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The Ephemeroptera (Hexapoda, Insecta) from the Lower Cretaceous Crato Formation (NE Brazil): a new genus and species, and reassessment of *Costalimella zucchii* Zamboni, 2001 and *Cratogenites corradinae* Martins-Neto, 1996

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ABSTRACT

A new genus and species of Ephemeroptera, *Astraeoptera cretacea* 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 Siphonuridae, as previously proposed. We also reanalysed the holotype of *Cratogenites corradinae* Martins-Neto, 1996, providing new and more accurate information about the species and confirming its junior synonymy to *Protoligoneuria 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.

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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; Staniczek, 2007) to recent, with

approximately 3500 extant species described so far (Sartori and Brittain, 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; Crampton, 1924; Haas and Kukalová-Peck, 2001; Kukalová-Peck, 2008; Regier et al., 2010; Blanke et al., 2013; Thomas et al., 2013; Song et al., 2019), (ii) as closely related to Neoptera (Chiasatomyaria 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; Staniczek, 2000; Wheeler et al., 2001; Ogden and Whiting, 2003; Grimaldi and Engel, 2005; Willkommen and Hörschemeyer, 2007; Zhang et al., 2008). Despite this long

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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). Fossil mayflies 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 Australiphemeridae (*Australiphemera revelata* McCafferty, 1990 and *Microphemera neotropica* McCafferty, 1990), Baetiscidae (*Protobaetisca bechlyi* Staniczek, 2007), Ephemeridae (*Cratonympha microcelata* Martins-Neto and Caldas, 1990), Euthyplociidae (*Pristiplocia rupestris* McCafferty, 1990), Hexagenitidae (*Protoligoneuria limai* Demoulin, 1955, *Cratohexagenites longicercus* Staniczek, 2007 and *Cratohexagenites minor* Staniczek, 2007), Oligoneuriidae (the recently described *Incogemina nubila* Storari et al., 2020, *Colocrus magnum* Staniczek, 2007 and *Colocrus indicum* McCafferty, 1990, recently reclassified as an hexagenitid by Storari et al., 2020), Polymitarciidae (*Carirynympha mandibulata* Martins-Neto and Caldas, 1990), Potamanthidae (*Olindinella gracilis* Martins-Neto and Caldas, 1990), and possibly Siphonuridae (*Costalimella nordestina* Martins-Neto, 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 corradinae* 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 Cretaceous strata of the Araripe Basin 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 redescribe the holotypes of *Cratogenites corradinae* 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; Arai 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 (LP/UFC), 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:zoo-bank.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.

(LSID: urn:lsid:zoo-bank.org:act:24C6C337-C976-4D63-9336-BA14F125D0BA).

Type species: *Astraeoptera cretacica* sp. nov., by monotypy.

Etymology. The generic name derives from Latin *Astræus* (Greek: Ἀστράϊω), 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 cretacica sp. nov.

(LSID: urn:lsid:zoo-bank.org:act:006809ED-8231-432A-86E6-AC1DA2671F01).

(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.

