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FOUR NEW DRAGONFLIES FROM THE UPPER JURASSIC OF GERMANY AND THE LOWER CRETACEOUS OF MONGOLIA (ANISOPTERA: HEMEROSCOPIDAE, SONIDAE, AND PROTEROGOMPHIDAE FAM. NOV.)

G. BECHLY[1], A. NEL[2], X. MARTÍNEZ-DELCLÒS[3] and G. FLECK[2]

[1] **Corresponding Author:** Institut und Museum für Geologie und Paläontologie, Geowissenschaftliche Fakultät der Eberhard-Karls-Universität, Sigwartstr. 10, D-72076 Tübingen, Germany – (email: GBechly@aol.com or Guenter.Bechly@t-online.de)

[2] Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, F-75005 Paris, France – (email: anel@cimrs1.mnhn.fr)

[3] Departament Geologia dinàmica, Geofísica i Paleontologia, Facultat de Geologia, Universitat de Barcelona, E-08071 Barcelona, Spain – (email: delclos@natura.geo.ub.es)

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Prohemeroscopus jurassicus gen. et sp. nov. and *P. kuehnapfeli* sp. nov. are described as first Hemeroscopidae from the Upper Jurassic of Germany (Solnhofen Lithographic Limestone). The monophyly of Hemeroscopidae is discussed and preliminarily advocated. The Mesozoic Hemeroscopidae are recognized as potential stem-group representatives of extant Chlorogomphoidea within Anisoptera - Cavilabiata. The status of the alleged hemeroscopid larvae is discussed and they are preliminarily transferred as new (unnamed) species to Sonidae. The family Sonidae is restricted to the referring larvae. The adult fossil dragonflies from the Lower Cretaceous of Mongolia that were previously attributed to *Sona nectes* (Sonidae) are here classified as a new taxon, *Proterogomphus krauseorum* gen. et sp. nov. (Proterogomphidae fam. nov.) within the monophylum Gomphides, as sister-group of Hageniidae. A new species, *Proterogomphus renateae* sp. nov. is described from the Upper Jurassic of Germany (Solnhofen Lithographic Limestone). A numerical cladistic analysis of Anisoptera could neither convincingly resolve the phylogenetic relationships within Hemeroscopidae, nor the phylogenetic positions of Gomphides and Proterogomphidae fam. nov., because of their lack of wing venational apomorphies, but otherwise confirmed the phylogenetic reclassification of dragonflies by BECHLY (1996, *Petalura* [Special Vol.] 2: 342-402).

INTRODUCTION

The fossil families Hemeroscopidae and Proterogomphidae fam. nov. (= Sonidae *sensu* auct) were previously only known as monospecific taxa from the Lower Cretaceous of Mongolia (PRITYKINA, 1977; 1986) and China (DONG, 1995). The discovery of new species of each of these families from the Upper Jurassic of Germany, provides further informations about these taxa. Since these new species turn out be the oldest known representatives of two large monophyla within Anisoptera (Cavilabiata and Gomphides), they significantly increase our knowledge of the early phylogeny and evolution of Anisoptera in the Mesozoic.

In the present study 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). We follow the phylogenetic classification of Anisoptera proposed by BECHLY (1996), amended by BECHLY (1997). 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; and BORICKI, 1996). All recognized monophyla have been named, since we reject the sequencing of stem-group representatives because of the logical and practical reasons described by WILLMANN (1989). The assignment of formal hierarchical ranks has been omitted whenever possible without violation of the International Rules of Zoological Nomenclature, because they are absolutely arbitrary and more or less superfluous (WILLMANN, 1989). For the new „higher" taxon names we provide phylogenetic definitions according to so-called „phylogenetic taxonomy" after DE QUEIROZ & GAUTHIER (1990, 1992).

SHORT SKETCH OF THE PHYLOGENETIC SYSTEM OF ANISOPTERA AFTER BECHLY (1996, 1997). – According to this new system, the Eurypalpida (= Libelluloidea *sensu* FRASER, 1957) and Chlorogomphida (Hemeroscopidae + Chlorogomphoidea) are sister-groups in the monophylum Brachystigmata. The latter group and the Neopetaliidae are sister-groups in the monophylum Cristotibiata. Cristotibiata and Cordulegastrida (Zoraenidae + Cordulegastridae) together form the monophylum Cavilabiata (= Libellulini *sensu* FRASER, 1957; = Libelluloidea *sensu* CARLE, 1995). Cavilabiata and Gomphides (= Gomphidae *sensu* FRASER, 1957; = Gomphoidea *sensu* CARLE, 1995) together form the monophyletic group Exophytica. The latter group and the Aeshnoptera (= Aeshnoidea *sensu* CARLE, 1995) are sister-groups in the monophylum Euanisoptera. Euanisoptera and Petalurida (Protolindeniidae + Cretapetaluridae + Aktassiidae + Petaluridae) are sister-groups in the monophylum Anisoptera (crown-group). The Aeshnoptera include the fossil Mesuropetalidae, the extant Austropetaliida (Archipetaliidae + Austropetaliidae), the fossil Cymatophlebioidea and the Euaeshnida (= Aeshnidae *sensu* FRASER, 1957). The positions of the fossil families Liassogomphidae and Aeschnidiidae remain somewhat uncertain, although CARLE's (1982) proposal

that Aeschnidiidae could be the sister-group of all extant Anisoptera indeed seems to be correct. At least it can be regarded as certain that the Aeschnidiidae are unrelated to Cordulegastrida (CARLE, 1995; BECHLY, 1996, 1997; *contra* FRASER, 1957). The attempted phylogenetic analysis by NEL & MARTÍNEZ-DELCLÒS (1993a) of the Aeschnidiidae has recently demonstrated that the lack of strong synapomorphies with any other group of Anisoptera hampers the determination of the correct phylogenetic position of the Aeschnidiidae. The presence of peculiar cells below the cubito-anal vein basal of the discoidal triangle might represent a synapomorphy of Liassogomphidae and Aeschnidiidae (together: Aeschnidioidea) and maybe even Stenophlebiidae (together: Aeschnidioptera).

However, some other characters (e.g. subdiscoidal triangle, PsA, second oblique vein 'O', etc.) rather suggest that Liassogomphidae is more basal than Aeschnidiidae and crown-group Anisoptera.

Very detailed informations concerning the new classification of Odonata (including the used terminology of odonate wing venation) are available on the World Wide Web under the address (URL): http://members.aol.com/odonatadat/phylogeny/bechly.htm (in the present publication referred to as BECHLY, 1997).

TAXONOMY OF HEMEROSCOPIDAE

Hemeroscopidae PRITYKINA, 1977

(Anisoptera: Euanisoptera: Exophytica: Cavilabiata: Cristotibiata: Brachystigmata: Chlorogomphida)

Type genus: *Hemeroscopus* PRITYKINA, 1977.

PHYLOGENETIC DEFINITION. – Hemeroscopidae shall include all dragonflies that are closer related to *Hemeroscopus baissicus* PRITYKINA, 1977 than to any of the type-species of the other type-genera of the Anisoptera family-group taxa *sensu* FRASER (1957) (stem-based definition).

NEW DIAGNOSIS. – The Hemeroscopidae are characterised by the following features: (1) a broad pentagonal hindwing anal loop, more or less posteriorly closed, without midrib; – (2) the fore- and hindwing subdiscoidal triangles are similar and unicellular; – (3) the postnodal crossveins are not aligned with the corresponding postsubnodal crossveins; – (4) vein Mspl is absent and vein Rspl is absent or only weakly developed, with only one row of cells between it and IR2; – (5) vein IR1 is short, originating on RP1 below the distal half of the pterostigma (pseudo-IR1 of Pananisoptera); – (6) the primary antenodal crossveins AX1 and AX2 are distinctly stronger than the secondaries with only few (1-4) secondaries between them; – (7) the area between IR2 and RP2 is distally widened, with two or three rows of cells basal of the pterostigma; – (8) there is only one oblique crossvein 'O', four or five cells distal of the subnodus; – (9) the hindwing vein CuAa has few (only 3-4) posterior branches , the most distal one being secondarily branched from CuAa; – (10) the area between CuA and MP is basally widened with at least one double cell below the discoidal triangle; – (11) the so-called „gaff" (= basal part of CuA be-

tween the fusion of CuA with AA and its frist branching into CuAa and CuAb) is very elongated and straight in the hindwing; – (12) the male hindwing has an anal angle and a three-celled anal triangle.

HEMEROSCOPUS PRITYKINA, 1977

Type species. – *Hemeroscopus baissicus* PRITYKINA, 1977.

DIAGNOSIS AND AUTAPOMORPHIES. – This genus is differing from *Prohemeroscopus* gen. nov. in the following features: (1) the hindwing anal loop is transversely elongated and divided into at least 8 cells (autapomorphy); – (2) Rspl is more distinct, but weakly zigzagged (autapomorphy); – (3) the hindwing vein CuAa is more strongly curved and has only three or four distinct posterior branches; – (4) the forewing discoidal triangle is not divided by crossveins (autapomorphy); – (5) the forewing MP reaches the posterior wing margin about the level of the nodus; – (6) pterostigmata not braced (autapomorphy); – (7) bigger size (wing length 52 mm, instead of about 30-40 mm).

HEMEROSCOPUS BAISSICUS PRITYKINA, 1977

1977, *Hemeroscopus baissicus* PRITYKINA, p. 91, text-figs 7-10, pl. 3, figs 2-3, pl. 4, figs 1-6.
1986, *Hemeroscopus baissicus* Pritykina; PRITYKINA, p. 171, 183.
1992, *Hemeroscopus baissicus* Pritykina; CARPENTER, pp. 84-85, fig. 6b.
1995, *Hemeroscopus baissicus* Pritykina; DONG, pp. 49-50, text-figs 3-2, pl. 1, figs 1-3.
1996, *Hemeroscopus baissicus* Pritykina; BECHLY, p. 16.

M a t e r i a l. – **Holotype**: ♀, specimen 3O64/141, Institute of Paleontology (PIN), Moscow, Russia; imprint and counter-imprint of a complete female hindwing of excellent preservation. – **Additional material**. – PRITYKINA (1977) photographically illustrated a second (male) hindwing and indicated the presence of about 2.500 further specimens from the Lower Cretaceous of Transbaikals and Mongolia, including some adults and many larvae, although the latter probably have been erroneously attributed to *Hemeroscopus* (see below); DONG (1995) described three adult specimens from the Lower Cretaceous of China (Beijing) that he attributed to *H. baissicus*.

STRATUM TYPICUM. – Bottom of Lower Cretaceous (Neocomian), Zazinsk series.

LOCUS TYPICUS. – Course of Bais at upper stream of Vitim River, Eravninsk region of Buryat ASSR.

DIAGNOSIS. – Same as for genus.

COMMENT. – The wing venation of the specimens described by DONG (1995) is nearly identical to that of the type specimen. Therefore the attribution to *H. baissicus* has to be regarded as very well founded. The Chinese material shows the fore- and hindwings in connection with the thorax and gives precise informations about the forewing of *Hemeroscopus*.

PROHEMEROSCOPUS GEN. NOV.

Type species. – *Prohemeroscopus jurassicus* sp. nov.

Etymology. – In reference to the similarity and probable relationship with *Hemeroscopus*.

DIAGNOSIS. – This new genus is rather similar to *Hemeroscopus*, but differs from it in the following characters: (1) hindwing anal loop is smaller (plesiomorphy); – (2) Rspl is absent (plesiomorphy); – (3) the hindwing vein CuA is longer and more smoothly curved (plesiomorphy); – (4) the forewing discoidal triangle is divided into three cells (unknown in *P. kuehnapfeli* sp. nov.); – (5) the forewing MP reaches the posterior wing margin well distal of the nodus (unknown in *P. kuehnapfeli* sp. nov.); – (6) pterostigmata more distinctly braced (plesiomorphy); – (7) smaller size (wing length 30-40 mm, instead of about 52 mm). None of these characters can be postulated as autapomorphy, so that the inclusion of *P. kuehnapfeli* sp. nov. to this genus is currently only based on overall similarity (symplesiomorphies). It should also be noted that the long CuAa with about five or six posterior branches in the hindwing, represents a uniquely retained plesiomorphy within Hemeroscopidae that even could indicate a more basal position of *Prohemeroscopus* gen. nov. and especially of *P. kuehnapfeli* sp. nov.

COMMENT. – The differences mentioned in the diagnoses of *Hemeroscopus* and *Prohemeroscopus* gen. nov. certainly justify the erection of a new genus, since traditionally most new genera within Odonata were based on likewise distinct differences.

Nevertheless, *Hemeroscopus* and *Prohemeroscopus* gen. nov. have a rather similar wing venation. Contrary to the drawing of PRITYKINA (1977: text-fig. 7) also the veins pseudo-IR1 are identical in *H. baissicus* (PRITYKINA, 1977: pl. 3, figs 2-3) and in *P. jurassicus* sp. nov. Even though the holotype of *H. baissicus* is a female (rounded anal margin), PRITYKINA (1977: pl. 3, fig. 3) has figured (photograph) a male specimen which has a distinct anal angle and anal triangle as in the Chinese specimen BL 92005 (DONG, 1995: figs 3-2 c) and in the holotypes of *P. jurassicus* sp. nov. and *P. kuehnapfeli* sp. nov.

PROHEMEROSCOPUS JURASSICUS SP. NOV.

Figures 1-2

Material. – **Holotype:** ♂, specimen SOS 1716a [Blumenberg, Eichstätt], Jura-Museum, Eichstätt, Germany.

STRATUM TYPICUM. – Upper Jurassic, („Weißer Jura"); Malm zeta 2b, Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

LOCUS TYPICUS. – Blumenberg quarry, Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Etymology. – In reference to the Jurassic age of the type specimen.

