- Leptophlebiidae (?) sp. 2 McCafferty (1990: 43–44; figure 33; AMNH 43476, adult)
- Leptophlebiidae (?) sp. 3 McCafferty (1990: 44, figure 34; AMNH 44312, adult)
- Family *incertae sedis* sp. 1 McCafferty (1990: 44; AMNH 43453, larva)
- Family *incertae sedis* sp. 2 McCafferty (1990: 44–45; AMNH 43423, larva)
- Family *incertae sedis* Grimaldi and Engel (2005: 166, figure 6.12; AMNH without number; small alate stage with two extremely long cerci but without paracercus)
- Family *incertae sedis* Bechly *et al.* (2001a: figure 30)
- Familia *incertae sedis* (Figures 11.5e and f); larval specimens SMNS 66622, SMNS 66625 and MSF Z2)
- *Comment*: these strange mayfly larvae (body length about 23 mm) have an absolutely unique habitus with broadened and flattened fore and hind femora, but slender mid femora.

Ephemeroptera *incertae sedis*

Costalimella nordestina Martins-Neto, 1996a (Figure 11.8a)
Costalimella zuechii Zamboni, 2001

Comment: these two species have each been described from a single adult specimen. Possibly both specimens resemble small species of †Hexagenitidae. In the forewing, the MA branch is located in the apical fourth of the wing, and in *C. zuechii* the branching of CuA is reported.

Insecta *incertae sedis*

Caririephemera marquesi Zamboni, 2001

Comment: Zamboni, 2001 described an insect larva with eight visible abdominal segments and without abdominal gills as a mayfly larva. Terminal filaments are either not present or not preserved. The author tentatively places the fossil within the Baetiscidae, because 'the lack of gills . . . occurs only in Baetiscidae'. In fact, the gills of the Baetiscidae lie under a gill chamber formed by the enlarged mesonotum. This fossil has no such gill chamber and nor does it exhibit any character that could identify it as a mayfly nymph, even though it might well represent a poorly preserved specimen of *Protoligoneuria limai*.

11.5 Odonata: damselflies and dragonflies

Günter Bechly

The order Odonata includes three Recent suborders (Zygoptera, 'Anisozygoptera' – Epiophlebiidae, and Anisoptera) with a total of 635 Recent genera and 5,538 described species. Odonates are relatively large insects and well known for their beautiful colours, their swift flight and the curious mating in the wheel-position.

Odonates have bristle-like antennae, biting mouthparts and large compound eyes. The thoracic segments have a distinct skew, so that their spiny legs are tilted anteriorly to form a 'catching basket'. The very powerful flight mechanism is driven by a unique combination of upstroke operated by indirect dorso-ventral muscles and a downstroke using direct flight musculature. The wings have a complete and dense venation with a characteristic that includes arculus, nodus, apical pterostigma, intercalary veins IR_1 and IR_2, and a distinct discoidal cell or discoidal triangle. The wing margins and wing veins are covered with spines, and the wing membrane is strongly pleated. The abdomen is long and slender. The primary genitalia are reduced in males, and in the females an ovipositor can be normally developed, hypertrophied or completely reduced. A unique feature within insects is the male secondary copulatory apparatus that is developed on the sternites of the second and third abdominal segments. In the three Recent suborders of Odonata different parts of this apparatus have been independently developed as copulation organs (Bechly *et al.*, 2001b), with structures for the removal of foreign sperm on the intromittent organ (ligula in Zygoptera, hamuli posteriores in Epiophlebiidae and vesicula spermalis in Anisoptera). The apex of the abdomen is provided with a grasping apparatus that is used in the formation of the mating wheel. This grasping apparatus comprises two pairs of claspers (cerci and paraprocts) in Zygoptera, but only a single pair of claspers (cerci), plus an unpaired appendage (epiproctal process) in Epiophlebiidae and Anisoptera.

Development is hemimetabolous, with a distinct aquatic larval stage. Larvae are characterized by a prehensile mask, twisted wing sheaths (convergent with Orthoptera), rectal gills (in Zygoptera also three caudal gill filaments). The larvae of Anisoptera are capable of locomotion by jet propulsion, except for the amphibious larvae of Petaluridae. Adult Odonata are important predators on other insects and have a worldwide distribution. They are only absent from very cold or very arid regions, and the larvae can be found in running water, stagnant water, swamps and phytotelmata, and a few even in brackish water.

Systematics and phylogeny

The systematics of Odonata is still largely based on the typological classification by Fraser (1957), but in the last two decades there have been attempts towards a phylogenetic classification (Carle, 1982; Lohmann, 1996; Trueman, 1996; Bechly, 1999a, 2002, 2003; Rehn, 2003; Hovmöller, 2006). Differences between the results of these attempts are based on different selection of characters or, perhaps even more so, on different methodological approaches (e.g. traditional Hennigian phylogenetic systematics and computer-based numerical cladistics).

There is a broad consensus that Epiophlebiidae and Anisoptera are both monophyletic sister groups, while 'Anisozygoptera' is a paraphyletic assemblage of Recent Epiophlebiidae (a single genus with only two relict species) and fossil stem group representatives of Anisoptera. In modern works there is also a wide consensus that ‘protodonates’ (e.g. †Meganisoptera), †Protanisoptera, †Triadophlebiomorpha and †Protozygoptera+†Archizygoptera are successive basal branches on the stemline of Odonata, and that the Mesozoic family †Tarsophlebiidae represents the sister group of crown group Odonata.

The monophyly of Anisoptera is supported by numerous morphological autapomorphies (sperm vesicle developed as a copulation organ, wing venation with hypertriangle, triangle, subtriangle and anal loop, and larval locomotion with jet propulsion) and this is also the case for Epiophlebiidae (hamuli posteriores developed as a copulation organ, interocellar lobe, ovoid pedicel, hairy eye tubercle and larval stridulation organs). It is also undisputed that Epiophlebiidae is the sister group of Anisoptera, because there are several good synapomorphies (discoidal cell distally distinctly widened in hind wing, male hind wing with anal angle, males with a secondary epiproctal projection, synthorax with the dorsal portion of the interpleural suture suppressed, and larvae with anal pyramid).

Most recent authors consider Zygoptera monophyletic, while Trueman (1996), in a cladistic analysis of wing venational characters, suggested that Zygoptera is a highly paraphyletic group, as previously indicated by Fraser (1957). However, the monophyly of Zygoptera is supported by several strong putative autapomorphies, including the transverse head, the more oblique pterothorax, abdominal sternites with triangular cross-section and longitudinal keel, formation of an ovipositor pouch by the enlarged outer valves (valvula 3 = gonoplacs) of the ninth abdominal sternite, and the highly specialized ligula developed as a copulatory organ. The presence of caudal gills, even though uniquely present in Zygoptera among Recent odonates, has been demonstrated to be a symplesiomorphy by the discovery of a fossil dragonfly larva. This larva has wing sheaths that clearly show the characteristic veinal features of the isophlebiid stem group representatives of Anisoptera, but still possesses three caudal gills.

A detailed phylogenetic system of fossil and Recent odonates with all synapomorphies, based on my results, is available at http://www.bernstein.naturkundemuseum-bw.de/odonata/phylosys.htm Bechly, 2002).

A comprehensive cladistic study of 122 morphological characters by Rehn (2003) basically confirmed this phylogeny: this includes the sister group relationship of †Tarsophlebiidae and crown group Odonata, the monophyly of Zygoptera, a lestinoid+coenagrionoid clade that is sister-group to Calopterygoidea, the position of the relict damselfly *Hemiphlebia* at the very base of lestinoid zygopteres, the position of Petaluridae at the base of Anisoptera, and the sister-group relationship of African Coryphagrionidae to the Neotropical Pseudostigmatidae. The only clear differences concern the positions of amphipterygid and megapodagrionid damselflies, which Rehn (2003) regards as a paraphyletic basal grade towards the lestinoid+coenagrionoid clade. However, the widely separated Zygoptera genera *Diphlebia* and *Philoganga* in this phylogeny indicate an artefact of the cladistic method without proper character weighting, because these two genera are united by very strong larval synapomorphies and some synapomorphies of the imagines.

Recent molecular studies concerning the higher phylogeny of odonates (Misof and Rickert, 1999a, 1999b) did not resolve the Zygoptera problem and in part conflicted with some monophyla; for example, Cavilabiata (Cordulegastridae, Neopetaliidae, Chlorogomphidae and libelluoids) that are very well established by morphological evidence beyond reasonable doubt. Methodological artefacts like long-branch attraction and 'noise' seem to be prevalent. Based on a study of rDNA, Hasegawa and Kasuya (2006) suggested that Zygoptera is paraphyletic (and incorrectly cited Bechly (1996) in support of this hypothesis) and confirmed that Epiophlebiidae is the sister group of Anisoptera.

The phylogenetic position of the Odonata in the tree of insects remains ambiguous. Fossil evidence and some morphological and molecular characters support the monophyly of Palaeoptera (†Palaeodictyopteroida+Ephemeroptera+Odonata), while rather strong characters of the Recent head morphology (Staniczek, 2000) and some molecular data support the monophyly of Metapterygota (Odonata+ Neoptera). Consequently, this issue still has to be considered unresolved.

Fossil record

The fossil record of Odonata is relatively well documented, with about 700 fossil species extending from Tertiary representatives of Recent families back to primitive protodonates of the lower-most Upper Carboniferous (320 mya). The biggest insect in Earth history was the protodonate *Meganeuropsis* from the Permian of North America, with a 75 cm wing span, while some protodonates from the Namurian belong to the oldest-known fossils of winged insects. Other Mesozoic localities with very diverse odonate faunas include the Madygan/Ferghana Basin (Late Triassic, Kyrgyzstan), the Solnhofen lithographic limestone (Upper Jurassic, Germany), the Weald Clay (Lower Cretaceous, southern England) and Liaoning (Lower Cretaceous, China).

Palaeobiology and palaeoecology

The large number of odonate species from the Crato Formation is typical for subtropical and tropical habitats with rather diverse aquatic biotopes. Some taxa, like libelluloid dragonflies, could indicate the presence of lacustrine biotopes, especially as no larvae of these dragonflies have been discovered yet. This is also supported by the occurrence of water striders (Hydrometridae) that are usually confined to standing water bodies or at least calmer water. Bechly (1998c) studied 351 fossil odonates from the Crato Formation (241 adults and 110 larvae): 54% of the adults and 56% of the larvae belonged to the gomphid clade (Plate 9a), and thus to a taxon of Anisoptera that is mostly adapted to lotic habitats. The presence of fast-flowing streams and rivers is therefore very likely, and also supported by the abundance of fossil mayfly larvae.

The somewhat larger percentage of female specimens among the Crato dragonflies (e.g. of the 46 adult holotypes and projected types, one is a larva, nine are of indeterminate sex, 21 are female and only 15 are male) could indicate that many specimens drowned during oviposition attempts.

Crato fossils

Even though they constitute only about 2% of the fossil insects found (Bechly, 1998c), dragonflies are not rare in the Crato Formation, so that more than 1,000 specimens of about 46 different species have been discovered so far. No other fossil locality yields more fossil odonates, either in the number of individuals or in the number of species, than the limestones of the Crato Formation. Furthermore, Crato Formation examples are outstanding because of their completeness and very beautiful preservation. A detailed statistical analysis of the Crato Formation odonate fauna was provided by Bechly (1998c: Table 1 and Appendix).

The first fossil dragonfly from this locality was mentioned by Westfall (1980) and described by Wighton (1987). Subsequently, important contributions with numerous descriptions of new species have been provided by Wighton (1988), Carle and Wighton (1990), Grimaldi (1991), Nel and Escuillié (1994), Nel and Paicheler (1994a, 1994b), Martill and Nel (1996), Bechly (1997a, 1997b, 1997c, 1998a, 1998b, 1998c), Nel *et al.* (1998), Jarzembowski *et al.* (1998), Bechly (1999a, 2000), Bechly *et al.* (2001b, 2001c), Bechly and Ueda (2002), Fleck *et al.* (2002), Martins-Neto (2005a, 2005b) and Grimaldi and Engel (2005).

Occasionally, falsified fossil dragonflies are offered for sale by local traders in Brazil. Such specimens often include the wings of a Recent dragonfly glued to a slab of Crato limestone, combined with a carved body. Such a specimen is deposited in the Paläontologische Staatssammlung (BSPGM) in Munich and was figured by Bechly *et al.* (2001b: Abb. 23), while a similar example was figured by Martill (1994).

Zygoptera: damselflies

Diagnosis: small-to-medium-sized damselflies (wing span less than 6 cm), with delicate bodies and a transverse head with large compound eyes; forewings and hind wings of very similar shape and venation, and without sexual dimorphism; wing venation of both pairs of wings with basally open or closed discoidal cells and a subdiscoidal cell. About 278 genera with more than 2,664 species. Up to now, no larvae of Zygoptera have been discovered among the hundreds of fossil dragonfly larvae from the Crato Formation, which suggests that they all lived in lacustrine habitats outside the Crato lagoon.

Family *incertae sedis* (probably Hemiphlebiidae)

Cretarchistigma Jarzembowski *et al.,* 1998

Cretarchistigma (?) essweini Bechly, 1998c

Material: female holotype SMNS 63071 (Figure 11.10a); female paratypes no. 51 and no. 1007 at NSMT; female paratype no. 101 at KMNH; specimen SMNS 66393 (Plate 2c); specimens no. MB.1999.3 MB.I.2055 (old no. D52) and no. MB.1999.3 MB.I.2056 (old no. C24) at MNB (ex MSF); several specimens in other collections (Plate 9b).

Diagnosis: wing length 9.8–10.5 mm; hind wing discoidal cell closed, elongate and narrow; pterostigmal brace distinct but not very oblique; IR_1 originates one cell basal of pterostigma or beneath stigmal brace; cell beneath pterostigma not widened; pterostigma with 'micraster-type' microsculptures; arculus aligned with Ax2; six non-aligned postnodal crossveins; thorax more gracile than in *Parahemiphlebia*; anal appendages very long and slender in males, but strongly reduced in females.

Comment: the new specimen SMNS 66393 (Plate 2c) demonstrates very rare preservation of the original metallic-green body colour (previously noted by Bechly, 1998c for *Parahemiphlebia cretacica*, Plate 9c), very similar to the colour of Recent Hemiphlebiidae. This is further evidence for referral of this species to Hemiphlebiidae. It is the first Mesozoic fossil record for preservation of interference colours.

Hemiphlebiidae Tillyard, 1926

Parahemiphlebia Jarzembowski *et al.,* 1998

Diagnosis: wings hardly petiolated; discoidal cell basally open in forewings; arculus somewhat distal of Ax2 in forewings; maximum of four to seven postnodal crossveins that are non-aligned; no intercalary veins (except IR_1 and IR_2) and no lestine oblique vein; RP_1 strongly kinked at stigmal brace; MP strongly bent at discoidal cell; anal area crossed by two transverse veinlets between AA and AP; head with distinct suture between vertex and occiput; metallic green body coloration (rarely preserved); males with long paraprocts (Bechly, 1998c, *contra* Jarzembowski *et al.*, 1998).

