Additions to the fossil dragonfly fauna from the Lower Cretaceous Crato Formation of Brazil (Insecta: Odonata)[1]

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Abstract

Several interesting new discoveries of fossil odonates from the Lower Cretaceous Crato Formation of NE Brazil are presented. Two new taxa of damselflies (*Euarchistigma peterknobli* n. sp. and *Santanagrion longipes* n. gen., n. sp.) are described, and a new specimen of *Euarchistigma marialuiseae* with preserved colour pattern, distinct from the type species, is featured. Among the dragonflies totally three new families (Megaphlebiidae n. fam., Magnathemidae n. fam., and Cratopetaliidae n. fam.), nine new genera, and ten new species (*Paracordulagomphus aberrans* n. gen., n. sp.; *Paracordulagomphus divergens* n. gen., n. sp.; *Pauciphlebia novaolindense* n. gen., n. sp.; *Cratogomphus erraticus* n. gen., n. sp.; *Cratohagenius erichweberi* n. gen., n. sp.; *Megaphlebia rayandressi* n. gen., n. sp.; *Magnathemis marcusthorhalli* n. gen., n. sp.; and *Cratopetalia whiteheadi* n. gen., n. sp.) are described. A further putative new dragonfly genus and species is discussed and featured, but not formally described because of the poor preservation of the single available specimen. The original descriptions of *Euarchistigma marialuiseae*, *Cratostenophlebia schwickerti*, *Eotanypteryx paradoxa*, *Paramesuropetala gigantea*, *Cordulagomphus hanneloreae* and *Cordulagomphus winkelhoferi* are emended with new data and supplemented with drawings and photos. The newly discovered counter plate of the holotype of *Cratopetalura petruleviciusi* is featured. Some errors concerning collection numbers and depositions of fossil odonates in Martill et al. (2007) are corrected and new collection numbers are updated for the Senckenberg museum collection.

Keywords: Fossil insects, Odonata, Zygoptera, Thaumatoneuridae, Euarchistigmatinae, Stenophlebioptera, Stenophlebiidae, Anisoptera, Cretapetaluridae, Liupanshaniidae, Proterogomphidae, Cordulagomphinae, Hageniidae, Megaphlebiidae n. fam., Magnathemidae n. fam., and Cratopetaliidae n. fam., Mesozoic, Lower Cretaceous, Crato Formation, Brazil.

Zusammenfassung

Einige interessante neue Funde fossiler Libellen aus der unterkretazischen Crato-Formation von NO-Brasilien werden vorgestellt. Zwei neue Kleinlibellentaxa (*Euarchistigma peterknobli* n. sp. und *Santanagrion longipes* n. gen., n. sp.) werden beschrieben, und ein neues Exemplar von *Euarchistigma marialuiseae* mit erhaltenem Farbmuster, welches sich von dem der Typusart unterscheidet, wird abgebildet. Unter den Großlibellen werden insgesamt drei neue Familien (Megaphlebiidae n. fam., Magnathemidae n. fam. und Cratopetaliidae n. fam.), neun neue Gattungen und zehn neue Arten beschrieben (*Paracordulagomphus aberrans* n. gen., n. sp.; *Paracordulagomphus divergens* n. gen., n. sp.; *Pauciphlebia novaolindense* n. gen., n. sp.; *Cratogomphus erraticus* n. gen., n. sp.; *Cratohagenius erichweberi* n. gen., n. sp.; *Megaphlebia rayandressi* n. gen., n. sp.; *Magnathemis marcusthorhalli* n. gen., n. sp.; und *Cratopetalia whiteheadi* n. gen., n. sp.). Eine weitere mögliche neue Gattung und Art von Großlibellen wird diskutiert und abgebildet, aber wegen der schlechten Erhaltungsqualität des einzigen verfügbaren Exemplars nicht formal beschrieben. Die Originalbeschreibungen von *Euarchistigma marialuiseae*, *Cratostenophlebia schwickerti*, *Eotanypteryx paradoxa*, *Paramesuropetala gigantea*, *Cordulagomphus hanneloreae* und *Cordulagomphus winkelhoferi* werden durch Zeichnungen, Fotos und zusätzliche Angaben ergänzt und erweitert. Die neu entdeckte Gegenplatte des Holotypus von *Cratopetalura petruleviciusi* wird abgebildet. Einige Fehler hinsichtlich der Angaben zu Sammlungsnummern und Aufbewahrungsorten von fossilen Libellen in Martill et al. (2007) werden berichtigt und neue Sammlungsnummern für Stücke aus dem Naturmuseum Senckenberg werden ergänzt.

Contents

[1] Contribution to the Willi-Hennig-Symposium on Phylogenetics and Evolution, University of Hohenheim, 29 September – 2 October 2009.

1. Introduction

The Crato Formation of NE Brazil is one of the most diverse fossil localities from the Lower Cretaceous and yields fossil plants, arthropods and vertebrates of exceptionally good preservation, sometimes even showing soft tissues and colour pattern (see Fig. 106 for the first record of colour pattern in Anisoptera). This fossil locality is especially important because of the combined occurrence of early flowering plants and putative early pollinating insects, so that there is direct fossil evidence available from the first stages of the co-evolution of insects and angiosperms which is one of the major events in the history of evolution on our planet. Consequently, the Lower Cretaceous Crato Formation of Brazil provides an important clue to the major radiation in insect evolution.

The fossil insects from this locality helped to solve one of WILLI HENNIG's major problems, who stated (1969): "One of the most unfortunate gaps in our knowledge of insect phylogeny is the nearly complete lack of fossils from the Cretaceous".

The insect fauna from the Crato Formation is represented by several ten-thousand specimens of most modern insect orders, except for tiny ground-dwelling and parasitic groups. However, the complete absence of any larval and adult Plecoptera still represents an unsolved mystery.

Several very interesting discoveries have recently been made (BECHLY 2007), such as the second record for the order Mecoptera, the first record of the odonate suborder "Anisozygoptera", the most primitive termite family Cratomastotermitidae and the oldest record of Kalotermitidae, the first New World record of the enigmatic Mesozoic Chresmododea (DELCLÒS et al. 2008), the first fossil record of the stick-insect-like orthopteran family Proscopiidae (HEADS 2008), and a strange family (Cratovitismidae) of roaches related to beetle-like Umenocoleoidea. Finally, a new order (Schwickertoptera) of neuropteroid insects and two new undescribed insect orders of paleopterous insects (stemgroup mayflies) have been recently discovered, including a relic group that still has features otherwise only known from Paleozoic insects (STANICZEK, BECHLY & GODUNKO in press 2011).

A statistical analysis of the relative abundance of the various orders of terrestrial arthropods based on more than 25000 fossil arthropods from this locality shows (MARTILL et al. 2007) that the insect orders Orthoptera, Blattodea, and Hemiptera each constitute about 1/4 of the fossil arthropods, while all other orders (except Ephemeroptera with 7 %) are only represented by 1–4 % of the fossils. The most frequent group is Orthoptera, followed by Heteroptera, Blattodea (incl. Umenocoleidae), and finally Auchenorrhyncha. Such an assemblage is characteristical for a semiarid environment with xerophytic vegetation, which is also suggested by the other available data.

BECHLY (1998, 2007) provided a synopsis of the fossil odonate fauna from the Crato Formation. These included 15 families, 24 genera, and 38 species. Subsequently Nel & Bechly (2009) described a further new genus and species. In the present publication three new families, ten new genera, and 12 new species are described. Thus, totally three suborders, 18 families, 35 genera, and 51 species of fossil damselflies and dragonflies are now known from this locality. For comparison, Solnhofen, which is one of the most proliferous localities concerning fossil odonate diversity, yealded six suborders, 18 families (plus two unpublished records), 28 genera (plus three undescribed genera), and 42 species (plus six undescribed species, but excl. all synonymous and/or dubious species names). There are no other fossil localities that could match these numbers. Consequently, the Crato Formation represents the fossil locality with the worldwide highest diversity of fossil odonate species.

Bechly (2007) described several new species. Due to the limitations of this book, the descriptions had to be brief and the printing quality of the illustrations unfortunately was rather poor. Therefore, a re-description of the type material of these new species is warranted and here provided.

Based on new fossil material from the Crato Formation some further odonate taxa are re-described and their diagnoses are emended. The eight new taxa of Anisoptera that had been discussed but not named by Bechly (2007: 218–222) are here formally described. Furthermore, several new discoveries are described.

Due to a rather chaotic technical editing process of Martill et al. (2007) in India, several collection numbers of fossil odonates from the Crato Formation have been confused (esp. the abbreviations for collections MSF and SMF). These disimprovements by the copy editors unfortunately made it into the book, because they were done after the proof reading process, so that some incorrect data are given in Bechly (2007). They are corrected in the present publication, and new collection numbers and places of deposition are provided in several cases.

Acknowledgements

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2. Material and methods

The drawings have been made with a camera lucida on a Wild M5 stereo microscope. Fossils have been "photographed" by direct scanning with a Canon CanoScan 4200F flatbed scanner, and with a Leica DFC490 digital macro camera on a Leica Z16-Apo microscope with Synchroscopy Auto-Montage™ software. All figures have been subsequently edited and polished with the Adobe Photoshop™ CS3 imaging software.

If plate and counter plate of a fossil haven been available, raw drawings of both sides have been made, and have then been combined for the final illustration of the fossil. When wing veins were only fragmentarily preserved they have been reconstructed in all those cases, where the complete course of the veins could be extrapolated unequivocally. Some fossils have been further prepared after the photos had been taken to show crucial characters for the description.

The terminology of odonate wing venation is based on Riek & Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). The used phylogenetic classification of the order Odonata is mainly based on Bechly (1996, 2003, 2007).

Acronyms of depositories

MNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum national d'Histoire naturelle, Paris, France
MSF	coll. Michael Schwickert, Sulzbachtal, Germany
MURJ	coll. Masayuki Murata, Kyoto, Japan
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
WDC	coll. Burkhard Pohl at the Wyoming Dinosaur Center – Crato (Thermopolis, Wyoming, USA)

3. Systematic palaeontology

3.1. Order Odonata Fabricius, 1793
3.1.2. Suborder Zygoptera Selys, 1854
Family Thaumatoneuridae Tillyard & Fraser, 1938
Subfamily Euarchistigmatinae Carle & Wighton, 1990

Genus *Euarchistigma* Carle & Wighton, 1990

Typus generis: *Euarchistigma atrophium* Carle & Wighton, 1990.

Revised diagnosis. – Wings 23–35 mm long, petiolated, and apically strongly broadened with numerous cells; discoidal cell elongate and free, with a more or less oblique distal side; subdiscoidal cell free; only two antenodal crosveins Ax1 and Ax2, with A2 aligned with arculus; nodus in a very basal position at about 25 % of wing length; subnodus somewhat distal of origin of IR2, but far basal of origin of RP2; pterostigma broad and unbraced, covering 4–6 cells; partly with two rows of cells between RA and RP1 distal of pterostigma; at least RA and RP1 are strongly curved towards hind margin; RA and RP1 are

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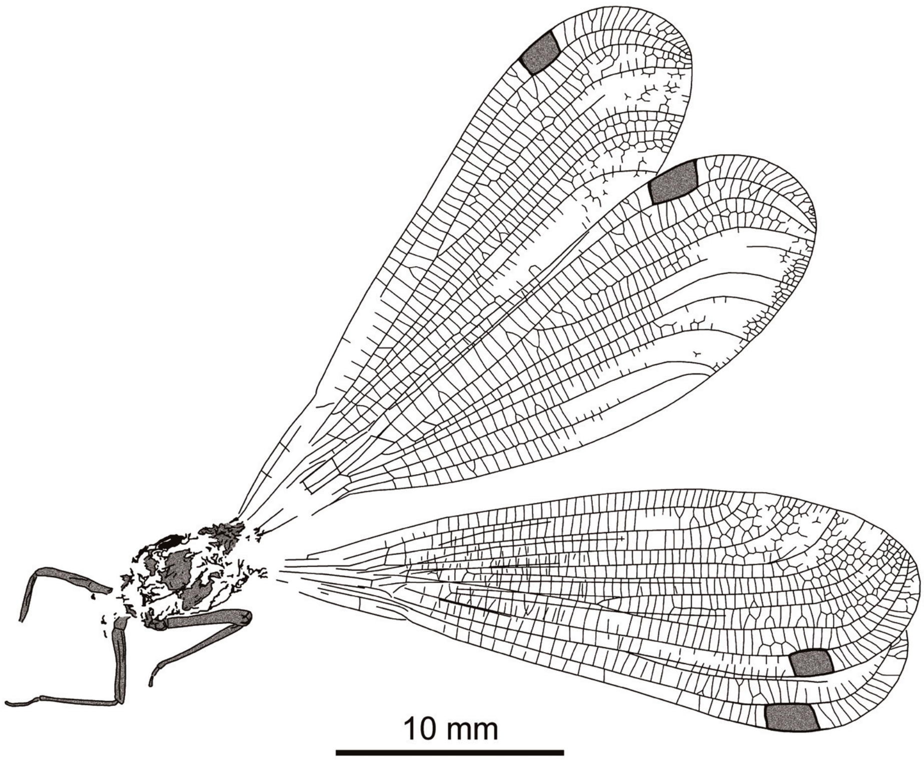

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Figs. 1–2. *Euarchistigma marialuiseae* Bechly, 2007, holotype; SMF VI 837.

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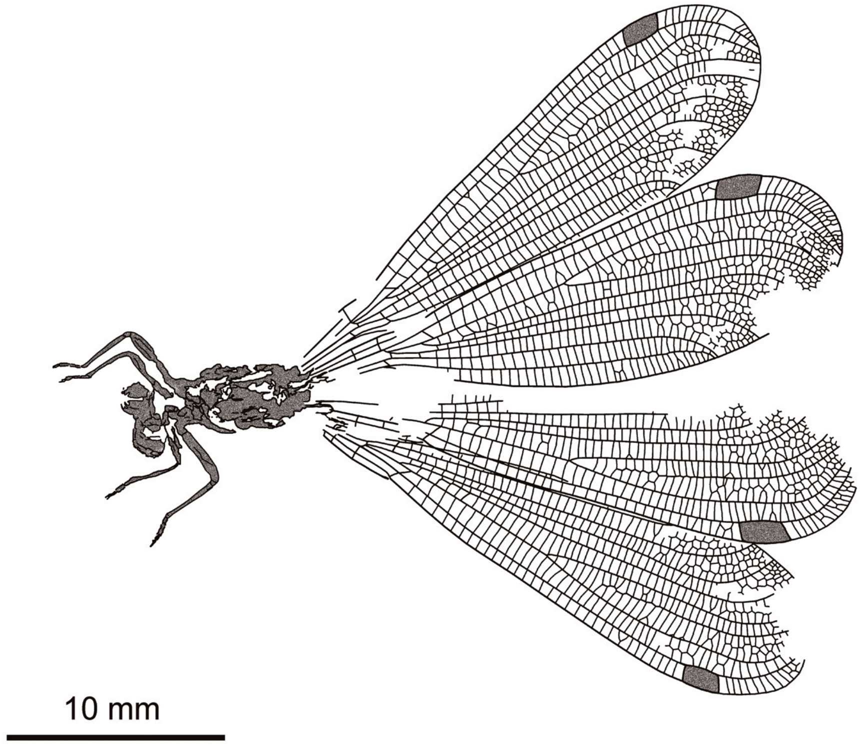

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Figs. 3–4. *Euarchistigma marialuiseae* Bechly, 2007; MSF E100411.

strongly converging towards hind margin; IR2 is basally approaching RP3/4, and often appears to originate from this vein, while the true origin on RP1/2 is less distinct. The imaginal labial plate has a deep median cleft (Fig. 3).

Contrary to the original description by CARLE & WIGHTON (1990) the discoidal cell is not rectangular, but has an oblique distal side in all three species including the type species (compare Fig. 6).

Discussion. – An attribution to Thaumatoneuridae is suggested by the following putative synapomorphies: Antesubnodal space without any crossveins; nodus and bases of IR2 and RP3/4 shifted to an extremely basal position, correlated with a large number of postnodal crossveins; IR2 apparently arising on RP3/4; very dense wing venation with a high number of cells; longitudinal wing veins distally distinctly curved to the posterior wing margin; dark colour pattern of wings; Neotropical distribution. This distally acute discoidal cell is plesiomorphic compared to the Recent genus *Thaumatoneura*.

Euarchistigma marialuiseae BECHLY, 2007
Figs. 1–5

Holotype: SMF VI 837 (old no. Q56) with a wing length of 28.5 mm (Figs. 1–2).

Paratypes: SMF VI 838 (old no. O35, incorrectly indicated as no. Q87 by BECHLY 2007: 193); MNB no. MB.1999.3 MB.I.2090 (old no. D29).

Further material: Specimen no. E100411 (Figs. 3–4) and male specimen no. D90929 (Fig. 5) in coll. MSF.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Smaller than type species (body length 36.7–37.2 mm; forewing length only 26.5–28.8 mm, instead of 30–35 mm in type species); dark colour pattern reaching till end of pterostigma (ending distinctly basal of pterostigma in type species); discoidal cell somewhat longer and narrower in hind wings (according to BECHLY (1998: 43, fig. 19) also present in some specimens of the type species); about 30 postnodal crossveins between

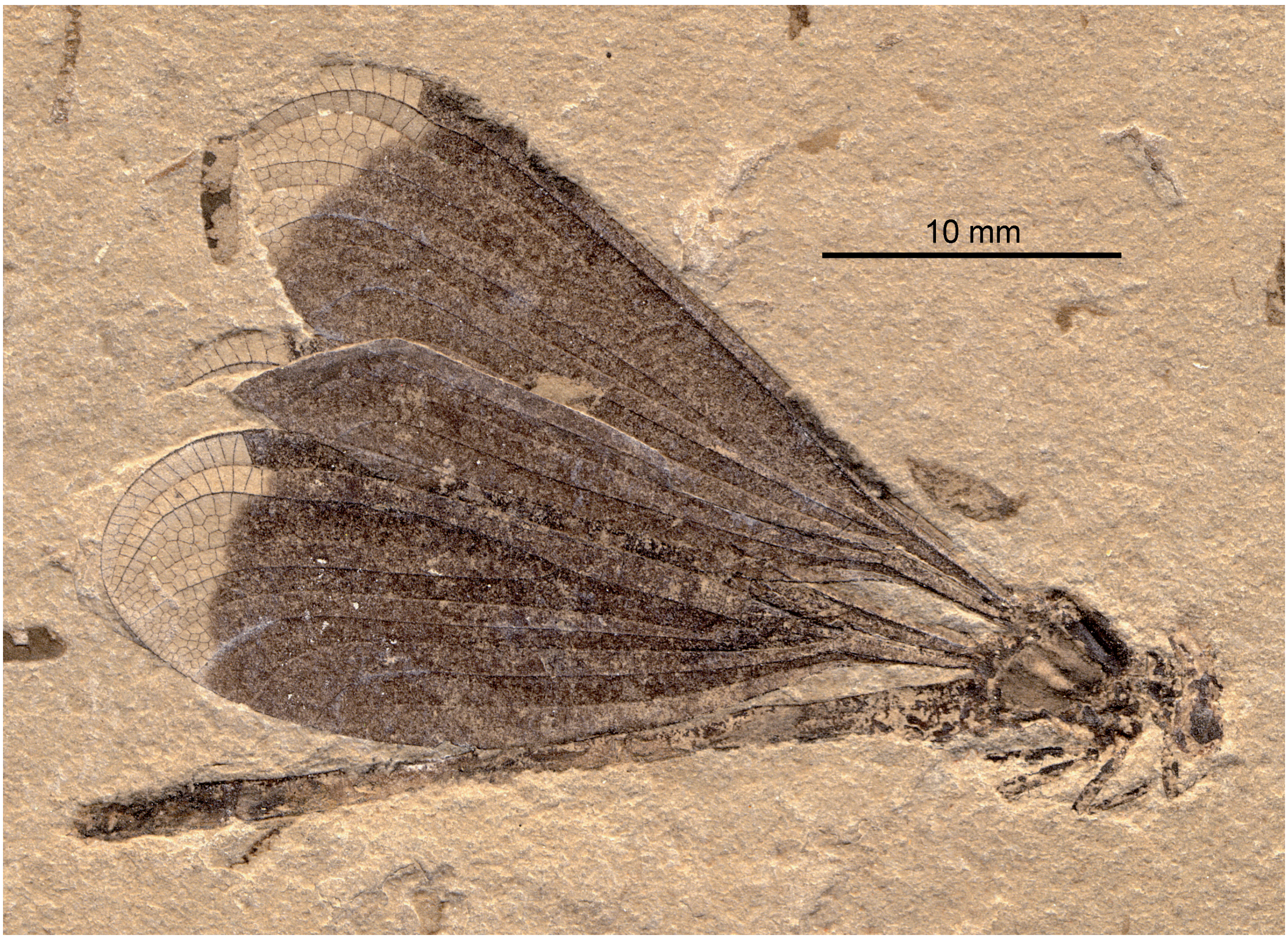

Fig. 5. *Euarchistigma marialuiseae* BECHLY, 2007, male specimen with colour pattern; MSF D90929.

nodus and pterostigma (as in type species); the forewing pterostigmata are shorter than the hind wing pterostigmata (as in type species); all longitudinal veins distally strongly curved towards hind margin (as in type species); IR1 distinct, long, and converging to RP1 near hind margin (as in type species); IR2 is basally approaching RP3/4 and appears to originate on this vein with a secondary prolongation, while its true origin on RP1/2 is indistinct and 1–3 cell more distal; IR2 originates 2–4 (Ø three) cells distal of midfork (instead of 3–6, Ø five, cells in type species, and only one cell in *E. peterknobli* n. sp.); only a single row of cells between CuA and hind margin in both pairs of wings (in type species there are distally two rows).

Discussion. – The number Q87 mentioned by Bechly (2007: 193) could no be verified at SMF and either represents and obsolete preliminary collection number of specimen SMF VI 838, or rather a different specimen in coll. MSF.

A further new male specimen no. D90929 in coll. MSF has a forewing length of 28.8 mm, a hind wing length of 28.5 mm, and a total body length of 37.2 mm (Fig. 5). This latter specimen shows for the first time the colour pattern of this species that is distinct from the colour pattern in the type species *Euarchistigma atrophium* (specimen SMF VI 836, old no. Q55, wing length 35 mm) (Fig. 6).

Even though there are only relatively small differences in size, wing venation and colour pattern between the two described species of the genus *Euarchistigma*, a sexual dimorphism (compare Crowley & Johansson 2002) can be ruled out, because completely preserved specimens of both sexes are known from both species (Fig. 7 features a female specimen of *E. atrophium* with no. 133 in coll. WDC that has a forewing length of 30.0 mm, a hind wing length of 28.3 mm, and a total body length of 38.0 mm).

Euarchistigma peterknobli n. sp.
Figs. 8–12

Holotype: SMNS 66823 (old no. E100409) (Figs. 8–10).

Paratype: Female specimen no. 132 in coll. WDC (Figs. 11–12).

Derivatio nominis: Named after my nephew Peter Maria Knobl (Langenzersdorf, Austria).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Much smaller size than type species (wings only 23.1–24.7 mm long; body less than 29 mm long); discoidal cell broader and shorter than in the other two species; only 17 postnodal crossveins between nodus and pterostigma (instead of more than 30 in the other two species); rows of crossveins in the basal half of the postnodal wing area are well aligned (instead of non-aligned or poorly aligned in the other two species); rectangular cells in the wing are quadratic (instead of vertically narrow rectangular in the other two species); pterostigmata of equal length in both pairs of wings; longitudinal veins (except RA and RP1) less strongly curved towards hind margin; between RP1 and RP2 there is no distinct IR1, but a meshwork of hexagonal cells; IR2 is basally fused to RP3/4, a single cell distal of midfork (instead of 2–6 cells in the other two species), but still also has an indistinct oblique or curved origin on RP1/2 a single cell distal of midfork.

Description of holotype (Figs. 8–10). – Pterothorax with four legs and all four wings (superimposed on both sides) in dorsal aspect. The left forewing has the best preserved wing venation and is here described: Length of forewing 24.7 mm; max. width 7.0 mm; Ax1 and Ax2 not preserved, but the right wings show that there are only the two primary antenodals; nodus in a very basal position at 22 % of the wing length; nodus and subnodus oblique, and slightly distal of the origin of IR2; no antesubnodal and antefurcal crossveins; 17 postnodal crossveins between nodus and pterostigma, the basal nine well aligned with the postsubnodal crossveins and the subsequent rows of crossveins; pterostigma broad with slanted distal side; 4–5 crossveins beneath pterostigma (best visible in right wing); two rows of cells between C and RA distal of pterostigma; RP1 strongly curved and distally convergent to RP2; IR1 absent; wing venation with hexagonal cells in the distal third of the wing, and with rectangular cells in the basal 2/3 of the wing that are more or les quadratic; longitudinal wing veins (except RA and RP1) distally not strongly curved towards wing margin; discoidal cell free and with and acute distal angle; distal side MAb of discoidal cell and subdiscoidal veinlet aligned and oblique; subdiscoidal cell free; only a single row of cells between MP and CuA and between CuA and wing margin.

Description of paratype (Figs. 11–12). – A completely preserved female damselfly in lateral aspect, with head, thorax, legs, wings (superimposed) and abdomen. Total body length of 28.8 mm; forewing length 24.4 mm; hind wing length 23.1 mm; max. width of wings 6.8 mm. Only two primary antenodals Ax1 and Ax2; nodus in a very basal position at 25 % of the wing length; nodus and subnodus oblique, and slightly distal of the origin of IR2; no antesubnodal and antefurcal crossveins; 17 postnodal crossveins between nodus and pterostigma in the forewing, the basal nine well aligned with the postsubnodal crossveins and the subsequent rows of crossveins; 4–5 crossveins beneath the pterostigma; RP1 strongly curved and distally convergent to RP2; no distinct IR1; longitudinal wing veins (except RA and RP1) distally not strongly curved towards wing margin; discoidal cell free and with and acute distal angle; distal side MAb of discoidal cell and subdiscoidal veinlet aligned and oblique; subdiscoidal cell free. Head with widely separated eyes;

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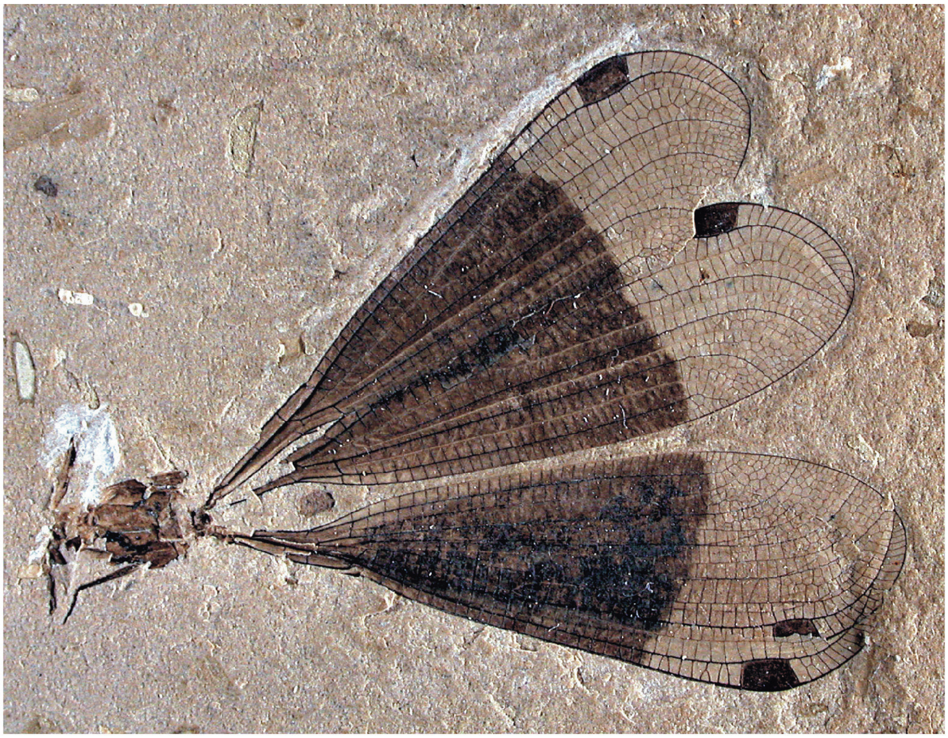

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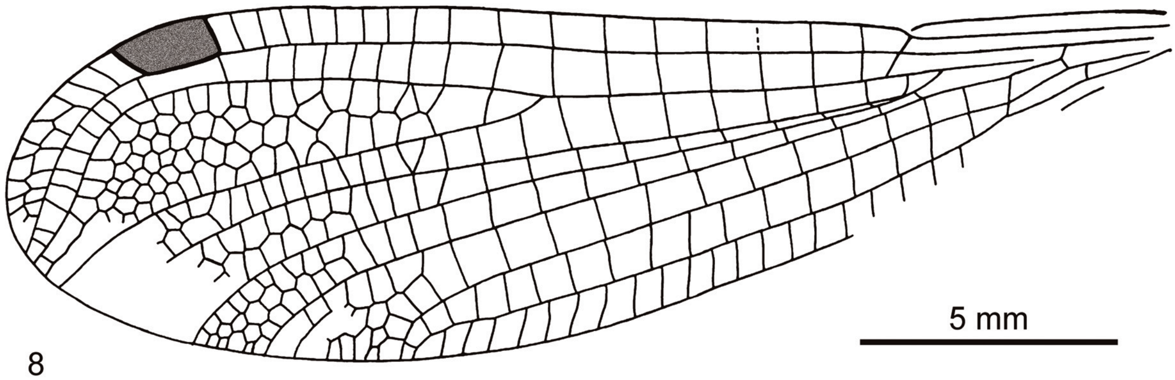
Figs. 6–7. *Euarchistigma atrophium* Carle & Wighton, 1990. – **Fig. 6**. Specimen with colour pattern; SMF VI 836. Scale: Wing length 35 mm. **Fig. 7**. Female; WDC 133. Scale: Ruler in mm.



