Stuttgarter Beiträge zur Naturkunde
Serie B (Geologie und Paläontologie)

Herausgeber:
Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 328	11 pp., 2 figs	Stuttgart, 31. 12. 2002

The first fossil record and first New World record for the dragonfly clade Chlorogomphida (Insecta: Odonata: Anisoptera: Araripechlorogomphidae n. fam.) from the Crato Limestone (Lower Cretaceous, Brazil)

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With 2 Figures

Summary

A new dragonfly is described from the Lower Cretaceous limestones of the Crato Formation (Brazil): *Araripechlorogomphus muratai* n. gen. n. sp. (Araripechlorogomphidae n. fam.) which clearly belongs to the chlorogomphid clade within Anisoptera. It is the first fossil record of Chlorogomphida and also the first New World record of this dragonfly group that is now exclusively distributed in East Asia. The phylogenetic and biogeographic implications of this new discovery are discussed. As consequence of the phylogenetic analysis the new higher taxa Cristotibiata, Paucipostnodalia, Eubrachystigmata, Neobrachystigmata, Paneurypalpidomorpha, Eurypalpidomorpha, and Eurypalpidiformia are introduced. A monotypic family Juracorduliidae n. fam. is established for the genus *Juracordulia*, and the genus *Prohemeroscopus* is transferred from Nannogomphidae to a new monotypic family Prohemeroscopidae n. fam. within Paucipostnodalia as sistergroup of Eubrachystigmata.

Zusammenfassung

Eine neue Libellenart wird aus den unterkretazischen Plattenkalken der Crato-Formation (Brasilien) beschrieben: *Araripechlorogomphus muratai* n. gen. n. sp. (Araripechlorogomphidae n. fam.) gehört zweifelsfrei zur monophyletischen Gruppe der Chlorogomphiden innerhalb der Anisoptera. Es handelt sich hierbei um den ersten Fossilnachweis der Chlorogomphida und auch um den ersten neuweltlichen Nachweis dieser Libellengruppe, die heute ausschließlich in Ostasien verbreitet ist. Die phylogenetischen und biogeographischen Implikationen dieser neuen Entdeckung werden diskutiert. Als Konsequenz der phylogenetischen Untersuchung werden die neuen höheren Taxa Cristotibiata, Paucipostnodalia, Eubrachystigmata, Neobrachystigmata, Paneurypalpidomorpha, Eurypalpidomorpha und Eurypalpidiformia eingeführt. Eine monotypische Familie Juracorduliidae n. fam. wird für die Gattung *Juracordulia* errichtet, und die Gattung *Prohemeroscopus* wird von den Nannogomphidae zu einer neuen monotypischen Familie Prohemeroscopidae n. fam. transferiert, die als Schwestergruppe der Eubrachystigmata innerhalb der Paucipostnodalia anzusehen ist.

1. Introduction

The Lower Cretaceous Crato Formation of Brazil already yielded a surprising diversity of fossil dragonflies (Carle & Wighton, 1990; Nel & Escuillié, 1994; Nel & Paicheler, 1994; Martill & Nel, 1996; Jarzembowski et al., 1998; Nel et al., 1998; Bechly, 1998a; Bechly, 2000; Bechly et al., 2001a). We here describe another interesting new dragonfly species (already figured and mentioned by Bechly, 1998a, Fig. 39 and Bechly et al., 2001b, Abb. 40) from this locality which belongs to the clade Chlorogomphida within Anisoptera. It is the first fossil record and the first New World record for this dragonfly group. Extant chlorogomphids are exclusively distributed in eastern Asia. Originally, chlorogomphids where classified as subfamily of Cordulegastridae, but Carle (1995) and Bechly (1996) have demonstrated that this taxon is closer to the rest of the libelluloid clade than to Cordulegastridae. Therefore, the separation from Cordulegastridae is clearly justified. The phylogenetic system of extant chlorogomphids was recently revised by Carle (1995) and Bechly (1996) as well. The latter author elevated the Carlean subfamilies Chloropetaliinae and Chlorogomphinae to family rank within a superfamily Chlorogomphoidea (= crowngroup chlorogomphids). The fossil species described in this work is a stemgroup chlorogomphid that warrants the erection of a separate new family as sistergroup of Chlorogomphoidea within Chlorogomphida (= panmonophylum chlorogomphids).

