
Natália C.A. Brandão a, b, *, Jonathas S. Bittencourt b, Adolfo R. Calor c, Marcio Mendes d, Max C. Langer e

a Programa de Pós-graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, 31270-901, Belo Horizonte MG, Brazil
b Laboratório de Paleontologia e Macroevolução, CPMTC, Departamento de Geologia, Instituto de Geociências, Universidade Federal de Minas Gerais, Av. Antônio Carlos 6627, 31270-901, Belo Horizonte MG, Brazil
c Laboratório de Entomologia Aquática (LEAQ), Instituto de Biologia, Universidade Federal da Bahia, Av. Barão de Jeremoabo, 147, Campus Ondina, 40170-115, Salvador BA, Brazil
d Laboratório de Paleontologia, Centro de Ciências, Universidade Federal do Ceará, campus do Pici, 60455-760, Fortaleza CE, Brazil
e Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, 14040-901, Ribeirão Preto SP, Brazil

**A R T I C L E  I N F O**

Article history:
Received 3 December 2020
Received in revised form 5 May 2021
Accepted in revised form 29 May 2021
Available online xxx

Keywords:
Aquatic insects
Fossil
Mayfly
Paleontology
Gondwana
Taxonomy

**A B S T R A C T**

A new genus and species of Ephemeroptera, Astraeoptera cretacica gen. et sp. nov., is described from the Lower Cretaceous limestone of the Crato Formation (Brazil). The new taxon has the following diagnostic characters: veins MP2 e CuA straight at their bases, MA branching in the apical half of wing length, CuA not forked, cubital field with longitudinal veins sub-parallel to CuA. It was compared with other adult mayflies worldwide, both fossil and extant, and could not be assigned to any known ephemeropteran family. In addition, holotypes of other two mayfly species were reanalyzed, resulting in taxonomical changes. A new description of the Costalimella zucchii Zamboni, 2001 holotype is provided, indicating its placement within Hexagenitidae, rather than Siphlonuridae, as previously proposed. We also reanalysed the holotype of Cratogenites corradiniae Martins-Neto, 1996, providing new and more accurate information about the species and confirming its junior synonymy to Proligoneuria limai Demoulin, 1955. Our results indicate that the diversity of Crato Formation mayflies, both at species and family level, is greater than previously thought, confirming the predominance of hexagenitids among Cretaceous ephemeropterans.

© 2021 Elsevier Ltd. All rights reserved.

1. Introduction

Ephemeroptera is a widespread order of amphibiotic insects (Dominguez et al., 2006; Da-Silva and Salles, 2012), popularly known as mayflies. Their temporal record spans minimally from Permian (Grimaldi and Engel 2005; Stanczak, 2007) to recent, with approximately 3500 extant species described so far (Sartori and Brittan, 2015). The phylogenetic position of the group is controversial and has been discussed on the basis of three hypothesis: (i) as closely related to Odonata (Palaeoptera hypothesis; Martynov, 1925; Cramp, 1924; Haas and Kukalová-Peck, 2001; Kukalová-Peck, 2008; Regier et al., 2010; Blanke et al., 2013; Song et al., 2019), (ii) as closely related to Neoptera (Chiasomyaria hypothesis; Carle, 1982a, 1982b; Kjer, 2004; Yoshizawa and Johnson, 2005; Misof et al., 2007; Simon et al., 2009), and (iii) sister group of clade Odonata + Neoptera (Metapterygota hypothesis; Stanczak, 2000; Wheeler et al., 2001; Ogden and Whiting, 2003; Grimaldi and Engel, 2005; Willkommen and Hörnschemeyer, 2007; Zhang et al., 2008). Despite this long
history of disagreement, there is a general consensus that mayflies constitute an early branch of winged insects (Grimaldi and Engel, 2005; Dominguez et al., 2006; Staniczek, 2007; Sartori and Brittain, 2015).

