THE CRATO FOSSIL BEDS OF BRAZIL

Window into an Ancient World

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Triangulifera but not with *Cretereisma*. Thus it appears that *Cretereisma* is the sister taxon of *Litophlebia*+Triangulifera. *Protereisma* and *Misthodotes* were abundant in the Lower Permian while *Litophlebia* lived about 60 myr later. Hence *Cretereisma*, with a phylogenetic position between *Litophlebia* and the two Permian taxa, is the only known representative of an ephemeroid lineage which had retained many plesiomorphic features for about 110–160 myr.

11.4 Ephemeroptera: mayflies

Arnold H. Staniczek

Mayflies represent one of the basal branches of winged insects and have a world wide distribution. Stem group representatives of mayflies date back to the Carboniferous. More than 3,000 Recent species have been described.

The larvae of mayflies are obligatorily bound to freshwater habitats. The imagines of mayflies are short-lived insects with a life span that varies from a few hours to a few days. Mayflies are the only pterygote insects to retain more than one fully winged stage. The subimago is the alate penultimate stage and undergoes another moulting to become the imago. The subimaginal moulting is generally regarded as a vestigial adult moulting as it is present in the apterygote insect groups. The adult stages of mayflies are easily recognized by the presence of usually very long cerci, often accompanied by a median long terminal filament (paracercus). At rest the wings are folded vertically over the abdomen. The hind wings are considerably smaller than the forewings and can also be entirely lost in some taxa. The imaginal wings are generally translucent and glabrous, but the subimaginal wings usually have a greyish or milky tinge and are equipped with setae. The venation is characterized by the presence of multiple crossveins, a pronounced costal brace especially in the forewing, and the presence of vein MP. The wings generally retain a pronounced pleating and corrugation of the longitudinal veins. The adult stages of mayflies do not feed, and their mouth parts are atrophied. The antennae are very short and bristle-like, convergent on Odonata. Other features are connected with the aerial mating flight that the males perform above the water: the male eyes are generally larger than the female ones, in some taxa (Baetidae, Leptophlebiidae) they are extended to so-called turbinate eyes, which are also morphologically divergent. The male forelegs are elongated to grasp the females around the base of the forewing during copulation. The male claspers, modified abdominal leglets of abdominal segment VIII, additionally clutch the female abdomen during copulation. Males have paired penes, and females have paired gonopores, respectively. The female ovipositor is completely reduced, and only some taxa have developed a secondary egg guide. After mating the female mayfly simply drops its eggs into the water. The eggs are equipped with highly variable adhesive structures to prevent drifting.

The larvae of mayflies undergo numerous moults until they reach the final instar. Extant species usually bear seven pairs of tracheal gills, which insert laterally on the first seven abdominal segments. The gills are of variable shape but often specific for higher taxa. They can be either simple or may be composed of an upper and a lower branch. The gills can be shaped like a leaf (Baetidae), fringed (Ephemeroidea), finger-like in some Leptophlebiidae, miniaturized in the Oligoneuriidae, or may be located beneath a specialized gill that functions as a gill cover (Caenidae). In the Heptageniidae the upper gill portion is leaf-like, and the lower portion is represented by a gill tuft. The larvae are also characterized by the presence of the tail filaments. The chewing mouth parts of mayfly larvae are well developed. The secondary mandibular joint is not fixed as a ball-and-socket joint, and the mandible is able to perform gliding movements similar to the conditions in silverfish. The hypopharynx retains side lobes (superlinguae), and maxillary and labial palps are both three-segmented. Mayfly larvae mostly feed on detritus accumulated with their maxillae and mandibles. The filter-feeding Setisura even use specialized setae to filter their food out of the water currents with their forelegs. A few taxa (Behningiidae, Ameletopsidae) have carnivorous larvae. Mayflies are important elements of the freshwater food chain and the nutrient base for many carnivorous fish. The emergence of mayflies is often highly synchronized, and at times millions of specimens can be observed in dense swarms.

Systematics and phylogeny

The monophyly of mayflies is well established and supported by numerous apomorphic characters such as the Palmen body, the atrophy of mouth parts, and an air-filled gut with aerostatic function. Apart from the Ephemeroptera, there are only two other Recent basal lineages of pterygote insects, the Odonata and Neoptera. There is, however, no general agreement on the sister group of Ephemeroptera. A potential sister-group relationship between Odonata and Ephemeroptera+Neoptera is only substantiated by few putative synapomorphic characters, namely by the presence of a direct sperm transfer in Ephemeroptera+Neoptera. A monophyletic taxon Paleoptera (Martynov, 1925; Ephemeroptera+Odonata) has mainly been advocated by Kukalová-Peck (1985, 1987, 1991). Potential synapomorphies of the Paleoptera include an anal wing brace that is similarly developed in stem group representatives of both groups, a media with common stem, and the presence of intercalary veins. Other workers have proposed a sister-group relationship between Ephemeroptera and all other pterygote insects, the Metapterygota (Börner, 1909). The rigid secondary mandibular joint together with a different arrangement of mandibular musculature, the loss of the terminal filament and superlinguae, and the loss of the imaginal moults are regarded as apomorphic characters of the

Metaptygota (see Kristensen, 1995 and Staniczek, 2000 for a detailed discussion). Molecular data are inconclusive (Ogden and Whiting, 2003), and a final decision cannot be made at present.

The phylogenetic systematics of Ephemeroptera is far from being fully resolved and remains controversial with regard to the composition and branching sequence of many higher taxa. There are about 37 monophyletic taxa recognized that are categorized as families. McCafferty and Edmunds (1979) divided the Ephemeroptera into the paraphyletic Schistonota and the Pannota, which are defined by medially fused larval wing pads. Later Kluge (in an oral conference contribution in 1992; and 1998) and then McCafferty (1997) excluded the Batiscidae+Prosopistomatidae from the Pannota and assumed the Prosopistomatoidea (Carapacea *sensu* McCafferty, 1997; Posteritorna *sensu* Kluge, 1998) to be the sister group of all other mayflies. Other similarities in both systematics are a proposed taxon of several rather plesiomorphic families, the Tridentiseta (Kluge, 2004) or Pisciforma (McCafferty, 1998), that consist of the Siphlonuroidea (Kluge *et al.*, 1995) and Baetoidea (Staniczek, 1997). There is also congruence in uniting all filter-feeding taxa with the Heptageniidae to a taxon Setisura (McCafferty, 1997) or Branchitergaliae (Kluge, 2004). The remaining groups, united into a taxon Furcatergaliae by Kluge (2004), are also considered to be monophyletic. Within these higher taxa, however, the arrangement of the different families differs considerably. Moreover, recent molecular systematics by Ogden and Whiting (2005) failed to support most of these groupings.

Evolution

One of the most important steps in insect evolution was the acquisition of wings. The development of insect wings from thoracic side lobes, the paranota, has been the prevailing hypothesis for a long time (Snodgrass, 1935), until Kukalová-Peck (1978, 1983) publicized the development of insect wings from modified thoracic gills. Both hypotheses claim to gain support from fossil evidence. The Recent ephemeropteran lineage is only one of several branches of early winged insects. The †Paleodictyopterida comprise several distinctive groups, all of which became extinct by the end of the Permian. At present there are some doubts whether the †Paleodictyopterida are monophyletic, as often assumed, because of the characteristic elongated, sucking mouth parts they share. In several groups of these Palaeozoic insects, huge prothoracic side lobes were developed as winglets. These prothoracic paranotal lobes had a similar venation to the meso- and metathoracic wings. The presence of prothoracic winglets in many of these Palaeozoic insects is generally taken as support for the above-mentioned paranotal hypothesis. However, paranota are rigid outgrowths that do not have any articulation with the prothorax. The gill hypothesis assumes that insect wings are serially homologous with the gills of mayfly larvae (Kukalová-Peck, 1991). In particular, gills and wing pads of Permian larvae of †Protereismatidae look similar to each other, and the wing pads, unlike in modern mayfly larvae, seem to articulate with the thorax. Consequently, an aquatic origin of pterygote insects has been postulated by the advocates of the gill hypothesis. On the other hand, all primarily apterous insect groups are terrestrial, and the basal taxa of ptergote insects with aquatic larvae (Ephemeroptera, Odonata, Plecoptera) have developed very different modes of respiration. This makes it unlikely that the pterygotes evolved in an aquatic environment (Pritchard *et al.*, 1993), although there are no terrestrial larvae of stem group representatives of mayflies known. Recently the gill hypothesis has been modified and the use of wings as a skimming device has been proposed as the trigger of wing development (Marden and Thomas, 2005). Given the fact that skimming in Recent mayflies and stoneflies only occurs in a few derived taxa, this scenario is not very likely.