2. Methods

The drawings were made with a camera lucida and a binocular microscope by K. Ueda, while the photo was made with a Nikon SLR camera by Mr B. Schuster (Hünstetten). The nomenclature of the dragonfly wing venation is based on the interpretations of Riek & Kukalová-Peck (1984), amended by Nel et al. (1993) and Bechly (1996), and the phylogenetic classification of Anisoptera is based on Bechly (1996, 2002). The systematic analysis is based on the principles of consequent Phylogenetic Systematics (sensu Hennig, 1966, 1969, and Bechly, 2000).

3. Systematic Palaeontology

Class Insecta LINNEAUS, 1758 (= Hexapoda LATREILLE, 1825)
Pterygota BRAUER, 1885
Order Odonata FABRICIUS, 1793
Suborder Anisoptera SELYS in SELYS & HAGEN, 1854
Cavilabiata BECHLY, 1996
Chlorogomphida BECHLY, 1996

Family Araripechlorogomphidae n. fam.

Type genus: *Araripechlorogomphus* n. gen., by present designation.

Diagnosis. – See diagnosis of type genus, since monotypic.

Autapomorphies: Hindwing discoidal triangle secondarily unicellular.

Taxonomic comment. – The mentioning of the family name Araripechlorogomphidae by BECHLY (2002) has to be regarded as a nomen nudum and as unpublished according to Art. 8 ICZN.

Genus *Araripechlorogomphus* n. gen.

Type species: *Araripechlorogomphus muratai* n. sp., by present designation.

Derivatio nominis: After the type locality Araripe and the extant genus *Chlorogomphus*.

Diagnosis. – See diagnosis of type species, since monotypic.

Araripechlorogomphus muratai n. sp.

Figs 1–2

Holotype: Female specimen no. KMNHIP000004 at the Kitakyushu Museum & Institute of Natural History, Kitakyushu, Japan (ex coll. MURATA, Kyoto, Japan).

Type locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, north-east Brazil (MAISEY, 1990).

Type horizon: Lower Cretaceous, Upper Aptian, Crato Formation – Nova Olinda Member (sensu MARTILL et al. 1993; = Santana Formation – Crato Member auct.).

Derivation of name: Named in honour of Mr MASAYUKI MURATA (Kyoto, Japan), who kindly donated this important holotype specimen from his magnificent private fossil collection and private museum to the Kitakyushu Museum.

Diagnosis. – This interesting new genus and species is distinguished by the following combination of hindwing characters: Basal space free; no accessory cubito-anal crossveins; no accessory antenodal crossveins basal of Ax1; short "libellulid gap" developed distal of subnodus; "cordulegastrid gap" basal of subnodus probably present; discoidal triangle transverse and free of crossveins; subdiscoidal triangle slanted towards wing base and distally narrowed; "gaff" long and straight; anal loop hexagonal, large, and divided into 8 cells; two rows of cells in the broadened area between MP and CuA directly distal of subdiscoidal veinlet; CuAa short and strongly curved with only two posterior branches; CuAb directed towards wing base; pterostigma relatively short, covering only 2.5 cells, and unbraced; no Rspl and Mspl; pseudo-IR1 originates beneath distal side of pterostigma; RP2 and IR2 as well as MA and RP3/4 are closely parallel up to wing margin; MA and RP3/4 slightly undulated.