The paleodiversity of mayflies is particularly noticeable during the Cretaceous, with 50 genera and 69 species described from all continents, except Antarctica, a distribution that is coincident with that of extant Ephemeroptera (Sartori and Brittain, 2015). Mayfly species are especially diverse in the Early Cretaceous, partly due to their abundance and exquisite preservation in the Aptian strata of the Crato Formation (Araripe Basin), northeast Brazil. Fifteen mayfly species have been described from this lithostratigraphic unit, including representatives of the families Australophiloxeridae (Australiphemera revelata McCafferty, 1990 and Microphemerina neotropica McCafferty, 1990), Baeticidae (Prisiptobasica bechlyi Staniczek, 2007), Ephemeridae (Cratonympha microlecuta Martins-Neto and Caldas, 1990), Euthyplociidae (Protoligoneuria limai Demoulin, 1955, Cratohexagenites longicus Staniczek, 2007 and Cratohexagenites minor Staniczek, 2007), Oligoneuriidae (the recently described Incogamenia nubila Storari et al., 2020, Colocorus magnus Staniczek, 2007 and Colocorus individivum McCafferty, 1990, recently redescribed as an hexagenitid by Storari et al., 2020), Poly- mitarciidae (Cariniphemera mandublata-Martins-Neto and Caldas, 1990), Potamanthiidae (Olinellina gracilis Martins-Neto and Caldas, 1990), and possibly Siphlonuridae (Costalimella nordestina Martins-Neto and Caldas, 1996 and Costalimella zuchii Zamboni, 2001). In fact, several previously proposed species not listed above have been synonymized in the last years (see review of Staniczek, 2007). This is the case of the putative hexagenitid Cratogenites corradianiae Martins-Neto, 1996, synonymized with Protoligoneuria limai by Staniczek (2007).

The above-mentioned record represents ca. 7.5% of the 121 insect families of the Crato Formation (Moura-Júnior et al., 2018). Also according to those authors, more than 100 species have been described in the last decade, which demonstrates the enduring potential of the Crato Formation as a haven for taxonomic studies of insects. Despite the significant, already known diversity, some of which requires new investigations, there are hundreds of mayfly specimens from the Crato Formation deposited in research institutions in Brazil and abroad still awaiting study. Those have the potential to reveal an even greater taxonomic and morphological diversity. In order to expand the available data about the ephemeropteran diversity in the Early Cretaceous, we describe a new species and genus that could not be assigned to any of the known mayfly families and redefine the holotypes of Cratogenites corradianiae and Costalimella zuchii, which have been subject of disagreement over their morphology due to insufficient description and/or illustration. We also discuss the implications of the new data for the taxonomy and paleodiversity of the Crato Formation mayflies.

2. Geological setting

The specimens dealt with here are preserved in laminated limestone slabs of the Crato Formation (Araripe Basin), northeast Brazil (Martill and Wilby, 1993; Viana and Neumann, 2002; Warren et al., 2017). Martill and Wilby (1993) and Martill and Heimhofer (2007) divided the Crato Formation into four members — Nova Olinda, Caldas (formerly Barbalha), Jamacaru, and Casa de Pedra — whereas other authors support the division of this stratigraphic unit into different carbonate sequences (Viana and Neumann, 2002). The exact locality of the holotype of the new species described here is unknown, yet its provenance from the Crato Formation is attested by historical records of the specimen, as well as its lithological and taphonomic features.

The Crato Formation paleoenvironment has been variously considered as a lake or lagoon, but recent data based on multiproxy analyses suggest that this Lagerstätte is better interpreted as a seasonal, semi-arid, shallow lacustrine wetland (Ribeiro et al., 2021). The age of the Crato Formation has been considered as late Aptian in most papers dealing with the biostratigraphy of the Araripe Basin (Ponte & Appi, 1990; Araújo et al., 2001; Coimbra et al., 2002; Heimhofer & Hochuli, 2010; Coimbra & Freire, 2021). A recent work suggested a latest Barremian—earliest Aptian deposition for the black shales of the Ipubi Formation (overlying the Crato Formation), based on Re–Os absolute ages (Lúcio et al., 2020).