However, notable differences from early stem group representatives of mayflies to modern Ephemeroptera can be observed. While a costal brace is present in most fossil and modern taxa, its basal course is slightly different in early groups such as the †Protereismatidae, where the costal brace is still well separated from the costal vein. Fore- and hind wings in the first fossil taxa are of the same size. Heteronomous wings first appear in the Jurassic, and all modern mayflies have significantly reduced hind wings. Other differences concern the development of a wing tornus in modern mayflies, while the hind margin of the wing in Palaeozoic stem group representatives has no sharp angle (Kluge, 2004). Generally the size of mayflies diminished during their evolution. Adults of Palaeozoic stem group representatives like the †Protereismatidae are also assumed to have functional mouth parts (Grimaldi and Engel, 2005). The articulated wing pads of the associated larvae grew out in a laterocaudad direction. In modern mayflies the wing pads are fused with the mesonotum and grow parallel to the longitudinal body axis. The amount of gill numbers has become reduced from nine pairs to seven.

Fossil record

Winged insects were already abundant in the Late Cretaceous, but the discovery of the Early Devonian *Rhyniognatha hirsti*, a species that may belong within the lineage of Metapterygota, suggests that the age of the Metapterygota and of its putative sister group, the Ephemeroptera, dates back to that time (Engel and Grimaldi, 2004). The first fossils that have been assigned to the ephemeropteran lineage date back to the Late Carboniferous. While the assignment of two enigmatic fossils, *Triblosoba pulchella* from the Late Carboniferous of Commentry and *Lithoneura lameerei* from the Late Carboniferous of Mazon Creek, to the stem group of mayflies is controversial (Willmann, 1999), most researchers agree on the assignment of *Bojophlebia prokopi*, from the Upper Carboniferous of Bohemia, to the stem group of mayflies (Kukalová-Peck, 1985). With a wing span of 45 cm it is also the largest mayfly precursor ever found.

There are many fossil stem group representatives from the Permian fauna preserved, among them the well-known †Protereismatidae from the Early Permian of Kansas, Oklahoma, Moravia and the Urals (Tillyard, 1932; Carpenter, 1979; Hubbard and Kukalová-Peck, 1980). Another well-known taxon is the †Misthodotidae that together with the †Protereismatidae disappeared by the end of the Permian (Tshernova, 1965). The stem group representatives were often placed in a separate suborder, '†Permoplectoptera', which is, however, regarded as paraphyletic with respect to the crown group. Most of these early taxa went extinct by the end of the Permian, but others could be recorded from the Triassic (Sinitshenkova *et al.*, 2005). The youngest stem group representatives of Ephemeroptera have been found within the Crato Formation and are described in detail in the preceding Section 11.3, by Willmann. A further, undescribed, stem group mayfly from this locality is featured in Figures 11.90i and j. For recent reviews on all stem group representatives of mayflies, see Kluge (2004) and Willmann (this volume, Section 11.3).

The first species that are positioned within the crown group of Ephemeroptera appear in the Lower Jurassic (Tshernova, 1967): *Stackelbergisca sibirica* turned out to be closely related to the Recent *Siphluriscus chinensis* (Siphluriscidae; Zhou and Peters, 2003). Species that are attributed to the Leptophlebiidae can be traced back to the Jurassic (Hubbard and Savage, 1981). Numerous other Jurassic genera have been placed in the extinct taxa †Epeoromimidae, †Aenigmephemeridae, †Mesephemeridae and †Hexagenitidae (McCafferty, 1990). The affinities to Recent mayfly groups remain mostly uncertain (Kluge, 2004).

The Cretaceous mayfly fauna apart from the Crato Formation has been documented by fossil records from Transbaykalia (Tshernova and Sinitshenkova, 1974; Sinitshenkova, 1986), China (Lin and Huang, 2001), England (Sinitshenkova and Coram, 2002), Australia (Jell and Duncan, 1986) and Algeria (Sinitshenkova, 1975).

The oldest mayflies in amber have been recorded from the mid-Cretaceous of Myanmar (Sinitshenkova, 2000), Lebanon (McCafferty, 1997) and New Jersey (Peters and Peters, 2000; Sinitshenkova, 2000). Several mayfly fossils from Baltic and Dominican amber have been recorded from the Eocene and Miocene that mostly reflect the modern fauna (Staniczek and Bechly, 2002; Staniczek, 2003; Godunko, 2004; Godunko and Neumann, 2006). New families of mayflies are defined only rarely, which, however, can all be attributed to Recent monophyletic groups (Kluge *et al.*, 2006). Kluge (1986) even reports a putative Recent species from Baltic amber.

Palaeobiology and palaeoecology

Mayflies are obligatorily bound to fresh water. Extant species of mayfly are generally halophobic and only a few species are reported to tolerate elevated salt concentrations as they are present in brackish water (Chadwick *et al.*, 2002). *Protoligoneuria limai* (Figures 11.4a and 11.9c; Plates 7i and 8a–c) is reported to be the most common fossil insect species of the Crato Formation (Martins-Neto, 1996a; D. Martill, personal communication), although mayflies only make up about 7% of the described Crato species (Bechly, 1998c). The mass occurrence of thousands of fossil larval mayflies in the Crato limestones clearly points to the presence of streams in the immediate vicinity of the deposit. McCafferty (1990) and Tshernova (1970) hypothesized quiet waters as a habitat for *P. limai* because of its larval swimming adaptations such as the minnow-like body shape, siphlonuroid caudal appendages and its enlarged seventh gill. The larvae of the burrowing Ephemeroidea (Figures 11.4c and g, 11.5a and b and 11.6h and i; Plate 8f) found in Crato also point to the presence of streams or at least stream sections with a rather low flow rate. However, a rheophilic habitat cannot entirely be ruled out. Similar to the Odonata fauna with a high percentage of Gomphidae found here, the oligoneuriid species found were probably more adapted to a lotic environment and generally depended on a high amount of oxygen. Most probably the Crato environment provided a diverse habitat suitable for both lotic and lentic species. The few adult records compared to the enormous amount of larval specimens found may be explained by two factors: mayfly larvae are sensitive to downstream drift, and this is counterbalanced by an upstream compensation flight of the female adults. Both effects may lead to a spatial separation of larvae and adults with the effect of an accumulation of larvae which have been swept into the area of deposition.

Crato fossils

The first fossil mayfly from this locality was reported by Costa-Lima (1950) and described by Demoulin (1955). According to Martins-Neto (2005b) there have been 15 species of fossil Crato mayflies described, not including the two species of stem group mayflies described by Willmann in Section 11.3 (a further undescribed specimen is featured on Figures 11.90i and j). Important contributions to Crato mayflies were made by McCafferty (1990) and Martins-Neto (1996a). Shorter contributions were provided by Brito (1987), Martins-Neto and Caldas (1990), Polegato and Zamboni (2001), Zamboni (2001) and Bechly *et al.* (2001a: figures 28, 30, 36 and 37).