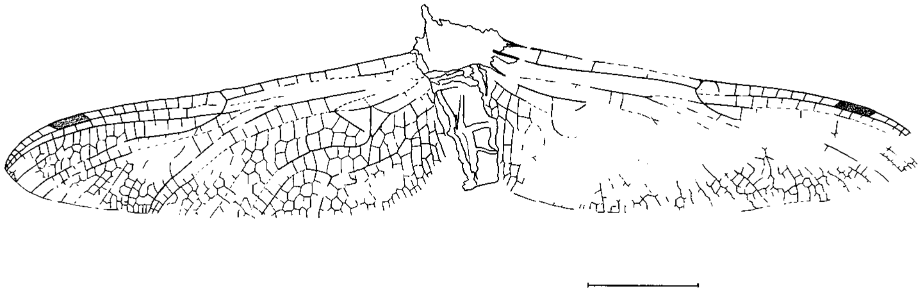

Fig. 1. *Araripechlorogomphus muratai* n. gen. n. sp., female holotype no. KMNHIP000004 Kitakyushu Museum. Scale 10 mm.

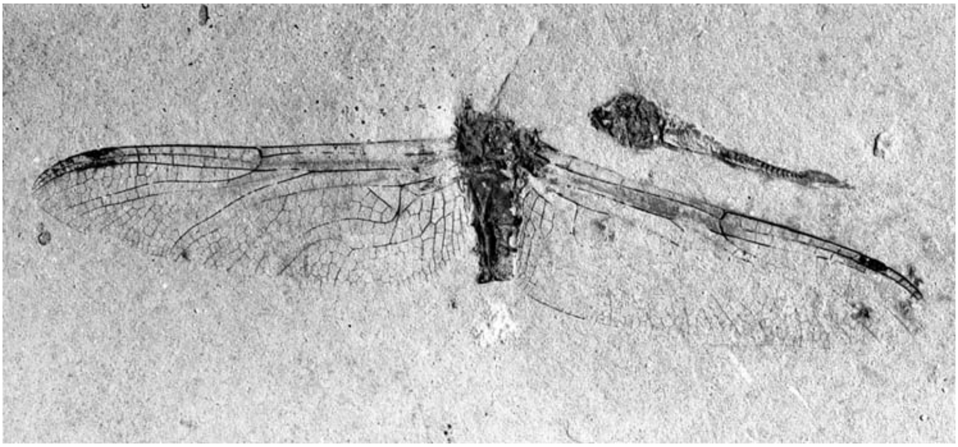

Fig. 2. *Araripechlorogomphus muratai* n. gen. n. sp., female holotype no. KMNHIP000004 Kitakyushu Museum. Without scale.

Description

A body fragment (thorax and base of abdomen) with two complete hindwings of a female dragonfly, preserved together with a small juvenile bony fish of the genus *Dastilbe* (Teleostei: Ostariophysi: Gonorynchiformes: Chanidae).

