THE CRATO FOSSIL BEDS OF BRAZIL

Window into an Ancient World

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Crato fossils

The first records of Zygentoma from the Crato Formation are those of Bechly (1998a). Two specimens of Lepismatidae were described by Sturm (1998). Since then, a further undescribed specimen (Plate 7a) was found in the Stuttgart (SMNS) collection. Due to their relatively poor state of preservation, neither a determination of the sex, nor a formal taxonomic description as a new species, has been possible. Consequently, these specimens have only been determined as "Lepismatidae gen. spec. 'Araripe'" by Sturm (1998).

Lepismatidae

Lepismatidae gen. spec. 'Araripe' Sturm, 1998

Material: no. B 99 at SMF; no 1998 III/4 at BSPGM; and no. SMNS 66535 (Plate a). A fourth specimen without number from AMNH was figured by Grimaldi and Engel (2005: 152, figure 5.6).

Diagnosis: body 10.5–14 mm long and 3–4 mm wide; head orthognathous; filiform antennae 10.5–13.5 mm long; filiform cerci (12–18 mm long, the only 8.8-mm-long cerci in specimen B 99 are obviously broken off) and terminal filum (13–21 mm long), all provided with setae; wingless; body robust; legs stout with flattened, broad and oval-shaped coxae.

11.3 Persisting-type stem group Ephemeroptera

Rainer Willmann

Organisms do not evolve at equal rates. While many Recent taxa are of entirely modern appearance, others are plesiomorphic in many respects, and in some insects plesiomorphic structures determine their body plan. This is not necessarily related to the age of the respective taxa, but of course some taxa, be it species or large species groups, have become separated from their sister group only recently, while others are very old and have changed little, even over several tens of millions of years. In both cases the latter types of organism have been called living fossils, a term introduced by Charles Darwin. However, such types have lived at any time in the history of life. As the term living fossil cannot well be applied to relatively plesiomorphic fossil species or species groups, the term persisting type, first introduced by Huxley, may be applied. Such types belonging to ephemeropteroid insects in its widest sense were in existence in the Lower Cretaceous of Brazil (Figures 11.2 and 11.3; Plates 7c–h).

Numerous mayflies of the crown group Ephemeroptera (about 3,100 described Recent species) have been described from Triassic, Jurassic, Cretaceous and Cenozoic strata including the Crato Formation (see review by McCafferty, 1990). No

