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Two new fossil dragonfly species (Insecta: Odonata: Anisoptera: Araripegomphidae and Lindeniidae) from the Crato Limestone (Lower Cretaceous, Brazil)

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With 10 Figures

Summary

Two new dragonfly taxa are described from the Lower Cretaceous limestones of the Crato Formation (Brazil): *Araripegomphus hanseggeri* n. sp. and *Cratolindenia knuepfae* n. gen. n. sp. which both belong to the gomphid clade within Anisoptera. With at least 10 known species the gomphids represent the most diverse and also most abundant group of dragonflies at this locality, which has to be regarded as strong evidence for the presence of rivers. While all other known gomphid species belong to the Araripegomphidae and Proterogomphidae – Cordulagomphinae, the new genus *Cratolindenia* appears to be the first record of Lindeniidae – Lindeniinae from this locality.

Zusammenfassung

Zwei neue Libellentaxa werden aus den unterkretazischen Plattenkalken der Crato-Formation (Brasilien) beschrieben: *Araripegomphus hanseggeri* n. sp. und *Cratolindenia knuepfae* n. gen. n. sp., die beide zur monophyletischen Gruppe der Gomphiden innerhalb der Anisoptera gehören. Mit mindestens 10 bekannten Arten sind die Flussjungfern die artenreichste und auch individuenreichste Libellengruppe dieser Fundstelle, was als ein deutliches Indiz auf das Vorhandensein von Fließgewässern zu werten ist. Während alle anderen bekannten Gomphidenarten zu den Araripegomphidae und Proterogomphidae – Cordulagomphinae gehören, ist die neue Gattung *Cratolindenia* offenbar der erste Nachweis der Lindeniidae – Lindeniinae von dieser Lokalität.

1. Introduction

In the last years numerous new fossil dragonflies from the Lower Cretaceous of the Crato Formation limestones in NE Brazil could be scientifically studied and described (Carle & Wighton, 1990; Bechly, 1998b). Meanwhile, 32 species and several hundred specimens are known (Bechly, 1998b) which suggests a rather high diversity of dragonflies in the surrounding habitats of the Crato lagoon. In this work I describe two further dragonfly species which belong to the clade Gomphides within Anisoptera. With totally 10 different species (about 29 % of all odonate species known from this locality) this clade proves to be the most diverse dragonfly group from the Crato limestones. This agrees with the fact that about 56 % of the fossil dragonfly larvae from this locality belong to the gomphid clade (Bechly, 1998b). Since the majority of extant gomphids are adapted to fluviatile habitats, the abundance of gomphid dragonflies at this locality strongly suggests the presence of various rivers and brooks that flew into the Crato lagoon (Bechly, 1998a).

2. Material and methods

The drawings were made with a camera lucida and a binocular microscope, while the photos were made by directly scanning the concerning fossil specimens with a flatbed scanner. The nomenclature of the dragonfly wing venation is based on the interpretations of Riek & Kukalová-Peck (1984), amended by Nel et al. (1993) and Bechly (1996), and the phylogenetic classification of Gomphides is based on Bechly (1996, 2000). The systematic analysis is based on the principles of consequent Phylogenetic Systematics (sensu Hennig, 1966, 1969, and Wägele, 2000).

3. Systematic Palaeontology

Class Insecta Linneaus, 1758 (= Hexapoda Latreille, 1825)
Pterygota Brauer, 1885
Order Odonata Fabricius, 1793
Suborder Anisoptera Selys in Selys & Hagen, 1854
Euanisoptera Bechly, 1996
Exophytica Bechly, 1996
Gomphides Bechly et al., 1998
Family Araripegomphidae Bechly, 1996

Genus *Araripegomphus* Nel & Paicheler, 1994

Araripegomphus hanseggeri n. sp.
Figs 1–8

Holotype: Female specimen SMNS no. 64415 (old no. H13) in collection of the Staatl. Museum f. Naturkunde, Stuttgart, Germany. This specimen was kindly donated to this museum by Mr Hans Egger (Erding).

Paratype and allotype: Male specimen SMNS no. 64416a,b (old nos H21 and H20) in collection of the Staatl. Museum f. Naturkunde, Stuttgart, Germany. Several further specimens with identical characters have been seen in the collections of a German fossil trader.

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

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

Derivation of name: Named in honour of Mr Hans Egger (Erding).

Diagnosis. – This new species is very similar to the type species *A. cretacicus* NEL & PAICHELER, 1994: About three intercalary veins between IR2 and RP3/4, and two intercalary veins between MA and MP; no Rspl and Mspl; male hindwing without any posterior branch of anal vein between anal loop and anal triangle; female hindwing with three posterior branches of anal vein; pterostigma distinctly braced in all wings and covering 3.5 cells. It differs from the other two species (*A. cretacicus* NEL & PAICHELER, 1994 and *A. andreneli* BECHLY, 1998) of the same genus by the following characters: Average wing length somewhat smaller (forewing only 32 mm long); only one secondary antenodal crossvein between the two primaries Ax1 and Ax2 in the forewing (autapomorphy); hindwing CuAa with 5–6 posterior branches, instead of 4–5 (usually 4); directly distal of the oblique vein there is a gap of crossveins between RP2 and IR2 in both pairs of wings (autapomorphy); area between RP2 and IR2 distally widened with 2–4 rows of cells between these veins in both pairs of wings (autapomorphy); hypertriangulum quadrangular, since the trigonal vein is ending on the distal side MAb of the discoidal triangle in both pairs of wings (autapomorphy); anal loop divided into 2–3 cells and distinctly closed posteriorly in both sexes. Furthermore, it differs from the type-species *A. cretacicus* by the presence of only two rows of cells in the basal part of the postdiscoidal area in both pairs of wings (as in *A. andreneli*).