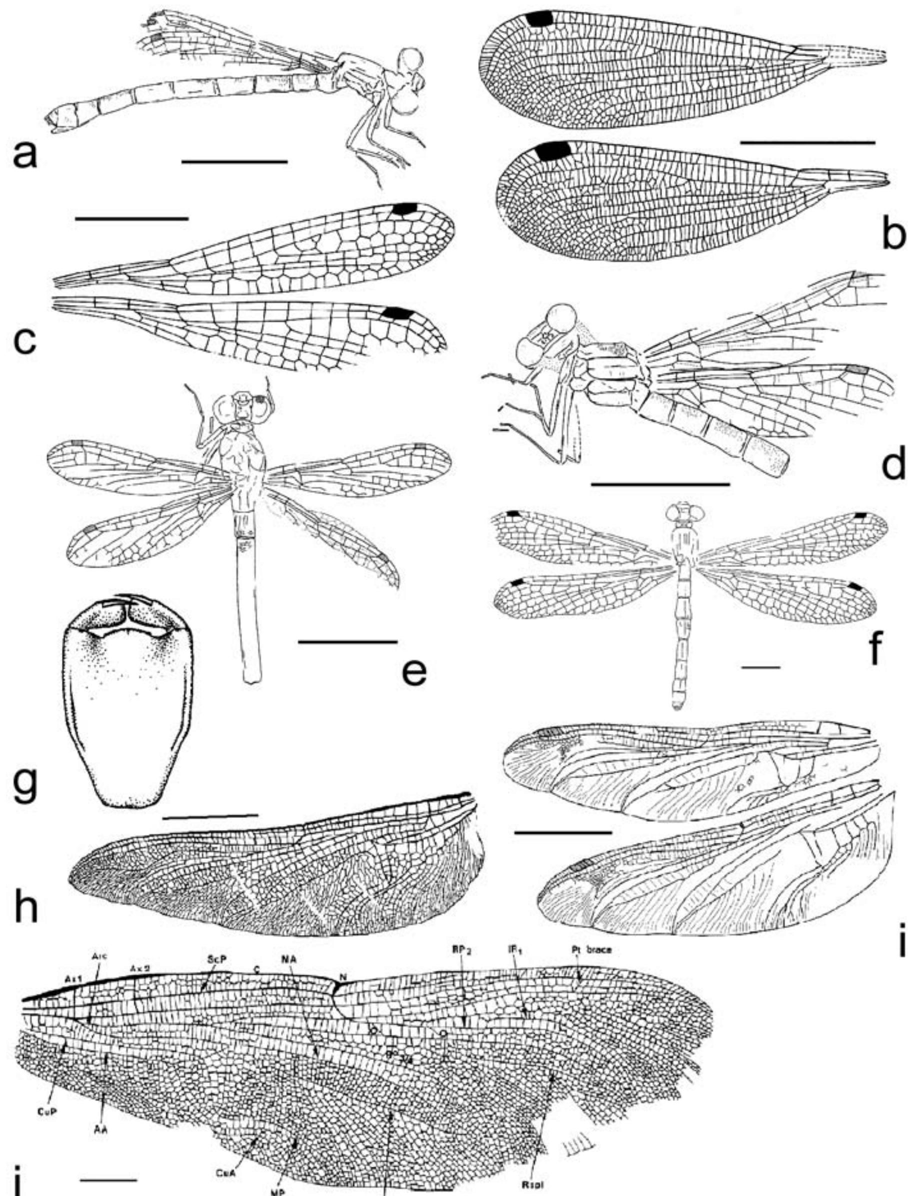

Fig. 11.10. Crato Formation Odonata: (a) Hemiphlebiidae?, *Cretarchistigma essweini*, female, holotype SMNS 63071; scale bar, 5 mm (after Bechly, 1998: figure 17): (b) Thaumatoneuridae, *Euarchistigma atrophium*, holotype AMNH 44204; scale bar, 3 mm (combined after Carle and Wighton, 1990: figures 2 and 3): (c) Protoneuridae, *Eoprotoneura hyperstigma*, male, holotype AMNH 44203; scale bar, 5 mm (after Carle and Wighton, 1990: figure 8); (d) Hemiphlebiidae, *Parahemiphlebia mickoleiti*, paratype SMNS 63072; scale bar, 5 mm (after Bechly, 1998: figure 16); (e) Hemiphlebiidae, *Parahemiphlebia mickoleiti*, holotype

Comment: about 11% of the Crato fossil odonates belong to the primitive damselfly family Hemiphlebiidae, which has only a single Recent relict species, *Hemiphlebia mirabilis*, in Australia.

Parahemiphlebia cretacica Jarzembowski *et al.*, 1998

Material: male holotype MNHN-LP-R.10451 (Figure 11.10f); female allotype MNHN-LP-R.10452; and male paratype MNHN-LP-R.10453 (Figure 11.10f); many specimens on other collections (Plate 9c).

Diagnosis: wing length 12.5–15.5 mm; five to seven postnodal crossveins; pterostigmal brace extremely oblique; IR_1 originates basal of pterostigma.

Parahemiphlebia mickoleiti Bechly, 1998c

Material: holotype without number (also figured in Grimaldi and Engel, 2005: figure 6.44) at AMNH, New York (Figure 11.10e); paratype SMNS 63072 (Figure 11.10d). Additional specimen SMNS 66385.

Diagnosis: wing length 8.9–9.9 mm; only four postnodal crossveins; pterostigmal brace highly oblique, but not as extreme as in *P. cretacica*; IR_1 originates beneath the distal side of pterostigma.

Parahemiphlebia spec. nov. (?) Bechly, 1998c

Material: specimen no. NSMT 563, and a further specimen mentioned by Bechly (1998c: 62).

Diagnosis: habitus, venation, and size similar to *P. cretacica* (wing length 13–14 mm), but pterostigmal brace not very oblique.

Comment: it is not yet possible to decide whether these two specimens really represent a new species or just slightly aberrant specimens of *P. cretacica*.

AMNH without number; scale bar, 5 mm (after Bechly, 1998: figure 14); (f) Hemiphlebiidae, *Parahemiphlebia cretacica*, reconstruction from holotype wings and paratype body (combined after Jarzembowski *et al.*, 1998: figures 3A–D, figure 4A); (g) Nothomacromiidae, *Nothomacromia sensibilis*, mask (after Carle and Wighton, 1990: figure 22); (h) Aeschnidiidae, *Wightonia araripina*, holotype AMNH 43268; scale bar, 10 mm (redrawn after Carle and Wighton, 1990: figure 21); (i) Aeschnidiidae, *Wightonia araripina*, B10 coll. MSF; scale bar, 10 mm (after Bechly, 1998: figure 24); (j) Aeschnidiidae, *Santanoptera gabbotti*, holotype LEIUG 115858; scale bar, 10 mm (after Martill and Nel, 1996: figure 2).

Protoneuridae Jacobson and Bianchi, 1905

Isostictinae Fraser, 1955

†Eoprotoneurini Carle and Wighton, 1990

Eoprotoneura Carle and Wighton, 1990

Eoprotoneura hyperstigma Carle and Wighton, 1990

Material: male holotype AMNH 44203 (also figured in Grimaldi and Engel, 2005: figure 6.39) (Figure 11.10c); female paratypes AMNH 44201 and AMNH 44202. A very nice female specimen with ovipositor is SMNS 66386; numerous specimens in other collections (Plate 9d).

Diagnosis: wing length 16.0–18.5 mm; only two antenodal crossveins and arculus somewhat distal of Ax2; discoidal cell rectangular, undivided, and closed in both pairs of wings; postnodal crossveins aligned; pterostigma braced; veins AA and CuA totally fused with hind margin; vein MP strongly shortened, ending at the level of the nodus.

Comment: about 6–7% of the fossil odonates belong to this taxon.

Thaumatoneuridae Tillyard and Fraser, 1938

Thaumatoneurinae Tillyard and Fraser, 1938

†Euarchistigmatini Carle and Wighton, 1990

Euarchistigma Carle and Wighton, 1990

Diagnosis: wings petiolated and apically broadened with a very dense venation; discoidal cell rectangular and undivided; subdiscoidal cell undivided; only two antenodal crossveins and Ax2 aligned with arculus; postnodal crossveins not well-aligned; nodus in very basal position at 25% of wing length; subnodus slightly distal of origin of IR_2, but far basal of origin of RP_2; pterostigma very broad and unbraced; all longitudinal veins strongly bent towards hind margin, especially at apex; RA, RP_1 and IR_1 apically converging; only a single row of cells between CuA and hind margin. The original diagnosis by Carle and Wighton (1990) was revised by Bechly (1998c).

Comment: approximately 1.5% of the Crato odonates belong to this taxon.

Euarchistigma atrophium Carle and Wighton, 1990

Material: holotype AMNH 44204 (Figure 11.10b); four further specimens were described by Bechly (1998c: 41–43) from SMNK, NSMT (no. 46), and MSF; specimen no. SMF Q55. SMNS 66387 (old no. H6) is a particularly nice example (wing length 32 mm) with anal appendages preserved.

Diagnosis: forewing length 30–35 mm; discoidal cell similar in both pairs of wings.

Comment: a new specimen no. SMF Q55 (Plate 9e) shows for the first time the original colour pattern of this calopterygoid-like damselfly, which has the basal two-thirds of all wings tinted in dark colour, while the apical thirds are hyaline.

Euarchistigma marialuiseae sp. nov.

Material: holotype with preliminary number Q56 (Plate 9f) and paratype no. Q87, deposited at SMF; paratype no. MB.1999.3 MB.I.2050 (old no. D29) (figured by Bechly, 1998c: figure 19) deposited at MNB (ex MSF); a further specimen with a wing length of only 26.5 mm is no. MSF O35.

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after my dear wife Maria Luise.

Diagnosis and description (Plate 9f): distinctly smaller than type species; forewing length only 26.5–28.5 mm; discoidal cell longer and narrower in hind wings. Otherwise, very similar to the *E. atrophium*, but potential colour pattern not preserved as in most specimens of *E. atrophium*.

‘Anisozygoptera’: ancient dragonflies

†Stenophlebioptera Bechly, 1996

†Stenophlebiidae Needham, 1903

Diagnosis: large dragonflies with a very dense wing venation with numerous small cells and many intercalary veins; both pairs of wings of similar shape and venation, long and slender, and more or less petiolated (at least in hind wings); both pairs of wings with hypertriangle and triangle; distinct subdiscoidal cell instead of a subtriangle; nodal and subnodal veinlets very oblique and elongated; IR_2 close to $RP_3{+}_4$, but far basal of RP_2; pterostigmata very long and shifted in a more basal position; hind wings of males often with an anal angle; larvae still unknown, but certainly of anisopterid type with anal pyramid instead of caudal gills (as in Epiophlebiidae).

Comment: new diagnoses and phylogenetic analyses of all Stenophlebiidae, as well as several descriptions of new species, are provided by Nel *et al.* (1993) and Fleck *et al.* (2003). A further new species *S. nusplingensis* was described by Bechly *et al.* (2003), while *S. casta* was re-described by Bechly (2005) and transferred from Stenophlebiidae to a new isophlebioid family Parastenophlebiidae.

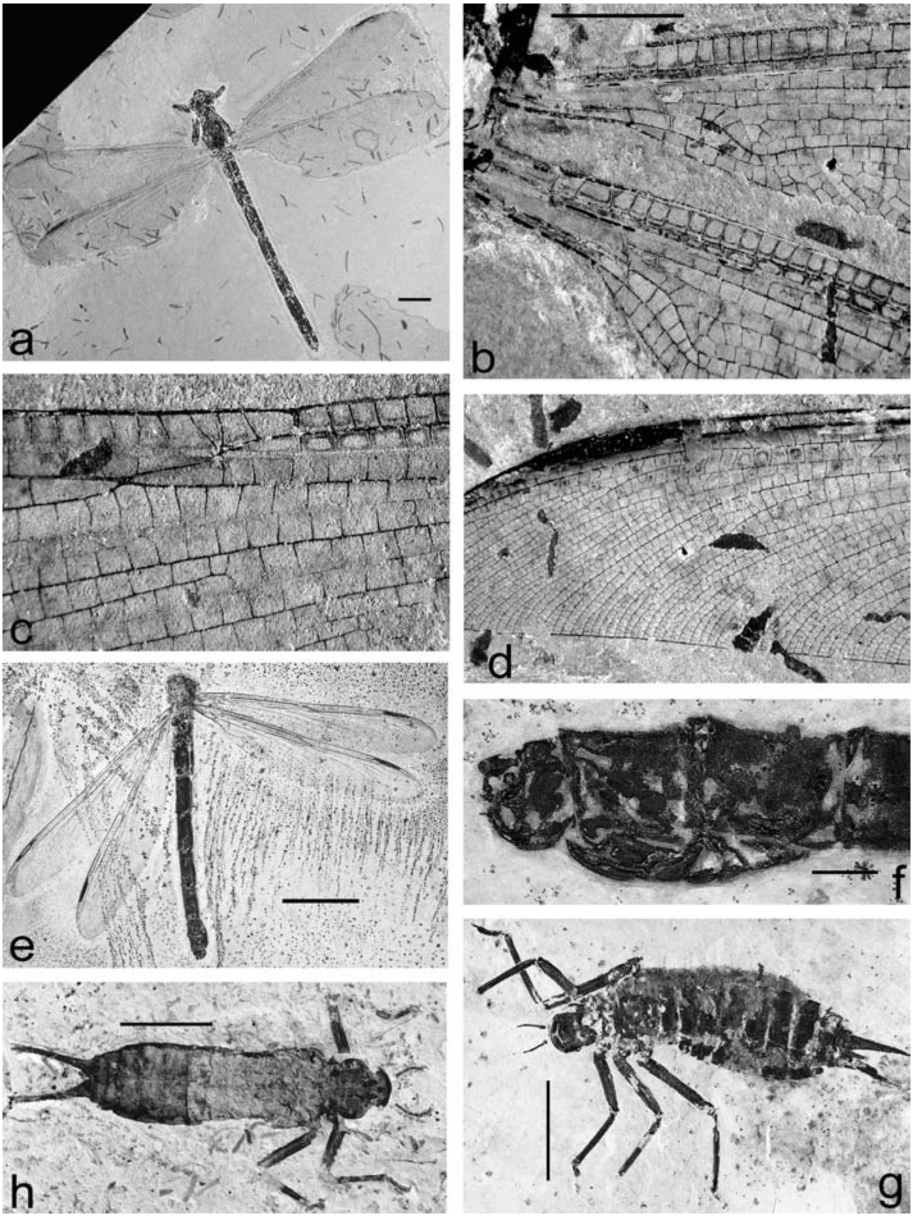

Fig. 11.11. Crato Formation Odonata: (a) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, holotype SMNS Z109; scale bar, 10 mm; (b) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, right wing bases, holotype SMNS Z109; scale bar, 5 mm; (c) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, left hind wing nodus, holotype SMNS Z109; (d) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., male, left hind wing pterostigma, holotype SMNS Z109; (e) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., female, paratype and allotype

Cratostenophlebia gen. nov.

Type species: *C. schwickerti* sp. nov., by present designation.

Derivation of name: named after the type locality and the fossil genus *Stenophlebia*.

