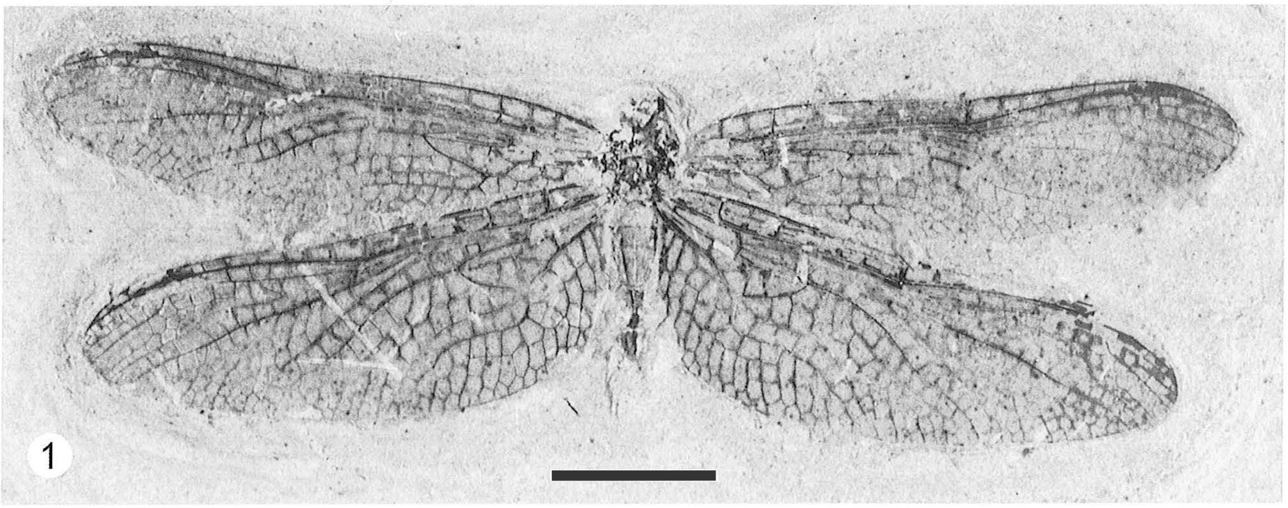

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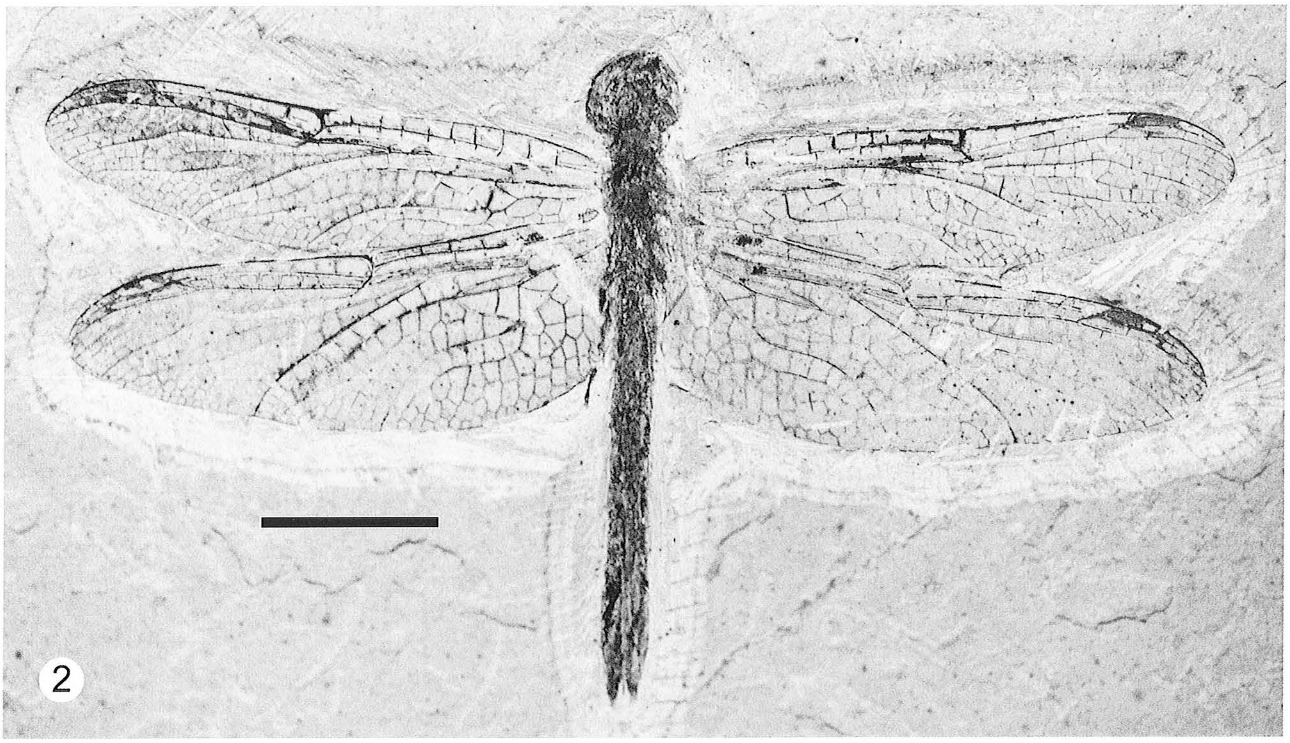