Description

Holotype specimen SMNS no. 64415 (Figs 1–5): A nearly complete and well-preserved fossil dragonfly with all four wings in outstretched position, preserved in ventral aspect. The apparent abdomen has been "reconstructed" (painted)

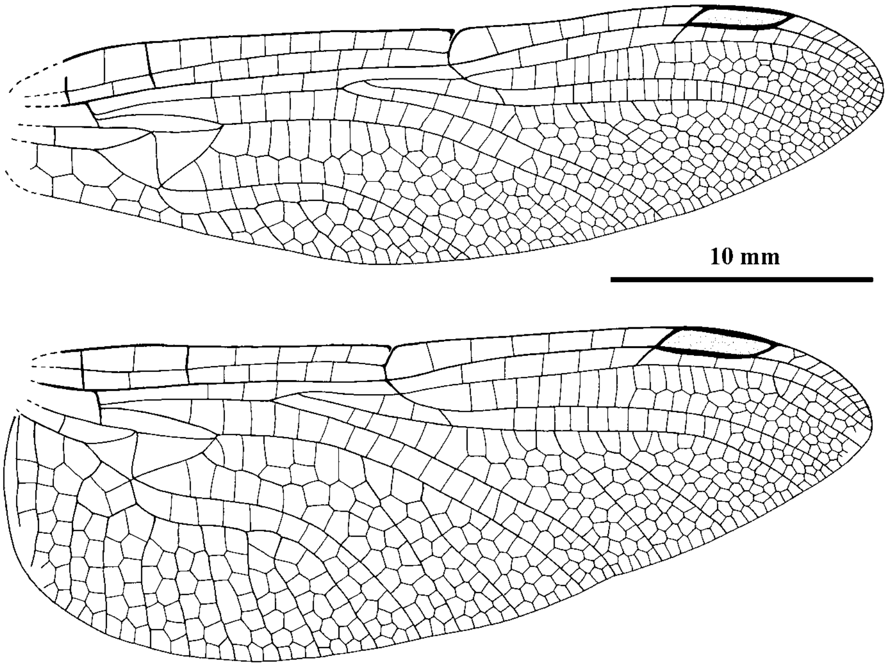

Fig. 1. *Araripegomphus hanseggeri* n. sp., female holotype SMNS no. 64415, left wings (in ventral aspect). Scale 10 mm.

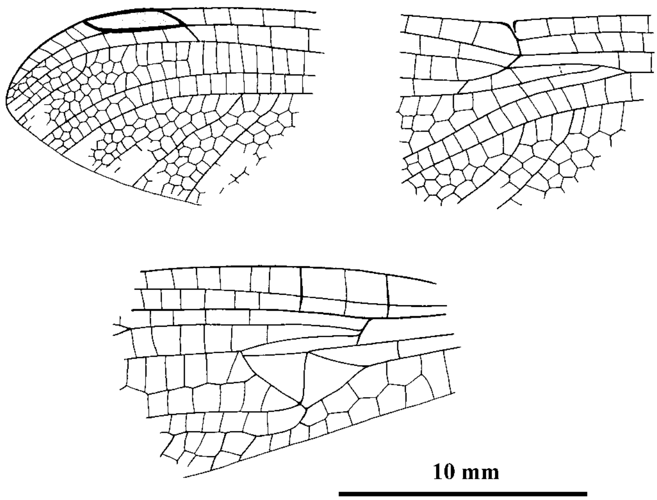

Fig. 2. *Araripegomphus hanseggeri* n. sp., female holotype SMNS no. 64415, right forewing (in ventral aspect). Scale 10 mm.

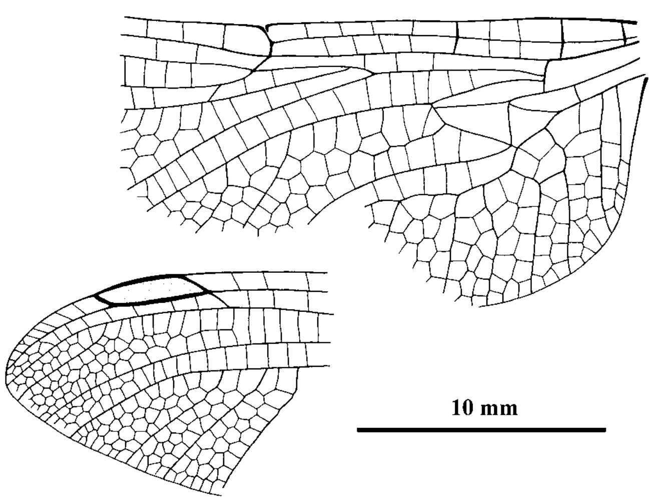

Fig. 3. *Araripegomphus hanseggeri* n. sp., female holotype SMNS no. 64415, right hindwing (in ventral aspect). Scale 10 mm.

by the Brazilian preparator, while the true abdomen is missing. The legs are preserved, but folded beneath the thorax, so that no details of thorax or legs are visible. The head is well-preserved (max. width 7 mm). The total wing span is 69.5 mm. The wings probably have been hyaline. The shape of the hindwing with rounded anal area and no anal triangle shows that it is a female specimen. The measurements were mostly taken from the left pair of wings (the right pair in the fossil, since preserved in ventral aspect).