Diagnosis: as for type species.

Cratostenophlebia schwickerti sp. nov.

Material: male holotype SMNS no. Z109 (Figures 11.11a–d; Plates 9g and h) and female paratype and allotype SMNS no. Z110 (Figures 11.11e and f; Plate 9i), both donated as permanent loans with later inheritance to SMNS by coll. MSF.

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: in honour of the collector Mr Michael Schwickert (Sulzbachtal, Germany).

Diagnosis and description (Figures 11.11a–f; Plates 9g–i): very large dragonfly with more than 140 mm wing span and a total body length of 94 mm; Anisoptera-like robust body and globular head with very large compound eyes that are only separated by a single-millimetre distance (Plate 9g); cerci short and stout (about 2.3 mm long and 1.0 mm broad) (Plate 9h); wings elongate and falcate, and both pairs of wings of very similar size, shape and venation (Figures 11.11a and e); discoidal cell indistinctly divided into hypertriangle and triangle by a crossvein that is not ending at the distal angle of triangle (Figure 11.11b); hypertriangle and triangle each divided by a crossvein (autapomorphy, unlike other Stenophlebiidae); triangles and subdiscoidal cells not transverse, because veins MP+Cu and AA are nearly straight (symplesiomorphy with *Prostenophlebia* and *Hispanostenophlebia*); nodal vein as in *Stenophlebia latreillei* with one or two postnodal crossveins above it, but none below it (Fig. 11.11c); subnodus elongate (about as long as nodal veinlet) but with only one crossvein above it and none below it (Figure 11.11c); in the putative male holotype RP_2 originates at subnodus in all four wings (symplesiomorphy with *Prostenophlebia* and *Cretastenophlebia*, unlike *Hispanostenophlebia* and *Stenophlebia*, which possess the characteristic stenophlebiid oblique veinlet beneath the subnodus between RP_1 and RP_2), while in the female paratype the 'stenophlebiid oblique veinlet' is completely absent only

←

SMNS Z110; scale bar, 20 mm; (f) Stenophlebidae, *Cratostenophlebia schwickerti* gen. et sp. nov., female, ovipositor,, paratype and allotype SMNS Z110; scale bar, 2 mm; (g) Nothomacromiidae, *Nothomacromia sensibilis*, SMNS 66399; scale bar, 10 mm; (h) Nothomacromiidae, *Nothomacromia sensibilis*, SMF no. 1002; scale bar, 15 mm.

in the right forewing, very tiny and indistinct in the right hind wing, but very distinct with two 'origins' of RP_2 in the left fore- and hind wing (consequently this feature seems to be much more variable than previously believed); origins of RP and MA widely separated in arculus; three rows of cells in basal area of postdiscoidal space in both pairs of wings (autapomorphy, unlike other Stenophlebiidae); Mspl well-defined; primary antenodals Ax1 and Ax2 as in *Cretastenophlebia*, with Ax0 in relatively distal position; no accessory antenodal crossveins between Ax0 and Ax1 and Ax2 (symplesiomorphy with *Cretastenophlebia*); pterostigmata very elongate and unbraced (Figure 11.11d); no distinct lestine oblique vein 'O'; both wings are strongly petiolated with a very long petiole and thus much reduced submedian area even in the forewing (autapomorphic difference to *Stenophlebia*, maybe similar to *Hispanostenophlebia* of which the forewing is unknown); the female has a normally developed endophytic ovipositor as in Aeshnidae (Figure 11.11f).

Anisoptera: dragonflies

Diagnosis: medium-sized to very large dragonflies (wing span at least 3–4 cm), with robust bodies and a globular head with very large compound eyes; hind wings distinctly broader than forewings; wing venation of both pairs of wings with discoidal triangles, hypertriangles and subtriangles (instead of a subdiscoidal cell), and often with an anal loop; sexual dimorphism of hind wings, with rounded anal margin in females, but with angulated anal margin (anal angle and anal triangle) in males of most taxa. About 356 Recent genera with more than 2,872 species.

†Nothomacromiidae Carle, 1995 (stat. rest.)

(subst. name for Pseudomacromiidae Carle and Wighton, 1990)

Nothomacromia Carle, 1995

(subst. name for *Pseudomacromia* Carle and Wighton, 1990)

(= genus *Conan* Martins-Neto, 1998c, new synonymy)

Nothomacromia sensibilis (Carle and Wighton, 1990)

(*Conan barbarica* Martins-Neto, 1998c, new synonymy)

Material: holotype AMNH 44205 (also figured in Grimaldi and Engel, 2005: figure 6.45) (Figure 11.10g); four specimens with nos SMNS 66397 (Figure 11.12a), SMNS 66398, SMNS 66399 (Figure 11.11g) and SMNS 66404; five specimens with no. MB.1999.3 MB.I.2036, no. MB.1999.3 MB.I.2037 (old no. B47), no. MB.1999.3 MB.I.2038 (old no. C47), no. MB.1999.3 MB.I.2039 (old no. C48a) and no. MB.1999.3 MB.I.2040 (old no. 1005) deposited at MNB; specimen no. SMF 1002 (Figure 11.11h); and specimens nos B42 (Plate 13c) and B53 in coll. MSF (figured by Bechly, 1998c: figures 28 and 29).

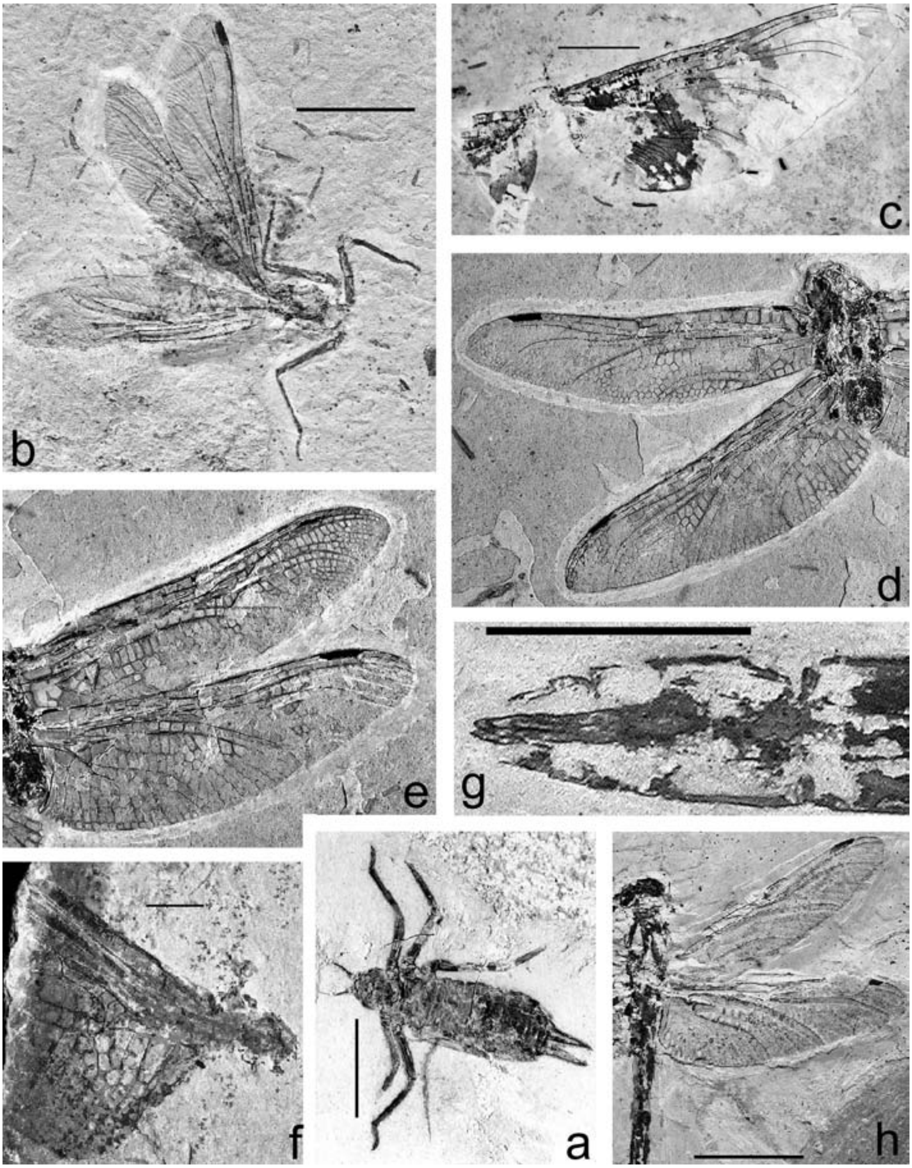

Fig. 11.12. Crato Formation Odonata: (a) Nothomacromiidae, *Nothomacromia sensibilis*, SMNS 66397; scale bar, 10 mm; (b) Aeschnidiidae, *Wightonia* cf. *araripina*, SMNS 66611; scale bar, 15 mm; (c) Aeschnidiidae, *Santanoptera gabbotti*, R4 coll. MSF; (d) Cretapetaluridae, *Eotanypteryx paradoxa* gen. et sp. nov., male, left wings, holotype SMF Q90; (e) Cretapetaluridae, *Eotanypteryx paradoxa* gen. et sp. nov., male, right wings, holotype SMF Q90; (f) Liupanshaniidae, *Paramesuropetala gigantea*, female, left hind wing base, SMNS 66613; (g) Araripegomphidae, *Araripegomphus andreneli*, female, ovipositor, SMNS 66392; (h) Anisoptera, gen. et sp. nov., male, SMNS 66592. Scale bars: f,g, 5 mm; a, 10 mm; b,c,h, 15 mm.

Diagnosis (Figures 11.10g, 11.12a and 11.11g and h; Plate 13c): body length 14.3–63.5 mm without antennae and anal appendages; antennae lyra-shaped; paraprocts hypertrophied and forcep-like (as in Aeschnidiidae); epiproct small and needle-like; mask of the flat gomphoid type with broad palps (Figure 11.10g); legs very long (as in Aeschnidiidae); the corresponding adults are still unknown.

Comment: about 7% of the Crato odonates belong to this family, and 22% of all the dragonfly larvae. Fleck *et al.* (2002: 178–179) demonstrated that the aeschnidiid affinities proposed by Bechly (1998c) cannot be upheld, and discussed possible affinities of the nothomacromiid larvae with anisozygopterous dragonflies, but dismissed this hypothesis (as did Bechly, 1998c) because of the complete lack of adult fossil anisozygopteres in the Crato Formation at the time of writing. However, the present discovery of two specimens of Stenophlebiidae from this locality, described above, suggests that the possibility of a correspondence with the *Nothomacromia*-type of larvae has to be reconsidered, also because the very large size of these adult Stenophlebiidae from Crato corresponds well with the giant size of the ultimate instar larvae.

Some apparent differences in the structure of the paraprocts (compare Figures 11.12a and 11.11g and h, and Plate 13c), for example the length and shape as well as the presence or absence of a serrated margin, previously seemed to suggest that there is more than one species of *Nothomacromia* larvae. However, specimen no. MB.1999.3 MB.I.2040 from MNB clearly shows that the apparent difference between broader forcep-like paraprocts (as in the holotype of *Nothomacromia sensibilis* and most other specimens) and very slim needle-like paraprocts (as in the holotype of *Conan barbarica*, or specimens no. SMF 1002 and no. B53) are an artefact of preservation, because the paraprocts are enforced by a tube-like structure, which sometimes is the only part preserved, while mostly the complete paraprocts are preserved. The absence or presence of a serrated margin is similarly due to differential preservation.

Conan barbarica was erroneously described as a larva of the beetle family Coptoclavidae by Martins-Neto (1998c), but was correctly recognized by Zamboni (2001) as a dragonfly nymph similar to *Nothomacromia*. There are no characters that justify generic separation of *C. barbarica* (*contra* Zamboni, 2001). Most differences (size, proportions and shape of body) are due to ontogeny, and the apparently different shape of the paraprocts is explained above. Furthermore, the different size is an insufficient criterion for generic distinction: for example specimen SMNS 66398 has all characters of *N. sensibilis* (including the shape of the paraprocts), but a larger size (body length about 4 cm) combined still with small wing sheaths (length only 6–7 mm), so that it would have even exceeded the size of *C. barbarica* in the final instar with fully developed wing sheaths. Finally, the different shape of the abdomen is a spurious character, as this is very flexible in Recent dragonfly larvae.

Consequently, *C. barbarica* is here regarded as a junior synonym of *Nothomacromia sensibilis*.

†Aeschnidiidae Needham, 1903

Diagnosis: large dragonflies; both pairs of wings of equal length, with a very dense venation, often partly or totally dark coloured; arculus close to Ax1; both pairs of wings with transverse and narrow triangles that are far removed from arculus, long and narrow hypertriangles, and hypertrophied subtriangles; a vein pseudo-ScP is developed in the postnodal area; two lestine oblique veins; Mspl and Rspl; anal area distinctly fan-like; hind wing strongly broadened, without anal angle and anal triangle in males; all wing spaces (e.g. median space, submedian space, triangle, and hypertriangle, etc.) traversed by numerous crossveins; compound eyes separated; abdomen thick and shorter than wings; females with very hypertrophied, long and thin ovipositor; larvae (still unknown from Crato) with concave spoon-shaped mask (unlike Nothomacromiidae), very long legs (like Nothomacromiidae), large forcep-like paraprocts (like Nothomacromiidae) and long ovipositor in female larvae (unlike Nothomacromiidae).

Wightonia Carle in Carle & Wighton, 1990

Wightonia araripina Carle in Carle & Wighton, 1990

Material: holotype AMNH 43268 (Figure 11.10h); female specimen no. KMNH; specimens SMNS 66610 and SMNS 66611 (Figure 11.12b); specimen MSF B10 (Figure 11.10i; also figured in Bechly, 1998c: figures 23–26); female specimen D28 at MNB (figured Bechly, 1998c: figure 22).

Diagnosis: forewing length 38–47.0 mm and hind wing length 38.0–46.0 mm; pterostigma well defined (Bechly, 1998c, *contra* Carle and Wighton, 1990), but traversed by about four crossveins and not always bulged, thus not visible in fossils without preserved colour of the stigma (e.g. in the holotype or in the isolated forewing SMNS 66610); stigmal brace present in some fossils, but very indistinct; triangle very narrow and divided into a single vertical row of about six cells; only one row of cells between ScP and C; one or two rows of cells between RA and RP_1; undulating complex intercalary vein (not IR_1) between RP_1 and RP_2.

Comment: the phylogenetic position was discussed by Nel and Martínez-Delclòs (1993: 64–65) and the original diagnosis was corrected and amended by Bechly (1998c: 43–47, figures 22–27), who described and figured additional specimens.

Some smaller specimens (e.g. SMNS 66610, SMNS 66611 = G28 and no. MSF B10 described by Bechly, 1998c) have a wing length of only about 38–40 mm. Specimen SMNS 66611 even has a preserved forewing length of only 35 mm, and an estimated total length of maximum 38 mm (Figure 11.12b). These fossils could belong to a new species, because a wing-length range of 38–47 mm seems to be too high to be attributed to infraspecific variability.