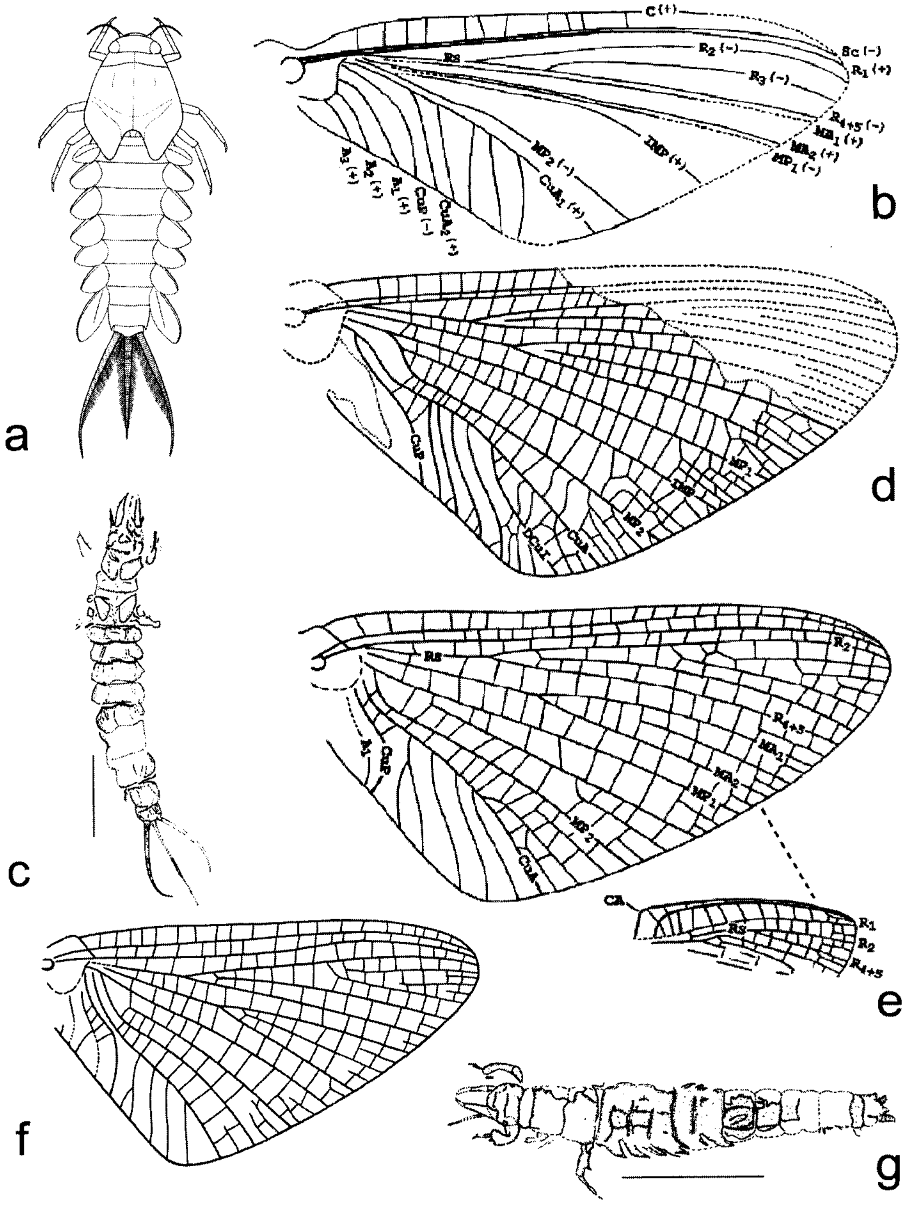

Fig. 11.4. Crato Formation Ephemeroptera: (a) Hexagenitidae, *Protoligoneuria limai*, composite reconstruction of larva (after McCafferty, 1990: figure 1); (b) Oligoneuriidae, *Colocrus indivicum*, reconstruction of forewing, adult paratype AMNH 43499 (after McCafferty, 1990: figure 19); (c) Ephemeroidea (Potamanthidae?), *Olindinella gracilis*, larval holotype AMA-I-028 (after Martins-Neto and Caldas 1990: figure 2); (d) Euthyplociidae, *Pristiplocia rupestris*, forewing, adult holotype AMNH 44308 (after McCafferty, 1990: figure 23); (e) Ephemeridae, *Australiephemera revelata*, forewing and hind wing fragment, composite from adult holotype AMNH 44300 and adult paratype AMNH 44310 (after McCafferty, 1990: figures 20 and 21); (f) Ephemeridae, *Microephemera neotropica*, forewing, adult holotype AMNH 43303 (after McCafferty, 1990: figure 22); (g) Ephemeroidea, (Ephemeridae?), *Cratonympha microcelata*, larval holotype GP/1T-1677 (after Martins-Neto and Caldas 1990: figure 1A).

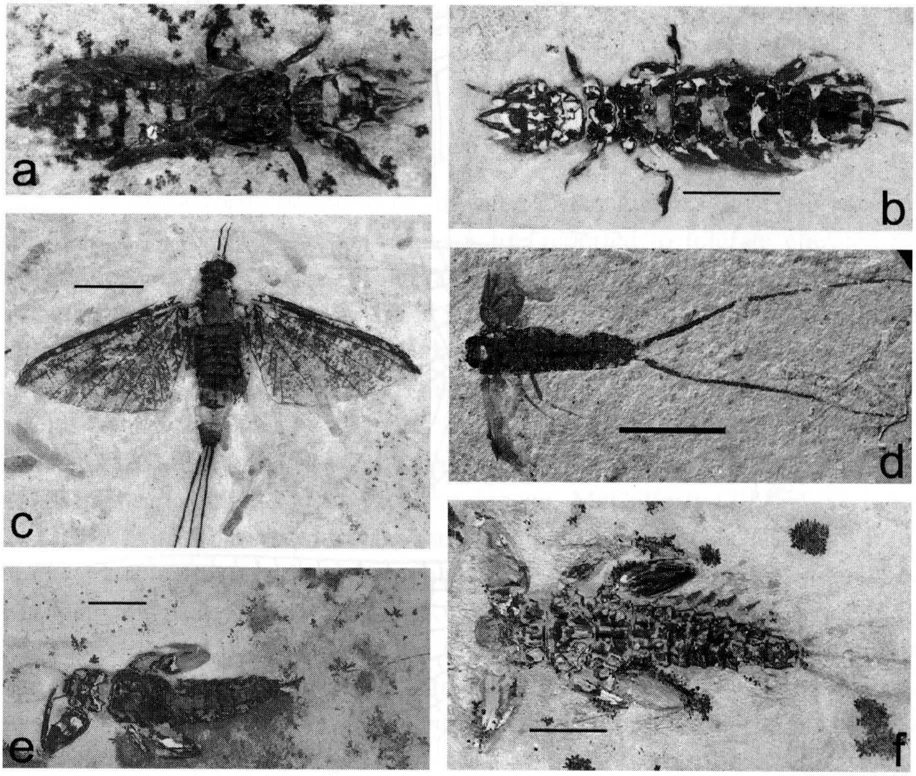

Fig. 11.5. Crato Formation Ephemeroptera: (a) Ephemeroidea indet., larva, SMNS 66630; (b) Ephemeroidea indet., larva, coll. MSF; (c) Ephemeroidea indet., adult, coll. MSF; (d) Leptophlebiidae (?) sp. 1 (*sensu* McCafferty 1990), subimago?, SMNS 66639; (e) Familia *incertae sedis*, gen. et sp. nov., larva Z2 coll. MSF; (f) Familia *incertae sedis*, gen. et sp. nov., larva, SMNS 66622. Scale bars, 5 mm.

†**Hexagenitidae** Lameere, 1917

Apart from the Crato fossils, there are five more genera that have been placed in the extinct †Hexagenitidae: *Hexagenites* Scudder 1880, *Ephemeropsis* Eichwald 1864, *Hexameropsis* Tshernova and Sinitshenkova 1974, *Mongologenites* Sinitshenkova 1986 and *Caenoephemera* Lin and Huang 2001. The first mayfly ever from Crato was mentioned by Costa-Lima (1950), who assigned three larval specimens to the Baetidae (equivalent to today's 'Siphlonuroidea'); however, no formal description was given. Based on these specimens, Demoulin (1955) formally named the species as *Protoligoneuria limai*, and placed it in the Oligoneuriidae. Brito (1987) described a new genus and species *Palaeobaetodes limai* but McCafferty (1990) synonymized Brito's species with *Protoligoneuria limai*. He placed the species in the †Hexagenitidae, based on the characteristic, significantly enlarged and outspread seventh gill that is also present in other hexagenitid larvae. This enlarged seventh gill is regarded as an autapomorphic larval character of the †Hexagenitidae

