Stuttgarter Beiträge zur Naturkunde
Serie B (Geologie und Paläontologie)

Herausgeber:

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

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 264	66 pp., 1 tab., 39 figs.	Stuttgart, 30. 9. 1998

New fossil dragonflies from the Lower Cretaceous Crato Formation of north-east Brazil (Insecta: Odonata)

By Günter Bechly, Tübingen

With 1 Table and 39 Figures

Summary

An overview of the fossil odonate fauna of the Crato Formation from the Lower Cretaceous of Brazil is given. Currently 351 specimens (241 adults and 110 larvae) in 12 families and 32 species are known to science. More than half of the adult and larval fossil odonates belong to the gomphid clade (= Gomphides), especially to the Cordulagomphinae which supports the hypothesis of an allochthonous origin of the aquatic insects. Six new species are described: *Araripegomphus andreneli* n. sp. (Araripegomphidae), *Cordulagomphus (Procordulagomphus* stat. nov.*) senckenbergi* n. sp. (Proterogomphidae – Cordulagomphinae), *Araripephlebia mirabilis* n. gen. et n. sp. (Araripephlebiidae n. fam.), *Cratocordulia borschukewitzi* n. gen. et n. sp. (Araripelibellulidae), *Cretarchistigma*(?) *essweini* n. sp. (Zygoptera incertae sedis), and *Parahemiphlebia mickoleiti* n. sp. (Hemiphlebiidae). With a wing length of only 9 mm the latter new species represents one of the smallest odonates of all times. *Araripephlebia mirabilis* n. gen. et n. sp. is classified in a new family Araripephlebiidae n. fam. which probably represents the sister-group of extant Chlorogomphoidea. A still unnamed new genus and species represents the first fossil record and the first New World record for Chlorogomphoidea s. str. Four further new species are illustrated, but not yet described.

The phylogenetic relationship of several known species is discussed, and some diagnoses are amended or corrected. Giant dragonfly larvae of up to 70 mm length are described, regarded as older stages of *Nothomacromia sensibilis* (Carle & Wighton, 1990), and considered as larval Aeschnidiidae. Consequently, the family-group taxa Sonidae Pritykina, 1986 and Nothomacromiidae Carle, 1995 (= "Pseudomacromiidae" sensu Carle & Wighton, 1990) are here regarded as junior subjective synonyms of Aeschnidiidae Needham, 1903. The position of Araripegomphidae in the stem-group of Gomphides rather than Eurypalpida (= Libelluloidea auct.) is advocated (contra Lohmann 1996). The former genus *Procordulagomphus* Nel & Escuillié, 1994 is down-ranked to a subgenus of *Cordulagomphus*. "*Cordulagomphus*" *santanensis* Carle & Wighton, 1990 is recognized as earwig and thus transferred from Odonata – Cordulagomphinae to Dermaptera incertae sedis. A comparison with the odonate fauna of the Upper Jurassic Solnhofen limestones reveals several remarkable differences. Because of the absence of typical Mesozoic odonate groups, such as "anisozygopteres", Archizygoptera and Steleopteridae, as well as the presence of extant families of Zygoptera, the odonate fauna of the Crato Formation appears to be significantly more advanced.

Zusammenfassung

Eine Übersicht der fossilen Libellenfauna der Crato Formation aus der Unterkreide Brasiliens wird vorgestellt. Derzeit sind 351 Exemplare (241 Imagines und 110 Larven) in 12 Familien und 32 Arten wissenschaftlich bekannt. Über die Hälfte der imaginalen und larvalen Libellenfossilien gehören zur Verwandtschaft der Gomphiden (Flußjungfern), insbesondere zu den Cordulagomphinae, was gut mit der Hypothese eines allochthonen Ursprunges der Wasserinsekten übereinstimmt. Sechs neue Libellenarten werden beschrieben: *Araripegomphus andreneli* n. sp. (Araripegomphidae), *Cordulagomphus (Procordulagomphus* stat. nov.*) senckenbergi* n. sp. (Proterogomphidae – Cordulagomphinae), *Araripephlebia mirabilis* n. gen. et n. sp. (Araripephlebiidae n. fam.), *Cratocordulia borschukewitzi* n. gen. et n. sp. (Araripelibellulidae), *Cretarchistigma*(?) *essweini* n. sp. (Zygoptera incertae sedis) und *Parahemiphlebia mickoleiti* n. sp. (Hemiphlebiidae), welche mit nur 9 mm Flügellänge eine der kleinsten bekannten Libellen aller Zeiten darstellt. *Araripephlebia mirabilis* n. gen. et n. sp. wird in einer neuen Familie Araripephlebiidae klassifiziert, welche vermutlich die Schwestergruppe der rezenten Chlorogomphoidea ist. Eine noch unbenannte neue Gattung und Art stellt den ersten Fossilnachweis und ersten neuweltlichen Nachweis der Chlorogomphoidea s. str. dar. Vier weitere neue Arten werden abgebildet, aber noch nicht beschrieben.

Die phylogenetische Verwandtschaft einiger bekannter Arten wird diskutiert, und einige Diagnosen werden ergänzt oder korrigiert. Riesige Libellenlarven von bis zu 70 mm Länge werden beschrieben, als ältere Stadien von *Nothomacromia sensibilis* (CARLE & WIGHTON, 1990) angesehen und als larvale Aeschnidiidae erkannt. Folglich sind die Familiengruppentaxa Sonidae PRITYKINA, 1986 und Nothomacromiidae CARLE, 1995 (= „Pseudomacromiidae" sensu CARLE & WIGHTON, 1990) als subjektive Juniorsynonyme der Aeschnidiidae NEEDHAM, 1903 anzusehen. Die Zugehörigkeit der Araripegomphidae zur Stammgruppe der Gomphides anstatt der Eurypalpida (= Libelluloidea auct.) wird belegt (contra LOHMANN 1996). Die frühere Gattung *Procordulagomphus* NEL & ESCUILLIÉ, 1994 wird zur Untergattung von *Cordulagomphus* herabgestuft. *„Cordulagomphus" santanensis* CARLE & WIGHTON, 1990 wird als Ohrwurm erkannt und daher von den Odonata – Cordulagomphinae zu den Dermaptera incertae sedis transferiert. Ein Vergleich mit der Libellenfauna der oberjurassischen Solnhofener Plattenkalke zeigt bemerkenswerte Unterschiede. Durch das Fehlen typisch mesozoischer Libellengruppen, wie der „Anisozygopteren", Archizygoptera und Steleopteridae, sowie das Vorkommen rezenter Zygopterenfamilien, erscheint die Libellenfauna der Crato Formation deutlich „moderner".

Contents

1. Introduction

Among the few localities for Cretaceous insects, the limestones of the Crato Formation are of outstanding importance because of the following three reasons:

1. A highly diverse fossil insect fauna with probably more than 300 species, of which less than the half are yet described.

2. The excellent preservation of the fossil insects.

3. The large number of specimens found (at least 16000 specimens in various collections).

This locality is also unique because it yields larval, as well as adult insects, and terrestrial species, as well as aerial or aquatic ones.

The referring limestone quarries are mostly located in the vicinity of Nova Olinda, along the northern slope of the Chapada do Araripe, – a Mesozoic plateau in the southern part of the state of Ceará, in the semiarid and poor north-east of Brazil.

On the Precambrian basement there are 700 m of Mesozoic sediments. Their lower part is formed by the Brotas group (= Val do Cariri group) with 300 m of Upper Jurassic sandstones and shales. The upper part is formed by up to 400 m of Cretaceous sediments of the Araripe group which has been dated as Lower Cretaceous (Aptian and Albian) on the basis of fossil pollen, ostracods and fishes. The upper part of the Araripe group is formed by the reddish sandstones and conglomerates of the Exu Formation which is more or less free of fossils and has been dated as Upper Albian to Cenomanian (lowest Upper Cretaceous).

The lower part has previously been classified as Santana Formation s.l. with three members. The latter have recently been elevated to separate formations by MARTILL et al. (1993). According to this new stratigraphical nomenclature, the uppermost part is the Santana Formation s. str. with the Romualdo Member that contains the calcareous concretions with the famous vertebrate fossils (fishes, pterosaurs, etc.). Below the latter is the Ipubi Formation that is mainly consisting of gypsum and anhydrite which indicate a progressive evaporation of the Santana lagoon. The Crato Formation is the lowermost formation of the Araripe Group and includes micritic dolomitic limestones of 3–8 m thickness (Nova Olinda Member sensu MARTILL et al. 1993). Fossil insects are exclusively found in these limestones which were probably deposited in the Upper Aptian, although some authors assumed a much older maximum age of origin (down to Lower Barremian).

Beside the numerous fossil arthropods (mainly insects and arachnids), the Crato limestones also yielded remains of terrestrial plants, but only very few vertebrate fossils, contrary to the mentioned concretions of the Romualdo Member. The only abundant vertebrates are juvenile specimens of the bonefish genus *Dastilbe*.

Meanwhile representatives of most extant insect orders have been recorded from this locality, but the majority of the material is still undescribed. The preservation of the fossil insects is generally excellent with most specimens being complete and only slightly flattened. Unweathered specimens may be organically preserved, but most specimens have been subject to weathering and thus are inorganically preserved with limonitised cuticle and calcite filled cavities (MARTILL & NEL 1996). Both types of preservation often show minute details, like bristles, ommatidia of the compound eyes, and surface sculptures of the cuticle, e.g. on the damselfly pterostigmata. Sometimes even soft parts are preserved, such as flight muscles or the gizzard. Very rare is the preservation of colour pattern (MARTILL & FREY 1995, BECHLY unpubl.), or even of original interference colours. For example a few specimens of the damselfly *Parahemiphlebia cretacica* (e.g. specimen no. 39, National Science Museum Tokyo) still show parts of the original metallic green body coloration (no secondary pyritisation!) that is also typical for their extant relatives (compare BECHLY 1996, 1997a). Even average fossil insects from the Crato Formation are generally by far better preserved than the best specimens from the famous Solnhofen limestones. Consequently, this locality has to be regarded as a typical "Konservat-Lagerstätte".

This important fossil locality was discovered in April 1819 by the two Bavarian naturalists JOHANN BAPTIST VON SPIX and CARL FRIEDRICH PHILIPP VON MARTIUS,

during a scientific expedition to Brazil on behalf of King MAXIMILIAN I. VON BAYERN. However, they did not yet find any fossil insects, but "only" concretions with fossil fishes. As first fossil insects some ephemerid larvae were described by COSTA-LIMA (1950). The first fossil dragonfly from Araripe, an isolated male hindwing of *Cordulagomphus* cf. *fenestratus*, was discovered by Prof. ANGELO MACHADO (University of Belo Horizonte). It was first mentioned in a short notice of WESTFALL (1980) and figured by MACHADO in SCHLÜTER & HARTUNG (1982, Abb. 5). Thorough palaeoentomological studies of the Santana fauna started in the mid eighties by BRITO (1984) and have been subsequently continued by Dr RAFAEL MARTINS-NETO (1987–1992) from the Zoological Museum of Sao Paulo and Dr DAVID GRIMALDI (1990–1991) from the American Museum of Natural History in New York, and several others. Currently the fossil Odonata of the Crato Formation are revised by Dr ANDRÉ NEL (MNHN, Paris) and me, which already led to a doubling of the known number of species. The majority of the new dragonfly species, which are partly still undescribed, have been discovered by me in the extensive collections of the fossil trader MICHAEL SCHWICKERT (ms-fossil) in Sulzbachtal (Germany).

2. Material and methods

The presented results are based on my examination of 309 specimens of fossil dragonflies (205 adults and 104 larvae) from the Crato Formation (308 specimens at ms-fossil and 1 specimen on loan from AMNH), as well as on 9 specimens on photos of ms-fossil (5 adults and 4 larvae), and on all 33 specimens that were mentioned or figured in the cited literature (31 adults and 2 larvae), thus totally on 351 specimens.

All holotypes and paratypes, and many of the further specimens, of all new species described in this publications are deposited in official museum collections (AMNH New York, JME Eichstätt, MNHN Paris, NSMT Tokyo, SMF Frankfurt, SMNK Karlsruhe, SMNS Stuttgart, and Museum of Kitakyushu). Specimen C13 (original) from my own collection will be deposited on permanent loan in the collection of the Staatl. Museum f. Naturkunde in Stuttgart (Inv. Nr. SMNS 63648). The remaining specimens, including a few originals, are still located in private collections, especially of ms-fossil (Sulzbachtal). However, some of the mentioned specimens that were still in collection of ms-fossil at the time of writing this manuscript, may already be deposited in official museum collections at the time of publication (the trader at least promised not to sell any of them to any private collectors at all). The mentioned large exhibition "Santana on Tour 97/98" (incl. specimens D28, D29, D45, and D58) will only be sold in whole and exclusively to an official museum. This exhibition was first displayed as special exhibition during the "Mineralientage" in Munich, 21.–23.11.97; afterwards it moved to the Jura-Museum Eichstätt, 01.10.97–15.03.98; Naturkundemuseum am Friedrichsplatz Karlsruhe, 01.04.98 till mid July 1998; Senckenberg-Museum Frankfurt, 22.07.98 till end of September 1998; Museum für Naturkunde Berlin, 06.10.98 till December 1998.

All drawings were made with camera lucida, and all photos were made with a SLR camera and macro lens. The nomenclature of the dragonfly wing venation is based on the interpretations of RIEK (1976) and RIEK & KUKALOVÁ-PECK (1984), amended by KUKALOVÁ-PECK (1991), NEL et al. (1993) and BECHLY (1996). The higher classifi-

cation is based on the new phylogenetic system of fossil and extant odonates of BECHLY (1996, 1997a). The systematical analysis is based on the principles of consequent Phylogenetic Systematics (sensu HENNIG 1966, 1969) rather than "numerical cladism" (also called "computer cladistics") which unfortunately still is mainstream, although it has more in common with phenetics than with genuine Hennigian methods (for the referring arguments see WÄGELE 1994, BORUCKI 1996, and BECHLY 1997a). The assignment of formal categorial ranks has been omitted as far as possible because they are more or less arbitrary and superfluous (WILLMANN 1989).

3. Description of seven new fossil odonate species from the Crato Formation

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 andreneli n. sp.
Figs 1–3

Holotype: ♂ specimen no. C1 in the private collection of the author (G. BECHLY, Böblingen), purchased from ms-fossil (Sulzbachtal) and deposited on permanent loan in the collection of the Staatl. Museum f. Naturkunde in Stuttgart (Inv. Nr. SMNS 63651).

Paratypes: ♂ specimen no. 31, and ♀ specimens nos 47 (allotype) and no. 1006 (National Science Museum Tokyo; ex coll. ms-fossil); specimens nos. 5, 12, 13, and 16, Museum of Kitakyushu.

Further material: Specimens nos D10, D27, E16, E18, and F1 (all in coll. ms-fossil). A further specimen was exhibited in the local museum of Santana do Cariri and figured in MARTILL et al. (1993, Text-Fig. 4.1), but is reported to have "disappeared".

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeast Brazil (MAISEY 1990).

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

Derivatio nominis: After my colleague Dr ANDRÉ NEL (Paris), for his numerous achievements in palaeoentomology.

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, hindwing CuAa with four to five (usually four) posterior branches; male hindwing without any posterior branch of anal vein between anal loop and anal triangle; female hindwing with three to four posterior branches of anal vein; pterostigma distinctly braced in all wings. The new species differs only in two characters from the type-species *A. cretacicus* which is only known by the female holotype: the wings are somewhat shorter, and there are only two rows of cells in the basal part of the postdiscoidal area of both

Table 1. Statistics of the fossil odonate fauna from the Crato Formation

FAMILY GROUP TAXA	SPECIES	ADULTS	LARVAE	SUM
Hemiphlebiidae	2 (+ 2 ?)	19 (+ 19 ?)	0	38
Protoneuridae – Isostictinae	1	20	0	20
Thaumatoneuridae – Euarchistigmatini	1	5	0	5
Aeschnidiidae (= Nothomacromiidae; = Sonidae)	2 (+ 1 ?)	7 (= 3 %)	20 (10 small + 10 big) (= 18 %)	27 (= 8 %)
Cretapetaluridae	1	1	0	1
Liupanshaniidae	2	3	0	3
Gomphaeschnidae – Gomphaeschnaoidinae	7 (= 22 %)	20 (= 8 %)	10 (+ 5 ?) (= 14 %)	35 (= 10 %)
Araripegomphidae	2 (+ 1 ?)	16	?	16
large gomphid larvae	?	–	16 (+ 10 ?)	26
Proterogomphidae – Cordulagomphinae	6 (= 19 %)	113 (= 47 %)	36 (= 33 %)	149 (= 42 %)
Araripephlebiidae	1	3	0	3
Chlorogomphidae	1	1	0	1
Araripelibellulidae	2	5	0	5
Anisoptera indet.	?	3	9 (+ 4 ?)	16
Odonata indet.	?	6	0	6
SUM	32 (= 100 %)	241 (= 69 %)	110 (= 31 %)	351 (= 100 %)

pairs of wings. The latter character is most significant, since it is not known to be variable within extant dragonfly species. Even the apparently negligible difference in body size is significant, since the wing length of the holotype of *A. cretacicus* is outside the variability of the fourteen known specimens of the new species (see Appendix). The correlation of this difference in size with a very stable wing venational character justifies the description of a new species.

LOHMANN (1996) mentioned three alleged autapomorphies of Araripegomphidae:

1. Anal loop only two-celled: this character is simply incorrect, since in all known specimens of Araripegomphidae the anal loop is either closed and three- to six-celled, or it is absent (not posteriorly closed). The sole exception is specimen no. D10 which does have a two-celled anal loop indeed that almost certainly has to be regarded as an individual aberration. However, the latter specimen was not known to LOHMANN (1996) whose arguments were only based on the description of the holotype of *A. cretacicus* which completely lacks an anal loop. Therefore, this erroneous autapomorphy is obviously based on a lapse, viz a confusion with Cordulagomphinae which indeed generally possess a two-celled anal loop.

2. "Gaff" (CuA between subdiscoidal veinlet and first branching) is secondarily shortened in the hindwing: this assumption of a secondarily shortened "gaff" is an

unjustified ad hoc hypothesis. The referring character state rather has to be regarded as a plesiomorphy, since it would otherwise represent the only known reversal of this character within Cavilabiata (see below).

3. Secondary antenodal crossveins between Ax1 and Ax2 are aligned: this character is variable within *Araripegomphus* (see below) and thus invalid.

Description

Holotype (Figs 1–2): A well-preserved male dragonfly with all four wings outspread (wing span 75 mm). Head and body are only preserved as faint imprint (maybe an artifact of preparation). The legs are not preserved, except for the bases of the forelegs. The wings probably have been hyaline.

Body: Width of head, 7.5 mm; the abdomen is 39.0 mm long and 2.1 mm wide; anal appendages (cerci) about 2.7 mm long, including the apical spine-like projection.

Forewing: Length, 36.2 mm; width at nodus, 8.3–8.4 mm; distance from base to nodus, 18.7 mm (the nodus is situated at about 52 % of the wing length); distance from nodus to pterostigma, 9.8–10.1 mm; distance from base to arculus, 3.6 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.6–0.7 mm basal of arculus and Ax2 is 3.6–3.8 mm distal of Ax1 (somewhat distal of basal side of discoidal triangle); only two secondary antenodal crossveins between Ax1 and Ax2 (inexactly aligned); distal of Ax2 there are ten secondary antenodal crossveins between costal margin and ScP and nine of them between ScP and RA; about five antesubnodal crossveins (only three of them visible in the left wing) with a distinct gap near the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; secondary antenodal crossveins and postnodal crossveins are non-aligned; six postnodal crossveins between nodus and pterostigma; no distinct "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 3.5 mm long and max. 0.9 mm wide; the pterostigma is distinctly braced and covers three to three and a half 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) somewhat separated at the arculus; the hypertriangle is 4.6–4.7 mm long and max. 0.6 mm wide; the hypertriangle is free and its costal side (MA) is slightly curved; discoidal triangle transverse and free; length of basal side of discoidal triangle, 2.1 mm; length of its costal side, 2.5–2.6 mm; length of its distal side MAb, 2.8–2.9 mm; MAb is more or less straight; 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 1.2 mm basal of arculus; anal area max. 2.1 mm wide with two rows of cells; cubito-anal area max. 1.9–2 mm wide with up to three rows of cells; CuA with five to six 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, 2.3 mm; width at hind margin, 6.9 mm or 7.4 mm respectively); no Mspl, but two intercalary veins in the distal postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between them, except near the hind margin (two rows of cells); first branching of RP ("midfork") 5.2 or 5.5 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 0.9 mm and one cell distal of subnodus; only one or two bridge crossveins between RP2 and IR2 basal of subnodus; RP2 and IR2 strictly parallel with only one row of

cells between them up to the hind margin; no Rspl, but three intercalary veins in the area between IR2 and RP3/4; RP1 and RP2 divergent with two rows of cells between them, even up to basal of 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, 33.9 mm; width at nodus, 10.7–11 mm; distance from base to nodus, 14.1 mm (the nodus is situated basal of midwing at about 42 % of the wing length); distance from nodus to pterostigma, 12–12.2 mm; distance from base to arculus, 3.4 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.3–0.5 mm basal of arculus and Ax2 is 4.0 mm distal of Ax1 (about the level of the distal edge of the discoidal triangle); only two secondary antenodal crossveins between Ax1 and Ax2 (more or less aligned); distal of Ax2 there are four to five secondary antenodal crossveins between the costal margin and ScP and six of them between ScP and RA; only two (left wing) or four (right wing) antesubnodal crossveins are visible, but there seems to be a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus, as well as a gap directly distal of the arculus; the secondary antenodal crossveins distal of Ax2 and the postnodal crossveins are non-aligned; seven postnodal crossveins between nodus and pterostigma; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 3.5–3.8 mm long and max. 0.9–1 mm wide; the pterostigma is distinctly braced and covers three to three and a half 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 somewhat separated at the arculus; the hypertriangle is 3.9–4 mm long and max. 0.8–0.9 mm wide (distinctly wider than in the forewing); the hypertriangle is free and its costal side (MA) is strongly curved; the discoidal triangle is transverse and free; length of basal side of discoidal triangle, 1.9–2 mm; length of its costal side, 2.7 mm; length of its distal side MAb, 3.1–3.2 mm; MAb is weakly angled and a weak postdiscoidal intercalary vein originates at this angle; pseudo-anal vein PsA is 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 1.1–1.2 mm basal of arculus; anal area max. 6.9–7.1 mm wide with eight to ten rows of cells; cubito-anal area max. 5–5.2 mm wide with up to six rows of cells; CuAa distinctly curved and thus relatively short with only four posterior branches; CuAb distinctly developed; "gaff" short; anal loop five-celled, but indistinct in the right wing and absent in the left wing; 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 two rows of cells); only two rows of cells in the basal part of the postdiscoidal area; the postdiscoidal area is distally strongly widened (width near discoidal triangle, 2.5 mm; width at hind margin, 7.6–7.8 mm); no Mspl, but two 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 them, except near the hind margin (two rows of cells); first branching of RP 5.1 or 4.7 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 0.7–0.8 mm and one cell distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus; RP2 and IR2 relatively straight and closely parallel with only one row of cells between them up to the hind margin; no Rspl, but three intercalary veins in the area between

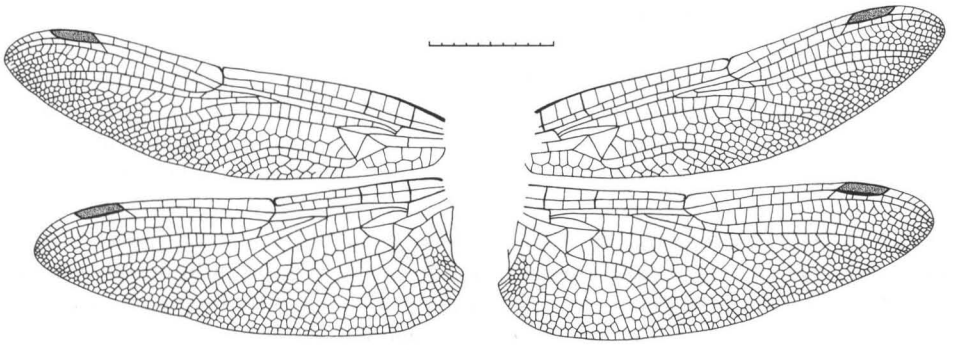

Fig. 1. *Araripegomphus andreneli* n. sp., ♂ holotype C1 (coll. BECHLY, SMNS). Scale 10 mm.

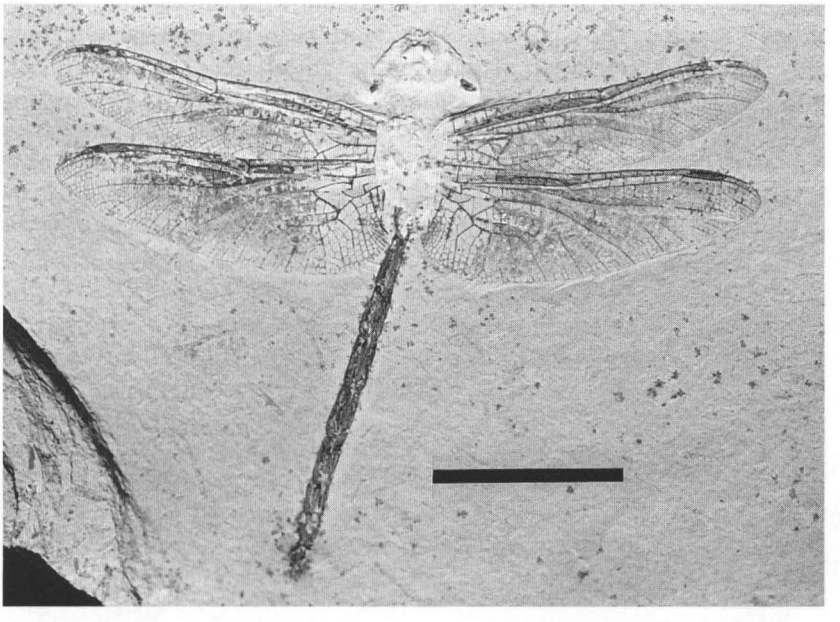

Fig. 2. *Araripegomphus andreneli* n. sp., ♂ holotype C1 (coll. BECHLY, SMNS). Scale 20 mm.

IR2 and RP3/4; RP1 and RP2 divergent and with two rows of cells between them, even up to basal 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; wing base with distinct anal angle in the hind margin and a three-celled anal triangle, thus it is a male specimen; only one posterior branch of anal vein between CuAb and anal triangle; no membranule is visible.

Paratype specimen no. 31: A male dragonfly with one fore- and hindwing, head, thorax, four legs and the basal 2/3 of the abdomen preserved. The compound eyes are shortly, but distinctly separated.