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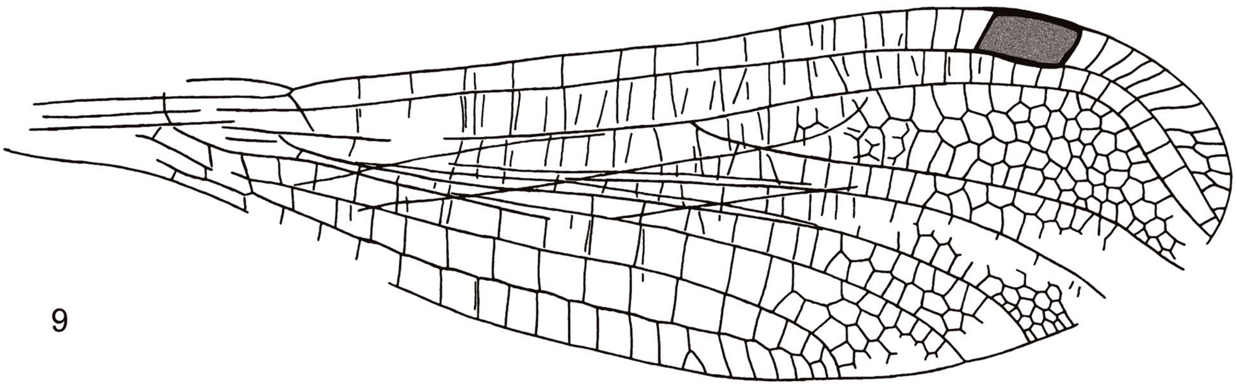

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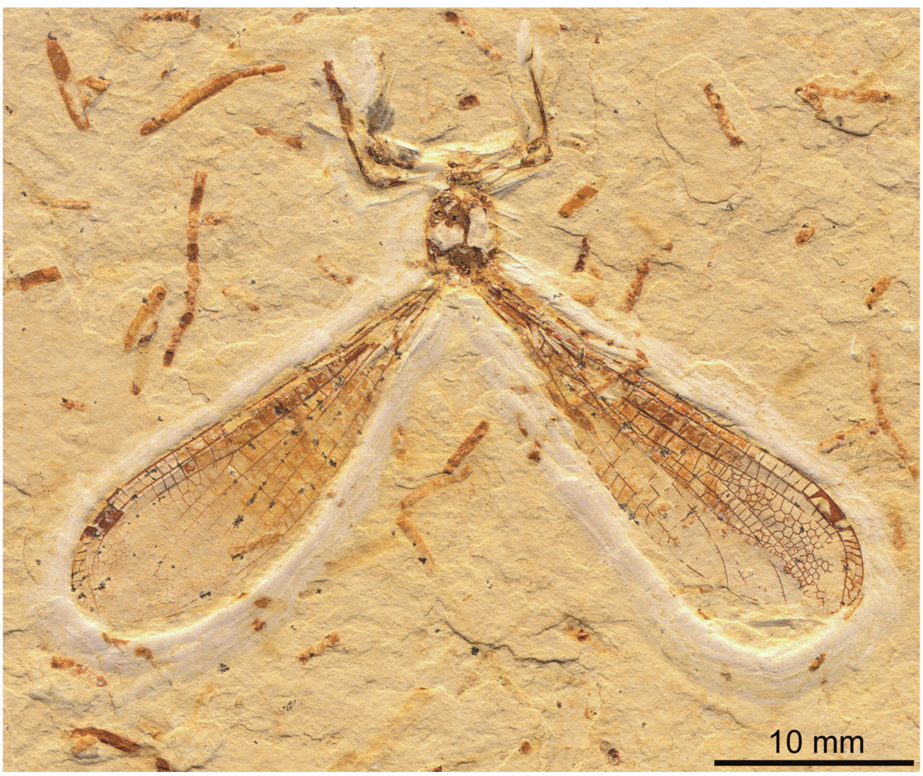

Figs. 8–10. *Euarchistigma peterknobli* n. sp., holotype; SMNS 66823. – **Fig. 8**. Right wing in ventral aspect. **Fig. 9**. Superimposed left wings in ventral aspect. **Fig. 10**. Complete specimen.

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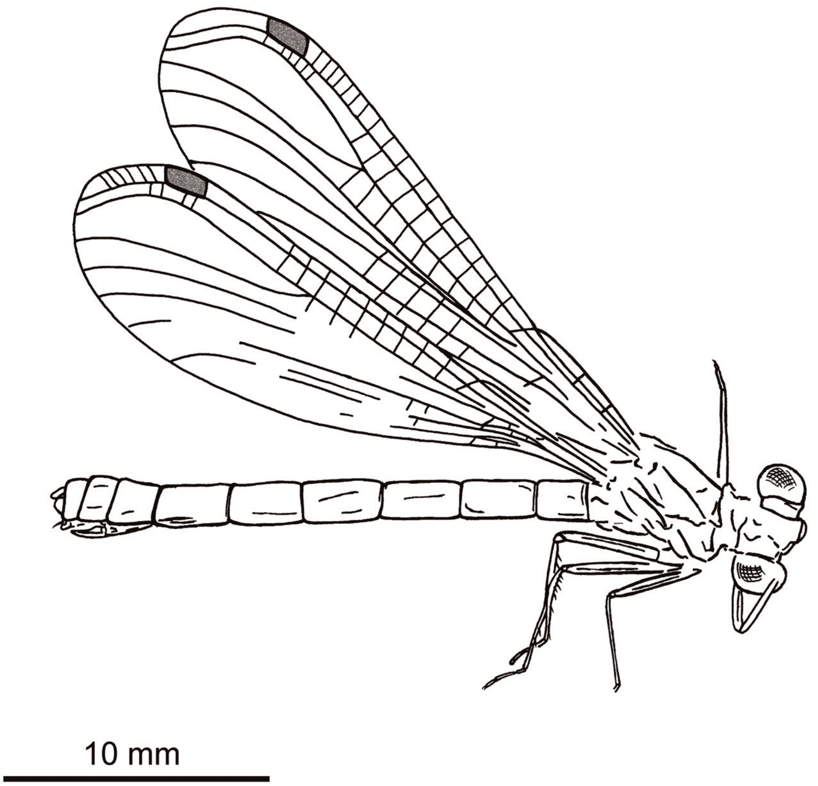

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Figs. 11–12. *Euarchistigma peterknobli* n. sp., female paratype; WDC 132.

thorax strongly oblique; legs relatively short; terminalia short; the well-preserved ovipositor proves that this is a female specimen.

Family incertae sedis

Genus *Santanagrion* n. gen.

Typus generis: *Santanagrion longipes* n. sp.

Derivatio nominis: Named after the locality Santana and the generic name *Agrion*.

Diagnosis. – Same as for type species since monotypic.

Santanagrion longipes n. sp.
Figs. 13–14

Holotype: SMNS 66803b (erroneously numbered as counter plate of SMNS 66803a, which is an *Eoprotoneura hyperstigma* Carle & Wighton, 1990) (Figs. 13–14).

Derivatio nominis: Named after the greatly elongated legs.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Wings about 12 mm long; pterostigmata short, strongly braced; RP1 with pronounced kink at stigmal brace; postnodal and postsubnodal crossveins aligned; nodus in a basal position. Thorax very long and slender; legs extremely elongated (hind femur and hind tibia each 6 mm long). The latter character clearly distinguishes this new taxon from all other known damselflies of the Crato Formation.

Description of holotype (Figs. 13–14). – A completely preserved damselfly, with head, thorax, abdomen, legs and wings. The wings are superimposed. The total body length is 27 mm. The prothorax is comparatively long (2 mm); the pterothorax is very elongate and slender, with a pronounced skewness of the thoracic sutures. The legs are extremely elongated (length of profemur 4.0 mm, of protibia 4.5 mm, of mesofemur 4.9 mm, of mesotibia 5.4 mm, of metafemur 5.8 mm, of metatibia 5.6 mm). The wings are 12.3 mm long and superimposed, so that the venation is only partly visible. The pterostigma is very short (only a single cell long) and strongly braced; RP1 is distinctly kinked at the stigmal brace; the postnodal and postsubnodal crossveins are aligned; RP2 originates beneath the third postsubnodal crossvein basal of the pterostigma; the nodus is in a relatively basal position at 36 % of the wing length. The terminalia and genitalia are not preserved, but the lack of a visible ovipositor suggests that this is a male specimen.

Discussion. – The general habitus (e. g. slender thorax and the extremely elongated legs) of this damselfly at first suggested that this fossil might be a Protomyrmeleontidae, but such an attribution is ruled out by the visible wing venation, which resembles that of the genus *Parahemiphlebia*. The prolonged legs are very unique for a crowngroup zygopteran and certainly justify a separate new genus. Unfortunately, important characters like the discoidal cell are not visible, and the available characters only allow an attribution of this strange new taxon to Zygoptera, but not yet to a specific damselfly family.

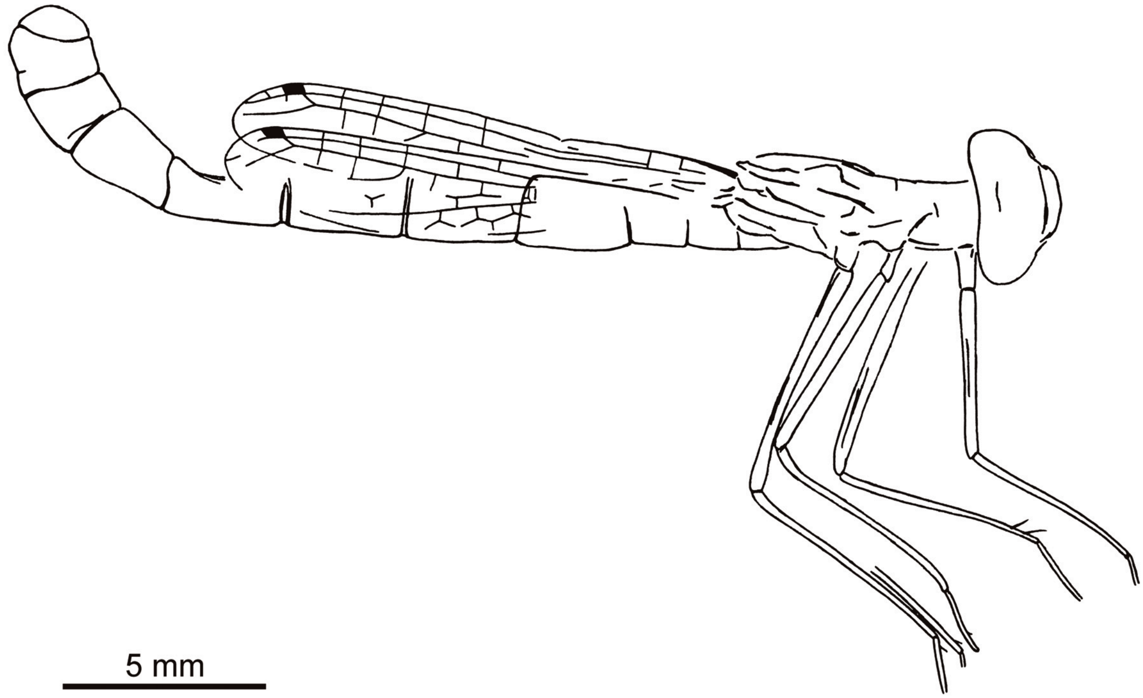
The circumstance that strongly prolonged legs are found in three unrelated Mesozoic damselfly-like odonate taxa (viz. Protomyrmeleontidae, Tarsophlebiidae, and the present new Zygoptera taxon) suggests that there may have been certain palaeoecological conditions in the Mesozoic favouring such a convergent adaptation (Nel, pers. comm. 2010, suggested that extinct large Thripida that lived only in the Mesozoic might have been the potential prey).

3.1.3. Suborder Stenophlebioptera Bechly, 1996
Family Stenophlebiidae Needham, 1903

Genus *Cratostenophlebia* Bechly, 2007

Typus generis: *Cratostenophlebia schwickerti* Bechly, 2007.

Emended diagnosis. – Very large "dragondamselflies" with about 13.5 cm wing span and a total body length of about 9 cm; wings very elongate and apically falcate; both pairs of wings of very similar size, shape, and venation; basal space free; discoidal cell indistinctly divided into hypertriangle and triangle by a crossvein that is not ending at the distal angle of triangle; hypertriangle and triangle each divided by a crossvein (autapomorphy, unlike other Stenophlebiidae); subdiscoidal cell with a single row of cells; triangles and subdiscoidal cells not transverse, because veins MP+Cu and AA are nearly straight (symplesiomorphy with *Prostenophlebia* and *Hispanostenophlebia*); nodal vein as in *Stenophlebia latreillei* with 1–2 postnodal crossveins above it, but none below it; subnodus elongate (about as long as nodal veinlet) but with only one crossvein above it and none below it; in the male holotype RP2 originates at subnodus in all four wings (symplesiomorphy with *Prostenophlebia* and *Cretastenophlebia*, unlike *Hispanostenophlebia* and *Stenophlebia*, which possess the characteristic "stenophlebiid oblique veinlet" beneath the subnodus between RP1 and RP2), while in the female allotype the "stenophlebiid oblique veinlet" is completely absent only in the right forewing, very tiny and indistinct in the right hind wing, but very distinct with two "origins" of RP2 in the left fore- and hind wing (consequently this feature seems to be much more variable than previously believed!); origins of RP and MA widely separated in arculus, with RA originating midway between MA and RA;



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Figs. 13–14. *Santanagrion longipes* n. gen., n. sp., holotype; SMNS 66803b.

three rows of cells in basal area of postdiscoidal space in both pairs of wings (autapomorphy, unlike other Stenophlebiidae, maybe except *Hispanostenophlebia*, of which the forewing is still unknown); Mspl well-defined; primary antenodals Ax1 and Ax2 as in *Cretastenophlebia*, with Ax0 in relatively distal position; no accessory antenodal crossveins between Ax0 and Ax1, and only a single secondary antenodal between Ax1 and Ax2 (symplesiomorphy with *Cretastenophlebia*); pterostigmata very elongate (covering 6–7 cells) and unbraced; distinct oblique vein between RP1 and IR1, about midway between origin of IR1 and pterostigma; no distinct lestine oblique vein 'O'; both wings are strongly petiolated with a very long petiole and thus much reduced submedian area even in the forewing (autapomorphic difference to *Stenophlebia*, maybe similar to *Hispanostenophlebia* of which the forewing is unknown); the female has a normally developed endophytic ovipositor as in Aeshnidae.

Discussion. – Fleck et al. (2003) suggested the following synapomorphies for Stenophlebioptera (Liassostenophlebiidae, Prostenophlebiidae, and Stenophlebiidae): Nodal and subnodal crossvein very oblique; CuAa with a broad area between the two most distal posterior branches; presence of straight supplementary longitudinal veins. All these characters are shared by *Cratostenophlebia*.

Within the Stenophlebioptera the Stenophlebioidea (Prostenophlebiidae and Stenophlebiidae) are characterized by the following synapomorphies according to Fleck et al. (2003): A long and not zigzagged (or only slightly zigzagged) secondary longitudinal convex vein in postdiscoidal area, parallel to MP; a long and not zigzagged concave Mspl; oblique vein "O" absent; wings elongate. Again all these characters are shared by *Cratostenophlebia*.

The family Stenophlebiidae is characterized by the following synapomorphies: (1) The secondary longitudinal convex vein in postdiscoidal area, parallel to MP, is not zigzagged and originates just distal of triangle; (2) the long nodal crossvein is covering more than 1–2 cells between RA and RP; (3) pterostigmata very long; (4) pterostigmata displaced basally; (5) forewing triangle long transverse; (6) hind wing subdiscoidal space transverse and divided by two or more crossveins; (7) more numerous and well defined straight intercalary secondary longitudinal veins reaching posterior wing margin; all wings very elongate and more or less falcate. Most of these character states are present in *Cratostenophlebia*. However, the zigzagged secondary vein parallel to MP, the less recessed pterostigmata (as in *Cretastenophlebia*), and the less transverse discoidal cells in both pairs of wings (as in *Hispanostenophlebia*), which are not clearly divided into triangle and hypertriangle (unlike in *Stenophlebia* s. str.), all seem to be plesiomorphic states that suggest a relatively basal position within Stenophlebiidae. On the other hand the extremely long wings and the presence of a "stenophlebiid oblique veinlet" (= real base of RP2) are derived characters that are still absent in the very basal genus *Cretastenophlebia*. However, the "stenophlebiid oblique veinlet" is very indistinct and only present in the female specimen (except in the right forewing), but not present at all in the male holotype.

Of all known stenophlebiid genera, the wing venation of *Cratostenophlebia* is most similar to *Hispanostenophlebia* (esp. petiole, arculus, discoidal and subdiscoidal cells, and nodal area) from the Lower Cretaceous of Spain. The position of the origin of RP at arculus and the long hind wing petiole are probable synapomorphies of *Cratostenophlebia* with *Hispanostenophlebia*. *Cratostenophlebia* differs from *Hispanostenophlebia* in the following characters: Wing length much larger; wings more elongate and falcate; "stenophlebiid oblique veinlet" less distinct (posterior prolongation of RP2 less than a cell in length) or absent; only a single crossvein is dividing the hypertriangle and the triangle; pterostigmata only covering 6–7 cells. These differences support the status as a distinct genus.

The absence of a male anal angle seems to be an autapomorphy of *Cratostenophlebia*, because a distinct anal angle is present in *Prostenophlebia*, *Cretastenophlebia* and *Stenophlebia*. Other genera without hind wing anal angle (e. g. *Hispanostenophlebia*) are only known from isolated wings, so that a determination of the sex is not possible.

Cratostenophlebia schwickerti Bechly, 2007
Figs. 15–28

Holotype: Male specimen no. 136 (old no. MSF Z109) in coll. WDC (Figs. 15–24).

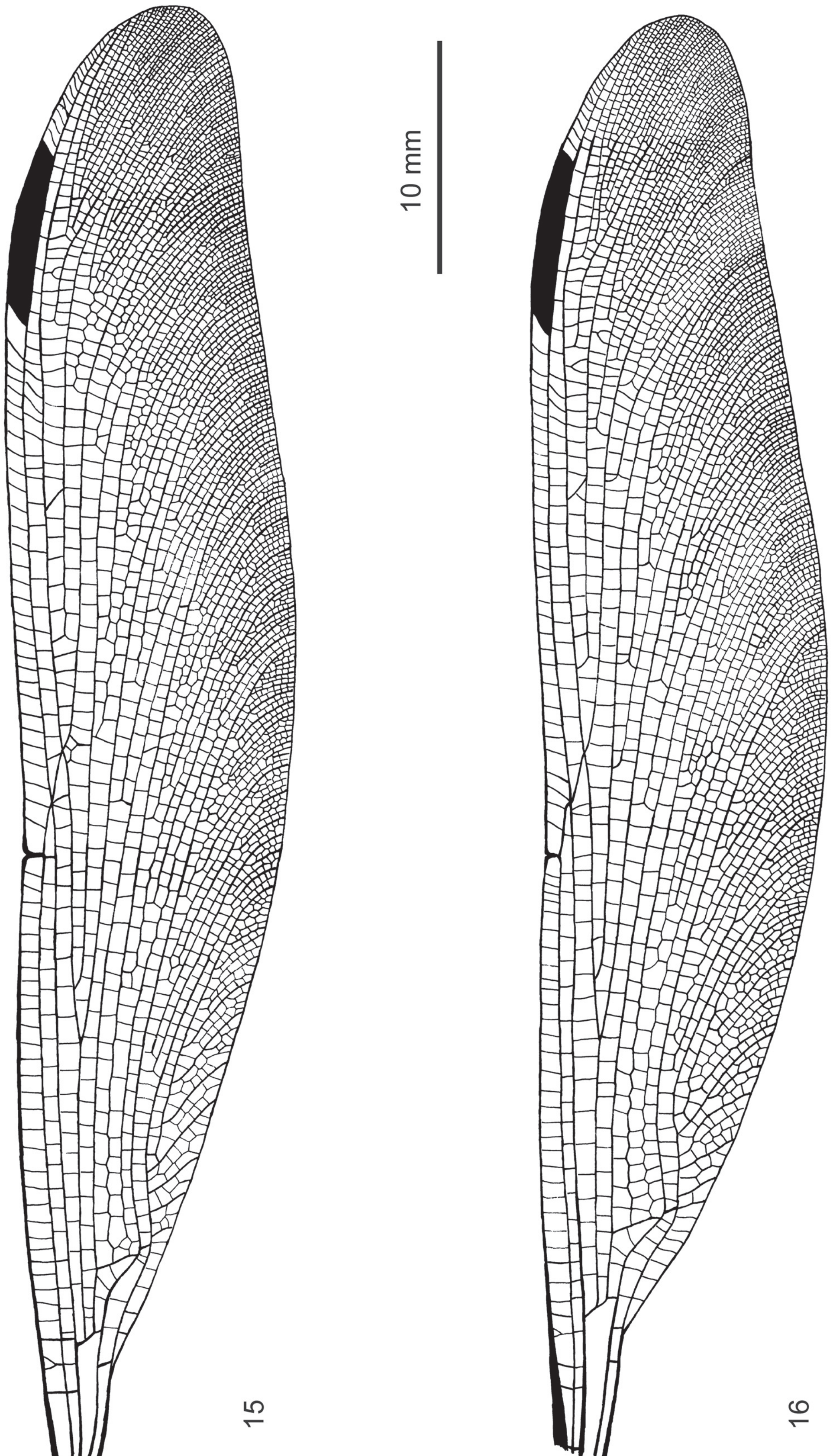
Allotype: Female specimen no. 137 (old no. MSF Z110) in coll. WDC (Figs. 25–28).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

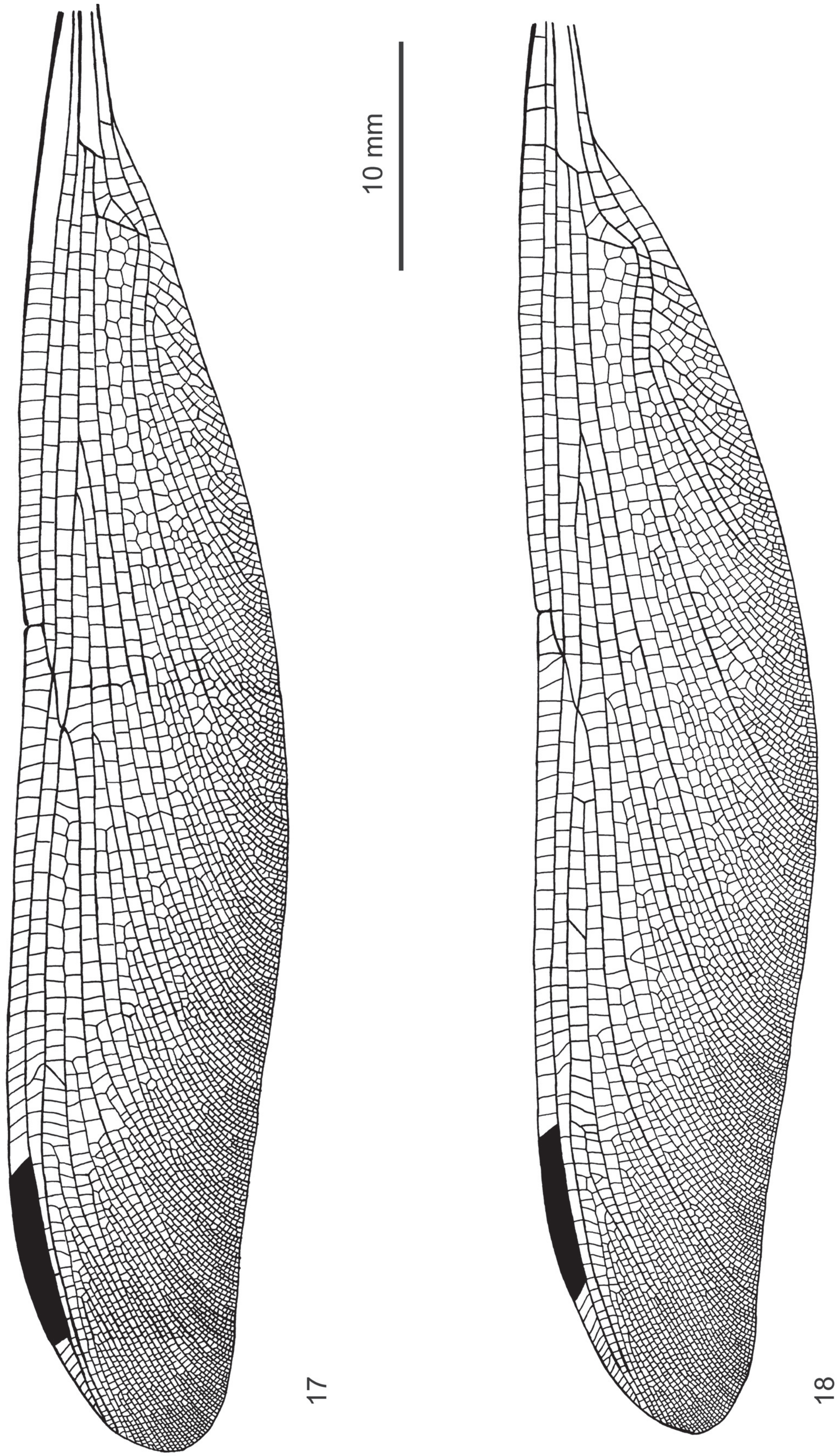
Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – As for genus since monotypic.

Redescription of male holotype (Figs. 15–24). – A completely and perfectly preserved male "dragondamselfly" with robust Anisoptera-like body (total body length 94 mm) and a wing span of 134 mm; globular head (width 8.9 mm) with very large compound eyes that are only separated by 0.8 mm distance (Fig. 23); legs very strong; cerci short and stout (about 2.3 mm long and 1.0 mm broad) (Fig. 24). Forewings 63 mm and 64 mm long respectively, and hind wings 63.5 mm and 64.2 mm long respectively; wing shape and venation more or less identical in forewings and hind wings (the hind wings only have a slightly broader cubital field); no secondary antenodals basal of Ax1 and only a single secondary antenod-



Figs. 15–16. *Cratostenophlebia schwickerti* BECHLY, 2007, male holotype; WDC Z109. – **Fig. 15**. Right forewing. **Fig. 16**. Right hind wing.