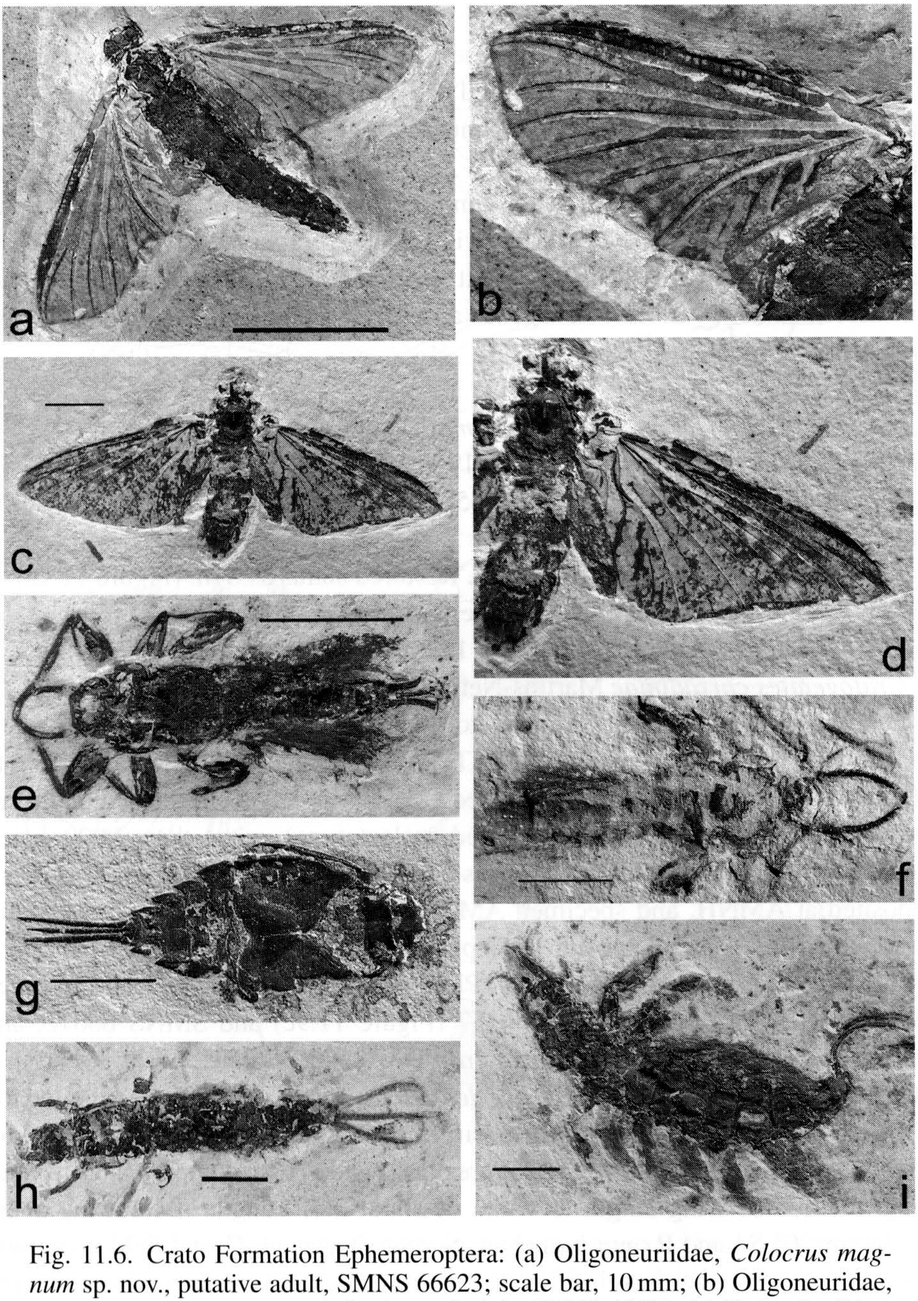

Fig. 11.6. Crato Formation Ephemeroptera: (a) Oligoneuriidae, *Colocrus magnum* sp. nov., putative adult, SMNS 66623; scale bar, 10 mm; (b) Oligoneuridae, *Colocrus magnum* sp. nov., left wings of adult, SMNS 66623; (c) Euthyplociidae, *Pristiplocia rupestris*, adult, SMNS 66541; scale bar, 5 mm; (d) Euthyplociidae, *Pristiplocia rupestris*, right wings of adult, SMNS 66541; (e) Euthyplociidae, *Pristiplocia* sp., larva, SMNS 66539; scale bar, 5 mm; (f) Euthyplociidae, *Pristiplocia* sp., larva, SMNS 66621; scale bar, 3 mm; (g) Baetiscidae, *Protobaetisca bechlyi* gen. et sp. nov., larval holotype SMNS 66620, scale bar, 3 mm; (h) Ephemeroidea indet., larva, MURJ without number; scale bar, 3 mm; (i) Ephemeroidea indet., larva, SMNS 66634; scale bar, 3 mm.

(Kluge, 2004), but according to McCafferty (1990) it may only be a synapomorphic character between some taxa within the †Hexagenitidae. Martins-Neto (1996a) reinstated *Palaeobaetodes* and described a second species, *Palaeobaetodes britoi*, from larvae, and also described a third genus *Cratogenites*, including *C. corradiniae*, from larvae.

The known imagines of the †Hexagenitidae all have a characteristic wing pattern with a branched CuA in the forewing and several successive triads present between CuA_1 and CuA_2. The first adult specimen of †Hexagenitidae from Crato was described as yet another new genus and species, namely *Cratogenitoides delclosi*, by Martins-Neto (1996a).

Protoligoneuria limai Demoulin, 1955

Baetidae (Siphlonurinae), Costa-Lima, 1950: 419

Protoligoneuria limai Demoulin, 1955: 271. (Figures 11.4a and 11.9c; Plates 7i and 8a–c)

Paleobaetodes costalima Brito, 1987. Restored status as Syn. (Figure 11.7a)

Siphgondwanus occidentalis McCafferty, 1990 Syn. nov. (Figure 11.7h)

Palaeobaetodes britoi Martins-Neto, 1996a Syn. nov. (Figures 11.7c–d)

Cratogenites corradiniae Martins-Neto, 1996a Syn. nov. (Figures 11.7e–f)

Cratogenitoides delclosi Martins-Neto, 1996a Syn. nov. (Figure 11.8b)

Material: larval holotype specimen CD 6616, Vulcano collection (according to Martins-Neto (2005a) it is the only specimen that is left from the original three syntypes, and thus it is here designated as lectotype); more than 2,000 specimens deposited in the collection Martins-Neto, São Paulo; 77+4 larval specimens deposited at AMNH, and specimen AMNH 43404 (holotype of *Siphgondwanus occidentalis*); 236 larval specimens deposited at SMF, including the two specimens with preliminary nos Q4 and Q9 (Plates 7i and 8a); three very well-preserved specimens SMNS 66536, SMNS 66537 (Figure 11.9c) and SMNS 66672; and numerous specimens in other collections. Two putative alate specimens are no. RGMN-T002 (holotype of *Cratogenitodes delclosi*) in the Martins-Neto collection at the University of São Paulo, and specimen SMNS 66635 (Figures 11.9a and b).

Diagnosis: putative alate stages (Figures 11.9a and b) with compact anteritornous wing, relation of wing length to width of about 2:1. Length of forewing about 18–20 mm. C, Sc and R_1 not branched; Sc not shortened. Costal field and entire wing with numerous crossveins. RS basally branched at about one-quarter of wing length. MA branched in apical half of wing at about three-quarters of wing length. MP basally branched, with very short common stem, CuA basally branched at about one-third of distance between wing base and tornus. CuA field with four successive 'hexagenitid' triads. CuP not branched. A_1 with common short stem and basally branched. Hind wing significantly reduced, without costal process, with RS, MA and MP apically branched. No conspicuous gemination of longitudinal veins.