Forewing: Length, 36.0 mm; pterostigma covers three and a half cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to basal of pterostigma; very short "libellulid gap"; "cordulegastrid gap" present; origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one cell distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2; costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Length, 34.7 mm; pterostigma covers nearly three cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to far basal of pterostigma; "cordulegastrid gap" apparently present (?); lestine oblique vein "O" one cell distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2 (inexactly aligned); costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly open; anal triangle present and three-celled.

Paratype and allotype specimen no. 47 (Fig. 3): A very well-preserved female dragonfly, of which only the tip of the left hindwing, all legs and the end of the abdomen are missing. The compound eyes appear to be widely separated, but this is probably due to a preservation of the head in ventral aspect (max. width of head, 6.2 mm).

Forewing: Length, 35.0 mm; pterostigma covers about four cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to basal of pterostigma; very short "libellulid gap"; arculus weakly angled and origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one and a half cells distal of

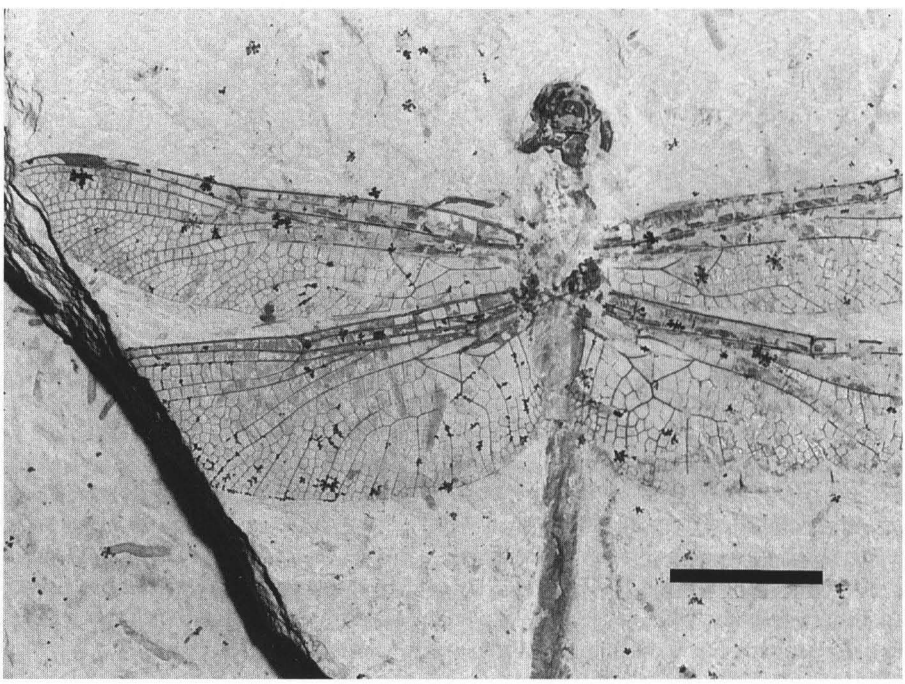

Fig. 3. *Araripegomphus andreneli* n. sp., ♀ paratype and allotype no. 47 (Nat. Sci. Mus. Tokyo). Scale 10 mm.

subnodus; only one secondary antenodal crossvein between Ax1 and Ax2 (aligned); costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Length, 34.0 mm; pterostigma covers two and a half cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to far basal of pterostigma; distinct "cordulegastrid gap"; arculus straight and origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one cell distal of subnodus; three (left wing) or only one (right wing) (?) secondary antenodal crossveins between Ax1 and Ax2 (aligned); costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly open in the left wing and indistinctly closed and five-celled in the right wing; three to four posterior branches of anal vein.

Paratype specimen no. 1006: A nearly complete, but not very well-preserved, female dragonfly. Only the distal half of the abdomen and the middle- and hindlegs are missing. The compound eyes are slightly separated (min. distance hardly 1.0 mm).

Forewing: Length, 36.1 mm; pterostigma covers about two and a half to three cells; pterostigma distinctly braced; lestine oblique vein "O" one cell distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2 (aligned); costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Length, 35.6 mm; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to basal of pterostigma; arculus straight and origins of RP and MA relatively widely separated at arculus (!); lestine oblique vein "O" one and a half cells distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2 (non-aligned!); costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop indistinctly closed and four- to five-celled; three to four posterior branches of anal vein.

Paratype specimen no. 5 (Kitakyushu): An isolated forewing (length, 36.3 mm).

Paratype specimen no. 12 (Kitakyushu): Two connected forewings (length, 33.3 mm).

Paratype specimen no. 13 (Kitakyushu): An adult female dragonfly.

Forewing: Length, 36.5 mm.

Hindwing: Length, 36.0 mm; anal loop closed and six-celled.

Paratype specimen no. 16 (Kitakyushu): Two connected forewings (length, 34.0 mm).

Specimen no. D10: Male dragonfly.

Forewing: Length, 32.0 mm; pterostigma distinctly braced; two rows of cells between RP1 and RP2 distal of basal side of pterostigma; very short "libellulid gap"; arculus nearly straight and origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one and a half cells distal of subnodus; only one secondary antenodal crossvein between Ax1 and Ax2 (more or less aligned); costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Length, 32.0 mm; pterostigma covers about three cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2 distal of basal side of pte-

rostigma; "cordulegastrid gap" present; arculus straight and origins of RP and MA somewhat separated at the arculus; lestine oblique vein "O" one and a half cells distal of subnodus; only one secondary antenodal crossvein between Ax1 and Ax2 (more or less aligned); costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly closed and two-celled (!); anal triangle present and three-celled.

Specimen no. D27: Female dragonfly; compound eyes only slightly separated.

Forewing: Length, 34.8 mm; pterostigma covers about three and a half cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2, even up to basal of the pterostigma; arculus straight and origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one cell distal of subnodus; one (left wing) or two (right wing) secondary antenodal crossveins between Ax1 and Ax2 (inexactly aligned); costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Length, 34.0 mm; pterostigma covers four to four and a half cells (!); pterostigma distinctly braced; two rows of cells between RP1 and RP2, even far basal of the pterostigma; "cordulegastrid gap" apparently present (?); arculus straight and origins of RP and MA somewhat separated at the arculus; lestine oblique vein "O" one cell distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2 (inexactly aligned); costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly open; three to four posterior branches of anal vein.

Specimen no. E16: Imprint of an adult female dragonfly with head, thorax, and all four wings (forewing length, 36.2 mm; hindwing length, 35.1 mm). The wing venation is rather poorly preserved, only the main veins are visible. The apices of the right wings are missing. The hindwings are very interesting since they clearly show a large membranule at the wing base. This character state has to be regarded as plesiomorphic, compared to the reduced membranule in crown-group Gomphides.

Specimen no. E18: A male specimen which is very similar to the other described specimens in all visible characters (forewing length, 36.0 mm; hindwing length, 35.5 mm).

Specimen without number in the local museum of Santana do Cariri: A very well-preserved and complete female dragonfly; compound eyes apparently widely separated, probably due to the preservation of the head in ventral aspect.

Forewing: Two rows of cells between RP1 and RP2 distal of basal side of pterostigma; origins of RP and MA hardly separated at the arculus; two secondary antenodal crossveins between Ax1 and Ax2; costal side of hypertriangle smoothly curved; two rows of cells in the basal part of the postdiscoidal area.

Hindwing: Two rows of cells between RP1 and RP2, even up to somewhat basal of pterostigma; costal side of hypertriangle strongly curved and hypertriangle distinctly wider than in the forewing; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly closed and with four or five cells; at least two posterior branches of anal vein are visible.

Phylogenetic position. – Contrary to the original description in Gomphidae by NEL & PAICHELER (1994a), LOHMANN (1996) recently suggested a position of Araripegomphidae in the stem-group of Eurypalpida (= Libelluloidea auct.). The evi-

dence of the new specimens renders this latter hypothesis quite doubtful. Of the nine alleged synapomorphies with Eurypalpida proposed by LOHMANN (1996), the following seven characters are very homoplastic anyway, and also occur in some or even most gomphids.

1. Pterostigma short, only covering about three cells: this character is not only somewhat variable within Araripegomphidae (see above), but also present in some gomphids.

2. Hindwing with straight arculus: although this is a derived similarity with most Brevistigmata (= Hemeroscopidae, Chlorogomphoidea, and Eurypalpida) indeed, it is rather worthless as potential synapomorphy, since it is also present in many gomphids as well. The plesiomorphic state in a new Hemeroscopidae from Solnhofen (BECHLY et al. 1998) furthermore indicates that the derived state convergently evolved several times within Brevistigmata. By the way: this character state is not only present in the hindwing of *A. andreneli* n. sp. but also distinct in the forewing.

3. The sectors of the arculus RP and MA have a common origin at the arculus: this character is correlated with the former character and thus involves the same counter arguments. Furthermore, this character is variable at least in *A. andreneli* n. sp.

4. Only two or less secondary antenodal crossveins between Ax1 and Ax2: this character is a derived similarity with Eurypalpida, but is also present in some gomphids (e.g. Proterogomphidae, incl. Cordulagomphinae). The alignment of these antenodals is certainly no predisposition (contra LOHMANN 1996) but just an individual feature of certain specimens of *Araripegomphus*, since the referring crossveins are hardly aligned or non-aligned in most specimens (see above).

5. Costal side (MA) of hypertriangle distinctly curved: this is another derived similarity with Eurypalpida that is also present in most gomphids.

6. The hindwing CuAa is shortened with max. four to five posterior branches: this derived character state is not only present in Araripegomphidae and most Cavilabiata (Cordulegastrida, Neopetaliidae, Chlorogomphida and Eurypalpida) but also in numerous gomphids.

7. The primary IR1 is reduced and a pseudo-IR1 originates on RP1 distal of the pterostigma: within the gomphid clade this character state is indeed only known from a few extant and fossil taxa (e.g. Proterogomphidae, incl. Cordulagomphinae). However, it is also present within Aeshnoptera, e.g. in Cymatophlebiidae and Gomphaeschnidae. Furthermore, only the reduction of the primary IR1 can be regarded as derived character, while the distal pseudo-IR1 seems to be a ground-plan character of Anisoptera (see BECHLY 1996).

Regarding the very limited value of the above mentioned characters, only two of LOHMANN's (1996) characters remain as potential synapomorphies for Araripegomphidae and Eurypalpida:

1. Forewing with "libellulid gap" (sensu BECHLY 1996) in the basal part of the postsubnodal area, and hindwing with "cordulegastrid gap" (sensu BECHLY 1996) in the distal part of the antesubnodal area: first of all it must be emphasised that the statement of LOHMANN (1996) is not fully correct, since all known specimens of *A. andreneli* n. sp. only have a very indistinct "libellulid gap" in both pairs of wings, but a long "cordulegastrid gap" in both pairs of wings! The supposed long "libellulid gap" in the forewing of the holotype of *A. cretacicus* could rather represent an artifact of preservation. Besides, a "cordulegastrid gap" is not only known from most Cavilabiata (except extant Chlorogomphoidea), but as well from Gomphaeschnidae

and Cordulagomphinae and a few other taxa. Consequently, it is a rather homoplastic character anyway which therefore has to be regarded as relatively weak evidence. The alleged "libellulid gap" is so weakly developed that it can hardly be coded as present and therefore cannot be regarded as a valid synapomorphy.

2. Compound eyes strongly approximated: the distance of the compound eyes in Araripegomphidae is indeed much smaller than in any other known gomphid! However, such an approximation of the eyes convergently evolved in Aeshnoptera anyway, so that it is quite possible that this character state evolved by convergence in Araripegomphidae, too.

The following three characters strongly contradict a close relationship of Araripegomphidae with Eurypalpida:

1. Vein RA is strongly broadened along the pterostigma, as in most gomphids: this character probably represents a derived ground-plan character of the gomphid clade (BECHLY 1996, 1997a) and thus a putative synapomorphy with Araripegomphidae.

2. The distal side MAb of the hindwing discoidal triangle is angled and a distinct postdiscoidal intercalary vein originates on this angle: this derived character is present in all gomphids (putative synapomorphy) and in the crown-group of Aeshnoptera (clearly a convergence). On the other hand this character state is completely absent in all known Cavilabiata.

3. In the hindwing the "gaff" is short, as in all Petalurida, basal Aeshnoptera, Gomphides and Cordulegastrida (symplesiomorphy), while it is distinctly elongated in all Brevistigmata, in which Eurypalpida have a subordinated position (synapomorphy). There exists no evidence whatever for a reversal of this character in any representative of Brevistigmata! For this reason, this important plesiomorphy excludes a close relationship of Araripegomphidae and Eurypalpida with great certainty. Correlated with the plesiomorphic "gaff" is the small anal loop (thus a plesiomorphy, too) which is even completely reduced in some specimens of *Araripegomphus*. Such a reduction of the anal loop is unknown in Cavilabiata, except in Cordulephyinae and Tetrathemistinae which have the complete cubito-anal area of the hindwing very much reduced, contrary to Araripegomphidae which have a very well-developed cubito-anal area.

Considering the total available evidence it must be stated that Araripegomphidae most probably belongs to the gomphid clade (see BECHLY 1996, 1997a) rather than to the stem-group of the libelluloid clade (Eurypalpida).

Araripegomphus n. sp. (?)

Figs 4–5

Material: ♂ specimen SMNS 63070 (Staatl. Museum f. Naturkunde in Stuttgart).

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

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

Diagnosis. – This specimen is very similar to the type-species *Araripegomphus cretacicus* NEL & PAICHELER, 1994 and *A. andreneli* n. sp. The only visible differences are the somewhat smaller size (hindwing only 30.5 mm long), and especially the more widely separated compound eyes. Considering the smaller distance of the eyes in the holotype of *A. cretacicus* and the specimens of *A. andreneli* n. sp., the

erection of a separate new species for this specimen could be justified, since this character is not intraspecifically variable. Because of the poor preservation of this specimen, this putative new species should not be named until better preserved specimens will be available.

Description (Figs 4 and 5): A rather poorly preserved male dragonfly. The head is max. 6.5 mm wide and the compound eyes are distinctly separated (min. distance about 1.3 mm), although the head is clearly preserved in dorsal aspect!

Forewing: Very incompletely preserved; two rows of cells in the distal part of the area between RP3/4 and MA; lestine oblique vein "O" one and a half cells distal of subnodus.

Hindwing: Length, only 30.5 mm; pterostigma covers about three and a half cells; pterostigma distinctly braced; two rows of cells between RP1 and RP2 up to somewhat basal of pterostigma; arculus straight and origins of RP and MA hardly separated at arculus; lestine oblique vein "O" one and a half cells distal of subnodus; two secondary antenodal crossveins between Ax1 and Ax2 (inexactly aligned); costal side of hypertriangle strongly curved and hypertriangle rather broad; two rows of cells in the basal part of the postdiscoidal area; anal loop posteriorly open (?); distinct anal triangle, thus it is a male specimen.

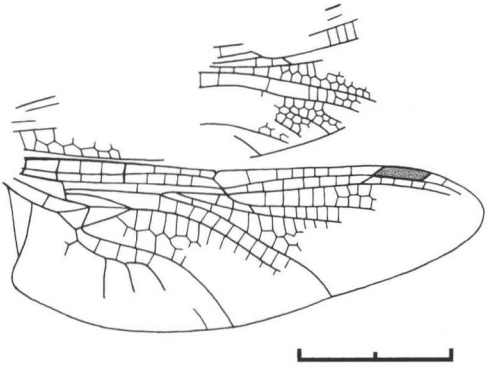

Fig. 4. *Araripegomphus* n. sp. (?) (combined from left and right pair of wings), ♂ SMNS 63070. Scale 10 mm.

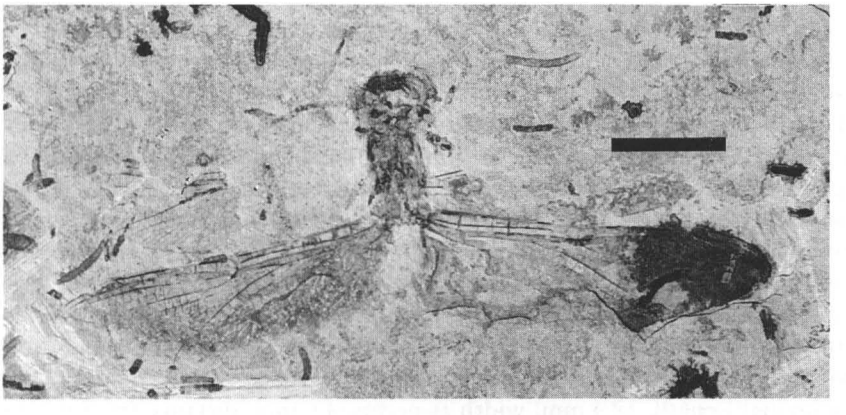

Fig. 5. *Araripegomphus* n. sp. (?), ♂ SMNS 63070. Scale 10 mm.

Suborder Anisoptera SELYS in SELYS & HAGEN, 1854
Euanisoptera BECHLY, 1996
Exophytica BECHLY, 1996
Gomphides BECHLY et al., 1998
Superfamily Hagenioidea TILLYARD & FRASER, 1940 sensu BECHLY 1997
Family Proterogomphidae BECHLY et al., 1998
Subfamily Cordulagomphinae CARLE & WIGHTON, 1990 stat. rest.

Genus *Cordulagomphus* CARLE & WIGHTON, 1990
Subgenus *Procordulagomphus* NEL & ESCUILLIÉ, 1994 stat. nov.

Cordulagomphus (Procordulagomphus stat. nov.*) senckenbergi* n. sp.
Figs 6–7

Holotype: ♂ specimen no. C7, donated by ms-fossil (Sulzbachtal) to the Senckenberg Museum in Frankfurt a.M., on the occasion of the opening of the large exhibition "Santana on Tour 97/98" in July 1998.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeast Brazil (MAISEY 1990).

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

Derivatio nominis: After the German naturalist JOHANN CHRISTIAN SENCKENBERG (* 1707, † 1772).

Diagnosis. – A very small species of Cordulagomphinae with a wing span of only about 37 mm. The following combination of characters distinguishes this new species from *Cordulagomphus (Procordulagomphus) xavieri* NEL & ESCUILLIÉ, 1994 and *Cordulagomphus fenestratus* CARLE & WIGHTON, 1990 that have a similar size: only one non-aligned secondary antenodal crossvein between Ax1 and Ax2; only four antenodal crossveins in the hindwing; only three postnodal crossveins in the forewing and four of them in the hindwing; only three postsubnodal crossveins; distal antefurcal (= postmedian) crossvein distinctly oblique in the hindwing; distal side MAb of the discoidal triangle is relatively straight without a pronounced angle; CuA in both pairs of wings without visible posterior branches; anal area of forewing with two rows of cells; anal loop unicellular; male with two-celled anal triangle.

Autapomorphies of this new species seem to be the small number of only three postnodal crossveins between nodus and pterostigma in the forewing, and the strongly reduced cubito-anal area in both pairs of wings with only one row of cells in the forewing and two to three rows of cells in the hindwing.

Description

Holotype (Figs 6–7): An excellently preserved male dragonfly of very small size (wing span, 37 mm; body length, 32 mm, incl. head and anal appendages). All four wings are outspread and head and body are well-preserved, too. Only the legs are not preserved, except for the bases of the forelegs. The wings probably have been hyaline.

Body: Max. width of head, 5.0 mm; the compound eyes are widely separated (distance, 1.3 mm); the abdomen is about 22 mm long (excl. anal appendages) and 1.3 mm wide (the terminal part of the abdomen is somewhat clubbed with a max. width of 2.0 mm); the anal appendages (cerci) are about 1.1 mm long and extremely slender (peg-like); the epiproct is not visible.

Forewing: Length, 17.4 mm; width at nodus, 4.6 mm; distance from base to nodus, 9.3 mm (the nodus is situated at about 53 % of the wing length); distance from

nodus to pterostigma, 4.5 or 4.8 mm respectively; distance from base to arculus, 2.6 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.9 mm basal of arculus and Ax2 is 2.3–2.4 mm distal of Ax1 (somewhat basal of the distal edge of the discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2 (inexactly aligned); distal of Ax2 there are three to four secondary antenodal crossveins between the costal margin and ScP and three of them between ScP and RA; only three antesubnodal crossveins with a distinct gap directly distal of the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; the secondary antenodal crossveins and the postnodal crossveins are non-aligned; only three postnodal crossveins and three postsubnodal crossveins between nodus and pterostigma; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 1.5–1.7 mm long and max. 0.6 mm wide; the pterostigma is distinctly braced and covers about one and a half cells; the arculus is between Ax1 and Ax2 and is distinctly angled; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the hypertriangle is 1.7–1.9 mm long and max. 0.3–0.4 mm wide; the hypertriangle is free and its costal side (MA) is curved; the discoidal triangle is transverse and free; length of basal side of discoidal triangle, 1.1 mm; length of its costal side, 1.1–1.2 mm; length of its distal side MAb, 1.5 mm; MAb is relatively straight (weakly angled in the right wing); a distinct pseudo-anal vein PsA delimits an unicellular subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 0.9 mm basal of arculus; anal area max. 0.9 mm wide with one to two rows of cells (including a large elongate cell beneath the cubital cell); cubito-anal area max. 0.6–0.7 mm wide with only one row of cells; CuA without visible posterior branches; MP ends on the level of the nodus; basal part of postdiscoidal area with only two rows of cells; the postdiscoidal area is somewhat widened distally (width near discoidal triangle, 1.1–1.2 mm; width at hind margin, 2.9–3 mm) with six cells between MA and MP at the hind margin; no Mspl; RP3/4 and MA relatively straight and parallel with only one row of cells between them, except directly at the hind margin (two cells); first branching of RP 2.7–2.8 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1–1.2 mm and one and a half cells distal des subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus; RP2 and IR2 strictly parallel with only one row of cells between them up to the hind margin; no Rspl; only one row of cells between RP1 and RP2 up to the pterostigma; pseudo-IR1 originates on RP1 beneath distal side of pterostigma; one row of cells between pseudo-IR1 and RP1 and two rows of cells between pseudo-IR1 and RP2 (three to four rows of cells near the hind margin).

Hindwing: Length, 16.7–16.9 mm; width at nodus, 5.5 mm; distance from base to nodus, 7.9 mm (the nodus is situated at 47 % of the wing length); distance from nodus to pterostigma, 4.7–4.9 mm; distance from base to arculus, 2.6–2.7 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.5–0.6 mm basal of arculus and Ax2 is 2.7–2.8 mm distal of Ax1 (about the level of the distal edge of the discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2 (inexactly aligned); distal of Ax2 there are only one to two secondary antenodal crossveins between the costal margin and ScP and only a single one between ScP and RA; only two antesubnodal crossveins are visible (none in the right wing) and there appears to be a long "cordulegastrid gap" (sensu BECHLY 1996)

directly basal of the subnodus, as well as a gap directly distal of the arculus; the secondary antenodal crossveins distal of Ax2 and the postnodal crossveins are nonaligned; four postnodal crossveins and two to three postsubnodal crossveins between nodus and pterostigma; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 1.7–1.8 mm long (distinctly longer than in the forewing) and max. 0.6 mm wide; the pterostigma is distinctly braced and covers about one to one and a half cells; the arculus is closer to Ax1 than in the forewing and is weakly angled; the origins of RP and MA (sectors of arculus) are somewhat separated at the arculus; the hypertriangle is 2.0 mm long and max. 0.4 mm wide; the hypertriangle is free and its costal side (MA) is curved; the discoidal triangle is transverse and free; length of basal side of discoidal triangle, 1.1–1.2 mm; length of its costal side, 1.4 mm; length of its distal side MAb, 1.6 mm; MAb is straight; the subdiscoidal veinlet (crossvein-like basal part of CuA between triangle and its fusion with the anal vein) is not shortened; the pseudo-anal vein PsA is as distinct as in the forewing; subdiscoidal triangle unicellular; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 0.9–1 mm basal of arculus; anal area max. 2.8 mm wide with three to four rows of cells; cubito-anal area max. 2.0 mm wide with two to three rows of cells; CuAa without any visible posterior branches (only the base of CuAb is still distinct, so that a short "gaff" can be recognized); CuA is smoothly approaching the hind margin; anal loop longitudinal elongate and unicellular (max. 1.6–1.7 mm long and 0.7 mm wide); MP ends on the level of the nodus; the area between CuA and MP is relatively narrow with only one row of cells, except directly at the hind margin (two cells); basal part of postdiscoidal area with only two rows of cells; the postdiscoidal area is distally widened (width near discoidal triangle, 1.3 mm; width at hind margin, 2.9–3.1 mm) with six cells between MA and MP at the hind margin; no Mspl; RP3/4 and MA relatively straight and parallel with only one row of cells between them, except directly at the hind margin (two cells); first branching of RP 2.4 or 2.8 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1.2–1.3 mm and one and a half cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus; RP2 and IR2 strictly parallel with only one row of cells between them up to the hind margin; no Rspl; only one row of cells between RP1 and RP2 up to the pterostigma, although these two veins are distinctly divergent; RP2 with a distinct kink at the lestine oblique vein "O"; pseudo-IR1 originates on RP1 beneath distal side of pterostigma; one row of cells between pseudo-IR1 and RP1 and two rows of cells between pseudo-IR1 and RP2 (three to four rows of cells near the hind margin); near the wing base there is a distinct anal angle in the hind margin and a two-celled anal triangle, thus it is a male specimen; between anal loop and anal triangle there are only two rows of cells, but no posterior branch of the anal vein; a long and narrow membranule is visible at the hind margin of the anal triangle.

Phylogenetic position. – The relationship of this new species with Proterogomphidae – Cordulagomphinae is documented by the following synapomorphies (compare BECHLY 1996, 1997a): discoidal triangle secondarily unicellular (convergent to Araripegomphidae and numerous extant gomphids); pterostigma covers only two cells; pseudo-IR1 originates on RP1 beneath the distal side of the pterostigma; anal loop longer than wide and only divided into one or two cells; distinct "cor-

dulegastrid gap" (sensu BECHLY 1996) of crossveins in the distal antesubnodal area (except in the most basal genus that is still undescribed); most distal antefurcal crossvein distinctly oblique and most basal postnodal crossvein distinctly slanted towards the nodus (the latter character is reduced in *C. xavieri* and an undescribed new species); only two antefurcal crossveins in both pairs of wings (convergent to Gomphidae sensu BECHLY 1996, 1997a); CuAa with reduced posterior branches in the hindwing (except in the most basal genus that is still undescribed).