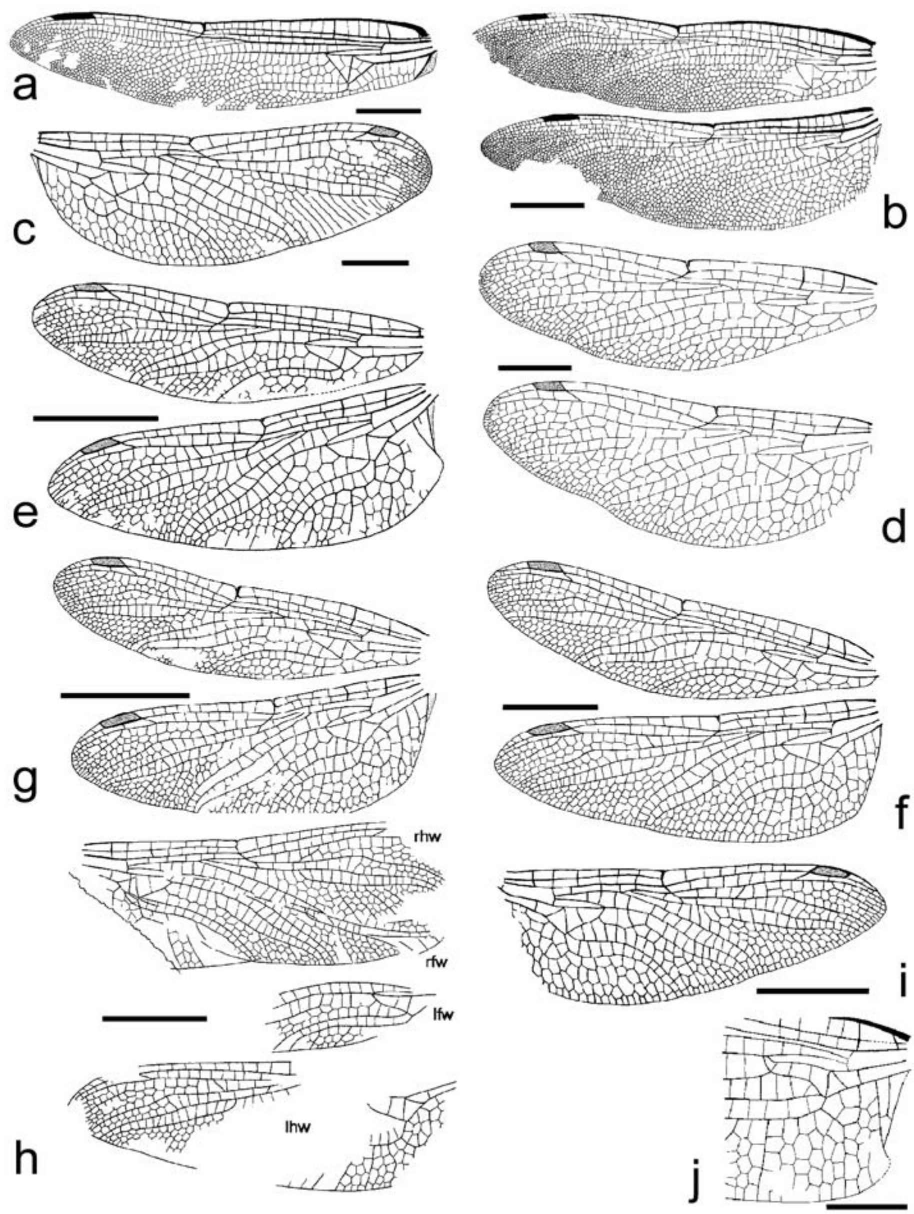

Fig. 11.13. Crato Formation Odonata: (a) Liupanshaniidae, *Paramesuropetala gigantea*, holotype MNHN-LP-R.55194; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 28); (b) Cretapetaluridae, *Cretapetalura brasiliensis*, female, holotype MCSNM I 9562; scale bar, 10 mm (redrawn after Nel *et al.*, 1998: figures 43 and 44); (c) Gomphaeschnidae, *Progomphaeschnaoides staniczeki*, female, holotype JME AP 1997–4a,b; scale bar, 5 mm (after Bechly *et al.*, 2001: figure 114); (d) Gomphaeschnidae, *Progomphaeschnaoides ursulae*, female, holotype SMNK 2357 PAL, scale bar, 5 mm (combined after Bechly *et al.*, 2001: figures 111 and

Santanoptera Martill & Nel, 1996

Santanoptera gabotti Martill & Nel, 1996

Material: holotype LEIUG 115858 (Figure 11.10j); SMNS 66609; nos R3 and R4 (Figure 11.12c) in coll. MSF.

Diagnosis: forewing length 62.3–64.1 mm; hind wing length 62–63 mm; arculus obliterated; pterostigma completely reduced, but a distinct stigmal brace is still present; triangle divided into two or three vertical rows of cells; two or three rows of cells between ScP and C; two or four rows of cells between RA and RP_1.

Comment: there is a fragmentary new specimen SMNS 66609 with two connected hind wings, which are 62 mm long and a maximum of 25 mm wide. Two further specimens, no. R3 (forewing length 64.1 mm) and R4 (hind wing length 63 mm), were in coll. MSF, and show more details of the hind wing venation (no pterostigma, narrow and oblique triangle with numerous cells, very broad and densely veined anal area; Figure 11.12c).

†Cretapetaluridae Nel *et al.*, 1998

Cretapetalura Nel *et al.,* 1998

Cretapetalura brasiliensis Nel *et al.,* 1998

Material: female holotype no. I 9562 at MCSNM (Figure 11.13b).

Diagnosis: length of fore- and hind wings 67.0 mm; two lestine oblique veins, the first one only one cell distal of subnodus; distal side of hind wing triangle strongly angulated, with a strong post-trigonal intercalary vein originating at the angle; triangle transverse and undivided in forewings, but elongate and two-celled in hind wings; forewing subtriangle large and three-celled, hind wing subtriangle widened and divided by a crossvein; very long and distinct vein IR_1 between RP_1 and RP_2; pterostigma very long and in basal position, with the stigmal brace displaced between stigma and nodus; hind wing anal loop longitudinally elongated.

112); (e) Gomphaeschnidae, *Gomphaeschnaoides obliquus*, male, SMNS 63069; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 118); (f) Gomphaeschnidae, *Gomphaeschnaoides magnus*, female, holotype JME AP 1997–2; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 120); (g) Gomphaeschnidae, *Gomphaeschnaoides betoreti*, female, holotype BSPGM no. 11; scale bar, 10 mm (after Bechly *et al.*, 2001: figure 123); (h) Gomphaeschnidae, *Gomphaeschnaoides petersi*, male, holotype JME AP 1997–3; scale bar, 10 mm (combined after Bechly *et al.*, 2001: figures 121 and 122); (i) Gomphaeschnidae, *Gomphaeschnaoides obliquus*, female holotype AMNH 43257; scale bar, 10 mm (redrawn after Wighton, 1987: figure 2); (j) Liupanshaniidae, *Araripeliupanshania annesusaea*, male, hind wing base, holotype MB.1999.3 MB.I.2047; scale bar, 5 mm (after Bechly *et al.*, 2001: figure 26).

Eotanypteryx gen. nov.

Type species: *E. paradoxa* sp. nov., by present designation.

Derivation of name: after the similarity to the Recent genus *Tanypteryx*.

Diagnosis: same as type species, since it is monotypic.

Eotanypteryx paradoxa sp. nov.

Material: male holotype (Figures 11.12d and e) no. SMF Q90.

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after the strange combination of plesiomorphic and apomorphic character states.

Diagnosis and description (Figures 11.12d and e): a thorax with all four wings; wing span 99 mm; forewing 45.1 mm long; hind wing 43.9 mm long and a maximum of 14.6 mm wide; stigmal brace shifted midway between nodus and pterostigma; only a single lestine oblique vein two cells distal of subnodus; hypertriangles free; forewing triangle free and very transverse and narrow; hind wing triangle free and acute; forewing subtriangle large and two-celled; hind wing subtriangle free and not enlarged; no Mspl or Rspl; IR_1 not hypertrophied; post-trigonal area with two rows of cells and a convex intercalary vein in both pairs of wings; anal loop posteriorly closed and two-celled; hind wing with anal angle and three-celled anal triangle (male).

Comment: this new genus and species is clearly a Petalurida and it looks quite similar to the Recent North American genus *Tanypteryx*, because it shares the autapomorphies of the subfamily Tachopteryginae (distal lestine oblique vein reduced) and the tribe Tanypterygini (wings shorter than 50 mm; IR_1 shorter and zigzagged; wing space between RP_1 and RP_2 not expanded, with less than eight to nine rows of cells; bridge-space less narrowed; hind wing triangle free; area between RP_3+_4 and MA not strongly widened near wing margin, and MA not undulate; distal side of hind wing triangle slightly angled, correlated with a convex intercalary vein in the post-trigonal area; basal part of post-trigonal area only with two rows of cells). However, the distal position of the forewing nodus at about 50% of the wing length, the long hind wing CuAa that nearly reaches the level of the nodus and the short pterostigmata (only two or three cells long) that do not reach the basally shifted stigmal brace are symplesiomorphies with Cretapetaluridae, that exclude a position within crown group Petaluridae.

†Liupanshaniidae Bechly *et al.*, 2001b

Diagnosis: hind wing triangle at least three-celled, longitudinally elongate, and narrow (anterior side distally curved and ending on the anterior side; distal side sigmoidally curved and with a strong angle); forewing triangle equilateral and three-celled; both pairs of wings with a strong intercalary vein in post-trigonal area; only a single lestine oblique vein; area between RP_1 and RP_2 very narrow; RP_2 and IR_2 distally undulate.

Comment: a phylogenetic analysis of this enigmatic fossil family was provided by Lin *et al.* (2002).

Paramesuropetala Bechly *et al.,* 2001b

Paramesuropetala gigantea Bechly *et al.,* 2001b

Material: holotype MNHN-LP.R.55194 (Figure 11.13a); specimen SMNS 66613 (Figure 11.12f).

Diagnosis: forewing length 67.0 mm; post-trigonal area with three rows of cells in forewing.

Comment: specimen SMNS 66613 is a basal fragment of a female hind wing (Figure 11.12f). The anal loop is indistinctly closed and the anal margin is rounded without anal angle and anal triangle (female), but otherwise the venation is identical to *Araripeliupanshania*, including the structure of the peculiar triangle. However, this fossil is much bigger than *Araripeliupanshania annesuseae*, with a maximum width of 19 mm (instead of only 12 mm in the holotype of *A. annesuseae*, which has a hind wing length of 38.5 mm) and a triangle that is about 7 mm long (instead of 4 mm in the holotype of *A. annesuseae*). Consequently, the estimated total hind wing length of this specimen is 61 mm, which corresponds quite well with the forewing length of the holotype of *Paramesurometala gigantea*. Therefore, this specimen strongly confirms the attribution of *Paramesurometala* to Liupanshaniidae.

Araripeliupanshania Bechly *et al.,* 2001b

Araripeliupanshania annesuseae Bechly *et al.,* 2001b

Material: male holotype MB.1999.3 MB.I.2047 (old no. D58) at the Museum für Naturkunde in Berlin (Figure 11.13j; Plate 10a); paratype and female allotype SMNS 64345 (old no. 72); male paratype SMNS 64343; a very well-preserved isolated forewing SMNS 66616 (old no. R9); an isolated hind wing without number in coll. MURJ; and two beautiful specimens with nos M56 and L75 in coll. MSF.

Diagnosis: forewing length 35.3–40.2 mm and hind wing length 34.7–38.5 mm; post-trigonal area with two rows of cells in forewing.

Comment: this species was previously mentioned (as *nomen nudum*) and figured by Bechly (1998c: figure 30).

Gomphaeschnidae Tillyard and Fraser, 1940

†Gomphaeschnaoidinae Bechly *et al.*, 2001b

Diagnosis: triangles elongate and two-celled; hypertriangles usually free (except in *Gomphaeschnaoides betoreti*); subtriangles free; only one secondary antenodal between Ax1 and Ax2 in forewings (except in *Progomphaeschnaoides*); short 'cordulegastrid gap' of antesubnodal crossveins; no accessory cubito-anal crossveins in the submedian space; pterostigmal brace very oblique and sigmoidal; a single lestine oblique vein one cell distal of subnodus; RP_2 strongly undulating, but IR_2 more or less straight; Mspl and Rspl present; anal loop closed and at least four cells large.

Comment: about 10% of the Crato fossil odonate larvae and adults belong to this family.

Gomphaeschnaoides Carle and Wighton, 1990

Type species: *Gomphaeschnaoides obliquus* (Wighton, 1987).

Diagnosis: wings usually longer than 30 mm (except in *Gomphaeschnaoides betoreti*); pseudo-IR_1 originates beneath middle of pterostigma; oblique crossvein slanted towards stigma between RP_1 and RP_2 about three or four cells distal of subnodus; one or two rows of cells between RP_2 and IR_2; posterior branches of CuAa well-defined; anal loop about circular; distinct posterior branches of AA basal of anal loop in females.

Gomphaeschnaoides obliquus (Wighton, 1987)

Material: female holotype AMNH 43257 (Figure 11.13i); numerous further specimens have been described by Bechly *et al.* (2001c), for example male specimen SMNS 63069 (Figure 11.13e).

Diagnosis: forewing length 31.0–35.0 mm and hind wing length 32.0–37.0 mm; six postnodals in forewing and seven or eight in hind wing; anal loop with four or five cells.

Gomphaeschnaoides petersi Bechly *et al.*, 2001b

Material: male holotype JME AP 1997/3 (Figure 11.13h); possible further specimen no. MSF G9/G24.

Diagnosis: wing length about 37.5 mm; nine or ten postnodal crossveins; anal loop with eight cells.

Gomphaeschnaoides betoreti Bechly *et al.*, 2001b

Material: female holotype no. 11 (old no. D9) at BSPGM (Figure 11.13g).

Diagnosis: forewing length 29.1 mm and hind wing length 28.2 mm; hypertriangles divided by a crossvein; eight postnodals in forewing and nine in hind wing; anal loop with seven cells.

Gomphaeschnaoides magnus Bechly *et al.*, 2001b

Material: female holotype JME AP 1997/2 (Figure 11.13f); paratypes SMNS 64344 and no. MSF M62; further specimen LEIUG 113603, figured in Martill (1993: plate 8, figure 2).

Diagnosis: wing span about 85 mm; forewing length 42.1–45.0 mm and hind wing length 41.0–43.0 mm.

Progomphaeschnaoides Bechly *et al.*, 2001b

Type species: *Progomphaeschnaoides ursulae* Bechly *et al.*, 2001b.

Diagnosis: wing length less than 30 mm; pseudo-IR_1 does not originate beneath middle of pterostigma; two antenodals between Ax1 and Ax2; two or three rows of cells between RP_2 and IR_2; basal posterior branches of CuAa weakly defined; anal loop longer than wide; no posterior branch of AA basal of anal loop in females; no oblique crossvein slanted towards stigma between RP_1 and RP_2.