Hindwing: Length, 39.4 mm; width at nodus, 12.2 mm (max. width, 13.8 mm); distance from base to nodus, 18.1 mm (the nodus is situated at about 46 % of the wing length); distance from nodus to pterostigma, 12.5 mm; Ax1 and Ax2 are stronger than the other antenodals (bracket-like); Ax1 is 3.3 mm distal of wing base and Ax2 is 5.3 distal of Ax1 (on the level of distal angle of discoidal triangle); apparently only one secondary antenodal crossveins between Ax1 and Ax2; distal of Ax2 there are 5 secondary antenodal crossveins between costal margin and ScP, the secondaries between ScP and RA are not preserved; the antesubnodal crossveins are not preserved, thus it is not possible to clearly verify if there was a long "cordulegastrid gap" (sensu BECHLY, 1996) directly basal of the subnodus, but it probably was present; 8–9 postnodal crossveins between nodus and pterostigma, and 6 corresponding postsubnodal crossveins between subnodus and pterostigma (not aligned with postnodal crossveins); there is a short "libellulid gap" (sensu Bechly, 1996) directly distal of the subnodus; the pterostigma is 3.2 mm long and max. 0.8 mm wide; pterostigma is not braced and covers 2.5 cells (in the left hindwing there is a crossvein aligned with the proximal stigmal margin, while there is no such veinlet in the right hindwing); the arculus is not clearly preserved; the bases of veins RP and MA (sectors of arculus) are not preserved, so that it is not visible if they have been distinctly separated at arculus; hypertriangle not very clearly preserved, but apparently distinctly longer than discoidal triangle, and divided by one crossvein at basal side of discoidal triangle; discoidal triangle transverse and unicellular (free of crossveins); length of basal side of discoidal triangle, 2.5 mm; length of its costal side, 3.2 mm; length of its distal side MAb, 3.9 mm; MAb is straight without any kink; a distinct pseudo-anal vein PsA (= AA0) delimits an unicellular subdiscoidal triangle (basally 1.9 mm wide, but distally only 0.3 mm wide); basal space apparently free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 2.8 mm distal of wing base; anal area max. 8.4 mm wide with 6 rows of cells; cubito-anal area max. 4.4 mm wide with up to 4 rows of cells; CuA with only two posterior branches; CuAb distinctly developed and directed towards wing base (parallel to hind margin of wing); "gaff" strongly enlarged, 2.7 mm long; anal loop hexagonal, large (6 mm long and 2.7 mm broad), and divided into 8 cells; MP apparently ending slightly basal of the level of the nodus; basal postdiscoidal area with two rows of cells; postdiscoidal area distally strongly widened (width near discoidal triangle, 3.1 mm; width at hind margin, 8.3 mm); no Mspl, but two strong intercalary veins in the distal postdiscoidal area, reaching the hind margin of wing; RP3/4 and MA only slightly undulated and parallel, with only one row of cells in-between, near the wing margin they are somewhat convergent with two cells between them; first branching of RP ("midfork") 5.3 mm basal of subnodus; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 2.5 mm and two and a half cells distal of subnodus; at least one bridge crossvein between RP2 and IR2 basal of subnodus (three basal of oblique vein); RP2 and IR2 parallel with only one row of cells between them up to the wing margin; no Rspl, but several intercalary veins in the area between IR2 and RP3/4, reaching the hind margin of wing; RP1 and RP2 basally parallel with one row of cells between them, but after seven cells becoming divergent with 2–3 rows of cells between them; pseudo-IR1 distinct and originating on RP1 below distal side of pterostigma; the anal margin of the wing is not preserved, but the venation in the anal area clearly indicates that there was no anal triangle and anal angle, thus it is a female specimen; three posterior branches of anal vein between CuAb and anal margin; no membranule is visible.

4. Phylogenetic and biogeographic considerations

Phylogenetic interpretation of wing venational characters with a reclassification of Cavilabiata based on these characters (characters present in Araripechlorogomphidae n. fam. are printed in bold face; a complete list of putative autapomorphies of all concerning taxa is provided by Bechly, 2002):

- Cavilabiata
  - Cordulegastrida
  - Cristotibiata
    - Neopetaliidae
    - Brachystigmata
      - † Nannogomphidae
      - Paucipostnodalia taxon nov.
        - † Prohemeroscopidae n. fam.
        - Eubrachystigmata
          - † Hemeroscopidae
          - Neobrachystigmata taxon nov.
            - Chlorogomphida
              - † Araripechlorogomphidae n. fam.
              - Chlorogomphoidea
            - Paneurypalpidomorpha taxon nov.
              - † Juracorduliidae n. fam.
              - Eurypalpidomorpha taxon nov.
                - † Valdicordulioidea stat. nov.
                  - † Valdicorduliidae
                  - † Araripephlebiidae
                - Eurypalpidiformia taxon nov.
                  - † Eocorduliidae
                  - Paneurypalpida