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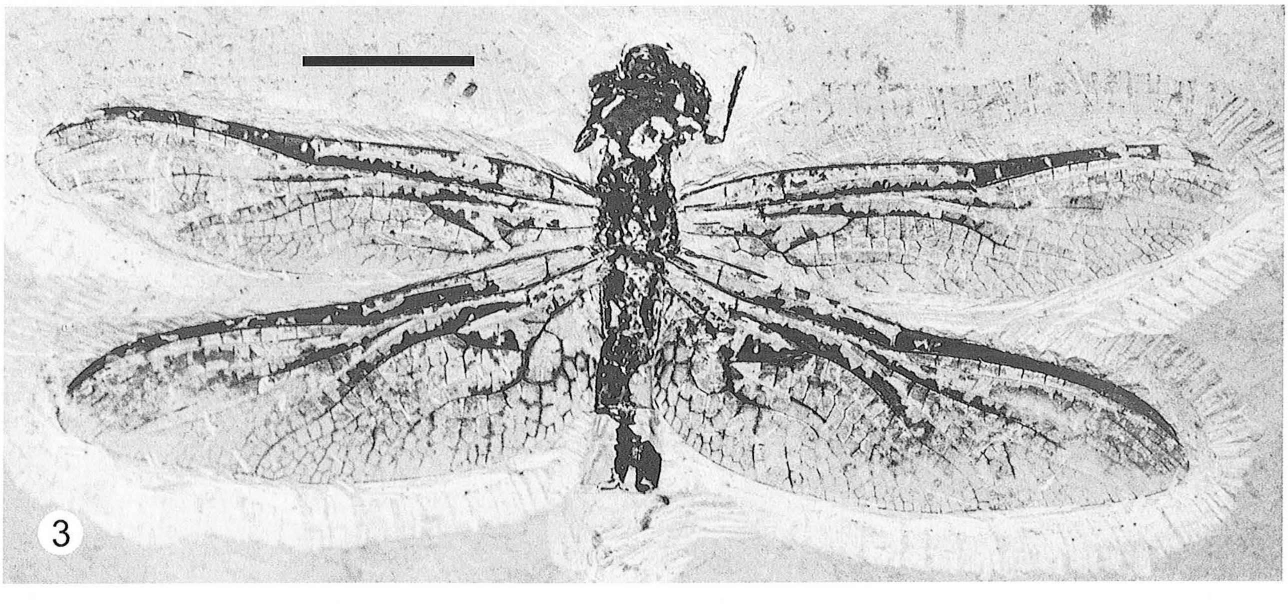

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