Progomphaeschnaoides ursulae Bechly *et al.*, 2001b

Material: female holotype SMNK 2357 PAL (Figure 11.13d).

Diagnosis: forewing length 27.5 mm and hind wing length 25.0–26.9 mm; pseudo-IR_1 originates beneath distal of pterostigma; five postnodals in forewing and seven in hind wing; Ax1 distinctly slanted towards wing base in hind wing; two rows of cells between RP_{3+4} and MA; one to three rows of cells between pseudo-IR_1 and RP_1 or RP_2 respectively.

Progomphaeschnaoides staniczeki Bechly *et al.,* 2001b

Material: female holotype JME AP 1197/4a,b an isolated hind wing (Figure 11.13c).

Diagnosis: hind wing length 29.3 mm; pseudo-IR_1 originates beneath basal side of pterostigma; 12 postnodals in hind wing; Ax1 not slanted towards wing base in hind wing; only a single row of cells between RP_{3+4} and MA; two to five rows of cells between pseudo-IR_1 and RP_1 or RP_2 respectively.

Paramorbaeschna Bechly *et al.,* 2001b

Paramorbaeschna araripensis Bechly *et al.,* 2001b

Material: female holotype SMNS 63068a,b (Figure 11.14e); paratypes MNHN-LP-R.55180, no. NSMT 29, SMNS 64218 and no. MURJ 518.

Diagnosis: forewing length 40.0–41.7 mm and hind wing length 37.7–40.6 mm; RP_2 distinctly undulate; three rows of cells between RP_2 and IR_2; two rows of

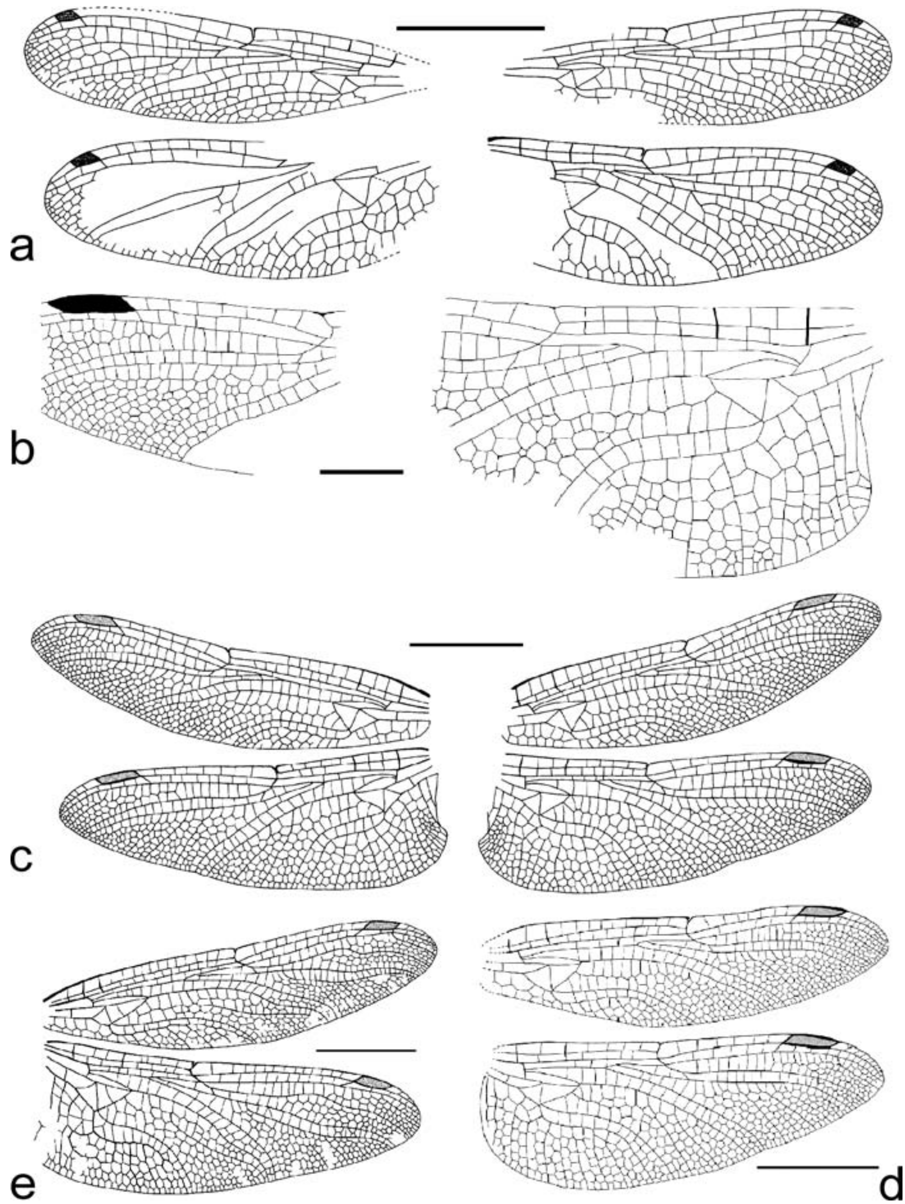

Fig. 11.14. Crato Formation Odonata: (a) Gomphaeschnidae, *Anomalaeschna berndschusteri*, female, holotype no. 515 MURJ (combined after Bechly *et al.*, 2001: figures 134–136); (b) Araripegomphidae, *Araripegomphus cretacicus*, female, holotype, forewing (left) and hind wing (right) (combined after Nel and Paichler, 1994: figures 5 and 6); (c) Araripegomphidae, *Araripegomphus andreneli*, male, holotype SMNS 63651 (after Bechly, 1998: figure 1); (d) Araripegomphidae, *Araripegomphus hanseggeri*, female, holotype SMNS 64415 (after Bechly, 2000: figure 1); (e) Gomphaeschnidae, *Paramorbaeschna araripensis*, female, holotype SMNS 53068 (after Bechly *et al.*, 2001: figure 109). Scale bars, 10 mm; except b, 4 mm.

cells between MA and Mspl; CuAa with five poorly defined posterior branches; accessory second anal loop (eight or nine cells) in hind wing.

Comment: a specimen that is nearly completely preserved in a large aggregation of insect remains and plant debris is featured in Figure 7.4e.

Anomalaeschna Bechly *et al.,* 2001b

Anomalaeschna berndschusteri Bechly *et al.,* 2001b

Material: female holotype no. 515 (old no. G22) at MURJ (Figure 11.14a).

Diagnosis: forewing length 28.4 mm and hind wing length 27.4 mm; triangles free (unique within subfamily); RP_2 originates distal of subnodus (unique autapomorphy within Anisoptera); RP_1 and RP_2 divergent; pterostigma only one cell long.

Araripegomphidae Bechly, 1996

Araripegomphus Nel and Paicheler, 1994d

Diagnosis: secondary antenodals between Ax1 and Ax2 more or less aligned (but not precisely so); arculus close to Ax1; hypertriangles, triangles and subtriangles free; anal loop reduced and posteriorly open; 'cordulegastrid gap'; bases of RP and MA approximated at arculus; three or four antefurcal crossveins (not oblique) in hind wings; no Mspl or Rspl; pterostigma three cells long and braced; compound eyes distinctly approximated but not connected (specimens with apparently widely separated eyes are preserved in ventral aspect).

Comment: about 5% of the adult fossil dragonflies from this locality belong to this taxon. The well-preserved female *Araripegomphus andreneli* specimen SMNS 66392 (old no. I38) shows a distinct ovipositor of about 3 mm length (Figure 11.12g; Plate 10b) with four valves, which strongly confirms the most basal position of Araripegomphidae within the gomphoid clade, as previously suggested by Bechly (2002), because all crown group gomphids have an obliterated ovipositor.

Araripegomphus cretacicus Nel and Paicheler, 1994d

Material: female holotype without number (Figure 11.14b) in coll. Baraffe in Paris, France.

Diagnosis: forewing length 38.5 mm and hind wing length 37.8 mm; post-trigonal area with three rows of cells in forewings.

Araripegomphus andreneli Bechly, 1998c

Material: male holotype SMNS 63651 (Figure 11.14c); paratypes no. 31, 47 (female allotype) and no. NSMT 1006; specimen MB.1999.3 MB.I.2057 (old no. D10) at MNB; male specimen SMNS 66394 and female specimen SMNS 66392, and numerous specimens in various collections.

Diagnosis: forewing length 32.0–36.7 mm (usually about 35 mm) and hind wing length 30.5–36.0 mm (usually about 34 mm); post-trigonal area with only two rows of cells in forewings.

Comment: the beautiful fossil dragonfly from the local museum in Santana do Cariri, figured by Martill (1993: front cover and text-figure 4.1), most probably belongs to this species. Specimen SMNS 66392 shows the female ovipositor (Figure 11.12g; Plate 10b), and a few male specimens (e.g. no. MSF G10) show extremely long cerci (4 mm) and an acute epiproct (Plate 10c). Specimen MSF G10 also shows the structure of the compound eyes in the same way as in the type species, *contra* Bechly (1998c), who was misled by ventrally preserved specimens.

Araripegomphus hanseggeri Bechly, 2000

Material: female holotype SMNS 64415 (Figure 11.14d); male paratype and allotype SMNS 64416a,b (Figure 11.15e).

Diagnosis: forewing length 32.9–33.6 mm and hind wing length 31.4–32.7 mm; only a single secondary antenodal between Ax1 and Ax2 in forewings; hind wing CuAa with five or six posterior branches; gap of crossveins distal of lestine oblique vein; area between RP_2 and IR_2 distally widened with two to four rows of cells in-between; hypertriangle quadrangular; anal loop posteriorly closed and divided into two or three cells; only two rows of cells in post-trigonal area in both pairs of wings.

Araripegomphus sp. nov. (?) Bechly, 1998c

Material: male specimen SMNS 63070.

Diagnosis: hind wing length only 30.5 mm; compound eyes apparently distinctly separated (distance 1.3 mm, head width 6.5 mm); otherwise very similar to *A. cretacicus* and *A. andreneli*.

Comment: a more detailed description, photograph and drawing, as well as phylogenetic discussion, was already provided by Bechly (1998c: 14–15, figures 4–5). It cannot be totally excluded that the apparently wide separation of the compound eyes is an artefact due to preservation of the head in ventral aspect. Therefore, this poorly preserved specimen could well represent a small male specimen of *A. andreneli*. The mention of the new species name '*A. imperfectus* n. sp.' in the acknowledgements section of Bechly (1998c: 64) was a *lapsus calami* and has to be considered as a *nomen nudum*.

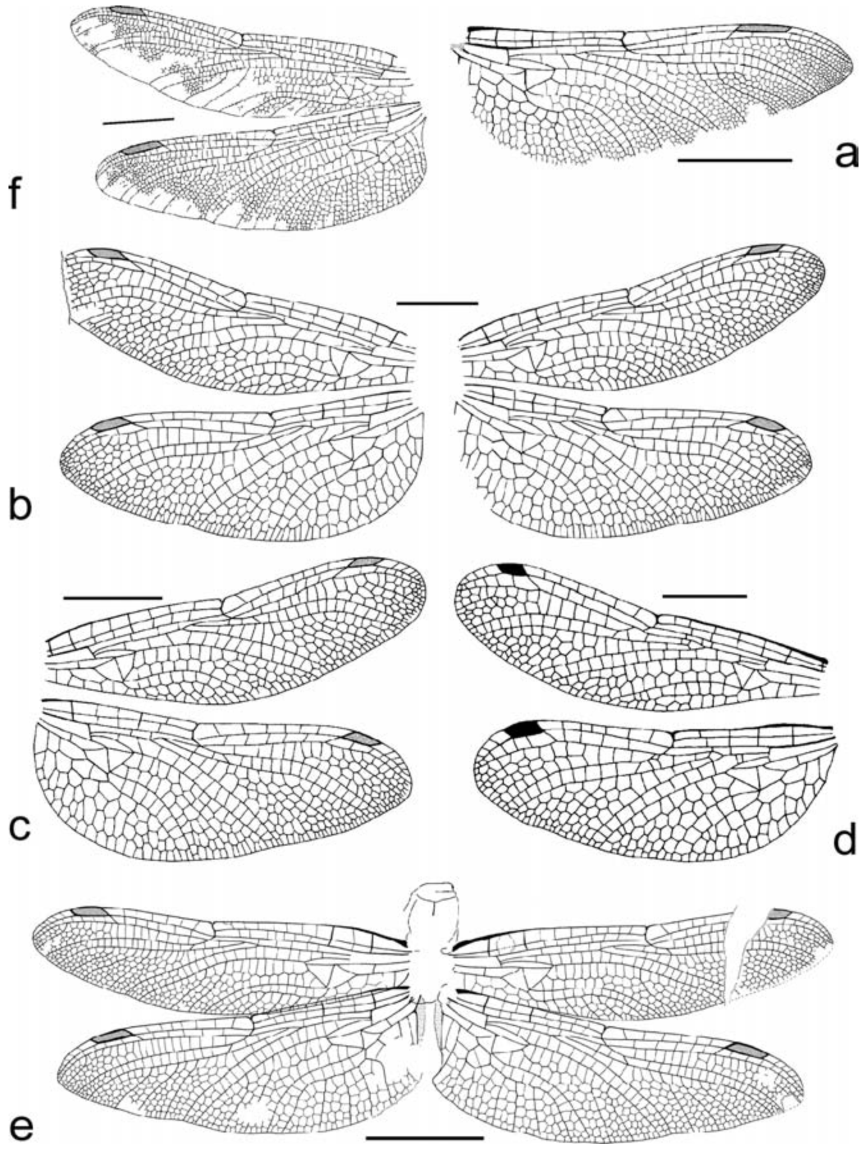

Fig. 11.15. Crato Formation Odonata: (a) Proterogomphidae, *Cordulagomphus winkelhoferi* sp. nov., female, paratype no. 513 MURJ (after Bechly, 1998: figure 31); (b) Proterogomphidae, *Cordulagomphus tuberculatus*, female, BSPGM C6 (after Bechly, 1998: figure 36); (c) Proterogomphidae, *Cordulagomphus fenestratus*, female, SMNS C13 (after Bechly, 1998: figure 35); (d) Proterogomphidae, *Procordulagomphus xavieri*, female, holotype MNHN-LP-R.10406 (redrawn after Nel and Escuillé, 1994: figure 2); (e) Araripegomphidae, *Araripegomphus hanseggeri*, male, allotype SMNS 64416a (after Bechly, 1998: figure 6); (f) Lindeniidae, *Cratolindenia knuepfae*, female, holotype SMNS 64414 (after Bechly, 2000: figure 9). Scale bars: d, 4 mm; b,c, 5 mm; a,e,f, 10 mm.

†Proterogomphidae Bechly *et al.*, 1998

†Cordulagomphinae Carle and Wighton, 1990

Diagnosis: 'cordulegastrid gap'; hypertriangles, triangles and subtriangles free; pterostigma two cells long and braced; pseudo-IR_1 originates beneath distal side of pterostigma; anal loop longer than wide and with only one or two cells; most basal postnodal crossveins very oblique; only two antefurcal crossveins in both pairs of wings; CuAa shortened and with reduced branching in hind wings (except in two new species).