- Cavilabiata Bechly, 1996:
  Included taxa: Cordulegastrida Bechly, 1996 and Cristotibiata taxon nov.
  Autapomorphies: Discoidal triangles at least somewhat longitudinal elongate in both wings (reversed in the forewing of Paneurypalpidomorpha), especially in the hindwing (reversed in Chlorogomphida); **distal part of antesubnodal area free of crossveins ("cordulegastrid gap") (convergent to Gomphaeschnidae, Araripegomphidae, Cordulagomphinae, and a few other Anisoptera; reversed in Chlorogomphoidea); "gaff" (= basal CuA before its branching) of the hindwing at least slightly prolonged (convergent to Aeshnodea); RP3/4 and MA slightly undulating in both pairs of wings (reversed in Juracorduliidae and Paneurypalpida).**
- Cristotibiata taxon nov. (cited as nomen nudum by Bechly, 2002):
  Included taxa: Neopetaliidae Tillyard & Fraser, 1940 and Brachystigmata Bechly, 1996.
  Autapomorphies: **Pterostigmata not parallel sided (distal side more oblique than basal side), and rather stout with length less than 8 times width;** forewing nodus shifted distinctly distal of midwing position (reversed in Libellulidae); **the hindwing CuAa is shortened, with fewer (1–6) posterior branches; anal loop at least elongated and enlarged, with more than 5 cells in the groundplan.**
- Brachystigmata Bechly, 1996:
  Included taxa: Nannogomphidae Bechly, 1996 and Paucipostnodalia taxon nov.
  Autapomorphies: **Wings with 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" (= basal CuA before its branching) is strongly prolonged (convergent to several Aeshnidae, especially Anacina) and very straight in the groundplan (but sigmoidal in Eurypalpidomorpha); area between MP and CuA basally widened with more than one row**

of cells (convergent to many Aeshnidae and the gomphid *Cacoides*; reversed in Chloropetaliidae, Valdicorduliidae and Eurypalpidiformia, but regained in a few Macromiidae); the terminal branch of CuAa is secondarily branched on CuA (convergent to a few Austropetaliidae and Aeshnidae, and *Octogomphus*; this character is of course not applicable in Nannogomphidae, Araripephlebiidae, and Eurypalpidiformia since CuAa is secondarily unbranched in these taxa); RP3/4 and MA strictly parallel up to the hind margin; area between RP2 and IR2 distally distinctly widened, with more than one cell row in the distal half (convergent to some Petaluridae, Austropetaliida, and Aeshnida; reversed in Chlorogomphida and Eurypalpida).

- Paucipostnodalia taxon nov. (cited as nomen nudum by BECHLY, 2002):
  Included taxa: Prohemeroscopidae n. fam. and Eubrachystigmata taxon nov.
  Autapomorphies: **Basal part of postsubnodal area free of crossveins ("libellulid gap")**. The name of this new taxon is based on this important character!
- Prohemeroscopidae n. fam.:
  Type genus *Prohemeroscopus* BECHLY et al., 1998, diagnosis as type genus.
  Autapomorphies: The forewing subdiscoidal triangle is widened with a curved or angled posterior margin (convergent to Juracorduliidae, Paneurypalpida, Petalurida, and some Gomphides). This character is unknown in *P. kuehnapfeli* which was only provisionally attributed to this genus and family by BECHLY et al. (1998) because of the overall similarity of the preserved hindwing venation with that of the type species *P. jurassicus*.
- Eubrachystigmata taxon nov. (cited as nomen nudum by BECHLY, 2002):
  Included taxa: Hemeroscopidae PRITYKINA, 1977 and Neobrachystigmata taxon nov.
  Autapomorphies: **In the hindwing CuAa is more distinctly curved towards the hind margin, and thus further shortened with less than five posterior branches.**
- Neobrachystigmata taxon nov. (cited as nomen nudum by BECHLY, 2002):
  Included taxa: Chlorogomphida BECHLY, 1996 and Paneurypalpidomorpha taxon nov.
  Autapomorphies: Arculus not distinctly angled but more or less straight (convergent to many gomphids; unknown in Araripechlorogomphidae); posterior part (crossvein) of arculus distinctly shorter than anterior part [RP & MA] (unknown in Araripechlorogomphidae); **hindwing MP distinctly curved towards the hind margin and thus somewhat shortened, ending basal of the level of the nodus**.
- Chlorogomphida BECHLY, 1996:
  Included taxa: Araripechlorogomphidae n. fam. and Chlorogomphoidea NEEDHAM, 1903.
  Autapomorphies: **Hypertriangles much longer than discoidal triangles in both pairs of wings (at least in the hindwing correlated with the transverse shape of the discoidal triangle); discoidal triangle more transverse in the hindwing; typical shape of the subdiscoidal triangle in the hindwing which is distinctly slanted towards the hind margin (correlated with the transverse shape of the discoidal triangle), basally dilated, but distally abruptly narrowed; pterostigmal brace vein reduced (convergent to Cordulegastrida, Hemeroscopidae, Valdicordulioidea, Eocorduliidae, and some Eurypalpida); anal loop longitudinally elongated and broad (at least 7–9 cells large) and of characteristical pen-**