DIAGNOSIS AND AUTAPOMORPHIES. – This new species differs from *P. kuehnapfeli* sp. nov. in the following hindwing characters: (1) distinctly smaller size (wing length about 30 mm); - (2) except the two most basal cells, there are always two rows of cells in the widened basal area between MP and CuA (autapomorphy); - (3) vein CuAa has two indistinct basal posterior branches that are separated by a wide „gap" from the two distinct distal posterior branches (autapomorphy); - (4) veins RP3/4 and MA are only slightly undulating (plesiomorphy); three rows of cells in the basal postdiscoidal area (autapomorphy); - (5) only one or two secondary (intercalary) veins in the distal part of the area between IR2 and RP3/4; - (6) the discoidal triangle is divided into two cells (plesiomorphy); - (7) there is only one secondary antenodal crossvein present between the two primaries AX1 and AX2 in both wing pairs (autapomorphy); - (8) AX2 is in a more basal position, somewhat basal of the level of the distal end of the discoidal triangle in both wing pairs (autapomorphy); - (9) the anal loop is somewhat less distinctly closed posteriorly (autapomorphy).

DESCRIPTION. – A nearly complete and well preserved adult male dragonfly, with excellent preservation of the right wing pair, while the left wing pair is only represented by the basal half which is only weakly preserved. The wings apparently have been hyaline, but the wing veins are traced by iron-oxide dendrites. Head, thorax and abdomen are preserved too, but only the abdomen shows some details.

F o r e w i n g. – Length 30.9 mm; width on the level of the nodus 7.4 mm; distance from base to arculus 3.8 mm; from base to nodus 16.3 mm; from nodus to pterostigma 8.6 mm; the pterostigma is not very long and narrow 3.2 mm long and max. 0.9 mm wide; the pterostigma is in a normal position, at about 59 % of the distance between nodus and apex; the pterostigma is not parallel sided, since its basal side is somewhat less oblique than its distal side; the pterostigmal brace is strong and distinctly oblique, aligned with the basal side of the pterostigma; the pterostigma covers three cells; there are seven postnodal crossveins between costal margin and RA distal of the pterostigma; only nine postnodal crossveins are present between nodus and pterostigma, non-aligned with the corresponding postsubnodal crossveins between RA and RP1; there is no distinct „libellulid gap" (*sensu* BECHLY, 1996) of postsubnodal crossveins directly distal of the subnodus; the nodus is of the „normal" Anisoptera-type; the subnodus is not extremely oblique; IR1 is a short vein, originating on RP1 slightly distal of the pterostigma (pseudo-IR1 of Pananisoptera); there are only two rows of cells in the area between pseudo-IR1 and RP1, and four rows of cells in the wider area between pseudo-IR1 and RP2; RP1 and RP2 are basally parallel with only one row of cells between them, but somewhat basal of the pterostigma they become divergent with three or more rows of cells between them; the base of RP2 is strictly aligned with the subnodus; there is only one oblique crossvein 'O' between RP2 and IR2, 2.3 mm and four cells distal of the subnodus; there is one row of cells in the basal area between RP2 and IR2, more distally there are two rows between them, and at the posterior wing

margin both veins are separated by six small cells; the area between RP2 and IR2 is distally widened; RP2 and IR2 are gently curved, but not undulating, and reach the posterior margin obliquely; the midfork (base of RP3/4) is 4.4 mm basal of the subnodus, and the origin of IR2 is 1.0 mm distal of the midfork; there are three bridge crossveins (Bqs) between RP and IR2 basal of the subnodus; six antesubnodal crossveins (between RA and RP basal of the subnodus and distal of the arculus) are concentrated in the median part of this wing space, so that there is a „gap" of antesubnodal crossveins directly distal of the arculus and directly basal of the subnodus (presence of a „cordulegastrid gap" *sensu* BECHLY, 1996); seven antefurcal (postmedian) crossveins between RP and MA basal of the RP-midfork; there is no Rspl and no long secondary vein in the area between IR2 and RP3/4; no Mspl; the postdiscoidal area is wide with four rows of cells directly distal of the discoidal triangle and fifteen cells between MA and MP at the posterior wing margin; the postdiscoidal area is distally somewhat narrowed (width near discoidal triangle, 2.2 mm; width near wing margin, 1.9 mm); RP3/4 and MA are more or less parallel, are slightly undulating on the level of the oblique crossvein 'O'; the area between RP3/4 and MA is slightly widened distally with two to three rows of cells between them (RP3/4 and MA separated by four cells at the wing margin), while there is only one row of cells between them till the level of the oblique crossvein 'O'; the discoidal triangle is very wide and somewhat longitudinal elongate, and divided into three cells; length of its anterior side, 2.9 mm; of its basal side, 1.8 mm; of its distal side MAb, 3.2 mm; the distal side MAb is straight; the hypertriangle is free, 4.2 mm long and max. 0.6 mm wide; the basal space and subbasal space are free of crossveins; a distinct secondary anterior branch PsA (pseudo-anal vein) of AA delimits an unicellular subdiscoidal triangle, which is 1.6 mm long, max. 1.3 mm wide (length of PsA) and min. 0.2 mm wide (length of subdiscoidal veinlet); there are one or two rows of cells in the anal area below AA which is 1.8 mm wide below PsA; the CuP-crossing (= anal cross-

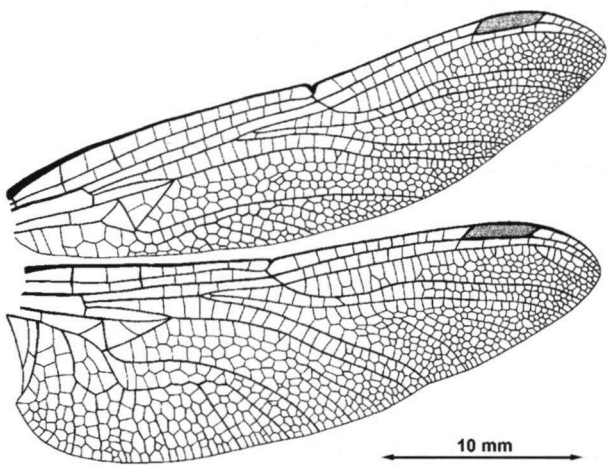

Fig. 1. *Prohemeroscopus jurassicus* gen. et sp. nov., holotype SOS 1716, fore- and hindwing venation, camera lucida drawing.

ing *sensu* FRASER, 1957) is 1.3 mm basal of the arculus; there are no supplementary cubito-anal crossveins; MP is very gently curved and very long, ending on the level of the oblique crossvein 'O'; the area between CuA and MP is distally widened near the wing margin; CuA is basally rather well-defined but it is obscured distally; the distal posterior branches of CuA look like secondary veins of the area between MP and the posterior wing margin, while only three or four basal posterior branches of CuA are rather well defined; there are four rows of cells in the median part of the cubito-anal area (max. 1.8 mm wide); the arculus is strongly angled, and the bases of RP and MA are shortly but distinctly separated at the arculus; only the two primary antenodal crossveins AX1 and AX2 (and the basal brace AX0) are aligned and stronger than the non-aligned secondary antenodal crossveins (twelve in the first row and ten in the second row); AX1 is 0.9 mm basal of the arculus and AX2 is 2.9 mm distal of AX1; there is only one secondary antenodal crossvein between AX1 and AX2 in each row, non-aligned with each other; the basal brace AX0 is preserved.

H i n d w i n g. – The venation is very similar to that of the forewing, especially in the distal half of the wing; length, 29.6 mm; width on the level of the nodus, 9.0 mm (max. width, 10.0 mm); distance from base to arculus, 3.7 mm; from base to nodus, 13.3 mm; from nodus to pterostigma, 9.6 mm; thus the nodus is in a relatively basal position, compared to the forewing; the pterostigma is not very long and narrow, 3.4 mm long and max. 0.9 mm wide; the pterostigma is in a normal position, at about 59 % of the distance between nodus and apex; the pterostigma is not parallel sided, since its basal side is somewhat less oblique than its distal side; the pterostigmal brace is strong and oblique, aligned with the basal side of the pterostigma; the pterostigma covers three cells; there are six postnodal crossveins

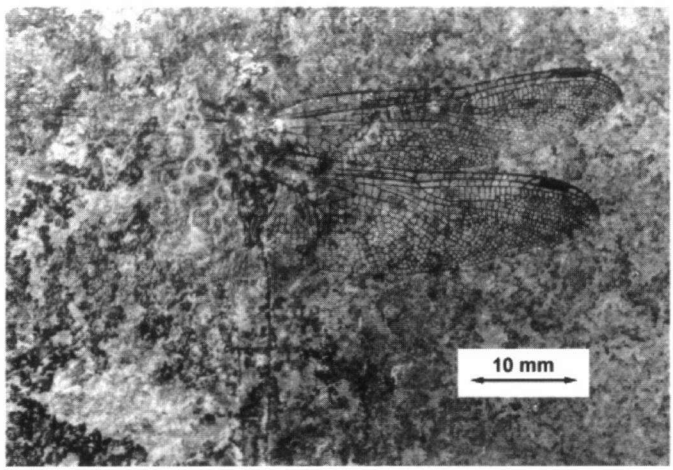

Fig. 2. *Prohemeroscopus jurassicus* gen. et sp. nov., holotype SOS 1716.

between costal margin and RA distal of the pterostigma; eleven postnodal crossveins are present between nodus and pterostigma, non-aligned with the corresponding postsubnodal crossveins between RA and RP1; there is no distinct „libellulid gap" (*sensu* BECHLY, 1996) of postsubnodal crossveins directly distal of the subnodus; the nodus is of the „normal" Anisoptera-type; the subnodus is not extremely oblique; IR1 is a short vein, originating on RP1 slightly distal of the pterostigma (pseudo-IR1 of Pananisoptera); there are only two rows of cells in the area between pseudo-IR1 and RP1, and four or five rows of cells in the wider area between pseudo-IR1 and RP2; RP1 and RP2 are basally parallel with mostly only one row of cells between them, but somewhat basal of the pterostigma they become divergent with three or more rows of cells between them; the base of RP2 is strictly aligned with the subnodus; there is only one oblique crossvein 'O' present between RP2 and IR2, 2.7 mm and four cells distal of the subnodus; there is one row of cells in the basal area between RP2 and IR2, more distally there are two rows between them, and at the posterior wing margin both veins are separated by four cells; the area between RP2 and IR2 is distally widened; RP2 and IR2 are gently curved, but not undulating, and reach the posterior margin obliquely; the midfork (base of RP3/4) is 3.7 mm basal of the subnodus, and the origin of IR2 is 0.5 mm distal of the midfork; there are three bridge crossveins (Bqs) between RP and IR2 basal of the subnodus; only four antesubnodal crossveins (between RA and RP basal of the nodus and distal of the arculus) are concentrated in the median part of this wing space, so that there is a „gap" of antesubnodal crossveins directly distal of the arculus and directly basal of the subnodus (presence of a „cordulegastrid gap" *sensu* BECHLY, 1996); four antefurcal (postmedian) crossveins between RP and MA basal of the RP-midfork; there is no Rspl, but one or two rather long and convex secondary veins (intercalaries) are present in the area between IR2 and RP3/4; there is no Mspl, but two rather long and convex secondary veins (intercalaries) are present in the distal postdiscoidal area between MA and MP; the postdiscoidal area is wide with three rows of cells directly distal of the discoidal triangle and fourteen cells between MA and MP at the posterior wing margin; the postdiscoidal area is distally widened (width near discoidal triangle, 2.1 mm; width at posterior wing margin, 4.9 mm); RP3/4 and MA are more or less parallel, but are slightly undulating on the level of the oblique crossvein 'O'; the area between RP3/4 and MA is slightly widened distally with two rows of cells between them (RP3/4 and MA are separated by three cells at the wing margin), while there is only one row of cells between them till the level of the oblique crossvein 'O'; the discoidal triangle is rather narrow and distinctly longitudinal elongate, and divided into two cells by an obliquely slanted transverse crossvein; length of its anterior side 3.4 mm long, of its basal side 1.5 mm; of its distal side MAb 3.6 mm; the distal side MAb is straight; the hypertriangle is free, 4.4 mm long and max. 0.6 mm wide; the costal side of the hypertriangle is rather straight; the basal space and subbasal space are free of crossveins; a distinct secondary anterior branch PsA of AA delimits an

unicellular subdiscoidal triangle which is 1.3 mm long, max. 1.4 mm wide (length of PsA) and min. 0.3 mm wide (length of subdiscoidal veinlet); there are eight rows of cells in the anal area below AA which is 6.1 mm wide below PsA; there is a distinct anal angle, and a large anal triangle that is divided into three cells by a Y-shaped vein (thus it is a male specimen); the CuP-crossing is 2.1 mm basal of the arculus, very close to the distal side of the anal triangle; there are no supplementary cubito-anal crossveins; MP is gently curved and ends slightly distal of the level of the nodus; the area between MP and CuAa is basally and distally distinctly widened with two rows of cells between both veins below the discoidal triangle, and with four rows of cells between them near the posterior wing margin; the „gaff" is straight and very elongated (1.8 mm long); CuAb (the most basal posterior branch of CuA) is strongly angular to the „gaff"-portion of CuA at the base, while the most basal part of CuAa is aligned with the „gaff" (unique curvature of the base of CuAa); CuAb and a posterior branch of AA enclose a relatively wide and transverse six-celled anal loop (max. 2.2 mm long and max. 3.1 mm wide) which is somewhat indistinctly closed posteriorly; there is one posterior branch of AA between the anal triangle and the anal loop; CuAa has two basal and two distal posterior branches which are separated by a wide cubito-anal area without any defined branch of CuAa, only divided by two secondary veins (intercalaries); there are five to seven rows of cells in the median part of the cubito-anal area (max. 3.8 mm wide); the arculus is distinctly angled, and the bases of RP and MA are distinctly separated at the arculus; only the two primary antenodal crossveins AX1 and AX2 are aligned and stronger than the non-aligned secondary antenodal crossveins (six or seven in the first row and five in the second row); AX1 is 0.5 mm basal of the arculus and AX2 is 3.5 mm distal of AX1, somewhat basal of the level of the distal end of the discoidal triangle; there is only one secondary antenodal crossvein between AX1 and AX2 in each row, not strictly aligned with eachother; the basal brace AX0 is not

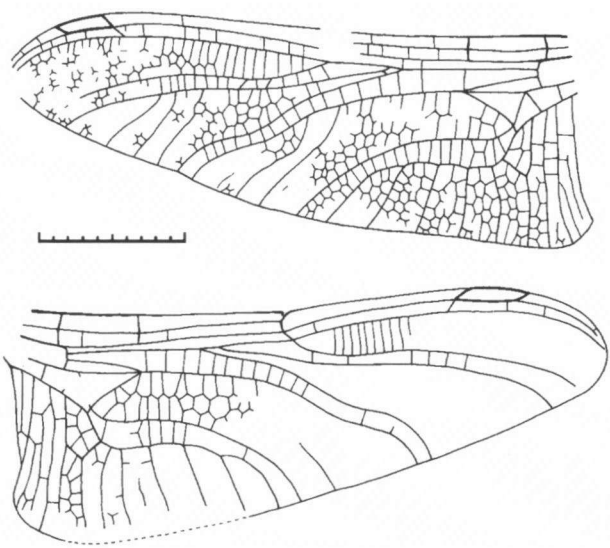

Fig. 3. *Prohemeroscopus kuehnapfeli* sp. nov., holotype SOS 1673, hindwing venation, camera lucida drawing.

preserved.