This new species shares with *Cordulagomphus (Procordulagomphus) xavieri* the small number of antenodal crossveins in the hindwing (generally not more than four), the unicellular anal loop, the reduced anal area in the hindwing, the strongly reduced cubito-anal area in the hindwing with only three rows of cells and without any visible posterior branches of CuA, and the relatively straight distal side MAb of the discoidal triangle (reversal), especially in the hindwing. These six derived characters probably represent synapomorphies of the two species and thus justify the attribution to the same subgenus *Procordulagomphus* stat. nov. Differences are the two-celled anal triangle (unicellular in *C. xavieri*), the strictly triangular shape of the discoidal triangle (slightly quadrangular in *C. xavieri*), the strongly oblique distal antefurcal crossvein (non-oblique in *C. xavieri*), and the presence of two rows of cells in the anal area of the forewings (only one row of cells in *C. xavieri*). The mentioned differences all seem to be plesiomorphies of *C. senckenbergi* n. sp. relative to the autapomorphic states in *C. xavieri*. The apparently plesiomorphic straight distal antefurcal crossvein of *C. xavieri* is clearly an autapomorphic reversal (contra NEL & ESCUILLIÉ 1994) as documented by the presence of the apomorphic state in *C. senckenbergi* n. sp. and in the most basal (undescribed) genus of Cordulagomphinae (Figs 31–32). NEL & ESCUILLIÉ (1994) mentioned two further potential autapomorphies of *C. xavieri*: quadrangular shape of the discoidal triangle in both pairs of wings of both sexes, and RP1 with a distinct kink at the pterostigmal brace vein. The latter character is also present in numerous specimens of *Cordulagomphus fenestratus* and because of this variability it is of dubious value as diagnostic character. At least in the forewings of one certain specimen of *C. xavieri* (no. 37, National Science Museum Tokyo; ex coll. ms-fossil) the discoidal triangles seem to be normal (triangular instead of quadrangular). On the other hand, female specimen E21 (coll. ms-fossil) has quadrangular triangles in all four wings, and agrees also in all the other characters exactly with the type specimens (this specimen has an extraordinarily well-preserved head and thorax in ventral aspect).

Because of several shared reductions and reversals *Procordulagomphus* seems to be more closely related to *Cordulagomphus fenestratus* than to *Cordulagomphus tuberculatus* CARLE & WIGHTON, 1990 which is the type species of the genus. If this should be correct, the genus *Cordulagomphus* would become paraphyletic unless *C. fenestratus* would be transferred to *Procordulagomphus*. The situation would become even more complicated through the discovery of two new species, of which one (Figs 31–32) clearly represents the most basal member of Cordulagomphinae, while the other (Figs 33–34) seems to be related to *Procordulagomphus,* too (see below). Furthermore, there are no known synapomorphies of *C. fenestratus* and *C. tuberculatus*. To avoid a paraphyletic genus *Cordulagomphus*, and to circumvent the necessity for an undesirable splitting of *Cordulagomphus* into several new monophyletic genera that would still be rather similar to each other, I decided to downrank *Procordulagomphus* from a separate genus to a subgenus of *Cordulagomphus*.

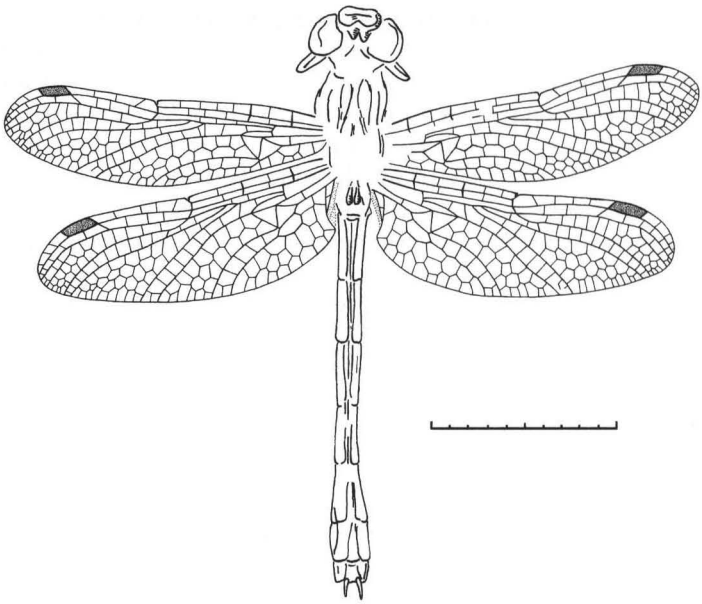

Fig. 6. *Cordulagomphus (Procordulagomphus) senckenbergi* n. sp., ♂ holotype C7 (Senckenberg Mus.). Scale 10 mm.

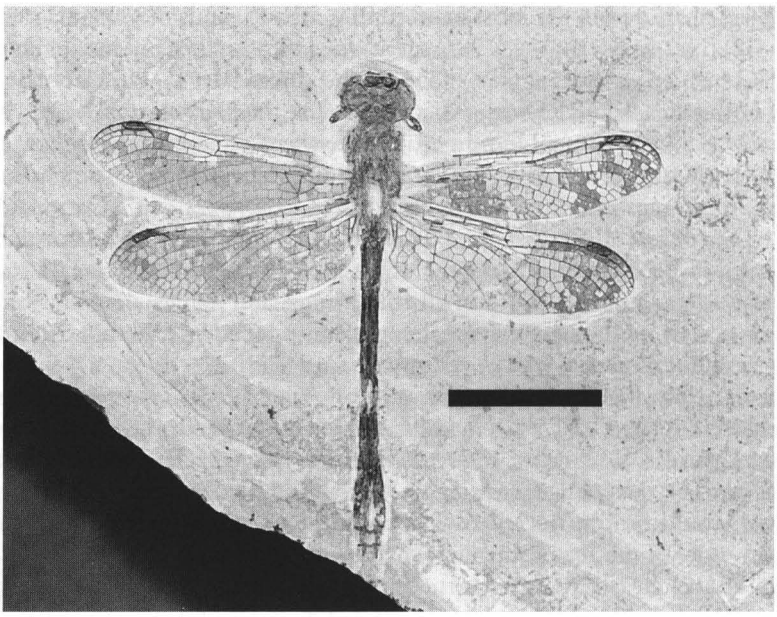

Fig. 7. *Cordulagomphus (Procordulagomphus) senckenbergi* n. sp., ♂ holotype C7 (Senckenberg Mus.). Scale 10 mm.

Suborder Anisoptera SELYS in SELYS & HAGEN, 1854
Euanisoptera BECHLY, 1996
Exophytica BECHLY, 1996
Cavilabiata BECHLY, 1996
Cristotibiata BECHLY, 1997
Brachystigmata BECHLY, 1996
Chlorogomphida BECHLY, 1996
Superfamily Chlorogomphoidea NEEDHAM, 1903 sensu BECHLY 1996

Family Araripephlebiidae n. fam.

Type-genus: *Araripephlebia* n. gen.

Phylogenetic definition. – The most inclusive clade that contains *Araripephlebia mirabilis* n. sp. but none of the type species of the type genera of the anisopteran family-group taxa sensu BECHLY (1996) (stem-based definition according to Phylogenetic Taxonomy sensu DE QUEIROZ & GAUTHIER 1990, 1992). Currently only including *Araripephlebia mirabilis* n. sp.

Diagnosis. – Same as genus, since monotypic.

Autapomorphies: The unique structure of the cubito-anal area with a concave secondary vein (definitely not a midrib of a so-called "italian" anal loop) parallel to the totally unbranched CuA.

Genus *Araripephlebia* n. gen.

Type-species: *Araripephlebia mirabilis* n. sp.
Derivatio nominis: After the type locality (Chapada do Araripe) and the Greek expression for vein.

Diagnosis. – Pterostigmata unbraced and relatively short (only covering two to three cells); pseudo-IR1 originates beneath pterostigma; discoidal triangles transverse in both pairs of wings with the two-celled hindwing discoidal triangle being even more transverse than the unicellular forewing discoidal triangle; subdiscoidal triangle unicellular in both pairs of wings, but larger in the forewing than in the hindwing; hypertriangle free in both pairs of wings, but shorter and wider in the hindwing than in the forewing; only two rows of cells in the basal part of the postdiscoidal area; only one secondary antenodal crossvein between Ax1 and Ax2; arculus straight and close to Ax1; Ax2 on the level of basal side of discoidal triangle in forewing; origins of RP and MA distinctly separated at arculus; only one lestine oblique vein "O" two cells distal of subnodus; no Rspl or Mspl; area between RP2 and IR2 somewhat widened distally; RP3/4 and MA parallel up to the hind margin; MP and CuAa strongly curved in the hindwing; area between MP and CuA basally and distally distinctly widened; CuA without any posterior branches; anal loop closed, but small (three to four cells); concave secondary vein in the cubito-anal area, parallel to CuA.

Araripephlebia mirabilis n. sp.
Figs 8–10

Holotype: ♀ specimen no. 49, National Science Museum Tokyo (ex coll. ms-fossil).
Paratypes: Specimen no. 14, Museum of Kitakyushu.

Further material: Specimen no. D45, part of the large exhibition "Santana on Tour 97/98" by ms-fossil in Germany.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeast Brazil (MAISEY 1990).

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

Derivatio nominis: After the Latin expression for "marvellous" because of the unique wing venation.

Diagnosis. – Same as genus, since monotypic.

Description

Holotype (Figs 8–9): A well-preserved female dragonfly with all four wings outspread (wing span about 72 mm), as well as head and body. Only the legs and the tip of the abdomen are missing. The wings probably have been hyaline.

Head: Width, 5.8 mm; compound eyes large and distinctly approximated, but not touching.

Forewing: Length, 34.2 mm; width at nodus, 8.8 mm; distance from base to nodus, 19.1 mm (the nodus is situated in a relatively distal position at about 56 % of the wing length); distance from nodus to pterostigma, 8.9 mm; distance from base to arculus, 3.2 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 3.1 mm distal of Ax1 (somewhat basal of the discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2; distal of Ax2 there are about eleven secondary antenodal crossveins between the costal margin and ScP and nine of them between ScP and RA; about eight antesubnodal crossveins (only four visible in the left wing) with a distinct gap directly distal of the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; the secondary antenodal crossveins and the postnodal crossveins are non-aligned; eight postnodal crossveins between nodus and pterostigma; the most basal postnodal crossvein is slanted towards the nodus; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.4 mm long and max. 0.9 mm wide; the pterostigma is unbraced and covers about two and a half cells; the arculus is close to Ax1 and only weakly angled; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the hypertriangle is 5.4 mm long and max. 0.7 mm wide; the hypertriangle is free and its costal side (MA) is distinctly curved; the discoidal triangle is transverse and free; length of basal side of discoidal triangle, 2.2 mm (right wing) or 2.0 mm (left wing); length of its costal side, 2.6 mm (right wing) or 2.3 mm (left wing); length of its distal side MAb, 2.7 mm (right wing) or 2.4 mm (left wing); MAb is straight; a distinct pseudo-anal vein PsA delimits an unicellular subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.0 mm basal of arculus; anal area max. 2.0 mm wide with two rows of cells; cubito-anal area max. 2.0 mm wide with up to three or four rows of cells; CuA probably with four posterior branches (only three are visible); MP ends on the level of the nodus; basal part of postdiscoidal area with only two rows of cells; the postdiscoidal area is distally widened (width near discoidal triangle, 2.3 mm; width at hind margin, 5.8 mm); no Mspl; RP3/4 and MA slightly undulating and closely parallel with only one row of cells between them, except at the hind margin (two small cells); first branching of RP 5.2 mm (right wing) or 4.8 mm (left wing) basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1.6 mm and two cells

(right wing) or 1.7 mm and two and a half cells (left wing) distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus; the area between RP2 and IR2 is distally widened, but there is only one row of cells between these veins, except near the hind margin (two rows of cells); no Rspl; RP1 and RP2 are basally parallel with only one row of cells between them, but about 3 mm basal of pterostigma the area between these veins widens progressively; pseudo-IR1 originates on RP1 beneath the pterostigma; two rows of cells between pseudo-IR1 and RP1 and between pseudo-IR1 and RP2.

Hindwing: Length, 34.1 mm (right wing) or 34.5 mm (left wing); width at nodus, 10.5 mm; distance from base to nodus, 16.0 mm (right wing) or 16.4 mm (left wing) (the nodus is situated basal of midwing at about 47 % of the wing length); distance from nodus to pterostigma, 11.8 mm (right wing) or 11.7 mm (left wing); distance from base to arculus, 3.5 mm (right wing) or 4.2 mm (left wing); Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.5 mm basal of arculus and Ax2 is 4.2 mm distal of Ax1 (slightly basal of the level of the distal edge of the discoidal triangle); only one secondary antenodal crossvein between Ax1 and Ax2 (aligned in the right wing, but non-aligned in the left wing); distal of Ax2 there are probably six secondary antenodal crossveins (only three or four are visible); only few antesubnodal crossveins are preserved, but there seems to be a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus, and no gap directly distal of the arculus; the secondary antenodal crossveins and the postnodal crossveins are non-aligned; about ten to twelve postnodal crossveins between nodus and pterostigma; the most basal postnodal crossvein is slanted towards the nodus; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.4 mm long and max. 0.9 mm wide; the pterostigma is unbraced and covers about two to two and a half cells; the arculus is totally straight and close to Ax1; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the hypertriangle is 3.8 mm long and max. 0.8 mm wide (distinctly wider than in the forewing); the hypertriangle is free and its costal side (MA) is strongly curved; the discoidal triangle is transverse (even more than in the forewing) and divided into two cells below each other; length of basal side of discoidal triangle, 2.2 mm; length of its costal side, 2.4 mm; length of its distal side MAb, 3.0 mm; MAb is straight; the pseudo-anal vein PsA is less distinct than in the forewing; subdiscoidal triangle smaller than in the forewing, but as well unicellular; basal space free; cubital cell free (except for CuP-crossing and PsA); CuP-crossing is 1.4 mm basal of arculus; anal area max. 8.2 mm wide with about ten rows of cells; cubito-anal area max. 3.7 mm (right wing) or 4.2 mm (left wing) wide with up to five rows of cells; CuA strongly sigmoidally curved and without any branchings (even a CuAb is not visible, so that it is not possible to delimit a "gaff"); anal loop small with three cells in the right wing and four cells in the left wing; concave secondary vein in the cubito-anal area, parallel to CuA (this unique intercalary vein originates and ends in the cross-venation); MP is strongly curved and end basal of the nodus; the area between CuA and MP is basally widened (with two rows of cells), and distally strongly widened, too (with four rows of cells between CuA and MP at the hind margin) (in the left hindwing a part of MP and the hind margin is torn off and folded over the wing!); basal part of postdiscoidal area with only two rows of cells; the postdiscoidal area is strongly widened distally (width near discoidal triangle, 2.4 mm; width at hind margin, 7.3 mm); no Mspl; MA is distally zigzagged; RP3/4

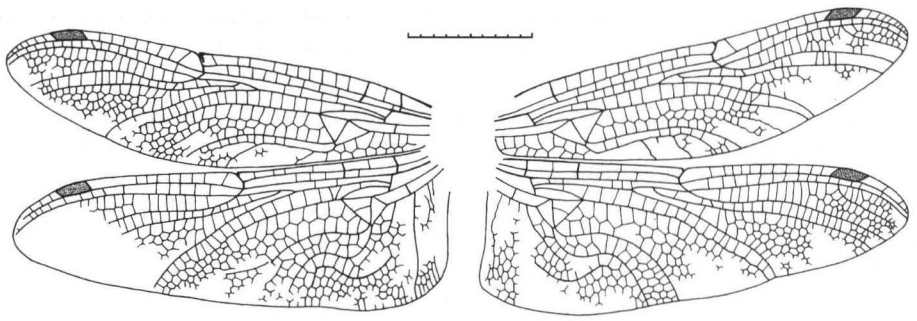

Fig. 8. *Araripephlebia mirabilis* n. gen. et n. sp., ♀ holotype no. 49 (Nat. Sci. Mus. Tokyo). Scale 10 mm.

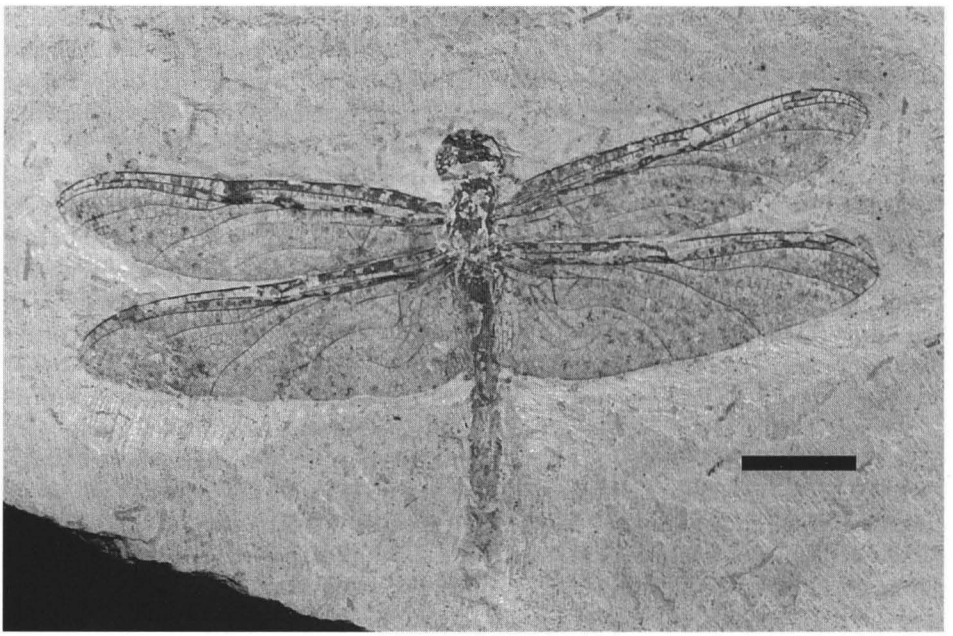

Fig. 9. *Araripephlebia mirabilis* n. gen. et n. sp., ♀ holotype no. 49 (Nat. Sci. Mus. Tokyo). Scale 10 mm.

and MA closely parallel with only one row of cells between them up to the hind margin; first branching of RP 4.7 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1.9 mm and three cells distal of subnodus; only one bridge crossvein between RP2 and IR2 basal of subnodus; the area between RP2 and IR2 is distally widened, but there is only one row of cells between these veins, except near the hind margin (two rows of cells); no Rspl; RP1 and RP2 are basally parallel with only one row of cells between them, but about 4 mm basal of the pterostigma the area between these veins widens progressively; pseudo-IR1 originates on RP1 beneath the pterostigma; two rows of cells between pseudo-IR1 and RP1 and

between pseudo-IR1 and RP2; the basal hind margin is rounded without an anal angle, and there is no anal triangle either, thus it almost certainly is a female specimen; a membranule is not visible.

Paratype no. 14: A thorax fragment with three legs and a single right forewing (length, 34.2 mm) with almost identical wing venation to the forewing of the holotype.

Forewing: Length, 34.2 mm; width at nodus, 8.1 mm; distance from base to nodus, 19.1 mm (the nodus is situated in a relatively distal position at about 56 % of the wing length); distance from nodus to pterostigma, 9.2 mm; distance from base to arculus, 4.5 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 1.1 mm basal of arculus and Ax2 is 3.6 mm distal of Ax1 (on the level of the basal side of the discoidal triangle); only one non-aligned secondary antenodal crossvein between Ax1 and Ax2; distal of Ax2 there are thirteen secondary antenodal crossveins between the costal margin and ScP, but only eight of them between ScP and RA; only five antesubnodal crossveins are present with a distinct gap directly distal of the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; the secondary antenodal crossveins and the postnodal crossveins are non-aligned; eight postnodal crossveins between nodus and pterostigma; the most basal postnodal crossvein is slanted towards the nodus just like the most distal costal antenodal crossvein; no "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 2.4 mm long and max. 0.9 mm wide; the pterostigma is unbraced and covers hardly more than two cells; the distal side of the pterostigma is much more oblique than the basal side; the arculus is closer to Ax1 and only weakly angled; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the hypertriangle is 4.9 mm long and max. 0.7 mm wide; the hypertriangle is free and its costal side (MA) is distinctly curved; the discoidal triangle is 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, 2.6 mm; MAb is straight; a distinct pseudo-anal vein PsA delimits an unicellular 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. 1.9 mm wide with two rows of cells; cubito-anal area max. 1.6 mm wide with up to three rows of cells; CuA probably with five posterior branches (only faintly preserved); MP ends on the level of the nodus; the cross-venation in the basal part of the postdiscoidal area is not preserved; the postdiscoidal area is distally widened (width near discoidal triangle, 2.1 mm; width at hind margin, 6.0 mm); no Mspl, but to convex intercalary veins are visible in the distal part of the postdiscoidal area; RP3/4 and MA slightly undulating and closely parallel with only one row of cells between them; first branching of RP 4.8 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 2.0 mm and slightly more than two cells distal of subnodus; only one bridge crossvein visible between RP2 and IR2 basal of subnodus; the area between RP2 and IR2 is distally somewhat wider than basally, but there is only one row of cells between these veins; no Rspl, but at least one convex intercalary vein is visible in the distal part of the area between IR2 and RP3/4; RP1 and RP2 are basally parallel with only one row of cells between them, but about 1.0 mm basal of pterostigma the area between these veins widens progressively; pseudo-IR1 originates on RP1 beneath the distal part of the pterostigma; two rows of cells between pseudo-IR1 and RP1 and two to three rows between pseudo-IR1 and RP2.

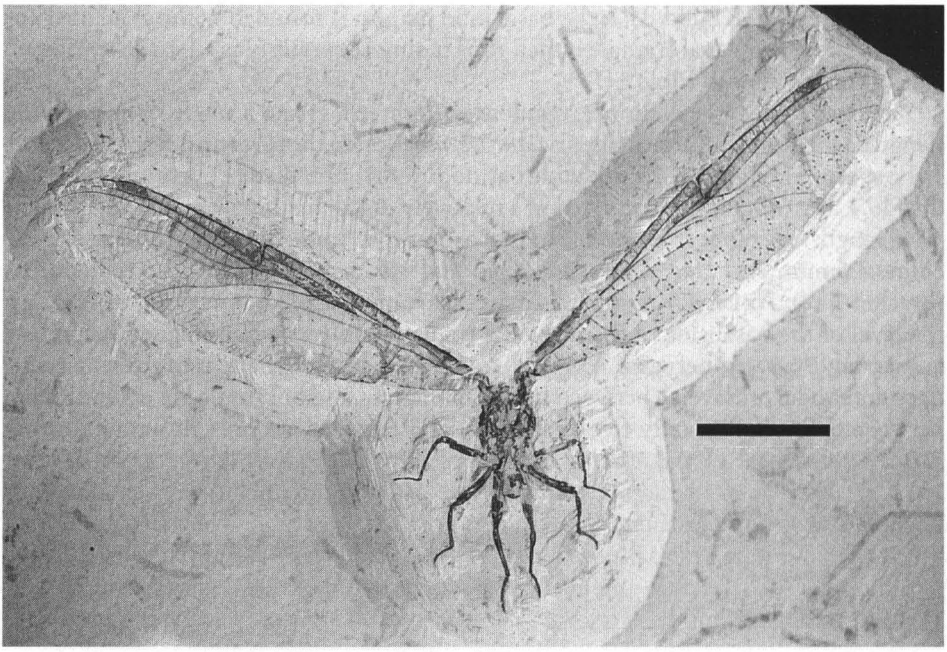

Fig. 10. *Araripephlebia mirabilis* n. gen. et n. sp., paratype D45 (ms-fossil). Scale 10 mm.

Specimen no. D45 (Fig. 10): Two well-preserved forewings (length, 34.0 mm) in connection with the thorax, and all six legs. The wing venation is nearly identical to the holotype. However, there are two intercalary veins visible in the distal post-discoidal area and three such veins in the area between IR2 and RP3/4. The apparent absence of these intercalary veins in the holotype is most probably due to an artifact of preservation.

Phylogenetic position. – This new family shares with all Exophytica (= Gomphides + Cavilabiata) the presence of only one lestine oblique vein "O". Although this is a homoplastic and thus rather weak character, it is the single known autapomorphy in the wing venation of Exophytica (BECHLY 1996, 1997a). Within Exophytica the Araripephlebiidae n. fam. share the presence of a so-called "cordulegastrid gap" as derived similarity with Cavilabiata (= Cordulegastrida + Cristotibiata) (convergent to Gomphaeschnidae, Araripegomphidae and Cordulagomphinae). Derived similarities with Cristotibiata (= Neopetaliidae + Brachystigmata) are the non-parallel sided pterostigmata (distal side more oblique than basal side) which are less than eight times longer than wide, and the shortened CuA in the hindwing with not more than five posterior branches (incl. CuAb). A relationship with Brachystigmata (= Chlorogomphida + Eurypalpida) is documented by the following putative synapomorphies: pterostigmata short, covering not more than two or three cells; pterostigmal brace vein displaced or reduced; MP more strongly curved in the hindwing and thus shortened; CuA more strongly curved in the hindwing and thus further shortened with not more than four posterior branches (incl. CuAb); nodus shifted in a more distal position in the forewing; arculus straight with a shortened posterior part; RP3/4 and MA parallel with only one row of cells between them up to the hind margin.

Within Brachystigmata the evidence from the characters is unfortunately somewhat conflicting, since there are derived similarities with Chlorogomphida, as well as with Eurypalpida (= Libelluloidea auct.). The putative synapomorphies with Chlorogomphida are: area between MP and CuA basally widened with two rows of cells; discoidal triangle more transverse in the hindwing than in the forewing; shape of the subdiscoidal triangle in the hindwing which is distinctly slanted towards the hind margin (correlated with the transverse shape of the discoidal triangle). Derived similarities with Eurypalpida include: CuA with not more than two posterior branches; costal side of hypertriangle distinctly curved, especially in the hindwing; Ax1 and Ax2 relatively close together with not more than one secondary antenodal crossvein between them.

While the mentioned similarities with Eurypalpida mostly include homoplastic characters that are partly also known from quite distantly related taxa (e.g. Gomphides), the putative synapomorphies with Chlorogomphida can be regarded as stronger evidence. Especially the hindwing discoidal triangle being more transverse than that of the forewing is a unique derived similarity with all extant Chlorogomphoidea which is not known from any other dragonflies. Therefore, Araripephlebiidae n. fam. probably represent the sister-group of extant Chlorogomphoidea. The derived similarities with Eurypalpida are better explained as convergences and parallelisms. The probable relationship of this new taxon with Chlorogomphoidea is of particular interest, since the distribution of all extant Chlorogomphoidea is restricted to East Asia. The other known putative stem-group representatives of chlorogomphids (viz Hemeroscopidae and maybe Valdicorduliidae) have an Old World distribution, too, except the fossil dragonfly described below as first fossil record and first New World record of Chlorogomphoidea s. str. However, because of the mentioned conflicting evidence the attribution of Araripephlebiidae to Chlorogomphida still has a somewhat preliminary status.