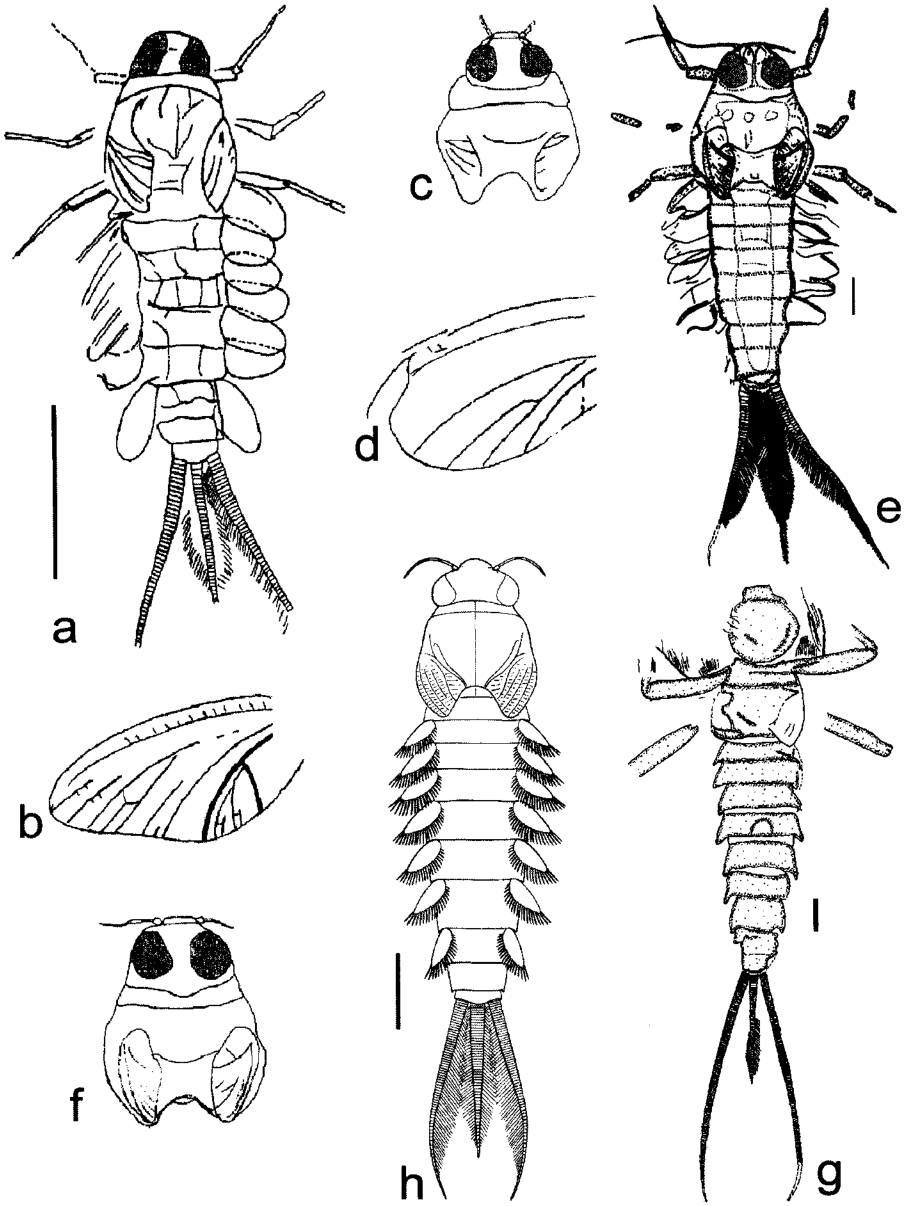

Fig. 11.7. Crato Formation Ephemeroptera (invalid taxa): (a, b) *Palaeobaetodes costalimai* Brito, 1987 (= *Protoligoneuria limai*); (a) mature nymph; scale bar, 5 mm, (b) alar; (c, d) *Palaeobaetodes britoi* Martins-Neto, 1996a (= *Protoligoneuria limai*); (c) head and thorax, RGMN-T006; (d) alar; (e, f) *Cratogenites corradiniae* Martins-Neto, 1996a (= *Protoligoneuria limai*), holotype, RGMN-T001; (e) mature larva; scale bar, 1 mm; (f) head and thorax; (g) *Cratoligoneuriella leonardii* Martins-Neto, 1996a (= *Colocrus indivicum*), holotype nymph, RGMN-T005; (h) *Siphgondwanus occidentalis* McCafferty, 1990 (= *Protoligoneuria limai*), larva in dorsal view, legs ommitted; scale bar, 1 mm. (a–h) After Martins-Neto (1996a); (i) after McCafferty (1990).

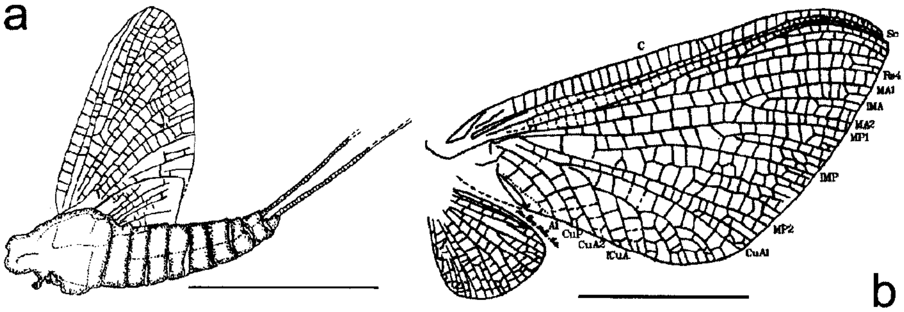

Fig. 11.8. Crato Formation Ephemeroptera: (a) Ephemeroptera *incertae sedis*, *Costalimella nordestina* Martins-Neto, 1996a, holotype, RGMN-T004; (b) *Cratogenites delclosi* Martins-Neto, 1996a (synonym of *Protoligoneuria limai*), holotype, RGMN T002. Scale bars, 5 mm. After Martins-Neto (1996a).

Larvae (Figures 11.4a and 11.9c; Plates 7i and 8a–c): body length up to 16 mm, excluding cerci. Siphlonuroid minnow-like appearance (Figures 11.4a and 11.9c), cerci at their inner sides and terminal filum with fringes of swimming hairs, cerci slightly longer than terminal filament, abdomen with seven pairs of tracheal gills, gill VII distinctively longer than other gills, all gills consisting of a leaf-like upper part and a lower gill tuft (Plates 7i and 8a) that previously had been overlooked. Anterior margin of gills I–VII strengthened, gill VII (Plate 8b) also with a second longitudinal rib in the posterior half of the gill, well apart from its posterior strengthened margin (often a small but distinctly protruding apical lobe is visible at the posterior end of this gill plate). Wing pads medially partially fused as in Recent species of Setisura (Plate 8c).

Comments: Brito (1987) described with *Palaeobaetodes costalima* (Figures 11.7a and b) a new genus and species of †Hexagenitidae from Crato. McCafferty (1990) synonymized *Palaeobaetodes* with *Protoligoneuria*, but Martins-Neto (1996a) reinstated the latter genus and described a second species, *Palaeobaetodes britoi* (Figures 11.7c and d). However, these authors mention only few differences to *Protoligoneuria*: according to Martins-Neto (1996a), *Paleobaetodes* differs from *Protoligoneuria* mainly in larger eyes, which occupy 50% of the head in *Palaeobaetodes* instead of 30% in *Protoligoneuria*. Obviously the author did not consider the sexual dimorphism of the eyes in many mayfly species. It is very common that male larvae have larger eyes than the females, and this has to be assumed in this case as well. A different ratio of gill lengths VII/VI was claimed to be the significant difference between the two described species of *Paleobaetodes* (Martins-Neto, 1996a), but I could not confirm a significant grouping in the material available (several hundred larvae). Consequently, both species of *Paleobaetodes* are here regarded as junior synonyms of *Protoligoneuria limai*.