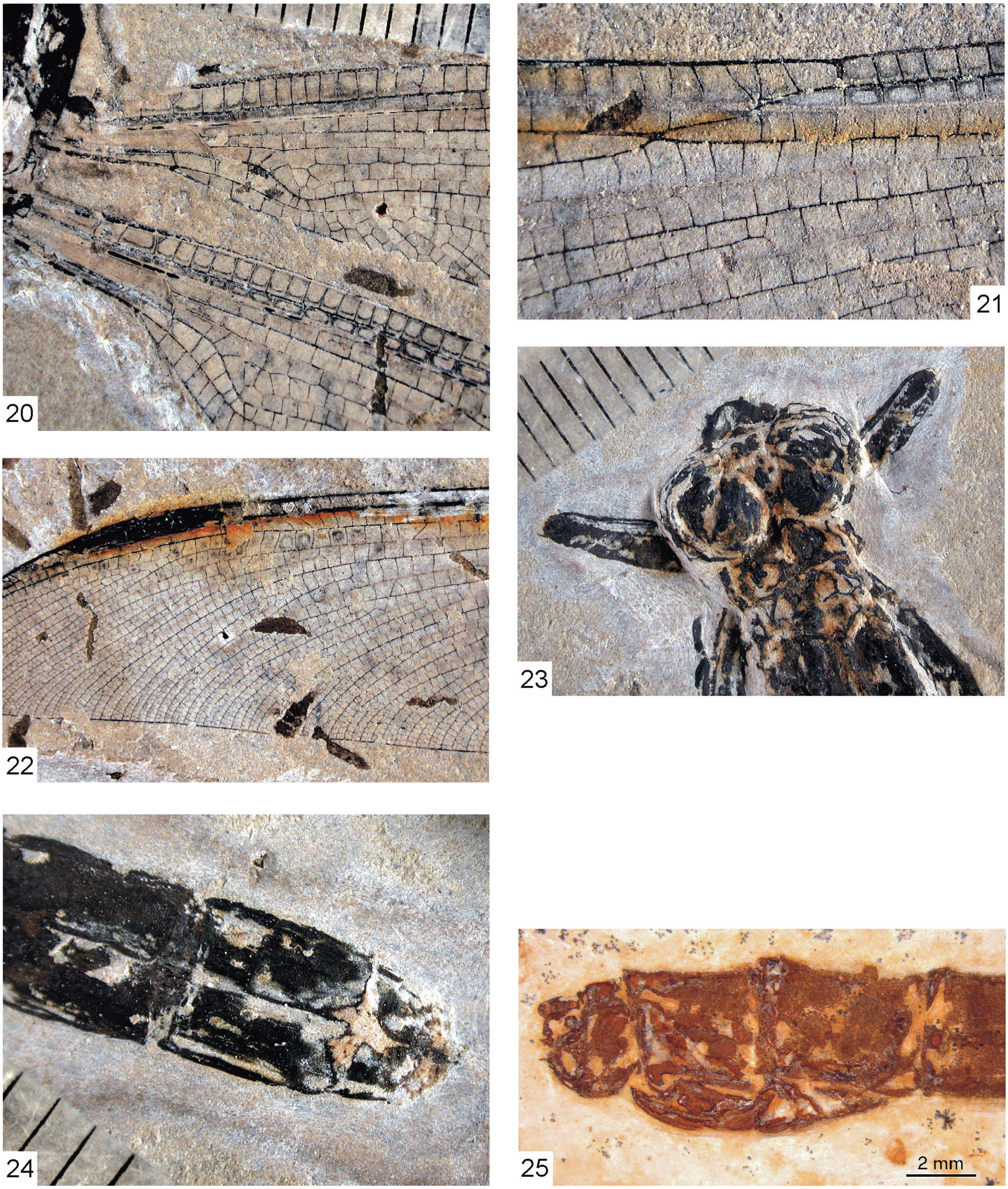


Figs. 17–18. *Cratostenophlebia schwickerti* BECHLY, 2007, male holotype; WDC Z109. – **Fig. 17**. Left forewing. **Fig. 18**. Left hind wing.

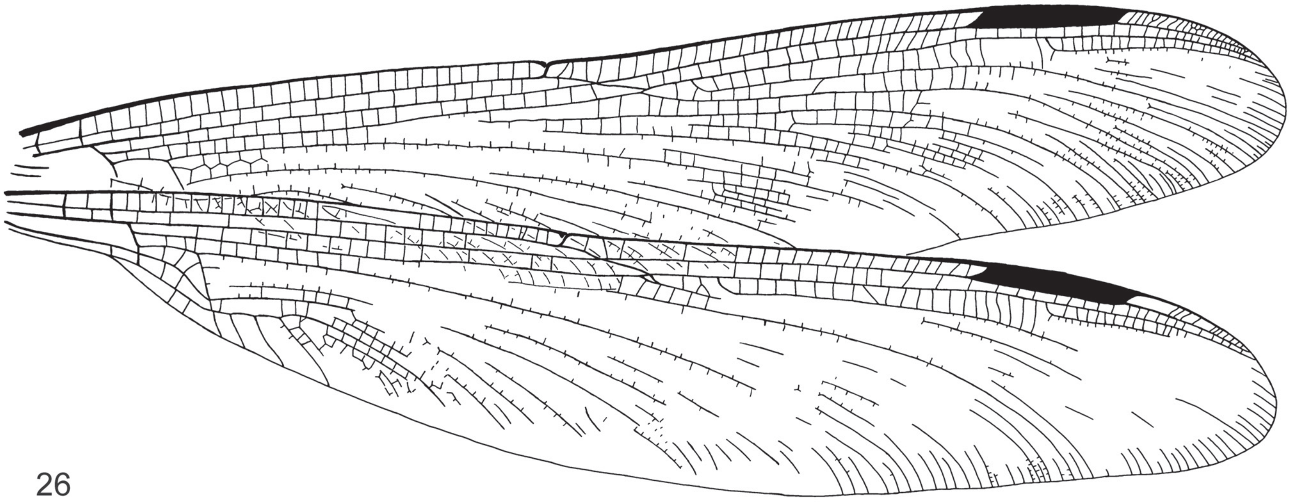
al between Ax1 and Ax2; Ax2 is very close to the arculus, but not strictly aligned with it; numerous non-aligned secondary antenodals distal of Ax2; nodus at 42–43 % of the wing length; nodal veinlet very oblique and long, covering two cells, and with 2–3 postnodal crossveins above it; subnodal veinlet very oblique and long, covering a single cell, and with a single postsubnodal crossvein above it; RP2 originating at subnodus without "stenophlebiid oblique veinlet"; IR2 originating on RP1/2; no lestine oblique vein between RP2 and IR2; distinct oblique vein between RP1 and IR1 at 2/3 of the distance between nodus and pterostigma; pterostigmata very long (covering 6.5 cells), unbraced, and slightly shifted basally; numerous very long and straight secondary longitudinal veins; distinct Mspl; postdiscoidal secondary vein parallel to MP is zigzagged; discoidal cell is divided by a crossvein, that does not precisely end at the distal angle, into an indistinct hypertriangle and triangle, that are each divided by a single crossvein; the triangle is not transverse in both pairs of wings; subdiscoidal cell divided by 5–6 crossveins into a single row of cells; three rows of cells directly distal of triangle in both pairs of wings; RP originating at arculus midway between the origin of MA and the fusion with RA; basal space free; there is no trace of an anal angle at the hind wing base.

Redescription of female allotype (Figs. 25–28). – A nearly complete and well-preserved female "dragondamselfly", of which only he prothorax, head and legs are missing. On abdominal segments seven and eight there is a distinctly endophytic ovipositor (Fig. 25), 7.4 mm long, which shows that this is a female specimen; the terminalia are very short. Forewings 61.3 mm and 62.1 mm long respectively, and left hind wing 62.4 mm long; wing shape and venation more or less identical in forewings and hind wings; the only differences to the wing venation of the holotype are the position of Ax2 somewhat basal of

Fig. 19. *Cratostenophlebia schwickert* BECHLY, 2007, male holotype; WDC Z109. – Scale: Ruler in mm.



Figs. 20–25. *Cratostenophlebia schwickert* BECHLY, 2007. – **Fig. 20**. Male holotype, right wing bases; WDC Z109. Scale: Ruler in mm. **Fig. 21**. Male holotype, nodus of left hind wing; WDC Z109. Without scale. **Fig. 22**. Male holotype, pterostigma of left hind wing; WDC Z109. Without scale. **Fig. 23**. Male holotype, head; WDC Z109. Scale: Ruler in mm. **Fig. 24**. Male holotype, terminalia; WDC Z109. Scale: Ruler in mm. **Fig. 25**. Female allotype, ovipositor; WDC Z110.



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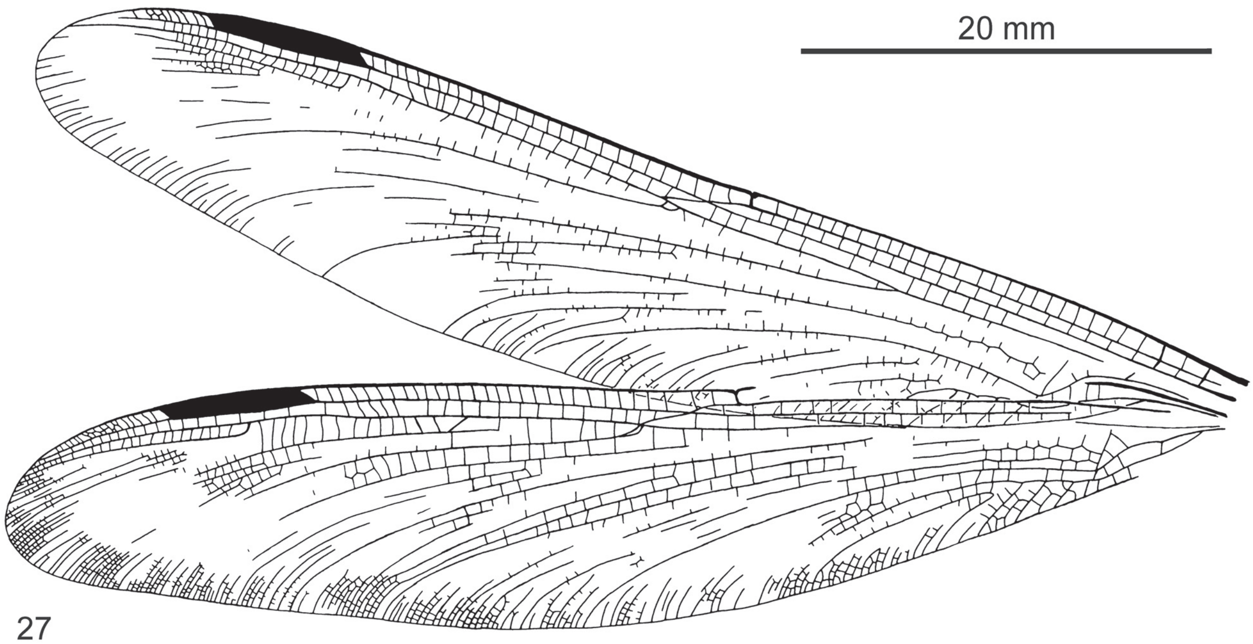

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Figs. 26–27. *Cratostenophlebia schwickerti* Bechly, 2007, female allotype; WDC Z110. – **Fig. 26**. Right wings. **Fig. 27**. Left wings.

the arculus and the origin of RP2, which is developed as a "stenophlebiid oblique veinlet" in the left pair of wings and in the right hind wing, but not in the right forewing; the posterior prolongation of RP2 is very short, less than a cell in length, giving the appearance of a bifurcated origin of RP2.

D i s c u s s i o n . – The deposition of the two type specimens was erroneously stated as SMNS by Bechly in Martill et al. (2007: 195). Both fossils are indeed deposited in coll. WDC.

The two type specimens belong to the best preserved Stenophlebiidae known and provide important information about this extinct Mesozoic family, which belongs to the stemgroup of Anisoptera, like the structures of the head, male and female terminalia, as well as the ovipositor.

Fig. 28. *Cratostenophlebia schwickerti* BECHLY, 2007, female allotype; WDC Z110.

3.1.4. Suborder Anisoptera SELYS, 1854
Family Cretapetaluridae NEL et al., 1998

Genus *Eotanypteryx* BECHLY, 2007

Typus generis: *Eotanypteryx paradoxa* BECHLY, 2007

Emended diagnosis. – This genus can be distinguished from the other two described cretapetalurid genera and species (*Cretapetalura brasiliensis* and *Cratopetalura petruleviciusi*) by the following combination of characters: wings about 45 mm long; stigmal brace midway between stigma and nodus, but well developed; hind wing triangle free; anal loop only 2-celled; true IR1 indistinct, pseudo-IR1 short and originating on RP1 beneath the distal end of pterostigma; pterostigma covering only 2.5 cells; only 1–2 secondary antenodals between Ax1 and Ax2; only 6–7 postnodal crossveins; only a single lestine oblique vein between RP2 and IR2 two cells distal of subnodus; subtriangle divided by a single crossvein into two cells.

Eotanypteryx paradoxa BECHLY, 2007
Figs. 29–34

Holotype: The male holotype specimen listed by BECHLY (2007: 202) with the old no. SMF Q90 has meanwhile received the new collection number SMF VI 853 (Figs. 29–32). The counter plate of this specimen is deposited at Senckenberg as well and has the collection number SMF VI 854 (old no. Q68) (Figs. 33–34).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – As for genus since monotypic.

Redescription of holotype (Figs. 29–34). – Plate and counter plate of the thorax fragment with all four wings (wing span 99 mm) of a male dragonfly. Forewing 45.1 mm long; basal space free; only 1–2 secondary antenodals between Ax1 and Ax2; Ax1 slightly distal of arculus, Ax2 on the level of the distal angle of triangle; about eight secondary non-aligned antenodals distal of Ax2; first postnodal crossvein slanted towards nodus; 6–7 postnodal crossveins, non-aligned with the postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basal-

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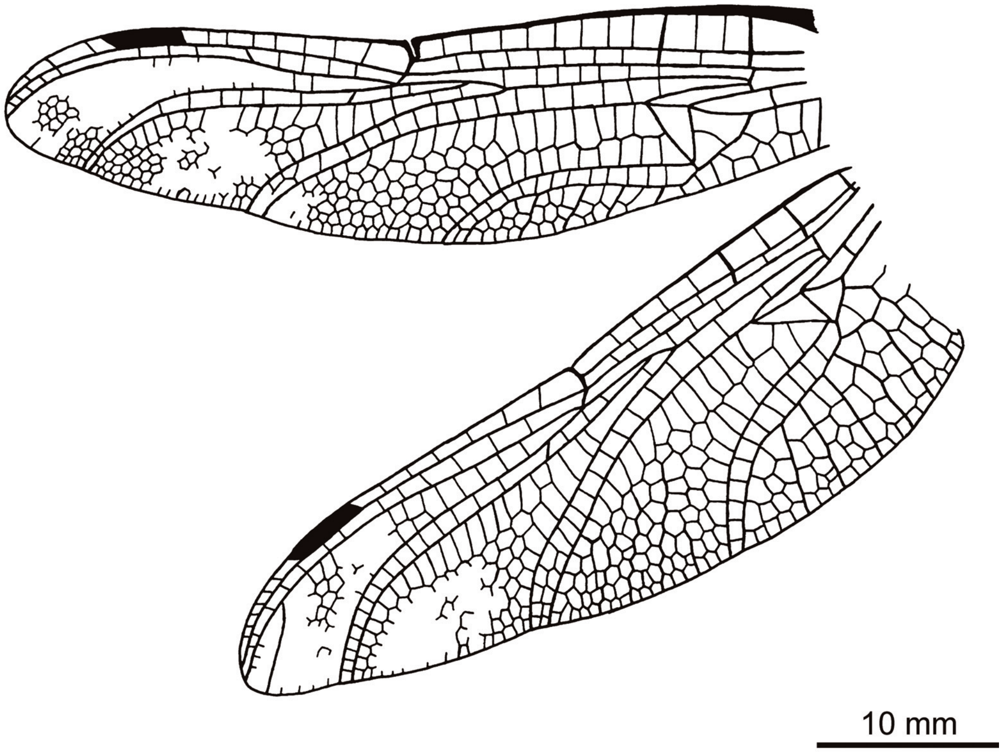

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Figs. 29–30. *Eotanypteryx paradoxa* Bechly, 2007, male holotype, left wings; SMF VI 853.

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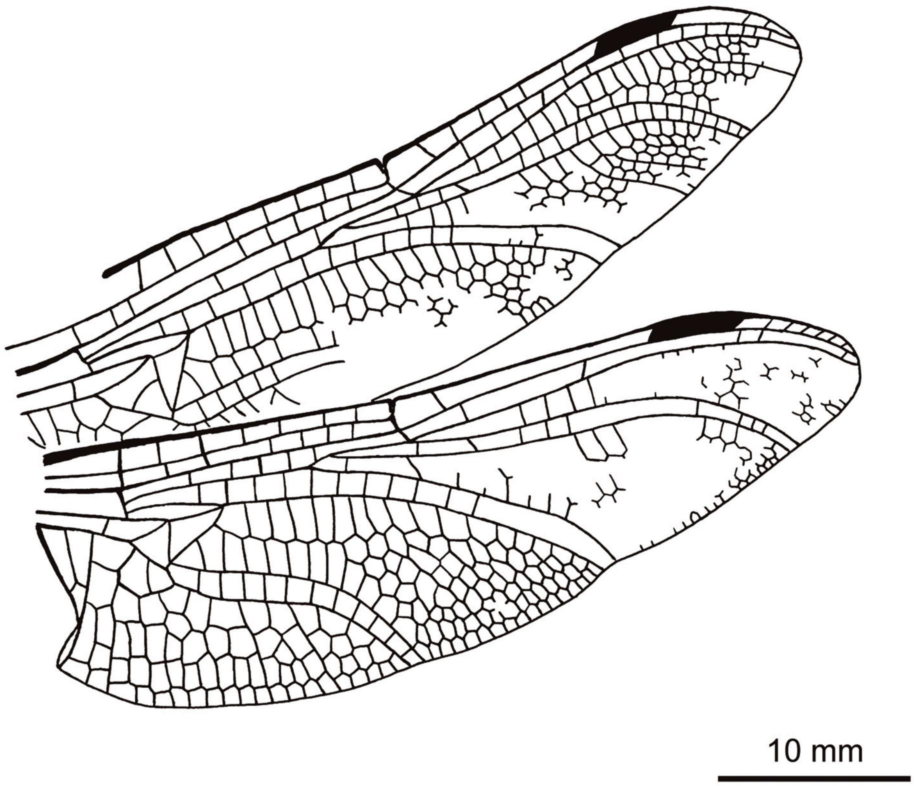

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Figs. 31–32. *Eotanypteryx paradoxa* BECHLY, 2007, male holotype, right wings; SMF VI 853.

Figs. 33–34. *Eotanypteryx paradoxa* Bechly, 2007, counter plate of male holotype; SMF VI 854. – **Fig. 33**. Left wings. **Fig. 34**. Right wings. – Without scale.

ly divergent, with a single row of cells in-between till the level of the stigmal brace; stigmal brace vein displaced basally midway between nodus and pterostigma; pterostigma somewhat shifted basally, covering 2.5 cells; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 two cells distal of subnodus; 2–3 bridge crossveins basal of oblique vein; RP3/4 and MA slightly undulate, but parallel, with two rows of cells in-between near the wing margin; no Rspl and no Mspl; six antefurcal crossveins; arculus angular with separate origins for RP and MA; posttrigonal space with two rows of cells, and with a weakly developed convex intercalary vein; hypertriangle free; triangle very transverse, narrow, and free; subtriangle widened and divided into two cells by a single "horizontal" crossvein; pseudo-analis hypertrophied; only a single row of cells between MP and CuA; CuA with five posterior branches (cubital area three cells wide).

Hind wing 43.9 mm long and max. 14.6 mm wide; basal space free; only a single secondary antenodal between Ax1 and Ax2; Ax1 slightly distal of arculus, Ax2 on the level of the distal angle of triangle; four secondary non-aligned antenodals distal of Ax2; first postnodal crossvein slanted towards nodus; about six postnodal crossveins, non-aligned with the postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally divergent, with a single row of cells in-between till the level of the stigmal brace; stigmal brace vein displaced basally midway between nodus and pterostigma; pterostigma somewhat shifted basally, covering about 2–3 cells; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 two cells distal of subnodus; three bridge crossveins basal of oblique vein; RP3/4 and MA slightly undulate, but parallel, with two rows of cells in-between near the wing margin; no Rspl and no Mspl; four antefurcal crossveins; arculus angular with separate origins for RP and MA; posttrigonal space with two rows of cells, and with a weakly developed convex intercalary vein; hypertriangle free; triangle elongate and free; distal side of triangle strongly slanted towards wing base and slightly kinked (however, the posttrigonal sector originating at the kink is relatively indistinct); subtriangle not widened and undivided; pseudo-analis distinct but not hypertrophied; gaff not elongated; only a single row of cells between MP and CuA; CuA with 5–6 posterior branches (cubital area four cells wide); anal loop posteriorly closed and 2-celled; a tree-celled anal triangle and a distinct anal angle are present and show that this is a male specimen.

D i s c u s s i o n . – The phylogenetic position was already discussed by Bechly (2007) and cannot be improved upon here.

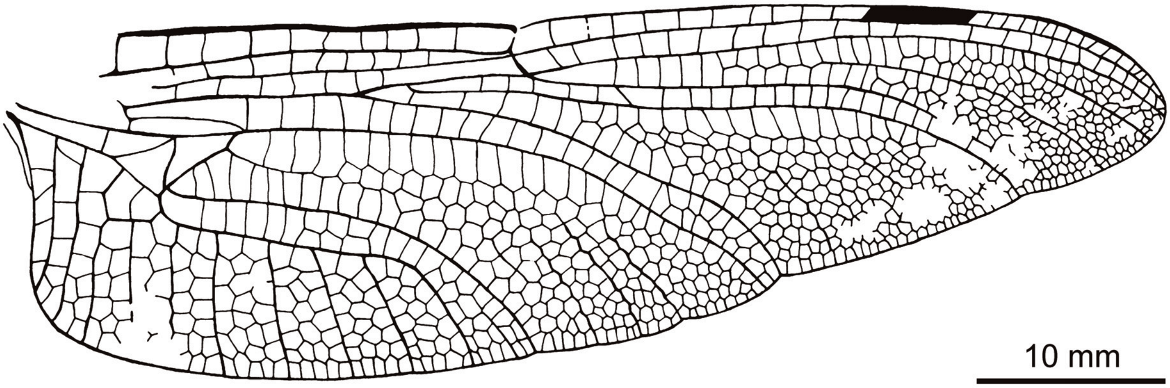
Genus *Cratopetalura* Nel & Bechly, 2009

T y p u s g e n e r i s : *Cratopetalura petruleviciusi* Nel & Bechly, 2009.

Cratopetalura petruleviciusi Nel & Bechly, 2009
Figs. 35–37

H o l o t y p e : Female specimen WDC CCFB-5, counter plate in coll. MSF (Fig. 37).

P a r a t y p e : Female specimen SMNS 66567 (Figs. 35–36).



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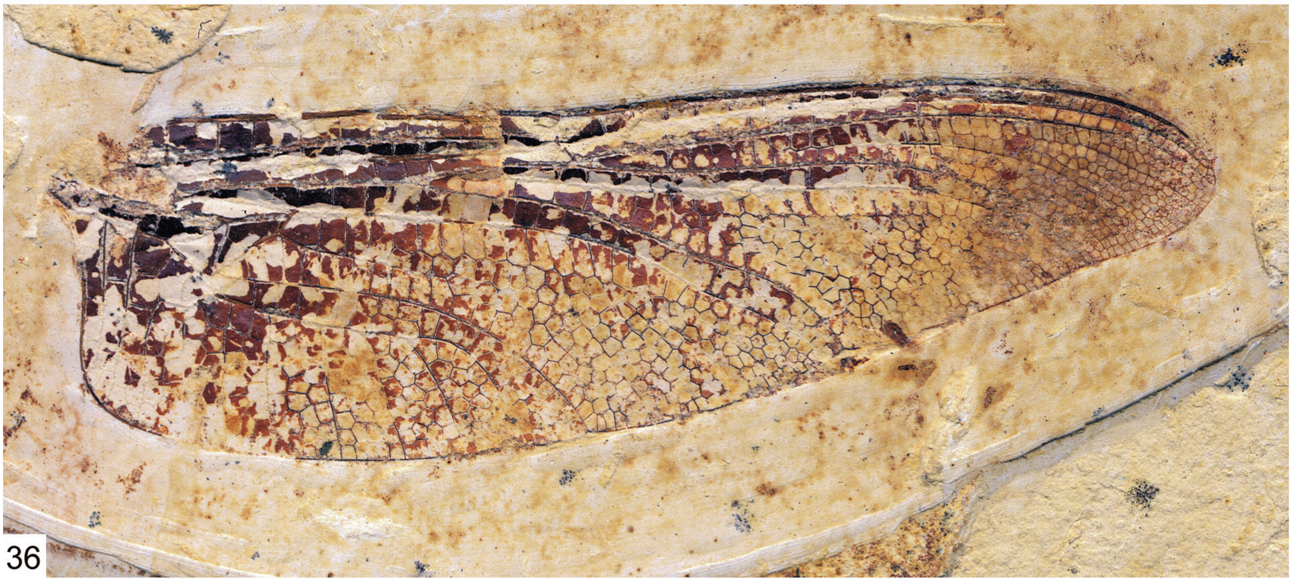

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Figs. 35–37. *Cratopetalura petrulevicius* NEL & BECHLY, 2009. – **Fig. 35**. Female paratype, right hind wing; SMNS 66567. **Fig. 36**. Female paratype, right hind wing; SMNS 66567. **Fig. 37**. Counter plate of female holotype, pair of hind wings; MSF, without number.

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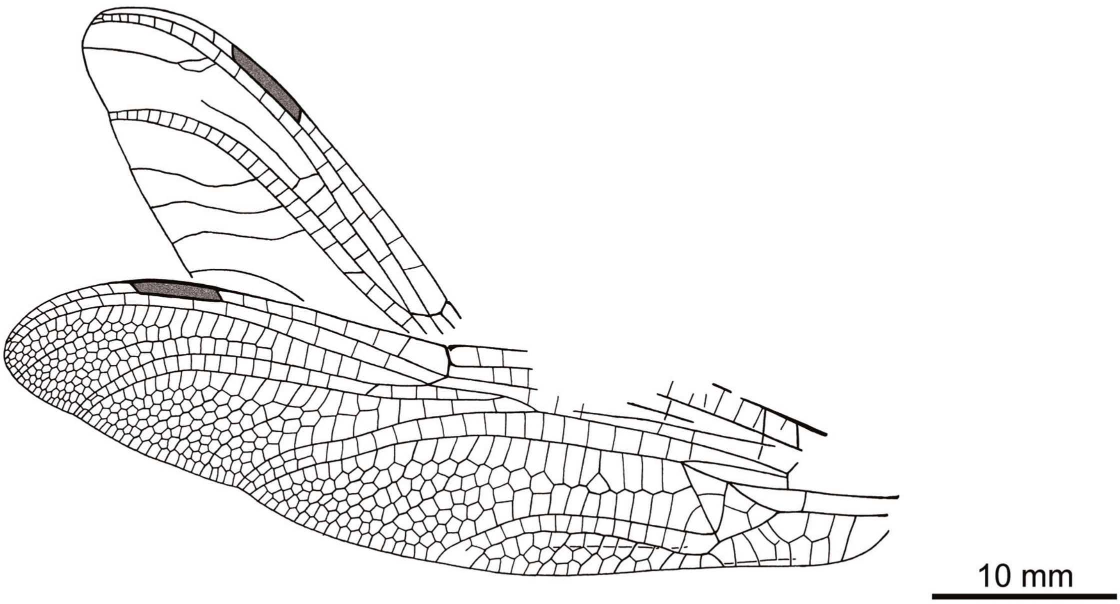

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Figs. 38–39. *Paraeschnopsis brasiliensis* n. gen., n. sp., holotype, right forewing in ventral aspect and left wing apex; SMNS 63648.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Discussion. – This second species of Cretapetaluridae that was mentioned but not named by BECHLY (2007: 218) was recently described as *Cratopetalura petruleviciusi* by NEL & BECHLY (2009) based on two type specimens. Recently, I discovered the counter plate of the holotype in coll. MSF (Fig. 37).

Family Mesuropetalidae BECHLY, 1996

Genus *Paraeschnopsis* n. gen.

Typus generis: *Paraeschnopsis brasiliensis* n. gen., n. sp.

Derivatio nominis: Named after the similarity to the fossil dragonfly genus *Aeschnopsis*.

Diagnosis (only forewing). – Wings nearly 50 mm long; pterostigma unbraced; only a single lestine oblique vein 2–3 cells distal of subnodus; four bridge crossveins; triangle very transverse and 2-celled; subtriangle 3-celled; posttrigonal area with two rows of cells; RP2 and IR2 closely parallel; IP1 long and zigzagged; pseudo-IR1 originating distal of pterostigma.