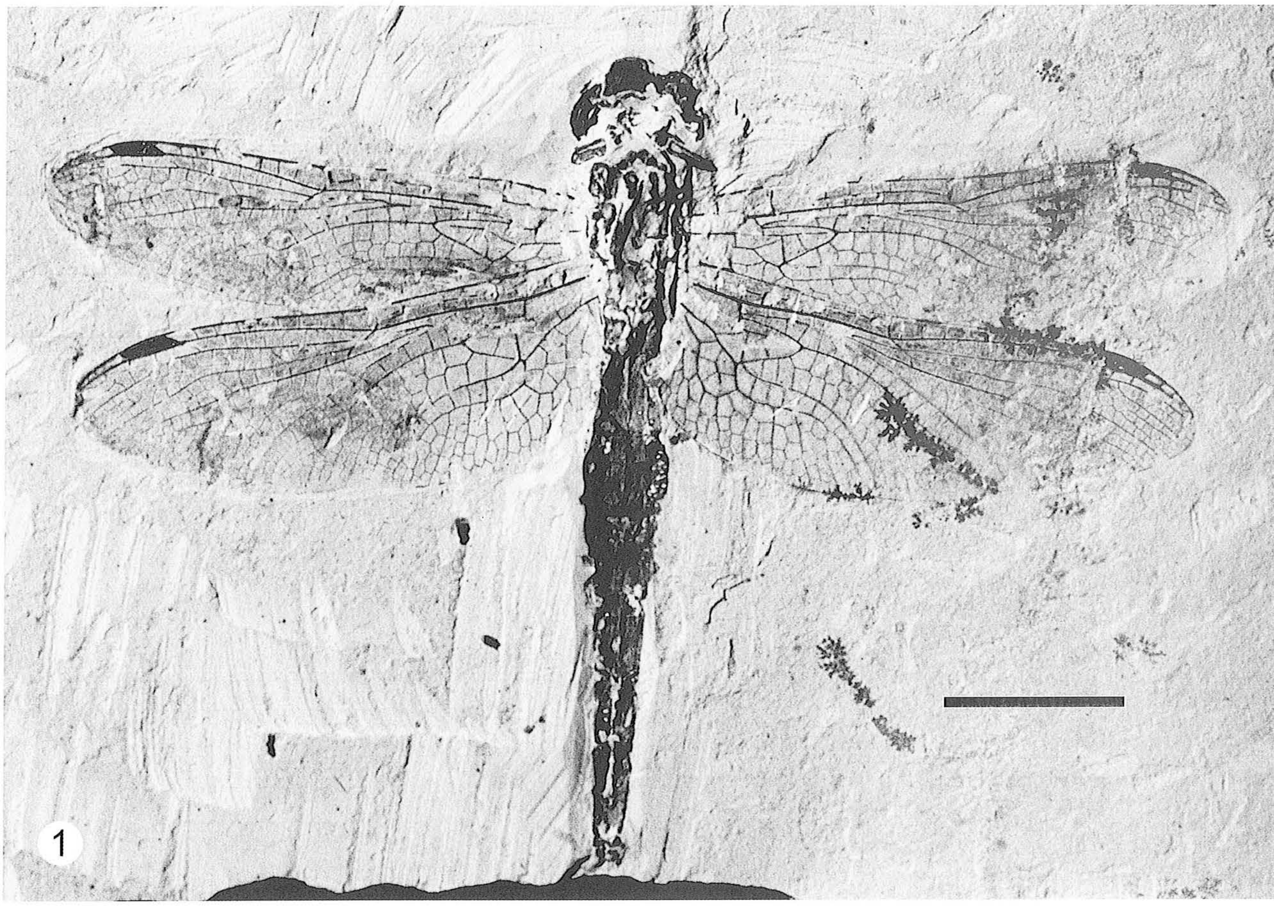
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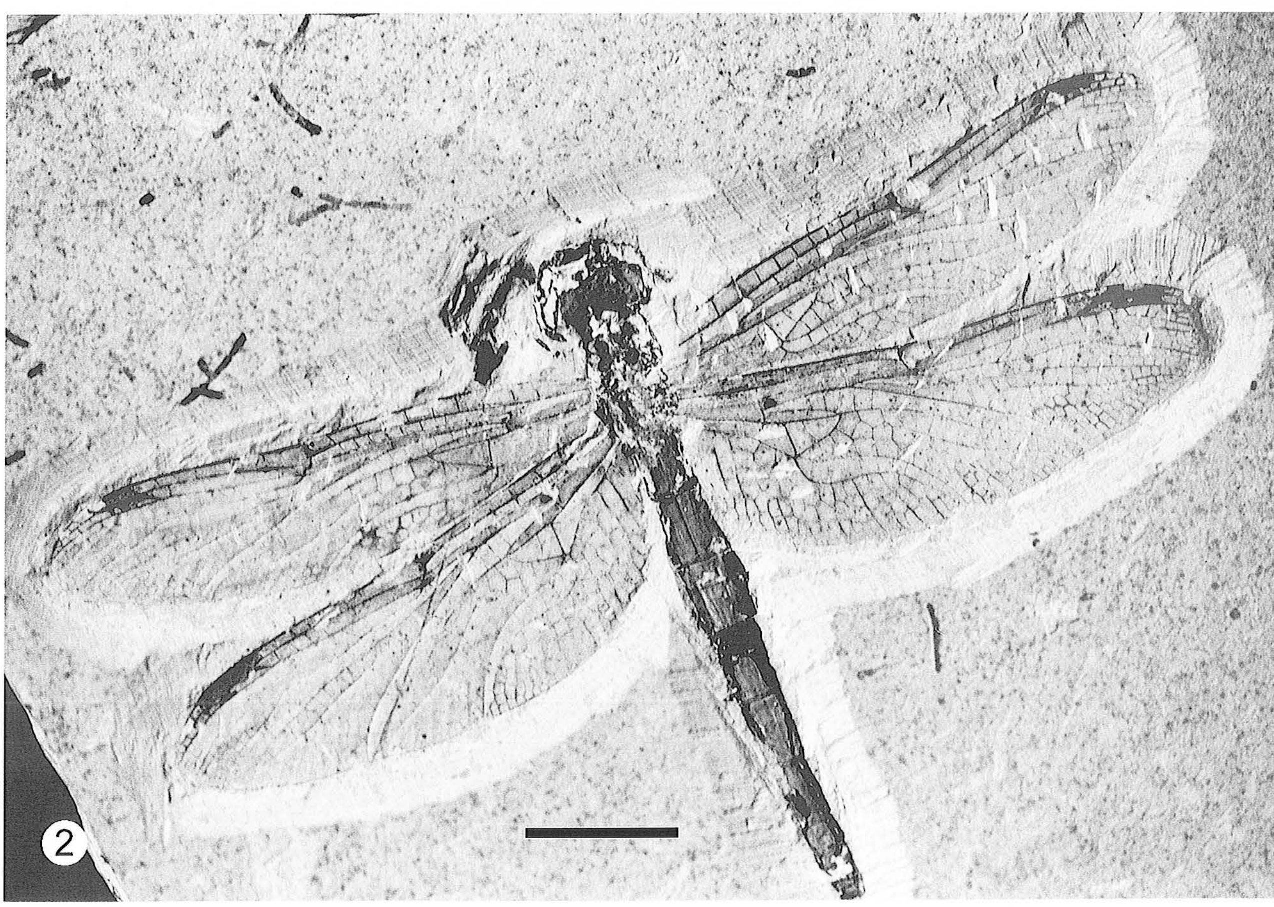