Based on those isotopic data, the authors proposed a Barremian—early Aptian age for the Crato Formation. Yet, this proposition has been criticized due to its inconsistency with the biostratigraphic data (Coimbra, 2021) and is open to scrutiny.

3. Material and methods

The specimens studied in this paper are housed in the fossil collections of the Laboratório de Paleontologia de Ribeirão Preto (LPRP/USP), Universidade de São Paulo, in Ribeirão Preto, Brazil, and Laboratório de Paleontologia, Centro de Ciências, Universidade Federal do Ceará (LUP/UFCE), in Fortaleza, Brazil.

Photographs were taken with a Leica DFC 295 camera, coupled to Leica M205C stereomicroscope. Image processing was made with Leica Application suite LAS v.3.8 and line drawings using a lightbox and later digitized and edited using Adobe Illustrator CC 2017. The descriptive terminology, including wing venation, follows Kluge (2004).

This work has been registered in the Official Register of Zoological Nomenclature (ZooBank) with LSID urn:lsid:zoobank.org:pub:77D723D8-55B1-4F55-94EB-DF746F59EC9F.

4. Taxonomy

Class Insecta Linnaeus, 1758
Order Ephemeroptera Hyatt and Arms, 1891
Suborder Euplectoptera Tillyard, 1932
Family Incertae sedis

Genus Astraeoptera gen. nov.
Type species: Astraeoptera cretica sp. nov., by monotypy.

Etymology. The generic name derives from Latin Astraeus (Greek: Αστραες), god of dusk; and ptera, wings (New Latin). In reference to Aristotle’s description of “ephemerum” in History of Animals, mentioning that these insects live and fly until evening and die at the sunset. Diagnosis. As for the species.

Astraeoptera cretica sp. nov.
(Figs. 1–2).

Holotype. A female imago, LPRP/USP 0504 (incomplete individual, exposed in right lateral view).

Etymology. The epithet refers to the Cretaceous strata of the Crato Formation.

Type locality and horizon. Unknown locality, Crato Formation (Araripe Basin), Northeast Brazil, upper Aptian.

Diagnosis. Pterothorax robust, wider than prothorax. MP2 e CuA straight at their bases; MA branching in the apical half of wing at about two-thirds of MA length; CuA not forked; cubital field with longitudinal veins sub-parallel to CuA.
**Description.** Female imago. Small size (7.5 mm, excluding cercus). Forewing length 5.0 mm, its width 3.5 mm. Head wider than long (length 0.5 mm). Eyes too incomplete to be described. Prothorax small (length 0.5 mm); pterothorax well-developed (length 2.0 mm), mesothorax large. Foreleg long, middle and hind legs fragmented; length of foreleg fragment 5.0 mm (femur preserved 1.5 mm, tibia + tarsus 3.5 mm). Forewing with tornoapical (outer) margin about two times longer than basitornal (anal) margin; costal area wide, narrowing toward tip; the field between Rs and RA is narrow in its basal portion, becoming wider in its apical half; entire forewing with numerous crossveins, except the cubital area; C, Sc and RA not branched and sub parallels; no conspicuous gemination of longitudinal veins; RS basally branched at about one-quarter of wing length (RS fork at 1.8 mm from wing base); RS formed triad RSa-iRS-RSp, iRS approximated RSp; RSa formed triad RSa1-iRSA-RSaa2; RSa2 formed triad RSa2-iRSA2-RSaa2`; RSp non-branched; MA branched in apical half of wing at about two-thirds of MA length; MA1 and MA2 uniformly diverging; iMA equidistant to MA1 and MA2; the distance between the forks RS and MA is approximately 2.3 mm; MP basally branched, with very short common stem; iMP slightly approximated with MP1; distinct intercalary veins existing between MP2 and CuA; MP2 and CuA veins are straight at their