Discussion. – This new taxon would be the first record for the extinct Mesozoic family Mesuropetalidae outside the Old World. The tentative attribution to Mesuropetalidae is based on the overall similarity of the wing venation to the mesuropetalid genus *Aeschnopsis*, and on the following putative synapomorphies (compare the revision of Mesuropetalidae and *Aeschnopsis* by BECHLY et al. 2001): Arculus shifted very close to the first primary antenodal Ax1; RP2 and IR2 very closely parallel and converging near the posterior wing margin; characteristical structure of the transverse and 2-celled forewing triangle; RP1 and RP2 basally divergent. However, all these characters are highly homoplastic. The absence of a stigmal brace vein and a second lestine oblique vein are otherwise unknown from Mesuropetalidae and could be autapomorphies of *Paraeschnopsis* (or conflicting evidence).

Paraeschnopsis brasiliensis n. sp.
Figs. 38–39

Holotype: SMNS 63648 (old no. E100404) (Figs. 38–39).

Derivatio nominis: Named after Brazil, the country of origin.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 38–39). – A thorax fragment with attached wings that are partly superimposed. Forewing (right forewing in ventral aspect) 48.9 mm long; arculus apparently close to Ax1; first postnodal crossvein slanted towards nodus; six postnodal crossveins, non-aligned with the postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally divergent; pterostigma elongate, covering 2–3 cells, and clearly unbraced; primary IR1 long but zigzagged; pseudo-IR1 distinct but short, originating on RP1 distal of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 2–3 cells distal of subnodus; four bridge crossveins basal of oblique vein; RP3/4 and MA slightly undulate, but closely parallel, with two rows of cells in-between near the wing margin; no Rspl and no Mspl; seven antefurcal crossveins; arculus angular; origins of RP and MA close but separate at arculus; posttrigonal space with two rows of cells, and with a weakly developed convex intercalary vein; hypertriangle free; triangle very transverse, narrow, and divided by a single "horizontal" crossvein; subtriangle widened and divided into three cells; pseudo-analis hypertrophied; only a single row of cells between MP and CuA; CuA with five posterior branches (cubital area three cells wide).

Family Liupanshaniidae BECHLY et al., 2001

Genus *Paramesuropetala* BECHLY et al., 2001

Typus generis: *Paramesuropetala gigantea* BECHLY et al., 2001.

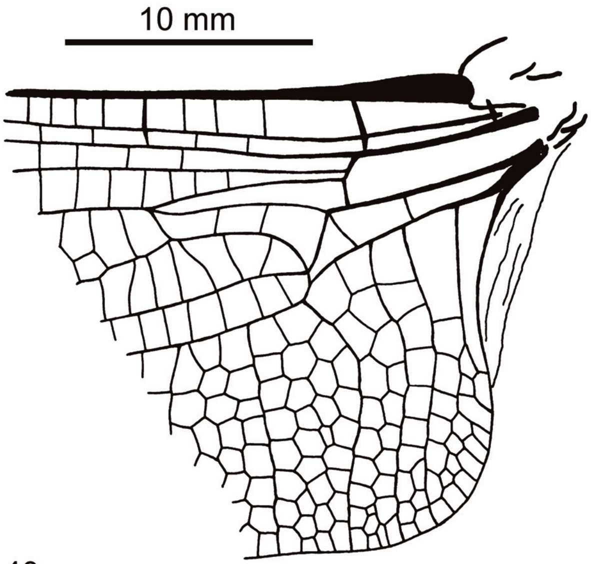
Emended diagnosis. – Forewing 70 mm long; posttrigonal area with three rows of cells; hypertriangle free; triangle and subtriangle 3-celled; RP1 closely parallel to RA with only a single row of cells in-between till the pterostigma; pterostigma five cells long and braced; RP2+IR2 and RP3/4+MA are strongly undulate; a single lestine oblique vein 1.5 cells distal of subnodus. Hind wing 19 mm wide; hypertriangle free; triangle very elongate and divided by two crossveins; distal side MAb of triangle strongly sigmoidal; subtriangle small and undivided; pseudo-analis not developed; cubital area with eight rows of cells. In both wings there are about 3–4 antenodals between Ax1 and Ax2, and there is a strong posttrigonal sector originating at the triangle.

Paramesuropetala gigantea BECHLY et al., 2001
Figs. 40–41

Holotype: MNHN-LP.R.55194.

Further material: Female specimen SMNS 66613 (Figs. 40–41).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.



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Figs. 40–41. *Paramesuropetala gigantea* Bechly et al., 2001, female, hind wing base; SMNS 66613.

L o c u s t y p i c u s : Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

D i a g n o s i s . – As for genus since monotypic.

D e s c r i p t i o n o f s p e c i m e n S M N S 6 6 6 1 3 (Figs. 40–41). – A well-preserved basal fragment of the hind wing of a very large female dragonfly. Width 19.0 mm; Ax1 at the arculus; at least three antenodals between Ax1 and Ax2; Ax2 at the level of the distal angle of triangle; secondary antenodals not aligned; seven antefurcal crossveins are visible; arculus angular with separate origins of RP and MA; hypertriangle undivided; triangle very elongate and divided by two vertical crossveins into three cells; upper side of triangle undulate; distal side of triangle strongly sigmoidal; strong posttrigonal sector originating at kink of triangle; two rows of cells in posttrigonal area directly distal of triangle; subtriangle small and undivided; pseudo-analis not developed (only a oblique crossvein is basally closing the subtriangle); CuA with strong posterior branches (cubital area eight cells wide); three secondary branches of AA between CuAb and wing base; anal loop absent or not closed. The rounded hind wing base strongly suggests that this is a female specimen. There is a large membranule at the base of the wing.

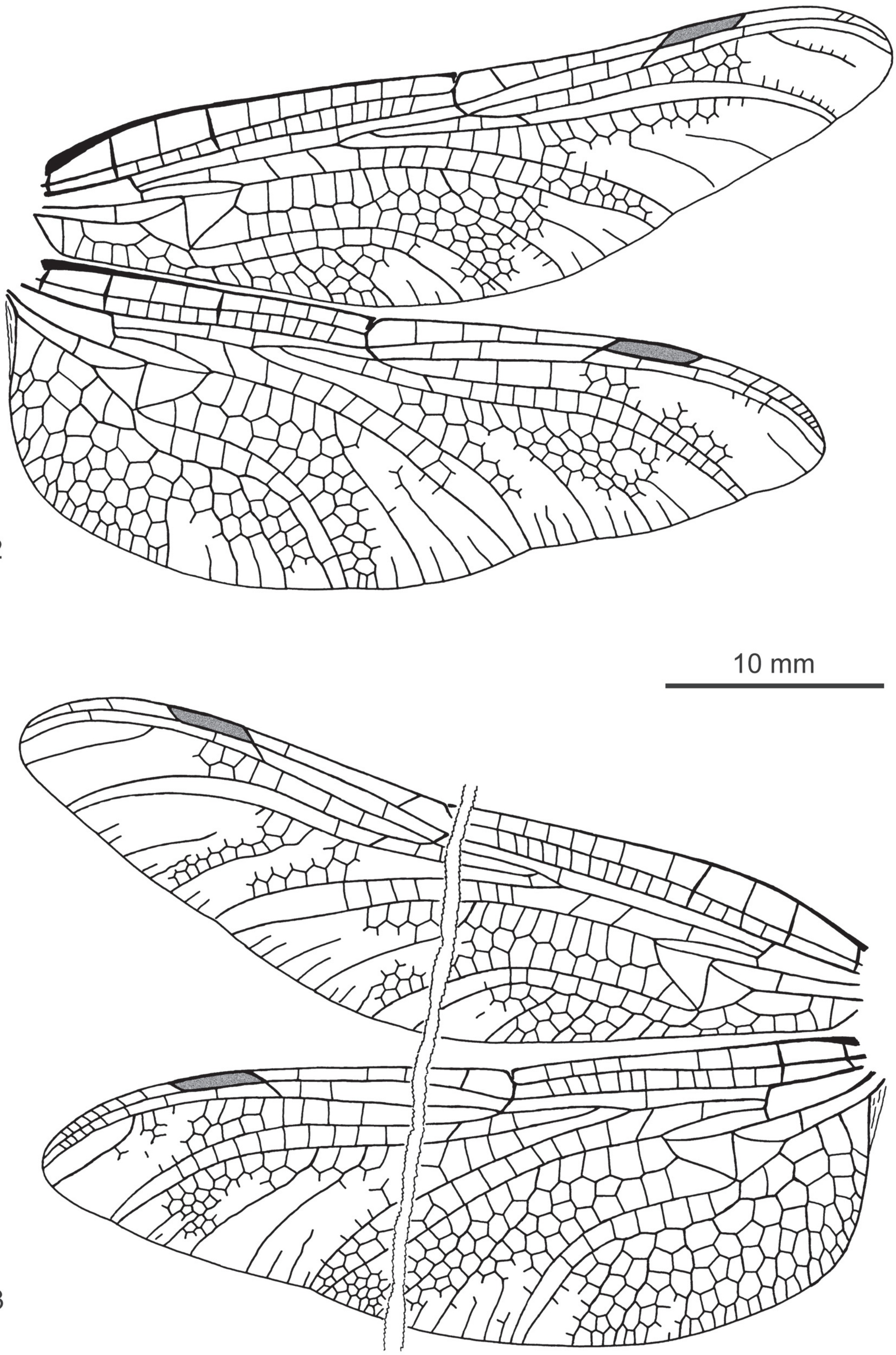
D i s c u s s i o n . – *Paramesuropetala gigantea* was first described by Bechly et al. (2001), based on a single isolated forewing as holotype. Bechly (2007, fig. 11.13a) featured a photo of the first record of a hind wing of this species. A drawing of this hind wing fragment is here provided together with a description and an emended diagnosis of this species. At Senckenberg museum there is a yet undescribed new specimen of this species with collection number SMF VI 855 (old no. O36) that has both pairs of wings preserved. This latter specimen confirms the attribution and conclusion of Bechly (2007: 203).

Family Proterogomphidae Bechly et al., 1998
Subfamily Cordulagomphinae Carle & Wighton, 1990

D i s c u s s i o n . – The following apomorphic characters of Proterogomphidae – Cordulagomphinae are also present in Araripegomphidae: Triangles undivided; distinct “cordulegastrid gap”; pseudo-IR1 originating beneath distal side of pterostigma; compound eyes approximated. On the other hand Araripegomphidae still have four antefurcals in the hind wing, three crossveins beneath the pterostigmata, the first postnodal not distinctly slanted towards nodus, and several other plesiomorphies (e. g. a long ovipositor) that seem to exclude a sistergroup relationship with Cordulagomphinae within Hagenioidea – Proterogomphidae. Nevertheless such a relationship remains a possibility that should be further evaluated.

Genus *Cordulagomphus* Carle & Wighton, 1990

T y p u s g e n e r i s : *Cordulagomphus tuberculatus* Carle & Wighton, 1990.



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Figs. 42–43. *Cordulagomphus hanneloreae* BECHLY, 2007, female holotype; SMNS 66591. – **Fig. 42**. Right wings. **Fig. 43**. Left wings.

Fig. 44. *Cordulagomphus hanneloreae* Bechly, 2007, female holotype; SMNS 66591.

Cordulagomphus hanneloreae Bechly, 2007
Figs. 42–45

Holotype: Female specimen SMNS 66591 (old no. O21) (Figs. 42–45).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Emended diagnosis. – Largest *Cordulagomphus* species (wings about 40 mm long); pseudo-IR1 originating on RP1 far distal of pterostigma; between Ax1 and Ax2 there is one (forewing) or two (hind wing) antenodal of the first row, and four (forewing) or 4–5 (hind wing) of the second row; hind wing cubital area with five rows of cells; pterostigmata in a more basal position than in the other species.

Redescription of holotype (Figs. 42–45). – A female dragonfly with all four wings, head and pterothorax preserved (a crack is running through the left pair of wings). The head is 8.1 mm wide and shows distinctly separated eyes, but this is insignificant because the head seems to be preserved in antero-ventral aspect (Fig. 45); wing span about 86 mm.

Forewing 40.5 mm long; basal space free; between Ax1 and Ax2 there is only one secondary antenodal in the first row, but four in the second row; Ax1 slightly basal of arculus, Ax2 on the level of the distal angle of triangle; about seven secondary antenodals distal of Ax2 in the first row, non-aligned with the 12 antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; four (maybe five) postnodal crossveins, non-aligned with the postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 very close basally, with a single row of cells in-between till the level of the pterostigma; pterostigma in a more basal position, strongly braced and with a single crossvein beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 far distal of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel, with two rows

Fig. 45. *Cordulagomphus hanneloreae* Bechly, 2007, female holotype, head in ventral aspect; SMNS 66591.

of cells between their distal parts; no Rspl and no Mspl; three antefurcal crossveins (the distal two are oblique); arculus angular with separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle transverse and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; an elongate cell in the anal area; CuA with five posterior branches (cubital area 1–4 cells wide).

Hind wing 38.8 mm long and 13.5 mm wide; basal space free; between Ax1 and Ax2 there are two secondary antenodals in the first row, but five in the second row; Ax1 slightly basal of arculus, Ax2 on the level of the distal angle of triangle; about four secondary antenodals distal of Ax2 in the first row, non-aligned with the seven antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; four (maybe five) postnodal crossveins, non-aligned with the postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma in a more basal position, strongly braced and with a single crossvein beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 far distal of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel, with two rows of cells between their distal parts; no Rspl and no Mspl; only two antefurcal crossveins (the distal one is strongly oblique); arculus angular with widely separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle elongate and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; gaff not elongated; only a single row of cells between MP and CuA; CuA with six posterior branches (cubital area five cells wide); anal loop longitudinal elongate, posteriorly closed, and 2-celled; the anal margin is rounded, thus it is a female specimen. There is a narrow membranule at the wing base.

D i s c u s s i o n . – The structure of the pterostigma and the "cordulegastrid gap" in both wings, of the antefurcal crossveins and the anal loop in the hind wing, and of the elongate anal cell in the forewing are synapomorphies that clearly confirm the attribution of this species to the genus *Cordulagomphus*.

Cordulagomphus winkelhoferi Bechly, 2007
Figs. 46–48

H o l o t y p e : Male hind wing SMNS 66607 (old no. M58) (Figs. 46–47).

P a r a t y p e : Male hind wing no. 513 (old no. C20) at MURJ (Fig. 48).

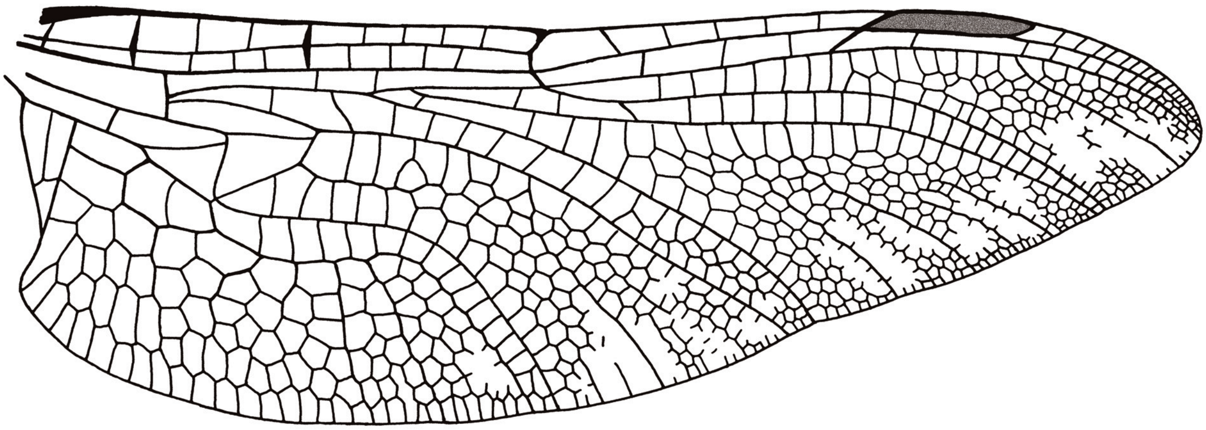
S t r a t u m t y p i c u m : Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

L o c u s t y p i c u s : Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

E m e n d e d d i a g n o s i s (hind wing). – Second largest *Cordulagomphus* species (wing about 35 mm long); pseudo-IR1 originating on RP1 beneath distal end of pterostigma; between Ax1 and Ax2 there are two antenodals of the first row and three of the second row; hind wing cubital area with six rows of cells; pterostigmata in a more basal position than in the other species (except for *C. hanneloreae*, which has the pterostigma even more basal); wing venation even more dense, thus with a distinctly higher number of cells, than in *C. hanneloreae*.

R e d e s c r i p t i o n o f h o l o t y p e (Figs. 46–47). – A well-preserved hind wing of a female dragonfly; length 34.2 mm; basal space free; between Ax1 and Ax2 there are two secondary antenodals in the first row, but three in the second row; Ax1 is distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; about four secondary antenodals distal of Ax2 in the first row, non-aligned with the four (three in he paratype) antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; five postnodal crossveins, non-aligned with the three postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent, but with only a single row of cells in-between till the pterostigma; pterostigma in a more basal position, strongly braced and with a single crossvein beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath the distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel, with 2–3 rows of cells between their distal parts; no Rspl and no Mspl; only two antefurcal crossveins (the distal one is strongly oblique); arculus slightly angular with separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle elongate and free, with a strongly kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; gaff not elongated; only a single row of cells between MP and CuA; CuA with six posterior branches (cubital area six cells wide); anal loop longitudinal elongate, posteriorly closed, and 2-celled; basal of anal loop there are two elongated cells above each other (also in the paratype); there is a 3-celled anal triangle and a distinct anal angle, thus it is a male specimen.

D i s c u s s i o n . – The paratype (Fig. 48) was already featured and discussed by Bechly (1998: 51, figs. 31–32) as putative new Cordulagomphinae. As already indicated by Bechly (2007: 211) the antenodal region was incorrectly figured in the drawing of Bechly (1998, fig. 31). Therefore,



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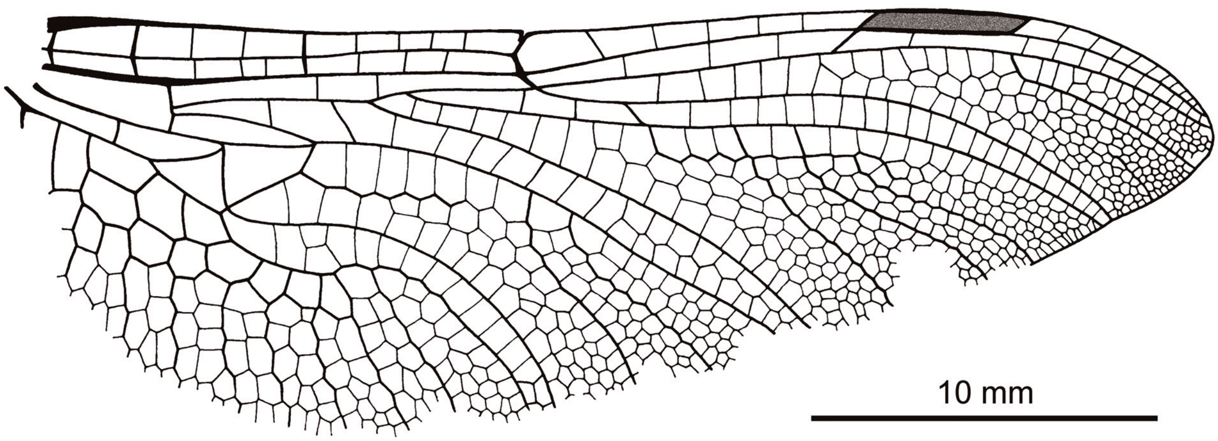

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Figs. 46–48. *Cordulagomphus winkelhoferi* Bechly, 2007. – **Fig. 46**. Male holotype, right hind wing; SMNS 66607. **Fig. 47**. Male holotype, right hind wing; SMNS 66607. **Fig. 48**. Male paratype, right hind wing (corrected drawing); MURJ 513.

a corrected drawing is here provided (Fig. 48). Contrary to the statements in BECHLY (1998, 2007), a comparison with the anal area of the male holotype shows that the paratype is not a female hind wing (and thus not an allotype), but also a male hind wing.

Again, the structure of the pterostigma and the "cordulegastrid gap" in both wings, of the antefurcal crossveins and the anal loop in the hind wing, and of the elongate anal cell in the forewing are synapomorphies that clearly confirm the attribution of this species to the genus *Cordulagomphus*.

Genus *Paracordulagomphus* n. gen.

Typus generis: *Paracordulagomphus aberrans* n. sp.

Derivatio nominis: Named after the overall similarity and probable relationship with the fossil dragonfly genus Cordulagomphus.

Diagnosis. – Quite similar in size and venation to large specimens of *Cordulagomphus tuberculatus* CARLE & WIGHTON, 1990, but the following differences distinguish this new taxon from *Cordulagomphus* and other genera: compound eyes more strongly separated; 2–3 cells distal of triangle there are three rows of cells in the hind wing posttrigonal area; 1–2 crossveins beneath pterostigmata; only a single antenodal in both rows between Ax1 and Ax2; only a single antefurcal crossvein in hind wings, which is not oblique; anal loop elongate but unicellular; RP3/4 and MA distally more or less divergent, with 5–11 cells in-between at the wing margin.

Discussion. – Most probably this new genus and species also belongs to Cordulagomphinae. The following synapomorphies are shared with Hagenioidea: Branching of RP at midfork symmetrical; distal side (MAb) of triangle strongly angulate (esp. in hind wings), correlated with a distinct posttrigonal sector. The following synapomorphies are shared with Proterogomphidae within Hagenioidea: Triangles secondarily unicellular; only two cells beneath pterostigmata; vein pseudo-IR1 very distinct and originating on RP1 beneath the distal side of the pterostigmata; anal loop longer than wide and with only one or two cells; forewings with a large elongated cell beneath the submedian area. Finally, the following synapomorphies are shared with Cordulagomphinae within Proterogomphidae: The most basal postnodal crossvein is very oblique; only 1–2 antefurcal crossveins in hind wings, and 2–3 in forewings; anal loop more distinctly longitudinal elongate; presence of a "cordulegastrid gap" of crossveins in the distal part of the antesubnodal area.

The plesiomorphic presence of more than a single crossvein beneath the pterostigma of the type-species might suggest a basal position within Cordulagomphinae, while the absence of the oblique distal antefurcal crossvein in hind wings could be an autapomorphic reduction. Also the distally divergent veins RP3/4 and MA in the forewings seem to be an autapomorphy of this new genus.

VERNOUX et al. (2010) described a new proterogomphid genus *Lingomphus* from the Lower Cretaceous of Liaoning in China. This genus seems to be even more basal than *Paracordulagomphus* n. gen. as is suggested by the presence of four crosveins beneath the pterostigma. It furthermore differs from *P. aberrans* n. sp. by the distally divergent veins RP1 and RP2, and from *P. divergens* n. sp. by the less divergent veins RP3/4 and MA. It also differs from both species in the presence of more rows of cells in the posttrigonal area.

Paracordulagomphus aberrans n. sp.
Figs. 49–60

Holotype: Male specimen SMF VI 1043 (old no. N40) (Figs. 49–54).

Allotype: Female specimen SMF VI 1044 (old no. Q86) (Figs. 55–58).

Paratype: Male specimen SMNS 66614 (old no. M67) (Figs. 59–60).

Derivatio nominis: Named after the aberrant wing venation for a Cordulagomphinae (viz. the distally divergent veins RP3/4 and MA).

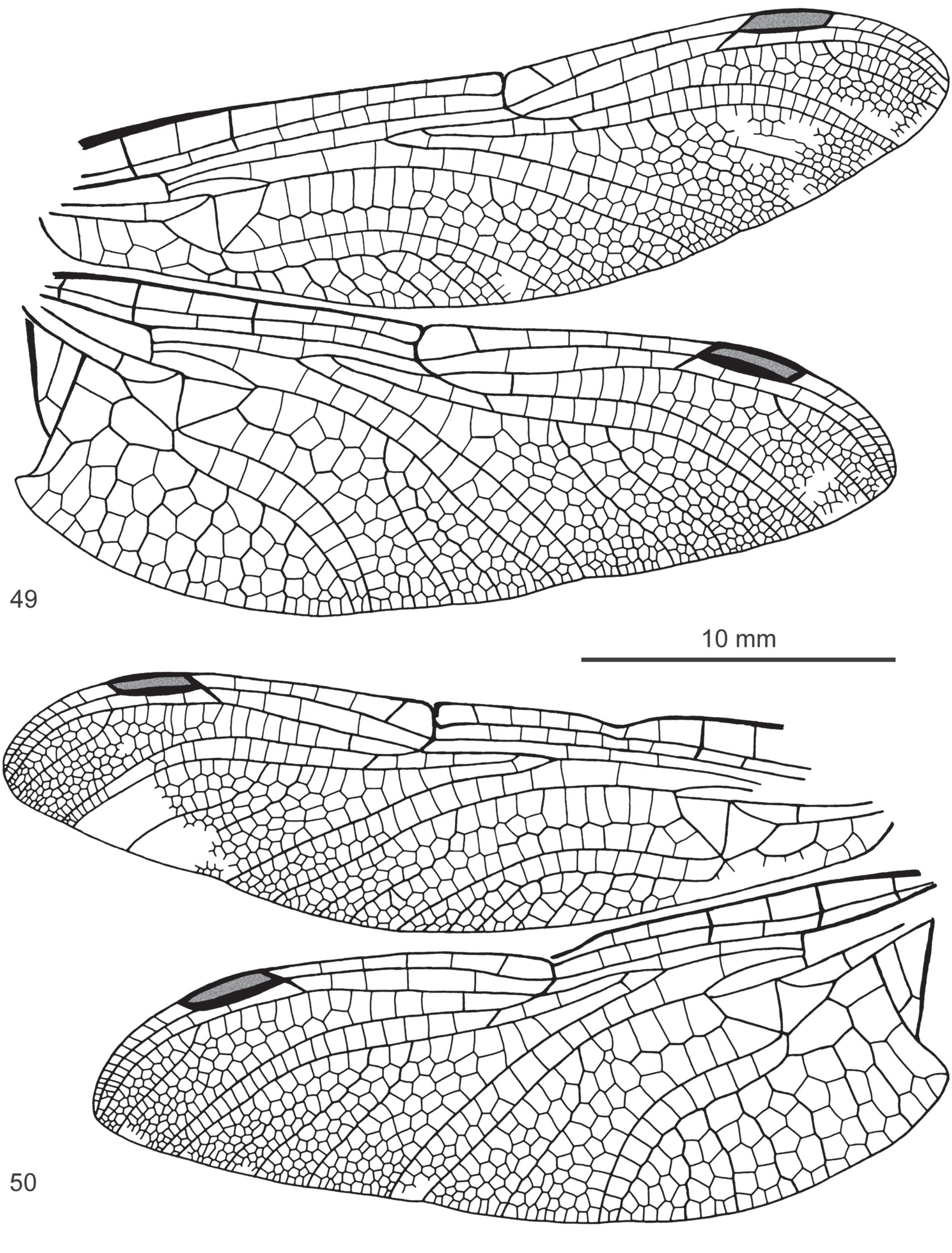
Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis (forewing). – In forewings RP3/4 and MA are less strongly divergent than in *P. divergens* n. sp., only separated by 5–7 cells at the wing margin (instead of 11); RP2 and IR2 are closely parallel in forewings, with only a single row of cells in-between; 1–2 crossveins beneath pterostigmata.

Description of male holotype (Figs. 49–54). – A complete and perfectly preserved male dragonfly; body length 53.3 mm; width of head 7.0 mm; the compound eyes are approximated but still distinctly separated (Fig. 53); the anal appendages (cerci) are 2.0–2.5 mm long and slender (Fig. 54); wing span 61.0 mm.