B o d y. – Head and thorax are not well preserved and rather useless. It is not visible if the compound eyes were separated or not. Abdomen. – Length 47.0 mm; width 3.0 mm; the abdomen is distinctly narrowed at the level of the second segment (length of the second abdominal segment 3.0 mm; width 2.0 mm) and distally slightly widened; the terminal appendages are not very well preserved, but the cerci are visible, 2.5 mm long and rather narrow, not leaf-like; no trace of any lateral auricles visible on the second segment (but this could also be an artefact of preservation); the male secondary genital apparatus is not visible, since the fossil is preserved in dorsal aspect.

PROHEMEROSCOPUS (?) *KUEHNAPFELI* SP. NOV.

Figure 3

M a t e r i a l. – **Holotype:** ♂, specimen SOS 1673 [Blumenberg, Eichstätt], Jura-Museum, Eichstätt, Germany.

STRATUM TYPICUM. – Upper Jurassic („Weißer Jura"), Malm zeta 2b, Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

LOCUS TYPICUS. – Blumenberg quarry, Eichstätt, southern Frankonian Alb, Bavaria, Germany.

E t y m o l o g y. – Named in honour of the first author's colleague Dr. Michael K ü h n a p f e l (Stuttgart, Germany), for numerous inspiring discussions on the theoretical problems of biosystematics and evolution.

DIAGNOSIS AND AUTAPOMORPHIES. – This new species differs from *P. jurassicus* sp. nov. in the following hindwing characters: (1) distinctly larger size (wing length about 40 mm); – (2) only one cell is double in the widened basal area between MP and CuA (plesiomorphy); – (3) vein CuAa has five or six distinct posterior branches (plesiomorphy); – (4) veins RP3/4 and MA are more distinctly undulating (autapomorphy); only two rows of cells in the basal postdiscoidal area; – (5) three secondary (intercalary) veins in the distal part of the area between IR2 and RP3/4; – (6) the discoidal triangle is free (autapomorphy); – (7) there are several secondary antenodal crossveins between the two primaries AX1 and AX2 (plesiomorphy); – (8) AX2 is in a more distal position on the level of the distal end of the discoidal triangle (plesiomorphy); – (9) the anal loop is more distinctly closed posteriorly (plesiomorphy).

DESCRIPTION. – A pair of rather poorly preserved hindwings of an adult male dragonfly. Some of the apparent differences in the wing venation of the right and the left hindwing of the holotype, especially concerning the position and length of the pterostigmata and concerning the width of the cubito-anal areas, might represent an aberration, or rather flaws in the referring drawings because of the bad state of preservation.

Hindwing. – Length, 41.3 mm; width on the level of the nodus, 11.3 mm (max. width, 13.6 mm); distance from base to arculus, 3.6 mm; from base to nodus, 19.0

mm; from nodus to pterostigma, 12.0 mm; the nodus is in a relatively basal position at 46 % of the wing length; the pterostigma is 4.3 mm long and max. 0.9 mm wide in the right wing, but apparently only 3.3 mm long in the left wing; the pterostigma is in a normal position, at about 54 % of the distance between nodus and apex in the right wing, but apparently in a more distal position at about 70 % in the left wing; the pterostigma is not parallel sided, since its basal side is somewhat less oblique than its distal side; the pterostigmal brace is well defined and oblique, aligned with the basal side of the pterostigma; the pterostigma probably covers three cells (though only one or two are visible); only one or two of the postnodal crossveins between costal margin and RA distal of the pterostigma are preserved; only one of the postnodal crossveins is preserved between nodus and pterostigma, and non-aligned with the corresponding postsubnodal crossveins between RA and RP1; there is no distinct „libellulid gap" (*sensu* BECHLY, 1996) of postsubnodal crossveins directly distal of the subnodus; the nodus is of the „normal" Anisoptera-type; the subnodus is not extremely oblique; IR1 is not preserved, but must have been a short vein (pseudo-IR1 of Pananisoptera); RP1 and RP2 are basally parallel with only one row of cells between them in the basal half of the area between nodus and pterostigma, while in the distal half they become divergent with three or more rows of cells between them; the base of RP2 is strictly aligned with the subnodus; there seem to be two oblique crossveins 'O' present between RP2 and IR2, the first one 4.1 mm and four and half cells distal of the subnodus, and the second one two cells further (the latter might either be an artefact, or an individual aberration like in some extant cordulegastrids); there is one row of cells between RP2 and IR2 till the level of the pterostigma, but more distally there are at least two rows of cells between them; the area between RP2 and IR2 is distally widened; RP2 and IR2 are gently curved, but not undulating, and reach the posterior margin obliquely; the midfork (base of RP3/4) is 6.4 mm (right wing) or 5.1 mm (left wing) basal of the subnodus, and the origin of IR2 is 1.3 mm (right wing) or 0.9 mm (left wing) distal of the midfork; there are no bridge crossveins (Bqs) preserved between RP and IR2 basal of the subnodus; only two of the antesubnodal crossveins (between RA and RP basal of the nodus and distal of the arculus) are preserved in the median part of this wing space, so that there might be a „gap" of antesubnodal crossveins directly distal of the arculus and directly basal of the subnodus (presence of a „cordulegastrid gap" *sensu* BECHLY, 1996); three or four antefurcal (postmedian) crossveins between RP and MA basal of the RP-midfork; there is no Rspl, but about three long and convex secondary veins (intercalaries) are present in the area between IR2 and RP3/4; there is no Mspl, but two rather long and convex secondary veins (intercalaries) are present in the distal postdiscoidal area between MA and MP; the postdiscoidal area is wide with only two rows of cells near the discoidal triangle; the postdiscoidal area is distally widened (width near discoidal triangle, 2.9 mm; width at posterior wing margin, 8.3 mm); RP3/4 and MA are strictly parallel, but distinctly undulating on the level of the oblique

crossvein 'O'; the discoidal triangle is rather narrow and distinctly longitudinal elongate, and apparently not divided by any crossveins; length of its anterior side, 4.3 mm; of its basal side, 2.1 mm; of its distal side MAb, 4.0 mm; the distal side MAb is straight or even slightly „concave"; the hypertriangle is free, 5.4 mm long and max. 0.7 mm wide; the costal side of the hypertriangle is rather straight; the basal space and subbasal space are free of crossveins; a somewhat oblique secondary anterior branch PsA (pseudo-anal vein) of AA delimits a well defined unicellular subdiscoidal triangle which is 2.0 mm long, max. 1.5 mm wide (length of PsA) and min. 0.3 to 0.4 mm wide (length of subdiscoidal veinlet); there are about seven rows of cells in the anal area below AA which is 8.1 mm wide below PsA; there is a distinct anal angle, and a large anal triangle that is divided into three cells by a Y-shaped vein (thus it is a male specimen); the CuP-crossing is 1.1 mm basal of the arculus, rather close to the distal side of the anal triangle; there are no supplementary cubito-anal crossveins; MP is gently curved and ends on the level of the nodus; the area between MP and CuAa is basally and distally distinctly widened with one cell being double below the discoidal triangle, and with probably four cells between MP and CuAa at the posterior wing margin; the so-called „gaff" is straight and very elongated (1.9 mm long); CuAb (the most basal posterior branch of CuA) is strongly angular to the „gaff"-portion of CuA; CuAb and a posterior branch of AA enclose a relatively large and transverse anal loop that is max. 3.3 mm long and max. 2.3 mm wide in the right wing, but somewhat aberrant in the left wing; the anal loop is distinctly closed posteriorly, and divided into six cells in the right wing and only four cells in the left wing; there is one posterior branch of AA between the anal triangle and the anal loop in the right wing, but two such branches in the left wing; CuAa has six distinct posterior branches in the right wing, and five in the left wing; the most distal branch is secondarily branched from CuAa; there are five to seven rows of cells in the median part of the cubito-anal area (apparently max. 5.4 mm wide in the right wing, but only max. 4.2 mm wide in the left wing); the arculus is distinctly angled, and the bases of RP and MA are distinctly separated at the arculus; only the two primary antenodal crossveins AX1 and AX2 are aligned and stronger than the non-aligned secondary antenodal crossveins that are incompletely preserved; AX1 is 0.4 mm basal of the arculus and AX2 is 5.5 mm distal of AX1, on the level of the distal end of the discoidal triangle; there is only one secondary antenodal crossvein preserved between AX1 and AX2, but there were probably about three of them.

PHYLOGENETIC POSITION OF THE HEMEROSCOPIDAE

PRITYKINA (1977) and CARPENTER (1992) considered that the Hemeroscopidae are related to the Cordulegastrida without any phylogenetic analysis. BECHLY (1995: 263) suggested a sister-group relationship of Cordulegastrida and Hemeroscopidae, based on the shared presence of a long „cordulegastrid gap" which

BECHLY (1996, 1997) and the authors of the present publication regard as symplesiomorphy, since it is present in Neopetaliidae and (less distinct) in Eurypalpida (= Libelluloidea *sensu* FRASER, 1957) too. BECHLY (1996, 1997) classified Hemeroscopidae as sister-group of Chlorogomphoidea, while LOHMANN (1996) regarded Hemeroscopidae as stem-group representatives of Brachystigmata (= Brevistigmata *sensu* LOHMANN 1996 who based this new taxon name on a personal information from BECHLY).

Since the larvae of Hemeroscopidae have to be regarded as unknown (see below) and the body characters are insufficiently preserved or based on dubious fragments (see below), only the wing venational characters allow an estimation of the phylogenetic position of Hemeroscopidae within Anisoptera.

RELATIONSHIP OF HEMEROSCOPIDAE WITH CAVILABIATA

The Hemeroscopidae can easily be distinguished from the Petalurida and the Gomphides by their elongated „gaff" and large anal loop. A similar type of anal loop is present in many Aeshnidae and Brachystigmata (Chlorogomphoidea, Synthemisti-dae, Gomphomacromiidae, and Macromiidae). The closed and six--celled anal loop of *Neopetalia* is quite similar too (symplesiomorphy), especially to that of *Prohemeroscopus* gen. nov. The anal loop of many Cordulegastrida is reduced (only two- or three-celled, more or less posteriorly open), but some Cordulegastrida have retained a posteriorly closed, two- to six-celled anal loop. The „more advanced" Eurypalpida (e.g. Neophyinae, Idomacromiinae, Corduliinae, Macrodiplacidae, and Libellulidae) have an elongate anal loop, with a mid-rib (Cuspl vein), as synapomorphy.

The Hemeroscopidae can be distinguished from the Aeshnoptera because they possess a subdiscoidal triangle that is defined by a secondary pseudo-anal vein PsA, their discoidal triangles are not longitudinal elongate and their Rspl and Mspl are rudimentary or absent. However, all these characters are plesiomorphies of Hemeroscopidae. The Hemeroscopidae have short veins pseudo-IR1, of libelluloid-type, which originate on RP1 below the distal side of the pterostigma, like some Gomphides, but unlike most Aeshnida. However, this character probably represents an autapomorphy of Pananisoptera, since Heterophlebioidea (sister-group of Pananisoptera) still have long primary IR1, like other „anisozygopteres" and Zygoptera, while a short pseudo-IR1 occurs in the Liassogomphidae, Aeschnidiidae (*Urogomphus*; Bechly, unpubl.), basal Aeshnoptera (e.g. *Mesuropetala*, *Cymatophlebia*, „*Morbaeschna*"), many Gomphides and most Cavilabiata (NEL *et al.*, 1993). As described by BECHLY (1996), the IR1 of crown-group Anisoptera is probably of complex origin and composed by a primary long IR1 and a secondary short pseudo-IR1 (autapomorphy of Pananisoptera), that can be either fused, or reduced in different ways.

The attribution of Hemeroscopidae to the Anisoptera - Cavilabiata can be based

on the following putative synapomorphies: No antesubnodal crossveins directly basal of the subnodus („cordulegastrid gap") (convergent to few other Anisoptera, e.g. Gomphaeschnidae; reversed in Chlorogomphoidea); presence of a wide anal loop that is divided into five or more cells (convergent to Euaeshnida); „gaff" of the hindwing at least slightly prolonged (convergent to Euaeshnida); hindwing CuAa is shortened with few (max. four) posterior branches (convergent to some Euaeshnida and Gomphides, like Cordulagomphinae), although the latter character seems to be plesiomorphic absent in *Prohemeroscopus* gen nov. The mentioned characters cannot be regarded as potential synapomorphies with Euaeshnidae, - Gomphaeschnidae, since the Hemeroscopidae lack all the autapomorphies of the more inclusive clades of aeshnoid dragonflies (Aeshnoptera, Aeshnomorpha, and Aeshnida; see BECHLY, 1996, 1997).

The attribution of Hemeroscopidae to the Anisoptera - Cristotibiata can be based on the following two putative synapomorphies: Pterostigmata not parallel sided, with length less than 8 times width; anal loop elongated and enlarged with more than 5 cells.