Forewing: Length, 33.6 mm; width at nodus, 8.9 mm; distance from base to nodus, 17.3 mm (the nodus is situated at about 51 % of the wing length); distance from nodus to pterostigma, 9.2 mm; distance from base to arculus, 3.3 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.7 mm basal of arculus and Ax2 is 3.3 mm distal of Ax1 (on the level of basal side of discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2 (more or less aligned); distal of Ax2 there are nine secondary antenodal crossveins between costal margin and ScP and eight of them between ScP and RA; only four antesubnodal crossveins, with a long gap near the arculus and a long "cordulegastrid gap" (sensu BECHLY, 1996) directly basal of the subnodus; secondary antenodal crossveins are non-aligned; seven postnodal crossveins between nodus and pterostigma, and only four postsubnodal crossveins (not aligned); no distinct "libellulid gap" (sensu BECHLY, 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 3.4 mm long and max. 0.9 mm wide; the pterostigma is distinctly braced and covers 3.5 cells; RA is distinctly broadened along the pterostigma; arculus is close to Ax1 and totally straight; bases of veins RP and MA (sectors of arculus) separated at arculus; the hypertriangle is 4.7 mm long and max. 0.6 mm wide; the hypertriangle is free and its costal side (MA) is slightly curved; the hypertriangle is quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; discoidal triangle transverse and free; length of basal side of discoidal triangle, 2.2 mm; length of its costal side, 2.7 mm; length of its distal side MAb, 3.3 mm; MAb is more or less straight, but there is a postdiscoidal intercalary vein originating at MAb; a distinct pseudo-anal vein PsA (= AA0) delimits a large unicellular subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.7 mm basal of arculus; anal area max. 2.1 mm wide with two rows of cells; cubito-anal area max. 2.2 mm wide with up to three rows of cells; CuA with four posterior branches; MP ends on the level of the nodus; basal postdiscoidal area with only two rows of cells; postdiscoidal area distally distinctly widened (width near discoidal triangle, 2.5 mm; width at hind margin, 6.1 mm); no Mspl, but two or three weak intercalary veins in the distal postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between their basal parts, but with 2–3 rows of cells between their distal parts; first branching of RP ("midfork") 4.7 mm basal of subnodus; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 1.3 mm and 1.5 cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus (two basal of oblique vein); directly distal of the oblique vein there is a gap of crossveins between RP2 and IR2; RP2 and IR2 relatively straight and parallel with only one row of cells between them up to the level of the distal end of the pterostigma, but distally with 2–3 rows of cells between these veins; no Rspl, but two distinct intercalary veins in the area between IR2 and RP3/4; RP1 and RP2 divergent with one rows of cells between them up to shortly basal of the level of the pterostigma; pseudo-IR1 originates on RP1 below distal side of pterostigma; two rows of cells between pseudo-IR1 and RP1 and three to four rows of cells between pseudo-IR1 and RP2.

Hindwing: Length, 32.7 mm; width at nodus, 11.5 mm (max. width, 12.1 mm); distance from base to nodus, 14.0 mm (the nodus is situated basal of midwing at about 43 % of the wing length); distance from nodus to pterostigma, 10.4 mm; distance from base to arculus, 2.9 mm; Ax1 and Ax2 are aligned and stronger than the

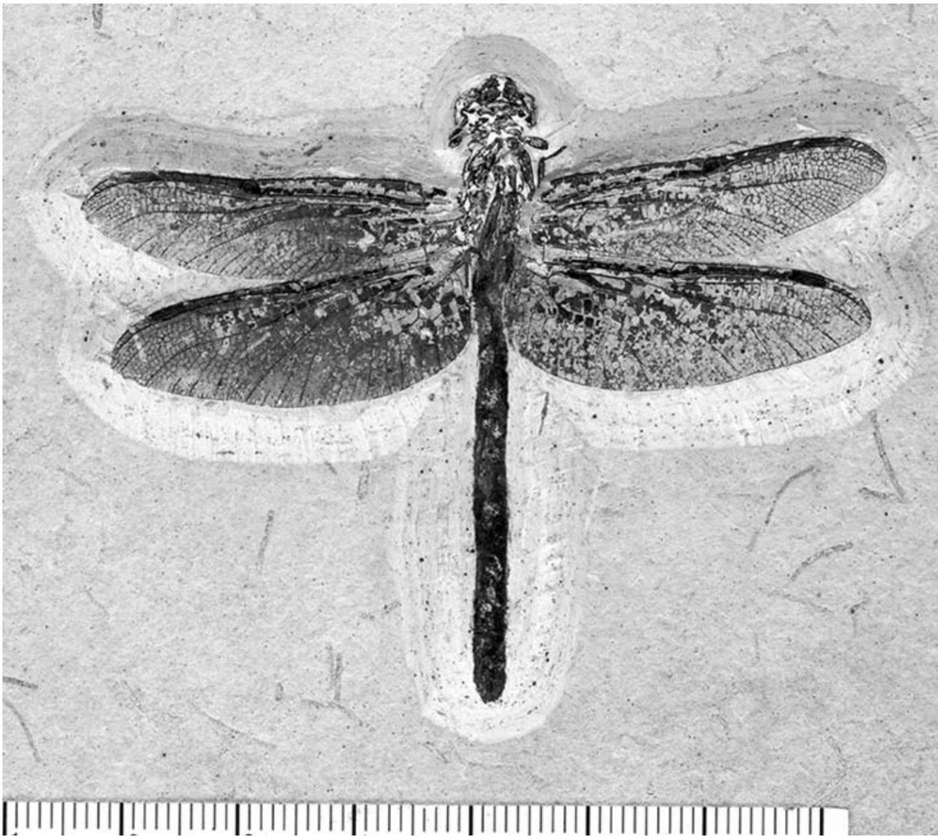

Fig. 4. *Araripegomphus hanseggeri* n. sp., female holotype SMNS no. 64415. Scale as indicated by rule.

other antenodals (bracket-like); Ax1 is 0.4 mm basal of arculus and Ax2 is 4.0 mm distal of Ax1 (about the level of the distal third of the discoidal triangle); one (left wing) or two (right wing) secondary antenodal crossvein(s) between Ax1 and Ax2 (more or less aligned); distal of Ax2 there are four secondary antenodal crossveins between the costal margin and ScP and five of them between ScP and RA; the secondary antenodal crossveins distal of Ax2 are non-aligned; three antesubnodal crossveins, with a long "cordulegastrid gap" (sensu BECHLY, 1996) directly basal of the subnodus, as well as a long gap directly distal of the arculus; six postnodal crossveins between nodus and pterostigma, and five postsubnodal crossveins (not aligned); no distinct "libellulid gap" (sensu BECHLY, 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 3.9 mm long and max. 1.1 mm wide; the pterostigma is distinctly braced and covers three (left wing) to three and a half (right wing) cells; RA is distinctly broadened along the pterostigma; arculus is close to Ax1 and totally straight; the origins of RP and MA (sectors of arculus) are shortly separated at the arculus; the hypertriangle is 4.4 mm long and max. 0.8 mm wide (distinctly wider than in the forewing); the hypertriangle is free and its costal side (MA) is curved; the hypertriangle is quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; the discoidal triangle is