Forewing 29.5 mm long; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; about seven secondary antenodals distal of Ax2 in the first row, non-aligned with the seven antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; six postnodal crossveins, non-aligned with the four postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally divergent; pterostigma strongly braced and with two crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a sin-

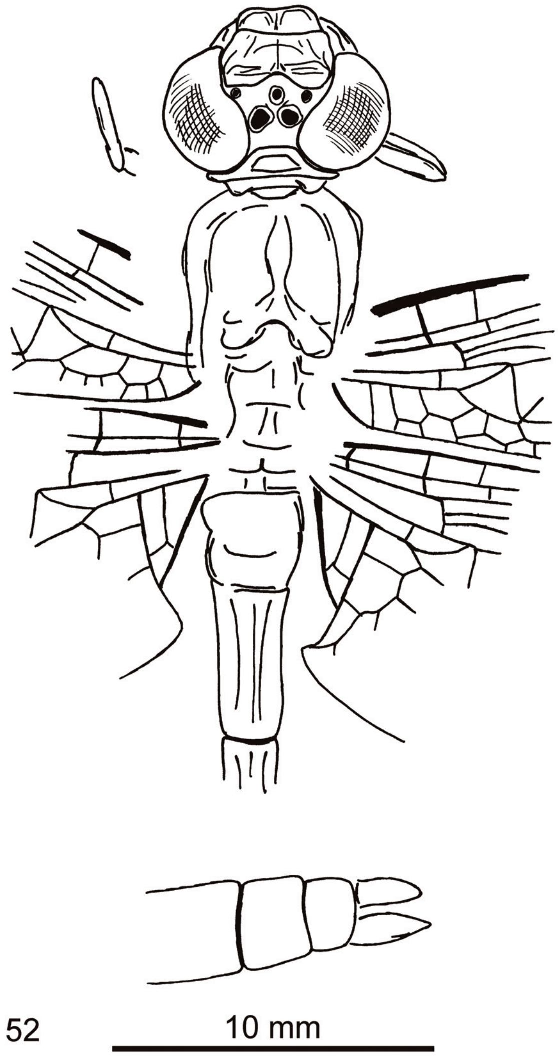


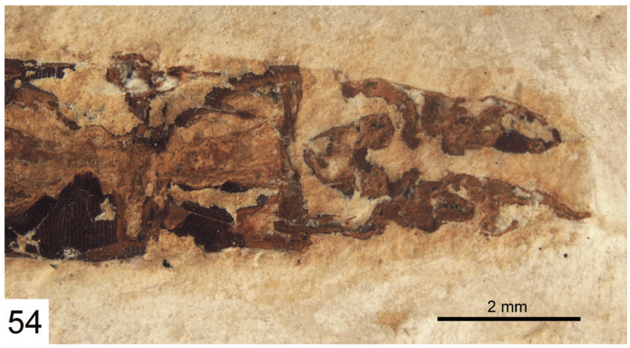
Figs. 49–50. *Paracordulagomphus aberrans* n. gen., n. sp., male holotype; SMF VI 1043. – **Fig. 49**. Right wings. **Fig. 50**. Left wings.

Fig. 51. *Paracordulagomphus aberrans* n. gen., n. sp., male holotype; SMF VI 1043.

gle lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; 2–3 bridge crossveins basal of oblique vein; RP3/4 and MA distally divergent, with 5–7 cells between them at wing margin; no Rspl and no Mspl; three antefurcal crossveins; arculus slightly angular with widely separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle transverse and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; an elongate cell in the anal area; CuA with 7–8 posterior branches (cubital area 3–4 cells wide).

Hind wing 28.6 mm long and 9.8 mm wide; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; about three secondary antenodals distal of Ax2 in the first row, non-aligned with the three antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; 5–6 postnodal crossveins, non-aligned with the four postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma strongly braced and with 1–2 crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2, except close to wing margin; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two



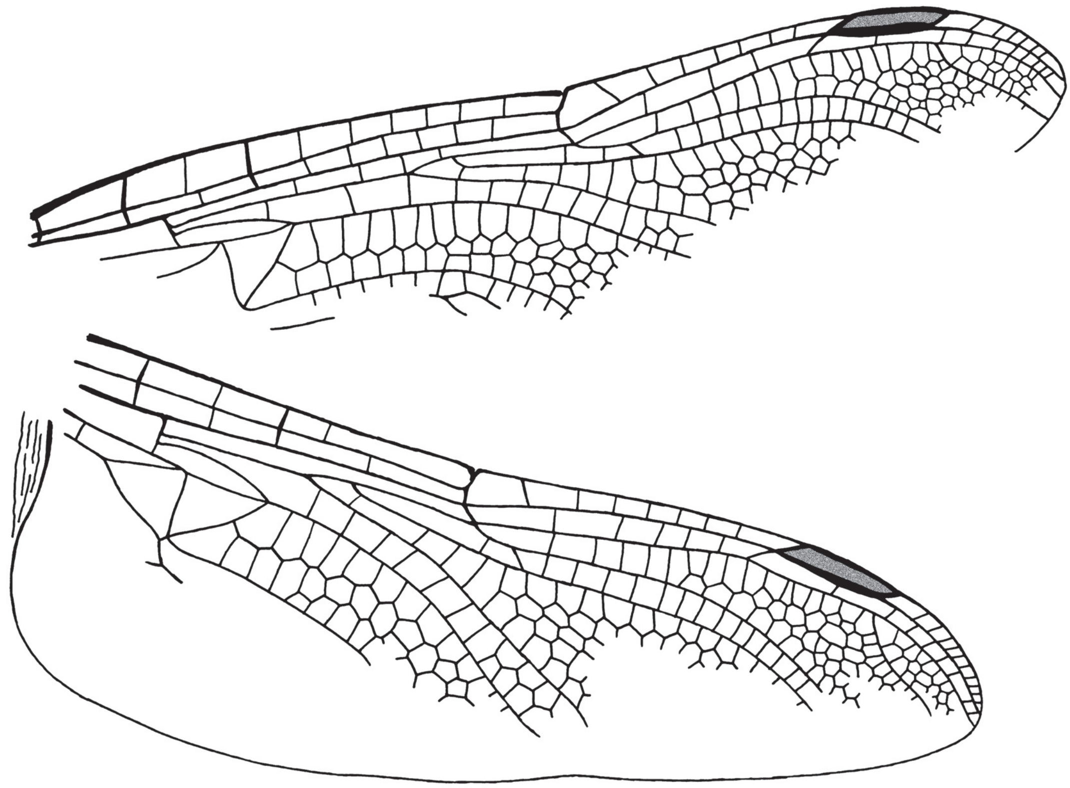


Figs. 52–54. *Paracordulagomphus aberrans* n. gen., n. sp., male holotype; SMF VI 1043. – **Fig. 52**. Body and terminalia. **Fig. 53**. Head. **Fig. 54**. Terminalia.

bridge crossveins basal of oblique vein; RP3/4 and MA parallel, with 2–3 rows of cells between their distal parts; no Rspl and no Mspl; only a single antefurcal crossvein that is not oblique; arculus rather straight with widely separate origins for RP and MA; posttrigonal space with three rows of cells already 2–3 cells distal of triangle, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle elongate and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; gaff not elongated; only a single row of cells between MP and CuA; CuA with six posterior branches (cubital area five cells wide); anal loop longitudinal elongate, posteriorly closed, and undivided; there is a 3-celled anal triangle and a distinct anal angle, thus it is a male specimen. There is no visible membranule at the wing base.

Description of female allotype (Figs. 55–58). – A complete female dragonfly, but the venation in the posterior areas of the wings is only poorly preserved; total body length 51.7 mm; the head is only poorly preserved; the anal appendages (cerci) are elongate (2.5 mm long) and lanceolate (Fig. 58); wing span 63.1 mm. The wing venation is very similar to the holotype.

Forewing 29.8 mm long; 6–7 secondary antenodals distal of Ax2 in the first row, non-aligned with the 6–7 antenodals in the second row; 6–7 postnodal crossveins, non-aligned with the 3–4 postsubnodal crossveins; one crossvein beneath pterostigma in right forewing, but two



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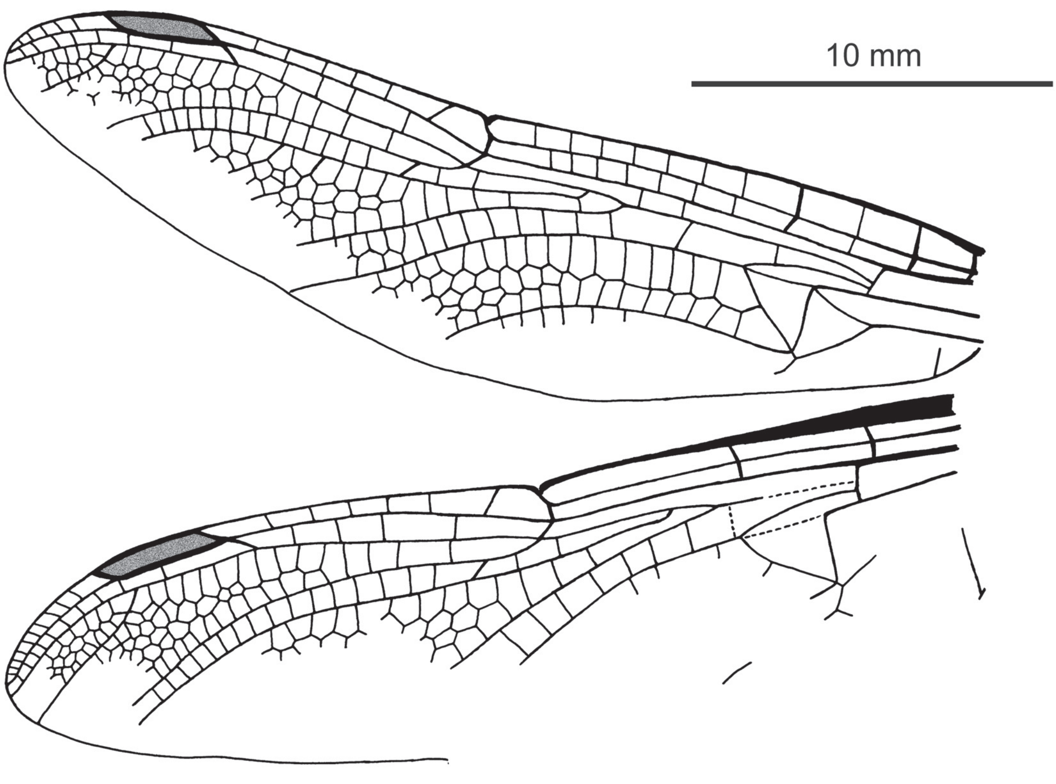

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Figs. 55–56. *Paracordulagomphus aberrans* n. gen., n. sp., female allotype; SMF VI 1044. – **Fig. 55**. Right wings. **Fig. 56**. Left wings.

Fig. 57. *Paracordulagomphus aberrans* n. gen., n. sp., female allotype; SMF VI 1044.

in the left one; two bridge crossveins basal of oblique vein; 2–3 antefurcal crossveins; arculus straight.

Hind wing 29.0 mm long and 9.9 mm wide; 6–7 postnodal crossveins, non-aligned with the 4–5 postsubnodal crossveins; one crossvein beneath pterostigma in right hind wing, but two in the left one; posttrigonal space with three rows of cells already two cells distal of triangle; anal margin rounded, thus it is a female specimen.

Description of male paratype (Figs. 59–60). – Thorax fragment with attached left pair of wings of a rather poorly preserved male dragonfly. The wing venation is very similar to the holotype.

Forewing 30.6 mm long and 8.3 mm wide; seven postnodal crossveins; pterostigma with a single crossvein beneath it; four bridge crossveins basal of oblique vein.

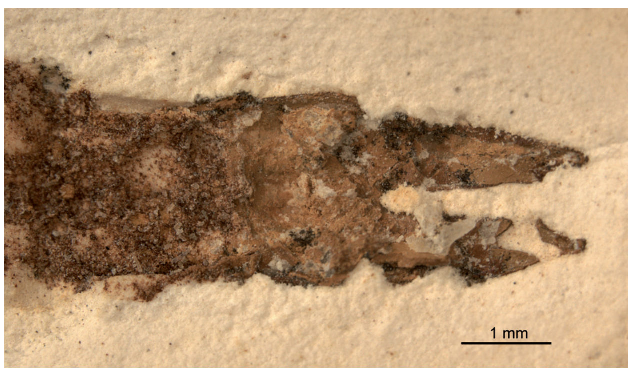

Fig. 58. *Paracordulagomphus aberrans* n. gen., n. sp., female allotype, terminalia; SMF VI 1044.

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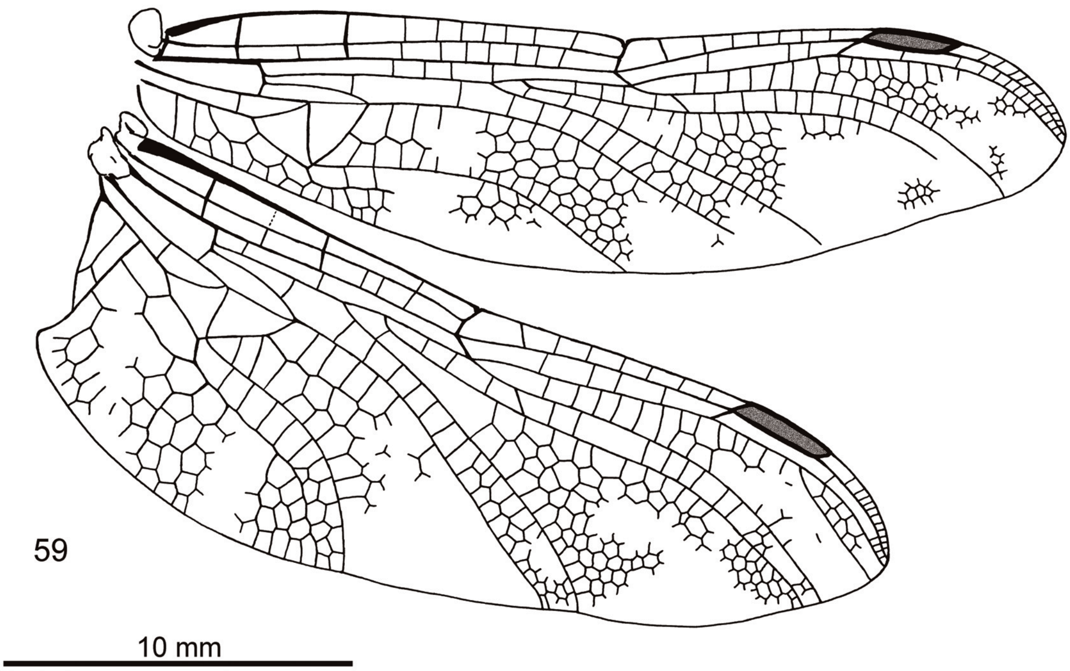

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Figs. 59–60. *Paracordulagomphus aberrans* n. gen., n. sp., male paratype, right wings; SMNS 66614.

Hind wing 29.0 mm long and 10.5 mm wide; seven postnodal crossveins; only a single row of cells between RP2 and IR2, except in the distal area; three bridge crossveins basal of oblique vein; arculus angular; posttrigonal space with three rows of cells already two cells distal of triangle; only a single row of cells between MP and CuA in the basal half, but two rows in the distal half; there is a 3-celled anal triangle and a distinct anal angle, thus it is a male specimen.

Paracordulagomphus divergens n. sp.
Figs. 61–63

H o l o t y p e : SMF VI 876 (old no. O38a) (Fig. 63) and counter plate SMF VI 877 (old no. O38b) (Figs. 61–62).

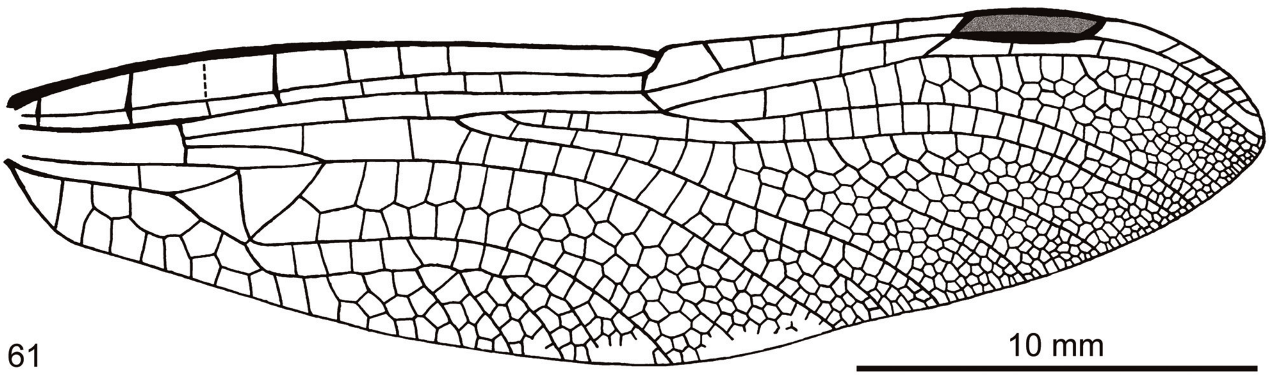
D e r i v a t i o n o m i n i s : Named after the distally strongly divergent veins RP3/4 and MA.

S t r a t u m t y p i c u m : Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

L o c u s t y p i c u s : Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

D i a g n o s i s (forewing). – Wing venation more or less identical to the type species, except for the following differences: RP3/4 and MA are more strongly divergent than in *P. aberrans* n. sp., separated by 11 cells at the wing margin (instead of only 5–7); two rows of cells between the distal parts of RP2 and IR2; only a single crossvein beneath pterostigma.

D e s c r i p t i o n o f h o l o t y p e (Figs. 61–63). – An isolated forewing with well-preserved venation; length 31.5 mm; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; only 3–4 antenodals distal of Ax2 are preserved; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; six postnodal crossveins, non-aligned with the postsubnodal crossveins (only two distal ones are preserved); RP2 originating at subnodus; RP1 and RP2 basally divergent; pterostigma strongly braced and with a single crossvein beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal end of pterostigma; two rows of cells between distal parts of RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; at least four bridge crossveins basal of oblique vein; RP3/4 and MA distal-



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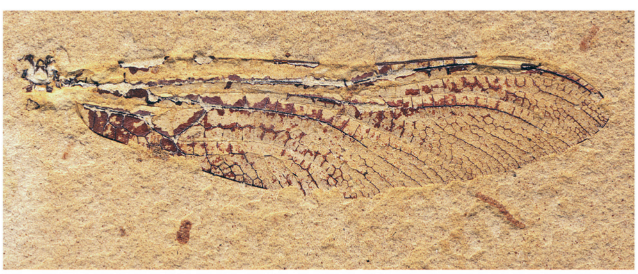

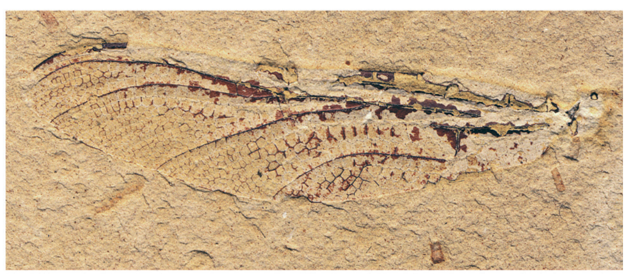

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Figs. 61–63. *Paracordulagomphus divergens* n. gen., n. sp., holotype; SMF VI 876, VI 877. – **Fig. 61**. Left forewing in ventral aspect (drawing supplemented with counter plate). **Fig. 62**. Left forewing in ventral aspect; SMF VI 877. **Fig. 63**. Left forewing in dorsal aspect; SMF VI 876, counter plate of SMF VI 877.

ly strongly divergent, with 11 cells between them at wing margin; no Rspl and no Mspl; two antefurcal crossveins; arculus slightly angular with widely separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle transverse and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; an elongate cell in the anal area; CuA with eight posterior branches (cubital area 3–5 cells wide).

Genus *Pauciphlebia* n. gen.

Typus generis: *Pauciphlebia novaolindense* n. sp.

Derivatio nominis: Named after the Latin word pauci for few, and the Greek word φλέβα (phleba) for vein, because of the reduced wing venation.

Diagnosis. – Quite similar in size and habitus to *Cordulagomphus fenestratus* CARLE & WIGHTON, 1990, but the following differences distinguish this new taxon from *Cordulagomphus* and other genera (incl. *Lingomphus* VERNOUX et al., 2010): compound nearly touching; only a single row of cells in the posttrigonal area of both pairs of wings (unique autapomorphy); only a single crossvein beneath pterostigmata; only a single antenodal in both rows between Ax1 and Ax2; long "libelluloid gap" of postsubnodal crossveins; two antefurcal crossveins in hind wings, which are not oblique; only a single row of cells between RP2 and IR2 and between RP3/4 and MA; hypertriangles, triangles, and subtriangles undivided; CuA with only five branches in forewing (cubital field 1–2 cells wide) and four branches in hind wings (cubital field three cells wide); anal loop elongate but unicellular; forewings with a single row of cells in the anal area.

Discussion. – This new genus and species can also be attributed to Cordulagomphinae. It shares the following synapomorphies with Hagenioidea: Branching of RP at midfork symmetrical; distal side (MAb) of triangle angulate. The following synapomorphies are shared with Proterogomphidae within Hagenioidea: Triangles secondarily unicellular; only two cells beneath pterostigmata; vein pseudo-IR1 very distinct and originating on RP1 beneath the distal side of the pterostigmata; anal loop longer than wide and with only one or two cells. Finally, the following synapomorphies are shared with Cordulagomphinae within Proterogomphidae: The most basal postnodal crossvein is very oblique; only 1–2 antefurcal crossveins in hind wings, and 2–3 in forewings; anal loop more distinctly longitudinal elongate; presence of a "cordulegastrid gap" of crossveins in the distal part of the antesubnodal area.

The non-obliquity of the distal antefurcal crossvein in hind wings is a plesiomorphic condition compared to *Cordulagomphus*. The parallel course of RP2+IR2 and RP3/4+MA is a plesiomorphic condition compared to *Lingomphus* and *Paracordulagomphus* n. gen. The reduced wing venation, with only a single row of cells in the posttrigonal areas of both wings and in the anal area of forewings is a unique autapomorphy of this new genus.

Pauciphlebia novaolindense n. sp.
Figs. 64–67

Holotype: Female specimen SMF VI 1045 (old no. N34) (Figs. 64–67).

Derivatio nominis: Named after the type locality Nova Olinda in Brazil.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 64–67). – A completely preserved female dragonfly with perfect wing venation; total body length 32.8 mm; width of head 4.3 mm; the compound eyes are approximated and apparently touch at one point, being only separated by a distance of 0.3 mm (Fig. 66); terminalia very short (0.6 mm long), styloid, and provided with setae (Fig. 67); wing span 40.9 mm.

Forewing 19.6 mm long; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; four secondary antenodals distal of Ax2 in the first row, non-aligned with the 3–4 antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; four postnodal crossveins, non-aligned with the three postsubnodal crossveins; distinct "libelluloid gap" of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel, with only a single row of cells till the pterostigma; pterostigma strongly braced, short and broad, with a single crossvein beneath it; primary IR1 absent; pseudo-IR1 distinct but very short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel with only a single row of cells between them (except near the wing margin in the right forewing); no Rspl and no Mspl; three antefurcal crossveins; arculus straight with separate origins for RP and MA; posttrigonal space with a single row of cells; hypertriangle free; triangle transverse and free, with a kinked distal side MAb (a posttrigonal crossvein originates at the kink); subtriangle not widened and undivided; pseudo-analis developed but not hypertrophied; anal area with a single row of cells; CuA with five posterior branches (cubital area 1–2 cells wide).

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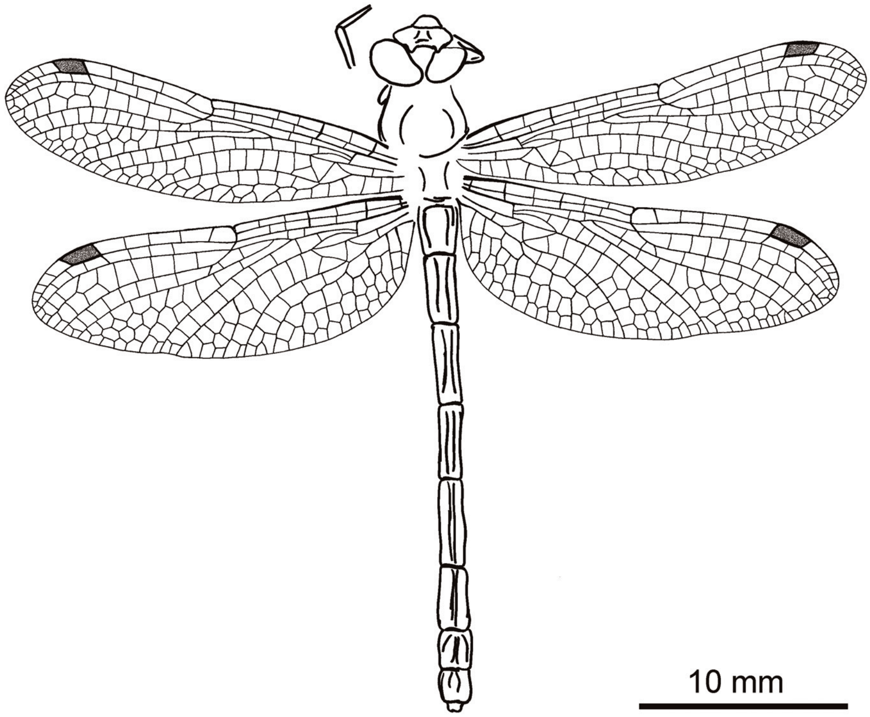

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Figs. 64–65. *Pauciphlebia novaolindense* n. gen., n. sp., female holotype; SMF VI 1045.

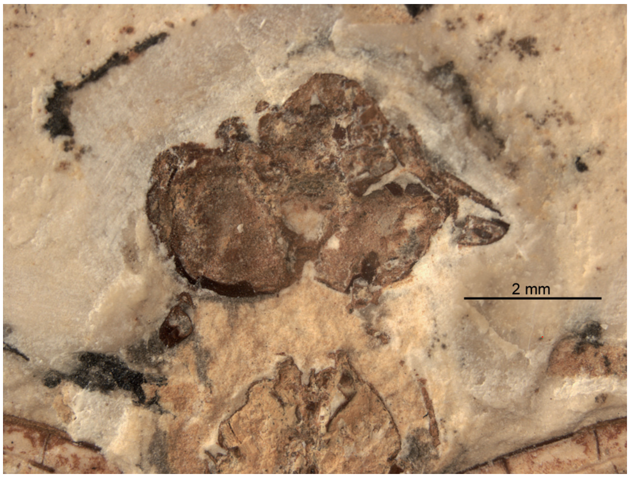


Fig. 66. *Pauciphlebia novaolindense* n. gen., n. sp., female holotype, head; SMF VI 1045.

Hind wing 18.4 mm long and 6.3 mm wide; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the distal angle of triangle; two secondary antenodals distal of Ax2 in the first row, non-aligned with the two antenodals in the second row; long “cordulegastrid gap” of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; 4–5 postnodal crossveins, non-aligned with the three postsubnodal crossveins; distinct “libelluloid gap” of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent, with only a single row of cells till the pterostigma; pterostigma strongly braced, short and broad, with a single crossvein beneath it; primary IR1 absent; pseudo-IR1 distinct but very short, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel with only a single row of cells between them; no Rspl and no Mspl; two antefurcal crossveins that are both not oblique; arculus straight with separate origins for RP and MA; posttrigonal space with a single row of cells till the level of nodus; hypertriangle free; triangle longitudinal and free, with a kinked distal side MAb (a posttrigonal crossvein originates at the kink); subtriangle widened, but undivided; pseudo-analis slightly hypertrophied; gaff not elongated; only a single row of cells between MP and CuA (except 2–3 cells near wing margin); CuA with four posterior branches (cubital area three cells wide); anal loop longitudinal elongate, posteriorly closed, and undivided; the anal margin is rounded, thus it is a female specimen. There is no visible membranule at the wing base.

Fig. 67. *Pauciphlebia novaolindense* n. gen., n. sp., female holotype, terminalia with setae; SMF VI 1045.

Genus *Cratogomphus* n. gen.

Typus generis: *Cratogomphus erraticus* n. sp.

Derivatio nominis: Named after the Crato Formation and the Recent dragonfly genus *Gomphus*.

Diagnosis. – Quite similar in size and habitus to *Cordulagomphus tuberculatus* Carle & Wighton, 1990, but the following differences distinguish this new taxon from *Cordulagomphus* and other genera (incl. *Lingomphus* Vernoux et al., 2010): two rows of cells in posttrigonal area; 2–3 crossveins beneath pterostigmata; pseudo-IR1 originates beneath the middle of pterostigma; only a single row of cells between RP1 and pseudo-IR1; only a single antenodal between Ax1 and Ax2; long "libelluloid gap" of postsubnodal crossveins; two antefurcal crossveins in hind wings, which are both not oblique; anal loop elongate but unicellular; RP2 and IR2 distally divergent, with 2–3 rows of cells between them; RP3/4 and MA undulate; shape of wings more elongate than in *Cordulagomphus*, combined with a more parallel fore- and hind margin.