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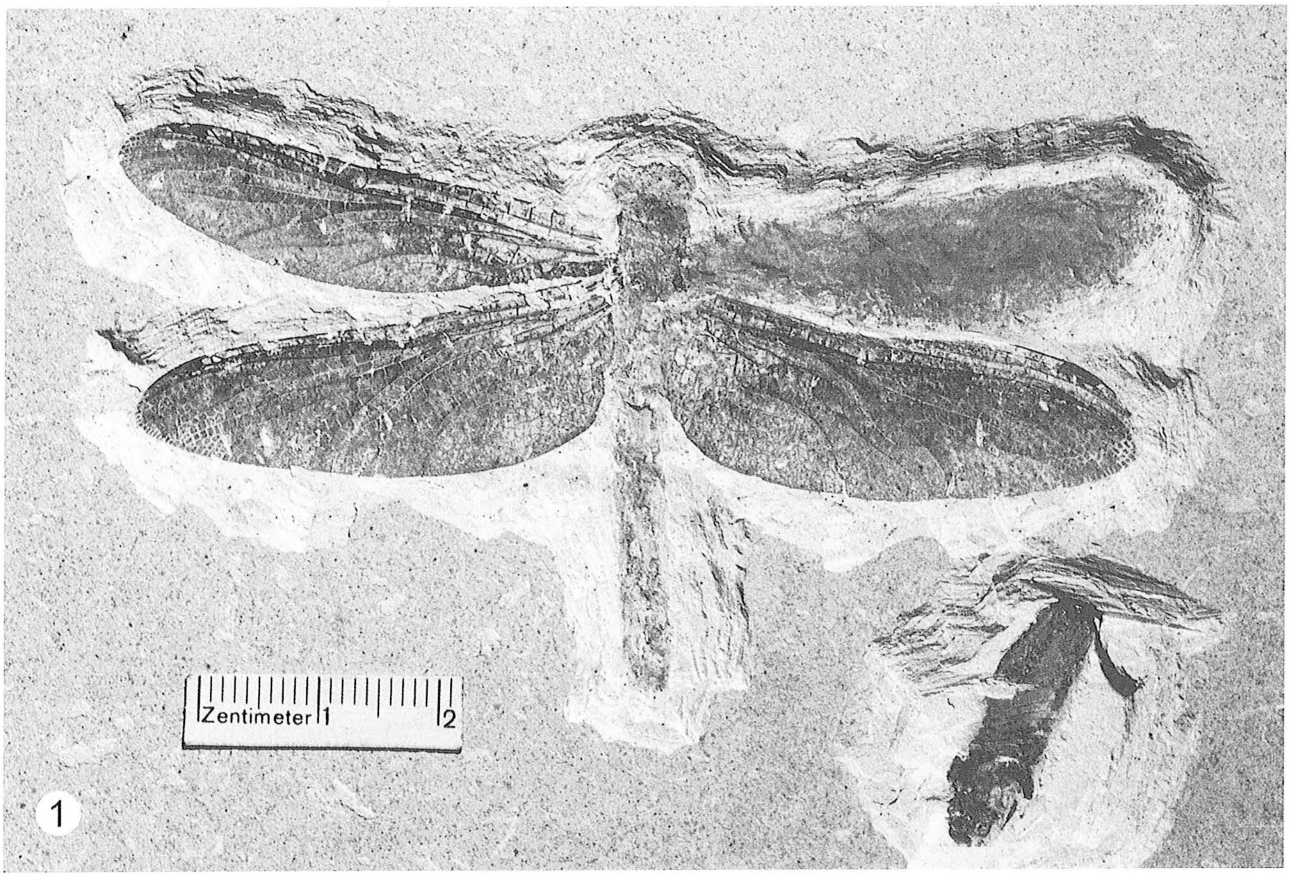

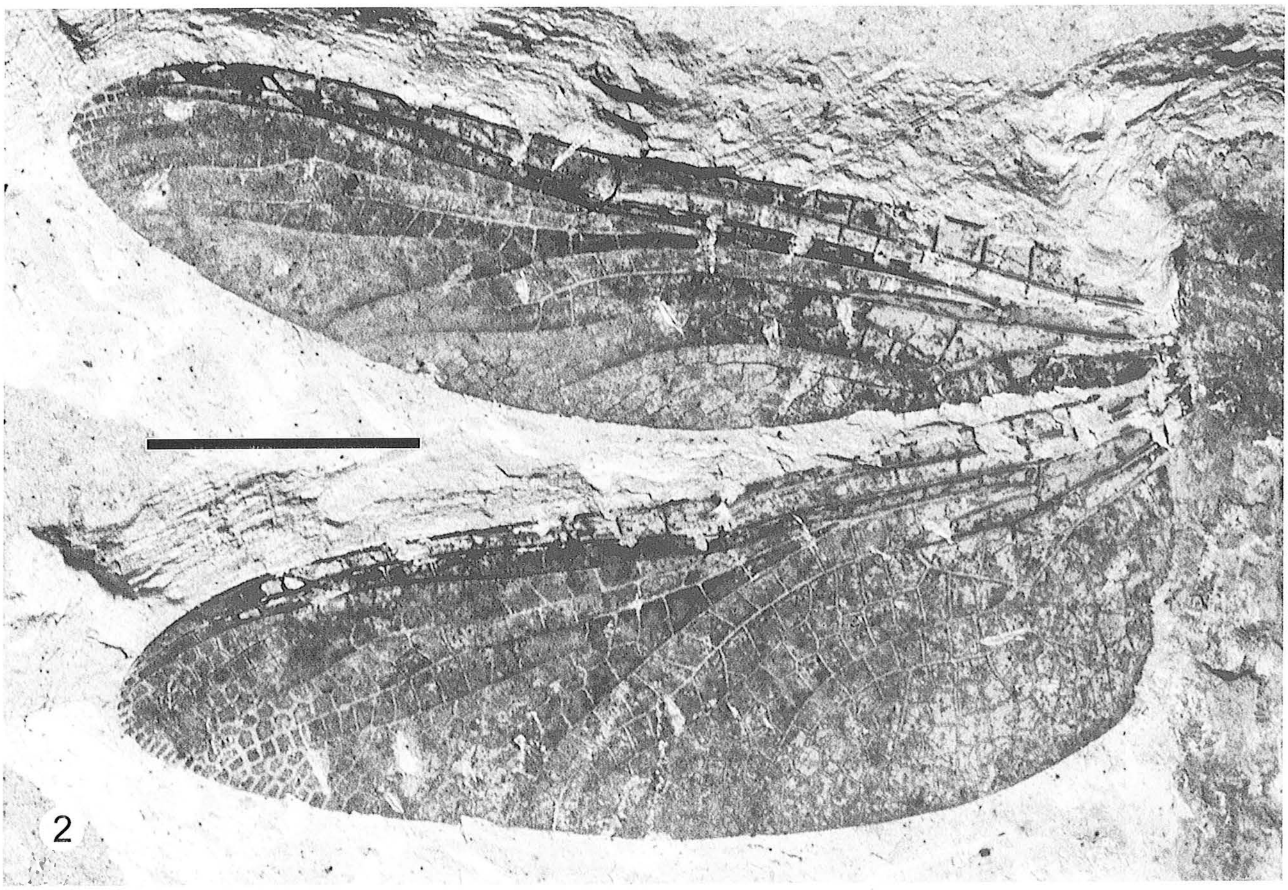