![Image of Astraeoptera cretacica sp. nov., female imago, holotype, LPRP/USP 0504.](image-url)

*Fig. 1.* Astraeoptera cretacica sp. nov., female imago, holotype, LPRP/USP 0504. (A) Photograph of lateral view. (B) Line drawing of lateral view. Captions: Ce, Cerci; Fl, fore leg; Fw, fore wing; He, Head; Hl, hind leg; Pt, Pterothorax; Ta, Tarsus of middle leg; VII–X, Abdominal tergum VII–X. Scale bar: 5 mm.
bases; cubital field with long longitudinal veins sub-parallel to CuA, which originate at the base of the wing and culminate in the outer margin. Abdomen with first segment covered by metathorax; segment VII widest (abdomen length 4.5 mm, maximum width segment VII 1.5); segment X apparently preserving one cercus. Paracercus not preserved. Cercus fragmented, almost the same length of body (length 6.5 mm).

Family Hexagenitidae Lamereere, 1917

**Costalimella zucchii** Zamboni, 2001

(Fig. 3)

2006b **Costalimella zucchii** Martins-Neto, p. 196
2007 **Costalimella zucchii** Zamboni, 2001, Staniczek, p. 184
2018 **Costalimella zucchii** Zamboni, 2001, Moura-Júnior et al., p. 150

Holotype. LP/UFC CRT 1276 (incomplete imago, exposed in lateral view).

**Revised diagnosis.** Forewing length 9 mm. RS basally branched at about one-quarter of wing length; RSa1 non-branched; RSa2 formed triad RSa2ʻiRSa2-RSa2, MA branched in apical half of wing, close to the origin of RSa1, at about three-quarters of MA length. CuA basally bifurcated to CuA1 and CuA2; CuA field with three successive 'hexagenitid' triads. Hindwing without costal process, with three bifurcated longitudinal veins described in the sequence: MA and CuA branch near its midlength, MP bifurcated in the apical third.

**Type locality and horizon.** Outcrop at Km 4 of the road Santana do Cariri – Nova Olinda, Ceará State, Northeast Brazil, Crato Formation (Zamboni, 2001, p. 130–131), upper Aptian.

**Fig. 2.** *Astraeoptera cretacea* sp. nov., holotype, LPRP/USP 0504. (A) Photograph of forewing. (B) Forewing drawing. Scale bar: 2 mm.

**Fig. 3.** *Costalimella zucchii* (holotype), LP/UFC CRT1276. (A) Photograph of lateral view. (B) Detail of the cubital field of the forewing; Scale bar, 1.0 mm. (C) Fore and hind wing drawing. Scale bars: 2 mm.

**Redescription.** Imago; sex unknown. Head (length 1.0 mm) and thorax (length 3.0) poorly preserved. Fore and hind wings are superimposed. Forewing length 9.5 mm, 5.0 mm maximal width. Forewing, Tornoapical (outer) margin about twice longer than basitolan (anal) margin. Relation of wing length to width of about 2:1. Costal area relatively wide, narrowing toward tip. C, Sc and RA not branched and subparallels; Sc and RA with semi-equal space...
between them; Sc not shortened. No conspicuous gcnimation of longitudinal veins. Costal field and entire wing with numerous crossveins. RS basally branched at about one-quarter of wing length (RS fork at 2.5 mm from wing base); RS formed triad RSA-iRS-RSp, iRS approximated RSp; RSA formed triad RSA1-iRSA-RSA2; RSA2 formed triad RSA2-iRSA2-RSA2*; RSp non-branched. MA length 7.0 mm; MA branched in apical half of wing, close to the origin of RSA3, at about three-quarters of MA length (MA fork at 5.0 mm from MA base); MA1 and MA2 uniformly diverging; IMa equidistant to MA1 and MA2. The distance between the forks RS and MA is approximately 3.0 mm. MP basally branched, with very short common stem; MP1 and MP2 slightly curved in their apical half; MP1 equidistant to MP2 and MP2; intercalary vein in the area between MP1-iMP and iMP-MP2. MP2 and CuA veins are straight at their bases. CuA vein basally bifurcated to CuA1 and CuA2, from the bifurcation a vein iCu formed three successive ‘hexagenitid’ triads, whose branches extend to the basiordinal margin of wing; anterior branch of each triad is arched and forms next triad; CuP not branched, subparalleling CuA basally and CuA2 distally. AA not discernible. Hind wing. Significantly reduced (length 3.5 mm, its width 2.5 mm), without evidence of costal process. Veins C and Sc unbranched and subparallels. RA field large, more than 3 times as wide as costal area; RA and RS apparently straight and unbranched; three bifurcated longitudinal veins described in the sequence: MA and CuA branch near its midlength, MP bifurcated in the apical third. Anal area unpreserved.