The attribution of Hemeroscopidae to the Anisoptera - Brachystigmata can be based on the following putative synapomorphies: Relatively short pterostigmata that cover only 1-3 complete cells (convergent to some derived Neoaeshnida and Gomphides; reversed in Libellulinae); in the hindwing the „gaff" is strongly prolonged (convergent to several Aeshnidae, especially Anactina); nodus shifted at least somewhat distally in forewings (reversed in Libellulidae).

Most of the remaining wing venational characters represent plesiomorphic character states within Anisoptera, e.g. the dense reticulation of the distal half of the wings; the absence of any Mspl and the rudimentary or absent Rspl; the presence of a subdiscoidal triangle delimited by a secondary branch PsA of the anal vein; the presence of an anal angle and anal triangle in the male hindwing; the distinctly braced pterostigmata (in *Prohemeroscopus* gen. nov.); the non-aligned antenodal crossveins; the absence of a „libellulid gap" (*sensu* BECHLY, 1996) in the basal postsubnodal space; and the bases of RP and MA well separated at the arculus which is distinctly angled, etc.

The presence of well-defined subdiscoidal triangles and a pseudo-anal vein PsA in both wing pairs is probably a symplesiomorphic character of Petalurida (JARZEMBOWSKI & NEL, 1996; NEL *et al.*, in press), Austropetaliida, Gomphides, and Hemeroscopidae, which is secondarily indistinct in Euaeshnida (still more distinct in „*Morbaeschna*", and vestigial in extant „Gomphaeschninae") and Cordule-gastrida, correlated with their longitudinal elongation of the discoidal triangles. The pseudo-anal vein PsA is also reduced in most Chlorogomphoidea (except *Chlorogomphus brunneus*) (JARZEMBOWSKI & NEL, 1996), but still visible as oblique crossvein. In all Eurypalpida the pseudo-anal vein PsA is very distinct in the forewing, even developed as main branch of AA in many „Corduliidae" and most Libellulidae, while the PsA of the hind wing is reduced to an oblique

crossvein or to a normal transverse crossvein, or is even completely suppressed.

The following potentially synapomorphic characters suggest a sister-group relationship of Hemeroscopidae and Chlorogomphoidea: (1) the basal area between CuAa and MP is widened in the hindwing, with at least one double cell (two rows of cells) below the discoidal triangle; – (2) the „gaff" is very long and straight in the hindwing; – (3) the anal loop is more or less pentagonal and rather wide; – (4) the most distal branch of CuAa seems to be secondarily branched on CuA.

Character (1) is a quite rare derived similarity between Hemeroscopidae and most Chlorogomphoidea, but it is absent in the most basal representatives of Chlorogomphoidea, like *Chloropetalia atkinsoni* (CARLE, 1995). Furthermore, it is also present by convergence in some Macromiidae (e.g. *Macromia funicularis*), the gomphid genus *Cacoides*, and several Aeshnidae (e.g. *Oplonaeschna armata*, *Cephalaeschna acutifrons*, *Staurophlebia gigantea*, *Neuraeschna harpya*, *Tetracanthagyna waterhousei*, some *Aeshna* species and all species of the Anactina). Consequently, this character could also be a convergence of Hemeroscopidae and Chlorogomphoidea. However, the assumption of convergence should never be an ad hoc hypothesis, but always implied by strong conflicting evidence.

Character (2) is very similarly developed in Hemeroscopidae and Chlorogomphoidea. The elongation of the „gaff" definitely represents a derived character state that is successively more strongly developed in the ground-plans of Cavilabiata (Cordulegastrida + Cristotibiata), Cristotibiata (Neopetaliidae + Brachystigmata) and Brachystigmata (Chlorogomphoidea + Hemeroscopidae + Eurypalpida). It is very long and straight in Chlorogomphoidea and Hemeroscopidae, while it is further elongated and sigmoidally curved in most Eurypalpida (except the most basal groups: Synthemistidae, Gomphomacromiidae, and Macromiidae). Since the „gaff" is more or less curved in Cordulegastrida, Neopetaliidae, and Eurypalpida, the straight course in Hemeroscopidae and Chlorogomphoidea could represent a synapomorphy indeed, while the strong elongation belongs to the ground-plan of Brachystigmata and therefore represents a symplesiomorphy of Hemeroscopidae and Chlorogomphoidea. A similarly straight and elongate „gaff" is present by convergence in some derived Aeshnidae, especially the Anactina.

A very large anal loop (character 3) is present in most Aeshnidae, *Hemeroscopus*, Chlorogomphoidea and Eurypalpida. The anal loop of *Prohemeroscopus* gen. nov. is more similar to the anal loop of *Neopetalia* which is already somewhat enlarged relative to the plesiomorphic state in Cordulegastrida, but not yet as large as in most Brachystigmata. Furthermore, the very wide anal loop is of different shape in *Hemeroscopus*, Chlorogomphoidea, and Eurypalpida. Although a more or less increased number of cells in the anal loop seems to represent a derived ground-plan character of Cristotibiata and Brachystigmata, the enormous enlargement in *Hemeroscopus*, Chlorogomphoidea, and Eurypalpida might be rather due to convergence, as in Aeshnidae.

Character (4) is a derived similarity of Hemeroscopidae and Chlorogomphoidea

as well, but since the same state also occurs as convergence in a few Aeshnoptera (e.g. *Hypopetalia pestilens*, *Phyllopetalia stictica*, *Oplonaeschna armata*, and *Hemianax ephippiger*), the gomphid genus *Octogomphus*, the stem-group eurypalpid genus *Valdicordulia*, and at least one species of Cordulegastridae (*Allogaster latifrons*), this character could also be the result of convergence between Hemeroscopidae and Chlorogomphoidea. Furthermore, it could even be an autapomorphy of Brachystigmata (thus a symplesiomorphy of Hemeroscopidae and Chlorogomphoidea), since the character is not applicable to Eurypalpida that have reduced all posterior branches of CuAa.

The compound eyes of *Hemeroscopus baissicus* are contiguous for a short distance (PRITYKINA 1977: 92, text-fig. 8a). This structure is unknown in *P. jurassicus* gen. et sp. nov., but it is of rather limited value, even if it suggests some affinities with the Cavilabiata - Brachystigmata, because within Chlorogomphoidea and even within the Libellulidae, some taxa have eyes dorsally meeting for a long distance, while others have the eyes only touching at a point. Since strongly contiguous compound eyes are also present in Aeshnida, this character has to be regarded as rather homoplastic and therefore of low weight for phylogenetic analyses within Anisoptera (FLECK, 1996). CARLE (1995) supposed that the character «eyes strongly approximate or meeting dorsally for a long distance» and the correlated character «occiput of triangular shape» are synapomorphies of Aeshnoptera (= Aeshnoidea *sensu* CARLE) and Cavilabiata (= Libelluloidea *sensu* CARLE), while he considered gomphids as the sister-group of all remaining extant Anisoptera. BECHLY (1996, 1997), LOHMANN (1996), and NEL *et al.* (in press) dismissed this hypothesis as based on unconvincing evidence, and instead considered gomphids to be the sister-group of Cavilabiata, while aeshnoids were shown to be a more basal group. FLECK (1996) could demonstrate that the approximation of the eyes within Aeshnidae and Libelluloidea is rather a convergence, since the subsequent reduction of the occiput is very different within the two groups. Within Gomphides only the Araripegomphidae BECHLY, 1996 do have approximated eyes by convergence too (BECHLY, 1996, 1997, in prep.), which led LOHMANN (1996) to the probably erroneous conclusion that *Araripegomphus* NEL & PAICHELER, 1994 belongs to the stem-group of Eurypalpida (Palpolabiata *sensu* LOHMANN, 1996). Therefore the approximation of the compound eyes is here regarded as a triple convergence within Anisoptera. Recent studies of new specimens of *Araripegomphus* by BECHLY (in prep.) confirmed the approximation of the eyes, that was previously only known from the holotype specimen, but also showed that the eyes are not in contact with eachother. These new specimens furthermore revealed that several of the alleged synapomorphies of Eurypalpida and Araripegomphidae proposed by LOHMANN (1996) are either incorrect, or variable in *Araripegomphus*, and thus of doubtful significance. The remaining alleged synapomorphies are very homoplastic and also occur in some, or even most, gomphids. The absence of an anal loop and the short „gaff" are characters of *Araripegomphus* that strongly con-

tradict a position in the stem-group of Eurypalpida. Most probably *Araripegomphus* is a gomphid, as suggested in the original description (NEL & PAICHELER, 1994c; BECHLY, in prep.).

The head of *Hemeroscopus* shows two high frontal spines. Similar structures (at least two humps on the upper part of the frons) are present in Brachystigmata (convergent to a few aeshnids, like *Austroaeschna atrata* and the male of *Nasiaeschna pentacantha*) and therefore might represent a further synapomorphy of Hemeroscopidae and Brachystigmata. The frons and postclypeus of *Hemeroscopus* are narrow, which clearly has to be regarded as plesiomorphic state, relative to the high frons and postclypeus in aeshnids (FLECK, 1996).

The other described body characters of *Hemeroscopus baissicus* (PRITYKINA, 1977) are either useless, since only showing plesiomorphies (e.g. thorax and legs), or based on body fragments that are only doubtfully attributed to this taxon (e.g. female terminalia without ovipositor). Nevertheless, two of the described body characters (confluent eyes and reduced ovipositor) would support the suggested position of Hemeroscopidae as sister-group of Chlorogomphoidea, while none of them conflicts with this hypothesis.

Although the venation in *Prohemeroscopus* gen. nov. and *Hemeroscopus* is very similar, these similarities are mostly based on symplesiomorphies (ground-plan characters of Anisoptera, Cavilabiata, Cristotibiata or Brachystigmata). The only strong putative synapomorphy between *Hemeroscopus* and *Prohemeroscopus* gen. nov. is the distinctly widened area between RP2 and IR2, although even this character is somewhat homoplastic: In many Heterophlebioidea (sister-group of Anisoptera) and in Liassogomphidae (very basal Anisoptera of uncertain position) this area is also greatly widened (NEL *et al.*, 1993; *contra* LOHMANN, 1996). In basal Euaeshnida (e.g. Gomphaeschnidae) this area is greatly widened too, although in a very different way, since being due to an undulation of RP2. In all other Anisoptera (incl. all other Cavilabiata) this area is generally distinctly less wide, with less than two rows of cells between RP2 and IR2. The state in Heterophlebioidea, Liassogomphidae and the mentioned aeshnids clearly does not belong to the ground-plan of Anisoptera, therefore the widening of this area is most parsimoniously interpreted as synapomorphy of *Prohemeroscopus* gen. nov. and *Hemeroscopus*, thus as autapomorphy of Hemeroscopidae which is rather unique in the crown-group Anisoptera.

The attribution of *Prohemeroscopus* gen. nov. to the Hemeroscopidae is consequently only based on a single good synapomorphy, several synapomorphies of Hemeroscopidae with Cavilabiata, Cristotibiata, Brachystigmata and Chlorogomphoidea, and numerous symplesiomorphic characters (that exclude a position in Eurypalpida). The lack of other strong autapomorphies makes a profound characterisation of the Hemeroscopidae quite difficult, and it cannot be totally excluded that Hemeroscopidae (incl. *Prohemeroscopus* gen. nov.) might be paraphyletic, as suggested by a numerical cladistic analysis (see below).

As a conflicting evidence to the proposed monophyly of Hemeroscopidae, *Prohemeroscopus jurassicus* gen. et sp. nov. shares with all Eurypalpida two potential synapomorphies: AX2 is shifted basal of the level of the distal end of the discoidal triangle in both wing pairs; there is not more than a single secondary antenodal crossvein retained between the two primaries AX1 and AX2. Both characters are of course correlated. Although the primary and secondary antenodal crossveins cannot be distinguished in numerous „Corduliidae" and all Libellulidae (except in a few genera like *Zenithoptera*, *Tramea*, and *Paleotramea*), the ground-plan condition of Eurypalpida can be reconstructed without great difficulty (BECHLY, 1996), i.e. a single secondary antenodal crossvein between the two primaries.

On the other hand, the longer vein CuAa in the hindwing, the rather small anal loop (only 6 cells), and the distinct pterostigmal brace are plesiomorphic states, relative to the derived states in *Hemeroscopus*, and in most Chlorogomphoidea and Eurypalpida. However, the relatively small anal loop and distinct pterostigmal brace in some stem-group representatives of Eurypalpida (e.g. *Araripelibellula*) clearly shows that the two mentioned derived similarities in *Hemeroscopus* and extant Brachystigmata must be due to convergence anyway.

As already indicated by BECHLY (1996, 1997) and LOHMANN (1996), there are several derived similarities between Chlorogomphoidea and Eurypalpida which could even suggest that Hemeroscopidae belong to the stem-group of all extant Brachystigmata rather than the stem-group of Chlorogomphoidea: Sectors of arculus (RP and MA) approximate; arculus rather straight and posterior part (basal discoidal crossvein) of arculus distinctly shorter than anterior part (RP+MA); oblique pterostigmal brace indistinct or obsolete, if present shifted distally beneath the pterostigma (no ground-plan character of Hemeroscopidae, since distinctly braced in *Prohemeroscopus* gen. nov.); hind wing MP somewhat shortened and more distinctly curved towards the hind margin (LOHMANN, 1996); the hindwing CuAa is further shortened, distinctly curved towards the hind margin, and supplied with less than four posterior branches; anal loop further enlarged (no ground-plan character of Hemeroscopidae, since still relatively small in *Prohemeroscopus* gen. nov.); presence of several accessory cubito-anal crossveins (CARLE, 1995; but reduced in many Eurypalpida); RP3/4 and MA closely parallel with only one row of cells even between the most distal parts of these veins. Nevertheless, some stem-group representatives of Eurypalpida (e.g. *Eocordulia*, *Condalia*, and *Araripelibellula*) do possess the plesiomorphic states too (in different combinations), so that most of the mentioned derived similarities of Chlorogomphoidea and Eurypalpida (e.g. arculus, pterostigmal brace, anal loop, cubito-anal crossveins) most probably are due to convergence (BECHLY, 1996, 1997). If Hemeroscopidae are regarded as monophyletic, the indistinct pterostigmal brace and the enlarged anal loop of *Hemeroscopus* must then be regarded as convergences anyway, since they are present in the plesiomorphic state in *Prohemeroscopus* gen. nov. As explained above, we

do not regard these (very homoplastic) character states as convincing evidence for a paraphyly of Hemeroscopidae, and thus give higher weight to the mentioned putative autapomorphy (widened area between RP2 and IR2), since it is quite unique within crown-group Anisoptera. However, the monophyly of Hemeroscopidae and their position as sister-group of Chlorogomphoidea are far from being well established, and it cannot be totally excluded that the correct position might be as indicated by our cladistic analysis (cf. Figure 7).