Suborder Anisoptera SELYS in SELYS & HAGEN, 1854
Euanisoptera BECHLY, 1996
Exophytica BECHLY, 1996
Cavilabiata BECHLY, 1996
Cristotibiata BECHLY, 1997
Brachystigmata BECHLY, 1996
Paneurypalpida BECHLY, 1996
Family Araripelibellulidae BECHLY, 1996

Genus *Cratocordulia* n. gen.

Type-species: *Cratocordulia borschukewitzi* n. sp.
Derivatio nominis: After the town of Crato and the genus *Cordulia*.

Diagnosis. – Similar to *Araripelibellula martinsnetoi* NEL & PAICHELER, 1994, the only other libelluloid from the Crato Formation, but differing in the following characters: distinctly bigger size (wing length about 24–25 mm); Ax2 is basal of the forewing discoidal triangle; the forewing arculus is straight; the sectors of the arculus have a common origin at the arculus in both pairs of wings; and the anal loop is longer and four-celled; no posterior branch of anal vein between anal loop and basal margin in the female hindwing; veins MA and IR2 are distally zigzagged; higher

number of postnodal and postsubnodal crossveins in both pairs of wings; the pterostigmal brace vein is slightly displaced distally; less distinct intercalary veins between IR2 and RP3/4 and between MA and MP in the hindwing.

Cratocordulia borschukewitzi n. sp.
Figs 11–12

Holotype: ♀ specimen C5, Muséum Nationale d'Histoire Naturelle in Paris (Laborat. Paleont.).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeast Brazil (MAISEY 1990).

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

Derivatio nominis: After Dr REINER BORSCHUKEWITZ (Offenburg) who donated the holotype and a collection of about 90 further interesting fossil insects from the Crato Formation to the Muséum National d'Histoire Naturelle in Paris.

Diagnosis. – Same as genus, since monotypic.

Description

Holotype (Figs 11–12): A female dragonfly with all four wings outspread. The wings are very well-preserved, only the apices of the right pair of wings are missing. Head, legs, and most of the abdomen are missing, only the thorax and the basal abdominal segments are preserved, but rather useless. The wings probably have been hyaline, although there might have been a dark coloration in the basal and costal parts of the wing.

Forewing: Length, 25.1 mm; width at nodus, 6.7 mm; distance from base to nodus, 14.5 mm (the nodus is situated in a relatively distal position at about 58 % of the wing length); distance from nodus to pterostigma, 6.2 mm; distance from base to arculus, 3.4 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.8 mm basal of arculus and Ax2 is only 2.3–2.4 mm distal of Ax1 (even slightly basal of basal side of discoidal triangle); no secondary antenodal crossveins between Ax1 and Ax2; distal of Ax2 there are only two secondary antenodal crossveins between the costal margin and ScP, strictly aligned with the two corresponding antenodals between ScP and RA; only one or two antesubnodal crossveins in the middle of the antesubnodal area with a distinct gap near the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; four postnodal crossveins between nodus and pterostigma, non-aligned with the three corresponding postsubnodal crossveins; distinct "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 1.7 mm long and max. 0.6 mm wide; the pterostigma is distinctly braced and covers only a half cell; the pterostigmal brace vein is slightly distally displaced, thus not exactly aligned with the basal margin of the pterostigma; RA is not distinctly broadened along the pterostigma; arculus is totally straight; bases of veins RP and MA (sectors of arculus) with a common origin at the arculus; the hypertriangle is 3.6 mm long and max. 0.5 mm wide; the hypertriangle is free and its costal side (MA) is distinctly curved; discoidal triangle transverse and free; length of basal side of discoidal triangle, 1.8 mm; length of its costal side, 1.8 mm; length of its distal side MAb, 2.1 mm; MAb is distinctly angled; a very well-defined pseudo-anal vein PsA (= AA0) delimits an unicellular subdiscoidal triangle; the hind margin of the subdiscoidal triangle is angled; basal space free; cubital cell free (except for CuP-crossing

and PsA); CuP-crossing is 1.0 mm (right wing) or 0.7 mm (left wing) basal of arculus; anal area max. 1.5 mm wide with two rows of cells; cubito-anal area max. 1.3 mm wide with two rows of cells; CuA with five to six posterior branches; MP ends somewhat distal of the level of the nodus; basal postdiscoidal area with only one row of cells; postdiscoidal area narrow, distally even more narrow than basally (width near discoidal triangle, 1.6 mm; min. distal width., 0.9 mm; width at hind margin, 1.1 mm in the right wing and 1.7 mm in the left wing); no Mspl and no other intercalary veins in the postdiscoidal area; RP3/4 and MA are somewhat undulating, but parallel with only one row of cells between them, except at the hind margin (two cells); distal part of MA zigzagged; first branching of RP ("midfork") 4.2 mm (right wing) or 4.0 mm (left wing) basal of subnodus (second branching of RP); IR2 originates on RP1/2; distal part of IR2 zigzagged; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1.4 mm and one and a half cells distal of subnodus; no bridge crossveins between RP2 and IR2 basal of subnodus; the area between RP2 and IR2 is very narrow at the oblique vein "O, but distinctly widened distally; there is only one row of cells between RP2 and IR2, except at the hind margin (two cells); no Rspl; RP1 and RP2 basally relatively parallel with only one row of cells between them, even below pterostigma; pseudo-IR1 is weakly defined and originates on RP1 below distal side of pterostigma; one row of cells between pseudo-IR1 and RP1 and between pseudo-IR1 and RP2 respectively.

Hindwing: Length, 24.2 mm; width at nodus, 8.4 mm; distance from base to nodus, 9.8 mm (the nodus is situated basal of midwing at about 40 % of the wing length); distance from nodus to pterostigma, 10.2 mm (right wing) or 9.6 mm (left wing); distance from base to arculus, 3.2 mm; Ax1 and Ax2 are aligned and stronger than the other antenodals (bracket-like); Ax1 is 0.2–0.3 mm basal of arculus and Ax2 is 2.5 mm distal of Ax1 (about the level of the distal edge of the discoidal triangle); no secondary antenodal crossveins between Ax1 and Ax2; distal of Ax2 there is only secondary antenodal crossveins between the costal margin and ScP which is strictly aligned with the corresponding antenodal between ScP and RA; only one antesubnodal crossvein in the middle of the antesubnodal area with a distinct gap near the arculus and a long "cordulegastrid gap" (sensu BECHLY 1996) directly basal of the subnodus; five (right wing) or six (left wing) postnodal crossveins between nodus and pterostigma, non-aligned with the four corresponding postsubnodal crossveins; distinct "libellulid gap" (sensu BECHLY 1996) of the postsubnodal crossveins directly distal of the subnodus; the pterostigma is 1.7 mm long and max. 0.6 mm wide; the pterostigma is distinctly braced and covers only a half cell; the pterostigmal brace vein is slightly distally displaced, thus not exactly aligned with the basal margin of the pterostigma; RA is not distinctly broadened along the pterostigma; arculus is close to Ax1 and totally straight; the bases of RP and MA (sectors of arculus) have a common origin at the arculus; the hypertriangle is 2.2 mm long and max. 0.4 mm wide (distinctly shorter than in the forewing); the hypertriangle is free and its costal side (MA) is very strongly curved; the discoidal triangle is free and less transverse than in the forewing; length of basal side of discoidal triangle, 1.3 mm; length of its costal side, 1.9 mm; length of its distal side MAb, 1.9 mm; the costal side of the discoidal triangle is distinctly curved; MAb is straight; pseudo-anal vein PsA is lacking (completely suppressed), thus there is no defined subdiscoidal triangle; basal space free; cubital cell free (except for CuP-crossing, 1.1 mm basal of arculus); anal area max. 6.1 mm wide with about five rows of cells; cubito-anal area max.

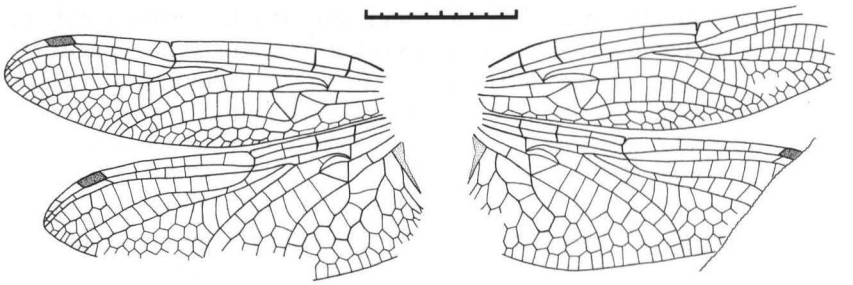

Fig. 11. *Cratocordulia borschukewitzi* n. gen. et n. sp., ♀ holotype C5 (MNHN). Scale 10 mm.

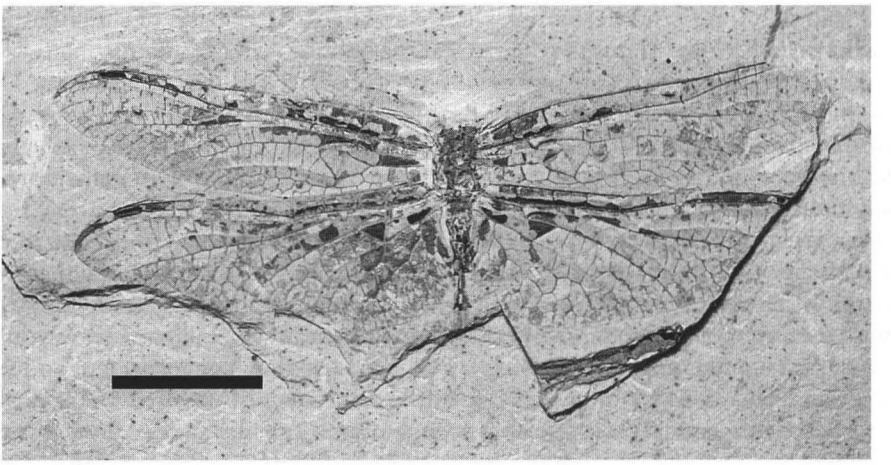

Fig. 12. *Cratocordulia borschukewitzi* n. gen. et n. sp., ♀ holotype C5 (MNHN). Scale 10 mm.

3.4 mm wide with three rows of cells; CuAa strongly curved and thus very short with only a single dichotomic branching into CuAb and CuAa (CuAa without any posterior branches); CuAb and CuAa strongly zigzagged; subdiscoidal veinlet strongly reduced; "gaff" very long and curved; anal loop well-defined, very elongate (max. length, 6.1 mm), and with a single row of four cells (quite similar to the extant species *Austrophya mystica* TILLYARD 1909); MP is strongly curved and thus shortened, ending somewhat basal of level of nodus; the area between CuA and MP is basally somewhat wider than distally, but always with only one row of cells; only one row of cells in the basal part of the postdiscoidal area; the postdiscoidal area is distally strongly widened (width near discoidal triangle, 1.6 mm; width at hind margin, 4.7 mm); no Mspl, but an indistinct intercalary vein in the distal part of the postdiscoidal area; RP3/4 and MA relatively straight and parallel with only one row of cells between them up to the hind margin; distal part of MA is zigzagged; first branching of RP 3.0 mm basal of subnodus (second branching of RP); IR2 originates on RP1/2; distal part of IR2 is zigzagged; RP2 aligned with subnodus; only one lestine oblique vein "O" between RP2 and IR2, 1.9 mm and one and a half cells distal of subnodus;

no bridge crossvein between RP2 and IR2 basal of subnodus; the area between RP2 and IR2 is very narrow at the oblique vein "O, but distinctly widened distally; there is only one row of cells between RP2 and IR2, except at the hind margin (two cells); no Rspl; RP1 and RP2 basally parallel with only one row of cells between them, even below pterostigma; pseudo-IR1 is weakly defined and originates on RP1 below distal side of pterostigma; one row of cells between pseudo-IR1 and RP1 and between pseudo-IR1 and RP2 respectively; the area of the potential anal angle is not preserved; there is no anal triangle (thus it is a female specimen, soince the male anal triangle is only reduced in crown-group Libellulidae, but not in the "corduliid" grade); no posterior branch of anal vein between anal loop and basal wing margin; a long membranule is visible.

Phylogenetic position. – This new genus and species is only known by the holotype. There are several derived similarities with *Araripelibellula martinsnetoi* (new specimen B39, coll. ms-fossil; Fig. 13): only one or two antesubnodal crossveins; only two to three secondary antenodal crossveins distal of Ax2; costal side of hypertriangle very strongly curved in the hindwing; area between RP2 and IR2 very narrow near the oblique vein "O", but more distally distinctly widened; elongate and narrow shape of the anal loop with only one row of cells; costal side of discoidal triangle distinctly curved (convergent to the extant species *Neophya rutherfordi* SELYS, 1881; contra NEL & JARZEMBOWSKI & ROSS in press); postdiscoidal area very narrow in the forewing (distal part even narrower than basal part) with only one row of cells; PsA suppressed in the hindwing (convergent to many crown-group Eurypalpida).

The numerous synapomorphies with Cavilabiata, Brachystigmata and Eurypalpida (= Libelluloidea auct.) include the following important characters: long "cordulegastrid gap" and "libellulid gap" (sensu BECHLY 1996) in both pairs of wings; distal position of nodus in the forewing; short pterostigmata in both pairs of wings; the approximated primary antenodal crossveins Ax1 and Ax2; very basal position of Ax2 in the forewing; and the curved costal side of the hypertriangles; straight arculus (at least in the hindwing); subdiscoidal veinlet strongly reduced in the hindwing; elongated "gaff" in the hindwing; CuA with only one dichotomic branching in the hindwing; MP and CuA strongly curved and shortened in the hindwing.

The following plesiomorphies of *Araripelibellula martinsnetoi* seem to contradict a position of Araripelibellulidae within the crown-group of Eurypalpida: Ax2 not situated basal of the discoidal triangle in the forewing; arculus still angled in the forewing; origins of RP and MA (sectors of arculus) still distinctly separated at the arculus in both pairs of wings; anal loop relatively small with only two cells; the pterostigmal brace vein is strictly aligned with the basal side of the pterostigma.

Unfortunately the discovery of *Cratocordulia borschukewitzi* n. gen. et n. sp. introduces some conflicting evidence, since it shows the same derived states like all extant Eurypalpida: Ax2 is basal of the forewing discoidal triangle; the forewing arculus is straight; the sectors of the arculus have a common origin at the arculus in both pairs of wings; and the anal loop is longer and four-celled; the pterostigmal brace vein is distally displaced in all wings. If these five derived similarities with extant Eurypalpida would be interpreted as synapomorphies, the five derived similarities with *Araripelibellula* would have to be interpreted as convergences in the new genus, or as reversals in all extant Eurypalpida. On the other hand, if the five derived similarities with *Araripelibelula* are interpreted as synapomorphies, the five derived simi-

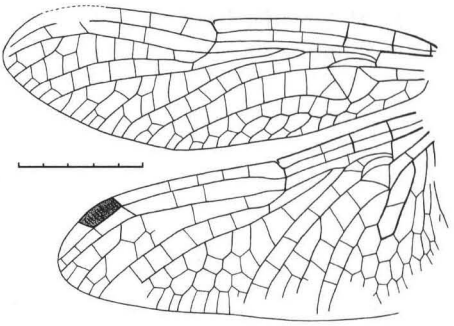

Fig. 13. *Araripelibellula martinsnetoi*, ♀ specimen B39 (ms-fossil). Scale 5 mm.

larities with Eurypalpida would have to be regarded as convergences in the new genus, or as reversals in *Araripellibelula*.

Obviously some wing venational characters either evolved several times by convergence, or have been reduced several times by convergence within Eurypalpida. This irritating homoplasy of the wing venational characters renders a phylogenetic analysis of the referring fossil dragonflies rather difficult, since unfortunately wing venation often is the only character complex that is sufficiently well-preserved in fossil dragonflies. Regarding the considerable amount of conflicting evidence, a mere numerical analysis of the character pattern with computer parsimony algorithms does not appear to be a satisfying solution at all. However, after careful consideration and weighting of the referring characters I preliminarily advocate a closer relationship of *Cratocordulia* n. gen. with *Araripelibellula* than with extant Eurypalpida. Several symplesiomorphies of the two genera, e.g. the anal loop without midrib, clearly show that they are no Libellulidae, but very basal members of the "corduliid" grade. Probable autapomorphies of *Cratocordulia borschukewitzti* n. gen. et n. sp. are the distally zigzagged veins MA and IR2, the distinctly angled distal side MAb of the forewing discoidal triangle, and the very short pterostigmata that only cover a half cell.

Contrary to Aeschnidiidae, Aeshnoptera and Gomphides, no larval Cavilabiata are known from the Crato Formation. A potential reason for this surprising absence could be the circumstance that most Eurypalpida are adapted to lentic or even lacustrine freshwater habitats, and therefore are rather unlikely to become displaced into a brackish lagoon.

Suborder Zygoptera SELYS, 1854
Euzygoptera BECHLY, 1996
Lestomorpha BECHLY, 1996
Family Hemiphlebiidae TILLYARD, 1926

Genus *Parahemiphlebia* JARZEMBOWSKI et al., in press

Parahemiphlebia mickoleiti n. sp.
Figs 14–16

Holotype: Specimen without number (Amer. Mus. Nat. Hist., New York), labelled «AMNH New and undescribed dragonfly / Crato Member – Santana Formation / Lower Cretaceous / Casa de Pedra, Araripe Plateau, Brazil» and «$800 / Geological Enterprises Inc., Box 996, Ardmore, Oklahoma 73402 / ordered by Herb Axelrod from Donna Cummings, Geol. Enterprises, Inc.».

Paratype: ♀ specimen no. SMNS 63072 (Staatl. Museum f. Naturkunde in Stuttgart).

Further material: Specimens nos D1 (?) and D22 (coll. ms-fossil).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda (Casa de Pedra), southern Ceará, north-east Brazil (MAISEY 1990).

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

Derivatio nominis: After my admired teacher Dr GERHARD MICKOLEIT (Tübingen).

Diagnosis. – One of the smallest odonates of all times with an average wing length of about 9 mm (only certain specimens of a few species of the extant damselfly genus *Agriocnemis* have a similar tiny size). The wing venation is very similar to *Parahemiphlebia cretacica* with the following few differences: pterostigmal brace vein not extremely oblique (plesiomorphy); only four postnodal crossveins and three postsubnodal crossveins (autapomorphy); IR1 originates beneath the distal side of the pterostigma (autapomorphy).

Description

Holotype (Figs 14–15): Plate and counter-plate of a well-preserved and nearly complete damselfly, of which only three legs and the tip of the abdomen are missing. The right hindwing is twisted.

Body: The head is max. 3.0 mm wide and 1.5 mm long; the compound eyes are distinctly separated (distance, 0.8 mm), and partly even the structure of the ommatidia is still visible; length of profemur, 1.6 mm; length of protibia, 1.6 mm; width of abdomen, 1.0 mm (length unknown, since the distal end of the abdomen is not preserved). Since the anal appendages and genital organs are not preserved it is not possible to determine the sex of this specimen. The coloration of the body is not preserved. The wings probably have been hyaline.

Forewing: Length, 9.9 mm; width at wing base, 0.7 mm; width at nodus, 1.9 mm; max. width (between nodus and pterostigma), 2.3 mm; distance from base to nodus, 4.3 mm (the nodus is situated at about 43 % of the wing length); distance from nodus to pterostigma, 4.1 mm; distance from base to arculus, 1.9 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 hardly 0.7 mm distal of Ax1; no secondary antenodal crossveins; no antesubnodal crossveins; four postnodal crossveins between nodus and pterostigma, non-aligned with the four postsubnodal crossveins; the pterostigma is very short (0.5 mm long and max. 0.3 mm wide); the pterostigma is distinctly braced and covers exactly one cell; the margins of the pterostigma are not distinctly broad-

ened; three postnodal crossveins distal of pterostigma; the arculus is slightly (about 0.1 mm) distal of Ax2 in both forewings; the posterior part of the arculus is missing, so that the discoidal cell is basally open; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the distal discoidal vein MAb is 0.5 mm long, concavely curved, and aligned with the arculus; there is a weak angle between arculus and MAb; basal space free; cubital cell free (except for CuP-crossing, on the level of Ax1); anal area max. 0.3 mm wide with one row of cells; cubito-anal area max. 0.3 mm wide with one row of cells; CuA zigzagged; although the subdiscoidal veinlet is aligned with MAb, there is a distinct angle between these two veins, since the subdiscoidal veinlet is slanted towards the wing base; MP is distinctly bent directly distal of the discoidal cell, and ends between nodus and pterostigma and several apical pseudo-branches; postdiscoidal area narrow with only one row of cells up to the hind margin; MA distally zigzagged and ending between nodus and pterostigma; RP3/4 and MA distally divergent, but always only one row of cells between them; RP3/4 ends on the level of the distal side of the pterostigma and has about four apical pseudo-branches; first branching of RP 0.9 mm basal of subnodus; IR2 originates 0.3 mm basal of subnodus in the left forewing, but is aligned with the subnodus in the right forewing (thus no bridge crossveins); IR2 ends somewhat distal of pterostigma; nodal crossvein and subnodus are oblique; RP3/4 and IR2 are parallel with only one row of cells between them up to the hind margin; RP2 originates between nodus and pterostigma, obviously in a rather variable position (1.8 mm distal of subnodus in the right wing, but only 1.3 mm distal of subnodus in the left wing); no lestine oblique vein "O" between RP2 and IR2; RP2 and IR2 are parallel with only one row of cells between them up to the hind margin; RP1 with a distinct kink at the pterostigmal brace vein, resulting in a distally widened substigmal cell; RP1 and RP2 divergent, but with only one row of cells between them up to the level of the pterostigma; IR1 originates in the cross-venation below the distal part of the pterostigma; one row of cells between IR1 and RP1 and between IR1 and RP2; RA and RP1 converging towards the wing apex; the wing base is narrow, but not petiolated (AA' and AA"+AP are not fused, so that the anal area reaches up to the wing base); there is only one crossvein in the anal area.

Hindwing: Length, 9.1 mm; width at wing base, 0.5 mm; width at nodus, 2.1 mm; max. width (between nodus and pterostigma), 2.4 mm; distance from base to nodus, 3.7 mm (the nodus is situated at about 40 % of the wing length); distance from nodus to pterostigma, 3.5 mm; distance from base to arculus, 1.7 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 0.7 mm distal of Ax1; no secondary antenodal crossveins; no antesubnodal crossveins; four postnodal crossveins between nodus and pterostigma, non-aligned with the three postsubnodal crossveins; the pterostigma is 0.5–0.6 mm long and max. 0.3 mm wide; the pterostigma is distinctly braced and covers exactly one cell; the margins of the pterostigma are not distinctly broadened; three postnodal crossveins distal of pterostigma; the arculus is aligned with Ax2; the posterior part of the arculus (= basal discoidal crossvein) is present, so that the discoidal cell is basally closed; the origins of RP and MA (sectors of arculus) are distinctly separated at the arculus; the discoidal cell is max. 0.7 mm long and max. 0.4 mm wide (= length of basal discoidal crossvein); the distal discoidal vein MAb is 0.5 mm long, concavely curved, and originates 0.3 mm distal of arculus; basal space free; cubital cell free (except for CuP-crossing, 0.3 mm basal of arculus); anal area max. 0.3 mm wide with

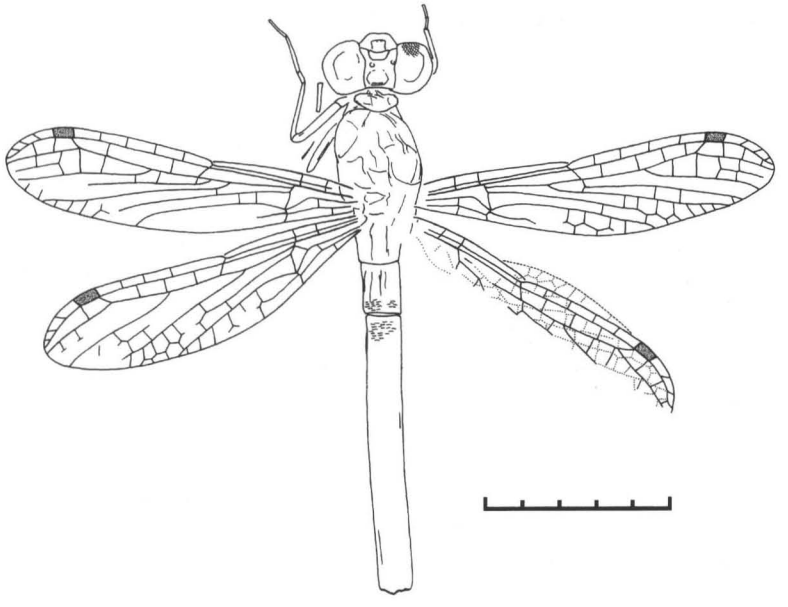

Fig. 14. *Parahemiphlebia mickoleiti* n. sp. (combined from plate and counter-plate), holotype AMNH without number. Scale 5 mm.

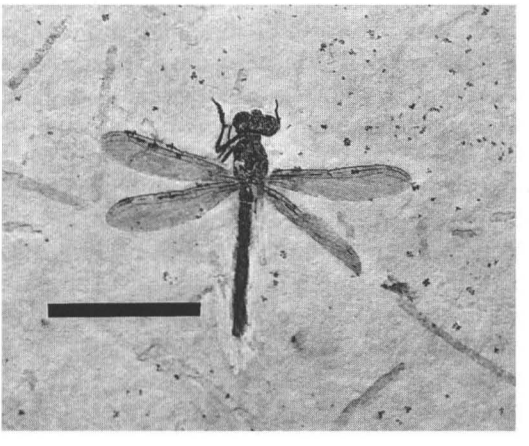

Fig. 15. *Parahemiphlebia mickoleiti* n. sp., holotype AMNH without number. Scale 10 mm.

one row of cells; cubito-anal area max. 0.3 mm wide with one row of cells; CuA zigzagged; although the subdiscoidal veinlet is aligned with MAb, there is a distinct angle between these two veins, since the subdiscoidal veinlet is slanted towards the wing base; MP is distinctly bent directly distal of the discoidal cell, and ends between nodus and pterostigma and has several apical pseudo-branches; postdiscoidal area narrow with only one row of cells up to the hind margin; MA distally zigzagged and ending somewhat basal of the level of the pterostigma; RP3/4 and MA with only one row of cells between them; the apical part of RP3/4 is not preserved; first branching

of RP 0.7 mm basal of subnodus; the base of IR2 is only preserved in the right hindwing (left hindwing of counter-plate) and originates 0.1 mm distal of subnodus; the distal part of IR2 seems to be zigzagged; nodal crossvein and subnodus are oblique; RP3/4 and IR2 seem to be parallel with only one row of cells between them up to the hind margin; RP2 originates between nodus and pterostigma (1.4–1.5 mm distal of subnodus); the area of the potential lestine oblique vein "O" between RP2 and IR2 is not preserved, but probably there was none as in the forewing; RP2 and IR2 with only one row of cells between them; RP1 with a distinct kink at the pterostigmal brace vein, resulting in a distally widened substigmal cell; RP1 and RP2 divergent, but with only one row of cells between them up to the level of the pterostigma; IR1 is not preserved, but must have originated distal of the pterostigma; RA and RP1 converging towards the wing apex; the wing base is narrow, but not petiolated (AA' and AA"+AP are not fused, so that the anal area reaches the wing base); there is only one crossvein in the anal area.