Family Hexagenitidae Lameere, 1917

*Protoligoneuria limai* Demoulins, 1955


**Type material, diagnosis, and synonym list for the type species:** see Staniczek (2007, p. 172—174).

*Reflected material.* LPRP/USP 0583 - holotype of *Cratogenites corradiniae* (male? nymph, exposed in dorsal view) (Fig. 4).

**Locality and horizon.** According to Martins-Neto (1996), the specimen LPRP/USP 0583 was collected in Fazenda Tatajuá, Santana do Cariri, Ceará State, Northeast Brazil, at 4 m from the base of a 15-m-thick outcrop of the Crato Formation (upper Aptian).

**Redescription.** Fusiform body (length 10 mm, excluding caudal filaments), siflonuroid minnow-like appearance. Head 1.4 times wider than long (length ca. 1.4 mm, its width 2.0 mm). Large compound eyes (length 1.0 mm, its width 0.7 mm) occupy most of the head; preserved ommatids. Filiform antenna, relatively short (length 1.6 mm); scape (length 0.3 mm) larger and wider than subsequent segments. Thorax length 2.6 mm, its maximal width 3.1 mm; mesothorax and metathorax wider than prothorax (prothorax width 2.4 mm, meso and metathorax width 3.1 mm); rect-angled pronotum, 7 times wider than long (length 0.3 mm, its width 2.4 mm); pterothorax carrying two pairs of wing pads (beside each other), semi-triangular and medially partially fused. Prothoracic, mesothoracic and metathoracic legs are preserved; thin legs with femurs slightly more robust than the tibiae, almost semi-qual in thickness; fore femur with spine-shaped projection at its apex. Prothoracic legs length: femur 0.6 mm, tibia 1.1 mm, tarsus 0.9 mm; its width: femur 0.3 mm, tibia 0.2 mm, tarsus 0.15 mm. Femur of the metathoracic legs (length 1.0 mm) 1.6 times longer than the femur of the prolegs. Segments abdomen (length 6.0 mm, maximal width 2.4 mm); segments gradually decrease in size as it approaches tergum X; two longitudinal lobes give the appearance of a three-lobed abdomen. Six pairs of leaf-shaped gills inserted posterolaterally on segments I-VI, subequal in size (length 1.2 mm); seventh gill not preserved or nonexistent; each gill with a sclerotized costal “rib” present on the anterior margin and an anal “rib” at a distance from posterior margin, close to the median region. From the distal portion of tergum X, the caudal filaments emerge, which becomes tapering towards the apex; cerci on its internal sides and terminal filament (paracercus) with fringes of dense swimming hairs, scarce at the distal ends; cerci (length 5.0 mm) slightly longer than the terminal filament (length 3.5 mm) and multisegmented.