PROBLEM OF THE SYSTEMATIC POSITION OF THE ALLEGED HEMEROSCOPID LARVAE

PRITYKINA (1977) partly based the attribution of the Hemeroscopidae to the libelluloid-like dragonflies (= Cavilabiata) on the spoon-shaped labial mask and the structure of the gizzard of the larvae that she attributed to *Hemeroscopus baissicus*. However, this conclusion has to be regarded as unjustified, since it is impossible to propose a reasonable hypothesis about the specific identity of fossil odonate larvae and fossil odonate adults because, at least in the order Odonata, the larvae and adults share nearly no diagnostic characters on the generic or specific level. On the other hand, it is often possible to attribute fossil larvae to higher taxa on the base of larval synapomorphies, e.g. the reduction of one tarsomere on the larval pro- and meso-tarsi of Gomphides. As a very rare example for an adult character that is visible in a fossil dragonfly larva, we can only mention the recent discovery of a genuine larva of the fossil family Aeschnidiidae (or Stenophlebiidae ?) from the Cretaceous of China which can be attributed to this family on the base of synapomorphic wing venational characters that are visible on the larval wing sheaths (NEL, unpubl.; FLECK, in prep.).

Consequently the larval mask and the gizzard described by PRITYKINA (1977) can only be regarded as belonging to a larval Cavilabiata *incertae sedis*. It is not even clear from her publication if the fossil larva with the spoon-shaped mask and the bilaterally symmetrical gizzard and the numerous fossil larvae with the hairy legs and the forcep-like paraprocts are really conspecific, or if for example the mask is a singular fragment which could also belong to a different type of larvae. The latter alternative is supported by a recent re-examination of the referring material in Moscow by one of the authors (NEL, unpubl.) who found the mask of the alleged hemeroscopid larvae to be of the flat gomphid type! The alleged preservation of the gizzard dentition in a fossil larva would be quite unique and surprising and definitely should be confirmed by a critical re-examination too.

The common presence of larvae and adults in the same layers is no sufficient evidence for an attribution to the same species, because several counter examples are known, with common presence of numerous fossil larvae and adults, even belonging to different families and suborders, in the same outcrop. For example, in the Upper Oligocene of Bes-Konak (Turkey), the Anisoptera (Libellulidae: *Palaeotramea aquisextana beskonakensis* NEL & PAICHELER, 1993) are known

by three doubtful larvae and fifty adults, while Zygoptera (Lestidae: *Lestes* (?) sp.) are known by one wing and more than two hundred larvae (NEL & PAICHELER, 1994a,1994b). If we would follow PRITYKINA's arguments, these zygopteroid larvae and anisopteroid adults would be attributed to the same species, because they are found together and both represent the most common odonate fossils from this outcrop. The same situation occurs in the Miocene of Ribesalbes (Spain). These examples demonstrate the fallaciousness of this kind of reasoning. Consequently, it is impossible to use the characters of the alleged hemeroscopid larvae for the analysis of the phylogenetic relationships of Hemeroscopidae. On the contrary, the results of a phylogenetic analysis of the adult specimens, allow predictions about the features of the unknown larvae. For example, it can be assumed that the hemeroscopid larvae indeed must have had a spoon-shaped mask and a bilaterally symmetrical gizzard, since Hemeroscopidae turned out to represent a subordinate group within the monophylum Cavilabiata (= Libellulini *sensu* FRASER, 1957) that does possess these larval features as derived ground-plan characters. However, we came to the preliminarily conclusion that the majority of the alleged „hemeroscopid" larvae belong to an undescribed genus and species in the Sonidae *sensu novo* (see below).

THE POSITION AND STATUS OF SONIDAE

PRITYKINA (1986) described *Sona nectes* and the monotypical Sonidae from the Lower Cretaceous of West Mongolia. She mentions the presence of about 300 specimens of which only 18 are adults while the rest are larvae of different stages. The holotype of *Sona nectes* is a well preserved young larva. Because of the above mentioned arguments there is no justification for the attribution of the alleged adult „Sonidae" to the larval „Sonidae". Since the holotype is a larva, BECHLY (1996, 1997) restricted the family Sonidae to these peculiar larvae and suggested a new genus and family (*Proterogomphus* and Proterogomphidae *sensu* BECHLY, 1996, 1997, *nomina nuda*) for the adult dragonflies that were formerly attributed to Sonidae. This suggestion was mainly based on arguments that support a different phylogenetic position of the referring larvae and adults. We follow this proposal and formally classify the adults as new genus and species in a new family (see below)

BECHLY (1996, 1997) already mentioned several potential autapomorphies of Proterogomphidae (*nomen nudum* in BECHLY, 1996, 1997) and suggested that this family probably belongs to the monophylum Gomphides (= Gomphata *sensu* LOHMANN, 1996), while the true Sonidae (larvae) seem to belong to the stem-group of Anisoptera (see below). A close relationship of the adult „sonids" (*sensu* PRITYKINA, 1986) with gomphids was already proposed by PRITYKINA (1986), while LOHMANN (1996) suggested that „Sonidae" belong to the stem-group of Exophytica (= Exophyticata *sensu* LOHMANN) without explaining why they should

not belong to the crown-group. Anyway, both statements are more or less meaningless, since they were largely based on a combination of characters of the obviously unrelated larvae and adults. The character of the adult male abdominal appendages („epiproct unifurcate") is rather dubious, since it is based on an abdominal fragment (specimen N 3152/142, PIN) which was very doubtfully attributed by PRITYKINA (1986) to the same species as the adult „Sonidae" without any evidence.

The holotypical larva of *Sona nectes* is very similar to the larvae that were previously attributed by PRITYKINA (1977) to *Hemeroscopus baissicus*, since they share two highly derived characters (dense fringe of hairs on the tibiae and forceplike paraprocts), as well as an aeshnid-like body without a true anal pyramid (symplesiomorphy). Nevertheless, PRITYKINA (1986) regarded these similarities as convergences, since the *Sona*-larvae clearly possess a flat gomphid-like mask, while the *Hemeroscopus*-larvae shall have a spoon-shaped libelluloid-like mask and a libelluloid-like gizzard. As already mentioned above, it rather looks like the alleged hemeroscopid larvae do not represent a single species, but rather a „chimera" of two different species: A sonid-like species with hairy legs and forcep-like paraprocts, and a libelluloid-like species with a spoon-shaped mask and a bilaterally symmetrical gizzard. We therefore regard the unique derived similarities of the sonid larvae and (at least a part of) the hemeroscopid larvae as homologous and thus as an indication for a very close relationship (synapomorphies).

The alleged larvae of Hemeroscopidae probably represent a new genus and species of Sonidae *sensu novo*. A potential autapomorphy of this new species are the dense fringes of hairs on the inner margin of the larval paraprocts. The unique forcep-like paraprocts are also known from some other fossil dragonfly larvae, e.g. the genera *Dissurus* and *Yixiangomphus* from the Mesozoic of China, and from *Nothomacromia sensiblis* and still undescribed giant larvae (with flat gomphid-like mask) from the Lower Cretaceous Santana Formation of Brazil, which therefore certainly belong to the same clade as *Sona nectes*. The mentioned Brazilian larvae share the needle-like larval epiproct as putative synapomorphy with the larvae that were previously assigned to *Hemeroscopus baissicus*. On the other hand, the dense fringes of hairs on the larval tibiae and tarsi are only known from the alleged „hemeroscopid" larvae and *Sona nectes*, but not from the Chinese and Brazilian larvae. Such „swimming legs" could indicate that these larvae were not capable of jet-prop locomotion, just like the larvae of Zygoptera, extant „anisozygopteres" (*Epiophlebia*), and the most basal Anisoptera (Petaluridae). The plesiomorphic absence of a true anal pyramid even suggests that all the sonid-like larvae belong to the stem-group of Anisoptera (e.g. Stenophlebiidae or Aeschnidiidae) rather than the crown-group. The reduced «Ovipositor-Anlagen» that have been described by PRITYKINA (1986) for female larvae of *Sona nectes* might indicate a relationship with Stenophlebioidea (BECHLY, 1996, 1997), since these are also known from the same layers and represent the only known stem-

group representatives of Anisoptera that have a reduced ovipositor in adult females (NEL et al., 1993). Nevertheless, this hypothesis is still rather weak.

On the wing sheaths of an undescribed fossil dragonfly larva of the sonid type from the Lower Cretaceous of China, the typical wing venation of Aeschnidiidae is visible (NEL, unpubl.; FLECK, in prep.). However, a similar venation (transverse discoidal triangles, many intercalaries) also occurs in Stenophlebiidae, so that a further confirmation would be important. On the other hand the complete absence of adult „anisozygopteres" and the presence of at least two species of adult Aeschnidiidae in the Santana Formation, also suggests that Aeschnidiidae are the more likely candidates as corresponding adults to the *Nothomacromia* larvae and the mentioned giant larvae. A further hint might be the facts that adult Aeschnidiidae, as well as *Nothomacromia* and the giant larvae are morphologically quite remote from the rest of Anisoptera, and that Aeschnidiidae and the giant larvae agree in their above average size. All together, the available evidence suggests that all the sonid-like larvae represent larval Aeschnidiidae (BECHLY, in prep.).

The fringe of hairs on the tibiae of at least the younger larvae of Sonidae was interpreted by PRITYKINA (1977, 1986) as a swimming device, correlated with a nectic way of life, that inspired her species name for *Sona nectes*. Although such a function cannot be excluded, there are no known extant examples for nectonic dragonfly larvae, but there exist several extant examples of gomphid larvae with hairy legs that use these structures as burrowing device. Furthermore a strikingly similar type of larva with nearly identical legs is known from the stonefly species *Perla marginata* (Plecoptera). Although its legs with the dense fringes of hairs shall be used as swimming device indeed (KARNY, 1934: 124), these perlids are not at all nectic, but benthic organisms. Therefore we do not regard PRITYKINA's original interpretation as compelling, as already noticed by NEL (1991).

Because of the very probable different phylogenetic position of Proterogomphidae fam. nov. („adult sonids") and the characteristical sonid larvae (Sonidae *sensu novo*) which show a strange combination of plesiomorphies and unique autapomorphies, we decided to restrict the family Sonidae to these larvae, and preliminarily regard this family as a potential junior subjective synonym of Aeschnidiidae (BECHLY, in prep.).

Our new phylogenetic definition of the taxon Sonidae *sensu novo* is: Sonidae shall include all dragonflies that are closer related to *Sona nectes* PRITYKINA, 1986 (holotypical larva) than to any of the type-species of the other type-genera of the extant Anisoptera family-group taxa *sensu* FRASER (1957) (stem-based definition).

TAXONOMY OF PROTEROGOMPHIDAE FAM. NOV.

Proterogomphidae fam. nov.

(Anisoptera: Euanisoptera: Exophytica: Gomphides: Hagenioidea stat. nov.)

Type genus. – *Proterogomphus* gen. nov.

PHYLOGENETIC DEFINITION. – Proterogomphidae fam. nov. shall include all dragonflies that are closer related to *Proterogomphus krauseorum* gen. et sp. nov. than to any of the type-species of the other type-genera of the Anisoptera family-group taxa *sensu* FRASER (1957) (stem-based definition).

INCLUDED TAXA. – Preliminarily only including the genus *Proterogomphus* gen. nov., but probably also including Cordulagomphinae according to BECHLY (in prep.).

DIAGNOSIS AND AUTAPOMORPHIES. – Triangles secondarily undivided; only two cells beneath the pterostigmata; vein pseudo-IR1 very distinct and originating on RP1 beneath the distal end of the pterostigma; anal loop reduced to one or two cells; enlarged cell beneath the subbasal space in the forewings; hindwing triangles more longitudinal elongate (convergent to Lindeniinae). All these characters seem to be auta-pomorphies. For further diagnostic characters see the new diagnosis of the type-genus below.

PHYLOGENETIC SYSTEMATICS. – PRITYKINA (1986) recognized that wing venation of Sonidae (auct.) does not differ from that of Gomphidae (auct.), and exclusively based her attribution to a separate family on the erroneous assumption that the adults are conspecific with the curious larvae (see above). Based on the phylogenetic system of Gomphides (BECHLY, 1996, 1997), we retain a separate family status for the adults (Proterogomphidae fam. nov.) which seem to be the sister-group to Hageniidae (BECHLY, 1997). In his modified phylogenetic classification, BECHLY (1997) transferrred the Hageniidae to a more basal position with Gomphides than in his previous classification (BECHLY, 1996). Proterogomphidae fam. nov. and Hageniidae are here classified in a new superfamily Hagenioidea stat. nov.