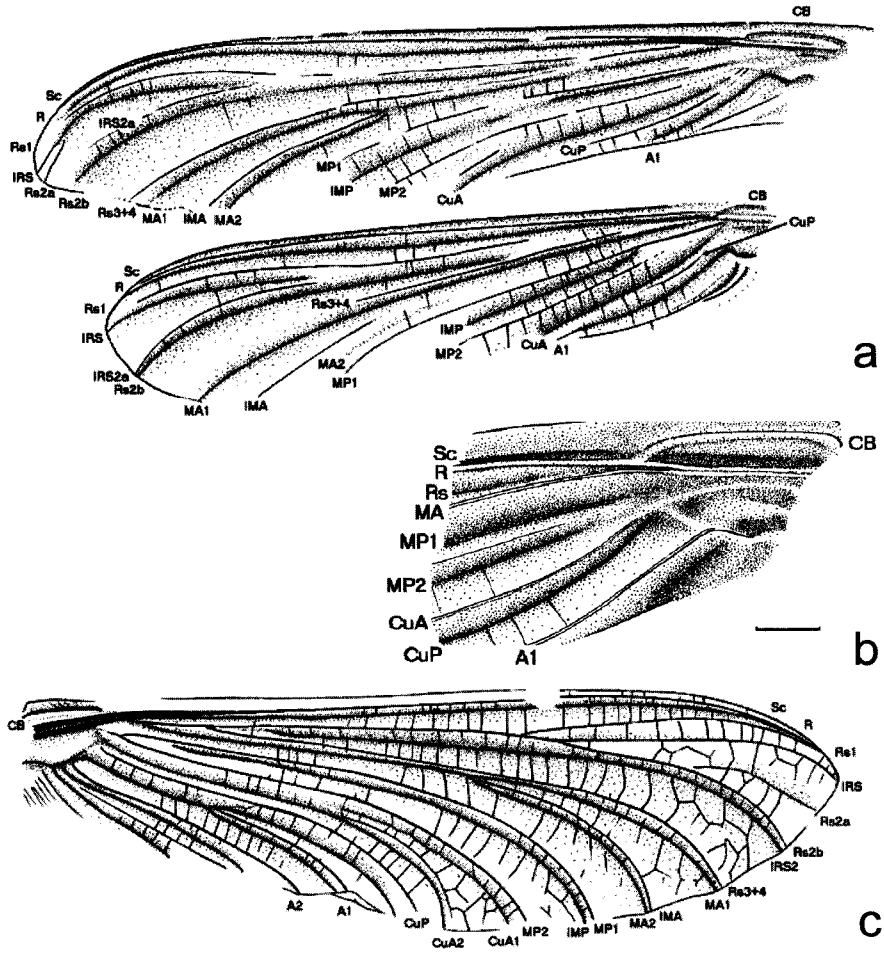

Fig. 11.2. Stem group Ephemeroptera; *Cretereisma* spp. wing venation of holotypes: (a) *Cretereisma antiqua* sp. nov., SMNS 66546, left fore- and hind wings (right wings of the living animal); (b) same specimen as (a), showing basis of left forewing (right wing of the living animal) with additional structures as observed in the right wing; (c) *Cretereisma schwickertorum*, SMNS 66598. Right forewing (left forewing of the living animal). Note the costal brace which does not reach the anterior wing margin. Both original specimens are seen in ventral view and convex veins are preserved as concave and vice versa. Drawings by R. Willmann.

such form is known from the Palaeozoic. On the other hand, numerous stem group representatives of Ephemeroptera are known from the Carboniferous and Permian, and it has been assumed that most of them, and all of those with more than seven pairs of nymphal abdominal gills, were extinct by the end of the Permian.

During a meeting of the fossil-insects network of the European Scientific Foundation in Portsmouth in 1998, David Martill exhibited specimens of a nymph from