Discussion. – This new genus and species shows a strange combination of characters that makes a familial attribution difficult.

It shares with Araripegomphidae the unicellular triangles and the "cordulegastrid gap", but these characters a also present as convergences in Cordulagomphinae.

The following synapomorphies are shared with Hagenioidea: Branching of RP at midfork symmetrical; distal side (MAb) of triangle strongly angulate, correlated with a distinct posttrigonal sector. The following synapomorphies are shared with Proterogomphidae within Hagenioidea: Triangles secondarily unicellular; anal loop longer than wide and with only one or two cells. However, the presence of more than two cells beneath pterostigmata, the more basal origin of vein pseudo-IR1, and the absence of the large elongated cell beneath the submedian area of forewings conflict with a position within Proterogomphidae. However, this new genus shares the following putative synapomorphies with Cordulagomphinae within Proterogomphidae: The most basal postnodal crossvein is very oblique; only two antefurcal crossveins in hind wings, and 2–3 in forewings; anal loop more distinctly longitudinal elongate; presence of a "cordulegastrid gap".

The new genus is here only tentatively attributed to Cordulagomphinae, but might alternatively belong to Araripegomphidae. Specimen SMNS 63070, which most probably belongs to this taxon, was indeed considered as a new unnamed species of *Araripegomphus* by Bechly (1998). The undulate RP3/4 and MA (esp. in forewings) also could suggest a relationship with *Araripegomphus*, but it is here considered as an autapomorphy. The distally divergent veins RP2 and IR2 and the long "libelluloid gap" represent further autapomorphies of this new genus.

Cratogomphus erraticus n. sp.
Figs. 68–73

Holotype: Male specimen SMNS 66606a (old no. L43) (Fig. 70) and counter plate SMNS 66606b (old no. L17) (Fig. 71).

Allotype: Female specimen SMF VI 1046 (old no. MSF O40) (Figs. 72–73).

Further material: Probably specimen SMNS 63070, described as *Araripegomphus* sp. by Bechly (1998: 14–15, figs. 4–5), also belongs to this new taxon.

Derivatio nominis: Named after the erratic phylogenetic position.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

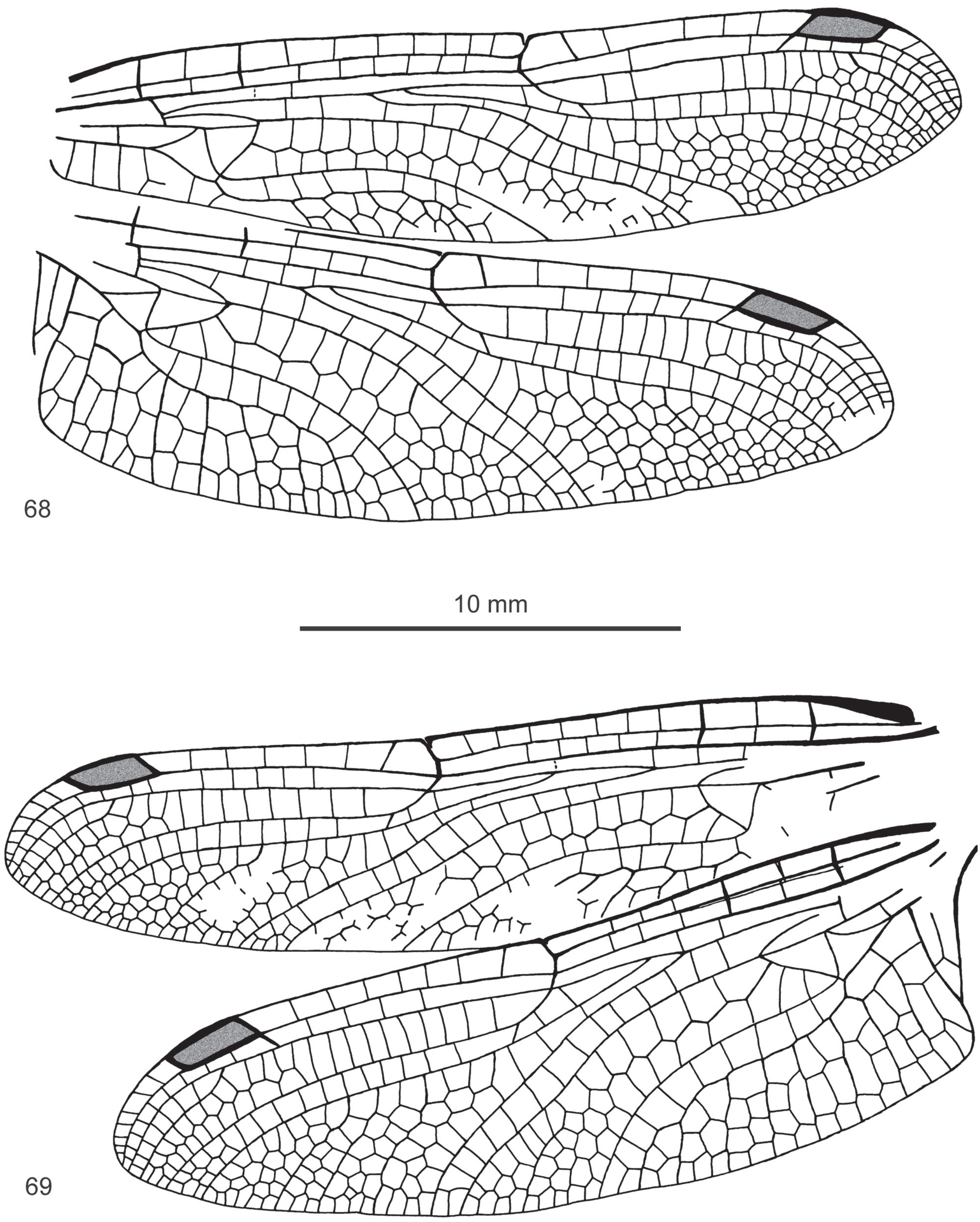
Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

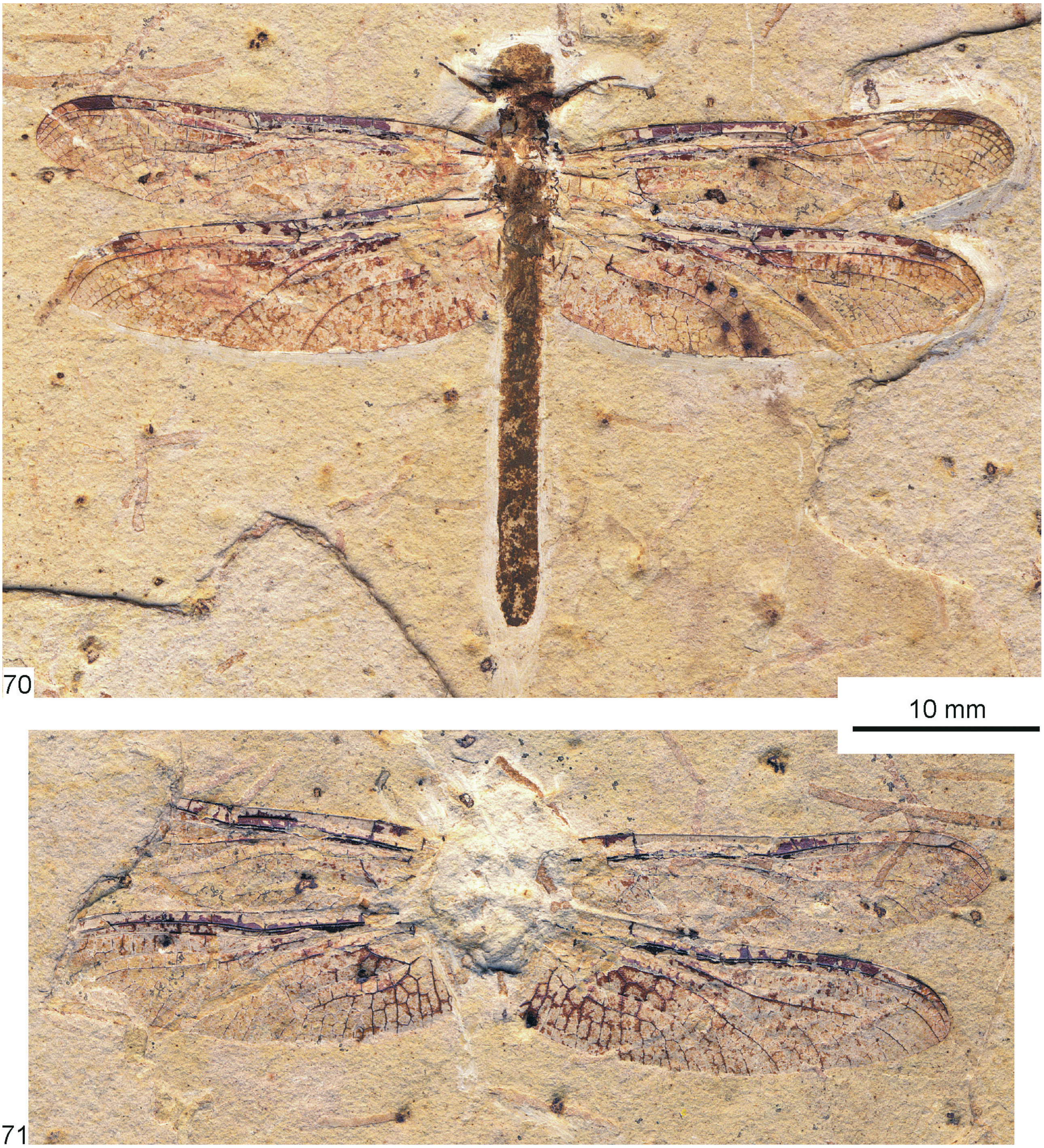
Description of male holotype (Figs. 68–71). – Plate and counter plate of a male dragonfly with all four wings and parts of the body preserved; total body length about 31 mm (but head and abdomen are mainly artificial colour supplemented by the preparator!); wing span 51.8 mm.

Forewing 24.0 mm long; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 slightly basal of arculus, Ax2 on the level of the distal angle of triangle; seven secondary antenodals distal of Ax2 in the first row, non-aligned with the six antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; six postnodal crossveins, non-aligned with the five postsubnodal crossveins; long "libelluloid gap" of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel, with a single row of cells between them till pterostigma; pterostigma strongly braced and with three crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct but short, originating on RP1 beneath distal third of pterostigma; only a single row of cells between RP1 and pseudo-IR1; RP2 and IR2 distally divergent, with 2–3 rows of cells between them; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA undulate and distally somewhat divergent; no Rspl and no Mspl; two antefurcal crossveins visible, but maybe more present; arculus slightly angular with separate origins for RP and MA; posttrigonal space narrow, with two rows of cells till the level of nodus, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle transverse and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; anal area with a single row of vertical rectangular cells; CuA with more than five posterior branches (cubital area two cells wide).

Hind wing 23.0 mm long and 7.3 mm wide; basal space free; between Ax1 and Ax2 there is only a single secondary antenodal in both rows; Ax1 slightly basal of arcu-



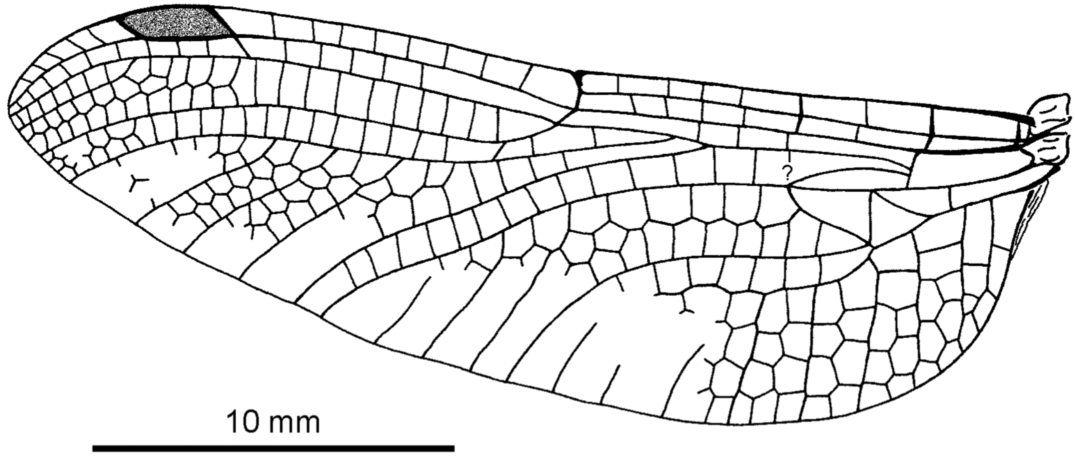
Figs. 68–69. *Cratogomphus erraticus* n. gen., n. sp., male holotype; SMNS 66606a+b. – **Fig. 68**. Right wings. **Fig. 69**. Left wings.



Figs. 70–71. *Cratogomphus erraticus* n. gen., n. sp., male holotype. – **Fig. 70**. SMNS 66606a. **Fig. 71**. Counter plate of male holotype; SMNS 66606b.

lus, Ax2 on the level of the distal angle of triangle; three secondary antenodals distal of Ax2 in the first row, non-aligned with the three antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; 6–7 postnodal crossveins, non-aligned with the 4–5 postsubnodal crossveins; long "libelluloid gap" of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel, with a single row of cells between them till pterostigma; pterostigma strongly braced and with two crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct, originating on RP1 beneath the middle of pterostigma; only a single row of cells between RP1 and pseudo-IR1; RP2 and IR2 distally divergent, with 2–3 rows of cells between them; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel and somewhat undulate, with a single row of cells between them; no Rspl and no Mspl; two antefurcal crossveins that are both not oblique; arculus rather straight with widely separate origins for RP and MA; posttrigonal space with two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle elongate and free, with a kinked distal side MAb; subtriangle widened but undivided; pseudo-analis hypertrophied; gaff not elongated; MP and CuA distally divergent; CuA with 6–7 posterior branches (cubital area 3–4 cells wide); anal loop longitudinal elongate, posteriorly closed, and undivided; there is a 3-celled anal triangle and a distinct anal angle, thus it is a male specimen. There is no visible membranule at the wing base.

Description of female allotype (Figs. 72–73). – A very well-preserved isolated hind wing of a female dragonfly. Wing 27.9 mm long and 9.2 mm wide. The wing venation is very similar to the holotype; three secondary antenodals distal of Ax2 in the first row, non-aligned with the four antenodals in the second row; eight postnodal crossveins, non-aligned with the five postsubnodal crossveins; long "libelluloid gap" of postsubnodal crossveins; pterostigma with three crossveins beneath it; pseudo-IR1 originating on RP1 beneath the distal end of pterostigma; CuA with six posterior branches (cubital area four cells wide); the undivided anal loop is small and only somewhat elongate; three secondary branches of AA be-



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Figs. 72–73. *Cratogomphus erraticus* n. gen., n. sp., female allotype, left hind wing; SMF VI 1046.

tween CuAb and wing base; the anal margin is rounded, thus it is a female specimen. There is a small and narrow membranule at the wing base.

Family Hageniidae TILLYARD & FRASER, 1940

Genus *Cratohagenius* n. gen.

Typus generis: *Cratohagenius erichweberi* n. sp.

Derivatio nominis: Named after the Crato Formation and the Recent dragonfly genus *Hagenius*.

Diagnosis. – Forewing length 34–39 mm; secondary branches of IR2 (three branches) and MA (two branches) distinctly developed; two rows of cells between the distal parts of RP3/4 and MA in both wings; usually only three (rarely up to five) antefurcal crossveins in hind wings; hypertriangles free; hypertriangle slightly quadrangular in hind wings; distal side MAb of triangles strongly kinked, with strong trigonal sector originating at kink in both wings; triangle transverse and 2-celled in forewings, but sigmoidally elongate and 2-celled (rarely 3-celled) in hind wings; forewing subtriangle 3-celled, hind wing subtriangle free; pterostigma with only two (rarely three) crossveins beneath it; brace vein slightly displaced basal of pterostigma; pseudo-IR1 originating on RP1 beneath distal end of pterostigma; long "cordulegastrid gap" of antesubnodal crossveins; lestine oblique vein 1.5 cells distal of subnodus; two antenodal crossveins between Ax1 and Ax2 in both wings; Ax1 basal of arculus; anal loop hexagonal and divided into 3–5 cells.

Discussion. – The small numbers of antefurcals (max. five), the symmetrical branching of the midfork, and the kinked hind wing triangle (correlated with a well-developed trigonal sector originating at the kink) suggest an attribution to the superfamily Hagenioidea. The sigmoidal shape of the hind wing triangles (convergent to Liupanshaniidae) and the not thickened margins of the pterostigmata suggest an attribution to Hageniidae. The fact that the forewing triangle is not elongated excludes a position within the crowngroup of Hageniidae. This is also corroborated by further plesiomorphies, such as still distinct subtriangles and pseudo-analis PsA, and an indistinct and not elongated primary IR1. Consequently, this new taxon is tentatively considered as a stemgroup Hageniidae.

The presence of a "cordulegastrid gap" is of conflicting evidence, and could rather suggest a relationship with Araripegomphidae and/or Cordulagomphinae, or rather with the lindeniid *Cratolindenia* described by BECHLY (2000). The widely separated eyes of *Cratohagenius* n. gen. would not contradict a relationship with *Cratolindenia*, but well with Araripegomphidae and Cordulagomphinae. Anyway, it is a strange phenomenon that many unrelated taxa of Anisoptera from the Crato Formation do have a "cordulegastrid gap" (e. g. Megaphlebiidae n. fam., Magnathemidae n. fam., Gomphaeschnidae – Gomphaeschnaoidinae, Araripegomphidae, Proterogomphidae – Cordulagomphinae, Lindeniidae – *Cratolindenia*, Araripephlebiidae, Araripechlorogomphidae?, and Araripelibellulidae), while this character state is much more rare among Recent dragonflies.

Cratohagenius erichweberi n. sp.
Figs. 74–89

Holotype: Female specimen SMNS 66615a (old no. H71a) and counter plate SMNS 66615b (old no. M71b) (Figs. 74–77).

Allotype: Male specimen SMNS 66612 (old no. R5) (Figs. 82–86).

Paratypes: Female specimen SMNS 66592 (old no. H29) (Figs. 78–81); female specimen SMNS 66390 (old no. E100401) (Figs. 87–89).

Derivatio nominis: Named in honour of the zoologist and ornithologist Dr. ERICH WEBER (Tübingen, Germany) with whom I enjoyed many interesting discussions on phylogenetics.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 74–77). – Plate and counter plate of a female dragonfly thorax with all four wings; wing span 78.8 mm.

Forewings 37.3 and 38.4 mm long; basal space free; between Ax1 and Ax2 there are two non-aligned secondary antenodals in both rows; Ax1 distinctly basal of arculus, Ax2 on the level of the lower angle of triangle; 8–9 secondary antenodals distal of Ax2 in the first row, non-aligned with the 7–8 antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; six postnodal crossveins, non-aligned with the 5–6 postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel; pterostigma strongly braced and with two crossveins beneath it; stigmal brace vein displaced slightly basal of pterostigma; primary IR1 indistinct; pseudo-IR1 distinct, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; 2–3 bridge crossveins basal of oblique vein; RP3/4 and MA slightly undulate, with two rows of cells between their distal parts; no Rspl and no Mspl, but three strong secondary sectors at IR2 and two strong secondary sectors at MA; five antefurcal crossveins; arculus rather straight with separate origins for RP and MA; posttrigonal space after 2–4 cells with three rows of cells, and with a convex intercalary vein originating at the kink of triangle; hypertriangle free; triangle transverse and 2-celled, with a strongly kinked distal side MAb; subtriangle widened and

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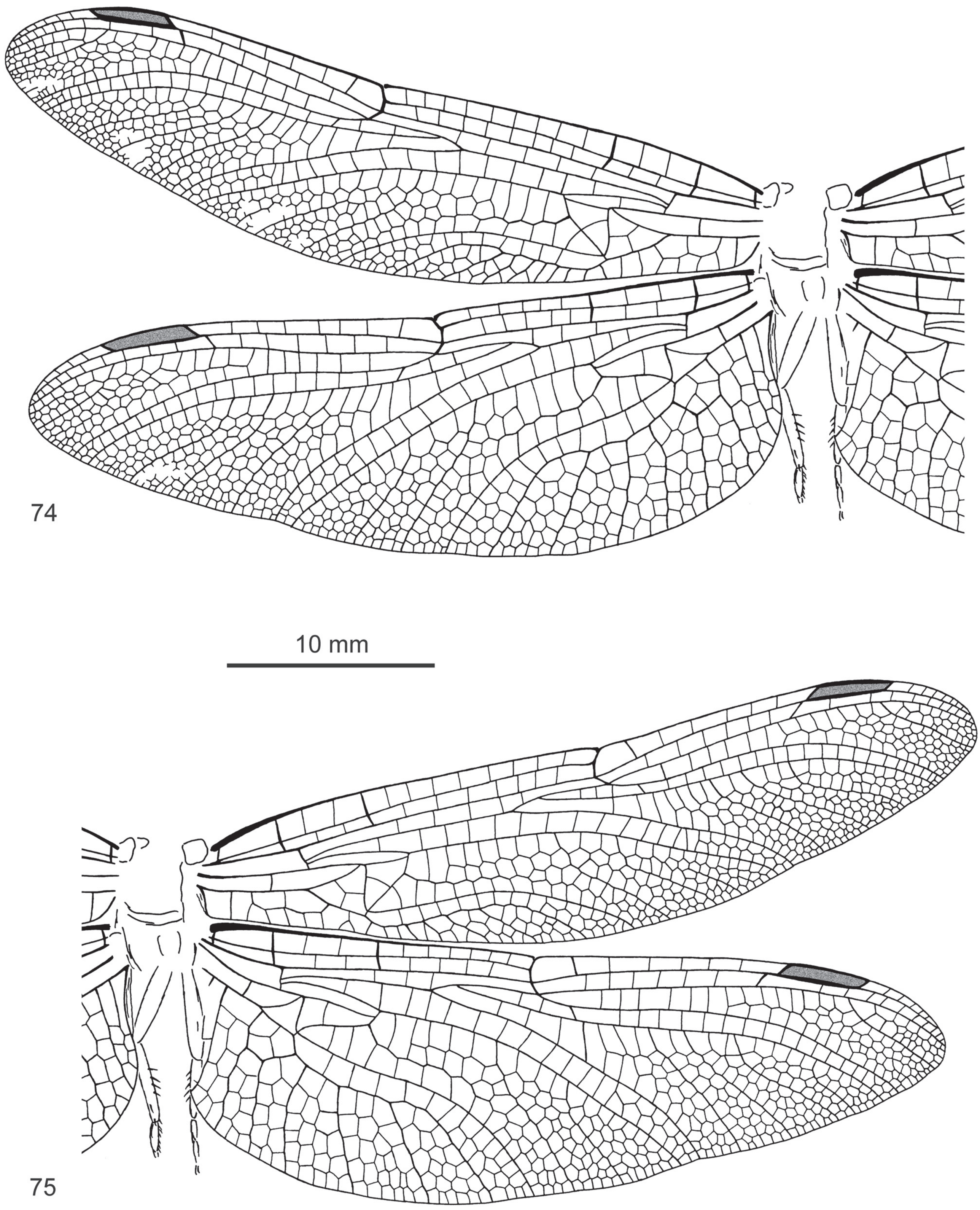

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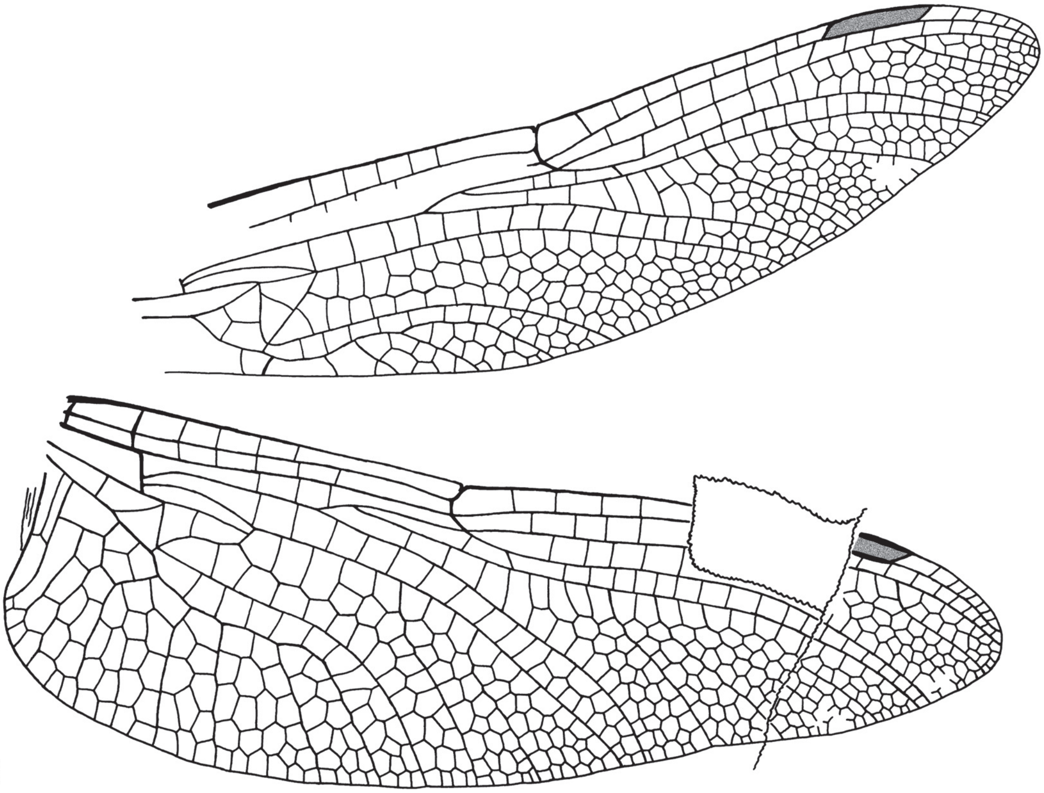
Figs. 74–75. *Cratohagenius erichweberi* n. gen., n. sp., female holotype; SMNS 66615a. – **Fig. 74**. Thorax and right wings in ventral aspect. **Fig. 75**. Thorax and left wings in ventral aspect.

Figs. 76–77. *Cratohagenius erichweberi* n. gen., n. sp., female. – **Fig. 76**. Holotype; SMNS 66615a. **Fig. 77**. Counter plate of holotype; SMNS 66615b.

3-celled; pseudo-analis hypertrophied; CuA with five posterior branches (cubital area max. three cells wide). There is a tiny membranule at the wing base.