5. Discussion

5.1. Comparisons and affinities of *Astraeoptera cretacica* gen. et sp. nov.

Comparisons of the new species (based on adult traits) with other Mesozoic epimeropterans worldwide and some extant mayfly taxa with fossil representatives have revealed a unique set of wing characters (i.e., MP1 e CuA straight at their bases; MA branching in the apical half of wing length; CuA not forked; cubital field with longitudinal veins sub-parallel to CuA). Those features weaken potential affinities with any family previously recorded in the Crato Formation. The MP4 and CuA veins, for instance, are straight at their bases, as opposed to those of *Fimbriatotergaliae* (Kluge, 2004), the MP4 and CuA veins of which are arched at their bases, as shown by the Australipheridae, Euthyplociidae, Epemeridae, Polymyctryciidae, and Potamantidiidae (Martins-Neto and Caldas, 1990; McCafferty, 1990) of that stratigraphic unit.

A close affinity with Hexagenitidae, the most common epimeropterans from the Crato Formation, is also not supported due to the absence of successive ‘hexagenitid’ triads within the CuA field. Unlike oligoneuriids, the entire forewing of *Astraeoptera cretacica* sp. nov. has numerous cross veins and no conspicuous twinning of longitudinal veins is seen.

The affinity of the new species with the baetiscid *Protobaetica bechlyi* also lacks support due to marked differences in wing venation. In Baeticidae and in other phylogenetically closed taxa, as Cretomitarcyidae (Sinitshenkova, 2000a) and Prospistomatidae (Lin et al., 2017), with fossils respectively from the New Jersey and Myanmar amber, the wing tornus is placed posterior to A1. Also, in Prosopistomatidae all longitudinal veins behind Rs veins are simple and detached (Lin et al., 2017), a condition not present in *Astraeoptera cretacica* sp. nov.

The holotype of *Astraeoptera cretacica* sp. nov. differs from Siphlonuridae by lacking CuA attached to the hind margin of forewing by a series of veinlets, often forking or sinuating (Edmunds et al., 1976). However, its assignment to Ametropodidae or Heptageniidae is hampered by differences in the MP sector. In ame-ropodidae, MP4 detaches basally, whereas MP1 and MP2 have a common branch in *Astraeoptera cretacica* sp. nov. In heptageniids,
MP₁ and MP₂ veins form a nearly symmetrical fork, as in the new species, but its MP forks closer to or at the same level of the RS split.

A possible assignment of the new species to Leptophelebiidae is also problematic, because the typical leptophelebiid characters cannot be assessed in *Astraeoptera cretacea* sp. nov. due to poor preservation. These include forewings usually with two intercalaries between CuA and CuP or one bifurcate vein arising from CuA and/or CUP (Kluge, 2004) and the CuP vein usually rather strongly recurved.

The wing morphology of *Astraeoptera cretacea* sp. nov. is similar to that of some metretopodids, because the MP fork is located more basally than the RS fork and the MP₂ vein of the forewing only slightly diverges from MP₁ at base (Staniczek and Godunko, 2012). Yet, winged stages of metretopodids can only be distinguished from other ephemeropterans by a combination of characters (from mesonotal, lateroparapsidal and tibiotapellate suture, furcasternal protuberances, pararccerus, tarsi and wings), which is not present in the new species. Given the comparisons presented above, the available evidence does not allow assigning *Astraeoptera cretacea* sp. nov. to any of the afore-mentioned families. Yet, caution is warranted as some diagnostic structures are not apparent in the type-specimen possibly due to its poor preservation.