Comment: about 44% of the fossil odonate larvae (41%) and adults (47%) belong to this taxon.

Cordulagomphus Carle and Wighton, 1990

Diagnosis: the second, distal antefurcal crossvein is very oblique in the hind wing (unique autapomorphy); anal loop usually divided in two cells; distal side of triangle angled; hind wing anal and cubito-anal area with at least three or four rows of cells and CuAa with visible posterior branches; hind wing with at least five antenodal crossveins.

Comment: Bechly (1998c) described new species and demonstrated great insufficiencies in the diagnoses of *Cordulagomphus tuberculatus* and *Cordulagomphus fenestratus*, based on a study of 98 specimens. Bechly (1998c: 57–58, figure 38) also identified the putative larvae of Cordulagomphinae and recognized that "*Cordulagomphus santanensis* Carle and Wighton, 1990' (specimen AMNH 43258) is not a dragonfly larva but a fossil earwig (see Section 11.6).

Cordulagomphus tuberculatus Carle and Wighton, 1990

Material: female holotype AMNH 43256; female specimen no. BSPGM C6 (described and figured by Bechly, 1998c: figures 36 and 37) (Figure 11.15b).

Diagnosis: forewing length 22.0–29.0 mm and hind wing length 21.0–28.0 mm; secondary antenodals usually non-aligned; distally two rows of cells between RP_3+_4 and MA; usually four or five postnodals in forewings and five or six in hind wings.

Comment: there could be a second, somewhat bigger, species 'hidden' among the very variable material (Plate 10d), because there are several specimens (e.g. SMNS 64362 = H10, SMNS 64361 = H11 and SMNS 66593 = M69) of very large size (forewing length 27–29 mm), but with more or less the same wing venation as the holotype. These specimens distinctly differ in size and venation from the two new large species of the same genus described below.

Cordulagomphus fenestratus Carle & Wighton, 1990

Material: male holotype AMNH 43262; female paratype and allotype AMNH 44200; female specimen SMNS C13 (described and figured by Bechly, 1998c: figure 35) (Figure 11.15c).

Diagnosis: forewing length 18.0–19.8 mm and hind wing length 17.5–19.6 mm; all antenodals aligned; distally only a single row of cells between RP_{3+4} and MA; usually five or six postnodals in forewings and six or seven in hind wings.

Cordulagomphus winkelhoferi sp. nov.

Material: male holotype SMNS 66607 (old no. M58; a very well-preserved hind wing; Plate 10e); female paratype and allotype no. 513 (old no. C20) at MURJ (Figure 11.15a).

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named in honour of my father-in-law, Mr Dipl.-Ing. Othmar Winkelhofer, Schwarzenau, Austria.

Diagnosis and description (Figure 11.15a; Plate 10e): hind wing length about 35 mm; CuAa with five or six well-defined posterior branches; six rows of cells in cubito-anal area; pterostigma and pseudo-IR_1 distinctly longer than in the other species of *Cordulagomphus*. Otherwise, the wing is very similar to *C. tuberculatus*, but with a more dense venation because of the much bigger size. A more detailed description, photo and drawing of this new species was already provided by Bechly (1998c: 51, figures 31 and 32), who also discussed the phylogenetic position as being most basal Cordulagomphinae. However, due to preservational circumstances Ax2 was incorrectly drawn by Bechly (1998c: figure 31); it is on the level of the distal angle of the triangle. In the hind wing there are two non-aligned secondary antenodals between Ax1 and Ax2 in the first row and three in the second row. Furthermore, there is a well-defined ‘cordulegastrid gap’ in the holotype.

Cordulagomphus hanneloreae sp. nov.

Material: female holotype SMNS 66591 (old no. O21; Plate 10f).

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after my dear aunt Hannelore Krause (née Schmidt; Kassel, Germany, 1943–2005).

Diagnosis and description (Plate 10f): the holotype is a nearly complete female dragonfly, of which only the abdomen is missing; the wing venation is very similar to *Cordulagomphus winkelhoferi* sp. nov., but pseudo-IR_1 is originating far distal of the pterostigma and the specimen is distinctly bigger (wing span 86 mm, hind wing 39 mm long and a maximum of 13.5 mm wide). This size difference to *C. winkelhoferi* (hind wing 35 mm long and a maximum of 11.5 mm wide) might appear minor at first sight, but is very obvious and striking in direct comparison. There is also a long 'cordulegastrid gap', and Ax2 is on the level of the distal angle of the triangle in both pairs of wings. In the forewing there is only one secondary antenodal between Ax1 and Ax2 in the first row but four antenodals in the second row, while in the hind wing there are two antenodals between Ax1 and Ax2 in the first row and five in the second row. Consequently, there is little doubt that this is a further new species of *Cordulagomphus*.

Cordulagomphus Carle and Wighton, 1990

Subgenus *Procordulagomphus* Nel and Escuillié, 1994

Diagnosis: anal loop unicellular; hind wing anal and cubito-anal area strongly reduced with only about three rows of cells and CuAa without distinct posterior branches; hind wing only with four antenodal crossveins (six in the new species).

C. (Procordulagomphus) xavieri Nel and Escuillié, 1994

Material: female holotype MNHN-LP-R.10406 (Figure 11.15d); male allotype MNHN-LP-R.10407; a further female specimen, with excellent three-dimensional preservation of the body, is SMNS 66391; specimens SMF Q79 and SMF Q82; MSF no. 37 and other specimens without numbers.

Diagnosis: forewing length 16.6–18.4 mm and hind wing length 15.6–17.5 mm; triangle slightly quadrangular; distal side of triangle MAb relatively straight, especially in hind wings; distal antefurcal crossvein usually not oblique or slanted but transverse; male anal triangle undivided; RP_1 bent posteriorly at stigmal brace; RP_3+_4 and MA closely parallel in forewings, with only a single row of cells in between (two rows at wing margin); anal area in forewings with only a single row of cells and without an enlarged elongate cell; anal loop usually unicellular, rarely two-celled in one wing. The secondary antenodal crossvein between Ax1 and Ax2 may be non-aligned in a few specimens.

Comment: the biggest specimen that otherwise completely agrees with all characters of the holotype, and strongly differs from *C. primaerensis*, is no. MSF 37, with a forewing length of 18.4 mm and a hind wing length of 17.5 mm.

C. (Procordulagomphus) senckenbergi Bechly, 1998

Material: male holotype SMF C7 (Figure 11.16c).

Diagnosis: forewing length 17.4 mm and hind wing length 16.8 mm; distal antefurcal antefurcal crossvein distinctly oblique; male anal triangle divided; forewings with only three postnodal crossveins; RP_3+_4 and MA closely parallel in forewings, with only a single row of cells in between (two rows at wing margin).

C. (Procordulagomphus) primaerensis Petrulevičius and Martins-Neto, 2007

Material: female holotype RGMN-T165 (Figure 11.16a).

Diagnosis: forewing length 20.6 mm and hind wing length 19.8 mm; distal antefurcal antefurcal crossvein distinctly oblique; forewings with five postnodal crossveins; RP_3+_4 and MA distally divergent in forewings, with two rows of cells in-between (three or four rows at wing margin); anal area of forewings with two rows of cells but without enlarged cell (or enlarged cell divided?).

Comment: the accessory cubito-anal crossvein in one forewing of the holotype is most probably not a diagnostic character, but an individual aberration.

C. (Procordulagomphus) michaeli sp. nov.

Material: male holotype no. 514 (old no. C14) at MURJ (Figure 11.16b; Plate 10g); further specimen nos E4 and E10 in coll. MSF.

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

Type horizon: Lower Cretaceous, Upper Aptian, Nova Olinda Member of the Crato Formation.

Derivation of name: named after Mr Michael Schwickert (Sulzbachtal, Germany).

Diagnosis and description (Figure 11.16b; Plate 10g): forewing length 17.0–21.5 mm and hind wing length 16.9–20.0 mm; forewings with seven and hind wings with six antenodal crossveins; forewings with four postnodal crossveins; distal antefurcal crossvein not very oblique; RP_3+_4 and MA distally divergent in forewings, with two rows of cells in between (four rows at wing margin); anal triangle very narrow and two-celled.

Comment: a more detailed description, photograph and drawing, as well as phylogenetic discussion, was provided by Bechly (1998c: 52–53, figures 33 and 34).

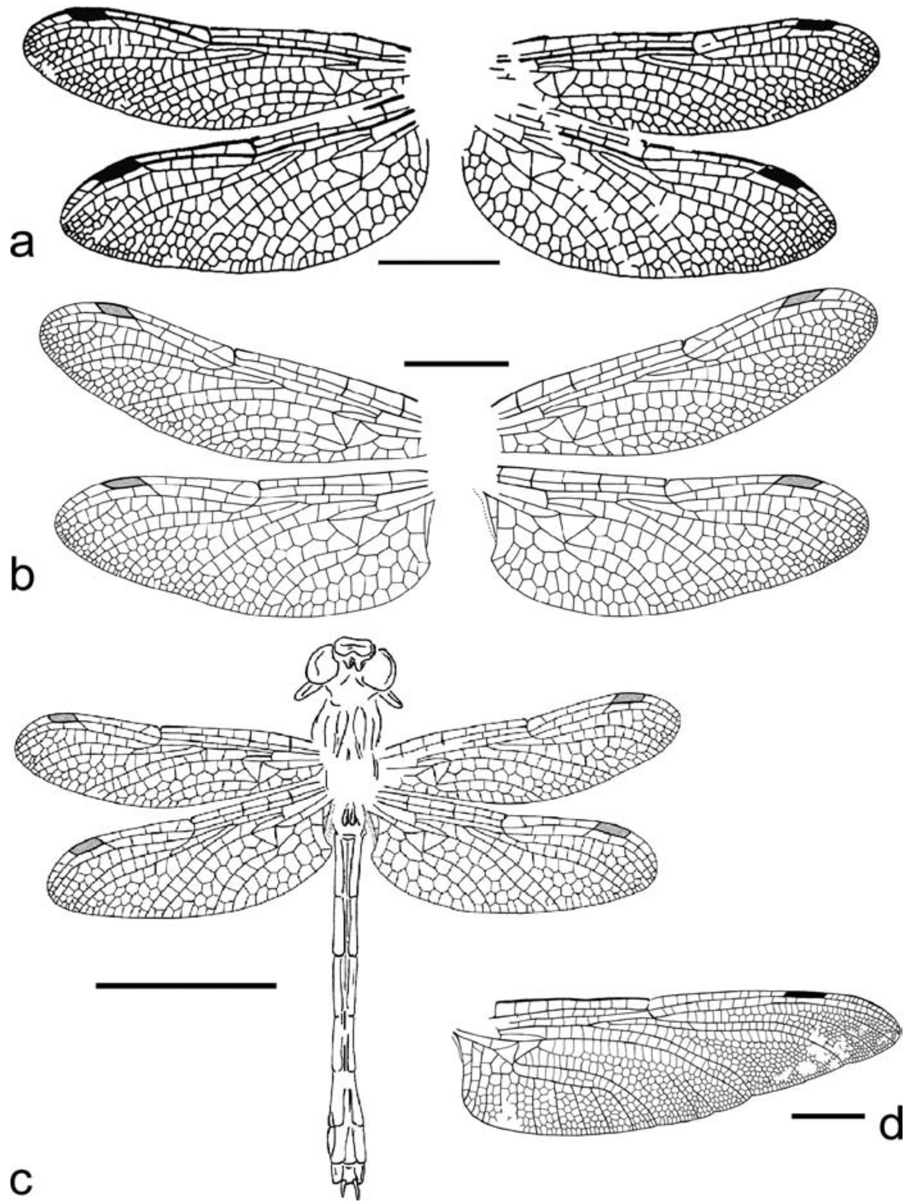

Fig. 11.16. Crato Formation Odonata: (a) Proterogomphidae, *Cordulagomphus (Procordulagomphus) primaerensis*, female, holotype RGMN-T165 (after Petrulevicius and Martins-Neto, 2007: figure 3); (b) Proterogomphidae *Cordulagomphus (Procordulagomphus) michaeli* sp. nov., male, holotype no. 514 MURJ (after Bechly, 1998: figure 33); (c) Proterogomphidae, *Cordulagomphus (Procordulagomphus) senckenbergi*, male, holotype SMF C7 (after Bechly, 1998: figure 6); (d) Petalurida? gen. et sp. nov., female, right hind wing, SMNS 66567. Scale bars: (a), 4 mm; b, 5 mm; c,d, 10 mm.

Lindeniidae Jacobson and Bianchi, 1905

Lindeniinae Jacobson and Bianchi, 1905

Cratolindenia Bechly, 2000

Cratolindenia knuepfae Bechly, 2000

Material: female holotype SMNS 64414 (Figure 11.15f).

Diagnosis: forewing length 49.6 mm and hind wing length 47.6 mm; short 'libelluloid gap' of postsubnodal crossveins and long 'cordulastrid gap' of antesubnodal crossveins; hypertriangle two-celled in forewing and undivided in hind wing; subtriangle large and three-celled in forewing and unicellular in hind wing; triangle transverse and three-celled in forewing and longitudinal elongate and two-celled in hind wing; costal side of triangle ends on its distal side below the distal angle in both wings (hypertriangle secondarily quadrangular); distal side of triangles strongly kinked in both wings with an post-trigonal intercalary vein originating at the kink; pterostigmata strongly braced and six cells long; IR_2 unforked; no Mspl or Rspl; only one lestine oblique vein three cells distal of subnodus; no accessory cubito-anal crossveins; anal loop elongate and two-celled; arculus close to Ax1 and about three secondary antenodals between Ax1 and Ax2.

†Araripephlebiidae Bechly, 1998c

Araripephlebia Bechly, 1998c

Araripephlebia mirabilis Bechly, 1998c

Material: female holotype no. 49 (Figure 11.17a) at NSMT; paratype no. 14 at KMNH; specimen MB.1999.3 MB.I.2058 (old no. D45) at MNB; SMNS 66618 (old no.K30), an isolated hind wing (Plate 10h); and complete specimen MSF G16 (Plate 10i).

Diagnosis: compound eyes approximated but not fused; forewing length 33.6–34.2 mm and hind wing length 32.5–36.0 mm; unique venation in the cubito-anal area with a very long anal loop with concave midrib (not homologous to libelluloid "italian loop"); a concave secondary vein beneath the anal loop, delimiting an elongate accessory anal loop with a single row of cells (Plates 10h and i); hind wing CuA short without CuAb and only a single dichotomic branching of CuAa (Plates 10h and i) or none at all (holotype); hypertriangles and subtriangles free; forewing triangle equilateral and free; hind wing triangle more transverse and divided by a horizontal crossvein; only a single antenodal between Ax1 and Ax2; 'cordulegastrid gap' of antesubnodal crossveins; a single lestine oblique vein two or three cells distal of subnodus; pterostigma two cells long and braced.