Fig. 5. *Araripegomphus hanseggeri* n. sp., female holotype SMNS no. 64415, left wings (in ventral aspect). Without scale.

elongate and free; length of basal side of discoidal triangle, 1.8 mm; length of its costal side, 3.0 mm; length of its distal side MAb, 3.6 mm; MAb is angled and a post-discoidal intercalary vein originates at this angle; pseudo-anal vein PsA is somewhat less distinct than in the forewing; subdiscoidal triangle smaller than in forewing, but as well free; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.4 mm basal of arculus; anal area max. 6.7 mm wide with seven rows of cells; cubito-anal area max. 5.0 mm wide with up to 6–7 rows of cells; CuAa with five posterior branches; CuAb distinctly developed; "gaff" short; anal loop quadrate and three-celled, and well-closed posteriorly; MP ends on level of nodus; the area between CuA and MP is basally narrow (with only one row of cells) and distally somewhat widened (with 2–3 rows of cells); only two rows of cells in the most basal part of the postdiscoidal area; the postdiscoidal area is distally strongly widened (width near discoidal triangle, 2.5 mm; width at hind margin, 6.5 mm); no Mspl, but two distinct intercalary veins in the distal part of the postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between their basal parts, but with 2–3 rows of cells between their distal parts; first branching of RP ("midfork") 5.0 mm basal of subnodus; three (left wing) or five (right wing) antefurcal crossveins between RP and MA basal of midfork; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 1.7 mm and 1.5 cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus (two basal of oblique vein); directly distal of the oblique vein there is a gap of crossveins between RP2 and IR2; RP2 and IR2 relatively straight and parallel with only one row of cells between them up to the level of the distal end of the pterostigma, but distally with 2–4 rows of cells between these

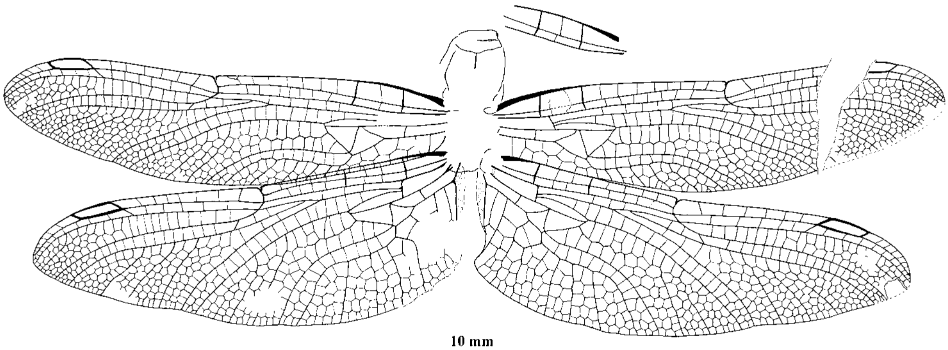

Fig. 6. *Araripegomphus hanseggeri* n. sp., male allotype SMNS no. 64416a, plate. Scale 10 mm (right and left pair of wings have been drawn separately and then mounted together, therefore their relative positions are slightly different from the original).

veins; no Rspl, but three distinct intercalary veins in the area between IR2 and RP3/4; RP1 and RP2 divergent, with one row of cells between them up to the basal end of pterostigma; pseudo-IR1 originates on RP1 below distal side of pterostigma; two rows of cells between pseudo-IR1 and RP1, and 3–4 rows of cells between pseudo-IR1 and RP2; wing base rounded without anal angle and anal triangle, thus it is a female specimen; three posterior branches of anal vein between CuAb and anal margin; no membranule is visible.

Paratype and allotype specimen SMNS no. 64416a,b (Figs 6–8): Plate (no. 64416a) and counterplate (no. 64416b) of a male dragonfly with all four wings preserved in connection with the thorax. Head, legs, and abdomen are missing. The total wing span is 68.0 mm.

Forewing: Length, 32.9 mm; width at nodus, 7.9 mm; distance from base to nodus, 17.1 mm (the nodus is situated at about 52 % of the wing length); distance from nodus to pterostigma, 9.2 mm; distance from base to arculus, 4.2 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.6 mm basal of arculus and Ax2 is 3.3 mm distal of Ax1 (on the level of basal side of discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2 (aligned); distal of Ax2 there are eight secondary antenodal crossveins between costal margin and ScP and seven of them between ScP and RA; five antesubnodal crossveins, with a long gap near the arculus and a long "cordulegastrid gap" (sensu Bechly, 1996) directly basal of the subnodus; secondary antenodal crossveins are non-aligned; six postnodal crossveins between nodus and pterostigma, and only 5–6 postsubnodal crossveins (not aligned); no distinct "libellulid gap" (sensu Bechly, 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.9 mm long and max. 0.9 mm wide; the pterostigma is distinctly braced and covers three cells; RA is broadened along the pterostigma; arculus is close to Ax1 and totally straight; bases of veins RP and MA (sectors of arculus) separated at arculus; the hypertriangle is 4.4 mm long and max. 0.6 mm wide; the hypertriangle is free and its costal side (MA) is slightly curved; the hypertriangle is quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; discoidal triangle transverse and free; length of basal side of discoidal triangle, 2.0 mm;