5.2. Comparisons and affinities of *Costalimella zucchii* and *Cratogenites corrдинiae*.

Siphlonuridae was firstly recorded in the Crato Formation based on *Costalimella nordestina* Martins-Neto, 1996, and the second species of the genus was described as *Costalimella zucchii* Zamboni, 2001 (Fig. 3A) (Martins-Neto, 2006). Both species were assigned to an undetermined family by Staniczek (2007), but possibly corresponding to small hexagenitids. At least for *Costalimella zucchii*, this hypothesis is confirmed, due to the bifurcation of CuA vein in CuA₁ and CuA₂ and the presence of successive ‘hexagenitid’ triads originating from iCu (Fig. 3B–C). Unfortunately, inferences about *Costalimella nordestina* are hampered by the unknown whereabouts of the holotype. In its description, Martins-Neto (1996) only figured the specimen with simple line drawing, in which the presence of cubital triads is uncertain. The occurrence of siphlonurids in the Crato Formation is unexpected, because most extant genera of this family are found in cold climates of higher latitudes, including Holarctic areas, Australia, New Zealand, and southern South America (Edmunds et al., 1976).

Martins-Neto (1996) described *Cratogenites corrдинiae* (Fig. 4A) with elongated and expanded gill VII, which is characteristic of Hexagenitidae. However, gill VII does not occur or is not preserved in the holotype (Fig. 4A–B). In addition, Martins-Neto (1996) diagnosed *Cratogenites corrдинiae* based on head shape, eyes and antennae sizes. However, Staniczek (2007) pointed out that, although the figure published in Martins-Neto (1996) shows elongated antennas, the corresponding photograph does not support that view. In addition, different head shapes can be explained by position of preservation, and sexual dimorphism may explain the large compound eyes, commonly seen in males. For all those reasons the species was considered a junior synonym of *Protoligoneuria limai* Demoulin, 1955 by Staniczek (2007).

The holotype of *Cratogenites corrдинiae* exhibits a left antenna (Fig. 4C) that is shorter than the width of the head and extends towards the foretibia; not shown in the photograph of Martins-Neto (1996). However, the antenna length measurement provided by that author is minimally 2.5 longer than that actually preserved in the holotype. McCafferty (1990) reported that the antenna is shorter than head width in *Protoligoneuria limai* (1.4 mm long in a specimen with body length of 8.9 mm and head width of 2.2 mm). Antennas of 2.0 mm have been reported for *Palaeoebatoches costalimal Brito, 1987* (Martins-Neto, 1996), also a junior synonym of *Protoligoneuria limai*. Therefore, the antenna length in *Cratogenites corrдинiae* does not allow distinguishing it from *Protoligoneuria limai*, confirming their synonym.

5.3. Cretaceous ephemeropterans.

The Early Cretaceous diversity of ephemeropterans is mostly concentrated in Eurasian deposits, including Russia, Mongolia, and China (>30 species), as well as in the Crato Formation, which represents the most prolific stratigraphic unit for Early Cretaceous mayflies. In Eurasia, this fauna is dominated by hexagenitids, followed by Mesoneitidae and Siphlonuridae (Huang et al., 2007, 2011; Sinitshenkova, 1989, 2000b, 2017), together encompassing nearly 90% of all species. In Brazil, the species distribution is more uniform; although Hexagenitidae is still more common, with five out of 15 valid species.

6. Conclusions.

A new mayfly, *Astraeoptera cretacea* gen. et sp. nov., from the Lower Cretaceous Crato Formation is described. After extensive comparisons, its assignment to any known family of Ephemeroptera remains elusive. Based on a revision of their holotypes, *Costalimella zucchii* is reallocated to Hexagenitidae and *Cratogenites corrδiniae* is confirmed as a junior synonymy of *Protoligoneuria limai*. The most diverse Cretaceous mayflies are the hexagenitids, notably for Eurasian faunas. The data discussed here supports a diversity of ephemeropterans for the Crato Formation greater than previously known, ratifying its potential to unveiling the evolution of Cretaceous insects.

Acknowledgements

We are grateful to Rodrigo da Rocha Machado (CPRM) for allowing examination of specimens under his care. Adalberto Santos (UFMG) is thanked for access to imagery equipment. We appreciate the valuable comments and constructive suggestion from two anonymous reviewers. This work was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) — Finance Code 001 (grant to NCAB); and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant to JSB).

References