Hind wings 36.3 and 36.5 mm long, and 12.5 mm wide; basal space free; between Ax1 and Ax2 there are two non-aligned secondary antenodals in both rows; Ax1 slightly basal of arculus, Ax2 on the level of the distal angle of triangle; about 5–6 secondary antenodals distal of Ax2 in the first row, non-aligned with the 4–5 antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; first postnodal crossvein slanted towards nodus; 6–7 postnodal crossveins, non-aligned with the six postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel; pterostigma strongly braced and with 2–3 crossveins beneath it; stigmal brace vein displaced slightly basal of pterostigma; primary IR1 indistinct; pseudo-IR1 distinct, originating on RP1 beneath distal end of pterostigma; only a single row of cells between RP2 and IR2, except close to wing margin; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; two bridge crossveins basal of oblique vein; RP3/4 and MA parallel, with two rows of cells between their distal parts; no Rspl and no Mspl, but three strong secondary sectors at IR2 and two strong secondary sec-



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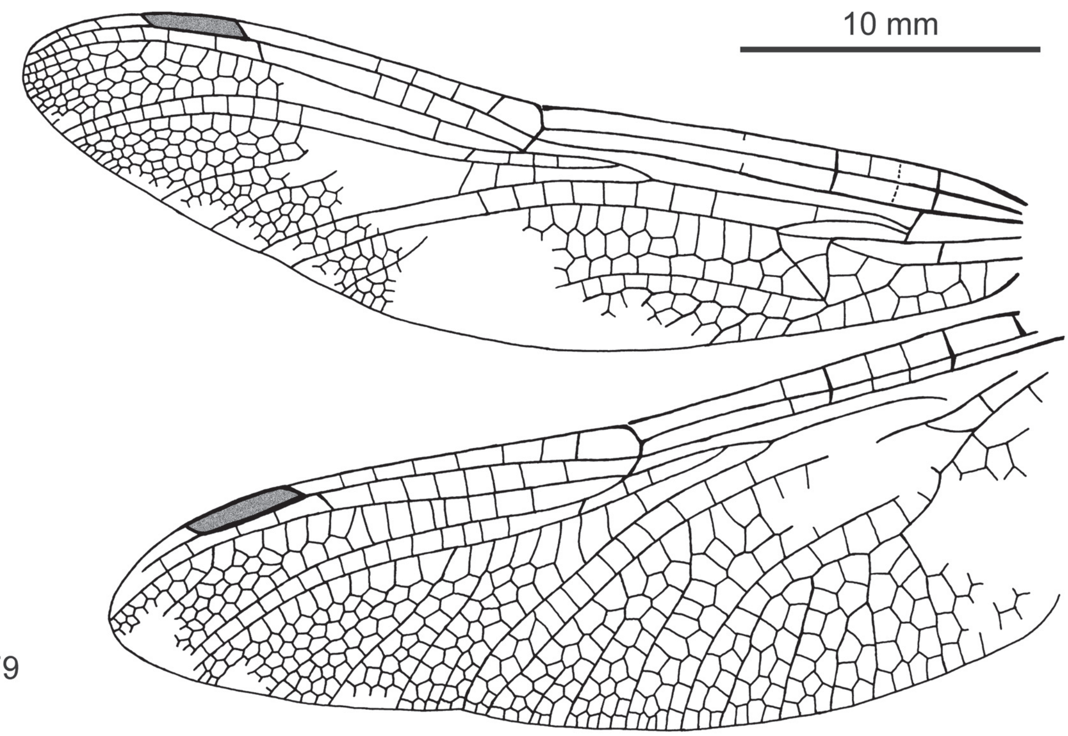

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Figs. 78–79. *Cratohagenius erichweberi* n. gen., n. sp., female paratype; SMNS 66592. – **Fig. 78**. Right wings. **Fig. 79**. Left wings.

tors at MA; 3–5 antefurcal crossveins (none oblique); arculus straight with separate origins for RP and MA; post-trigonal space with 2–3 rows of cells, and with a convex intercalary vein originating at kink of triangle; hypertriangle free and slightly rectangular, because the upper side of the triangle is not ending precisely at the distal angle; triangle sigmoidally elongate and 2-celled, with a strongly kinked and sigmoidal distal side MAb; subtriangle undivided; pseudo-analis not hypertrophied; gaff not elongated; MP and CuA distally divergent with 2–4 rows of cells between them; CuA with five posterior branches (cubital area 5–6 cells wide); anal loop hexagonal, posteriorly closed, and divided into 3–5 cells; two secondary branches of AA between CuAb and wing base; the anal margin is rounded, thus it is a female specimen. There is a narrow membranule at the wing base.

Description of paratype SMNS 66592 (Figs. 78–81). – A complete and well-preserved female dragonfly in dorsal aspect; body length about 50 mm but the apex of abdomen is missing; compound eyes widely separated (Fig. 81); wing span 68.2 mm (forewings) and 70.5 mm (hind wings). The wing venation is very similar to the holotype.

Forewing 33.7 mm long; Ax1 slightly basal of arculus, Ax2 on the level of the basal angle of triangle; eight postnodal crossveins, non-aligned with the six postsubnodal crossveins; three bridge crossveins basal of oblique vein; no Rspl and no Mspl, but two strong secondary sectors at IR2 and 0–1 strong secondary sectors at MA.

Hind wings 32.6 mm long, and 11.2 mm wide; seven postnodal crossveins, non-aligned with the seven postsubnodal crossveins; pterostigma with two crossveins beneath it; only a single row of cells between RP2 and IR2 till the wing margin; RP3/4 and MA slightly; only two antefurcal crossveins (none oblique); MP and CuA distally divergent with 2–3 rows of cells between them; anal loop

Fig. 80. *Cratohagenius erichweberi* n. gen., n. sp., female paratype; SMNS 66592.

Fig. 81. *Cratohagenius erichweberi* n. gen., n. sp., female paratype, head and thorax; SMNS 66592.

hexagonal, posteriorly closed, and divided into three cells; two secondary branches of AA between CuAb and wing base; the anal margin is rounded, thus it is a female specimen. There is a narrow membranule at the wing base.

Description of male allotype SMNS 66612 (Figs. 82–86). – A male dragonfly preserved in lateral aspect with superimposed wings; body about 45 mm long but abdominal segments 6–10 are missing; compound eyes relatively small and probably separated (Fig. 86); thorax very robust; the presence of a secondary genital apparatus at the basal abdomen shows that this is a male specimen. The wing venation is only poorly preserved, but agrees with the holotype. Length of forewings 38 mm, of hind wings 37 mm.

Description of female paratype SMNS 66390 (Figs. 87–89). – A complete and perfectly preserved female dragonfly in grey Crato limestone, which only has a few damages in the wings from the prepara-

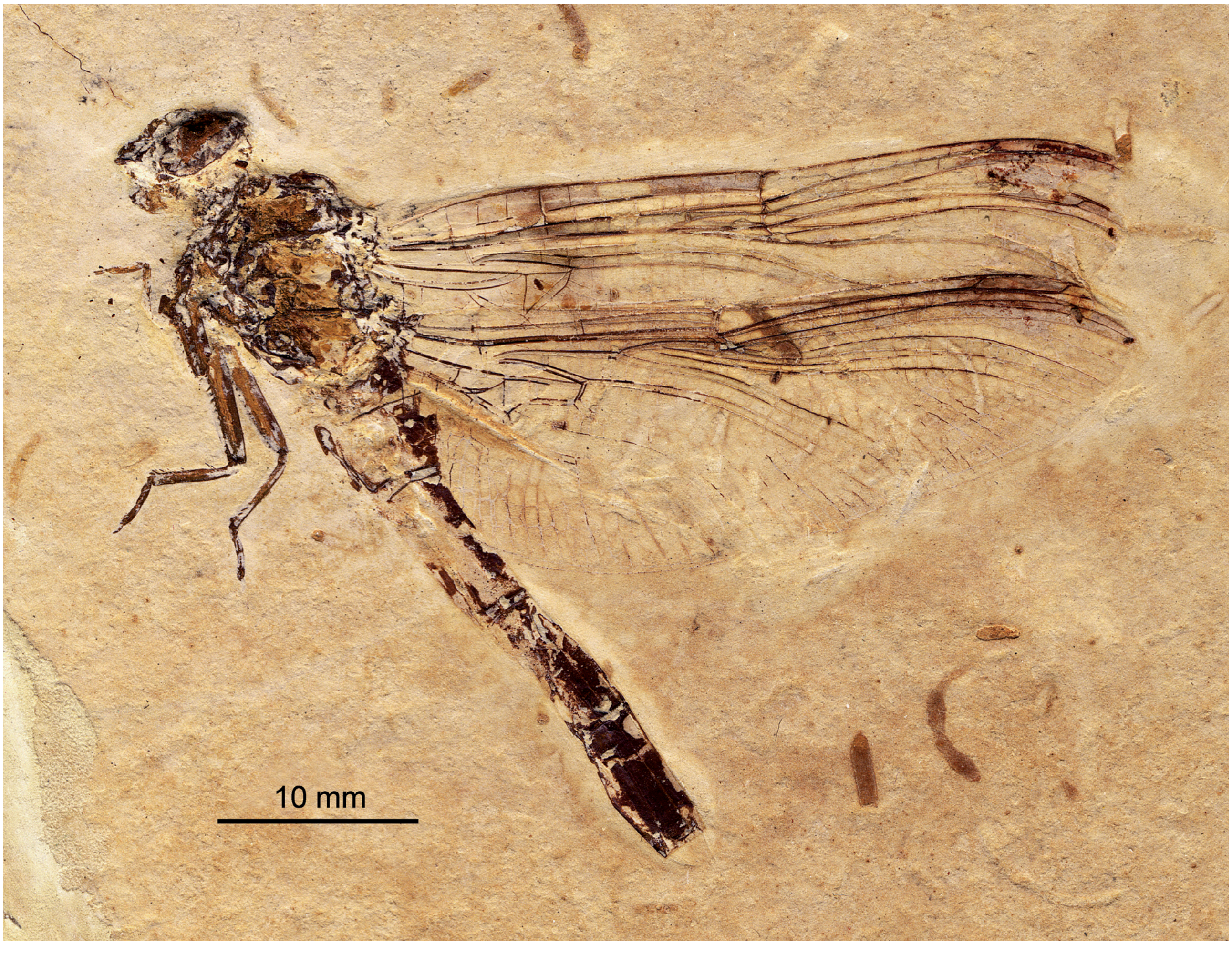


Fig. 82. *Cratohagenius erichweberi* n. gen., n. sp., male allotype; SMNS 66612.

tion. Total body length 59 mm and wing span 79.5 mm. The wing venation is again very similar to the holotype.

Forewings 36.8 mm long; seven postnodal crossveins, non-aligned with the 6–7 postsubnodal crossveins; stigmal brace vein displaced distinctly basal of pterostigma; three bridge crossveins basal of oblique vein; CuA with at least five posterior branches (cubital area max. four cells wide).

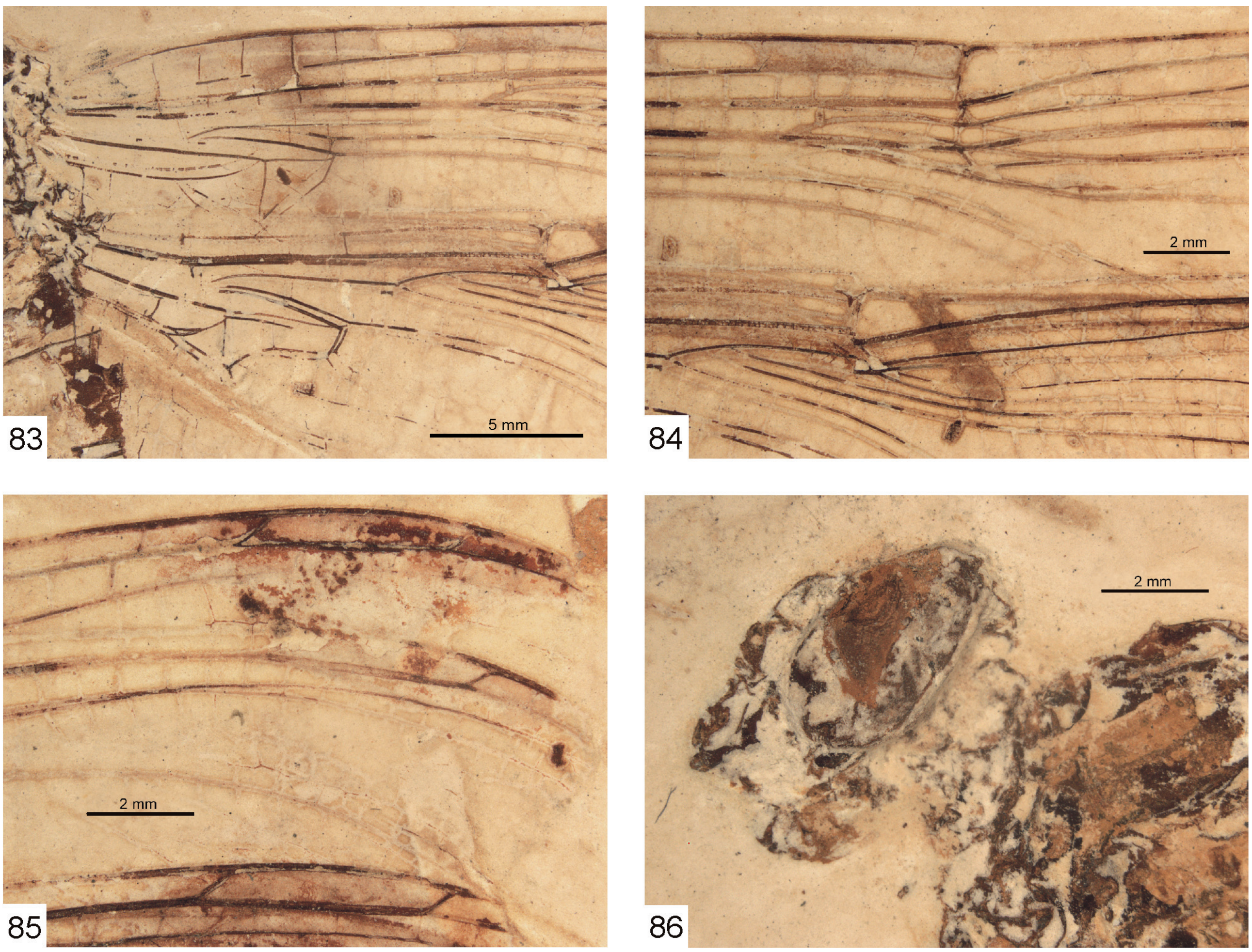
Hind wings 35.3 mm long, and 13.0 mm wide; four secondary antenodals distal of Ax2 in the first row, non-aligned with the four antenodals in the second row; eight postnodal crossveins, non-aligned with the six postsubnodal crossveins; stigmal brace vein displaced distinctly basal of pterostigma; only a single row of cells between RP2 and IR2 till the wing margin; a single lestine oblique vein between RP2 and IR2 two cells distal of subnodus; three bridge crossveins basal of oblique vein; only two antefurcal crossveins (none oblique); triangle sigmoidally elongate and 3-celled; MP and CuA distally more strongly divergent with 2–5 rows of cells between them; cubital area six cells wide; anal loop hexagonal, posteriorly closed, and divided into 3–5 cells; two secondary branches of AA between CuAb and wing base; the anal margin is rounded, thus it is a female specimen.

D i s c u s s i o n . – Obviously all these specimens belong to the same new genus and species of gomphid relationship, because they share the same unique combination of characters and show only minor differences in venation and dimensions.

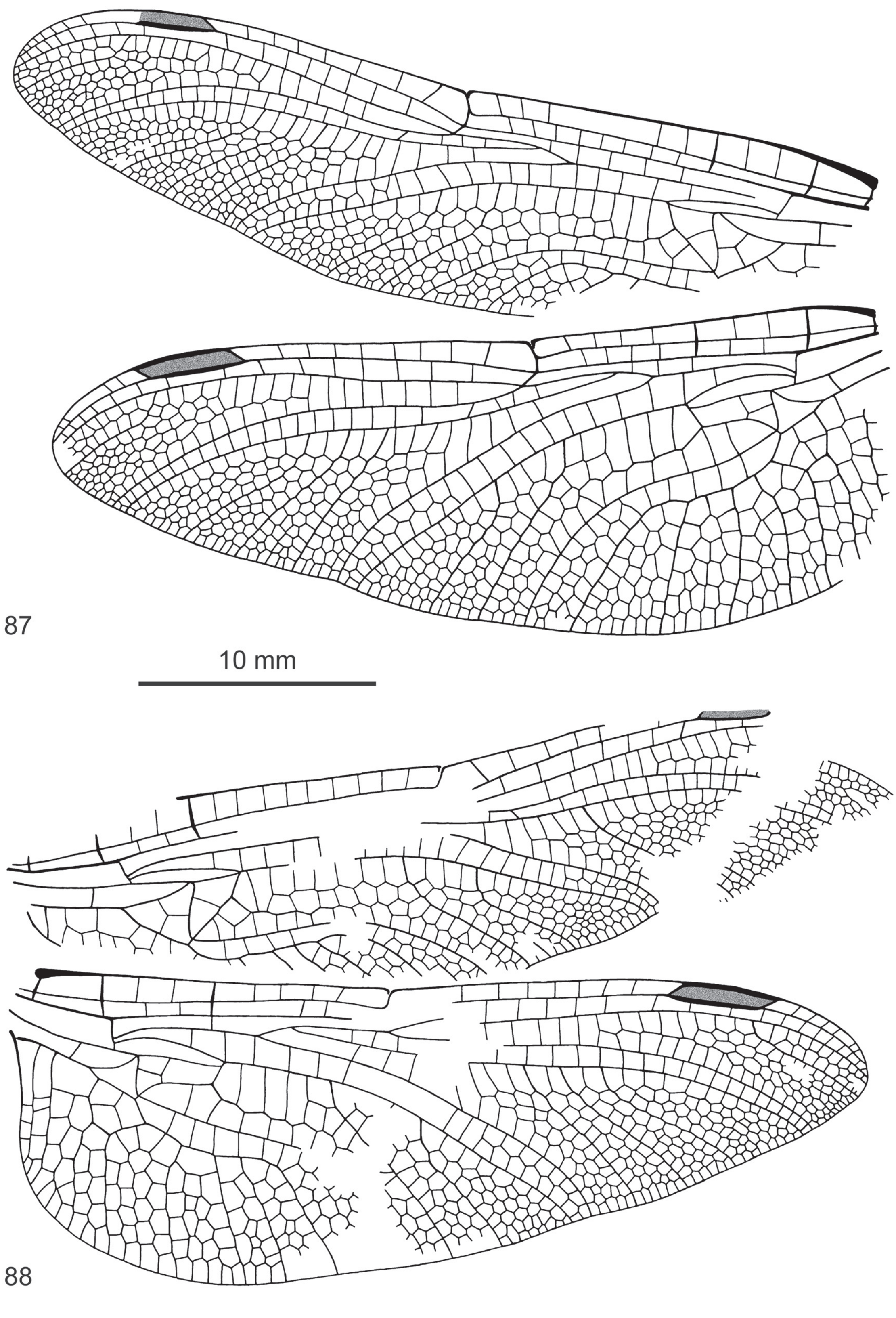
Family Megaphlebiidae n. fam.

T y p u s f a m i l i a r i s : *Megaphlebia* n. gen.

D i a g n o s i s . – Same as for type genus since monotypic.



Figs. 83–86. *Cratohagenius erichweberi* n. gen., n. sp., male allotype; SMNS 66612. – **Fig. 83**. Wing bases. **Fig. 84**. Nodus area. **Fig. 85**. Pterostigmata. **Fig. 86**. Head in lateral aspect.



Figs. 87–88. *Cratohagenius erichweberi* n. gen., n. sp., female paratype; SMNS 66390. – **Fig. 87**. Right wings. **Fig. 88**. Left wings.

Fig. 89. *Cratohagenius erichweberi* n. gen., n. sp., female paratype; SMNS 66390.

Genus *Megaphlebia* n. gen.

Typus generis: *Megaphlebia rayandressi* n. sp.

Derivatio nominis: Named after the Latin word mega for large and the prefix "phleb" (based on the Greek word φλέβψ = phleps) for vein, because of the very large size of the wings.

Diagnosis (forewing). – Wing strongly elongated (autapomorphy) and very large (58.6 mm long); nodus in very distal position at 56 % of wing length; pterostigma braced and with a single crossvein beneath it (autapomorphy); primary IR1 absent; pseudo-IR1 originates on RP1 beneath distal end of pterostigma; RP2 and IR2 distally divergent with three rows of cells between them; Rspl present and closely parallel to IR2; RP3/4 and MA strongly undulate; posttrigonal area with 2–3 rows of cells; distal side MAb of triangle straight but with a strong trigonal sector originating at triangle (a quite unique and autapomorphic combination of character states); field between MP and CuA distally strongly widened; only a single antenodal between Ax1 and Ax2; long "cordulastrid gap"; a single lestine oblique vein 2.5 cells distal of subnodus; eight non-aligned antenodals distal of Ax2, and eight non-aligned postnodals between nodus and pterostigma; hypertriangle free; triangle longitudinal and free; subtriangle small and free, without hypertrophied pseudo-analis; anal area with two rows of cells.

Discussion. – The weakly defined Rspl and the undulating veins RP3/4 and MA as well as the elongate triangle suggest a phylogenetic position within Aeshnoptera. Except for the elongate forewing triangle all synapomorphic characters of Aeshnomorpha are absent. Therefore, this new family and genus is here tentatively considered as putative plesiomorphic sistergroup of all other Aeshnomorpha (Austropetaliidae + Aeshnidae in the traditional classification).

Megaphlebia rayandressi n. sp.
Figs. 90–91

Holotype: SMNS 66617 (old no. R6) (Figs. 90–91).

Derivatio nominis: Named after the British amateur odonatologist Mr. RAYMOND ANDRESS (London, UK), who is a specialist on Recent Petaluridae and skilful painter of these animals.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 90–91). – A well-preserved isolated forewing with the enormous length of 58.6 mm; basal space free; a single aligned secondary antenodal crossvein between Ax1 and Ax2 in both rows; Ax1 distinctly basal of arculus, Ax2 near the level of the distal angle of triangle; eight non-aligned secondary antenodals distal of Ax2; long "cordulegastrid gap" of antesubnodal crossveins; nodus in extremely distal position at about 56 % of the forewing length (32.7 mm); first postnodal crossvein not slanted towards nodus; eight (only seven preserved) postnodal crossveins, non-aligned with the seven postsubnodal crossveins; no "libelluloid gap" of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 basally parallel; pterostigma strongly braced and with a single crossvein beneath it; primary IR1 absent; pseudo-IR1 distinct, originating on RP1 beneath distal end of pterostigma; very broad area between pseudo-IR1 and RP1; RP2 and IR2 distally strongly divergent with three rows of cells between them; a single lestine oblique vein between RP2 and IR2 2.5 cells distal of subnodus; three bridge crossveins basal of oblique vein; RP3/4 and MA strongly undulate, but parallel; Rspl present and parallel to IR2, with a single row of cells in between; no Mspl and no secondary sectors at IR2 and MA; six antefurcal crossveins; arculus weakly angular with separate origins for RP and MA; post-trigonal area narrow, basally with only two rows of cells, and with a convex intercalary vein originating at the triangle; hypertriangle free; triangle elongate (aeshnoid-like) and free; subtriangle small and free; pseudo-analis not hypertrophied; MP and CuA distally strongly divergent; CuA with six posterior branches; anal area with two rows of cells.

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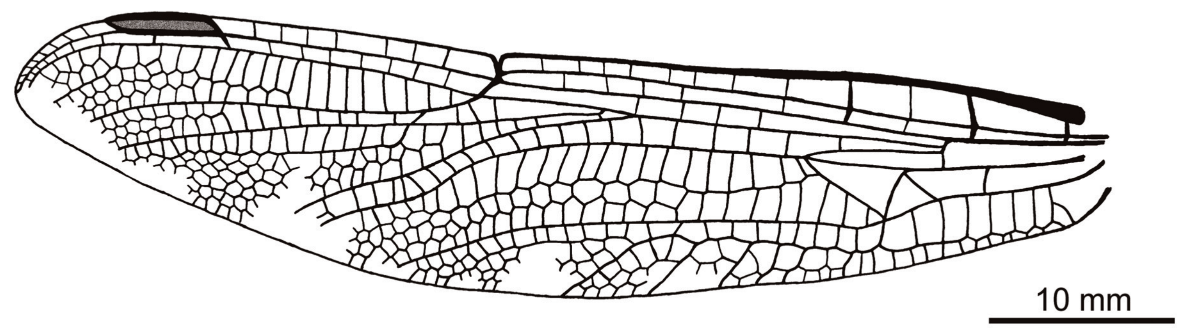

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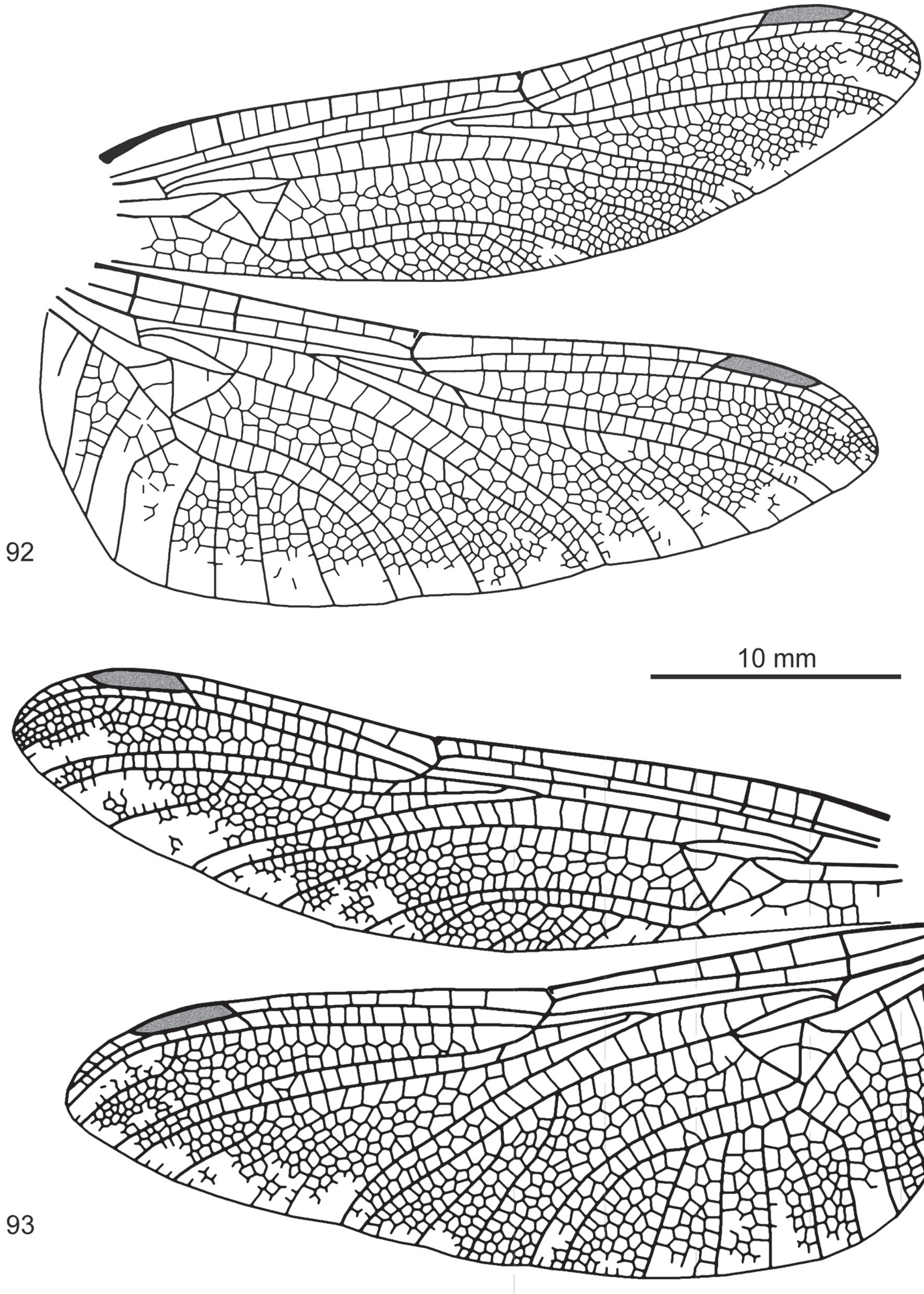
Figs. 90–91. *Megaphlebia rayandressi* n. gen., n. sp., holotype, left forewing; SMNS 66617.



Figs. 92–93. *Magnathemis marcusthorhalli* n. gen., n. sp., female holotype; WDC 105. – **Fig. 92**. Right wings. **Fig. 93**. Left wings.

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Figs. 94–95. *Magnathemis marcusthorhalli* n. gen., n. sp., female holotype, right wings; WDC 105. – **Fig. 94**. Right wings. **Fig. 95**. Left wings. – Scales: Ruler in mm.

Family Magnathemidae n. fam.

Typus familiaris: *Magnathemis* n. gen.

Diagnosis. – Same as for type genus since monotypic.

Genus *Magnathemis* n. gen.

Typus generis: *Magnathemis marcusthorhalli* n. sp.

Derivatio nominis: Named after the Latin word magn(a) for large and the Greek goddess Themis, who is often used for generic names in dragonflies.

Diagnosis. – Wing length about 37 mm; pterostigma braced and with 5–6 crossveins beneath it (plesiomorphy); primary IR1 absent; pseudo-IR1 originates on RP2 beneath distal third of pterostigma (autapomorphy); a single lestine oblique vein two cells distal of subnodus (autapomorphy); long "cordulegastrid gap" and short "libelluloid gap" present; only 7–8 antefurcals in forewings and 4–5 in hind wings (autapomorphy); arculus straight; hypertriangles free; triangles of equilateral shape and divided by a single "horizontal" crossvein in both wings (autapomorphy); subtriangles narrow and 2-celled in both wings, with non-hypertrophied pseudo-analis; posttrigonal area with three rows of cells directly distal of triangle in forewings, and four rows in hind wings (autapomorphies); gaff slightly elongated in hind wings; anal loop posteriorly open in hind wings; two rows of cells between distal parts of RP2+IR2 and RP3/4+MA.