length of its costal side, 2.5 mm; length of its distal side MAb, 2.9 mm; MAb is weakly angled, with a postdiscoidal intercalary vein originating at the angle of MAb; a distinct pseudo-anal vein PsA (= AA0) delimits a large unicellular subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.4 mm basal of arculus; anal area max. 1.9 mm wide with two rows of cells; cubito-anal area max. 2.0 mm wide with up to three rows of cells; CuA with 5–6 posterior branches; MP ends on the level of the nodus; basal postdiscoidal area with only two rows of cells; postdiscoidal area distally distinctly widened (width near discoidal triangle, 2.2 mm; width at hind margin, 5.4 mm); no Mspl, but two weak intercalary veins in the distal postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between their basal parts, but with 2–3 rows of cells between their distal parts; first branching of RP ("midfork") 4.4 mm basal of subnodus; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 1.5 mm and 1.5 cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus (two basal of oblique vein); directly distal of the oblique vein there is a gap of crossveins between RP2 and IR2; RP2 and IR2 relatively straight and parallel with only one row of cells between them up to the level of the distal end of the pterostigma, but distally with 2–4 rows of cells between these veins; no Rspl, but three distinct intercalary veins in the area between IR2 and RP3/4; RP1 and RP2 divergent with one rows of cells between them up to the level of the basal end of pterostigma; pseudo-IR1 originates on RP1 below distal side of pterostigma; two rows of cells between pseudo-IR1 and RP1 and three rows of cells between pseudo-IR1 and RP2.

Hindwing: Length, 31.4 mm; width at nodus, 10.1 mm (max. width, 10.7 mm); distance from base to nodus, 13.7 mm (the nodus is situated basal of midwing at about 44 % of the wing length); distance from nodus to pterostigma, 10.6 mm; distance from base to arculus, 3.6 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.4 mm basal of arculus and Ax2 is 4.1 mm distal of Ax1 (about the level of the distal angle of the discoidal triangle); two secondary antenodal crossveins between Ax1 and Ax2 (imprecisely aligned); distal of Ax2 there are four secondary antenodal crossveins between the costal margin and ScP and also four of them between ScP and RA; the secondary antenodal crossveins distal of Ax2 are non-aligned; three or four antesubnodal crossveins, with a long "cordulegastrid gap" (sensu BECHLY, 1996) directly basal of the subnodus, as well as a long gap directly distal of the arculus; six or seven postnodal crossveins between nodus and pterostigma, and five postsubnodal crossveins (not aligned); no distinct "libellulid gap" (sensu BECHLY, 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 3.3 mm long and max. 0.9 mm wide; the pterostigma is distinctly braced and covers three cells; RA is distinctly broadened along the pterostigma; arculus is close to Ax1 and totally straight; the origins of RP and MA (sectors of arculus) are separated at the arculus; the hypertriangle is 4.2 mm long and max. 0.7 mm wide (distinctly wider than in the forewing); the hypertriangle is free and its costal side (MA) is curved; the hypertriangle is quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; the discoidal triangle is elongate and free; length of basal side of discoidal triangle, 1.8 mm; length of its costal side, 2.9 mm; length of its distal side MAb, 3.4 mm; MAb is angled and a postdiscoidal intercalary vein originates at this angle; pseudo-anal vein PsA is somewhat less distinct than in the forewing; subdiscoidal triangle small-

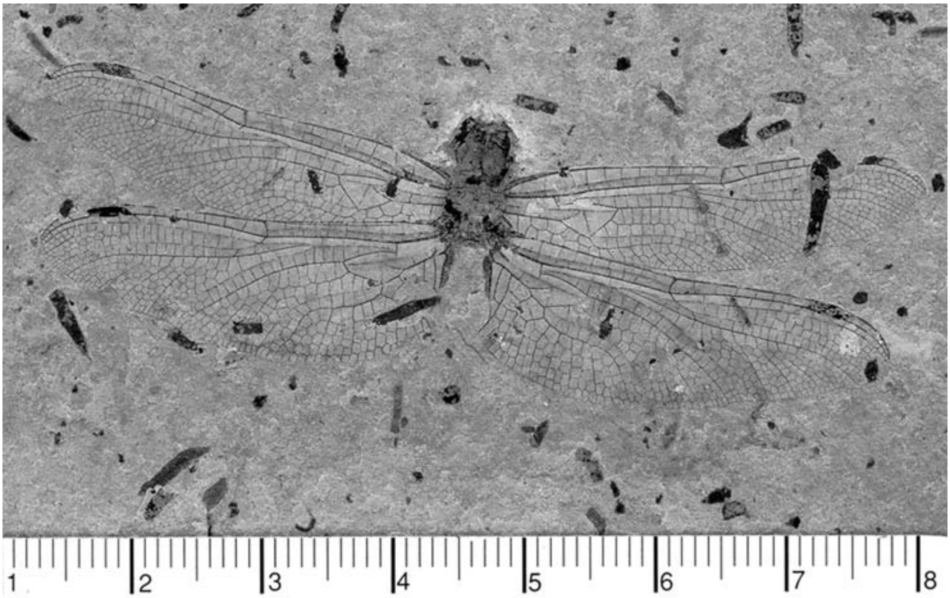

Fig. 7. *Araripegomphus hanseggeri* n. sp., male allotype SMNS no. 64416a, plate. Scale as indicated by rule.