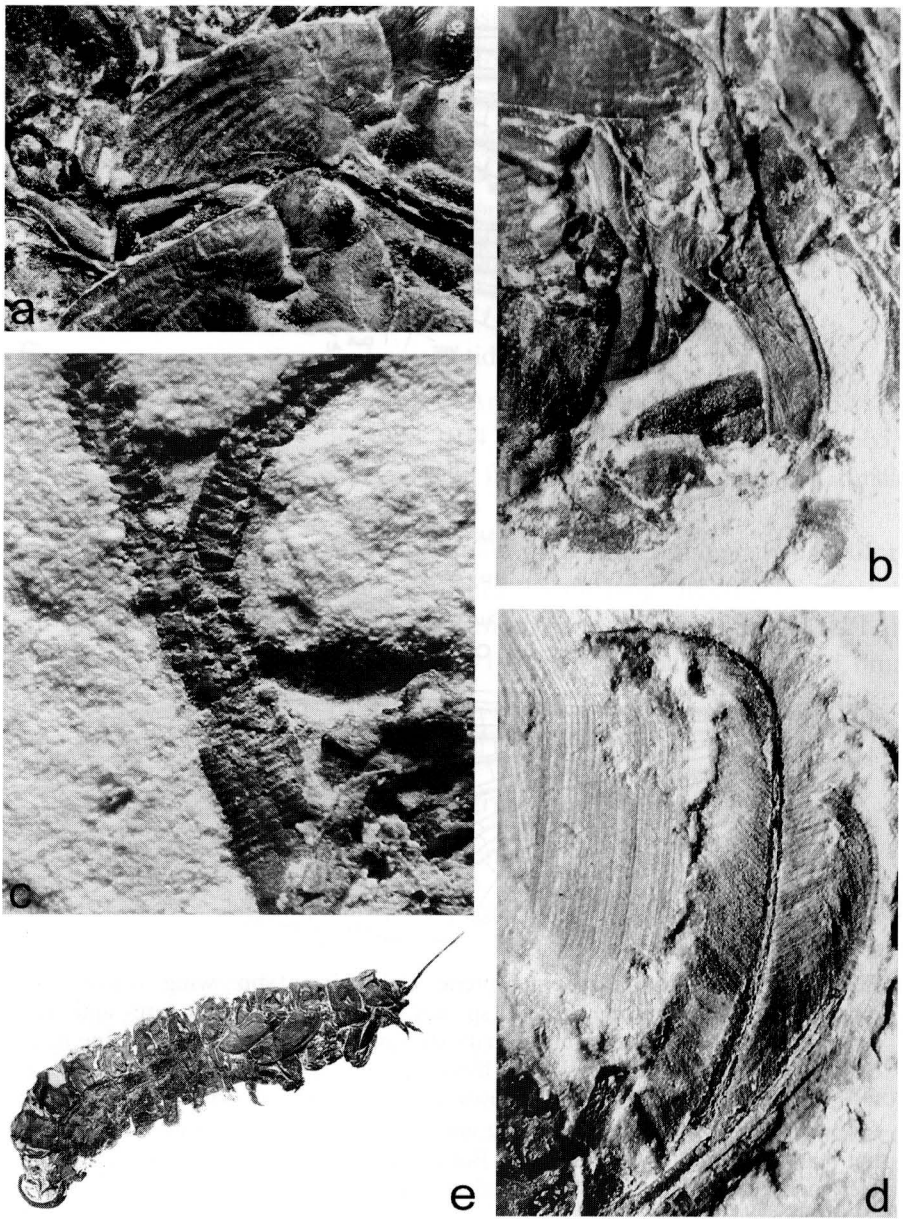

Fig. 11.3. Stem group Ephemeroptera; *Cretereisma* sp. nov., anatomical details of nymphs. (a) Forewing pad and proximal part of hind wing pad, SMNS 66673. (b) First abdominal left gill plate overlying femur-tibia-joint of hind leg. Its basal area is overlain by the tip of the hind wing pad. The dark area near the left margin is the posterior part of the coxa, SMNS 66673. (c) Bases of terminal appendages, SMNS 66601. (d) Left circus (on the right) and paracercus, showing setation, SMNS 66604. (e) *Cretereisma* sp., nymph, no. 512 MURJ. Photographs (a)–(d) by R. Willmann, photograph (e) by G. Bechly.

the Crato Beds that appeared to belong in mayflies but clearly not into any taxon previously known from the late Mesozoic. Comparison with stem group representatives of mayflies showed that the new finds belong here. Later, Günter Bechly obtained specimens of large adult mayflies that showed characters that were as plesiomorphic as those of the nymphs. I completely agree with Bechly *et al.* (2001a), who discussed and figured beautiful larval and adult specimens as ancestral mayflies similar to Protereismatidae, that both nymphs and adults belong to the same archaic taxon. These specimens are described below.

Systematics

Including ephemeroid-like insects, the mayflies have been classified into the crown group and the stem group representatives. An early example is Handlirsch (1908: 1292 and plate LX), who distinguished between a subclass Ephemeroidea including the Plectoptera (= Agnatha), and the Protephemeroidea. Crampton (1938: 170) wrote that the Ephemerida were probably derived from the Protephemerida, and that the Ephemerida and Protephemerida might be grouped into a superorder called the Panephemeroptera or Ephemeropteria. The names Protephemeroptera and Protephemerida refer to the Carboniferous *Triplosoba pulchella* (Brongniart, 1893), which is, however, possibly not a stem group representative of the mayflies (Willmann, 1999). Therefore, one might abandon the names Panephemeroptera or Ephemeria. Lauterbach (1973), however, proposed to call a crown group and the entirety of its stem group representatives with the prefix Pan-, and accordingly, under a phylogenetic view, the name Panephemerida would still be both useful and acceptable. Numerous stem group representatives of the mayflies have been described since the discovery of *Triplosoba*.

Categorical ranks have varied from subclass (Ephemeroidea *sensu* Handlirsch, 1908) through superorder (Ephemeroidea *sensu* Weber, 1933), cohorts (Ephemeriformes; Rohdendorf, 1977) to order (Ephemeroptera), suborder and infraorder. The latter two ranks have been applied to the crown group mayflies, or Euplectoptera, which were, however, consistently called Ephemeroptera, Ephemerida or Plectoptera when only Recent species were considered. Carpenter (1992) called the mayflies *sensu latissimo* (including *Triplosoba*) Ephemeroptera and assigned them ordinal rank. Categorical ranks will not be used here because of the inapplicability in a phylogenetic context.