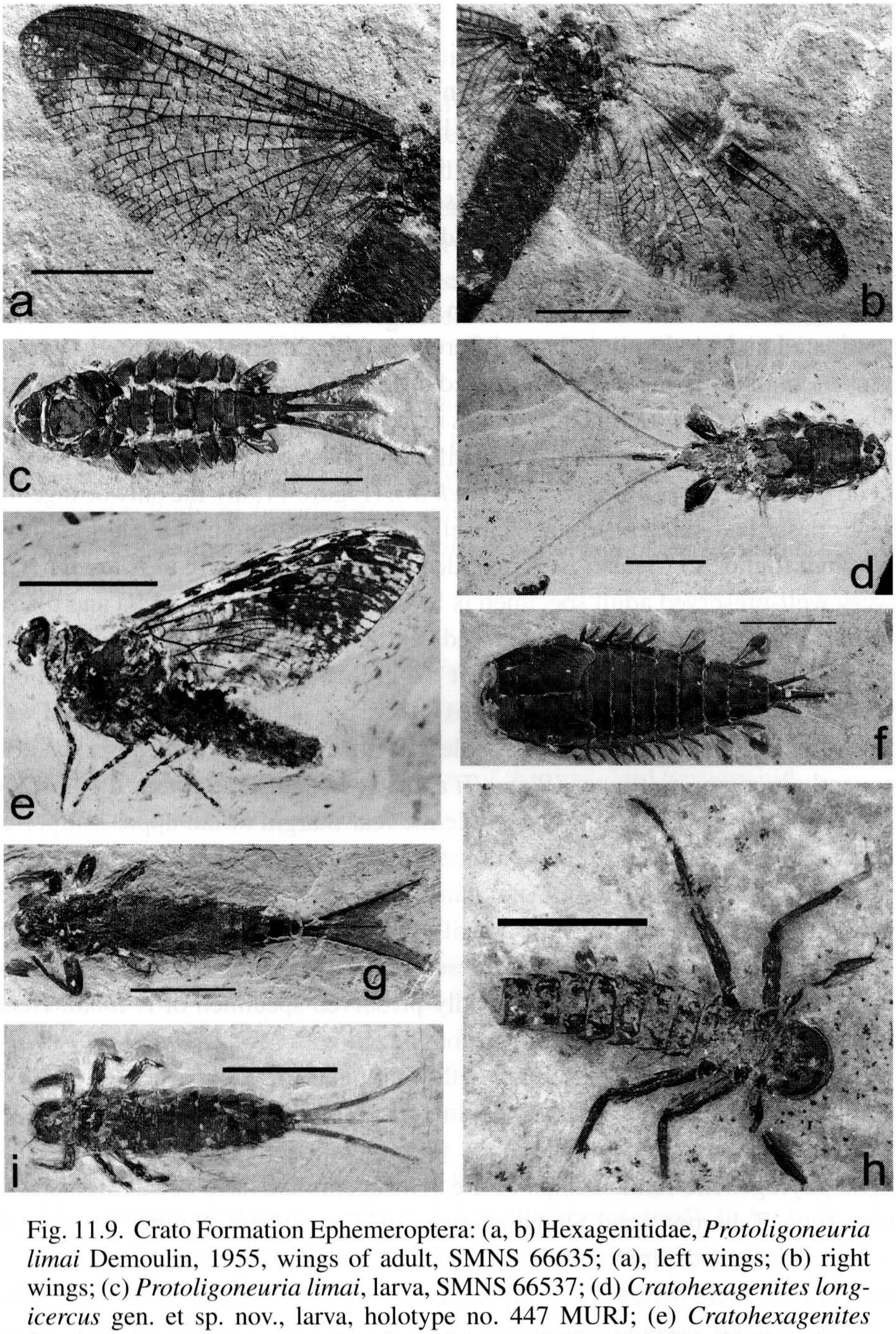

Fig. 11.9. Crato Formation Ephemeroptera: (a, b) Hexagenitidae, *Protoligoneuria limai* Demoulin, 1955, wings of adult, SMNS 66635; (a), left wings; (b) right wings; (c) *Protoligoneuria limai*, larva, SMNS 66537; (d) *Cratohexagenites longicercus* gen. et sp. nov., larva, holotype no. 447 MURJ; (e) *Cratohexagenites longicercus* gen. et sp. nov., putative adult, no. O46 coll. MSF; (f) *Cratohexagenites minor* gen. et sp. nov., larva, holotype MB.I.2026; (g) Oligoneuriidae, *Colocrus indivicum*, larva, SMNS 66538; (h) Oligoneuriidae, *Colocrus indivicum*, larva, MB.I.2025; (i) Oligoneuriidae, *Colocrus magnum* sp. nov., larva, holotype, SMNS 66624.

Martins-Neto (1996a) also described *Cratogenites corradiniae* (Figures 11.7e and f). Apart from larger eyes the only differences to *P. limai* mentioned are longer antennae (about twice the head width) in *C. corradiniae*. However, while the line drawing of the holotype (Martins-Neto, 1996a: figure 2A) shows an elongated left antenna, the corresponding photograph (Martins-Neto, 1996a: Plate 1, figure 1) does not support this view. Hence I also synonymize *Cratogenites corradiniae* with *Protoligoneuria*, until there is sound proof that it can indeed be distinguished as a separate species from *P. limai*.

Martins-Neto also noted differences in the larval head shape of the specimens he investigated and tried to link these differences with different species. However, it seems more likely to me that the observed differences are due to different positions of the head. I also noted slight differences in the body shape, but this could be caused by a different state of nutrition or by a different phase of the moulting period.

The body length of *Cratogenitoides delclosi* (Figure 11.8b), the only hexagenitid species described in the alate state, closely matches the length of the largest larvae of *P. limai* found. So *C. delclosi* is regarded as a junior synonym of *P. limai* herein. A very well-preserved adult specimen is SMNS 66635 (Figures 11.9a and b).

None of the previous authors observed ventral gill tufts in the larvae they investigated. This may be due to the fact that the gill tufts are inconspicuous and only visible in very well-preserved specimens. However, once I had encountered well-preserved specimens with clearly visible gill tufts, they could be observed quite frequently in many specimens (Plates 7i and 8a). In some specimens the fibrillous endings of the tufts just slightly protrude the rear margin of the upper gill portion and give the leaf-like gills the appearance of having a fringed rear margin. McCafferty (1990) described a single siphlonurid larva as *Siphgondwanus occidentalis* (Figure 11.7h) having exactly the same gill shape as mentioned above. Furthermore, the seventh pair of gills is not well preserved in this specimen. It is very probable that this in fact is nothing but a badly preserved specimen of *P. limai*. Hence *Siphgondwanus occidentalis* is also synonymized with *Protoligoneuria limai*.

Demoulin (1955) assigned *P. limai* to the Oligoneuriidae, but McCafferty (1990) demonstrated that there are larval and imaginal apomorphies present that clearly point to a position of *P. limai* within the †Hexagenitidae.

The phylogenetic relationships of the †Hexagenitidae have been enigmatic for a long time. Tshernova and Sinitshenkova (1974) maintain affinities between the †Hexagenitidae and Siphlonuridae, but the characters they have in common are genererally thought to be plesiomorphic. Demoulin (1971) emphasized similarities between the basal Recent oligoneuriid genus *Chromarcys* and the †Hexagenitidae, assuming a closer phylogenetic relationship between these taxa. However, *Chromarcys* is generally regarded as the sister group to all other Recent Oligoneuriidae (McCafferty, 1991), and the †Hexagenitidae are clearly lacking the autapomorphies of the Oligoneuriidae, so the †Hexagenitidae cannot be an ingroup taxon of the Oligoneuriidae. If the gill tufts now found in *P. limai* should be confirmed as groundplan characters of the †Hexagenitidae, a position of the †Hexagenitidae within the Setisura (McCafferty, 1991) = Branchitergaliae (Kluge, 2004), or a sister-group relationship between the two taxa, would be likely. However, a detailed structural analysis of the gill tufts is yet to be undertaken. A second character also supports this hypothesis: in some very well-preserved specimens a partial medial fusion of the wing pads is visible (Plate 8c). The same character state is also present in the filter-feeding taxa of the Branchitergaliae.

Cratohexagenites gen. nov.

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

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

Diagnosis: Body of broader drop-like shape; seventh gill distinctly larger in proportion to the other gills than in *Protoligoneuria*, and of trapezoidal shape with angular instead of rounded hind margin.

Cratohexagenites longicercus sp. nov.

Material: larval holotype (Figure 11.9d) no. 447 (old no. G76) in coll. MURJ; larval paratype MB.I.2026 at MNB; putative adult specimen no. MSF O46 (Figure 11.9e), deduced from the corresponding large size of this imaginal hexagenitid.

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 its elongated caudal filaments.

Diagnosis and description (Figure 11.9d): hexagenitid larva with enlarged seventh gill of trapezoid shape, differs from *P. limai* by body length of about 27 mm, length of cerci 28 mm, length of terminal filament 24 mm. General body shape is drop-like. Length of gills I–VI is about 5 mm, length of gill VII is 11 mm. Otherwise quite similar to *P. limai.*

Comment: adult specimen no. MSF O46 has the characteristic CuA branch and apical MA branch of †Hexagenitidae (CuA field not preserved). Its body length of 23.5 mm corresponds to the large size of the holotypical larva. Like *Protoligoneuria* and Recent Setisura this new taxon also has the larval wing pads medially partially fused (Figure 11.9d).