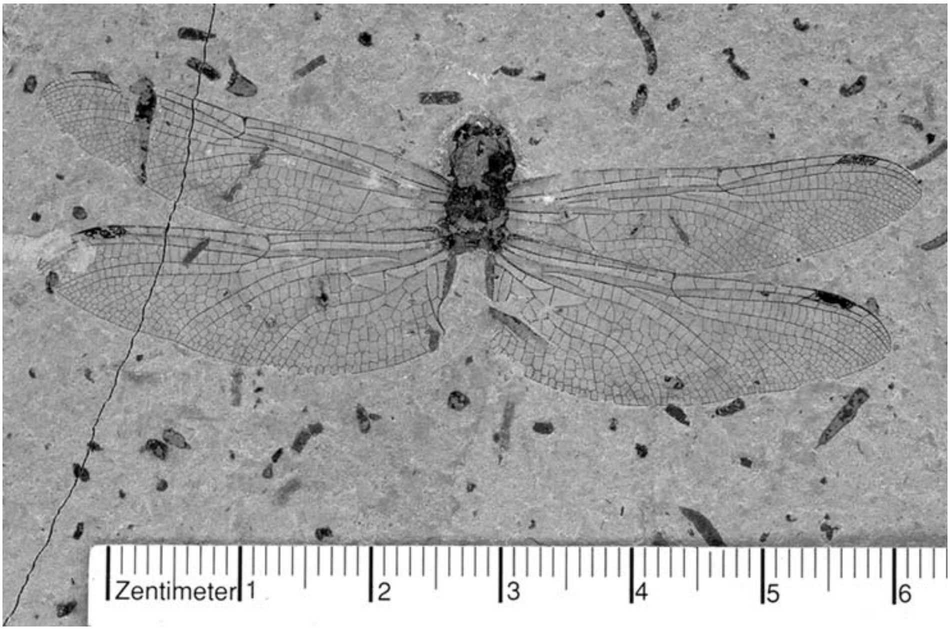

Fig. 8. *Araripegomphus hanseggeri* n. sp., male allotype SMNS no. 64416b, counterplate. Scale as indicated by rule.

er than in forewing, but as well free; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.2 mm basal of arculus; anal area max. 5.9 mm wide with six rows of cells; cubito-anal area max. 4.2 mm wide with five rows of cells; CuAa with four (right wing) or five (left wing) posterior branches; CuAb distinctly developed; "gaff" short; anal loop quadrate and two-celled, and well-closed posteriorly; MP ends on level of nodus; the area between CuA and MP is basally narrow (with only one row of cells) and distally somewhat widened (with 2–3 rows of cells); only two rows of cells in the most basal part of the postdiscoidal area; the postdiscoidal area is distally strongly widened (width near discoidal triangle, 2.3 mm; width at hind margin, 5.9 mm); no Mspl, but two distinct intercalary veins in the distal part of the postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between their basal parts, but with two rows of cells between their distal parts; first branching of RP ("midfork") 4.8 mm basal of subnodus; three (left wing) or four (right wing) antefurcal crossveins between RP and MA basal of midfork; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 1.8 mm and 1.5 cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus (two basal of oblique vein); directly distal of the oblique vein there is a gap of crossveins between RP2 and IR2; RP2 and IR2 relatively straight and parallel with only one row of cells between them up to the level of the distal end of the pterostigma, but distally with 2–3 rows of cells between these veins; no Rspl, but three distinct intercalary veins in the area between IR2 and RP3/4; RP1 and RP2 divergent, with one row of cells between them up to the basal end of pterostigma; pseudo-IR1 originates on RP1 below distal side of pterostigma; two rows of cells between pseudo-IR1 and RP1, and 3–4 rows of cells between pseudo-IR1 and RP2; wing base with anal angle and a long three-celled anal triangle (hind margin of anal triangle with straight basal part and a concave distal part, separated by a kink), thus it is a male specimen; only one posterior branch of anal vein between CuAb and anal triangle; a long and narrow membranule is visible in both hindwings.

Family Lindeniidae JACOBSON & BIANCHI, 1905

Genus *Cratolindenia* n. gen.

Type species: *Cratolindenia knuepfae* n. sp., by present designation.

Derivatio nominis: After the town of Crato near the type locality and the genus *Lindenia*.

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

Phylogenetic position. – Within Gomphides this new genus shares with Lindeniidae – Lindeniinae the following putative synapomorphies: Hypertriangle divided; IR2 and MA with a more or less distinct secondary branch; hindwing discoidal triangle longitudinal elongate with a strongly sigmoidal and angulated distal side, caused by the development of a more distinct supplementary sector (trigonal planate) in the postdiscoidal area (convergent to Hagenioidea); forewing discoidal triangle divided in more than two cells (convergent to a few Progomphidae and some Gomphoidini); forewing subdiscoidal triangle divided into three cells; arculus very close to Ax1 in both pairs of wings. Furthermore, the plesiomorphic presence of more than 5 antefurcal crossveins between RP and MA in the hindwing excludes a position within "higher" gomphids (clade Oligophlebiata). The plesiomorphic absence of some other groundplan apomorphies of Lindeniinae (e.g. IR2 apparently dichotomously forked shortly distal of oblique vein; hindwing discoidal triangle divided into more than 2 cells; supplementary cubito-anal-crossveins in forewing) indicates that this new genus belongs to the stemgroup of this taxon.

Cratolindenia knuepfae n. sp.

Figs 9–10

Holotype: Female specimen SMNS no. 64414 (old no. K29) in collection of the Staatl. Museum f. Naturkunde, Stuttgart, Germany. This specimen was kindly donated to this museum by Mrs Lotti Knüpf (Erbstadt).

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

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

Derivation of name: Named in honour of Mrs Lotti Knüpf (Erbstadt).

Diagnosis. – This interesting new genus and species is distinguished by the following combination of characters: Absence of an apparent dichotomic forking of IR2 (plesiomorphy), but secondary branches of IR2 and MA distinctly developed; absence of accessory cubito-anal crossveins (plesiomorphy); 2–3 rows of cells between the distal parts of RP3/4 and MA; 6–7 antefurcal crossveins between RP and MA in the hindwing (plesiomorphy); hypertriangulum quadrangular in both pairs of wings (autapomorphy); distal side MAb discoidal triangles strongly kinked; discoidal triangle transverse and three-celled in the forewing, but elongate and two-celled in the hindwing; forewing subdiscoidal triangle divided into three cells; pterostigma very long, covering six cells, and distinctly braced; presence of a short