The Proterogomphidae fam. nov. share with Exophytica the presence of only one oblique vein (potential synapomorphy, but very homoplastic character), and with Gomphides the very distinct subdiscoidal triangles in both wings (polarity unclear) and the angled distal side MAb of the discoidal triangle (synapomorphy) that is correlated with a supplementary sector in the postdiscoidal area (convergent to Euaeshnida). The distinctly separated compound eyes agree with a position in Gomphides, but of course represent a symplesiomorphy. The same is true concerning the general similarity of the wing venation, since Proterogomphidae fam. nov. and Gomphides have retained a very plesiomorphic wing venation. Within Gomphides, the Proterogomphidae fam. nov. share with most groups (except the most basal Progomphidae and Lindeniidae) the presence of less than five antefurcal

crossveins between RP and MA in the hindwings. With Hageniidae they share the following putative synapomorphies: Branching of RP at midfork symmetrical (convergent to Eugomphida); hindwing discoidal triangles distinctly longitudinal elongate (convergent to Lindeniinae), correlated with somewhat less distinct pseudo-anal veins PsA and subdiscoidal triangles (convergent to Lindeniinae); distal side of triangle (MAb) strongly angulate, correlated with the development of a more distinct supplementary sector (trigonal planate) in the postdiscoidal area (convergent to the hindwing of Lindeniinae). Furthermore, Proterogomphidae fam. nov. and Hageniidae share two important symplesiomorphies that exclude a position in „higher" gomphids: Hindwing CuAa long with numerous posterior branches; hindwing still with more than two antefurcal crossveins between RP and MA. However, all above mentioned characters are relatively weak and homoplastic, so that the proposed phylogenetic position of Proterogomphidae fam. nov. as sister-group of Hageniidae within Gomphides is still somewhat uncertain.

BECHLY (in prep.) suggests that Cordulagomphinae from the Lower Cretaceous of Brazil is the sister-group of *Proterogomphus* gen. nov. (Proterogomphinae) within Proterogomphidae fam. nov. The proposed synapomorphies are: Discoidal triangle secondarily free (unicellular); not more than two cells below the pterostigma; vein pseudo-IR1 originates below the distal side of the pterostigma; anal loop only one- or two-celled; the enlarged cell beneath the subbasal space in the forewings.

PROTEROGOMPHUS GEN. NOV.

Type species. – *P. krauseorum* sp. nov.

E t y m o l o g y. – After the Greek word for „former" and the genus *Gomphus*.

DIAGNOSIS AND AUTAPOMORPHIES. – Wing length about 37-42 mm; pterostigma very elongate and strongly braced; both rows of secondary antenodals non-aligned; arculus situated between AX1 and AX2, but much closer to AX1; only one oblique vein 'O', distinctly distal of the subnodus; no distinct veins Rspl or Mspl (maybe a weakly defined Rspl in the hindwing); forewings with a distinctly enlarged cell of the anal area, directly beneath the subbasal space; hypertriangles, discoidal triangles, and subdiscoidal triangles free of crossveins; hindwing discoidal triangle elongate and with a strongly angled distal side MAb; hindwing postdiscoidal area with a supplementary sector that originates on the angle of MAb; postdiscoidal area of both wings basally with only two rows of cells; hypertriangles with more or less curved anterior side; both subdiscoidal triangles very well defined by a strongly oblique pseudo-anal vein PsA; anal loop reduced to a single cell; „gaff" not elongated; no accessory cubito-anal crossveins present (except CuP-crossing); males with an anal angle and a three-celled anal triangle in the hindwing; pseudo-IR1 originating beneath the distal side of the pterostigma; RP1 and RP2 basally divergent, but with only one row of cells between them till the pterostigma; RP2 and IR2 strictly parallel and straight with only one row of cells between them; RP3/4 and

MA more or less parallel and straight, but distally somewhat diverging with two or three rows of cells between them.

A putative autapomorphy of *Proterogomphus* gen. nov. seems to be the unicellular anal loop (convergent to *Procordulagomphus* and many Gomphida). Probably an unifurcate epiproct of the adult males represents a further autapomorphy, although this character state is very dubious in the type-species (see above), since it is present in the new species *P. krauseorum* sp. nov. as well. Unfortunately the epiproct is unknown in the probably related Cordulagomphinae.

PROTEROGOMPHUS KRAUSEORUM SP. NOV.

Figure 4

Material. – **Holotype**: ♂, specimen N 3152/2118, Institute of Paleontology (PIN), Moscow, Russia; a rather well preserved specimen, described and figured in PRITYKINA, 1986: figs 18 and 25. – **Paratypes**: N 3152/2124, N 3152/2128, N 3152/2132, all from the same collection. – **Additional material**: At least some of the remaining 14 adult specimens mentioned by PRITYKINA (1986: 171) might belong to this species, but several of them certainly have to be regarded as Anisoptera *incertae sedis*.

STRATUM TYPICUM. – Lower Cretaceous (Neocomian), Gurvan-Eren Formation.

LOCUS TYPICUS. – Kobdo aimak, 8 km SE of Myangad somon, Mongolia.

Etymology. – Named in honour of Hannelore and Werner Krause (Kassel, Germany), dear relatives of the first author.

DIAGNOSIS. – Only differing from *P. renateae* sp. nov. by a slightly larger wing length (38-42 mm); the presence of a weak Rspl in the hindwing; the larger distance between CuP-crossing and arculus in the forewing.

A reconstruction of the wing venation of *Proterogomphus krauseorum* gen. et sp. nov. is provided in Figure 4. It is based on a (computer-aided) combination of the fragments figured by PRITYKINA (1986).

PROTEROGOMPHUS RENATEAE GEN. ET SP. NOV.

Figures 5-6

Material. – **Holotype**: ♂, specimen 6D, Coll. Dieter Kümpel (Wuppertal, Germany); will be deposited in the Jura-Museum, Eichstätt, Germany.

STRATUM TYPICUM. – Upper Jurassic („Weißer Jura"), Malm zeta 2b, Lower Tithonian, *Hybonotum*-Zone, Solnhofen Lithographic Limestone.

LOCUS TYPICUS. – Eichstätt, southern Frankonian Alb, Bavaria, Germany.

Etymology. – Named in honour of Mrs. Renate Kümpel (Wuppertal, Germany), wife of the collector.

DIAGNOSIS. – Wing venation extremely similar to *P. krauseorum* sp. nov.; even the pattern of the cross venation, e.g. in the anal area, is nearly identical. Only differing from the type-species by a slightly shorter wing length (less than 37 mm); the absence of any trace of a vein Rspl; and the smaller distance between CuP-

crossing and arculus in the forewing. These slight differences alone could hardly justify a specific separation, would there not be a significant geographic and temporal distance to *P. krauseorum* sp. nov. which excludes a conspecific status. Therefore „Upper Jurassic of Germany" might well be regarded as an accessory diagnostic property of this new species.

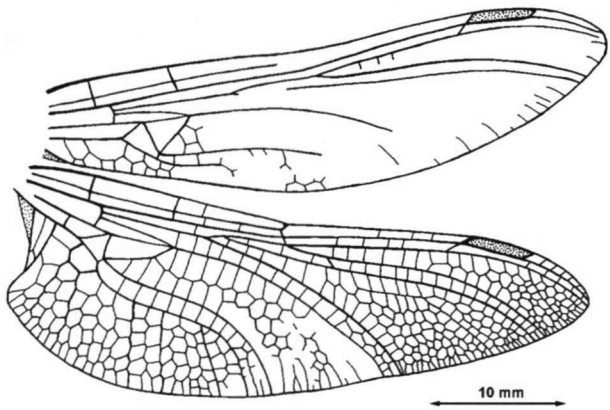

Fig. 4. *Proterogomphus krauseorum* gen. et sp. nov., reconstruction after the fragments illustrated by PRITYKINA (1986: FIGS 13, 14, 15, 18).

DESCRIPTION. – A nearly complete and well preserved adult male dragonfly, only the left hindwing is missing and the right forewing is less well preserved than the right one. The wing veins are not traced by dendrites. Head, thorax and abdomen are preserved too, but are rather useless.

F o r e w i n g. – Length 36.6 mm; width on the level of the nodus 8.4 mm; distance from base to arculus 4.6 mm; from base to nodus 19.4 mm; from nodus to pterostigma 9.9 mm; the pterostigma is elongate 3.6 mm long and max. 0.7 mm wide with distinctly thickened anterior and posterior margins; the pterostigma is in a normal position, at about 58 % of the distance between nodus and apex; the basal side of the pterostigma is somewhat more oblique than the distal side; the pterostigmal brace is strong and distinctly oblique, aligned with the basal side of the pterostigma; the pterostigma covers two and a third cells, and the first crossvein beneath the pterostigma distal of the brace seems to be somewhat stronger than the others; there are only six postnodal crossveins present between nodus and pterostigma, non-aligned with the corresponding postsubnodal crossveins between RA and RP1; there is no distinct „libellulid gap" (*sensu* BECHLY, 1996) of postsubnodal crossveins directly distal of the subnodus; the nodus is of the „normal" Anisoptera-type; the subnodus is not extremely oblique; IR1 is originating on RP1 below the distal side of the pterostigma (pseudo-IR1 of Pananisoptera); there are only two rows of cells in the area between pseudo-IR1 and RP1, and four rows of cells in the wider area between pseudo-IR1 and RP2; RP1 and RP2 are basally slightly divergent with only one row of cells between them till the pterostigma, but below the pterostigma they become more divergent with two or more rows of cells between them; the base of RP2 is strictly aligned with the subnodus; there is only one oblique crossvein 'O' between RP2 and IR2, 1.9 mm and two cells distal of the

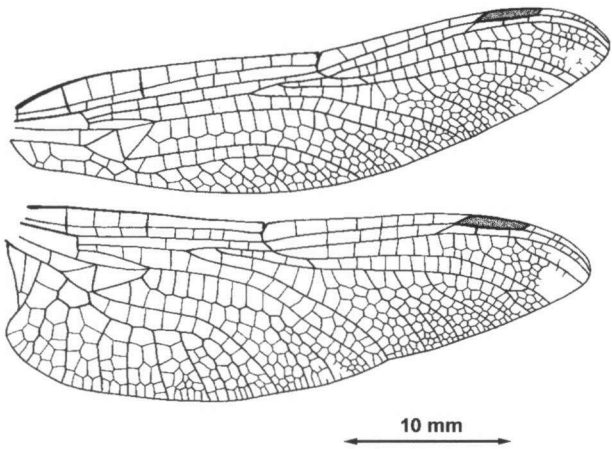

Fig. 5. *Proterogomphus renateae* sp. nov., holotype 6D, fore- and hindwing venation (camera lucida drawing).

subnodus; there is one row of cells between RP2 and IR2 till the wing margin; the area between RP2 and IR2 is distally narrowed; RP2 and IR2 are gently curved, but not undulating, and reach the posterior margin obliquely; the midfork (base of RP3/4) is 4.7 mm basal of the subnodus, and the origin of IR2 is 2.9 mm distal of the midfork; there are three crossveins between RP and IR2 basal of the oblique vein 'O', including two bridge crossveins (Bqs); eight antesubnodal crossveins are visible between RA and RP basal of the subnodus and distal of the arculus, but there is no distinct „gap" of antesubnodal crossveins directly distal of the arculus and directly basal of the subnodus („cordulegastrid gap" *sensu* BECHLY, 1996); seven antefurcal (postmedian) crossveins between RP and MA basal of the RP-midfork; there is no Rspl, but there are three distinct convex secondary veins (intercalaries) in the area between IR2 and RP3/4; no Mspl, but at least two convex secondary veins in the distal part of the postdiscoidal area; the postdiscoidal area is basally narrow with two rows of cells directly distal of the discoidal triangle, but distally somewhat widened with probably about fourteen cells between MA and MP at the posterior wing margin (width near discoidal triangle, 2.1 mm; width at wing margin, 4.9 mm); RP3/4 and MA are more or less parallel and not distinctly undulate; the area between RP3/4 and MA is somewhat widened distally with two to three rows of cells between them (RP3/4 and MA separated by four cells at the wing margin), while there is only one row of cells between them till the level of the oblique crossvein 'O'; the discoidal triangle is very wide, somewhat transverse, and free of crossveins; length of its anterior side, 2.4 mm; of its basal side, 1.9 mm long; of its distal side MAb, 2.8 mm; the distal side MAb of the discoidal triangle is more or less straight (only slightly bent); the hypertriangle is rather broad and free of crossveins, 4.0 mm long and max. 0.6 mm wide, and has a distinctly curved anterior side; the basal space and subbasal space are free of crossveins; a distinct secondary anterior branch PsA (pseudo-anal vein) of AA delimits an unicellular subdiscoidal triangle which is about 2.1 mm long, max. 2.1 mm wide (length of PsA) and min. 0.3 mm wide (length of subdiscoidal

veinlet); there are two rows of cells in the anal area below AA which is 1.7 mm wide below PsA; the CuP-crossing is only 0.5 mm basal of the arculus, very close to the origin of PsA; there are no supplementary cubito-anal crossveins; MP is gently curved and ending slightly distal of the level of the nodus; the area between CuA and MP is distally somewhat widened (separated by three cells at the wing margin); the first crossvein between MP and CuA is distinctly slanted, parallel to the distal side of the discoidal triangle; CuA is well-defined with seven or eight parallel posterior branches; there are four rows of cells in the median part of the cubito-anal area (max. 2.2 mm wide); the arculus is angled, and the bases of RP and MA are distinctly separated at the arculus; only the two primary antenodal crossveins AX1 and AX2 (and the basal brace AX0) are aligned and stronger than the non-aligned secondary antenodal crossveins (eight in the first row, but only five preserved in the second row); AX1 is 0.6 mm basal of the arculus and AX2 is 4.6 mm distal of AX1, slightly basal of the level of the distal angle of the discoidal triangle; there are two secondary antenodal crossveins between AX1 and AX2 in each row, not strictly aligned with eachother; the basal brace AX0 is preserved.