Cratohexagenites minor sp. nov.

Material: larval holotype (Figure 11.9f) no. MB.I.2026 at MNB.

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 its smaller size compared to the type species.

Diagnosis and description (Figure 11.9f): hexagenitid larva with enlarged seventh gill of trapezoid shape, differs from type species by body length of 15.5 mm, length of terminal filaments about 6 mm (comparatively shorter than in type species). General body shape is drop-like (maximum width of body, 6.1 mm). Length of gill VII is about 2.4 mm. Otherwise it is very similar to the type species, including the larval wing pads that are medially partially fused (Figure 11.9f). Adults are still unknown.

Oligoneuriidae

Colocrus McCafferty, 1990 (see Figure 11.4b)

Cratoligoneuriella Martins-Neto, 1996a Syn. nov.

Diagnosis: larva: abdomen with pronounced posterolateral projections. Paracercus significantly shorter than cerci. Siphlonuroid setation of terminal filaments: cerci at their inner sides and terminal filum with swimming hairs. Abdomen with leaf-like tracheal gills preserved on segments I–VI (I–III in holotype AMNH 43483, III–V in SMNS larva 66538, I–VI in SMNS larva 66619). Gill I with dorsal insertion (McCafferty, 1990). Ventral gill tufts are not present or not preserved. Abdominal segments with posterolateral projections are present on segments IV–IX. Fore femora and fore tibiae on inner sides are equipped with a row of filtering setae (Plate 8d). Head capsule is broadened; the labium with enlarged and basally fused glossae forms a labial plate (Figure 11.9h; Plate 8e).

Alate stages: forewing with crossveins in costal field only. Gemination of Sc and R_1, R_{4+5} and MA_1, MA_2 and MP_1, MP_2 and CuA. Series of veins running from CuA to posterior wing margin. Intercalaries absent except IMP.

Comments: Martins-Neto (1996a) established a new genus, *Cratoligoneuriella*, based on putative differences of the femoral base of the larval filter hairs. He claimed the presence of a 'sclerotic process in the middle length of the fore femur' of *Cratoligoneuriella* without further explanation or figure. Judging from the picture he gives, there is no difference between the detailed structure and origin of the filtering hairs in *Cratoligoneuriella* and *Colocrus*. However, the row of filtering hairs is sometimes detached and dislocated in some specimens (Figure 11.9g; Plate 8d). It is likely that Martins-Neto's observation can be traced back to this artefact. I regard *Cratoligoneuriella leonardii* as a synonym of *Colocrus*.

Martins-Neto (2002b), in his unpublished doctoral thesis, described another species, *Cratoligoneuriella ninae*, and listed this species in a recent publication (Martins-Neto, 2005a). As the description in this doctoral thesis was never properly published, *Cratoligoneuriella ninae* has to be considered as a *nomen nudum*. This thesis was not available to me, so that I cannot comment on the description given there.

Colocrus indivicum McCafferty, 1990

Cratoligoneuriella leonardii (Martins-Neto, 1996a) Syn. nov.
Cratoligoneuriella ninae (Martins-Neto, 2005b) *nomen nudum*

Material: larval holotype AMNH 43484; adult paratype AMNH 43499 (Figure 11.4b); larvae SMNS 66538 (Figure 11.9g; Plate 8d) and SMNS 66619 (Plate 8e); larva RGMN-T005 coll. Martins-Neto; larvae MB.I.2025 (Figure 11.9h) and MB.I.2027 at MNB.

Diagnosis: larva (Figures 11.9g and h; Plate 8d and e): body length up to 15 mm excluding terminal filaments. Length of cerci up to 7 mm. Fore femora short and broad, middle and hind legs longer and slender. Filtering hairs on forelegs.

Alate stage (Figure 11.4b): forewing length 11 mm. Body length 13.2 mm. Wing venation see generic diagnosis, above.

Comment: McCafferty (1990) assigned an adult specimen (Figure 11.4b) of an oligoneuriid with a body length of 13.2 mm to *Colocrus indivicum*. Judging from the size of the holotype larva, it is most likely that it is indeed the alate stage of *C. indivicum*. Figure 11.9h and Plate 8e show in excellent preservation the labial plate that is characteristic for the larvae of all Oligoneuriidae. The filter apparatus is very well visible in specimen SMNS 66538 (Figure 11.9g; Plate 8d).

Colocrus? magnum sp. nov.

Material: larval holotype SMNS 66624 (Figure 11.9i). Putative adults are not rare in the collections; for example, specimen SMNS 66623 (Figures 11.6a and b), which is a fossil oligoneuriid of corresponding size, but the wing venation (Figures 11.6a and b) differs significantly from the adults attributed to *Colocrus indivicum*, so that the generic attribution is only very preliminary.

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 its large body size compared to the other species of the genus.

Diagnosis and description (Figure 11.9i): body length 22.5 mm without terminal filaments. Length of cerci 12 mm; length of terminal filament 9 mm. Femora short and broad.

Ephemeroidea (*sensu* McCafferty, 1991)

There are currently eight different species in eight different genera of Ephemeroidea described from Crato by McCafferty (1990) and Martins-Neto and Caldas (1990). While McCafferty (1990) described only alate stages, the contribution of Martins-Neto and Caldas (1990) only deals with larval specimens. A definite attribution of all larval and imaginal specimens to each other cannot be made at present.

Moreover, the larval specimens are not adequately described, and judging from the figures presented there, the contribution of Martins-Neto and Caldas rather deals with three specimens of a single species than three different genera and species from three different families. However, as I do not have the type material at hand, I here still refrain from synonymizing the three larval specimens described by Martins-Neto and Caldas (1990). The material and diagnoses given by the authors are merely listed.

Four undetermined larval specimens (two specimens SMNS 66630 and SMNS 66634, as well as two specimens without number in collections MURJ and MSF, respectively) and an undetermined adult specimen (MSF without number) of Ephemeroidea are featured in Figures 11.5a–c and 11.6h and i and Plate 8f.

Potamanthidae?

Olindinella gracilis Martins-Neto and Caldas, 1990

Material: larval holotype AMA-I-028 (Figure 11.4c), coll. Federal University of Ceará.

Diagnosis: burrowing larva with rostrum, long mandibular tusk, pubescent, robust tibia, paracercus longer than cercus.

Comment: validity and status doubtful, as discussed above.

Euthyplociidae

Pristiplocia rupestris McCafferty, 1990

Material: adult holotype AMNH 44308 (Figure 11.4d); adult SMNS 66541 (Figures 11.6c and d); various adult specimens in coll. MSF; larvae SMNS 66539 (Figure 11.6e) and SMNS 66621 (Figure 11.6f; Plates 8g and h) (probably two different species).

Diagnosis: alate stage (Figures 11.4d and 11.6c and d): body length 13–14 mm. Forelegs developed, about 4 mm long. Length of forewing 13 mm. Extensive crossvenation throughout wing. RS fork at one-quarter distance from base, MA fork in basal third of wing, MP_2 and CuA strongly decurved posteriorly at base. Cubital field with sigmoid veinlets from CuA to hind margin. A_1 not forked.

Larva (specimen SMNS 66621; Figure 11.6f; Plates 8g and h): body length up to 12 mm excluding terminal filaments (Figure 11.6f). Length of cerci and paracercus up to 2 mm. Abdominal segments II(?)–VII with fringed, doubled, lateral tracheal gills (Plate 8g). Femora flat and broad. Tibial spur not visible. Long, convex mandibular tusks up to 3 mm length, with numerous hairs (Plate 8h).

Comment: the very characteristic larval mandibular tusks equipped with long hairs unambiguously determine the larva as belonging to the Euthylociidae. As there have been only adult specimens of *P. rupestris* found so far, and because there are probably at least two species (Figures 11.6e and f) of euthyplociid larvae (compare the different length and shape of mandibles) from this locality, a definite attribution of one of these two types to the present species is not possible.

Ephemeridae

Australiephemera revelata McCafferty, 1990

Material: adult holotype AMNH 44300 (Figure 11.4e); adult paratype AMNH 44310 (Figure 11.4e).

Diagnosis: ephemeroid forewing, MA forked at midlength, distinct distal arch of CuP, A_1 nearly straight, no cubital intercalaries, hind wing with costal angulation, RS shorter than R_2 and R_{4+5}.