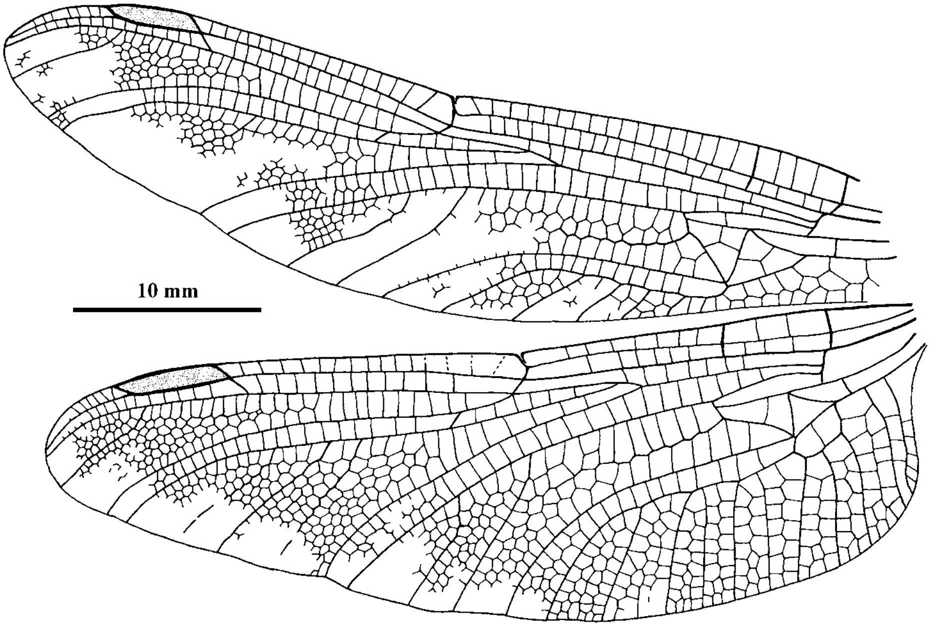

Fig. 9. *Cratolindenia knuepfae* n. gen. n. sp., female holotype SMNS no. 64414. Scale 10 mm.

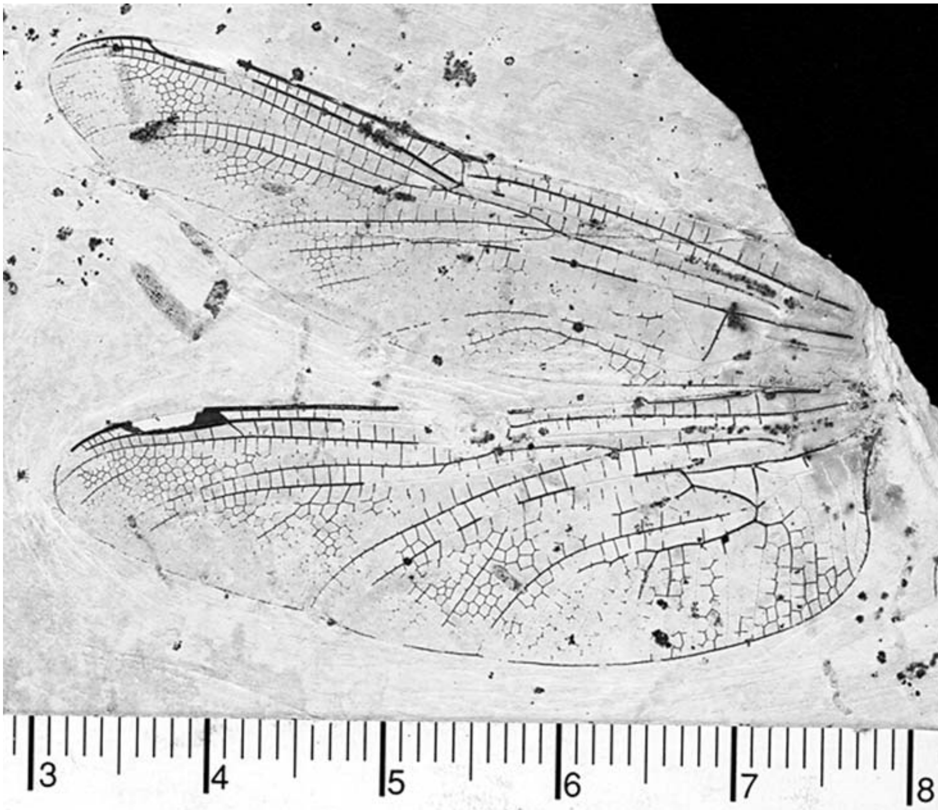

Fig. 10. *Cratolindenia knuepfae* n. gen. n. sp., female holotype SMNS no. 64414. Scale as indicated by rule.

"libelluid gap" (sensu BECHLY, 1996) and a long "cordulegastrid gap" (sensu BECHLY, 1996) directly distal and basal of the subnodus respectively (autapomorphy); oblique vein three cells distal of subnodus; 3–4 secondary antenodal crossveins between Ax1 and Ax2 in the forewing, and 2–3 in the hindwing; arculus very close to Ax1; anal loop elongate and two-celled.

Description

An isolated left pair of wings (preserved in dorsal aspect).