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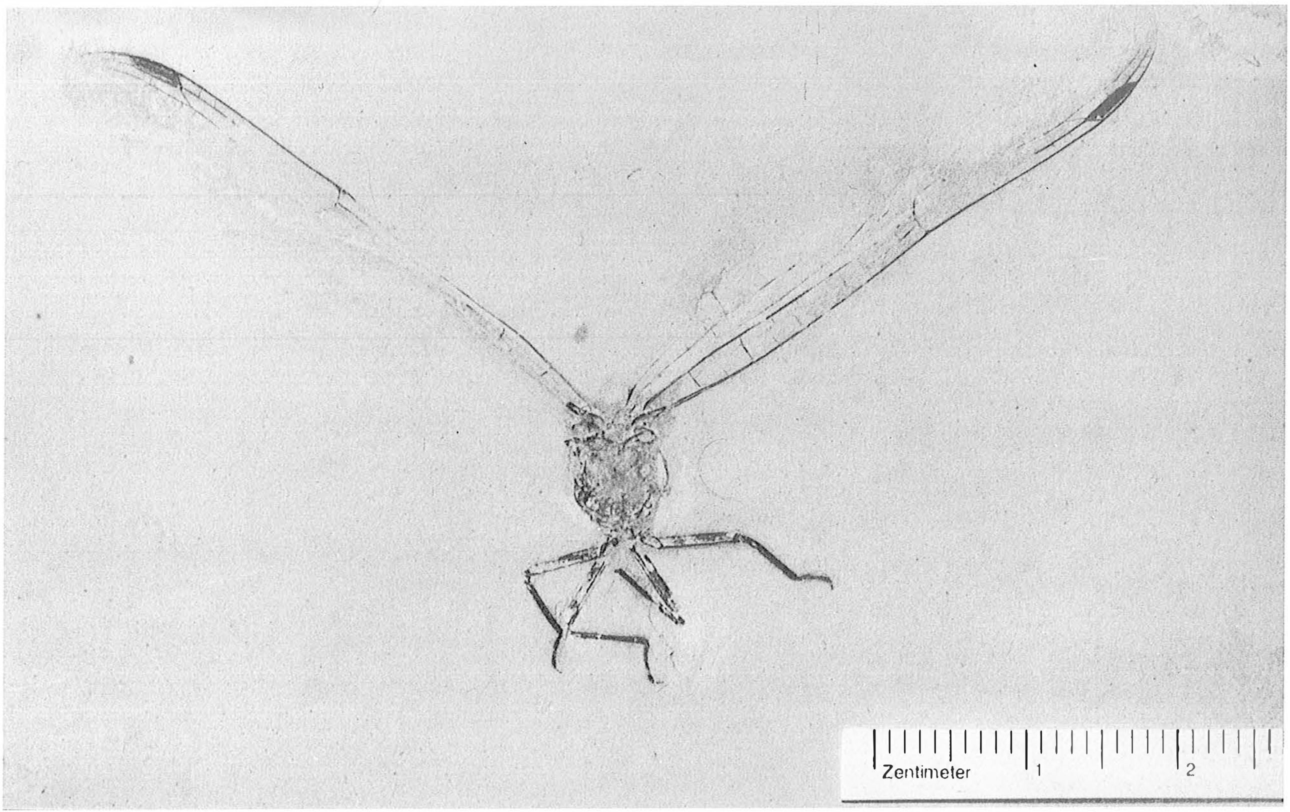

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