Microephemera neotropica McCafferty, 1990

Material: adult holotype AMNH 43303 (Figure 11.4f).

Diagnosis: ephemeroid forewing, MA forked in basal half of wing, moderate distal arch of CuP, A_1 not forked.

Cratonympha microcelata Martins-Neto & Caldas, 1990

Material: larval holotype USP GP/1T-1677 (Figure 11.4g).

Diagnosis: burrowing nymphs with rounded head, mandible long and smooth, foreleg with expanded tibia, apically with at least two spines.

Comment: validity and status doubtful, as discussed above.

Polymitarcyidae?

Caririnympha mandibulata Martins-Neto & Caldas, 1990

Material: larval holotype GP/1T-1678 coll. University of São Paulo.

Diagnosis: burrowing nymphs with trapezoid head, without rostrum, mandibular tusk short, foreleg with femur and tibia of same length.

Comment: validity and status doubtful, as discussed above.

Baetiscidae

Protobaetisca gen. nov.

Type species: *Protobaetisca bechlyi* sp. nov., by present designation.

Derivation of name: compound noun made up of the Greek prefix *protos* (first) and the Recent genus *Baetisca*.

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

Protobaetisca bechlyi sp. nov.

Material: larval holotype SMNS 66620 (Figure 11.6g).

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 colleague Günter Bechly, curator of fossil insects and amber at the SMNS, who pointed me to fossil mayflies.

Diagnosis and description (Figure 11.6g): larva with stout, rotund body of ovoid shape. Length 8 mm without terminal filaments. Length of cerci 3 mm. Abdominal segments VI–IX with prominent posterolateral projections, without median spines. Lateral margins of abdominal segments I–V bent up. Abdominal segment VI slightly enlarged, longest abdominal segment, with prominent longitudinal crest most probably representing the caudal closure of a gill chamber. Mesonotum posteriorly extending up to abdominal segment VI, forming a gill chamber ('carapace'). Anterior part of gill chamber torn and flaked off. It cannot be decided with certainty if the pronotal part of the gill chamber is preserved in its entity or partly broken off together with the anterior part of the mesonotum). Carapace without dorsal spines, lateral parts of carapace not preserved. Length of preserved part of foreleg 4 mm, length of femur 2 mm, length of tibia 0.8 mm. Head with two frontal carinae. Antennae not preserved.

Comment: apparently, this is the fourth record of a fossil stem group representative of the Prosopistomatoidea. Staniczek and Bechly (2002) described *Balticobaetisca velteni* from Eocene Baltic amber extending the distribution of the

Baetiscidae to the Palaearctic. Jell and Duncan (1986) described a specimen from the Lower Cretaceous as Siphlonuridae? gen. nov. It has the general shape of a baetiscid mayfly with a mesonotum that extends posteriorly to abdominal segment VI. The pronotum is separated from the mesonotum. The authors mentioned its similarities to Baetiscidae but refrained from assigning the fossil to this family because its Recent distribution is Nearctic. Nevertheless this fossil either belongs to the stem group of Baetiscidae or Prosopistomatoidea. Sinitshenkova (2000) described *Cretomitarcys luzzi* from the Upper Cretaceous of New Jersey. She assigned the adult male specimen to the †Cretomitarcyinae, a new subfamily of the Polymitarcyidae. McCafferty (2004) realized its affinities and transferred the fossil to the Prosopistomatoidea (= Carapacea *sensu* McCafferty = Posteritorna *sensu* Kluge). He placed it in a new family, the †Cretomitarcyidae. Judging from the figures given in Sinitshenkova (2000), *C. luzzi* indeed clearly belongs to the Prosopistomatoidea: the wing tornus is situated posterior to A_1. The rounded hind wing with multiple intercalaries points to a phylogenetic position in the stemline of Baetiscidae. *C. luzzi* is plesiomorphic in retaining gonopods with several segments and an entirely separated basitarsus of the foreleg. However, I see no reason in placing this species in a separate family.

Protobaetisca bechlyi sp. nov. is the first record of a fossil Baetiscidae from the Crato Formation. The frontal head projections confirm its placement at least in the stem group of Baetiscidae. If the pronotum was separated a placement in the stem group of Prosopistomatoidea cannot be excluded.

The alleged fossil Baetiscidae *Cariephemera marquesi* (Zamboni, 2001) definitely does not belong to the Baetiscidae (see below).

Other records of unnamed Ephemeroptera

- Siphlonuridae (?) sp. 1 McCafferty (1990: 30, figure 11; AMNH 44306, adult)
- Siphlonuridae (?) sp. 2 McCafferty (1990: 30, figure 12; AMNH 44313, adult)
- Siphlonuridae (?) sp. 3 McCafferty (1990: 31, figure 13; AMNH 43477, adult)
- Oligoneuriidae gen. et sp. indet. Martins-Neto (1996a: 188, figure 6c; adult)
- Ephemeroidea *incertae sedis* (Figures 11.5a and b and 11.6h and i; Plate 8f); larval specimens SMNS 66630, SMNS 66634, without number in collections MURJ and MSF)
- Ephemeroidea *incertae sedis* (Figure 11.5c; adult specimen, MSF without number)
- Ephemeroidea sp. 1 McCafferty (1990: 42, figure 30; AMNH 44311, adult)
- Ephemeroidea sp. 2 McCafferty (1990: 42–43, figure 31; AMNH 43480, adult)
- Leptophlebiidae (?) sp. 1 McCafferty (1990: 43, figure 32; AMNH 43474, adult)
- *Comment*: this taxon is relatively frequently found. Other specimens (e.g. SMNS 66639, Figure 11.5d) demonstrate that specimen AMNH 43474 is not a larva, but an adult without preserved wings. The other fossils generally have entangled or wizened wings (probably subimagines) and also only two terminal filaments (cerci).

- 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 belong to the same genus. A careful revision by a specialist on fossil Trichoptera would be very useful. Furthermore, there are several putative new genera and species to be described, such as specimens nos SMNS 66282 (Figure 11.87d), SMNS 66287 (Figure 11.88a) and SMNS 66568 (Figure 11.88b), which are clearly distinct from any described species.

Crato Lepidotera: moths and butterflies

Lepidoptera are extremely rare in the Crato Formation and only members of the microlepidopteran grade occur. Martins-Neto and Vulcano (1989b) and Martins-Neto (1999, 2001b) described the following five taxa.

- *Parasabatinca caldasae*: Micropterygidae; body length 3.5–5 mm; forewing length 3–3.5 mm; R_2 and R_3 ending near apex. Besides the holotype, a single specimen (SMNS 66279) has been identified as this species (Figure 11.87c).
- *Undopterix caririensis*: Undopterygidae; hind wing length 3.1 mm; M_1+M_2 fork slightly posterior to R_4+R_5 fork; CuA ending at anal margin near apex.
- *Gracilepterix pulchra*: in familia *incertae sedis*; similar to *Undopterix*; body length and forewing length about 3 mm; hind wing length 2.3 mm; R_1 forking anteriorly of R_2+R_3 and R_4+R_5 forks in forewings; Sc and R_1 unbranched in hind wings. One specimen of this species (SMNS 66277) has been identified (Figure 11.87d). This fossil butterfly was incorrectly listed as *Gracilepteryx* (*sic*) by Martins-Neto (2005b).
- *Xena nana* Martins-Neto, 1999b: Eolepidopterigidae. This taxon seems to be similar to *Eolepidopterix* and is said to be described by 'Martins-Neto, 2000' according to Martins-Neto (2005b), which seems to be a *lapsus* and should be 'Martins-Neto, 1999b'.
- *Psamateia calipsa* Martins Neto, 2002: the present author could not locate the publication with this description, which is mentioned by Martins-Neto (2005b).

All the above species belong to the most primitive and most basal grade of Lepidoptera, and thus not within the Glossata, although Martins-Neto (2005b: 480) attributed all five species to the Eolepidopterigidae, but without explication. However, Grimaldi and Engel (2005: 562, figure 13.16) figured an unnamed primitive moth (AMNH SF 46441) with a piercing oviscapt similar to the Recent families Eriocraniidae and Acanthopteroctetidae that are indeed basal Glossata. This fossil could be the most derived Lower Cretaceous lepidopteran yet discovered, if it should not turn out to be just a small trichopteran like *Cratorella media*.

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