Forewing: Length, 49.6 mm; width at nodus, 11.8 mm; distance from base to nodus, 25.0 mm (the nodus is situated at about 50 % of the wing length); distance from nodus to pterostigma, 14.6 mm; distance from base to arculus, 4.4 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.4 mm basal of arculus and Ax2 is 5.1 distal of Ax1 (only slightly distal of basal side of discoidal triangle); only three (first row) or four (second row) secondary antenodal crossveins between Ax1 and Ax2 (not aligned); distal of Ax2 there are 17 secondary antenodal crossveins between costal margin and ScP and 16 of them between ScP and RA; ten antesubnodal crossveins with a short gap near the arculus and a long "cordulegastrid gap" (sensu BECHLY, 1996) directly basal of the subnodus; secondary antenodal crossveins are non-aligned; 17 postnodal crossveins between nodus and pterostigma, and 13 postsubnodal crossveins between subnodus and stigmal brace (not aligned with postnodal crossveins); a short "libellulid gap" (sensu Bechly, 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 4.6 mm long and max. 1.1 mm wide; the pterostigma is distinctly braced and covers six cells; RA is somewhat broadened along the pterostigma; arculus is very close to Ax1 and totally straight; bases of veins RP and MA (sectors of arculus) distinctly separated at arculus; the hypertriangle is 6.9 mm long and max. 0.8 mm wide; hypertriangle divided by a single crossvein and its costal side (MA) is slightly curved; the hypertriangle is distinctly quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; discoidal triangle transverse and three-celled; length of basal side of discoidal triangle, 3.1 mm; length of its costal side, 3.4 mm; length of its distal side MAb, 4.4 mm; MAb is strongly kinked with a strong but short postdiscoidal intercalary vein originating at the kink; a distinct pseudo-anal vein PsA (= AA0) delimits a large three-celled subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.6 mm basal of arculus; anal area max. 2.6 mm wide with 2–3 rows of cells; cubito-anal area max. 2.9 mm wide with up to five rows of cells; CuA with five posterior branches; MP ends distal of the level of the nodus; basal postdiscoidal area with three rows of cells; postdiscoidal area distally distinctly widened (width near discoidal triangle, 3.2 mm; width at hind margin, 9.0 mm); no Mspl, but two strong intercalary veins in the distal postdiscoidal area; RP3/4 and MA relatively straight and parallel, with only one row of cells between their basal parts, but with 2–3 rows of cells between their distal parts; first branching of RP ("midfork") 6.7 mm basal of subnodus; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 2.7 mm and three cells distal of subnodus; two bridge crossveins between RP2 and IR2 basal of subnodus (five basal of oblique vein); RP2 and IR2 parallel with only one row of cells between them up to the level of the distal end of pterostigma, but more distally 2–3 rows of cells between them; no Rspl, but one strong intercalary vein in the area between IR2 and RP3/4; RP1 and RP2 divergent with one row of cells between them in the basal half of the area basal of pterostigma, but with 2–3 rows of cells between them in the distal half of this area; pseudo-IR1 very distinct and originating on RP1 below distal side of pterostigma; three rows of cells between pseudo-IR1 and RP1, and about six rows of cells between pseudo-IR1 and RP2.

Hindwing: Length, 47.6 mm; width at nodus, 14.6 mm (max. width, 15.1 mm); distance from base to nodus, 21.3 mm (the nodus is situated at about 45 % of the wing length); distance from nodus to pterostigma, 16.0 mm; distance from base to arculus, 5.3 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.4 mm basal of arculus and Ax2 is 5.9 distal of Ax1 (slightly basal of distal angle of discoidal triangle); only two (first row) or three (second row) secondary antenodal crossveins between Ax1 and Ax2 (not aligned); distal of Ax2 there are seven secondary antenodal crossveins between costal margin and ScP and six of them between ScP and RA; seven antesubnodal crossveins with a long gap near the arculus and a long "cordulegastrid gap" (sensu Bechly, 1996) directly basal of the subnodus; secondary antenodal crossveins are non-aligned; about 15 postnodal crossveins between nodus and pterostigma, and at least 11 postsubnodal crossveins between subnodus and stigmal brace (not aligned with postnodal crossveins); the postnodal area directly distal of the nodus is destroyed, so that it is not visible if there was a short "libellulid gap" (sensu BECHLY, 1996); the pterostigma is 5.4 mm long and max. 1.0 mm wide; the pterostigma is distinctly braced and covers six cells; RA is somewhat broadened along the pterostigma; arculus is very close to Ax1 and totally straight; bases of veins RP and MA (sectors of arculus) distinctly separated at arculus; the hypertriangle is 6.0 mm long and max. 1.0 mm wide; hypertriangle not divided by crossveins and its costal side (MA) is distinctly curved; the hypertriangle is distinctly quadrangular, since the trigonal vein ends on MAb instead of the distal angle of discoidal triangle; discoidal triangle elongate and two-celled; length of basal side of discoidal triangle, 2.4 mm; length of its costal side, 4.0 mm; length of its distal side MAb, 4.9 mm; MAb is strongly kinked with a strong but short postdiscoidal intercalary vein originating at the kink; a distinct pseudo-anal vein PsA (= AA0) delimits an unicellular subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.1 mm basal of arculus; anal area max. 8.2 mm wide with 7–8 rows of cells; cubito-anal area max. 6.5 mm wide with up to nine rows of cells; CuA with four strong posterior branches; CuAb distinctly developed; "gaff" short; anal loop elongate (3.1 mm long) and two-celled; MP ends distal of the level of the nodus; basal postdiscoidal area with two rows of cells; postdiscoidal area distally strongly widened (width near discoidal triangle, 3.2 mm; width at hind margin, 8.7 mm); no Mspl, but two strong intercalary veins in the distal postdiscoidal area; RP3/4 and MA relatively straight and parallel, with only one row of cells between their basal parts, but with 2–3 rows of cells between their distal parts; first branching of RP ("midfork") 7.0 mm basal of subnodus; IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein 'O' between RP2 and IR2, 2.9 mm and three cells distal of subnodus; three bridge crossveins between RP2 and IR2 basal of subnodus (six basal of oblique vein); RP2 and IR2 parallel with only one row of cells between them up to the level of the distal end of pterostigma, but more distally at least two rows of cells between them; no Rspl, but three intercalary vein in the area between IR2 and RP3/4, one of which is rather strong; RP1 and RP2 divergent with one row of cells between them in the basal half of the area basal of pterostigma, but with 2–3 rows of cells between them in the distal half of this area; pseudo-IR1 distinct and originating on RP1 below distal side of pterostigma; 3–4 rows of cells between pseudo-IR1 and RP1, and about 6–7 rows of cells between pseudo-IR1 and RP2; wing base rounded without anal angle and anal triangle, thus it is a female specimen; three posterior branches of anal vein between CuAb and anal margin; no membranule is visible.

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