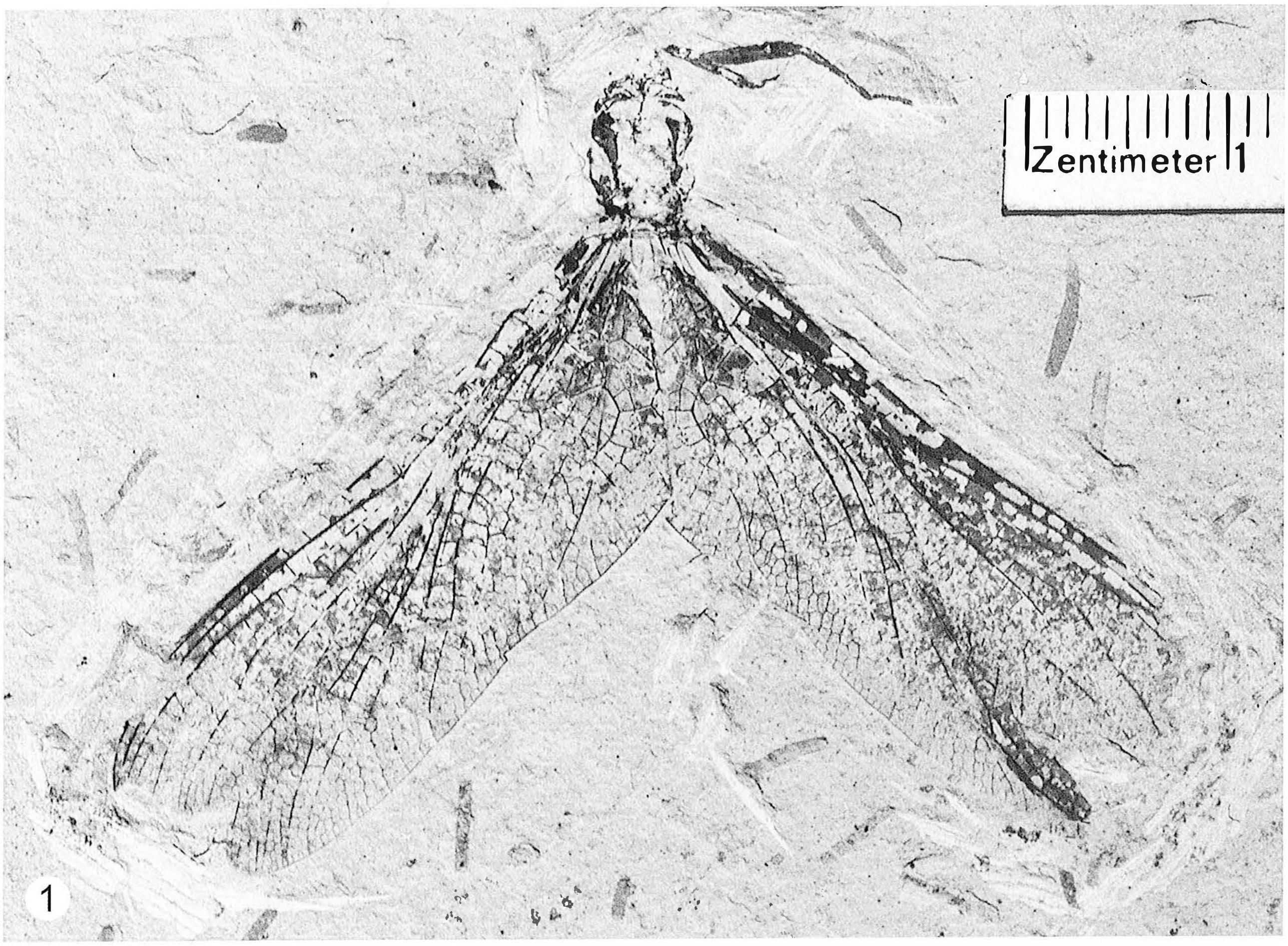

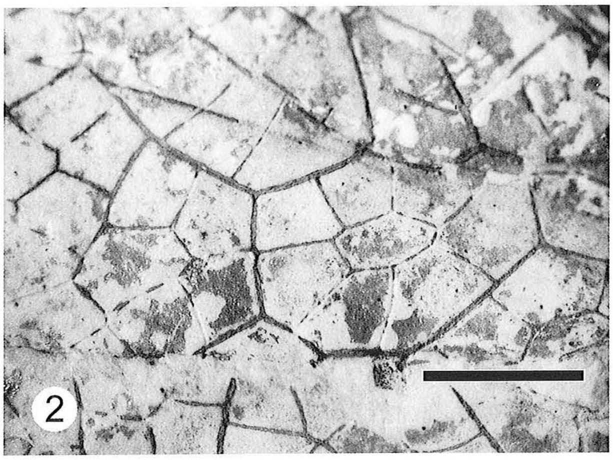

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