Paratype (Fig. 16): A well-preserved female damselfly, of which only the wing tips and the distal half of the abdomen are missing. The specimen is preserved in lateral aspect, so that the two pairs of wings are folded over each other.

Body: The head is max. 2.8 mm wide and 0.9 mm long; the compound eyes are distinctly separated (distance, 0.8 mm); a distinct suture is visible between vertex and occiput; all three ocelli are visible; the pterothorax is max. 2.5 mm long and 2.2 mm high, and has a distinctly developed interpleural suture; the skewness of the pterothorax is about 25°, measured as angled between thoracic sutures and abdominal axis; length of protibia, 1.3 mm; of mesofemur, 1.9; of mesotibia, 1.8 mm; of metafemur, 2.9 mm; of metatibia, 2.3 mm; width of abdomen, about 1.0 mm. Although preserved in lateral aspect, there is no secondary genital apparatus visible on the second and third abdominal segment, thus it is most probably a female specimen.

Wings: The wing length (hindwing only 8.9 mm long) and the wing venation is very similar to the holotype with the following differences: MA is not distally zigzagged; the arculus is exactly aligned with Ax2 in both pairs of wings; IR2 is exactly aligned with the subnodus in both pairs of wings.

Specimen D22: A complete, but not very well-preserved damselfly. The body length is 18.8 mm and the wing length is about 9 mm. The discoidal cell is basally open in the forewing, and the pterostigmal region is identical with the holotype and

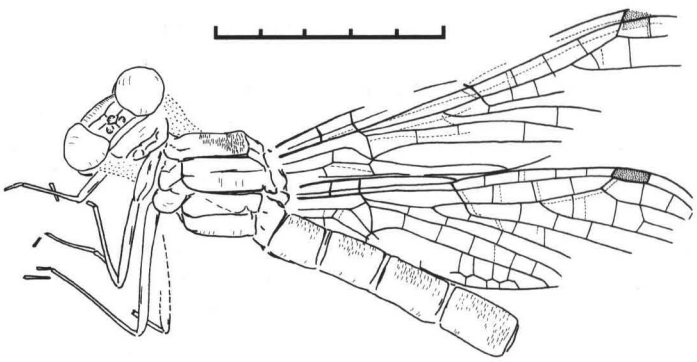

Fig. 16. *Parahemiphlebia mickoleiti* n. sp., ♀ paratype SMNS 63072. Scale 5 mm.

paratype, too. A secondary genital apparatus is clearly visible on the second abdominal segment, thus it is a male specimen. The cerci are relatively long (length, nearly 1 mm).

Phylogenetic position. – This new species shares the following characters with *Parahemiphlebia cretacica* JARZEMBOWSKI et al., in press and the extant relict species *Hemiphlebia mirabilis* SELYS, 1868: distinct suture between vertex and occiput (symplesiomorphy); discoidal cell basally open in forewing (symplesiomorphy; among extant Odonata only preserved in the two species *Chorismagrion risi* MORTON, 1914 and *Hemiphlebia mirabilis*); postnodal- and postsubnodal crossveins non-aligned (symplesiomorphy, also preserved in calopterygoid damselflies); lestine oblique vein "O" suppressed (potential synapomorphy with Hemiphlebiidae, but very homoplastic); very small body size and wing length (potential synapomorphy with Hemiphlebiidae); only five to seven postnodal crossveins (potential synapomorphy with Hemiphlebiidae); no intercalary veins, except IR1 and IR2 (potential synapomorphy with Hemiphlebiidae); petiolation of wing base reduced (potential synapomorphy with Hemiphlebiidae). The remarkably short and stout basal abdominal segments probably represent a further symplesiomorphy with *Hemiphlebia*, since this state is more similar to Epiophlebiidae and Anisoptera than to other damselflies.

Several synapomorphies with *Parahemiphlebia cretacica* justify an attribution to the same genus, such as the very distinct kink of RP1 at the pterostigmal brace vein, and the more strongly reduced petiolation with totally unfused veins AA' and AA"+AP (sensu BECHLY 1996). A further derived similarity is the distinct bend of MP directly distal of the tip of the discoidal cell, but this could rather represent a derived ground-plan character of Lestomorpha (sensu BECHLY 1996) that was convergently reduced in *Hemiphlebia* and *Cretacoenagrion* JARZEMBOWSKI, 1990 (contra BECHLY 1996). The pterostigmal brace vein not being extremely oblique is a plesiomorphy of this new species relative to the autapomorphic state in *Parahemiphlebia cretacica*. Autapomorphies of the new species are the small number of only four postnodal crossveins and three postsubnodal crossveins, and the very short vein IR1, since the latter originates basal of the pterostigma in *Parahemiphlebia cretacica* and *Hemiphlebia mirabilis*.

Suborder Zygoptera SELYS, 1854
Euzygoptera BECHLY, 1996
Familia incertae sedis (probably Hemiphlebiidae)

Genus *Cretarchistigma* JARZEMBOWSKI et al., in press

Cretarchistigma(?) *essweini* n. sp.
Figs 17–18

Holotype: ♀ specimen no. SMNS 63071 (Staatl. Museum f. Naturkunde in Stuttgart).

Paratypes: ♀ specimens nos 51 and no. 1007 (National Science Museum Tokyo; ex coll. ms-fossil); ♀ specimen no. 101 (Museum of Kitakyushu; ex coll. ms-fossil).

Further material: Specimen without number (Staatl. Museum f. Naturkunde, Karlsruhe); specimens nos B9 (relatively poorly preserved specimen that meanwhile seems to be "disappeared"), C24, C28 / C29 (?), D52 (?), D53, and E26 (all in coll. ms-fossil).

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, northeast Brazil (MAISEY 1990).

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

Derivatio nominis: After my gifted fellow student Dipl. Biol. STEFAN ESSWEIN who most tragically died before he could finish his PhD thesis on the phylogeny of tortoises at the University of Tübingen.

Diagnosis. – A very small damselfly (wing length about 10–11 mm) with the following diagnostic characters in the wing venation: arculus aligned with Ax2; hindwing discoidal cell basally closed and relatively long and narrow (basal and distal discoidal vein distinctly shorter than in *Parahemiphlebia*); about six postnodal crossveins non-aligned with the corresponding postsubnodal crossveins; pterostigma distinctly braced and rather short, covering only one cell; pterostigma with "micraster-type" sculptures; the pterostigmal brace vein is not very oblique; RP1 with a slight kink at the pterostigmal brace vein; IR1 originates one cell basal of pterostigma; only two antenodal crossveins (Ax1 and Ax2); only one row of cells between each pair of adjacent longitudinal veins. The thorax appears to be more gracile, compared to head and abdomen, as in *Parahemiphlebia*. At least the female anal appendages are strongly reduced (very short and peg-like).

Description

Holotype (Figs 17–18): A well-preserved and nearly complete female damselfly. The specimen is preserved in lateral aspect with all four wings are folded over each other, so that the wing venation is largely obscured. The total length of the body is 18.3 mm, and the wing length is about 9.8 mm. All visible characters of the wing venation have already been listed in the diagnosis (see above).

Body: The head is 3.2 mm wide and about 1.3 mm long; the compound eyes are widely separated; the pterothorax is max. 2.4 mm long and 1.7 mm high, and apparently has a well-developed interpleural suture; the skewness of the pterothorax is nearly 30°, measured as angle between the thoracic sutures and the abdominal axis; length of profemur, 1.5 mm; of protibia, 1.5 mm; of mesofemur, 1.9 mm; of mesotibia, 1.9 mm; of metafemur, 2.3 mm; of metatibia, 2.2 mm; the abdomen is 13.9 mm long and 0.8 mm wide (the fifth abdominal segment being the longest one); the anal appendages are extremely short (only 0.2 mm long) and very slender (peg-like); an ovipositor is distinctly visible, thus it is a female specimen.

Paratype specimen no. 51: A very well-preserved and complete female damselfly with the wings folded over each other. The head is max. 3.1 mm wide; the pterothorax is 2.8 mm long and 1.7 mm high, and relatively gracile; the abdomen is 15.3 mm long and max. 1.0 mm wide (except at the ovipositor). Wing length, about 10.4 mm; the pterostigmal brace is not very oblique; RP1 with a weak kink at the pterostigmal brace vein; IR1 originates one cell basal of pterostigma; IR2 and MA are distally distinctly zigzagged.

Paratype specimen no. 1007: A not very well-preserved damselfly with the distal third of the abdomen missing and the wings folded over each other. Since there is no secondary genital apparatus visible on the second and third abdominal segment, it probably is another female specimen. The high percentage of females among the damselfly fossils can be explained by the higher risk during oviposition. The wing length is 10.5 mm. The wing venation is poorly preserved, but the size, the less oblique pterostigmal brace vein, and the longer IR1, strongly suggest an attribution to the present species.

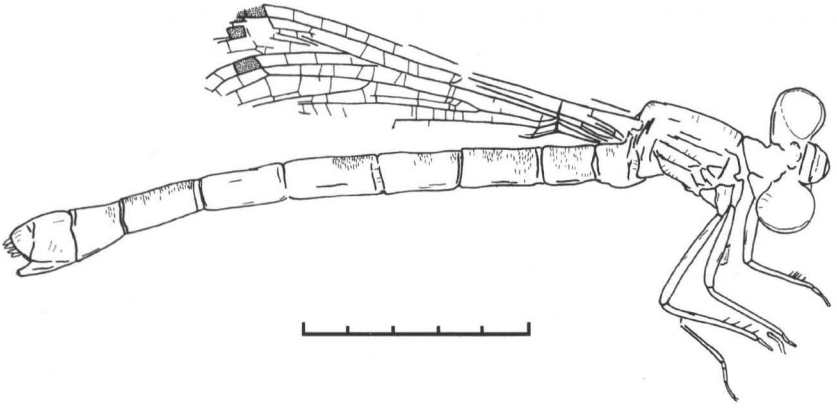

Fig. 17. *Cretarchistigma*(?) *essweini* n. sp., ♀ holotype SMNS 63071. Scale 5 mm.

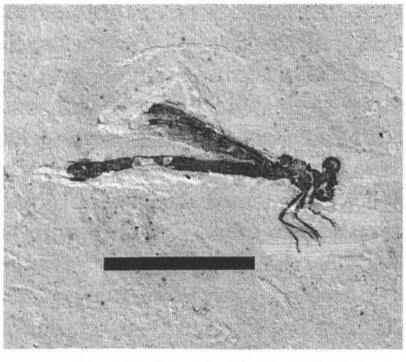

Fig. 18. *Cretarchistigma*(?) *essweini* n. sp., ♀ holotype SMNS 63071. Scale 10 mm.

Paratype specimen no. 101: A very well-preserved female damselfly with remarkably preserved body. Total length of body about 19 mm; max. width of head, 3.1 mm. The distance of the compound eyes is 1.1 mm. The thoracic sutures seem to be complete. Length of the abdominal segments: I 0.9 mm, II 1.4 mm, III 1.9 mm, IV 2.0 mm, V 2.0 mm, VI 2.0 mm, VII 1.9 mm, VIII 1.2 mm, I♀ 1.0 mm ♀ 0.6 mm. The ovipositor is clearly visible, but there are no visible anal appendages. Unfortunately the wings (length, 11 mm) are overlapping, so that several important parts of the wing venation (e.g. the discoidal cells) are not visible. The pterostigma is perfectly preserved and clearly shows the so-called "micraster-type" sculptures (sensu BECHLY 1996), just like extant Hemiphlebiidae and other extant Lestomorpha. The pterostigmal brace vein is of normal obliquity; RP1 does not make a distinct kink at this brace vein.

Phylogenetic position. – This new species shares the following characters with the hemiphlebiid genera *Parahemiphlebia* and *Hemiphlebia*: postnodal- and postsubnodal crossveins are non-aligned; very small body size and wing length; only five to seven postnodal crossveins; no intercalary veins, except IR1 and IR2. However, these few similarities with Hemiphlebiidae are either symplesiomorphies,

or very weak characters (reductions). With the genus *Parahemiphlebia* there are only some symplesiomorphic similarities. The strongly reduced anal appendages in the female holotype of *Cretarchistigma*(?) *essweini* n. sp. are similar to those described for the female allotype of *Parahemiphlebia cretacica*, but at least the males of the latter species had long anal appendages like *Parahemiphlebia mickoleiti* n. sp. (see below). Therefore, this character which is very homoplastic anyway, and e.g. evolved several times by convergence within the coenagrionoid clade, is not sufficient as evidence for a potential relationship with *Parahemiphlebia cretacica*. The very small size (wing length about 9–11 mm) and the position of the arculus at Ax2 could be potential synapomorphies with *Parahemiphlebia mickoleiti* n. sp., but as well have to be regarded as very weak evidence. An attribution of the new species to the Hemiphlebiidae is still somewhat uncertain, and a close relationship with the genus *Parahemiphlebia* is even less certain, although the possibility cannot be excluded.

On the other hand there are several similarities with *Cretarchistigma greenwoodi* JARZEMBOWSKI et al., in press from the Lower Cretaceous of England, especially with specimen no. 018658 BMB, that include most above mentioned similarities with Hemiphlebiidae, except the number of the postnodal crossveins; the long and narrow (hindwing) discoidal cell; the alignment of the arculus with Ax2; and the relatively straight course of MP distal of the discoidal cell (no bent). For these reasons I have preliminarily attributed this new species to the genus *Cretarchistigma*. This latter genus is certainly not related to Coryphagrionidae + Pseudostigmatidae, or to Euarchistigmatidae (contra JARZEMBOWSKI et al., in press), but more likely related to Hemiphlebiidae. Although the "micraster-type" sculptures of the pterostigma of *Cretarchistigma*(?) *essweini* n. sp. are a derived similarity with Hemiphlebiidae and other Lestomorpha, it is still uncertain whether the genus *Cretarchistigma* indeed belongs to Hemiphlebiidae, since it is not even known if the discoidal cell is basally open in the forewing of *Cretarchistigma*(?) *essweini* n. sp. and *Cretarchistigma greenwoodi*. A definite attribution will only be possible when better preserved specimens will become available.

4. Miscellaneous notes on other odonates from the Crato Formation

Parahemiphlebia cretacica JARZEMBOWSKI et al., in press
(Zygoptera, Euzygoptera, Lestomorpha, Hemiphlebiidae)

In the original description of this interesting species the authors discussed the potential relationship with the extant south Australian relic species *Hemiphlebia mirabilis*, but preliminarily preferred to classify it as Zygoptera incertae sedis. Meanwhile nine further specimens have been studied by me and now allow a more definite conclusion: this species indeed is the first fossil representative of Hemiphlebiidae. The latter have often been regarded as most "primitive" extant Odonata, but according to the phylogenetic study of BECHLY (1996, 1997a), Hemiphlebiidae is just the most basal taxon of Lestomorpha (= Lestinoidea auct.). *Italophlebia gervasuttii* WHALLEY, 1986 from the Upper Triassic of Italy was erroneously described in Hemiphlebioidea, since it is not even a Zygoptera, but clearly an "anisozygoptere" of the isophlebioid clade (BECHLY 1997e).

The following unique combination of symplesiomorphic and synapomorphic similarities supports the attribution of *Parahemiphlebia cretacica* to Hemiphlebii-

dae: distinct suture between vertex and occiput (rare symplesiomorphy); discoidal cell basally open in the forewing (very rare symplesiomorphy that is only preserved in two extant species); at least in the forewing the arculus is situated distal of Ax2 (rare symplesiomorphy); postnodal- and postsubnodal crossveins are non-aligned (symplesiomorphy); body with metallic green coloration (synapomorphy with Lestomorpha, incl. Hemiphlebiidae) (the peculiar preservation of the original body colour was already mentioned in the introduction); lestine oblique vein "O" suppressed (synapomorphy with Hemiphlebiidae); very small body size and wing length (synapomorphy with Hemiphlebiidae); only five to seven postnodal crossveins (synapomorphy with Hemiphlebiidae); no intercalary veins, except IR1 and IR2 (synapomorphy with Hemiphlebiidae); wing base with distinctly reduced petiolation (synapomorphy with Hemiphlebiidae; certainly no symplesiomorphy according to BECHLY 1996).

Although most of the mentioned putative synapomorphies are relatively weak characters (homoplastic characters, reversals or reductions), they include all wing venational apomorphies that are known for *Hemiphlebia*. Furthermore, there are several important and rather unique symplesiomorphies, and there are no conflicting characters that would suggest a different relationship. The extremely oblique pterostigmal brace vein, and maybe the reduced anal appendages of the female sex, represent autapomorphies of this species, since its probable sister-species *P. mickoleiti* n. sp. still preserved the plesiomorphic states.

In the original description of *Parahemiphlebia cretacica* short coenagrionid-like anal appendages (cerci and paraprocts) have been described for both sexes of this species. However, at least in the male this apparent character state must have been due to an artifact of preservation, since an indisputable male specimen of this species (specimen no. E8, coll. ms-fossil) clearly has plesiomorphic long anal appendages just like the male of *Parahemiphlebia mickoleiti* n. sp. Therefore, the alleged short appendages cannot be regarded as potential synapomorphy of *Parahemiphlebia* with extant coenagrionids.

Euarchistigma atrophium CARLE & WIGHTON, 1990
(Zygoptera, Caloptera, Thaumatoneuridae, Euarchistigmatini)
Figs 19–21

This strange species was described by CARLE & WIGHTON (1990) in the extant neotropical family Pseudostigmatidae. However, this attribution is only based on superficial similarities and probable convergences. As already demonstrated in two previous publications (BECHLY 1996, JARZEMBOWSKI et al., in press), *Euarchistigma* is a basal representative of the calopterygoid clade, and most probably the sister-group of the extant relic species *Thaumatoneura inopinata* MCLACHLAN, 1897 that is only known from waterfalls and rapids of the Costa Rican rainforest.

Nevertheless, the finding of three new specimens of *Euarchistigma* showed that one of the putative synapomorphies with Thaumatoneuridae is invalid, since the referring character (base of IR2 apparently fused to RP3/4) is variable in *Euarchistigma*: the base of IR2 is distinct and clearly originating on RP1/2 in specimen D29 (coll. ms-fossil; Fig. 19), and it is indistinct in specimen B52 (coll. ms-fossil; Fig. 20), while it is apparently originating from RP3/4 in the holotype and specimen no. 46 (National Science Museum Tokyo; Fig. 21). Nevertheless, the majority of the "good" characters still supports the hypothesis of a relationship with Thaumatoneu-

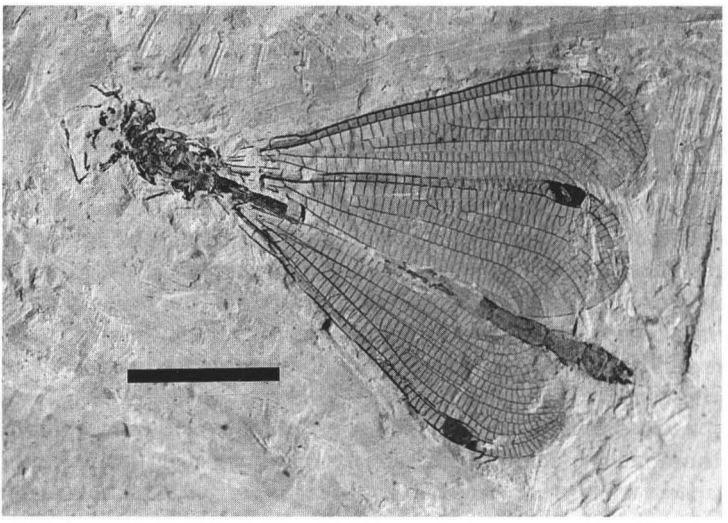

Fig. 19. *Euarchistigma atrophium*, specimen D29 (ms-fossil). Scale 10 mm.

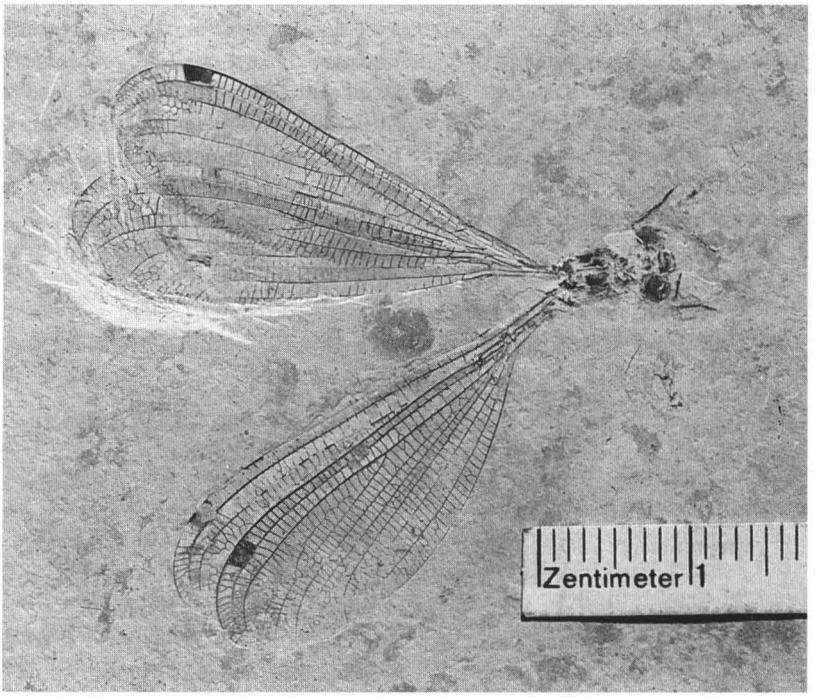

Fig. 20. *Euarchistigma atrophium*, specimen B52 (ms-fossil). Scale as indicated by rule.

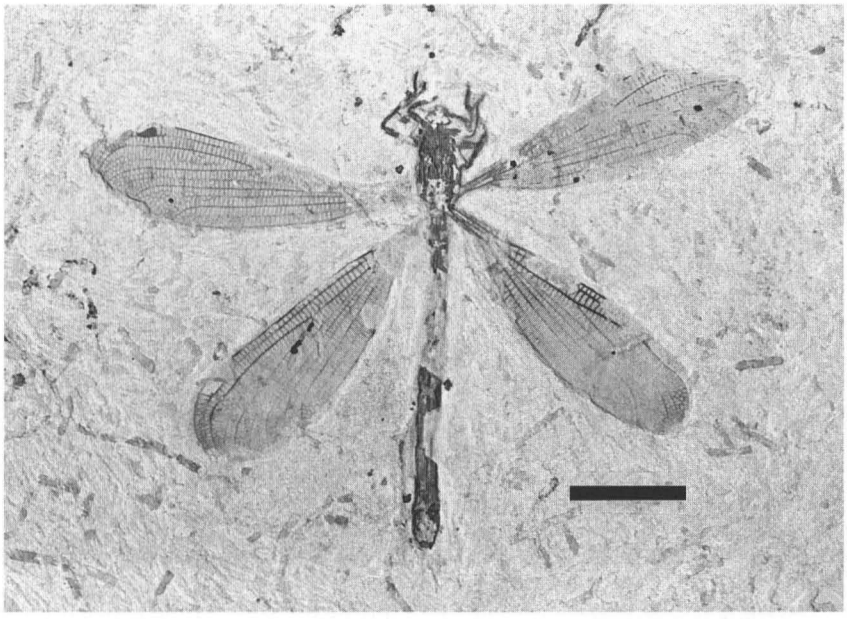

Fig. 21. *Euarchistigma atrophium*, specimen no. 46 (Nat. Sci. Mus. Tokyo). Scale 10 mm.

"good" characters still supports the hypothesis of a relationship with Thaumatoneuridae rather than Pseudostigmatidae (BECHLY 1996, 1997a).

Specimen D29 also shows two other interesting characters: the discoidal cell is somewhat longer and more narrow in the hindwing than in the forewing, and the arculus is situated distinctly distal of Ax2 in the right forewing. This latter feature of course has to be regarded as an individual aberration, since the arculus is aligned with Ax2 in all the other wings.

Another interesting but not very well-preserved specimen is present in the collection of the Staatliches Museum für Naturkunde in Karlsruhe. It is a plate and counterplate of a complete female specimen (forewing length, 30 mm; hindwing length, 29 mm). The abdomen is 28 mm long and 1.8 mm wide and clearly shows a 2.1 mm long ovipositor that is gently curved.

Wightonia araripina CARLE & WIGHTON, 1990
(Anisoptera, Aeschnidiidae)
Figs 22–27

Five new specimens of this species have recently been found by me in the collections of ms-fossil. These new specimens include the first female specimen (no. D28, coll. ms-fossil; forewing length, 43.6 mm and hindwing length, 44.5 mm; Fig. 22) which is nearly completely preserved, a further nearly complete specimen of uncertain sex (no. B10, coll. ms-fossil; forewing length, 39.3 mm and hindwing length, 39.0 mm; Figs 23–26), and an isolated hindwing (B19, coll. ms-fossil; hindwing length, 40.5 mm; Fig. 27) which is of uncertain sex, too. Finally there is a second complete female specimen (no. 17, Museum of Kitakyushu, ex. coll. ms-fossil; wing

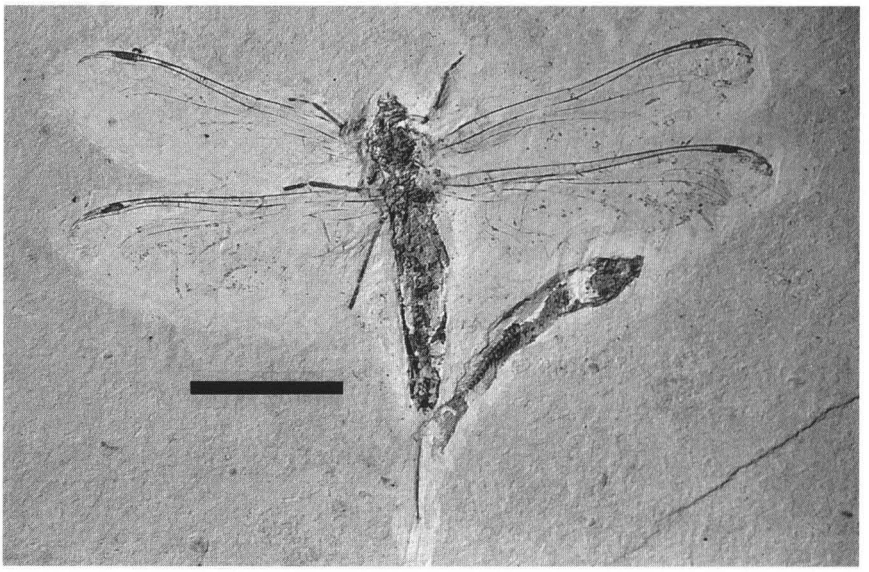

Fig. 22. *Wightonia araripina*, ♀ specimen D28 (ms-fossil), with very long ovipositor. Scale 20 mm.