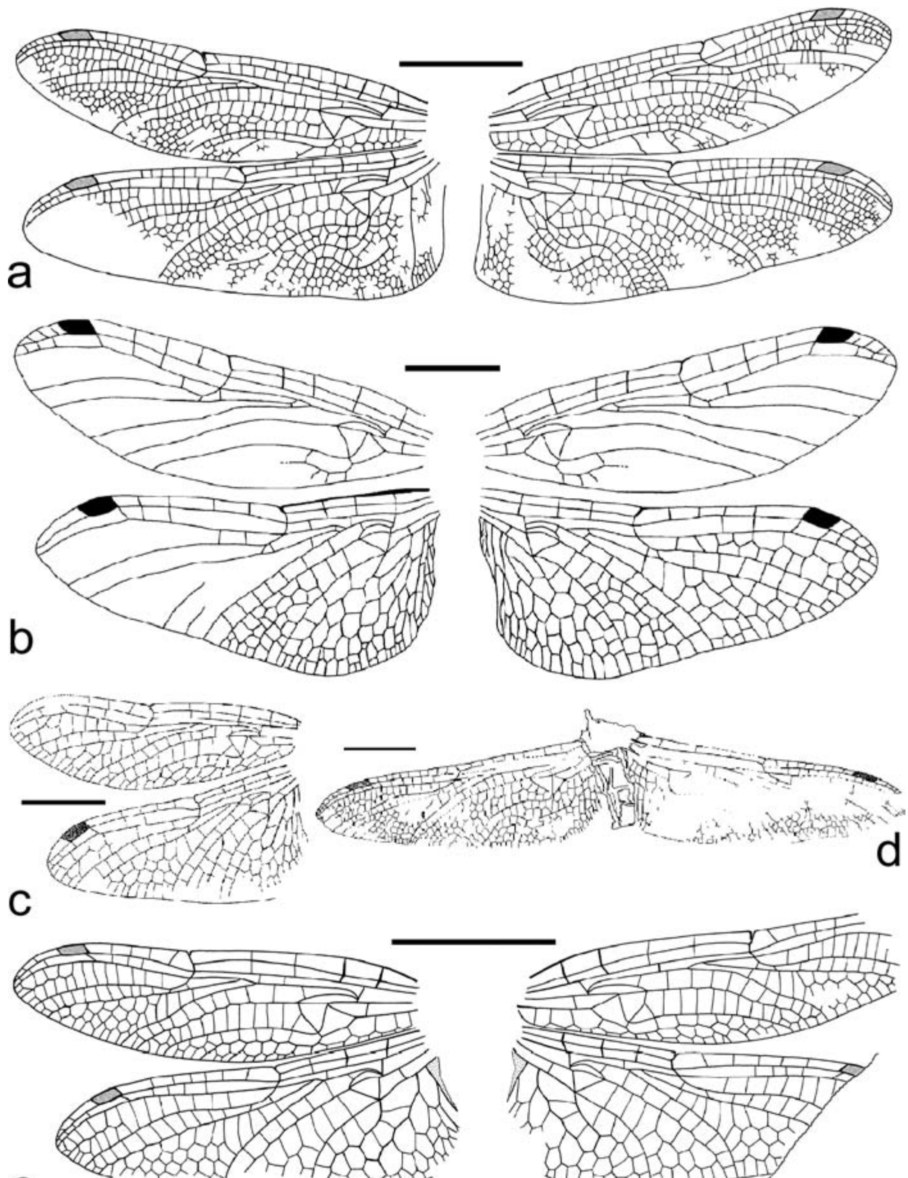

Fig. 11.17. Crato Formation Odonata: (a) Araripephlebiidae, *Araripephlebia mirabilis*, female, holotype NSM Tokyo 49 (after Bechly, 1998: figure 8); (b) Araripelibellulidae, *Araripelibellula martinsnetoi*, holotype MNHN-LP-R54376 (combined after Nel and Paichler, 1994: figures 1–3); (c) Araripelibellulidae, *Araripelibellula martinsnetoi*, female, B39 coll. MSF (after Bechly, 1998: figure 13); (d) Araripechlorogomphidae, *Araripechlorogomphus muratai*, female, holotype KMNH IP 000004 (after Bechly and Ueda, 2002: figure 1); (e) Araripelibellulidae, *Cratocordulia borschukewitzi*, female, holotype MNHN C5 (after Bechly, 1998: figure 11). Scale bars: b, 4 mm; c,d, 5 mm; a,e, 10 mm.

Comment: specimen no. G16 (complete dragonfly, forewing 33.6 mm long, hind wing 32.5 mm long) in coll. MSF, and specimen SMNS K30 (an isolated hind wing with 36 mm length) belong to the same species and show further details of the strange cubito-anal area (Plates 10h and i). All three known specimens with preserved hind wings lack an anal angle and anal triangle, thus they are either all females, or this taxon has reduced these structures in the male hind wing. Bechly (1998c) listed as a further diagnostic character the ‘distal half of MA distinctly zigzagged in hind wings’, but this is probably rather an individual aberration of the holotype, because this state is absent in the other specimens.

†Araripechlorogomphidae Bechly and Ueda, 2002

Araripechlorogomphus Bechly and Ueda, 2002

Araripechlorogomphus muratai Bechly and Ueda, 2002

Material: female holotype KMNH IP 000004 (Figure 11.17d), (ex coll. MURJ). This holotype was previously discussed and figured by Bechly (1998c: figure 39) and Bechly *et al.* (2001b: Abb. 40).

Diagnosis: hind wing length 39.4 mm; short ‘libelluloid gap’ of postsubnodal crossveins; triangle and subtriangle transverse and undivided; basal space free; CuAa with only two posterior branches; anal loop large, transverse, hexagonal, and seven-celled; very long ‘gaff’; only a single lestine oblique vein two or three cells distal of subnodus; no Mspl or Rspl; pterostigma unbraced and covering two or three cells.

†Araripelibellulidae Bechly, 1996

†Araripelibellulinae Bechly, 1996

Diagnosis: all antenodal crossveins aligned; no antenodals between Ax1 and Ax2 and only two or three antenodals distal of Ax2; ‘cordulegastrid gap’ (only one or two antesubnodal crossveins); forewing with only three or four postnodals; pterostigma braced and short (one cell long); hypertriangle strongly curved in hind wings; hypertriangles, triangles and subtriangles free; post-trigonal area very narrow in the forewings with only a single row of cells; anal loop transversely elongate, narrow, with a single row of two to four cells; area between RP_2 and IR_2 very narrow near the single lestine oblique vein; PsA and subtriangle suppressed in the hind wing.

Comment: only about 2% of the Crato odonates belong to this taxon.

Araripelibellula Nel and Paicheler, 1994

Araripelibellula martinsnetoi Nel and Paicheler, 1994

Material: holotype MNHN-LP-R.54376 (Figure 11.17b); specimen no. MSF B39 (discussed and figured by Bechly, 1998c: 31–32, figure 13) (Figure 11.17c); and several further specimens in other collections.

Diagnosis: forewing length 17.4–18.0 mm and hind wing length 16.5–17.1 mm; anal loop two-celled.

Cratocordulia Bechly, 1998c

Cratocordulia borschukewitzi Bechly, 1998c

Material: female holotype with preliminary no. C5 (Figure 11.17e) at the MNHN in Paris (coll. A. Nel, Laborat. Paleont.). A further putative specimen (two connected forewings) is SMF Q66.

Diagnosis: forewing length 23.5–25.1 mm and hind wing length 24.2 mm; anal loop with row of four cells.

Undescribed new taxa

Several further species of Anisoptera remain to be described, but due to time constraints it has not been possible to include all these new descriptions, which therefore will be published elsewhere. Among these new taxa are the following new genera and species.

Specimen SMNS 66567 (Figure 11.16d; Plate 10j): an isolated but complete and very well-preserved female hind wing (length 57.3 mm, maximum width 17 mm): pterostigma long, unbraced and in basal position and a well-defined and long vein IR_1 (all characters as in Petaluridae), but only a single lestine oblique vein (as in Recent Petaluridae-Tachopteryginae) 3.5 cells distal of subnodus; pseudo-IR_1 originating far distal of pterostigma; no Mspl or Rspl; RP and MA separated in arculus (unstalked); four antefurcal crossveins (none oblique); hypertriangle free; triangle transverse, free and with a strongly kinked distal side; distinct intercalary vein originating at this kink, dividing the post-trigonal area into two rows of cells; subtriangle free; CuAa with six posterior branches; anal loop round, posteriorly closed, and two-celled; anal margin rounded without anal angle or anal triangle (female); no accessory veins. This undescribed new genus and species most probably represents a further fossil petalurid that has some similarities to the Recent North American genera *Tachopteryx* and *Tanypteryx*, but differs from all crown group Petaluridae by its very long and multi-branched CuAa in the hind wing and the structure of the pterostigma.

Specimen SMNS 66608 (old no. H19) (Plate 10k): head, thorax, two forelegs and both forewings (complete but poorly preserved): compound eyes approximated but not fused; forelegs very short; wing length 38 mm; pterostigma elongate (4.5–5 cells long) and braced; pseudo-IR_1 originates distal of pterostigma; RP_2 closely parallel to RP_1 with only one row of cells in between them, even below basal part of pterostigma (strongly different from *Araripegomphus*, which otherwise looks quite similar); RP_2 and IR_2 as well as RP_3+_4 and MA slightly undulate; lestine oblique vein one cell distal of subnodus; triangle somewhat transverse, distal side straight; hypertriangles elongate, narrow and apparently undivided; subtriangle transverse, narrow and apparently undivided; no Mspl or Rspl, and no post-trigonal intercalary vein at triangle; only two rows of cells in post-trigonal area. Most probably it is a new species of †Mesuropetalidae or rather †Liupanshaniidae.

Specimen SMNS 66614 (old no. M67) (Plate 10.l): left pair of wings with thorax fragment (rather poorly preserved): forewing 30.4 mm long and 8 mm wide, hind wing 29 mm long and a maximum of 10.5 mm wide; pterostigma only two cells long and distinctly braced; anal loop closed and elongate; hind wing with anal angle and a very broad and three-celled anal triangle (male). Overall the visible venation is quite similar to *Cordulagomphus tuberculatus*, but the wings are of very different shape and there are three post-trigonal rows of cells in the hind wing (beginning two cells distal of triangle). Probably it is a new species of †Cordulagomphinae.

Specimen SMNS 66592 (old no. H29) (Figure 11.12h): a complete and well-preserved male dragonfly; body length about 5 cm; compound eyes separated; forewing length 34.0 mm, hind wing length 32.5 mm; pterostigma elongate and braced; space between RP_1 and RP_2 basally very narrow; no Mspl or Rspl; a single lestine oblique vein one cell distal of subnodus; apparently only two antefurcal crossveins in hind wing (none oblique); the anterior side of the triangles ends on the distal side MAb beneath the distal angle (hypertriangles quadrangular) in all four wings; forewing triangle transverse and two-celled (as in *Mesuropetala*); hind wing triangle elongated, two-celled, and with sigmoidal distal side; distinct posttrigonal intercalary vein originating at distal side of triangle in both pairs of wings; subtriangle large and three-celled in forewing, but smaller and unicellular in hind wing; CuAa with four posterior branches in hind wing; anal loop closed and three-celled; anal triangle three-celled but extremely narrow and anal angle much reduced (a unique feature). A second specimen (SMNS 66612, old no. R5, forewings 38 mm long, hind wings 37 mm long) is preserved in lateral aspect with superimposed wings (Figure 11.18a). A third specimen (SMNS 66615a, b, old no. M71a,b, plate and counterplate of a female dragonfly thorax with all four wings, forewings 38.3 mm long, hind wing 37.0 mm long) also agrees with the above description, but there are three or four antefurcals in the hind wings (none oblique), a short ‘libellulid gap’ and a long ‘cordulegastrid gap’ are visible, and vein

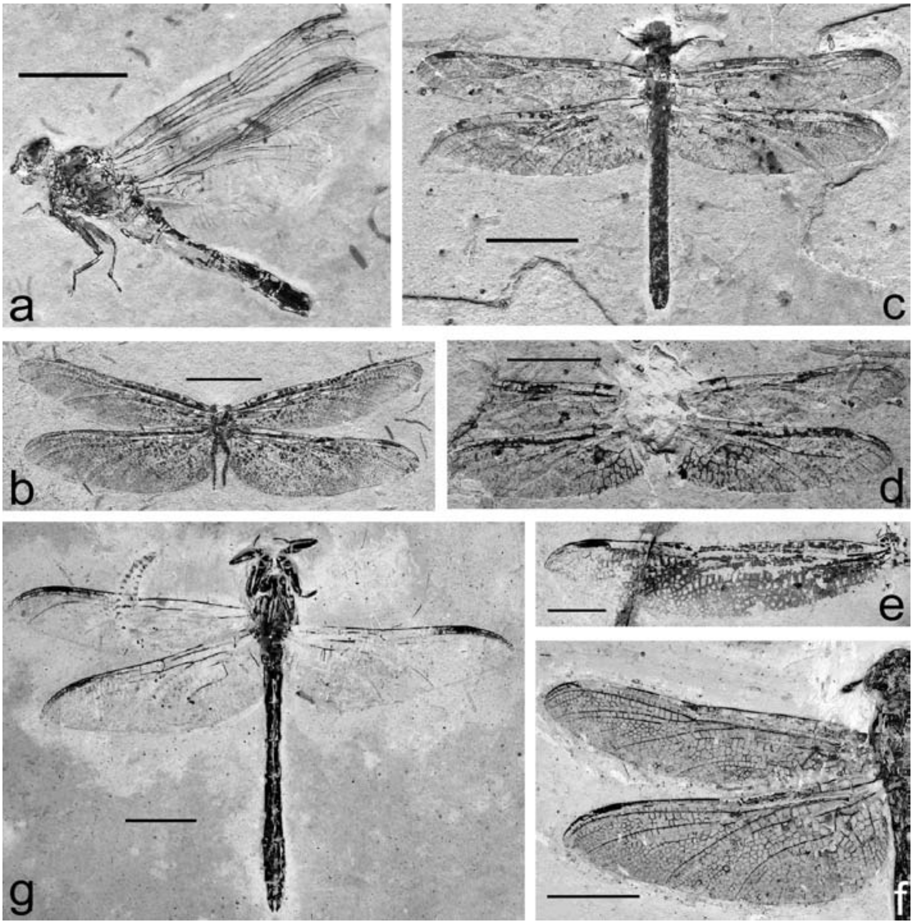

Fig. 11.18. Crato Formation Odonata: (a) Anisoptera, gen. et sp. nov., SMNS 66612; (b) Anisoptera, gen. et sp. nov., female, SMNS 66615b; (c) Anisoptera, gen. et sp. nov., male, SMNS 66606a; (d) Anisoptera, gen. et sp. nov., male, SMNS 66606b; (e) Anisoptera, gen. et sp. nov., SMNS 66617; (f) Anisoptera, gen. et sp. nov., female, Z43 coll. MSF; (g) Anisoptera, gen. et sp. nov., male, Z52 coll. MSF. Scale bars: a,b, 15 mm; c–g, 10 mm.

pseudo-IR_1 originates beneath distal side of stigma (Figure 11.18b). Most probably all these specimens belong to the same new genus and species of gomphid relationship, because they share the same combination of characters and show only a minor difference in size. The small numbers of antefurcals and the shape of the triangle in the hind wings suggests an attribution to the superfamily Hagenioidea.