Discussion. – The long "cordulegastrid gap" and the similar shapes of the triangles and subtriangles in both pairs of wings are derived character states share with basal Cavilabiata like Cordulegastridae, Neopetaliidae, Hemeroscopidae and Chlorogomphidae. Nevertheless the defining autapomorphies of each of these families are all absent in the new family and genus, which is characterized by several autapomorphies mentioned above. The more oblique distal side of the pterostigmata is a putative synapomorphy with Cristotibiata (the monophyly of this group is doubtful according to modern phylogenomic studies), but the presence of five crossveins beneath the pterostigmata excludes a position in Brachystigmata. Consequently, this new taxon is here considered as a basal Cavilabiata incertae sedis.

Bechly & Ueda (2002) described the only previously known "cordulegastroid" dragonfly from the Crato Formation, which is easily distinguished from the two new basal "corulegastroid" dragonflies described below by its large anal loop and the much more elongated gaff.

Magnathemis marcusthorhalli n. sp.
Figs. 92–96

Holotype: Female specimen no. 105 (old no. MSF Z43) in coll. WDC (Figs. 92–96).

Derivatio nominis: Named after my nephew Marcus Thorhall Winkelhofer (Vienna, Austria).

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 92–96). – A complete and very well-preserved female dragonfly; body length 56.1 mm; compound eyes widely separated; wing span 79.7 mm.

Forewings 37.5 mm long; basal space free; between Ax1 and Ax2 there are two secondary antenodals; Ax1 is slightly distal of arculus, Ax2 on the level of the basal angle of triangle; about 13 secondary antenodals distal of Ax2 in the first row, non-aligned with the antenodals in the second row; long "cordulegastrid gap" of antesubnodal crossveins; nine postnodal crossveins, non-aligned with the ten postsubnodal crossveins; a short but distinct 'libelluloid gap' of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 strongly divergent with 3–4 rows of cells in between at stigmal brace; pterostigma strongly braced and with 4–5 crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct, originating on RP1 beneath distal third of pterostigma; two or three rows of cells between RP1 and pseudo-IR1; two rows of cells between distal parts of RP2 and IR2; a single lestine oblique vein between RP2 and IR2 1.5 cells distal of subnodus; three bridge crossveins basal of oblique vein; two rows of cells between the distal parts of RP3/4 and MA; no Rspl and no Mspl, but a secondary sector at IR2 and MA respectively; 7–8 antefurcal crossveins; arculus straight with widely separate origins for RP and MA; posttrigonal space with three rows of cells directly distal of triangle, with no convex intercalary vein originating at triangle; hypertriangle

Fig. 96. *Magnathemis marcusthorhalli* n. gen., n. sp., female holotype; WDC 105. – Scale: Ruler in mm.

free; triangle equilateral and divided into two cells by a single curved crossvein that connects the upper and the distal side of the triangle; distal side MAb straight; subtriangle elongate, narrow and 2-celled; pseudo-analis not hypertrophied; MP and CuA distally divergent; CuA with six posterior branches (cubital area max. 3–4 cells wide).

Hind wings 36.8 mm long, and 13.2 mm wide; basal space free; between Ax1 and Ax2 there are two secondary antenodals; Ax1 is close to the arculus, Ax2 on the level of the distal angle of triangle; secondary antenodals only partly preserved but non-aligned; long "cordulegastrid gap" of antesubnodal crossveins; nine postnodal crossveins, non-aligned with the 11–12 postsubnodal crossveins; a short but distinct 'libelluloid gap' of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 strongly divergent with 3–4 rows of cells in between at stigmal brace; pterostigma strongly braced and with 5–6 crossveins beneath it; primary IR1 indistinct; pseudo-IR1 distinct, originating on RP1 beneath distal third of pterostigma; two or three rows of cells between RP1 and pseudo-IR1; two rows of cells between distal parts of RP2 and IR2; a single lestine oblique vein between RP2 and IR2 two cells distal of subnodus; 2–3 bridge crossveins basal of oblique vein; two rows of cells between the distal parts of RP3/4 and MA; no Rspl and no Mspl, but a secondary sector at IR2 and MA respectively; 4–5 antefurcal crossveins; arculus straight and oblique, with widely separate origins for RP and MA; posttrigonal space with four rows of cells directly distal of triangle, and with a convex intercalary vein originating at triangle; hypertriangle free; triangle equilateral and divided into two cells by a single horizontal crossvein; distal side MAb straight; subtriangle elongate, narrow and 2-celled; pseudo-analis not hypertrophied; gaff slightly elongated; MP and CuA distally divergent with 2–3 rows of cells between them; CuA with six posterior branches (cubital area eight cells wide); anal loop ill-defined and posteriorly open; 2–3 secondary branches of AA between CuAb and wing base; the anal margin is rounded, thus it is a female specimen.

Family Cratopetaliidae n. fam.

Typus familiaris: *Cratopetalia* n. gen.

Diagnosis. – Same as for type genus since monotypic.

Genus *Cratopetalia* n. gen.

Typus generis: *Cratopetalia whiteheadi* n. sp.

Derivatio nominis: Named after the Crato Formation and the (invalid) dragonfly genus *Petalia* Hagen, 1854.

Diagnosis. – Wings about 43 mm long; pterostigmata unbraced and covering six cells; RA and RP1 strongly divergent at wing apex; pseudo-IR1 absent; primary IR1 strong and very long, originating on RP2 but distally closely parallel to RP1; RP2 and IR2 closely parallel with a single row of cells between them; a single lestine oblique vein 2–5 (usually four) cells distal of subnodus; 4–5 bridge crossveins in forewings and 6–7 in hind wings; two rows of cells between distal parts of RP3/4 and MA that are not undulate; five antefurcals in forewings and 2–4 in hind wings; three secondary antenodals between Ax1 and Ax2; short "cordulegastrid gap" and "libelluloid gap"; sectors (RP and MA) of arculus with separate origins on RA; hypertriangles free; in both wings the triangles are very elongate and 2-celled, with a slightly sigmoidal distal side; subtriangles unicellular, smaller in the hind wing; CuA with eight posterior branches in hind wing; anal loop closed and 3-celled; gaff somewhat elongated in hind wings; male anal triangle 3-celled, but not divided by a Y-shaped vein as in most other Anisoptera.

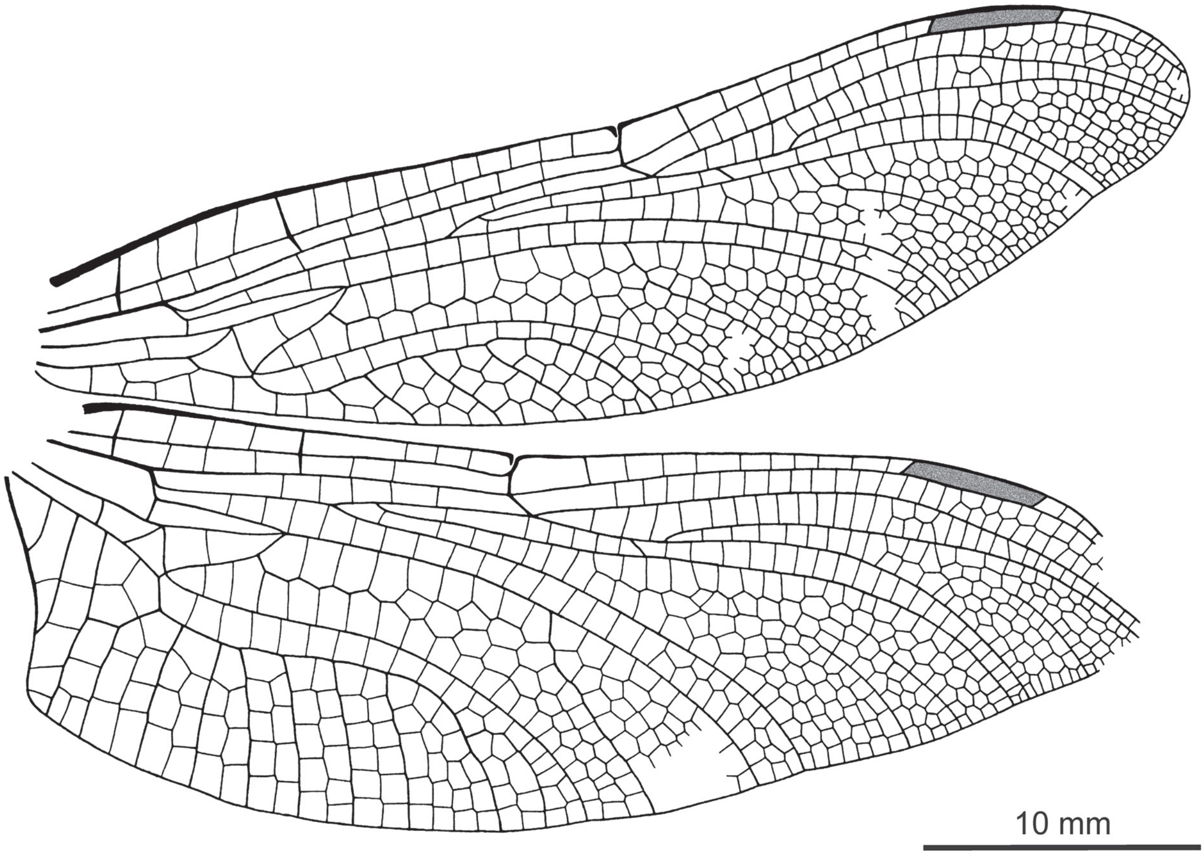
Discussion. – A "cordulegastrid gap", longitudinal triangles in both wings, and a slightly elongated gaff in hind wings, are putative synapomorphies with Cavilabiata, especially with Cordulegastridae and Neopetaliidae. Plesiomorphic characters like numerous cells beneath pterostigmata and numerous branches of CuA in hind wings and some other differences exclude a relationship with Brachystigmata. There are no visible synapomorphies with Cordulegastridae. The strongly developed and elongated primary IR1 is a putative synapomorphy with Neopetaliidae. However, all other defining characteristics of the latter family are absent in this new taxon. Furthermore, it has two rather unique character states within Anisoptera: RP and MA have parallel, but separate origins from RA at the angular arculus; and RA and RP1 are strongly divergent at the wing apex with 2–3 rows of cells between them. The latter character is even a unique autapomorphy among all fossil and Recent Odonata! The unbraced pterostigmata, absent pseudo-IR1, course of primary IR1, and the pattern of the male anal triangle are further rare or unique autapomorphies. Consequently, a separate new family appears to be well-justified.

A reviewer questioned if the very strange feature of the divergent veins RA and RP1 could be a teratology. However, this can be clearly excluded, because the character is invariably present in all four wings. Furthermore, teratological wings typically do not show such a regular pattern of wing venation but exhibit a messed up venation with fusing and unfusing wing veins.

Cratopetalia whiteheadi n. sp.
Figs. 97–99

Holotype: Male specimen SMNS 66389 (old no. E100415) (Figs. 97–99).

Derivatio nominis: Named after the late Anglo-American mathematician and philosopher Alfred North Whitehead,



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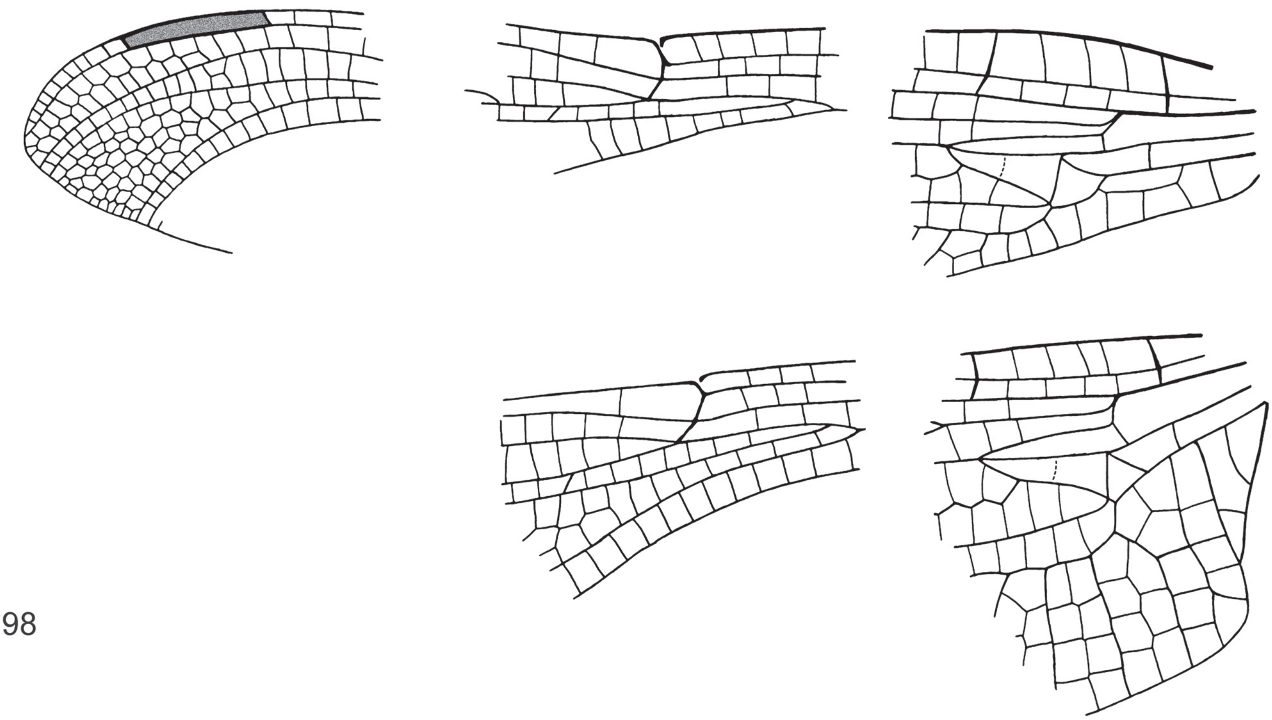

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Figs. 97–98. *Cratopetalia whiteheadi* n. gen., n. sp., male holotype; SMNS 66389. – **Fig. 97**. Right wings. **Fig. 98**. Details of base, nodus, and apex of left forewing, and base and nodus of left hind wing.

Fig. 99. *Cratopetalia whiteheadi* n. gen., n. sp., male holotype; SMNS 66389.

the founder of modern Process Philosophy, because his contribution to philosophy is at least as unique as the strange wing venation of this dragonfly.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, north-east Brazil.

Diagnosis. – Same as for genus since monotypic.

Description of holotype (Figs. 97–99). – A pterothorax with two legs and all four wings of a male dragonfly.

Forewings 43.2 mm long; basal space free; between Ax1 and Ax2 there are three non-aligned secondary antenodals in both rows; Ax1 is far basal of arculus, Ax2 on the level of the distal angle of triangle; about ten secondary antenodals distal of Ax2 in the first row, non-aligned with the seven antenodals in the second row; short “cordulegastrid gap” of antesubnodal crossveins; eight postnodal crossveins, non-aligned with the postsubnodal crossveins; a short but distinct ‘libelluloid gap’ of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma unbraced and with 5–6 crossveins beneath it; RA and RP1 become strongly divergent at the pterostigma with 2–3 rows of cells between them; primary IR1 hypertrophied, strong and very long, originating on RP2 but distally closely parallel to RP1; pseudo-IR1 absent; RP2 and IR2 strictly parallel and even converging towards wing margin, with a single rows of cell between them; a single lestine oblique vein between RP2 and IR2 two (right wing) or 3.5 (left wing) cells distal of subnodus; 4–5 bridge crossveins basal of oblique vein; two rows of cells between the distal parts of RP3/4 and MA that are not undulate; no Rspl and no Mspl, but a secondary sector at IR2 and MA respectively; five antefurcal crossveins; arculus angular with RP and MA having parallel and separate origins at RA; posttrigonal space with two rows of cells directly distal of triangle, and with a convex intercalary vein originating at triangle; hypertriangle free; triangle strongly elongate and divided into two cells by a single vertical crossvein; distal side MAb somewhat sigmoidal; subtriangle of normal size and undivided; pseudo-analis slightly hypertrophied; MP and CuA distally divergent; CuA with five posterior branches (cubital area max. four cells wide); anal area with an elongate cell.

Hind wings 41.9 mm long and 14.2 mm wide; basal space free; between Ax1 and Ax2 there are 3–4 non-aligned secondary antenodals in both rows; Ax1 is far basal of arculus, Ax2 on the level of the distal angle of triangle; secondary antenodals distal of Ax2 only partly preserved but non-aligned; short “cordulegastrid gap” of antesubnodal crossveins; ten postnodal crossveins, non-aligned with the postsubnodal crossveins; a short but distinct ‘libelluloid gap’ of postsubnodal crossveins; RP2 originating at subnodus; RP1 and RP2 divergent; pterostigma unbraced and with 6–7 crossveins beneath it; RA and RP1 become divergent at the pterostigma with two rows of cells between them; primary IR1 hypertrophied, strong and very long, originating on RP2 but distally closely parallel to RP1; pseudo-IR1 absent; RP2 and IR2 strictly parallel and even converging towards wing margin, with a single rows of cell between them; a single lestine oblique vein between RP2 and IR2 4.5 cells distal of subnodus; 6–7 bridge crossveins basal of oblique vein; two rows of cells between the distal parts of RP3/4 and MA that are not undulate but somewhat divergent; no Rspl and no Mspl, but a secondary sector at IR2 and MA respectively; three antefurcal crossveins; arculus angular with RP and MA having parallel and separate origins at RA; posttrigonal space with two rows of cells directly distal of triangle, and with a convex intercalary vein originating at triangle; hypertriangle free; triangle strongly elongate and divided into two cells by a single vertical crossvein; distal side MAb somewhat sigmoidal; subtriangle small and undivided; pseudo-analis not hypertrophied; gaff somewhat elongated; MP and CuA distally divergent with 2–4 rows of cells between them; CuA with eight posterior branches (cubital area five cells wide); anal loop transvers, posteriorly closed, and 3-celled; there is a 3-celled anal triangle (not divided by the usual Y-shaped vein) and a distinct anal angle, thus it is a female specimen.

3.1.5. Other putative new dragonfly taxa from the Crato Formation

M a t e r i a l : Specimen no. 106 (old no. MSF Z52) in coll. WDC.

D e s c r i p t i o n (Fig. 100). – A nearly complete male dragonfly, of which only the head and one forewing is missing; the wing venation is only poorly preserved; forewing 34.0 mm long; hind wing 32.5 mm long and a maximum of 11.0 mm wide; hind wing triangle and subtriangle transverse and free; RP1 and RP2 very close together up to level of the pterostigma; pterostigma long with a very acute basal edge and a very slightly basally displaced stigmal brace, which is very oblique as well; apparently no Mspl or Rspl, and no hypertrophied vein IR1; two rows of

Fig. 100. Gen. et sp. nov. incertae sedis, male specimen; WDC 106 (Z52). – Scale: Ruler in mm.

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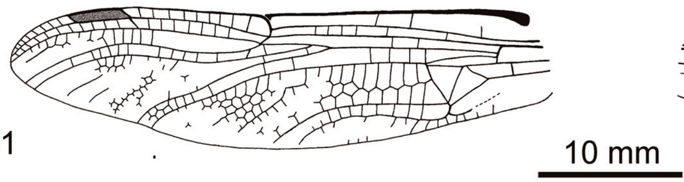

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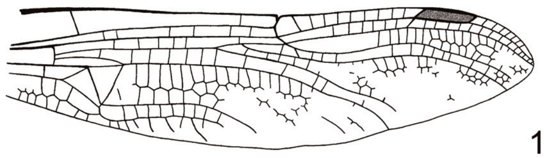

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Figs. 101–103. *Araripeliupanshania annesuseae* BECHLY et al., 2001; SMNS 66608. – **Fig. 101**. Left forewing. **Fig. 102**. Right forewing. **Fig. 103**. Head, thorax, and pair of forewings.

cells in post-trigonal area of both wings; hind wing with anal triangle (male); cerci 1.9 mm long.

Discussion. – As already suggested by BECHLY (2007: 222) this specimen probably represents a further new taxon of uncertain familial affinities, but the poor preservation of the wing venation suggests that a formal description of a new genus and species should be postponed until better preserved specimens are eventually discovered.

Material: Specimen no. SMNS 66608 (old no. H19).

Description (Figs. 101–104). – Head, thorax, two forelegs and both forewings (complete but poorly preserved): width of head 10.1 mm; compound eyes approximated but not fused (Fig. 104); forelegs very short (Fig. 104); wing span 82.3 mm; forewing length 38.0 mm; pterostigma elongate (4.5–5 cells long) and braced; pseudo-IR1 originates distal of pterostigma; RP2 closely parallel to RP1 with only one row of cells in between them, even below basal part of pterostigma; RP2 and IR2 as well as RP3+4 and MA slightly undulate; lestine oblique vein one cell distal of subnodus; triangle somewhat transverse, distal side straight; hypertriangles elongate, narrow and apparently undivided; subtriangle transverse and narrow; no Mspl or Rspl, and no post-trigonal intercalary vein at triangle; only two rows of cells in post-trigonal area.

Discussion. – This specimen was briefly discussed and figured by BECHLY (2007: 219, pl. 10k) as putative new species of Mesuropetalidae or rather Liupanshaniidae. A careful re-examination of this poorly preserved specimen showed that it is indeed a Liupanshaniidae that can be attributed to the described species *Araripeliupanshania annesuseae* BECHLY et al., 2001, because all visible characters agree with such an attribution and there are no significant differences.

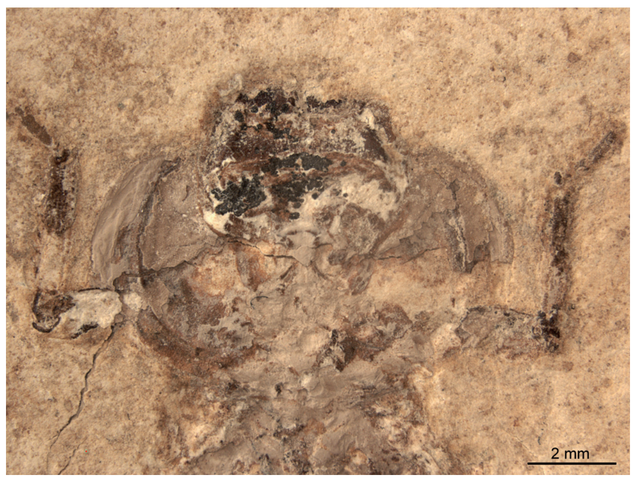

Fig. 104. *Araripeliupanshania annesuseae* BECHLY et al., 2001, head; SMNS 66608.

3.1.6. Further new findings of already known species

A new complete male specimen of *Araripegomphus andreneli* BECHLY, 1998 in coll. WDC (without number) shows for the first time a preserved colour pattern for this species and for Crato Anisoptera (Fig. 105). A new complete specimen of *Araripephlebia mirabilis* BECHLY, 1998 in coll. WDC (without number), probably a male specimen (Fig. 106), has a very well preserved head with approximated compound eyes and well preserved anal appendages (foliate and hairy cerci that are 3.2 mm long and 1.0 mm wide, and an elongate, clublike epiproct that is 3.0 mm long and 0.6 mm wide) (Fig. 107). Finally, a new specimen of the aeschnidiid *Wightonia araripina* CARLE & WIGHTON,

Fig. 105. *Araripegomphus andreneli* BECHLY, 1998, complete female specimen with preserved colour pattern (body length 57 mm, wing span 77 mm); WDC without number. – Without scale.

Fig. 107. *Araripephlebia mirabilis* BECHLY, 1998, anal appendices; WDC without number.

Fig. 106. *Araripephlebia mirabilis* BECHLY, 1998, complete specimen with well preserved head and anal appendices; WDC without number. – Scale: Ruler in mm.

Fig. 108. *Wightonia araripina* CARLE & WIGHTON, 1990; MSF without number. – Scale: Ruler in mm.

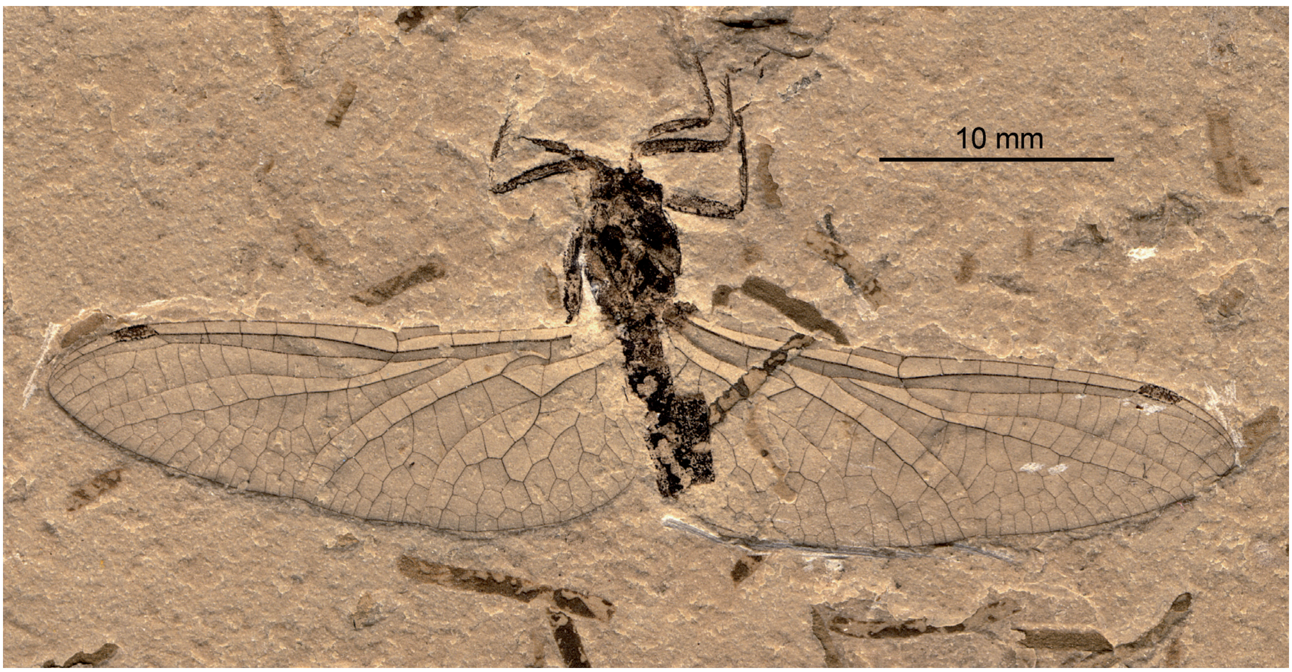

Fig. 109. *Cratocordulia borschukewitzi* BECHLY, 1998, body fragment and pair of hind wings; MSF E100407.

1990 in coll. MSF (without number, Fig. 108) shows that the pterostigmata are indeed completely absent in both wings as suggested by the original description of CARLE & WIGHTON (1990). Specimens that clearly do possess dark pterostigmata have been featured by BECHLY (1998) either represent sexual dimorphism or a different new species. Furthermore, the new specimen confirms the presence of two rows of cells in the antenodal space, contrary to the original description.

3.1.7. Additional corrections of collection numbers and depositions of fossil dragonflies mentioned in BECHLY (2007)

C. (Procordulagomphus) xavieri NEL & ESCUILLIÉ, 1994: BECHLY (2007: 212) mentions two specimens of this species from the Senckenberg collection with the old numbers SMF Q79 and SMF Q82. Specimen SMF Q82 has received the new collection number SMF VI 874. The second specimen at Senckenberg has the old number N33 and the new number SMF VI 875. A specimen with no. Q79 could not be found at Senckenberg and might be in collection MSF instead of SMF.

Cratocordulia borschukewitzi BECHLY, 1998: The only specimen in the Senckenberg collection has the collection number SMF VI 875 (old no. N37). The specimen with no. SMF Q66, mentioned by BECHLY (2007: 218), could not be found at Senckenberg and might be in coll. MSF as well. A new specimen no. E100407 in coll. MSF with very well-preserved hind wings is featured in Fig. 109.

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