tagonal or hexagonal shape; area between RP2 and IR2 not distinctly widened distally (reversal; convergent to Eurypalpida).

- Araripechlorogomphidae n. fam. (cited as nomen nudum by BECHLY, 2002): Type genus *Araripechlorogomphus* n. gen., diagnosis as type genus (see above). Autapomorphies: **Hindwing discoidal triangle unicellular (convergent to Nannogomphidae, Hemeroscopidae, and Paneurypalpidomorpha)**.
- Chlorogomphoidea NEEDHAM, 1903 (sensu BECHLY, 2002): Included taxa: All extant chlorogomphids (crowngroup). Autapomorphies: Sectors of arculus approximate (convergent to Eurypalpida and some Araripelibellulidae); basal accessory antenodal crossveins present in the subcostal space between Ax0 and Ax1 (maybe not a groundplan character); hindwing discoidal triangle divided into 3–6 cells (maybe not a groundplan character); wings secondarily with crossveins immediately basal of the subnodus ("cordulegastrid gap" reduced); median space of wings is traversed by one or more crossveins; hypertriangles traversed by several crossveins in both pairs of wings; cubital cell (between CuP-crossing and PsA) divided by accessory cubito-anal crossveins (convergent to Synthemistidae, Macromiidae, Idomacromiidae, and some Idionychidae and Libellulidae); male hindwing with a less distinct anal angle.
- Paneurypalpidomorpha taxon nov. (cited as nomen nudum by BECHLY, 2002): Included taxa: Juracorduliidae n. fam. and Eurypalpidomorpha taxon nov. Autapomorphies: Anterior margin of hypertriangle distinctly convex, especially in the hindwings, because of a basally arched MA; forewing Ax1 shifted basal of the level of the distal angle of the discoidal triangle (convergent to Nannogomphidae); in both pairs of wings Ax1 and Ax2 are relatively close together with not more than one secondary antenodal crossvein between them (convergent to Nannogomphidae); lestine oblique vein only 1–2 cells distad of the subnodus in both pairs of wings; forewing discoidal triangle more or less transverse instead of elongate (reversal); discoidal triangles unicellular in both pairs of wings (convergent to Nannogomphidae, Hemeroscopidae, and Araripechlorogomphidae; reversed in the hindwing of Araripephlebiidae and in some Eurypalpida).
- Juracorduliidae n. fam. (cited as nomen nudum by BECHLY, 2002): Type genus *Juracordulia* BECHLY, 1998b, diagnosis as type genus. Autapomorphies: Pterostigma further shortened, only 1–2 cells long (convergent to Nannogomphidae and Eurypalpidiformia); the forewing subdiscoidal triangle is widened with a curved or angled posterior margin (convergent to *Prohemeroscopus jurassicus*, Paneurypalpida, Petalurida, and some Gomphides); unique shape of the transversely elongate anal loop; postdiscoidal area very narrow and strongly bent in both pairs of wings; RP2 and IR2 more strongly divergent; RP3/4 and MA secondarily not undulating in both pairs of wings (convergent to Paneurypalpida).
- Eurypalpidomorpha taxon nov. (cited as nomen nudum by BECHLY, 2002): Included taxa: Valdicordulioidea stat. nov. (sensu BECHLY, 2002) and Eurypalpidiformia taxon nov. Autapomorphies: In the hindwing the elongated "gaff" (= basal CuA before its branching) is sigmoidally curved; CuAb shifted very far distally, and CuAa with only one or two posterior branches.