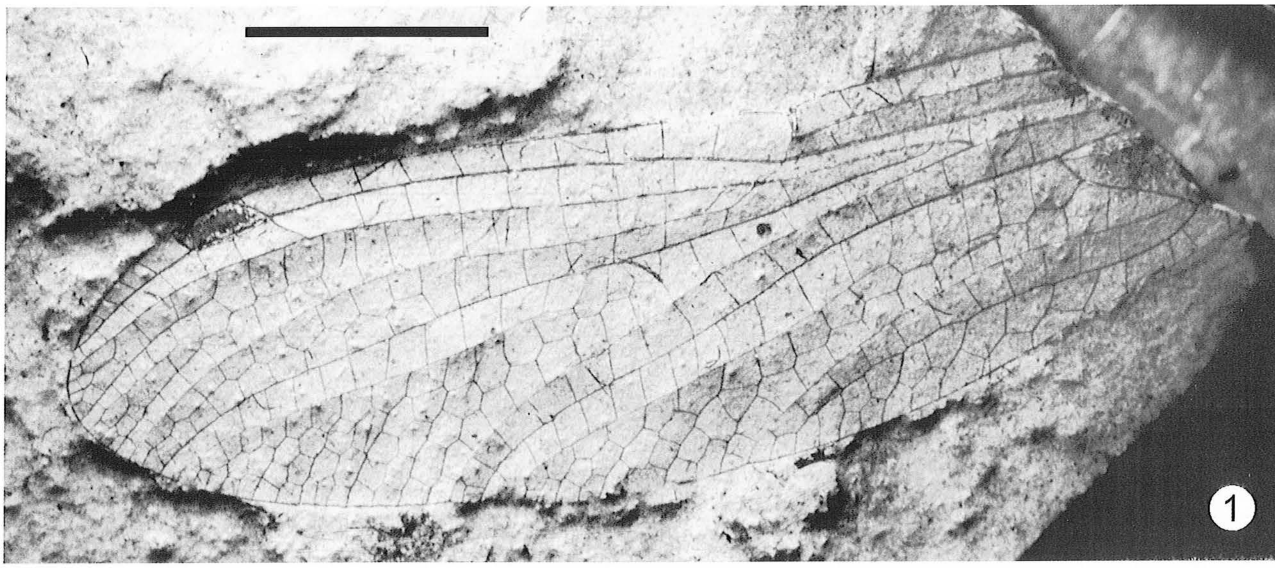

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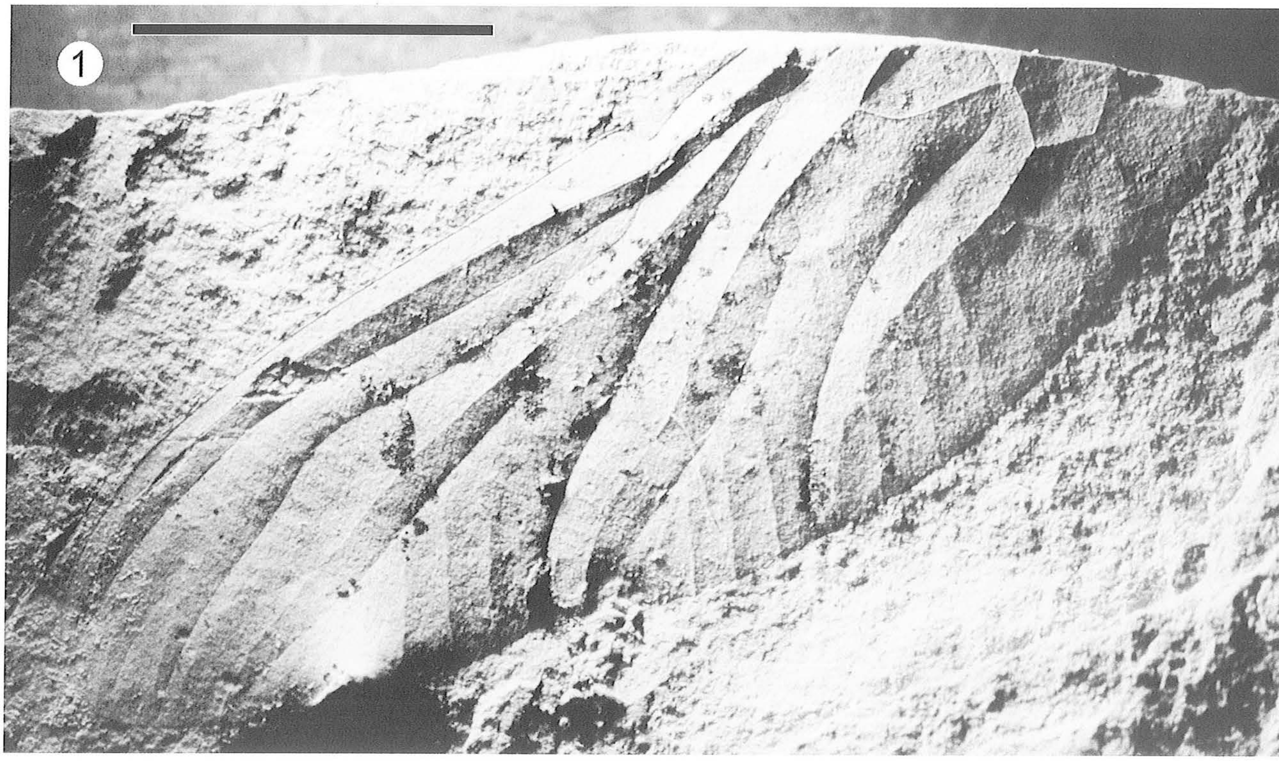