Specimens SMNS 66606b (old no. L17) and SMNS 66606a (old no. L43) (Figures 11.18c–d): plate and counterplate of a complete male dragonfly; forewing length 24.0 mm, hind wing length 23.0 mm; pterostigma braced, relatively short

(2.5 cells long) and broad; pseudo-IR_1 originates beneath middle of pterostigma; only a single row of cells between pseudo-IR_1 and RP_1; only a single row of cells between RP_1 and RP_2 up to level of stigmal brace; Ax1 and Ax2 close together without secondary antenodals between them; the arculus is straight; very long 'libellulid gap' of antesubnodal crossveins and long 'cordulegastrid gap' of postsubnodal crossveins in both pairs of wings; three antefurcal crossveins in hind wing (not oblique); a single lestine oblique vein 1.5–2 cells distal of subnodus; no Mspl or Rspl; hypertriangles and subtriangles free; forewing triangle transverse, hind wing triangle elongate; triangles free and with slightly angled distal side in both pairs of wings; two rows of cells in posttrigonal area in both pairs of wings; CuAa long and with six posterior branches; cubito-anal area with three rows of cells, anal area with four rows; anal loop elongate and undivided (as in *Procordulagomphus*); hind wing with anal angle and three-celled anal triangle (male). Specimen MSF O40 is a very well-preserved isolated hind wing (length 28 mm) of the same taxon. The combination of characters is rather strange and very unusual. It is certainly a new gomphid genus and species, most probably closely related to †Araripegomphidae or †Cordulagomphinae.

Specimen SMNS 66617 (old no. R6) (Figure 11.18e): a well-preserved isolated forewing with the enormous length of 58.7 mm; a single secondary antenodal between Ax1 and Ax2; pterostigma about two cells long and braced; pseudo-IR_1 originates beneath distal end of stigma, with a very broad area between pseudo-IR_1 and RP_1; RP_2 and IR_2 distally divergent with two or three rows of cells in between; Rspl present and parallel to IR_2, with a single row of cells in between; a single lestine oblique vein 3.5 cells distal of subnodus; RP_3+_4 and MA strongly undulate, but closely parallel, with a single row of cells in between; post-trigonal area narrow, basally with only two rows of cells, and a convex intercalary vein; hypertriangle free; triangle elongate (aeshnoid-like) and free; subtriangle small and free; nodus in extremely distal position at about 56% of the forewing length (32.7 mm); no 'libellulid gap' of postsubnodal crossveins; no accessory veins. Again, no familial attribution of this new taxon is possible yet.

Specimen MSF Z43 (Figure 11.18f): a complete and very well-preserved female dragonfly; body length 56.1 mm; compound eyes widely separated; wing span 79.7 mm; forewings 37.5 mm long; hind wings 36.8 mm long and a maximum of 13.2 mm wide; pterostigma 4.5–5 cells long and braced; pseudo-IR_1 originates between distal part of pterostigma (two or three rows of cells between RP_1 and pseudo-IR_1); RP_1 and RP_2 strongly divergent with three or four rows of cells in between at stigmal brace; one lestine oblique vein one or two cells distal of subnodus; two rows of cells between RP_3+_4 and MA from the level of oblique vein up to hind margin; no Mspl or Rspl; triangles equilateral and two-celled in both pairs of wings; subtriangles elongate in forewings and two-celled in both pairs of wings;

anal loop absent (not posteriorly closed); three rows of cells in basal part of post-trigonal area in forewings, and four rows in hind wings; hind wing CuA with six distinct posterior branches (including CuAb); about two antenodals between Ax1 and Ax2; arculus close to Ax1 in hind wing (Ax2 aligned with distal angle of hind wing triangle), and apparently even basal of Ax1 in forewings (Ax2 aligned with basal angle of forewing triangle); a short but distinct 'libelluloid gap' of postsubnodal crossveins is visible. It is a new genus and species of uncertain familial affinity.

Specimen MSF Z52 (Figure 11.18g): a nearly complete male dragonfly, of which only the head and one forewing is missing; unfortunately the wing venation is poorly preserved; forewing 34.0 mm long; hind wing 32.5 mm long and a maximum of 11.0 mm wide; hind wing triangle and subtriangle transverse and free; RP_1 and RP_2 very close together up to level of the pterostigma; pterostigma long with a very acute basal edge and a very slightly basally displaced stigmal brace, which is very oblique as well; apparently no Mspl or Rspl, and no hypertrophied vein IR_1; two rows of cells in post-trigonal area of both wings; hind wing with anal triangle (male); cerci 1.9 mm long. Familial attribution of this new taxon is not possible.

11.6 Dermaptera: earwigs

Fabian Haas

Dermaptera constitute a uniform and highly derived monophyletic taxon among the insects, with a moderate diversity of about 2,200 species, including fossils. Almost all species belong to the Forficulina: the earwigs of common parlance. Earwigs are rather long and slender insects, often 10–20 mm in length, with a disc-like pronotum, short to moderately long walking legs, and have, without exception, forceps-like cerci. Earwigs are omnivorous. The common or European earwig (*Forficula auricularia* Linnaeus, 1758) provides a typical example for description. The extremes, however, are quite different: the smallest earwig is *Eugerax peocilium* Hebard, 1917, at 3 mm long, while the largest, now probably extinct, was *Labidura herculeana* (Fabricius, 1798), from St. Helena in the Atlantic Ocean, at 80 mm in length. *Titanolabis colossea* (Dohrn, 1864) from Australia is the largest Recent species at 55–60 mm long. The nutrition, as far is known at all, varies between carnivory (*Labidura riparia* (Pallas, 1773)), omnivory, herbivory and spongivory in many Spongiphoridae, although no species seems to be highly specialized on a food source (for an exception see below). Earwigs usually prefer narrow spaces and hide under stones, under bark, in decaying wood, in leaf axles, in leaf litter or in flowers, in a wide range of habitats.

One of their most interesting features is the complex folding mechanics of the hind wings. They are unfolded by the cerci and, due to intrinsic elasticity, folded

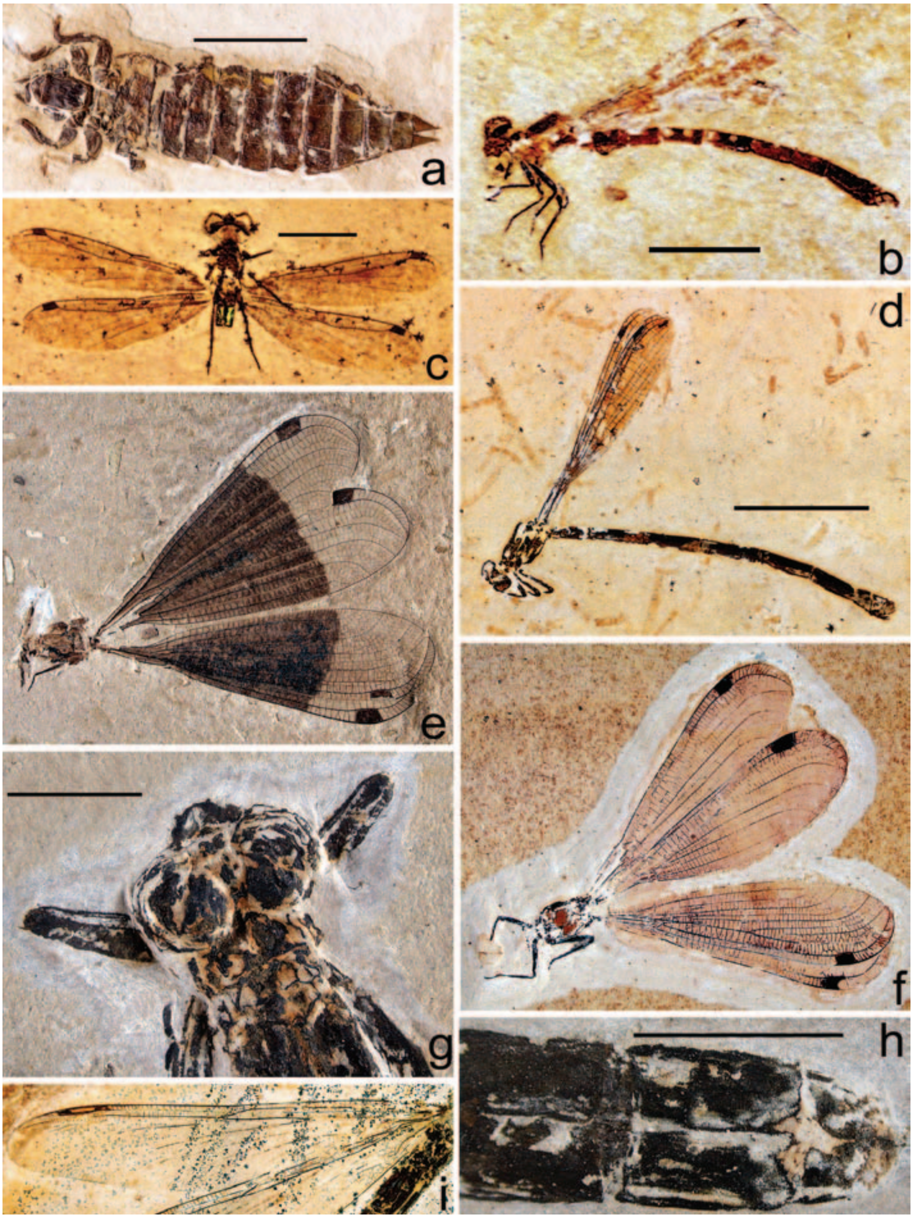

Plate 9. Crato Odonata: (a) gomphid larva with mask, SMNS 66402; (b) Hemiphlebidae?, *Cretarchistigma essweini*, male with anal appendages, MSF G3; (c) *Parahemiphlebia cretacica* with preserved green metallic colour on first abdominal segment, MSF 39; (d) *Eoprotoneura hyperstigma*, female with ovipositor, MSF O6; (e) *Euarchistigma atrophium* with colour pattern, SMF Q55; (f) *Euarchistigma marialuiseae* sp. nov., holotype SMF Q56; (g) *Cratostenophlebia schwickerti* gen. et sp. nov., male head, holotype SMNS Z109; (h) *Cratostenophlebia schwickerti* gen. et sp. nov., male anal appendages, holotype SMNS Z109; (i) *Cratostenophlebia schwickerti* gen. et sp. nov., female, left forewing, paratype and allotype SMNS Z110. Scale bars, 10 mm, except (a), 5 mm.

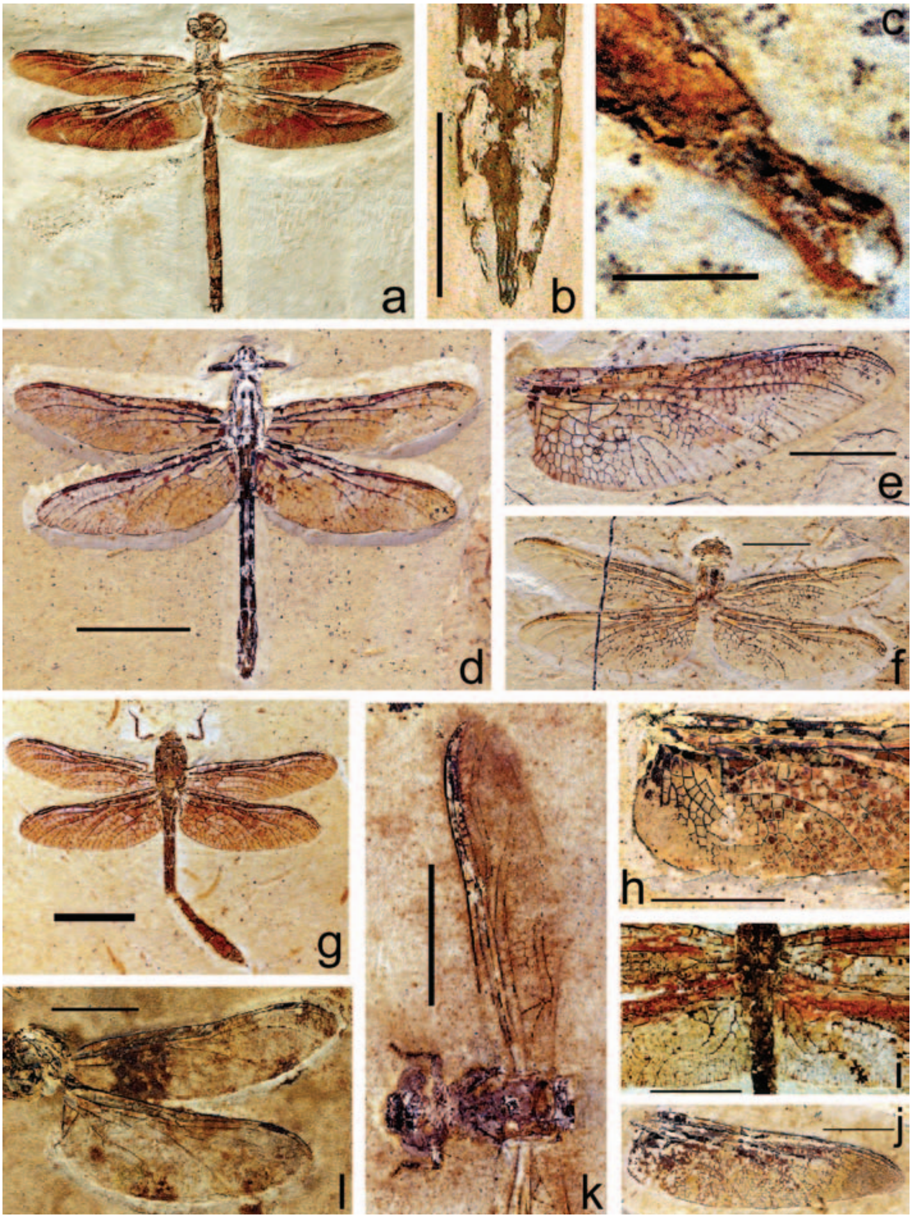

Plate 10. Crato Odonata: (a) *Araripeliupanshania annesuseae*, male, holotype MB. 1999.3 MB.I.2047; (b) *Araripegomphus andreneli*, female, ovipositor, SMNS 66392; (c) *Araripegomphus andreneli* male, anal appendages, MSF G10; (d) *Cordulagomphus* cf. *tuberculatus*, female, SMNS 64361; (e) *Cordulagomphus winkelhoferi* sp. nov., male, holotype SMNS 66607; (f) *Cordulagomphus hanneloreae* sp. nov., female, holotype SMNS 66591; (g) *Procordulagomphus michaeli* sp. nov., male, holotype MURJ no 514; (h) *Araripephlebia mirabilis*, female?, right hind wing, SMNS 66618; (i) *Araripephlebia mirabilis*, female?, wing bases, MSF G16; (j) Odonata, Anisoptera, gen. et sp. nov., female, SMNS 66567; (k) Odonata, Anisoptera, gen. et sp. nov., SMNS 66608; (l) Odonata, Anisoptera, gen. et sp. nov., male, SMNS 66614. Scale bars: (b), 5 mm; (c), 3 mm; (d, f, j, k), 15 mm; (e, g, h, i, l), 10 mm.