Several taxon names for stem group representatives do not refer to monophyla and should be abandoned (for Permoplectoptera, see remark of Illies, 1968: 6). Willmann (2006) reviewed the phylogenetic relationships among the early mayflies *sensu lato* and systematized the stem group representatives, including *Cretereisma*,

as follows, attempting to preserve established names (synonyms are given only as examples).

1. Panephemeroptera Crampton (= Ephemerata Boudreaux; = Ephemeridea Rasnitsyn, 2002 (in Rasnitsyn and Quicke, 2002), = Ephemeroptera *sensu* Tshernova, 1962, Carpenter, 1992 and others, = Ephemerida *sensu* Kukalová-Peck, 1985)

? 1.1 *Triplosoba* ('Protephemeroptera')
1.2.1 *Bojophlebia*
1.2.2 Ephemerontoida (= Ephemerida *sensu* Boudreaux, 1979: 271)
1.2.2.1 *Syntonoptera*
1.2.2.2 Ephemeronta
1.2.2.2.1 *Lithoneura*
1.2.2.2.2 Reticulata (= Plectoptera *sensu* Tshernova, 1962, 1970, = Ephemerida *sensu* Kluge and Sinitshenkova, 2002 (in Rasnitsyn and Quicke, 2002) and others, = Ephemeroptera *sensu* Grimaldi and Engel, 2005)
1.2.2.2.2.1 *Protereisma* (+*Misthodotes*?)
1.2.2.2.2.2 Heptabranchia
1.2.2.2.2.2.1 *Cretereisma*
1.2.2.2.2.2.2 n.n.
1.2.2.2.2.2.2.1 *Litophlebia*
1.2.2.2.2.2.2.2 Triangulifera (= Euplectoptera *sensu* Tshernova, 1962, 1970,? = Euplectoptera *sensu* Tillyard, 1932) (= *Paedephemera multinervosa*+remaining ephemeroids, which include, among others, the Ephemerida) (Ephemereida = Ephemeroptera *vel* Plectoptera auct., = Euplectoptera *sensu* Grimaldi and Engel, 2005,? = Euplectoptera *sensu* Tillyard, 1932; = crown group of the entire ephemeropteran lineage).

In the following, the vernacular term ephemeroid is used for any taxon which is considered to be more closely related to modern mayflies (Ephemerida) than to any other Recent taxon.

Cretereisma gen. nov.

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

Etymology: named after the Cretaceous age and the similar fossil genus *Protereisma*.

Diagnosis: adult fore- and hind wings of almost equal size, narrow, distal portions only slightly broader than their basal parts. Costal brace long and only slightly arched. Anal veins long, meeting the hind margin of the wings at low angle (plesiomorphies shared with *Protereisma* and, in part, earlier branches of ephemeroids). Several longitudinal veins run pairwise and almost parallel to each other towards the wing margin, each pair consisting of a concave and a convex

vein (IRS_{2a} and R_{2b}; RS_{3+4} and MA_1; IMA and MA_2; MP_1 and IMP; MP_2 and CuA_1; ICuA and CuA_2 respectively). Nomenclature of veins as developed by Tillyard (1932) for *Protereisma*. The main CuA vein appears to be CuA_2, while this is CuA_1 in *Protereisma*.

Nymph caterpillar-like or gammarid-like in appearance, with undivided tarsus bearing one claw. Pro-, meso- and metathorax subequal in size, hind wing pads only slightly shorter than forewing pads. Abdomen with seven pairs of elongated plate-like gill appendages.

Comment: these generic characters – that is, characters found in both species of *Cretereisma* – are not repeated in the following descriptions of the two species.

Cretereisma antiqua sp. nov. (Figures 11.2a and b; Plate 7c)

Material: holotype SMNS 66546 (old no. 28) (figured by Bechly *et al.*, 2001a: 48, Abb. 37).

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

Etymology: *antiquus*, Latin, old. The name refers to the very archaic structure of the species, which resembles the Permian *Protereisma* in many aspects.