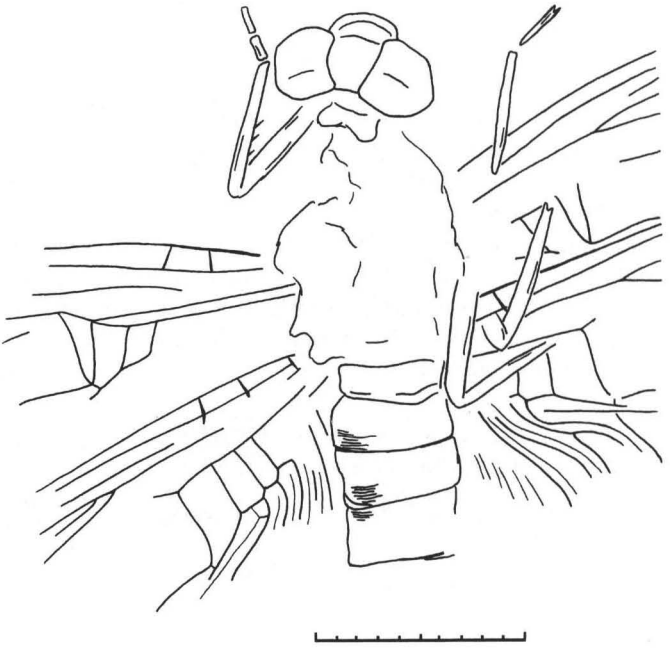

Fig. 23. *Wightonia araripina*, specimen B10 (ms-fossil), body. Scale 10 mm.

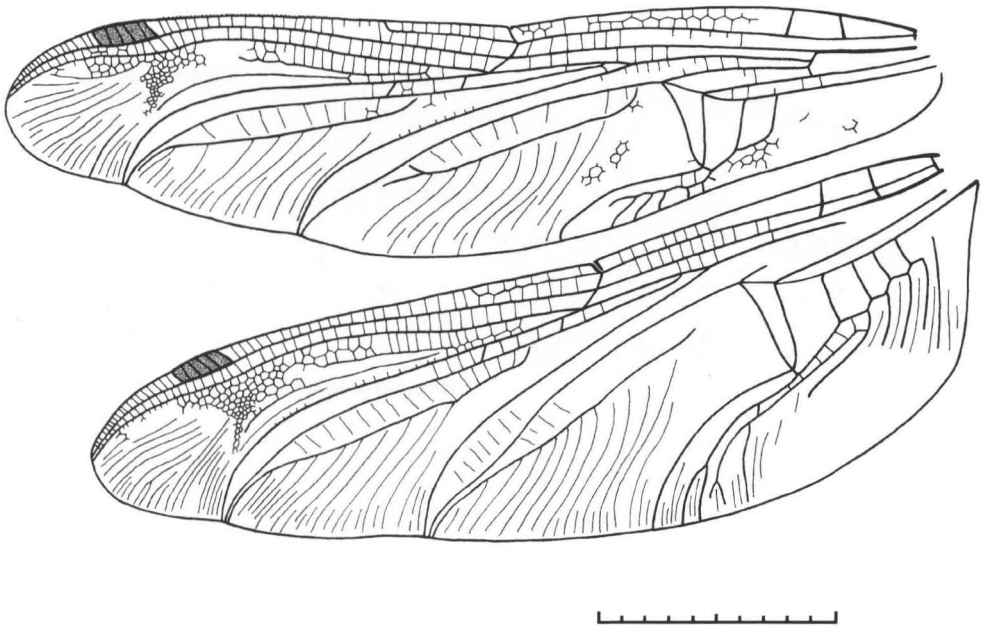

Fig. 24. *Wightonia araripina*, specimen B10 (ms-fossil), left pair of wings. Scale 10 mm.

Fig. 25. *Wightonia araripina*, specimen B10 (ms-fossil). Scale 10 mm.

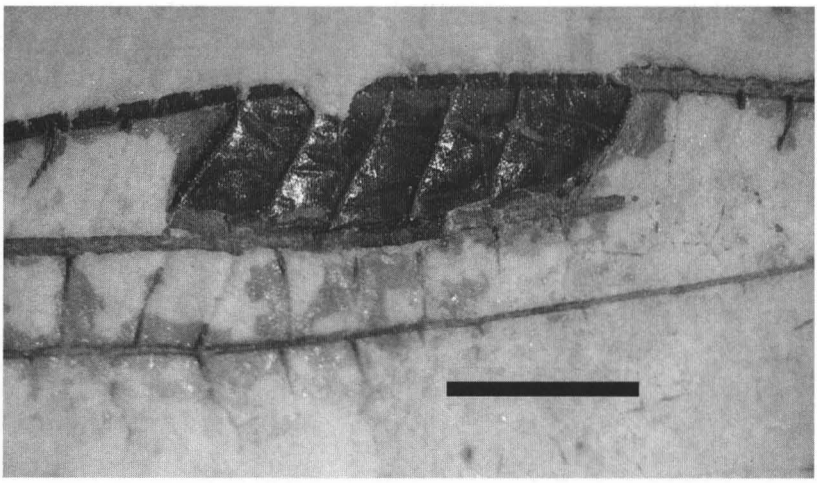

Fig. 26. *Wightonia araripina*, specimen B10 (ms-fossil), pterostigma of right forewing traversed by four crossveins. Scale 1 mm.

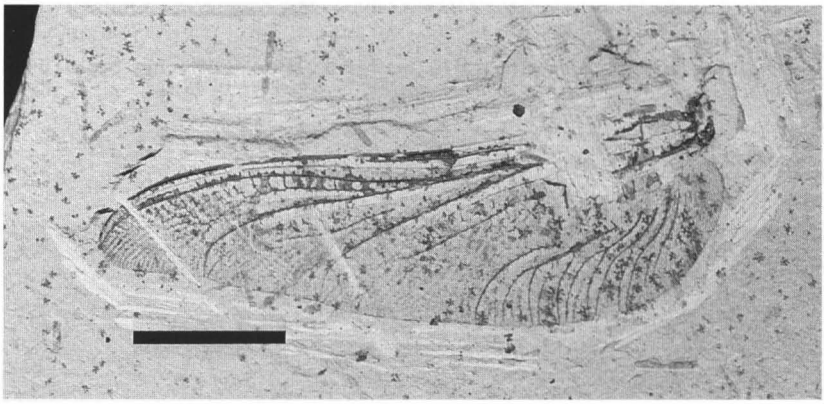

Fig. 27. *Wightonia araripina*, specimen B19 (ms-fossil). Scale 10 mm.

length, about 38–39 mm), and an isolated forewing with a length of 47.0 mm (E7, coll. ms-fossil).

Because of these new specimens, some amendations and corrections of the previous diagnosis of this species are necessary, since the latter was only based on an isolated and not very well-preserved hindwing as holotype (hindwing length, 46.0 mm). The most important correction is the definite presence of a well-defined pterostigma which is clearly visible in specimens B10 and D28. This pterostigma is traversed by about four crossveins (Fig. 26), just like in some other Aeschnidiidae, e.g. *Aeschnidium densum*. The apparent absence of the pterostigma in the holotype and in specimen B19 is simply due to an artifact of preservation: when the pigmentation of the pterostigma is not preserved it can appear to be absent because of the traversing crossveins! Besides, the pterostigma is indistinctly braced. A further correction concerns

the alleged undulating intercalary vein IR1 between RP1 and RP2, which indeed is a complex vein that is composed of a basal concave vein and a distal convex vein (Fig. 24). These two veins are autapomorphic features of this species and certainly not homologous to the generally convex primary IR1 (= IR2 sensu CARLE & WIGHTON 1990) in the ground-plan of Anisoptera which is completely suppressed in all Aeschnidiidae. The compound nature of this vein is even visible on a photo of the holotype (GRIMALDI 1991: 340), contrary to the figure in CARLE & WIGHTON (1990: 63).

Specimen B10 has a very well-preserved head (width, 7.2 mm; length, 4.7 mm) with large compound eyes that are distinctly separated (min. distance, 1.4 mm). The female specimen D28 has a relatively short and broad abdomen (28.5 mm long and max. 6.2 mm wide) with an extremely long and slender ovipositor (length, 14.3 mm) (Fig. 22). The other female specimen has a total body length of about 41 mm, and the visible part of the ovipositor is about 8 mm long. The pterostigmata are well-defined, but traversed by three weak crossveins in the left wings, though no traversing crossveins are visible in the pterostigma of the right hindwing.

The five new specimens perfectly agree in most characters with the holotype. All major differences to the original description that could not be explained with intraspecific variability, are either erroneous interpretations in the original description (IR1), or due to artifacts of preservation of the holotype (pterostigma), or due to a somewhat careless drawing of the cross-venation by CARLE & WIGHTON (1990, Fig. 21). The significant difference in size between the smallest and the largest specimens is bridged by intermediate specimens. Therefore, it is preliminarily justified to regard the five new specimens as conspecific with the holotype of *Wightonia araripina*, especially since they all stem from the same locality (Araripe) and layer (Crato Formation – Nova Olinda Member).

Nothomacromia sensibilis (CARLE & WIGHTON, 1990)

(Anisoptera, Aeschnidiidae)
Figs 28–29

CARLE & WIGHTON (1990) described a very curious dragonfly larva (*Pseudomacromia sensibilis*) with forcep-like anal appendages, very long legs, and a petalurid-like mask. The homonymous generic name *Pseudomacromia* was later replaced with *Nothomacromia* by CARLE (1995).

Because of several alleged "primitive" features which were believed to indicate a basal position in Anisoptera (like adult Aeschnidiidae), and because of an alleged lentic life style of this larva, CARLE & WIGHTON (1990) suggested a classification in a separate family Nothomacromiidae (= Pseudomacromiidae) within the superfamily Aeschnidioidea which was regarded by these authors as sister-group of the other Anisoptera. However, the mentioned arguments are unconvincing because of the following reasons: (1) Plesiomorphic similarities are invalid as evidence for phylogenetic relationship; (2) at least one of the alleged plesiomorphies of *Nothomacromia* rather represents an autapomorphy anyway (petalurid-like palps; convergent to Petaluridae); (3) some of the alleged "primitive" characters, mentioned by CARLE & WIGHTON (1990) as evidence for the basal position of Aeschnidiidae (e.g. poorly developed arculus, nodus and pterostigma, and presence of numerous intercalary veins) without doubt are autapomorphic reversals and not symplesiomorphies with "protodonates", since these states do not belong to the ground-plan of crown-group

Odonata (see BECHLY 1996, 1997a); (4) the alleged lentic adaptation of these larvae is mere speculation and even improbable, since all aquatic insect larvae of the Crato Formation are of allochthonous origin (see below), thus washed in by adjacent streams. Furthermore, this argument is most doubtful anyway, since there is no evidence whatever for lentic adaptations in the adult Aeschnidiidae, so that the lentic adaptations of *Nothomacromia* larvae (even if correct) could not indicate a close relationship with adult Aeschnidiidae. The long forcep-like appendages are formed by the paraprocts and not by the cerci (contra CARLE & WIGHTON 1990). A further incorrect assumption of CARLE & WIGHTON (1990) is the interpretation of the holotype of *Nothomacromia sensibilis* as a penultimate larval instar, since the wing sheaths are not sufficiently developed for this stage (also see below).

In spite of all these dubious arguments and incorrect statements, CARLE & WIGHTON (1990) seem to be right for the wrong reasons, not only concerning the basal position of Aeschnidiidae (documented by BECHLY 1996, 1997a), but as well concerning the close relationship of *Nothomacromia* with Aeschnidiidae. The plesiomorphic absence of a true anal pyramid excludes a position of *Nothomacromia* in the crown-group of Anisoptera. Therefore, it can only belong to the stem-group of Anisoptera, thus to an adult dragonfly of either the "anisozygopteroid" grade, or the Aeschnidiidae (compare BECHLY 1996, 1997a). The complete absence of adult "anisozygopteres", and the presence of at least two species of adult Aeschnidiidae in the Crato Formation, already suggests that Aeschnidiidae are the more likely candidates. A further hint might be the facts that adult Aeschnidiidae, as well as *Nothomacromia* larvae are morphologically quite remote from the rest of Anisoptera, and that Aeschnidiidae and the referring larvae agree in their above average size (see below). Of course these two arguments can only be regarded as relatively weak circumstantial evidence. On the other hand, a very compelling evidence was recently discovered by NEL (unpubl., pers. comm.) who recognized the typical aeschnidiid discoidal triangle and veinal supplements on the wing sheaths of a *Nothomacromia*-like larva (with long legs and forcep-like appendages) from the Lower Cretaceous of China.

As already documented in detail by BECHLY et al. (1998), *Nothomacromia sensibilis* and previously undescribed giant dragonfly larvae from the same locality, belong to the same clade as the larvae of Sonidae (their alleged adults are unrelated and are described in a new gomphid family Proterogomphidae by BECHLY et al., 1998), and the larvae that have been erroneously attributed to Hemeroscopidae by PRITYKINA (1977) (their alleged scoop-like mask indeed is gomphid-like and flat according to NEL, pers. comm.), as well as the larval genera *Dissurus* HONG, 1982 and *Yixiangomphus* LIN, 1986 from the Mesozoic of China. This monophylum is clearly diagnosed by several unique synapomorphies, such as the enormously enlarged and forcep-like paraprocts. All these larvae most likely represent larval Aeschnidiidae. Therefore, the family-group taxa Sonidae PRITYKINA, 1986 and Nothomacromiidae CARLE, 1995 (= "Pseudomacromiidae" sensu CARLE & WIGHTON, 1990) are here regarded as junior subjective synonyms of Aeschnidiidae NEEDHAM, 1903.

The above mentioned giant dragonfly larvae from the Crato Formation (Fig. 28) seem to be very closely related to *Nothomacromia sensibilis* (Fig. 29), since they not only share the forcep-like paraprocts, but as well the lyre-shaped antennae and the spine-like epiproct. These characters are highly derived and unique, and therefore have to be regarded as strong synapomorphies. Symplesiomorphic similarities are

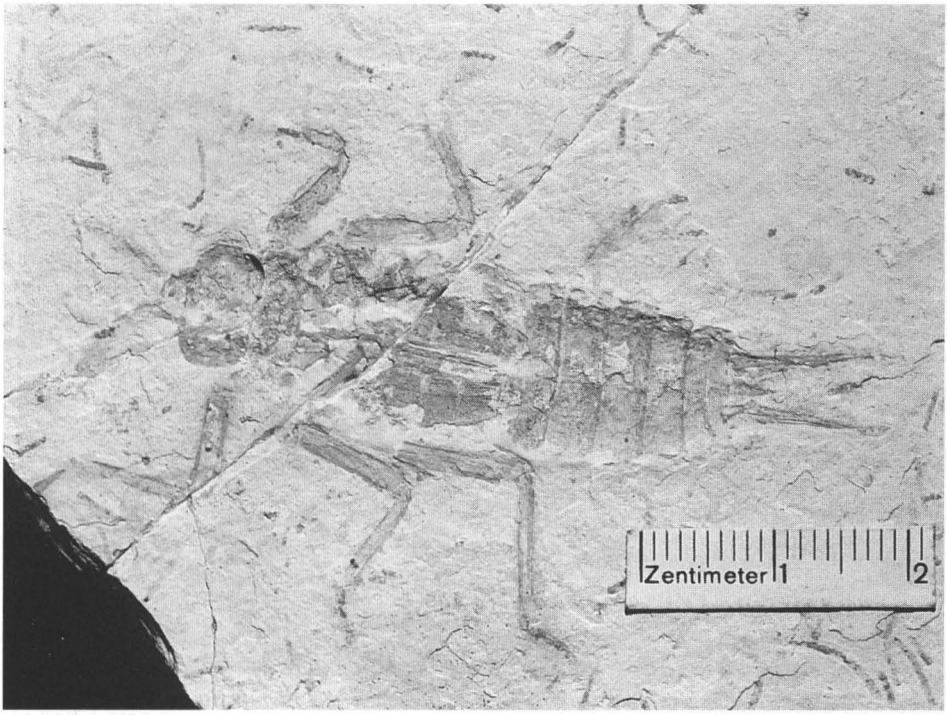

Fig. 28. Giant dragonfly larva (*Nothomacromia sensibilis* ?), specimen B42 (ms-fossil). Scale as indicated by rule.

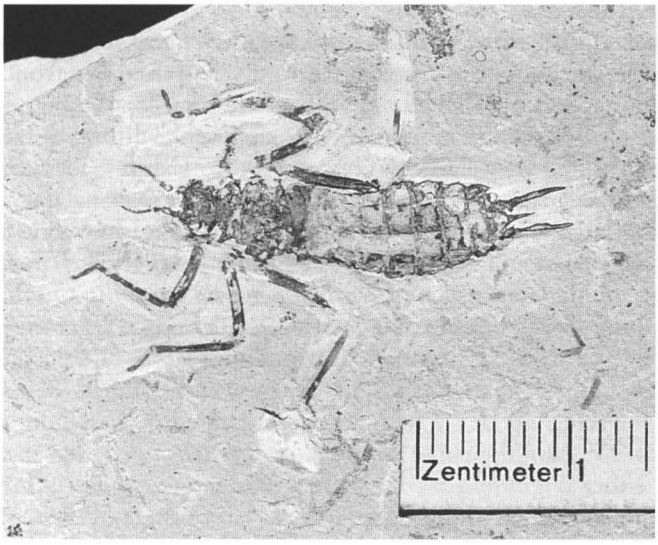

Fig. 29. *Nothomacromia sensibilis*, specimen B53 (ms-fossil). Scale as indicated by rule.

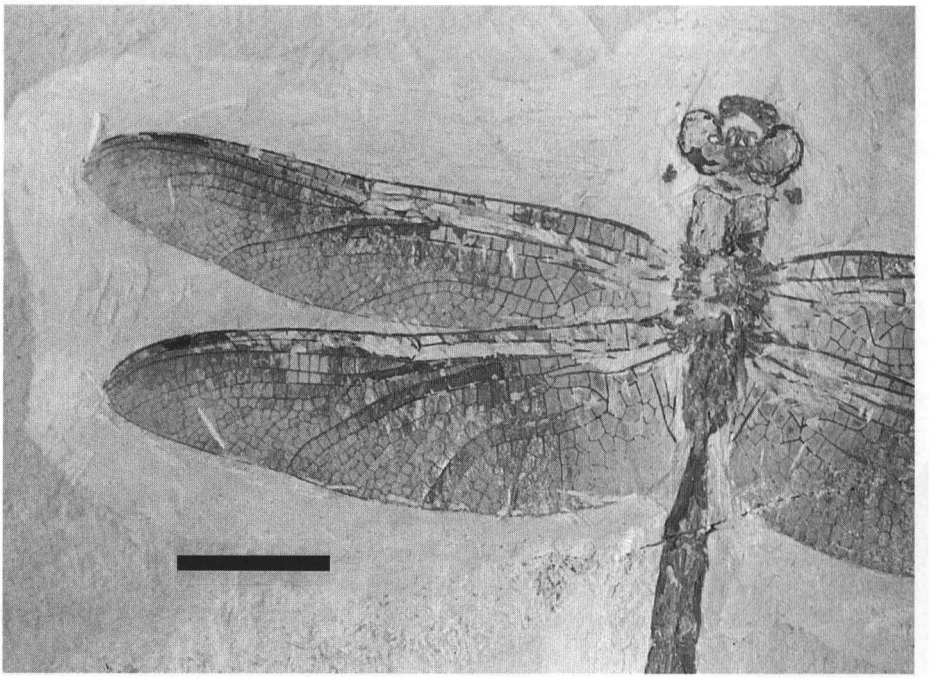

Fig. 30. *Araripeliupanshania annesuseae* (n. gen. et n. sp. in BECHLY et al., in prep.), first record of Liupanshaniidae from the Crato Formation, ♂ specimen D58 (ms-fossil). Scale 10 mm.

the flat gomphid-like mask, the elongate body, and the lack of a true anal pyramid. There are larvae of different size which form a gradual morphocline from small *Nothomacromia*-like larvae to the giant larvae (body length varies from 14.3 mm to 63.5 mm without appendages). The only difference between the biggest larvae and the small larvae (*Nothomacromia sensibilis*), except for the different size, are the relatively shorter legs and the relatively bigger eyes. Both differences could be easily explained by allometric growth. It is very interesting that the small larvae (*Nothomacromia sensibilis*) always have poorly developed wing sheaths, while the giant larvae have well-developed wing sheaths. Consequently, it is very well possible that the giant larvae are simply later instars of *Nothomacromia sensibilis*. On the other hand there are two different species of adult Aeschnidiidae known from this locality, and differ significantly in size, so that the corresponding larvae should be expected to differ in size, too. Unfortunately it will hardly be ever possible to decide the specific identity of the referring larvae with any described adult Aeschnidiidae. For this reason I suggest to retain the name *Nothomacromia sensibilis*, even though it could be the larva of either *Wightonia araripina*, or *Santanoptera gabbotti* MARTILL & NEL, 1996, and preliminarily regard the giant larvae as later instars of the same species.

Undescribed new genus and species of Cordulagomphinae (Anisoptera, Gomphides, Proterogomphidae)

Figs 31–32

This new genus and species is only known by the single isolated female hindwing (specimen C20, coll. ms-fossil, holotype in spe) that is illustrated in Fig. 31. Beside the synapomorphies with Proterogomphidae that are discussed below, the following synapomorphies strongly suggest an attribution to Cordulagomphinae: anal loop longer than wide; only two antefurcal crossveins of which the most distal one is strongly oblique; most basal postnodal crossvein distinctly slanted towards the nodus. The oblique distal antefurcal crossvein is an unique apomorphic character of Cordulagomphinae which therefore has to be regarded as very strong evidence.

This new genus and species is most interesting, since it has retained some "primitive" characters that are not present anymore in any of the other Cordulagomphinae: larger wing length (hindwing about 35 mm long); more densely reticulated wing venation; very well-defined postdiscoidal intercalary vein; no "cordulegastrid gap" of the antesubnodal crossveins directly basal of the subnodus; very well-defined posterior branches of CuA which is not distinctly shortened. These unique plesiomorphies within Cordulagomphinae clearly indicate that this new taxon represents the most basal member of this group. A probable autapomorphy of the new genus and species is the presence of only one secondary antenodal crossvein between Ax1 and Ax2, correlated with the distinct displacement of Ax2 into a very basal position.

Because of its mosaic-like character pattern (heterobathmy sensu HENNIG 1966), this new taxon also proved to be particularly useful for the reconstruction of the phylogenetic relationship of Cordulagomphinae within Gomphides (see BECHLY 1997a). The following derived similarities suggest a close relationship with the genus *Proterogomphus* (Proterogomphidae) that is described by BECHLY et al. (1998) for those fossil gomphids that have been erroneously believed by PRITYKINA (1986) to represent the adults of the larval genus *Sona* (Sonidae): discoidal triangle secondarily free (unicellular); not more than two cells below the pterostigma; vein pseudo-IR1 originates below the distal side of the pterostigma; anal loop only one- or two-celled; elongated cell beneath the submedian cell in the forewings. Besides these putative synapomorphies there are also numerous symplesiomorphies, resulting in a surprisingly similar wing venation of these two genera (compare BECHLY et al., 1998). Therefore, it is reasonable to classify Cordulagomphinae as subfamily of the Proterogomphidae, while *Proterogomphus* is classified in the nominate subfamily.

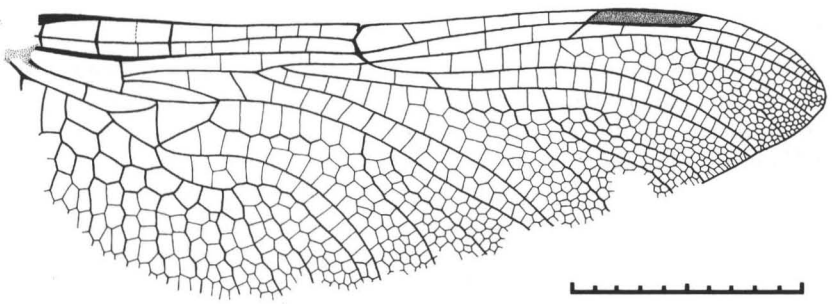

Fig. 31. Cordulagomphinae n. gen. et n. sp., ♀ specimen C20 (ms-fossil). Scale 10 mm.

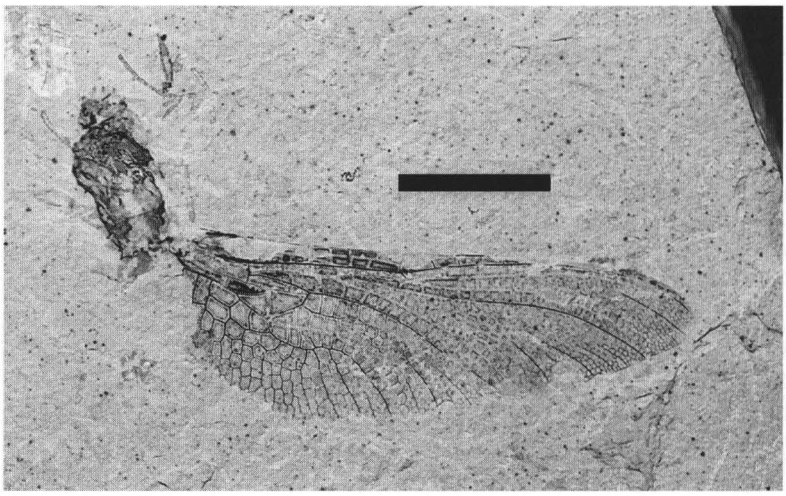

Fig. 32. Cordulagomphinae n. gen. et n. sp., ♀ specimen C20 (ms-fossil). Scale 10 mm.