- Valdicordulioidea stat. nov. (sensu Bechly, 2002):
  Included taxa: Valdicorduliidae Bechly, 1996 and Araripephlebiidae Bechly, 1998a.
  Autapomorphies: Pterostigmal brace vein reduced (convergent to Cordulegastrida, Hemeroscopidae, Chlorogomphida, Eocorduliidae, and some Eurypalpida); hindwing subdiscoidal triangle more strongly transverse.
- Eurypalpidiformia taxon nov. (cited as nomen nudum by Bechly, 2002):
  Included taxa: Eocorduliidae Bechly, 1996 and Paneurypalpida Bechly, 1996.
  Autapomorphies: Pterostigma further shortened, only 1–2 cells long (convergent to Nannogomphidae and Juracorduliidae; reversed in Libellulinae).

The distribution of derived character states described above clearly demonstrates that Araripechlorogomphidae n. fam. is most closely related to extant Chlorogomphoidea, but does not belong within this crowngroup. The absence of a “libellulid gap” in Cordulegastridae, Neopetaliidae and Nannogomphidae (excl. *Prohemeroscopus*) (see Bechly et al., 1998b and Bechly, in prep.) and the presence of a short “libellulid gap” in both wings of Araripechlorogomphidae n. fam. and Hemeroscopidae (see Bechly et al., 1998b) strongly suggests that this character is a groundplan autapomorphy of Paucipostnodalia rather than of Paneurypalpidomorpha (contrary to Bechly, 2002). The genus *Prohemeroscopus* was tentatively attributed by Bechly (2002) to Nannogomphidae, even though there are no strong synapomorphies. The presence of a short “libellulid gap” requires the removal of this genus from Nannogomphidae and its attribution to Eubrachystigmata as most basal taxon within a new monotypic family Prohemeroscopidae n. fam.. The above conclusion implies that the lack of a “libellulid gap” in crowngroup chlorogomphids must be regarded as a reversal, just like the reduction of the “cordulegastrid gap” in all extant chlorogomphids (see Bechly, 2002). The presence of the “libellulid gap” in Araripechlorogomphidae n. fam. is a plesiomorphy that demonstrates, that this fossil taxon belongs to the stemgroup of extant chlorogomphids. Some further plesiomorphies (viz. no accessory antenodals between Ax0 and Ax1; median space free; no accessory cubito-anal crossveins) support this conclusion.

Because all 44 extant species of chlorogomphids are distributed in Eastern Asia, the present discovery of a stemgroup representative of Chlorogomphoidea from the Lower Cretaceous of South America allows two conclusions:

1.) The clade Chlorogomphida originated at least about 120 Million years ago in the Lower Cretaceous (“terminus post quem non” sensu Hennig, 1966). The real age of origin must even be older, because the sistergroup (Paneurypalpidomorpha) is represented with *Juracordulia schiemenzi* Bechly, 1998b in the Upper Jurassic Solnhofen Limestone that is about 150 Million years old.

2.) The clade Chlorogomphida either originated in South America or its stemgroup was more widespread than the extant representatives. Because of the very close proximity of the South American and the African continent in the Lower Cretaceous (the Crato area was then only 200 km separated from West Africa, while the southern halves of both continents where still together) it appears quite likely that stemgroup chlorogomphids where also distributed in parts of Africa in this period of earth history. The potential reasons for the subsequent disappearance of chlorogomphids from South America (and Africa?) are still unknown, because similar suitable habitats were always present in this region.

5. Acknowledgements

We are most grateful to Mr M. Murata (Kyoto) for the kind loan of the holotype in his collection and its subsequent donation to the Kitakyushu Museum. We thank Mr B. Schuster (Hünstetten) for providing a photo of the holotype. We are indebted to Dr G. Bloos (SMNS, Stuttgart) for his careful proof-reading of this manuscript.

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ISSN 0341-0153

Schriftleitung: Dr. Gert Bloos, Rosenstein 1, D-70191 Stuttgart
Gesamtherstellung: Gulde-Druck GmbH, D-72072 Tübingen