Description (Figures 11.2a and b): specimen with all four wings spread out, visible from its ventral side. Body length 18 mm. Forewing length 24 mm. Hind wing measuring about four-fifths of forewing length. Sc running towards wing apex, curving posteriorly towards R. CuA and CuP simple. A_1 short (not extending beyond the first quarter of the wing), probably simple; remaining anals difficult to trace (the veinal description applies for both the fore- and the hind wings). Abdominal segments as broad as those of the thorax, head as broad as thorax, with large bulging eyes. Antennae and abdominal appendages not preserved.

Cretereisma schwickertorum sp. nov. (Figure 11.2c; Plate 7d)

Material: holotype SMNS 66598 (old no. H51).

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

Etymology: the species is named in honour of Mr and Mrs Schwickert, Sulzbachtal, Germany, for generously supporting scientific research on Crato Formation fossils for nearly 15 years.

Description (Figure 11.2c): left wings missing except the very bases, right hind wing very fragmentary. Body length 32 mm. Forewing length 31 mm. Wing venation as in *C. antiqua* but A_1 almost extending to the middle of the wing and with a well-developed triad. With more anal veins behind A_1 than in the previous species.

Head, thorax and abdomen of almost the same width. Antennae, legs and abdominal appendages not preserved.

Comment: the circumstance that almost no crossveins have been noticed in the costal areas of both *C. antiqua* and *C. schwickertorum* is certainly due to preservation.

Comparison with *C. antiqua*: the differences in venation between the two species are a result of size differences, *C. schwickertorum* being considerably larger. In the latter, more anal branches are present to strengthen the posterior basal wing area. I do not believe that the differences, especially the absence/presence of a well-pronounced triad on A_1, is due to intraspecific variation or sexual dimorphism.

Two further well-preserved adult specimens of *Cretereisma* spp. are deposited without number in the collection of SMF.

Nymphs (Figures 11.3a–d; Plates 7e–h)

According to the size and morphology of the flying stages, the nymphs of the two species described above must have been of considerable size, have had four wing pads of almost equal size and, as a necessity of the latter property, a well-developed meso- and metathorax. Many specimens fulfilling these requirements have been found in the Crato Formation and are considered to be members of *Cretereisma*. These nymphs are not so rare in the Crato Formation, and are well-known to the local quarry workers under the vernacular term *Ananas* or pineapple.

Material: there are 10 nymphs with the nos SMNS 66547 (old no. 33; figured by Bechly *et al.*, 2001a: 47, Abb. 36), SMNS 66548 (old no. L74), SMNS 66549, SMNS 66599 (old no. 30), SMNS 66600 (old no. 31), SMNS 66601 (old no. 32), SMNS 66602 (old no. H54), SMNS 66603 (old no. L73), SMNS 66604 (old no. H52), and SMNS 66605 (old no. 29); three further specimens have been recently donated to SMNS (SMNS 66673, SMNS 66674, SMNS 66675). A very nice nymph is specimen MB.I.2028 at MNB, and additional specimens are held by SMF. One of the best-preserved nymphs is specimen no. 512 in coll. MURJ (Figure 11.3e). Another nymph from AMNH was figured by Grimaldi and Engel (2005: 166, figure 6.13).

Specimen SMNS 66673 (Figures 11.3a and b; Plate 7e) was chosen as the basis of nymphal description mainly because of its good general state and the complete preservation of its left wing pads): the animal is visible from its left side. Body length 33 mm. Thoracomeres and abdominal segments are very high (body not flattened), which give the animal a somewhat caterpillar-like appearance. Sclerites with numerous fine pores are present which may have been the insertion points of bristles (see description of additional material).

Description (Figures 11.3a and b): head short, about as long as prothorax, and probably with burrowing devices. Mouthparts only fragmentarily preserved.

Antenna long, with big basal segments (only a very faint impression of one antenna directed forwards is left). Pro-, meso- and metathorax of almost equal length, mesothorax slightly longer than the other two thoracomeres. Thoracic terga with pronounced hind margins. Meso- and metathorax with wing pads of subequal shape, the hind wing pad being slightly shorter than that of the forewing. The forewing base is attached to the thorax as follows: laterally, the tergite has two knob-like elevations opposite to the anterior basal wing area; these elevations being set apart from the wing pad by a deep longitudinal incision. The posterior lateral area of the tergite is slightly elevated and separated by a longitudinal groove from a still more lateral elevation near the middle of the wing base. The hind margin of the wing pad runs continuously into the hind margin of the mesothoracic tergite. The situation in the metathorax is the same, but the structures are less pronounced due to the slightly smaller size of the hind wing pad. As already proposed by Bechly *et al.* (2001a: 48), it appears that the wing pads were moveable along the deep incision mentioned above. Such moveable wing pads represent a very archaic character state, which is otherwise only known from Palaeozoic pterygote larvae. Legs stout; coxae very large and broad. Fore coxa slightly shorter than the fore femur, middle and hind coxae almost as long as the respective femora. The fore legs are the longest.