H i n d w i n g. – The venation is very similar to that of the forewing, especially in the distal half of the wing; length 35.1 mm; width on the level of the nodus 10.8 mm (max. width 11.5 mm); distance from base to arculus 4.1 mm; from base to nodus 15.5 mm; from nodus to pterostigma 11.8 mm; thus the nodus is in a relatively basal position, compared to the forewing; the pterostigma is elongate 3.8 mm long and max. 0.8 mm wide with distinctly thickened anterior and posterior margins; the pterostigma is in a normal position, at about 60 % of the distance between nodus and apex; the basal side of the pterostigma is somewhat more oblique than the distal side; the pterostigmal brace is strong and oblique, aligned with the basal side of the pterostigma; the pterostigma covers two and a half cells, and the first crossvein beneath the pterostigma distal of the brace seems to be somewhat stronger than the others; there are seven postnodal crossveins present between nodus and pterostigma, non-aligned with the corresponding postsubnodal crossveins between RA and RP1; the apparent „libellulid gap" (*sensu* BECHLY, 1996) of postsubnodal crossveins directly distal of the subnodus rather seems to be an artefact of preservation; the nodus is of the „normal" Anisoptera-type; the subnodus is not extremely oblique; IR1 is originating on RP1 beneath the distal side of the pterostigma (pseudo-IR1 of Pananisoptera); there are only two rows of cells in the area between pseudo-IR1 and RP1, and four or five rows of cells in the wider area between pseudo-IR1 and RP2; RP1 and RP2 are basally somewhat divergent with only one row of cells between them till the pterostigma, but below the pterostigma they become more divergent with two or more rows of cells between them; the base of RP2 is strictly aligned with the subnodus; there is only one oblique crossvein 'O' present between RP2 and IR2, 2.1 mm and two cells distal of the subnodus; there is one row of cells in the basal area between RP2 and IR2, only close to the wing margin there are three rows of cells between them; the distal

widened area between RP2 and IR2 is preceded by an apparent secondary branch of IR2 towards RP2 (most probably an teratological aberration; the normal state probably was one row of cells between RP2 and IR2 till the wing margin, as in the forewing); RP2 and IR2 are gently curved, but not undulating, and reach the posterior margin obliquely; the midfork (base of RP3/4) is 5.3 mm basal of the subnodus, and the origin of IR2 is 3.5 mm distal of the midfork; there are three crossveins between RP and IR2 basal of the subnodus, including two bridge crossveins (Bqs); only three antesubnodal crossveins (between RA and RP basal of the nodus and distal of the arculus) are preserved, two of them very distally, so that there was obviously no „gap" of antesubnodal crossveins directly basal of the subnodus („cordulegastrid gap" *sensu* BECHLY, 1996); four antefurcal (postmedian) crossveins between RP and MA basal of the RP-midfork; there is no Rspl, but there are three distinct convex secondary veins (intercalaries) in the area between IR2 and RP3/4; there is no Mspl, but two or three convex secondary veins (intercalaries) are present in the distal postdiscoidal area between MA and MP, originating from a furcation of the zigzagging secondary vein that originates on the distal side of the discoidal triangle; postdiscoidal area with two rows of cells directly distal of the discoidal triangle and probably fifteen cells between MA and MP at the posterior wing margin; the postdiscoidal area is distally widened (width near discoidal triangle 2.6 mm; width at posterior wing margin 5.8 mm); RP3/4 and MA are more or less parallel and not distinctly undulate; the area between RP3/4 and MA is slightly widened distally with two rows of cells between them (RP3/4 and MA are separated by three cells at the wing margin), while there is only one row of cells between them till the level of the oblique crossvein 'O'; the discoidal triangle is rather elongate, and not divided by crossveins; length of its anterior side 3.2 mm long, of its basal side 1.7 mm; of its distal side MAb 3.7 mm; the distal side MAb of the discoidal triangle is distinctly angled; the hypertriangle is rather broad and free of crossveins, 4.4 mm long and max. 0.8 mm wide, and has a distinctly curved anterior side; the basal space and subbasal space are free of crossveins too; a distinct secondary anterior branch PsA of AA delimits an unicellular subdiscoidal triangle which is 1.6 mm long, max. 2.1 mm wide (length of PsA) and min. 0.3 mm wide (length of subdiscoidal veinlet); there is only one posterior branch of AA between the distal side of the anal triangle and CuAb; there are five or six rows of cells in the anal area below AA, which is 6.7 mm wide below PsA; there is a distinct anal angle, and a large anal triangle that is divided into three cells by a Y-shaped vein (thus it is a male specimen); the membranule is not preserved; the CuP-crossing is 1.6 mm basal of the arculus, rather close to the distal side of the anal triangle; there are no supplementary cubito-anal crossveins; MP is gently curved and ends on the level of the nodus; the area between MP and CuAa is distally somewhat widened, with two or three rows between both veins near the posterior wing margin; the „gaff" is not elongated (only 0.7 mm long); CuAb (the most basal posterior branch of CuA) is strongly angular to the „gaff"-portion of CuA at the base; CuAb and a

posterior branch of AA enclose a small unicellular anal loop (max. 2.1 mm long and max. 1.4 mm wide) which is distinctly closed posteriorly; CuAa has six parallel posterior branches; there are five rows of cells in the median part of the cubito-anal area (max. 4.3 mm wide); the arculus is slightly angled, and the bases of RP and MA are distinctly separated at the arculus; only the two primary antenodal crossveins AX1 and AX2 are aligned and stronger than the non-aligned secondary antenodal crossveins (only two are preserved the first row and six in the second row); AX1 is 0.6 mm basal of the arculus and AX2 is 4.8 mm distal of AX1, on the level of the distal angle of the discoidal triangle; there are only two secondary antenodal crossvein between AX1 and AX2 in each row, not strictly aligned with eachother; the basal brace AX0 is not preserved.

B o d y. – Head and thorax are not well preserved and rather useless. It is not visible if the compound eyes were separated or not. None of the legs has been preserved. Body length from head to the tip of the abdomen (incl. appendages) 55 mm; length of abdomen 42 mm; width, 2-2.5 mm; the abdomen is neither narrowed, nor dilated in any part; the terminal appendages are not very well preserved, but the cerci are visible, about 2 mm long, and slender (not leaf-like); the epiproct apparently was unifurcate; no lateral auricles are visible on the second abdominal segment, but this could also be an artefact of preservation.

CLADISTIC ANALYSIS OF ANISOPTERA

Additionally to the phylogenetic analysis by „hand and brain" (BECHLY, 1996, 1997), we performed a computerised cladistic analysis of a restricted character set

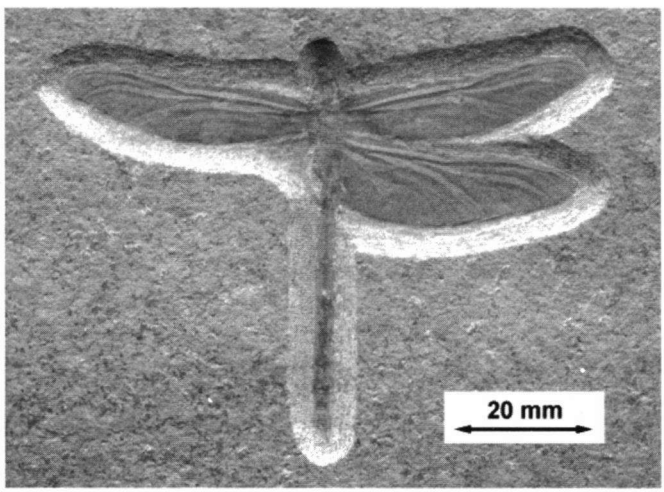

Fig. 6. *Proterogomphus renateae* sp.nov., holotype 6D.

Table I
Data-matrix of Anisoptera

Taxa / Characters	1	2	3	4	5	6	7	8	9	10
Hypanc	0	0	0	0	0	0	0	0	0	0
Petalurida	0	0/1	0	0	0	0	0	0	0	0
Austropetaliida	0	0	0	0	0	0	0	1	0/1	0
Cymatophlebiidae	0	0	0	0	0	0	0	0	0	0
Euaeshnida	0	0/1	0/1	0	0	0	0/1	0/1/2	0/1	0
Proterogomphidae	0	?	?	0	?	0	1	?	0	0
Gomphides	0	0/1	0	0	0	0/1	0/1	0/1/2	0/1	0/1
Cordulegastrida	0	0	1	0	0	0	0	0	0/2	0
Neopetaliidae	0	0	1	0	0	1	1	0	0	0
Prohemeroscopus	0	3	1	0	0	0	1	1	0	0
H. baissicus (Russia)	0	1	1	0	0	1	1	1	1	0
H. baissicus (China)	0	1	1	0	0	1	1	?	1	0
Chlorogomphoidea	0	0	0	0	0	1	1	1	2	1
Synthemistidae	1	2	1	1	1	1	1	1/2	1	1
Macromiidae	1	2	0/1	3	1	1	1	1/2	1	1
"Corduliidae" s.l.	1	2/3	1	2/3	1	0/1	1	1/2	1	1
Macrodiplacidae	1	3	1	3	1	0	1	2	1	1
Libellulidae	1	3	1	3	1	0	0/1	0/1/2	1	1

Taxa / Characters	11	12	13	14	15	16	17	18	19	20
Hypanc	0	0	0	0	0	0	0	0	0	0
Petalurida	0	0	0	0	0/1	0	0	0/1	1	0
Austropetaliida	0	0	0/1	0	0/1	1	1	0/2	?	1
Cymatophlebiidae	0	0	1	1	1	1	2	0	0/1	3
Euaeshnida	0	0	0/1	0	0/1	1	0/1	0/1	1	2/3
Proterogomphidae	0	1	0	1	0	0	0	1	1	1
Gomphides	0/1	0/1	0/1	0/1	0	0/1	0	1	0/1	0
Cordulegastrida	0	0	0	0	0	0	0	1	0	0
Neopetaliidae	0	0	0	0	0	0	0	1	0	0
Prohemeroscopus	0	0	0	1	1	0	0	1	0	0
H. baissicus (Russia)	0	0	0	1	1	0	0	1	0	1
H. baissicus (China)	0	0	0	1	1	0	0	1	0	1
Chlorogomphoidea	1	0	0	1	0	0	0	1	0/1	0
Synthemistidae	2	0	0	1	0	0	0	1	1	1
Macromiidae	2	0	0	1	0	0	0	1	1	1
"Corduliidae" s.l.	2	0	0	1	0/1	0	0	1	1	1/2/3
Macrodiplacidae	2	0	0	1	0	0	0	1	1	3
Libellulidae	2	0	0	1	0/1	0/1	0/1	1	1	2/3

Taxa / Characters	21	22	23	24	25	26	27	28	29	30
Hypanc	0	0	0	0	0	0	0	0	0	0
Petalurida	0	0	1	0	0	0	0/1	0	0/2	0
Austropetaliida	0	0	0	0	0	0	0/1	0/1	0	2
Cymatophlebiidae	0	2/3	0	0	0	1/2	0	0	0	0
Euaeshnida	0/1	2/3	0/1	0/1	0	0	0/1	0/1	0/1	0/1
Proterogomphidae	0	0	1	1	0	0	0	0	0	0
Gomphides	0/1	0	0/1	0/1	0	0	0/1/2/3	0/1	0/2	0/2
Cordulegastrida	0	0	0	0	0	1	1	0	1	1
Neopetaliidae	0	0	0	0	0	1	1/2	0	0/1	0
Prohemeroscopus	0	0	0	1	0	2	1	1	0	0
H. baissicus (Russia)	0	0	1	1	0	2	1/2	1	0	0
H. baissicus (China)	0	0	0	1	0	2	1/2	1	0	0
Chlorogomphoidea	1	0	1	1	0	2	1/2	1	0/1	1
Synthemistidae	1	0	1	0	1	3	3	?	2	1
Macromiidae	0/1	0	1	0/1	1	3	3	?	2	1
"Corduliidae" s.l.	0/1	1/2/3	1	0	1	3	3	?	2	1
Macrodiplacidae	1	3	1	0	1	3	3	?	2	1
Libellulidae	0/1	3	1	0/1	1	3	3	?	2	1

Table I, continued

Taxa / Characters	31	32	33	34	35	36	37	38	39	40	41	42
Hypanc	0	0	0	0	0	0	0	0	0	0	0	0
Petalurida	0/1	0/1	0	0	0/1	0	0/1	0/1	0/1	1	0	0
Austropetaliida	0/1	0	0	0	1	1	0	1/2	0	0	0	1
Cymatophlebiidae	0/1	0	0	0	1	1	0/1	2	0/1	1	0	1
Euaeshnida	1	0/1	0/1	0	0/1	2	1	1/2	0/1	0/1	0	1
Proterogomphidae	1	0	0	1	0	0	1	0	0	0	?	0
Gomphides	0/1	0/1	0/1	0/1	0/1	0	1	0/1	0/1	0/1	0	0/1
Cordulegastrida	0/1	0/1	0	0	0/1	2	0	0/1	0	0/1	1	1
Neopetaliidae	1	2	0	0	1	1	0	1	0	0	1	1
Prohemeroscopus	0	2	0	0	0	0	0	1	0	0	?	?
H. baissicus (Russia)	1	3	?	0	0	1	0	0	0	0	?	1
H. baissicus (China)	1	3	0	0	0	1	0	0	0	0	?	?
Chlorogomphoidea	1	3	0	0	1	0	0	1	1	0/1	1	1
Synthemistidae	1	2/3	1	1	1	0	0	0	1	0	1	1
Macromiidae	1	2/3	1	1	1	0	0	0	1	0/1	1	1
"Corduliidae" s.l.	1	2/3/4	1	1	0/1	0	0	0/1	0/1	0/1	1	1
Macrodiplacidae	1	5	1	1	0	0	0	0	0	0/1	1	1
Libellulidae	1	5	1	1	0/1	0	0	0/1	0/1	0/1	1	1

of mostly wing venational characters (42 characters for 17 terminal taxa plus hypothetical all-zero outgroup) with the software packages PAUP 3.1.1 and MacClade 3.01 (for characters and data-matrix see Appendix and Table 1).

The terminal taxa are defined in BECHLY (1996, 1997): Austropetaliida corresponds to the traditional Austropetaliidae *sensu* CARLE. Gomphides include all the fossil and extant taxa traditionally included in the Gomphidae; the group Euaeshnida corresponds to the traditional fossil and extant Aeshnidae (incl. „*Morbaeschna*"); Cordulegastrida corresponds to the traditional Cordulegastridae. The other taxa were already explained in the Introduction. The characters for *Prohemeroscopus* gen. nov. were exclusively coded on the basis of the type-species, because of the fragmentary preservation and somewhat uncertain position of *P. kuehnapfeli* sp. nov. Autapomorphies of the terminal taxa were excluded from the analysis. The characters were equally weighted and not regarded as irreversible. The multistate characters were generally treated as ordered, except characters 18, 21, 29, and 30 that were treated as unordered. An hypothetical all-zero outgroup was used for the rooting of the tree. A strict consensus tree (Fig. 7) was calculated from the nine equally parsimonious trees (step-length = 239; CI = 0.883; RI = 0.81) obtained by the heuristic and branch-and-bound searches.