Undescribed new species of *Cordulagomphus (Procordulagomphus)* (Anisoptera, Gomphides, Proterogomphidae, Cordulagomphinae)

Figs 33–34

This new species is quite similar to *C. fenestratus* and only known by one male and two female specimens (specimens nos C14, E4, E10, coll. ms-fossil), and shares the following synapomorphies with the other species of the genus *Cordulagomphus*: discoidal triangle secondarily free (convergent to Araripegomphidae and numerous extant gomphids); pterostigma only covering two or less cells; pseudo-IR1 originates beneath the distal side of the pterostigma; anal loop longer than wide and only one- or two-celled; distinct "cordulegastrid gap" (sensu BECHLY 1996) of the antesubnodal crossveins directly basal of the subnodus (except in the most basal genus that is still undescribed; Figs 31–32); only two antefurcal crossveins in both pairs of wings (convergent to Gomphidae s. str.); most distal antefurcal crossvein at least somewhat oblique in the hindwing; hindwing CuAa shortened and with reduced posterior branches (except in the most basal genus that is still undescribed; Figs 31–32); anal triangle with only one or two cells.

Furthermore, there are some potential synapomorphies with *Cordulagomphus (Procordulagomphus) xavieri*: anal loop unicellular; cubito-anal area strongly reduced in the hindwing with only three rows of cells and with reduced posterior branches of CuA (somewhat doubtful, since better defined in the female specimen E10); most distal antefurcal crossvein less oblique in the hindwing (somewhat doubtful, since well oblique in the female specimen E4 and not preserved in specimen E10). However, these potential synapomorphies are in conflict with some other characters that rather indicate a sister-group relationship of *Cordulagomphus (Procordulagomphus) senckenbergi* n. sp. and *Cordulagomphus (Procordulagomphus) xavieri*, such as number of only four antenodal crossveins in the hindwing (still five in the new species), and the reduced angulation of the distal side MAb of the discoidal triangle in both pairs of wings (still angled in specimen C14 and E4, but

not in specimen E10). The circumstance that *Cordulagomphus (Procordulagomphus) senckenbergi* n. sp. has retained the distinctly oblique distal antefurcal crossvein in the hindwing, even increases the incongruence of the derived similarities. This is another case of very homoplastic wing venational characters that prohibit a sound phylogenetic analysis.

The presence of only four postnodal and three postsubnodal crossveins in all wings of the specimens C14 and E4 could be a derived similarity with *Cordulagomphus (Procordulagomphus) senckenbergi* n. sp., but the specimen E10 has five postnodal and four postsubnodal crossveins in all wings. While the male specimen (no. C14) has a second incomplete antenodal crossvein between Ax1 and Ax2 in the hindwing, the female specimens (nos E4 and E10) only have a single secondary antenodal crossvein between the primaries.

Further differences between the female specimen E10 and the male specimen are the somewhat smaller size (wing span, 37.0 mm; total body length, 32.5 mm), the presence of only one costal antenodal crossvein distal of Ax2 in the hindwing, the absence of the kink of RP2 at the oblique vein "O", the more longitudinal elongate discoidal triangle in the hindwing, the better defined three posterior branches of CuA in the hindwing, and of course the absence of an anal angle and anal triangle. All other characters are very similar to the male specimen. Differences between the female specimen E4 and the male specimen are the distinctly bigger size (forewing length, 21 mm, hindwing length 20 mm), the more distinct angle in MAb in both pairs of wings, the somewhat more pronounced obliquity of the distal antefurcal crossvein in the hindwing, and the rounded anal margin (female). The kink of RP2 at the oblique vein "O" is present, but somewhat less distinct than in the male specimen. All other characters are nearly identical to the male specimen. A distinct and long membranule is preserved at the hindwing base of specimen E4.

A unique diagnostic character of this new species within Cordulagomphinae, that is present in all three specimens, is the distal divergence of the veins RP3/4 and MA, especially in the forewings. The costal and radial margins of the pterostigmata are strongly thickened as in the other Cordulagomphinae and most other Gomphides (except Hageniidae).

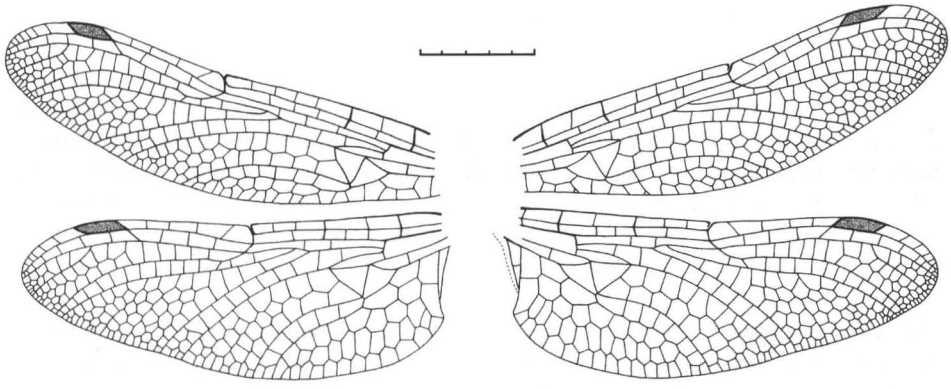

Fig. 33. *C. (Procordulagomphus)* n. sp., ♂ specimen C14 (ms-fossil). Scale 5 mm.

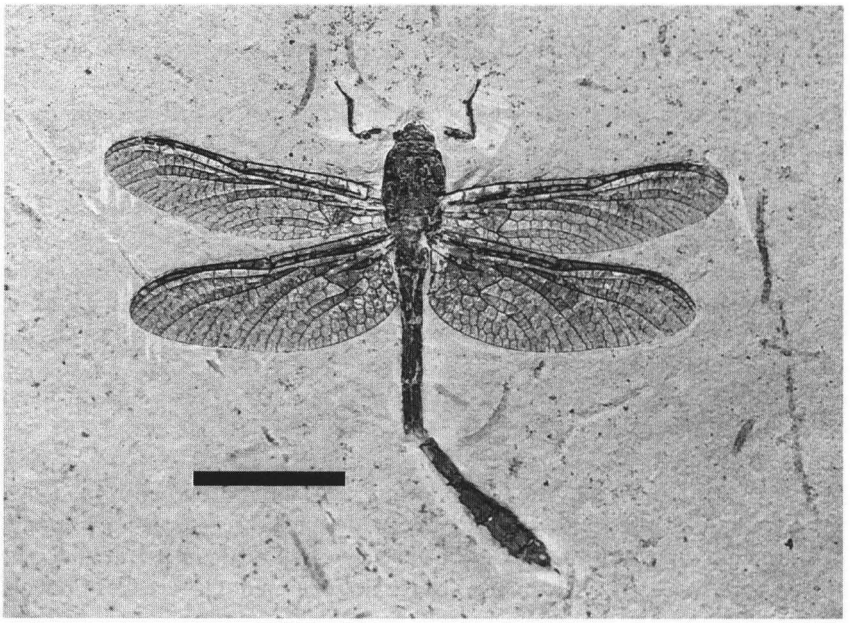

Fig. 34. *C. (Procordulagomphus)* n. sp., ♂ specimen C14 (ms-fossil). Scale 10 mm.

New diagnosis of *Cordulagomphus tuberculatus* CARLE & WIGHTON, 1990 versus *C. fenestratus* CARLE & WIGHTON, 1990 (Anisoptera, Gomphides, Proterogomphidae, Cordulagomphinae)

Figs 35–37

According to the original description of CARLE & WIGHTON (1990), the following characters distinguish *C. fenestratus* from the type species *C. tuberculatus*:

1. All antenodal crossveins are aligned (instead of non-aligned).
2. Even between the distal parts of RP3/4 and MA there is only one row of cells (instead of two).
3. In the hindwing there are only two cells in the postdiscoidal area, adjacent to the distal side MAb of the discoidal triangle (instead of three).
4. Hindwing anal area with only three rows of cells (instead of four).

The careful analysis of totally 98 potential specimens of these two species revealed that all above mentioned diagnostic characters are either invalid, or at least unreliable. This conclusion was derived from the surprising circumstance that although numerous specimens perfectly agreed with the diagnosis of *C. fenestratus* (e.g. specimen C13, coll. Bechly, ex coll. ms-fossil, Fig. 35), and a few (three) specimens even perfectly agreed with the diagnosis of *C. tuberculatus*, nearly half of the material showed a mixture (!) of the diagnostic characters of both species (e.g. specimen C6, BSPGM in Munich, ex coll. ms-fossil; Figs 36–37).

Please note: Specimens with a wing length of more than 20 mm and at least one of the diagnostic characters of *C. tuberculatus* are called "potential specimens of *C. tuberculatus*" in the following discussion.

Re. 1. The alignment of all antenodal crossveins is indeed present in all unequi-

vocal specimens of *C. fenestratus*, but is as well present in some potential specimens of *C. tuberculatus* (Fig. 36). Besides, even in specimens of *C. fenestratus* (Fig. 35) the secondary antenodal crossveins are often only inexactly aligned, and they are never reinforced like the primary antenodals Ax1 and Ax2 or like all antenodals in Libellulidae.

Re. 2. The presence of one or two rows of cells between the distal parts of RP3/4 and MA is very variable in specimens with more than 20 mm wing length. Even within the same specimen one wing may show the state of *C. tuberculatus*, while the other shows the state of *C. fenestratus* (Fig. 36). Nevertheless, unequivocal specimens of *C. fenestratus* only have two rows of cells between RP3/4 and MA close to the wing margin at best.

Re. 3. The presence of three postdiscoidal cells at the distal side MAb of the discoidal triangle in both pairs of wings of the holotype of *C. tuberculatus* seems to be a very rare character state that might rather be an individual feature, since it is only present in very few of the potential specimens of *C. tuberculatus*. Anyway, this character is never present in unequivocal specimens of *C. fenestratus*.

Re. 4. The character of the number of rows of cells in the anal area is even incorrect in the holotypes described by CARLE & WIGHTON (1990), since the holotype of *C. fenestratus* has four rows of cells in the anal area and the holotype of *C. tuberculatus* has four to five rows of cells in this area. Although the anal area of the holotype of *C. tuberculatus* is indeed somewhat wider than that of all unequivocal specimens of *C. fenestratus*, this character is still problematic, since numerous potential specimens of *C. tuberculatus* also have only four rows of cells in the anal area (Fig. 36).

Two further diagnostic characters have not been mentioned by CARLE & WIGHTON (1990): (1) The number of postnodal crossveins which is generally somewhat higher in unequivocal specimens of *C. fenestratus* (five to six in the forewing and six to seven in the hindwing) than in potential specimens of *C. tuberculatus* (four or five in the forewing and five or six in the hindwing); (2) unequivocal specimens of *C. fenestratus* have two rows of cells in the basal postdiscoidal area of the hindwing up to four or five cells distal of the discoidal triangle, while this is only the case up to three or four cells distal of the discoidal triangle in potential specimens of *C. tuberculatus*. Unfortunately both characters are overlapping and therefore unreliable, too.

Two better diagnostic characters could be the more distinct posterior branches of CuA and the more distinct postdiscoidal intercalary vein in the hindwing of most potential specimens of *C. tuberculatus*. The only 100 % "save" diagnostic character seems to be the wing length which is always less than 20 mm (17.5 mm to 19.8 mm) in all unequivocal specimens of *C. fenestratus*, and always above 20 mm (21.0 mm to 25.0 mm) in all potential specimens of *C. tuberculatus*. This character is of course correlated with the total number of wing cells that appears to be somewhat higher in *C. tuberculatus* than in *C. fenestratus*. The problem with the size-related characters is that the very wing length was used as one of the key characters to recognize (or rather define) potential specimens of *C. tuberculatus* which could result in a perfect example of circular reasoning.

Consequently, it must be asked if there are two different species at all, or maybe just one highly variable species. However, the presence of more than one species is strongly suggested by the mere circumstance that certain character states, e.g. two rows of cells between RP3/4 and MA or five rows of cells in the anal area, only occur in specimens with a wing length of more than 20 mm. Furthermore, the extreme

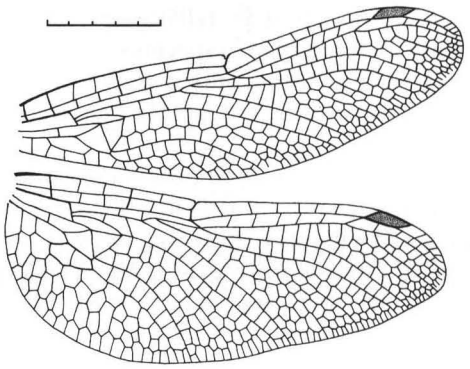

Fig. 35. *Cordulagomphus fenestratus*, ♀ specimen C13 (coll. BECHLY, SMNS). Scale 5 mm.

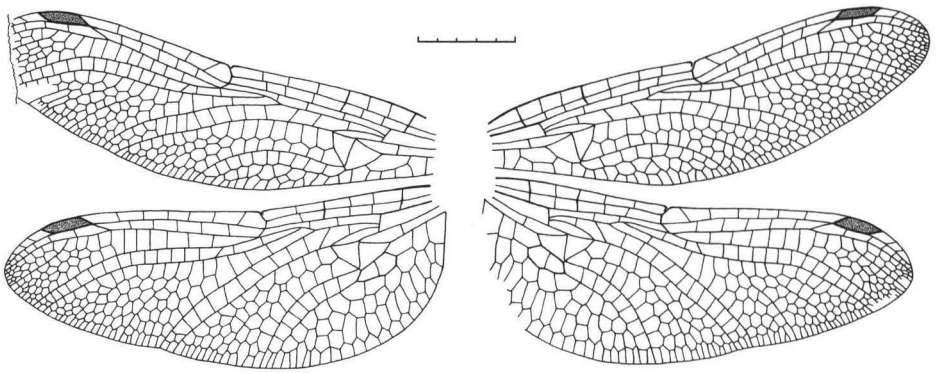

Fig. 36. *Cordulagomphus* cf. *tuberculatus*, ♀ specimen C6 (BSPGM). Scale 5 mm.

morphotypes are simply too dissimilar in size and wing venation to be conspecific, at least if one sticks to the reasonable assumption that the variability may not be significantly higher than in certain extant species that are notorious for their variable size and wing venation.

Since only three specimens among the 98 specimens studied by me, possess the complete set of diagnostic characters of the holotype of *C. tuberculatus*, it cannot be excluded that only these three specimens are indeed conspecific with this holotype. In this special case there could be two possible explanations for the variability among the remaining specimens: either the *fenestratus-tuberculatus*-complex includes three species rather than only two, or *Cordulagomphus fenestratus* is extremely variable in size and only larger specimens sometimes possess certain characters of *C. tuberculatus*. An above average variability of the wing venation of *Cordulagomphus* is documented by a few (rare) specimens of *C. fenestratus* and *C. tuberculatus* which have an unicellular anal loop in one hindwing (like the subgenus *Procordulagomphus* stat. nov.) and a normal two-celled anal loop in the other (e.g. specimen no. E2 in coll. ms-fossil has a forewing length of 22.0 mm, a wing venation

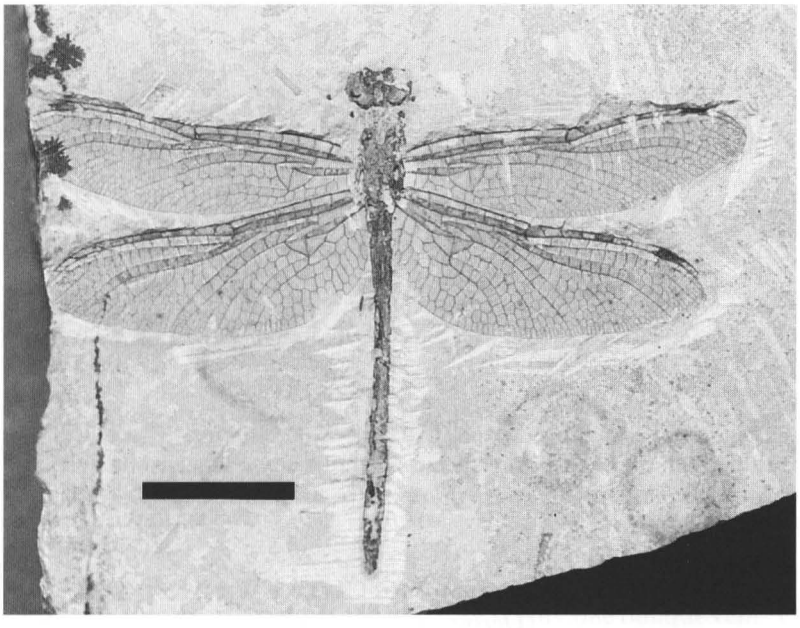

Fig. 37. *Cordulagomphus* cf. *tuberculatus*, ♀ specimen C6 (BSPGM). Scale 10 mm.

more similar to *C. fenestratus*, and an unicellular anal loop only in the right hindwing, while the anal loop is two-celled in the left hindwing). A definite answer to this complex species problem is not yet possible, in spite of the extensive available material, or maybe especially for this very reason!

Putative larvae of Cordulagomphinae (Anisoptera, Gomphides, Proterogomphidae) Fig. 38

About a third of all known dragonfly larvae from the Crato Formation are small gomphid larvae. Since these larvae generally possess well-developed wing sheaths, they do not seem to be early instars, but rather late instars of one or more small gomphid species. The attribution to the gomphid clade (= Gomphides) is possible because of the general habitus, the relatively small head with rather short and thick antennae, the bent femora, and especially because of the two-segmented fore- and middle-tarsi which represent an unique autapomorphy of the gomphid clade.

Of all known adult gomphids from the Crato Formation, only some species of the Cordulagomphinae have the correct size to be the corresponding adults for these larvae. Furthermore, the relative frequency of the referring larvae (33 %) agrees well with that of the adult Cordulagomphinae (47 %). Although an attribution of fossil dragonfly larvae to certain adult taxa is always problematical, in this special case the evidence indeed strongly suggests that the small gomphid larvae belong to the Cordulagomphinae. A separate specific naming of these larvae (e.g. *Cordulagomphus santanensis* CARLE & WIGHTON, 1990; see below) is not appropriate, since there are five different species of Cordulagomphinae with small adults known which could all

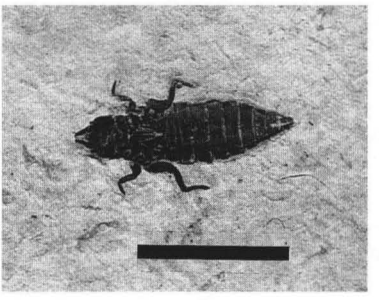

Fig. 38. Small gomphid larva (Cordulagomphinae ?), specimen B58 (ms-fossil). Scale 10 mm.

be represented in the larval material. Thus, any "larval species" would involve the risk of double naming of the same species without any chance to be ever able to recognize this. All referring larvae are therefore best classified as "Cordulagomphinae gen. et sp. indet.".

"Cordulagomphus" santanensis CARLE & WIGHTON, 1990 (Dermaptera pos. nov.)

The original description of this species only includes a very brief diagnosis and description, as well as a photo of the holotype (specimen no. AMNH 43258). NEL & PAICHELER (1994a) argued that it represents a gomphid larva of uncertain generic affinity. However, the photographic figure in the original description clearly shows no dragonfly larva at all, but obviously an adult earwig! Especially the characteristical shape of the head, pronotum and abdomen, as well as the forcep-like anal appendages (cerci), prove the dermapteran relationship of this fossil. The alleged larval wing sheaths are nothing but the typical elytrae and wings of Dermaptera, and the supposed antennae obviously represent the maxillary palps. Even a long filamentous right antenna seems to be preserved (artifact?). *"Cordulagomphus" santanensis* therefore has to be excluded from the list of fossil Odonata and transferred to Dermaptera incertae sedis.

First fossil record and first New World record of Chlorogomphoidea s. str. (Anisoptera, Exophytica, Cavilabiata, Cristotibiata, Brachystigmata) Fig. 39

The figured specimen shows two hindwings of an adult female dragonfly, still attached to a fragment of the pterothorax and basal abdomen. The wing venation is nearly identical to extant chlorogomphids: a large and longitudinal elongate anal loop that is divided into seven cells; a strongly elongated and very straight "gaff"; the basal part of the area between MP and CuA is widened with two rows of cells; CuAa has only two posterior branches, and the distal branch is distinctly curved on the main branch of CuA; the discoidal triangle is rather transverse; the subdiscoidal triangle is narrowed distally; there is no Mspl, but a secondary vein originating on MA in the distal half of the postdiscoidal area; there are two rows of cells in the basal part of the postdiscoidal area; RP3/4 and MA are parallel with one row of cells between them; there is no Rspl, but several secondary veins originate on IR2; RP2 and IR2 are

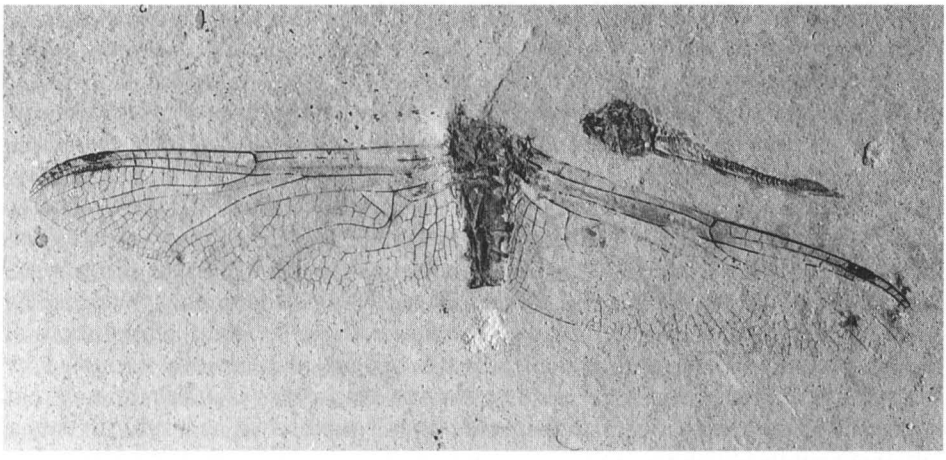

Fig. 39. Chlorogomphidae n. gen. et n. sp., first fossil record and first New World record, ♀ specimen (private coll. Murata, Japan). Scale unknown. Photo by BERND SCHUSTER (Hünstetten).

parallel with one row of cells between them; there is only one oblique vein "O", two or three cells distal of the subnodus; nine postnodal crossveins between nodus and pterostigma, non-aligned with the corresponding postsubnodal crossveins; the pterostigma is short, covering hardly three cells, and it is unbraced; vein pseudo-IR1 originates on RP1 below the distal end of the pterostigma. The area of the potential "cordulegastrid gap" and the basal space are not well-preserved, so that the presence of crossveins can neither be confirmed, nor refuted. Nevertheless there seems to be at least one character that is more plesiomorphic than in all extant chlorogomphids, since there seem to be no accessory cubito-anal crossveins in the subbasal space. The discoidal triangle seems to be free, but the hypertriangle might be divided by a crossvein. Anyway, there can be no doubt that this fossil belongs to Chlorogomphoidea, and thus represents the first fossil record and the first New World record of this taxon that now is restricted to east Asia. Unfortunately this remarkable specimen is in a private collection in Japan (coll. Murata, Kyoto).

5. Discussion

The relative frequency of odonates among the fossil insects of the Crato Formation is only about 2 %, since among 16000 specimens of fossil insects in various collections only 351 odonates are known to science (241 adults and 110 larvae). 309 specimens could be examined by myself, most of them in the collections of ms-fossil (Sulzbachtal). The Odonata of the Crato Formation belong to 32 different species, of which only 18 are described yet, including the six new species in the present publication. The descriptions of two new species are in print (JARZEMBOWSKI et al., in press; NEL et al., in press), and further eight species will be described soon by me (BECHLY et al. in prep.). The above mentioned undescribed chlorogomphid and the two undescribed taxa of Cordulagomphinae will be described by me, too, as soon as the final deposition of the referring holotypes in an official collection will be settled

(the only known specimen of the new chlorogomphid is in a private collection in Japan, and the four known specimens of the two new cordulagomphine taxa are still in the collections of ms-fossil).

With about 54 % of the adults and 56 % of the larvae, the majority of the odonate fossils belongs to the gomphid clade (Araripegomphidae and Proterogomphidae – Cordulagomphinae). This remarkable abundance of gomphids supports the hypothesis of an allochthonous origin of the aquatic insects of the Crato Formation (contra CARLE & WIGHTON 1990; contra BECHLY 1997b-d), since most extant gomphids are adapted to lotic habitats, and this even has to be regarded as the groundplan habitat of the gomphid clade (= Gomphides). This is also strongly confirmed by the evidence from the ephemerid larvae. Further evidence against the hypothesis of an autochthonous lacustrine fauna of aquatic insects was recently compiled by BECHLY (1998), for example the absence of any aquatic plants (although numerous terrestrial plants are preserved), the absence of mosquito larvae and caddisfly larvae (although adults of these groups have been found), and geological proves for a saline habitat (dolomitisation of the limestones and so-called medusoid salt-pseudomorphs). A further clue is the relative rarity of aquatic insects, contrary to their conspicuous occurrence at first sight, which was revealed by my recent screening of 3651 fossil arthropods from the Crato Formation in the collections of ms-fossil:

Scorpiones = 5; Uropygi = 2; Araneae = 48; Solifugae = 1; Acari = 1; Crustacea – Decapoda = 2; "Myriapoda" = 0; Diplura = 1; Zygentoma = 2; Ephemeroptera = 176 (adults) + 97 (larvae) (together 7 %); Odonata = 57 (adults) + 25 (larvae) (together 2 %); Plecoptera = 1; Dermaptera = 3; Blattodea (incl. Protocoleoptera) = 960 (26 %); Isoptera = 37 (1 %); Mantodea = 5; Phasmatodea = 2; Saltatoria = 1004 (27 %); Psocoptera = 3; Auchenorrhyncha = 282 (8 %); Heteroptera (mainly aquatic bugs) = 537 (15 %); Megaloptera = 4; Raphidioptera = 23 (1 %); Planipennia = 129 (4 %); Coleoptera = 93 (3 %); Hymenoptera = 64 (2 %); Trichoptera = 6; Lepidoptera = 1; Diptera = 81 (2 %); holometabolan larvae indet. = 2. There were no specimens of the orders Protura, Collembola, Archaeognatha, Zoraptera, Embioptera, Notoptera (Grylloblattodea), Phthiraptera ("Mallophaga" and Anoplura), Thysanoptera, Sternorryncha, Coleorrhyncha, Strepsiptera, Siphonaptera, and Mecoptera. Most of these "missing" groups are very small and cryptic insects that are either ground dwellers, or parasites.