The first eight abdominal segments are of subequal length, the remaining ones being considerably shorter. Segments 1–7 each with a pair of strongly scleritized elongated lateral gill appendices which are directed downwards in the fossil. Their distal parts appear to have been strongly scleritized into plate-like structures and are slightly curved forwards. Gill plates with a pronounced margin around their distal portions. The gill appendices insert laterally at the abdomen with a broad base. As the bases are irregularly crumbled it appears that this portion was not developed as a plate in the living animal. Abdominal tergites 8–10 extend more ventrally than the preceding ones. Cerci are lacking in this specimen due to preservation.

Additional material as listed above shows well-preserved long antennae and fairly long cerci and paracercus. Antennae about as long as head and thorax combined (e.g. SMNS 66599, SMNS 66600, SMNS 66547). Paracercus with row of long setae on each side, cerci with one row of setae only. Cercal joints and joints of paracercus short. Femora with strong bristles or hairs (SMNS 66599 and SMNS 66604), coxa similarly equipped (SMNS 66547; other leg segments do not show such structures possibly due to preservation of the specimens available for study). Tarsi one-segmented, claws pointed. Specimen SMNS 66674, which is partly preserved as a negative imprint, shows impressions of longitudinally directed long body hairs on the abdomen. The small pores on the sclerites of other specimens may correspond to these hairs and might have been insertion places. Gill appendages fringed with hairs.

Body lengths in the additional material range from 10.5 mm (SMNS 66605) to 26 mm (SMNS 66547 and SMNS 66604) and even 30 mm in one specimen (SMNS 66549), without antennae and abdominal appendages.

It was not possible to distinguish, in the nymphs, between the two species described above from adult specimens.

With exception of specimen no. MSF Z78, all nymphs of *Cretereisma* are embedded in a lateral position. Furthermore, these nymphs clearly have a laterally compressed body, which seems to be a unique autapomorphy, because such a habitus is unknown from other fossil and Recent mayfly nymphs. Bechly *et al.* (2001a: 49) therefore suggested that these peculiar larvae had a very different lifestyle than all other known mayflies.

Comparisons

The general wing structure of *Cretereisma* resembles closely that of *Protereisma*. A main difference is the pairwise alignment of some of the longitudinal veins which is an autapomorphy of *Cretereisma*. Another difference lies in the structure of the first anal vein, which is simple in the forewing of *Protereisma* and *Misthodotes* while it has a triad in the hind wing (Carpenter, 1933). In *Cretereisma*, however, A_1 is apparently either simple in both wings (*C. antiqua*) or has a triad at least in the forewing (*C. schwickertorum*; structure of hind wing anals unknown). The general tendency towards a reduction of anal branches is probably correlated to the reduction of wing width. Nymphs are different from those of *Protereisma* (and *Phthartus*) in their unique body shape and their plate-like gill appendages, and both *Protereisma* and *Phthartus* have nine abdominal gill pairs while *Cretereisma* is more derived in having seven. Epeoromimidae have seven pairs of plate-like gill appendages as well; however, this is the only remarkable similarity worth mentioning. In other structures, epeoromimid nymphs differ fundamentally from *Cretereisma*, for example in body shape, a small prothorax and posteriorly directed wing pads, of which the hind pair is only small.

Phylogenetic position

Cretereisma shares with the Permian *Protereisma* and *Misthodotes* a reduced anal area in the hind wing and the possession of a costal brace which is only slightly curved and does not reach the costal margin. These characters were not present (or have not been observed) in earlier ephemeroids. *Cretereisma* is more derived than *Protereisma* in having only seven gill appendages in the nymph. On the other hand, the Upper Triassic *Litophlebia*, which resembles *Protereisma* in many aspects, possibly shares at least one synapomorphy (shortened anal veins) with the

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.

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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