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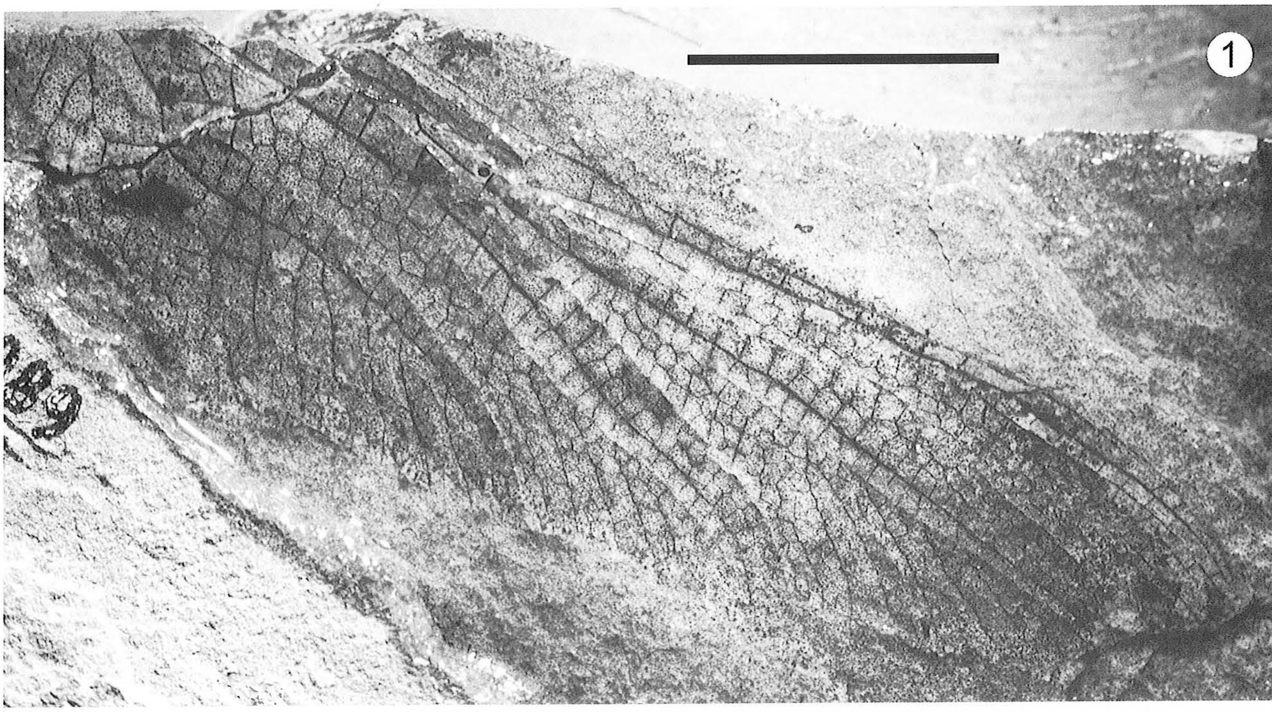

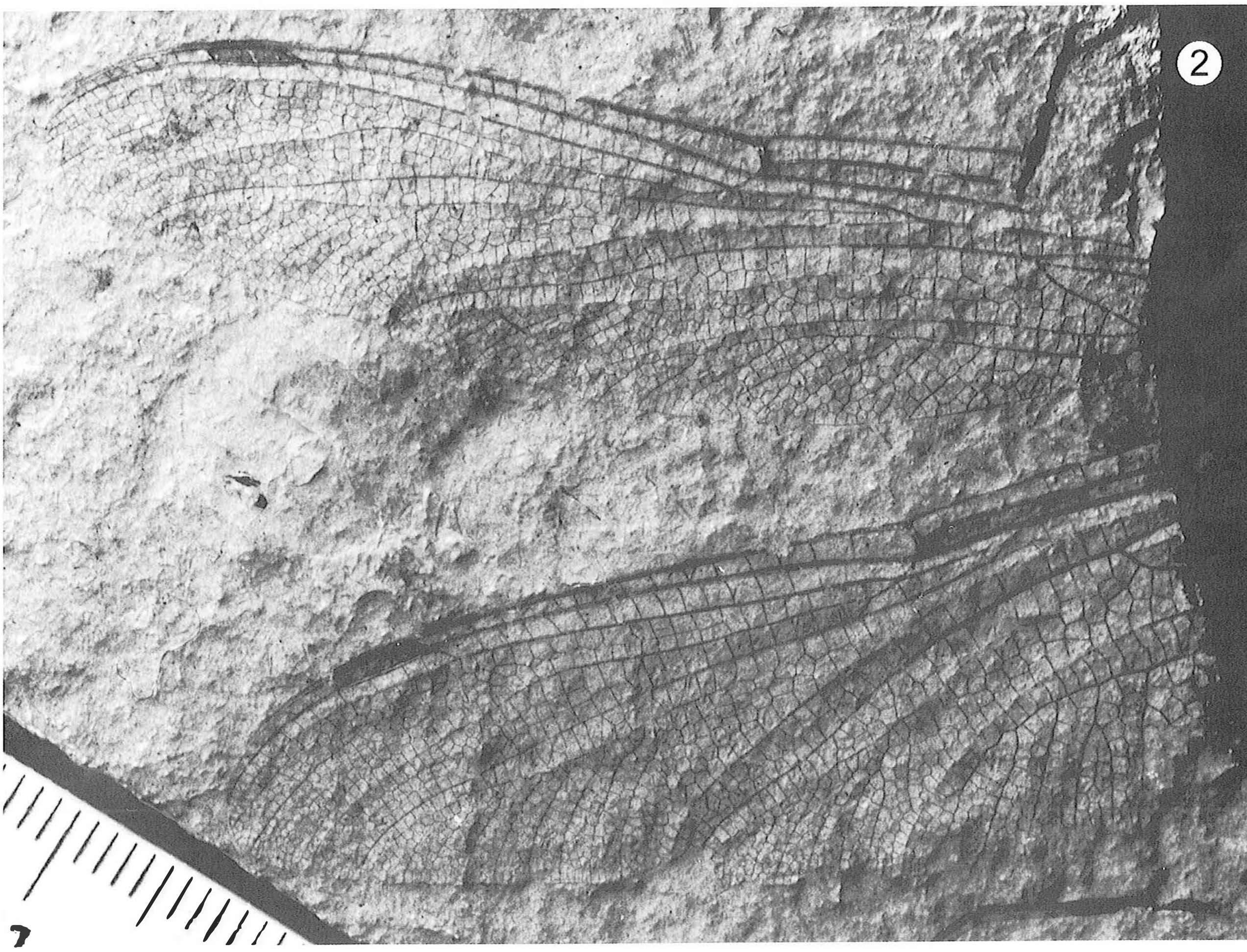

Plate 48