The by far most abundant groups of insects are the Saltatoria (Orthoptera) and Blattodea, followed by Hemiptera, which together constitute about 76 % of this insect taphocoenosis. Odonata and Ephemeroptera are much more rare (together 9 %), and other aquatic insects (e.g. Plecoptera, Megaloptera, and Trichoptera) are even only known by a few specimens. The most frequent aquatic insects are water bugs (Notonectidae, Nepidae, Naucoridae, Belostomatidae, Hydrometridae, etc.), of which most are known to be excellent and avid fliers and thus do not necessarily indicate an autochthonous aquatic fauna anyway.

Altogether, the available evidence strongly suggests that the Araripe / Santana palaeo-habitat has been a brackish lagoon without any autochthonous aquatic insects (also see MARTILL et al. 1993).

A comparison of the odonate fauna of the Crato Formation with that of the Solnhofen limestones shows two remarkable differences:

1. The frequent occurrence of dragonfly larvae (31 % of the fossil odonates) and other aquatic insect larvae in the Crato Formation, contrary to the complete lack of

aquatic insect larvae in Solnhofen. However, this difference can be easily explained by the significant distance of the marine Solnhofen sedimentation area from the next emergent land which prohibited that such larvae could be drifted into the area by adjacent streams. In case of the Araripe area there obviously have been streams flowing into the brackish lagoon where the Crato limestones have been deposited. This is also documented by the excellent preservation of numerous delicate ephemerid larvae which is only possible if there was no long transportation. A yet unexplained oddity of the Araripe entomofauna is the complete absence of any damselfly larvae, compared to the relative abundance of dragonfly larvae. Maybe the referring larval habitats were exclusively confined to lacustrine freshwater or even phytotelmata and therefore could hardly be displaced into the lagoon.

2. The odonate fauna of the Crato Formation appears to be much more "modern" than the Solnhofen fauna, since there are already representatives of extant damselfly taxa (e.g. Hemiphlebiidae, Thaumatoneuridae, and Protoneuridae), while typical Mesozoic elements such as "anisozygopteres" (Tarsophlebiidae, Stenophlebiidae, and Isophlebiidae), Steleopteridae and Archizygoptera (Protomyrmeleontidae) are completely lacking. Regarding the large amount of material already found and determined, it can be regarded as most unlikely that these taxa occurred and have just been overlooked, or have only not been found by chance. True Zygoptera or even crown-group Zygoptera are unknown from Solnhofen, maybe except Steleopteridae, although these rather seem to be "anisozygopteres", since the arculus is between Ax1 and Ax2 (Bechly 1996, 1997a; Nel pers. comm.). Numerous species of "anisozygopteres" are frequently found in Solnhofen, as well as in nearly all other Mesozoic localities with fossil odonates. Archizygoptera are known from the Triassic of Australia, the Upper Triassic of Italy, the Liassic of Central Europe, the Upper Jurassic of Solnhofen, and the Lower Cretaceous of England. Steleopteridae are only known from the Upper Jurassic of Solnhofen and Kazakhstan. The single Mesozoic elements among the Odonata of the Santana fauna are the Liupanshaniidae (Mesuropetaloidea) and especially the Aeschnidiidae that both went extinct in the Cretaceous. While only stem-group representatives of aeshnids have been found in Solnhofen, there are several species of crown-group aeshnids from Santana, even though all of them belong to the most basal clade Gomphaeschnidae. Such Gomphaeschnidae are either absent, or at least much rarer in all other Cretaceous localities (e.g. Wealden, NE Asia). Concerning the libelluloid dragonflies (Eurypalpida), comparably "derived" representatives like *Araripelibellula* are not yet known from Solnhofen, but are well present in the Lower Cretaceous of England (Wealden).

The evolution of Odonata obviously was more advanced in the Lower Cretaceous of Brazil than in the Upper Jurassic of the Palaearctic. This impression is confirmed by the evidence from numerous "modern" insect groups which have their oldest fossil records in the Crato Formation (e.g. Zygentoma, Oligoneuriidae, Potamanthidae, Euthyplociidae, Mantodea, Stenopelmatidae, Myrmecophilidae, Gryllotalpidae, Tridactylidae, Achilidae, Cicadidae, Ochteridae, Nepidae, Hydrometridae, Macroveliidae, Corydalidae, Hemerobiidae, Osmylidae, Nemopteridae, Myrmeleontidae, Ascalaphidae, Passalidae, Cerambycidae, Pyrochroidae, Rhopalosomatidae, Tiphiidae, Formicidae?, Apoidea?, Lepidoptera, Xylophagidae, Xylomyidae, Asilidae; Bechly 1998; Bechly & Nel unpubl.), although there are also several typical Mesozoic taxa, like Protocoleoptera, Palaeontinoidea, Brongniartiellidae, Kalligrammatidae, Ephialtitidae, and even relatives of *Chresmoda* (Bechly 1998; Bech-

LY & NEL unpubl.). This phenomenon can be either explained by a significant general progress in the evolution of the Odonata and many other insect groups between the Upper Jurassic and the Lower Cretaceous, or rather by an early local progress of this evolution on the southern hemisphere.

The fossils of the Crato Formation consequently provide a unique source of information about a very interesting period in the evolution of odonates and other insects which after all include more than 90 % of all known species on our planet. Since this locality also yields a diverse fossil angiosperm flora, it might even allow the study of the early co-evolution of insects and flowering plants.

6. Appendix: List of the fossil odonate species from the Crato Formation

Zygoptera (= damselflies)
- Familia incertae sedis, probably Hemiphlebiidae
  1. *Cretarchistigma*(?) *essweini* n. sp. in this publ.
     (13 spec.; wl. about 9.8–10.5 mm)
  2. *Parahemiphlebia*(?) n. sp. (undescribed new species)
     (2 spec., e.g. no. 563 at National Science Museum Tokyo; size as *Parahemiphlebia cretacica*, but "pterostigmal brace" not extremely oblique)
- Hemiphlebiidae
  3. *Parahemiphlebia cretacica* n. gen. et n. sp. in JARZEMBOWSKI et al. (in press)
     (15 spec.; wl. 12.5–14.5 mm)
  4. *Parahemiphlebia mickoleiti* n. sp. in this publ.
     (4 spec.; wl. 8.9–9.9 mm)
- Protoneuridae – Isostictinae
  5. *Eoprotoneura hyperstigma* CARLE & WIGHTON, 1990
     (20 spec.; wl. 16–18.5 mm)
- Thaumatoneuridae – Euarchistigmatini
  6. *Euarchistigma atrophium* CARLE & WIGHTON, 1990
     (5 spec.; wl. 27.7–31.8 mm)

Anisoptera (= dragonflies s. str.)
- Aeschnidiidae (= Nothomacromiidae; = Sonidae)
  7. *Nothomacromia sensibilis* CARLE & WIGHTON, 1990
     (10 small and 10 large spec.; bl. 14.3–63.5 mm without anal appendages)
  8. *Wightonia araripina* CARLE & WIGHTON, 1990
     (6 spec.; fwl. 39.7–47 mm; hwl. 39–46 mm)
  9. *Santanoptera gabbotti* MARTILL & NEL, 1996
     (1 spec.; fwl. 62.3 mm)
- Cretapetaluridae n. fam. in NEL et al. (in press)
  10. *Cretapetalura brasiliensis* n. gen. et n. sp. in NEL et al. (in press)
      (1 spec.; fwl. 67 mm; hwl. 67 mm)
- Liupanshaniidae n. fam. in BECHLY et al. (in prep.)
  11. *Paramesuropetala gigantea* n. gen. et n. sp. in BECHLY et al. (in prep.)
      (1 spec.; fwl. 67 mm)
  12. *Araripeliupanshania annesuseae* n. gen. et n. sp. in BECHLY et al. (in prep.)
      (2 spec.; fwl. 40.2 mm; hwl. 38.5 mm; Fig. 30)
- Gomphaeschnidae – Gomphaeschnaoidinae n. subfam. in BECHLY et al. (in prep.)
  13. *Gomphaeschnaoides obliquus* (WIGHTON, 1987)
      (10 spec.; fwl. 31–35 mm; hwl. 32–37 mm)
  14. *Gomphaeschnaoides petersi* n. sp. in BECHLY et al. (in prep.)
      (1 spec.; wl. about 37.5 mm)
  15. *Gomphaeschnaoides betoreti* n. sp. in BECHLY et al. (in prep.)
      (1 spec.; fwl. 29.1 mm; hwl. 28.2 mm)
  16. *Gomphaeschnaoides magnus* n. sp. in BECHLY et al. (in prep.)
      (2 spec.; fwl. 42.1–45 mm; hwl. 41–43 mm)

17. *Progomphaeschnaoides ursulae* n. gen. et n. sp. in BECHLY et al. (in prep.)
(2 spec.; fwl. 27.5 mm; hwl. 25–26.9 mm)
18. *Progomphaeschnaoides staniczeki* n. sp. in BECHLY et al. (in prep.)
(1 spec.; hwl. 29.3 mm)
19. *Paramorbaeschna araripensis* n. gen. et n. sp. in BECHLY et al. (in prep.)
(3 spec.; fwl. 40–41.7 mm; hwl. 37.7–40.6 mm)

Araripegomphidae

20. *Araripegomphus cretacicus* NEL & PAICHELER, 1994
(1 spec.; fwl. 38.5 mm; hwl. 37.8 mm)
21. *Araripegomphus andreneli* n. sp. in this publ.
(14 spec.; fwl. 32–36.7 mm, generally about 35 mm; hwl. 32–36 mm, generally about 34 mm)
22. *Araripegomphus* n. sp. (?) in this publ.
(1 spec.; hwl. 30.5 mm)

Proterogomphidae n. fam. in BECHLY et al. (1998) – Cordulagomphinae

23. *Cordulagomphus fenestratus* CARLE & WIGHTON, 1990
(40 spec.; fwl. 18–19.8 mm; hwl. 17.5–19.6 mm)
24. *Cordulagomphus tuberculatus* CARLE & WIGHTON, 1990
(58 spec.; fwl. 22–25 mm; hwl. 21–23 mm)
25. *Cordulagomphus (Procordulagomphus* stat. nov.*)* sp. (undescribed new species; Figs 33–34)
(3 spec.; fwl. 17–21.5 mm; hwl. 16.9–20 mm)
26. *Cordulagomphus (Procordulagomphus* stat. nov.*) xavieri* NEL & ESCUILLIÉ, 1994
(5 spec.; fwl. 16.6–18 mm; hwl. 15.6–17.2 mm)
27. *Cordulagomphus (Procordulagomphus* stat. nov.*) senckenbergi* n. sp. in this publ.
(1 spec.; fwl. 17.4 mm; hwl. 16.7–16.9 mm)
28. (undescribed new genus and species; Figs 31–32)
(1 spec.; hwl. 35 mm)

Araripephlebiidae n. fam. in this publ.

29. *Araripephlebia mirabilis* n. gen. et n. sp. in this publ.
(3 spec.; fwl. 34–34.2 mm; hwl. 34.1 mm)

Chlorogomphidae

30. (undescribed new genus and species; Fig. 39)
(1 spec. in private collection in Japan; size unknown)

Araripelibellulidae

31. *Araripelibellula martinsnetoi* NEL & PAICHELER, 1994
(4 spec.; fwl. 17.4–18 mm; hwl. 16.5–17.1 mm)
32. *Cratocordulia borschukewitzi* n. gen. et n. sp. in this publ.
(1 spec.; fwl. 25.1 mm; hwl. 24.2 mm)

Abbreviations: spec. = number of known specimens, excluding all specimens with uncertain determination; bl. = body length; wl. = wing length; fwl. = forewing length; hwl. = hindwing length; s. str. = sensu stricto.

Please note: Some of the mentioned scientific names are still unpublished manuscript names, since the referring publications are either in press, or in preparation (submitted).

7. Acknowledgements

I am most grateful to ANNESUSE and MICHAEL SCHWICKERT (Sulzbachtal, Germany) for the unique opportunity to study the marvellous collections at ms-fossil (and even providing a working place with binocular microscope, etc.), their generous providing of numerous specimens on loan and various photos, and of course for their kind hospitality. This is a very positive example for the significant promotion of paleontological research by a trader of fossils, who also takes care that all scientifically important specimens are exclusively sold to public museums. I also owe many thanks to Dr DAVID GRIMALDI (AMNH, New York) for a loan of the holotype of *Parahemiphlebia mickoleiti* n. sp., to Dr ANDRÉ NEL (MNHN, Paris) and Dr

EBERHARD FREY (SMNK, Karlsruhe) for interesting discussions, to Dr GERD DIETL and Dr GÜNTER SCHWEIGERT (SMNS, Stuttgart) for their friendly support of my studies at the Staatl. Museum f. Naturkunde in Stuttgart, and to Dr GERT BLOOS (SMNS, Stuttgart) for his careful proof-reading of this manuscript.

My sincere thanks also go to Dr GÜNTER VIOHL (Eichstätt) who purchased three important specimens for the Jura-Museum (B40 *Gomphaeschnaoides magnus* n. sp.; B41 *Gomphaeschnaoides petersi* n. sp.; B48a,b *Progomphaeschnaoides ursulae* n. gen. et n. sp.) that will be described in BECHLY et al. (in prep.), and to the "Gesellschaft zur Förderung des Naturkundemuseums" in Stuttgart, for sponsoring the purchase of five originals and types for the referring museum (SMNS 63070 *Araripegomphus imperfectus* n. sp., holotype; SMNS 63068a,b *Paramorbaeschna araripensis* n. gen. et n. sp., holotype; SMNS 63071 *Cretarchistigma*(?) *essweini*, holotype; SMNS 63072 *Parahemiphlebia mickoleiti* n. sp., paratype; SMNS 63069 = B22 *Gomphaeschnaoides obliquus*, original) that are partly described in the present publication and partly will be described in BECHLY et al. (in prep.).

Last but not least I thank Dr REINER BORSCHUKEWITZ (Offenburg) who generously donated the holotype of *Cratocordulia borschukewitzi* n. gen. et n. sp., and more than 90 further interesting fossil insects from the Crato Formation, to the Muséum National d'Histoire Naturelle in Paris.

This publication is part of my PhD thesis on the phylogeny of dragonflies at the Eberhard-Karls-University in Tübingen, and was supported from 1996–1998 by the "Graduiertenförderung" of the State Baden-Württemberg (Germany).

8. References and bibliography of fossil Odonata from Araripe

BECHLY, G. (1996): Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und der Grundplanes der *Odonata. – Petalura, spec. vol. **2**: 1–402; Böblingen.

– (1997): Phylogenetic Systematics of Odonata. – website on the Internet (URL: http://members.aol.com/odonatadat/phylogeny/bechly.htm). – [1997a]

– (1997): Die Libellen (und einige andere fossile Insekten) aus der Unterkreide von Brasilien (Santana). – 4. Fachgespräch "Fossile Insekten", Clausthal-Zellerfeld, 28–29 Juni 1997, Abstracts. – [1997b]

– (1997): Dragonflies from the Lower Cretaceous of Brazil. – Inclusion Wrostek, **27**: 9; Kraków. – [1997c]

– (1997): Dragonflies from the Lower Cretaceous of Brazil. – Meganeura, **1**: 27–28; Strasbourg. – [1997d]

– (1997): New fossil odonates from the Upper Triassic of Italy, with a redescription of *Italophlebia gervasuttii*, and a reclassification of Triassic dragonflies (Insecta: Odonata). – Riv. Mus. Civ. Sci. Nat. 'E. Caffi', **19**: 31–70; Bergamo. – [1997e]

– (1998): Santana – Die Schatzkammer fossiler Insekten aus der Unterkreide Brasiliens. – Fossilien, **2**: 95–99 (first part), **3**: 148–156 (second part); Korb.

BECHLY, G., NEL, A., MARTÍNEZ-DELCLÒS, X. & FLECK, G. (1998): Four new dragonfly species from the Upper Jurassic of Germany and the Lower Cretaceous of Mongolia (Anisoptera: Hemeroscopidae, Sonidae, and Proterogomphidae fam. nov.). – Odonatologica, **27**(2): 149–187; Bilthoven.

BECHLY, G., NEL, A., MARTÍNEZ-DELCLÒS, X., JARZEMBOWSKI, E.A., CORAM, R., MARTILL, D., FLECK, G., ESCUILLIÉ, F., WISSHAK, M. M. & MAISCH, M. (in prep.): A revision and phylogenetic study of Mesozoic Aeshnoptera, with description of several new families, genera and species (Insecta: Odonata: Anisoptera). – N. paläont. Abh.; Dresden. – [Submitted]

BORUCKI, H. (1996): Evolution und Phylogenetisches System der Chilopoda (Mandibulata, Tracheata). – Verh. naturwiss. Ver. Hamburg, (NF) **35**: 95–226; Hamburg.

BRITO, I.M. (1984): Nota preliminar sobre os insetos da Formaçao Santana, Cretáceo inferior da Chapada do Araripe. – XXXIII Congr. Brasil. Geol., Rio de Janeiro: 530–535.

CARLE, F.L. (1995): Evolution, taxonomy, and biogeography of ancient Gondwanian Libellu-

loids, with comments on anisopterid evolution and phylogenetic systematics (Anisoptera: Libelluloidea). – Odonatologica, **24**(4): 383–424; Bilthoven.

CARLE, F.L. & WIGHTON, D.C. (1990): Odonata. Chapter 3. – *In*: GRIMALDI, D.A. (Eds.): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bull. Amer. Mus. nat. Hist., **195**: 51–68; New York.

CARPENTER, F.M. (1992): Superclass Hexapoda. – *In*: MOORE, R.C. & KAESLER, R.L. (Eds.): Treatise on Invertebrate Paleontology. (R), Arthropoda 4, 3–4. xxii + 655 pp.; Boulder – Lawrence (Geological Society of America – University of Kansas).

DE QUEIROZ, K. & GAUTHIER, J. (1990): Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. – Syst. Zool., **39**(4): 307–322; Washington.

– & – (1992): Phylogenetic taxonomy. – Ann. Rev. Ecol. Syst., **23**: 449–480.

Digital Fossil & National Science Museum Tokyo (1996): Santana 1 for Windows. Volume #1: The insects and spiders of the Santana Formation, Lower Cretaceous of Brazil. – CD-ROM for MS-Windows™.

GRIMALDI, D.A. (Ed.) (1990): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bull. Amer. Mus. nat. Hist., **195**: 1–191; New York.

– (1991): The Santana Formation insects. – *In*: MAISEY, J.G. (Ed.) (1991): Santana fossils: an illustrated atlas: 379–406 ; Neptune City (T.H.F. Publications).

HANDLIRSCH, A. (1906–1908): Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. 1430 pp.; Leipzig (Engelmann).

HENNIG, W. (1966): Phylogenetic Systematics. – Urbana (Univ. Illinois Press).

– (1969): Die Stammesgeschichte der Insekten. 436 pp.; Frankfurt a.M. (Kramer).

JARZEMBOWSKI, E.A., MARTÍNEZ-DELCLÒS, X., BECHLY, G., NEL, A., CORAM, R. & ESCUILLIÉ, F. (in press): The Mesozoic non-calopterygoid Zygoptera: descriptions of new genera and species from the Lower Cretaceous of England and Brazil and their phylogenetic significance (Odonata, Zygoptera, Coenagrionoidea, Hemiphlebioidea, Lestoidea). – Cretaceous Res., **19**: 1–42; London. – [1998]

KUKALOVÁ-PECK, J. (1991): Chapter 6: Fossil history and the evolution of hexapod structures. – *In*: NAUMANN, I. D. (Ed.): The insects of Australia, A textbook for students and research workers (2nd ed.). **1**: 141–179; Melbourne (Melbourne University Press).

LOHMANN, H. (1996): Das Phylogenetische System der Anisoptera (Odonata). – Entomologische Zeitschrift, **106**(6): 209–252 (first part); **106**(7): 253–296 (second part); **106**(9): 360–367 (first postscript); Frankfurt a.M.

MAISEY, J.G. (1990): Stratigraphy and depositional environment of the Crato Member (Santana Formation, Lower Cretaceous of N.E. Brazil). – *In*: GRIMALDI, D.A. (Ed.): Insects from the Santana Formation, Lower Cretaceous, of Brazil. – Bull. Amer. Mus. nat. Hist., **195**: 15–19; New York.

MARTILL, D.M., BRITO, P.M., WENZ, S. & WILBY, P.R. (1993): Fossils of the Santana and Crato Formations, Brazil. – *In*: JARZEMBOWSKI, E. A. (Ed.): Palaeontological Association Field Guides to Fossils Series, **5**. 159 pp.; London (The Palaeontological Association).

MARTILL, D.M. & FREY, E. (1995): Colour patterning preserved in Lower Cretaceous birds and insects: The Crato-Formation of N.E. Brazil. – N. Jb. Geol. Paläont. Mh., **1995**: 118–128; Stuttgart.

MARTILL, D.M. & NEL, A. (1996): A new dragonfly from the Crato Formation (Lower Cretaceous, Aptian) of N.E. Brazil. – N. Jb. Geol. Paläont. Mh., **1996**: 279–292; Stuttgart.

MARTINS-NETO, R.G. (1987): A paleoentomofauna Brasileira: estagio atual do conhecimento. – Anais X Congr. Brasil. Palaeontol., Rio de Janeiro, **1987**: 567–591.

– (1991): A Paleoentomofauna do Nordeste Brasileiro: Estado da Arte. – Atas XIV Simposio de Geologia do Nordeste, Recife, 1991, **12**: 59–62.

– (1992): A paleoentomofauna das bacias mesozoicas brasileiras e seu potencial para possiveis correlacoes bioestratigraficas entre depositos nao-marinhos. – *In*: I. Encontro sobre a sedimentacao continental das bacias mesozoicas brasileiras. – Acta Geologica Leopoldensia, **36**: 125–126.

MARTINS-NETO, R.G., CASTILLO, D.C., FRAGOSO, L.M., SANTOS, J.C. & VIEIRA, F.R. (1992): Paleofisiologia de insetos da Formaçao Santana, Cretáceo do nordeste do Brasil; Parte 1, Um caso de extrema especializacao em gafanhotoss. – *In*: II. Simposio sobre as bacias cretacicas brasileiras. – Boletim do Simposio sobre o Cretáceo do Brasil, **2**: 65–68.

NEEDHAM, J.G. (1903): A genealogic study of the dragonfly wing venation. – Proc. U.S. natn. Mus., **26**(1331): 703–764.

NEL, A., BECHLY, G., JARZEMBOWSKI, E.A. & MARTÍNEZ-DELCLÒS, X. (in press): A revision of the fossil petalurid dragonflies (Insecta: Odonata: Anisoptera: Petalurida). – Paleontologia Lombarda; Milano.

NEL, A. & ESCUILLIÉ, F. (1994): A new dragonfly from the Lower Cretaceous of Brazil. – Palaeontology, **37**(4): 923–930; London.

NEL, A., JARZEMBOWSKI, E.A. & ROSS, A. (in press): Revision of *Araripelibellula martinsnetoi* Nel & Paicheler, 1994, fossil dragonfly from the Lower Cretaceous of Brazil (Odonata: Libelluloidea: Corduliidae). – Cretaceous Res.; London.

NEL, A., MARTÍNEZ-DELCLÒS, X., PAICHELER, J.-C. & HENROTAY, M. (1993): Les „Anisozygoptera" fossiles. Phylogénie et classification. (Odonata). – Martinia, Numéro hors-série, **3**: 1–311; Bois-d'Arcy.

NEL, A. & PAICHELER, J.-C. (1994): Les Gomphidae fossiles. Un inventaire critique (Odonata: Gomphidae). – Ann. Soc. entomol. Fr., (N.S.) **30**(1): 55–77; Paris. – [1994a]

– & – (1994): Les Libelluloidea fossiles autres que Libellulidae. Un inventaire critique (Odonata, Corduliidae, Macromiidae, Synthemistidae, Chlorogomphidae et Mesophlebiidae). – Nouv. Rev. Ent., (N.S.) **11**: 321–334; Toulouse. – [1994b]

PRITYKINA, L.N. (1977): New dragonflies from Lower Cretaceous deposits of Transbaikalia and Mongolia. – Trudy sovm. sov.-mongol. paleont. Eksped., **4**: 81–96. – [Russian]

– (1986): Two new dragonflies from the Lower Cretaceous deposits of West Mongolia (Anisoptera: Sonidae fam. nov., Corduliidae). – Odonatologica, **15**(2): 169–184; Bilthoven.

RIEK, E.F. (1976): A new collection of insects from the Upper Triassic of south Africa. – Ann. Natal Mus., **22**(3): 791–820; Pietermartitzburg, etc.

RIEK, E.F. & KUKALOVÁ-PECK, J. (1984): A new interpretation of dragonfly wing venation based upon early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic characters states in pterygote wings. – Can. J. Zool., **62**: 1150–1166; Ottawa.

SCHLÜTER, T. & HARTUNG, M. (1982): *Aegyptidium aburasiensis* gen. nov., spec. nov. (Aeschnidiidae) und *Gondvanogomphus bartheli* gen. nov., spec. nov. (Gomphidae) aus mutmasslicher Unterkreide Südwest-Ägyptens (Anisoptera). – Odonatologica, **11**(4): 297–307; Bilthoven.

WÄGELE, J.W. (1994): Review of methodological problems of "computer cladistics" exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). – Z. zool. Syst. Evolut.-forsch., **32**: 82–107; Hamburg, etc.

WESTFALL, M.J. (1980): Cretaceous dragonfly discovery in Brazil. – Selysia, **9**(2): 22; Gainesville.

WIGHTON, D.C. (1987): *Gomphaeschna obliqua* spec. nov., a new species of Gomphaeschninae from the Lower Cretaceous of northeastern Brazil (Anisoptera, Aeshnidae). – Odonatologica, **16**(3): 311–314; Bilthoven.

– (1988): Odonate fossils from the Lower Cretaceous of Northeastern Brazil. – Proc. 18th Internat. Congr. Entomol., Vancouver, Abstracts: 64.

WILLMANN, R. (1989): Palaeontology and the systematization of natural taxa. – *In*: SCHMIDT-KITTLER, M. & WILLMANN, R. (Eds.): Phylogeny and the classification of fossil and recent organisms. – Abh. naturwiss. Ver. Hamburg, (NF) **28**: 267–291; Hamburg.

Author's address:

Dipl.-Biol. Günter Bechly, Institut und Museum für Geologie und Paläontologie, Eberhard-Karls-Universität Tübingen, Sigwartstr. 10, D-72076 Tübingen, Germany.
Email: Guenter.Bechly@t-online.de or GBechly@aol.com

ISSN 0341-0153

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