The result generally confirmed the new classification of BECHLY (1996, 1997), although the latter was based on traditional Phylogenetic Systematics rather than an so-called „Computer Cladistics". The Cavilabiata were supported as monophylum, after the introduction of a single non-venational character concerning the structure of the larval labial mask which is a very strong autapomorphy for this monophylum (CARLE, 1995; BECHLY, 1996, 1997; LOHMANN, 1996). Concerning the extant taxa, the only difference is the placement of Gomphides (and Proterogomphidae) as a sister-group of Petalurida. This almost certainly incorrect

result is caused by the almost exclusive use of wing venational characters which are rather useless for the assessment of the phylogenetic position of Gomphides, since the latter retained an overall plesiomorphic venation. The position of Proterogomphidae fam. nov. could not be convincingly resolved for the same reasons, especially since the potential synapomorphies with derived in-group gomphids were not considered (see above). The use of further morphological characters rather suggests that Gomphides (including Proterogomphidae fam. nov.) are the sister-group to all Cavilabiata (see BECHLY, 1996, 1997).

The results concerning Hemeroscopidae were somewhat unexpected, since they were resolved as paraphyletic grade between Neopetaliidae and Chlorogomphoidea with *Prohemeroscopus* gen. nov. being more basal than *Hemeroscopus*. However, the minimal trees are very sensitive to the missing data, as is clearly shown by the unresolved relative positions of the Chinese and Russian specimens of *Hemeroscopus baissicus*. Although this phylogenetic analysis would suggest the paraphyly of Hemeroscopi-dae, because of the lack of strong autapomorphies of this family, and would furthermore confirm the phylogenetic relationships proposed by LOHMANN (1996), we do not regard these results as really significant. As explained above, most of the putative synapomorphies of Chlorogomphoidea and Eurypalpida that would imply a more basal position of Hemeroscopidae, can clearly be recognized as convergences or parallelisms if fossil stem-group representatives of Eurypalpida are also taken into consideration (e.g. *Eocordulia*, *Condalia*, and *Araripelibellula*), since these do show the plesiomorphic states like *Hemeroscopus* and/or *Prohemeroscopus* gen. nov. The same argument applies to the two possible synapomorphies of *Hemeroscopus* (but not *Prohemeroscopus* gen. nov.) and extant Brachystigmata. After a priori weighting of the characters, based on their compatibility and homoplasy, we preliminarily prefer to include *Prohemeroscopus* gen. nov. and

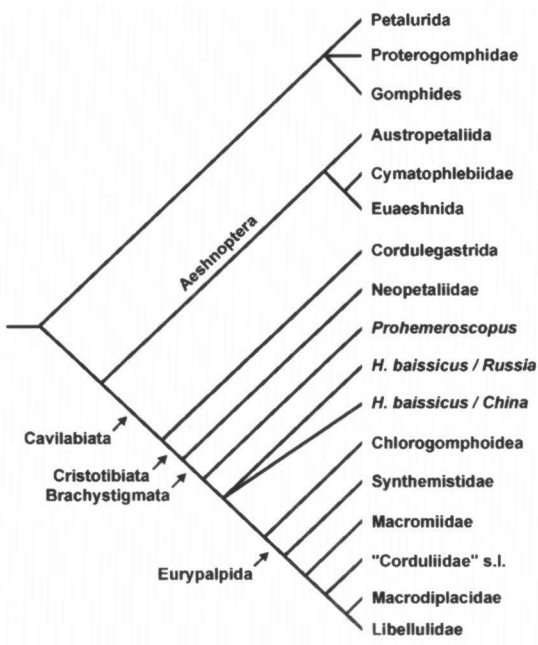

Fig. 7. Strict consensus tree of a numerical cladistic analysis of Anisoptera (239 septs; CI - 0.83).

Hemeroscopus in the same family Hemeroscopidae, and to consider this family as the sister group of the extant Chlorogomphoidea, even if these attributions are based on a relatively few putative synapomorphies (for a justification of a priori character weighting and a profound criticism of computer-parsimony see WÄGELE, 1994; BORICKI, 1996). Further investigations and better preserved material will be necessary to test these preliminary hypotheses.

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APPENDIX

List of polarised characters (all wing venational characters, except the last two characters):

(1) 0 = the primary antenodal AX2 is situated distal of the discoidal triangle in fore wings
1 = the primary antenodal AX2 is situated basal of the discoidal triangle in fore wings

(2) 0 = there are 4 or more secondary antenodals between the two primaries AX1 and AX2
1 = only 2-3 (rarely 4) secondary antenodals between the two primaries AX1 and AX2
2 = only 1 secondary antenodal present between the two primaries AX1 and AX2
3 = no secondary antenodals present between the two primaries AX1 and AX2

(*treated as ordered multistate character*)

(3) 0 = wings with crossveins in the distal antesubnodal area
1 = wings without crossveins in the distal antesubnodal area („cordulegastrid gap")

(4) 0 = secondary antenodal and antesubnodal crossveins not aligned, so that the two primaries AX1 and AX2 are very distinct from the secondaries
1 = antenodal and antesubnodal crossveins more or less aligned, and at least the hindwings with more than two aligned and bracket-like antenodals
2 = nearly all antenodals and antesubnodals are aligned in both wing pairs, and at least all the hindwing antenodals are more or less enforced and bracket-like
3 = all antenodals and antesubnodals aligned and bracket-like in both wing pairs, so that the two primaries AX1 and AX2 are indistinguishable from the secondaries
(*treated as ordered multistate character*)

(5) 0 = wings with crossveins in the basal postsubnodal area („libellulid gap")
1 = wings without crossveins in the basal postsubnodal area („libellulid gap")

(6) 0 = nodus in mid wing position in forewings
1 = nodus shifted in a more distal position in forewings

(7) 0 = pterostigmata parallel sided, with length more than 8 times width
1 = pterostigmata not parallel sided, with length less than 8 times width

(8) 0 = pterostigmata long, with more than 3 cells beneath them
1 = pterostigmata relatively short, with only 1-3 complete cells beneath them
2 = pterostigma further shortened, with only 1-2 cells beneath them
(*treated as ordered multistate character*)

(9) 0 = oblique pterostigmal brace vein present and aligned with the basal end of the pterostigma
1 = oblique pterostigmal brace indistinct or obsolete, if present shifted distally beneath the pterostigma
2 = pterostigmal brace vein completely suppressed
(*treated as ordered multistate character*)

(10) 0 = arculus broken, and the posterior part (arcular crossvein) not shortened
1 = arculus rather straight, and the posterior part much shorter than the anterior part (RP + MA)

(11) 0 = sectors of arculus (RP and MA) basally widely separated
1 = sectors of arculus basally more or less approximate
2 = sectors of arculus diverging from one point or even shortly fused basally (arculus stalked)
(*treated as ordered multistate character*)

(12) 0 = costal margin and RA not distinctly thickened along the pterostigmata
1 = costal margin and RA distinctly thickened along the pterostigmata

(13) 0 = the veins RP1 and RP2 are basally diverging, with more than two rows of cells basal of the pterostigma
1 = the veins RP1 and RP2 are basally strictly parallel, with only one row of cells basal of the pterostigma

(14) 0 = the base of vein IR1 is basal of the middle of the pterostigma
1 = the base of vein IR1 is below or distad of the distal side of the pterostigma

(15) 0 = the area between RP2 and IR2 is distally not widened
1 = the area between RP2 and IR2 is distally distinctly widened, with more than one cell row in the distal half, and more than three cell rows near the wing margin

(16) 0 = RP2 is more or less straight
1 = RP2 is distinctly undulate or curved beneath the pterostigma

(17) 0 = IR2 is more or less straight
1 = IR2 is at least somewhat undulate
2 = IR2 is strongly undulate and parallel to the undulate RP2
(*treated as ordered multistate character*)

(18) 0 = presence of two oblique veins between RP2 and IR2
1 = presence of only the basal oblique vein
2 = presence of only the distal (accessory) oblique vein
(*treated as unordered multistate character*)

(19) 0 = basal oblique vein is situated more than 3 cells distal of the subnode in both wing pairs
1 = oblique vein less than three cells distal of the subnode in both wing pairs

(20) 0 = Rspl absent
1 = at least a weakly defined Rspl, parallel to IR2
2 = very well defined Rspl present in both wing pairs, and parallel to IR2
3 = very distinct and strongly curved Rspl present in both wing pairs
(*treated as ordered multistate character*)

(21) 0 = RP3/4 and MA more or less parallel
1 = RP3/4 and MA strictly parallel with only one row of cells till the hind margin
2 = RP3/4 and MA more or less undulate and distinctly divergent near the hind margin
(*treated as unordered multistate character*)

(22) 0 = Mspl absent
1 = at least a weakly defined Mspl, parallel to MA
2 = very well defined Mspl present in both wing pairs, and parallel to MA
3 = very distinct and strongly curved Mspl present in both wing pairs
(*treated as ordered multistate character*)

(23) 0 = hindwing MP not shortened and smoothly curved towards the hind margin
1 = hindwing MP somewhat shortened and more distinctly curved towards the hind margin

(24) 0 = the hindwing area between MP and CuAa is narrow, with only one row of cells near the discoidal triangle
1 = the hindwing area between MP and CuAa is widened, with two rows of cells near the discoidal triangle

(25) 0 = the subdiscoidal veinlet (basal part of CuA that is aligned with the distal trigonal vein MAb) is distinct in hindwings
1 = the subdiscoidal veinlet (basal part of CuA that is aligned with the distal trigonal vein MAb) is reduced in hindwings

(26) 0 = „gaff" (= basal part of CuA between the subdiscoidal veinlet and its first branching into CuAa and CuAb) is short in the hindwing
1 = „gaff" is at least somewhat prolonged
2 = „gaff" is very long and straight
3 = „gaff" is very long and sigmoidally curved
(*treated as ordered multistate character*)

(27) 0 = the hindwing CuAa is smoothly curved, and has many posterior branches
1 = the hindwing CuAa is more strongly curved (thus shortened), and has only four or less posterior branches
2 = the hindwing CuAa is further shortened, with less than 3 posterior branches
3 = CuAa is further shortened, and has no defined posterior branch at all (CuA is only branched in CuAa and CuAb)
(*treated as ordered multistate character*)

(28) 0 = the terminal posterior branch of CuAa is not secondarily branched on CuA in the hindwing
1 = the terminal posterior branch of CuAa seems to be secondarily branched on CuA in the hindwing

(29) 0 = a well-defined secondary branch AA (pseudo-anal vein PsA) is separating a subdiscoidal triangle in the forewings
1 = the pseudo-anal vein PsA is reduced to a „normal" crossvein in the forewings
2 = the forewing pseudo-anal vein PsA is hypertrophied and the subdiscoidal triangle is widened with a curved or angled posterior margin, correlated with a more transverse forewing

discoidal triangle
(*treated as unordered multistate character*)

(30) 0 = a well-defined secondary branch PsA of AA (pseudo-anal vein) is delimiting a subdiscoidal triangle in the hindwing
1 = pseudo-anal vein PsA less distinct in the hindwing (crossvein-like or absent)
2 = pseudo-anal vein PsA and subtriangle of hindwings somewhat hypertrophied
(*treated as unordered multistate character*)

(31) 0 = the hindwing anal loop is absent or posteriorly open
1 = the hindwing anal loop is posteriorly closed

(32) 0 = the hindwing anal loop is less than four-celled
1 = the anal loop is broad, more than four-celled, it is pentagonal or hexagonal in shape
2 = the anal loop is enlarged with at least 5 cells
3 = the anal loop is elongated with at least 8 cells (but without a well-defined midrib)
4 = the anal loop transversely elongated and with a well-defined midrib (= Cuspl)
5 = the anal loop is foot-shaped with a well-defined midrib and a distinct toe
(*treated as ordered multistate character*)

(33) 0 = male hindwings with a three-celled anal triangle, which is divided by a distally branched longitudinal vein
1 = male hindwings with a two-celled anal triangle, which is divided by a longitudinal crossvein or undivided

(34) 0 = anterior margin (MA) of hypertriangle more or less straight
1 = anterior margin (MA) of hypertriangle distinctly curved

(35) 0 = hypertriangles without crossveins
1 = hypertriangles divided by several parallel crossveins

(36) 0 = the discoidal triangles are of somewhat different shape and not elongate (both wing pairs)
1 = the forewing discoidal triangle is less transverse therefore both discoidal triangles of a similar shape
2 = the discoidal triangles are longitudinal elongate and narrow (both wing pairs)
(*treated as ordered multistate character*)

(37) 0 = discoidal triangles with a straight distal side MAb, and postdiscoidal area without distinct sup-plementary sector
1 = at least the hindwing discoidal triangle with a more or less angulated distal side MAb, correlated with a supplementary sector (trigonal planate) in the postdiscoidal area

(38) 0 = forewing discoidal triangle free of crossveins
1 = forewing discoidal triangle only divided by one (rarely two parallel) crossvein(s)
2 = forewing discoidal triangle divided by more than two crossveins
(*treated as ordered multistate character*)

(39) 0 = basal part of the subdiscoidal cell (between CuP-crossing and pseudo-anal vein PsA) without accessory cubito-anal crossveins
1 = basal part of the subdiscoidal cell (between CuP-crossing and pseudo-anal vein PsA) traversed by one or more accessory cubito-anal crossveins

(40) 0 = forewing subdiscoidal triangle free of crossveins
1 = forewing subdiscoidal triangle traversed by one or more crossveins

(41) 0 = larval mask flat, with elongate side lobes and without setae
1 = larval mask spoon-shaped, with broad side lobes and numerous setae

(42) 0 = compound eyes widely separated in adults
1 = compound eyes more or less approximated in adults