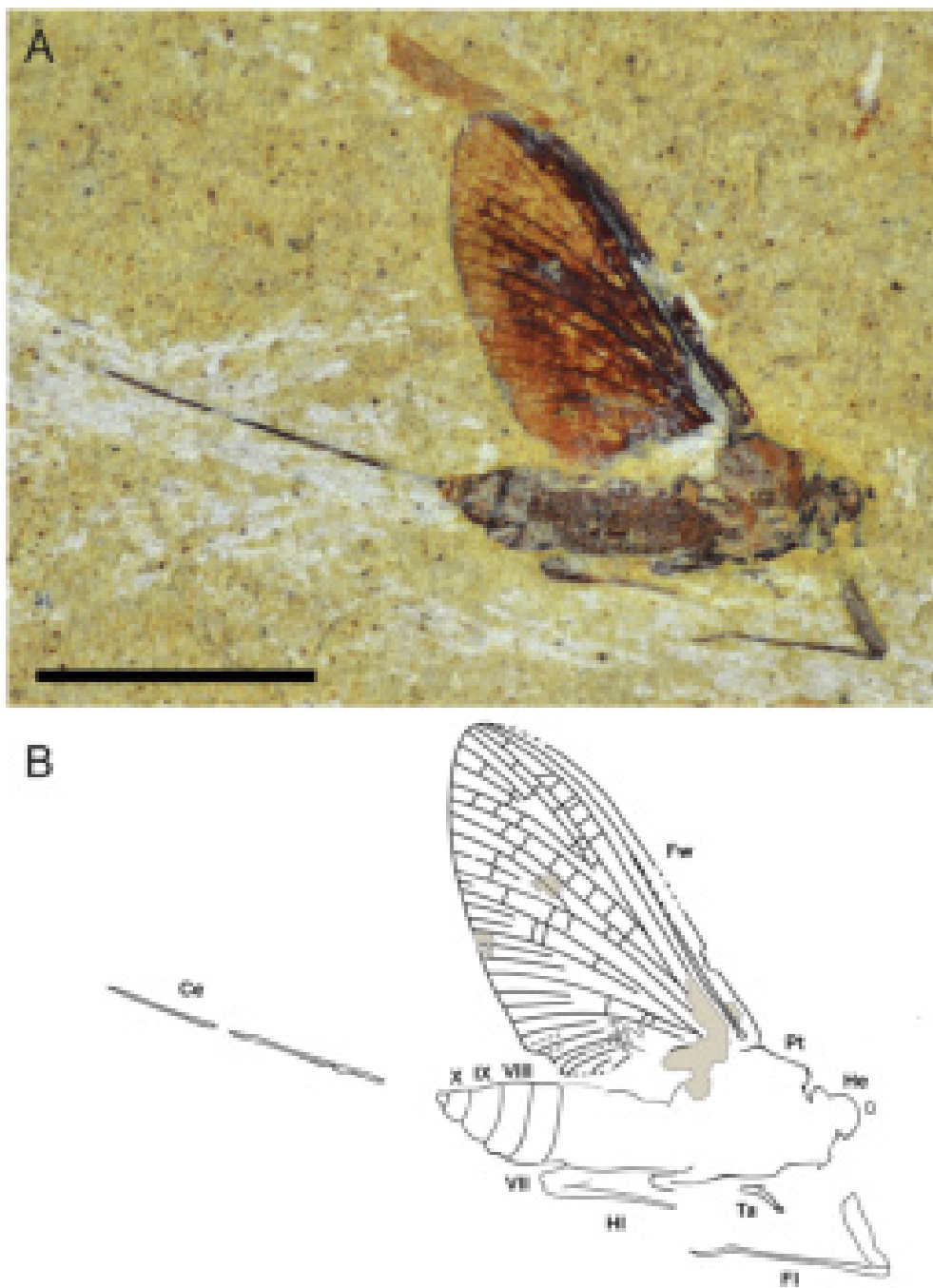


Fig. 1. *Astraeoptera cretacica* sp. nov., female imago, holotype, LPRP/USP 0504. (A) Photograph of lateral view. (B) Line drawing of lateral view. Captions: Ce, Cerci; Fl, fore leg; Fw, fore wing; He, Head; HI, hind leg; Pt, Pterothorax; Ta, Tarsus of middle leg; VII–X, Abdominal tergum VII–X. Scale bar: 5 mm.

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 tornapical (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 $RSa_1-iRSa-RSa_2$; RSa_2 formed triad $RSa_2'-iRSa_2-RSa_2''$; RSp non-branched; MA branched in apical half of wing at about two-thirds of MA length; MA_1 and MA_2 uniformly diverging; iMA equidistant to MA_1 and MA_2 ; 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 MP_1 ; distinct intercalary veins existing between MP_2 and CuA ; MP_2 and CuA veins are straight at their

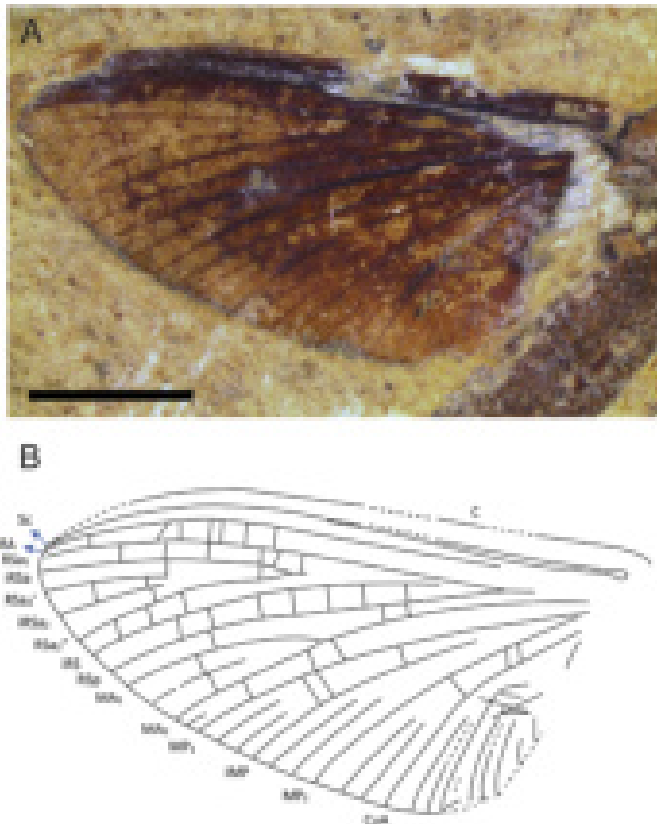


Fig. 2. *Astraeoptera cretacica* sp. nov., holotype, LPRP/USP 0504. (A) Photograph of forewing. (B) Forewing drawing. Scale bar: 2 mm.

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 [Lameere, 1917](#)

***Costalimella zucchini* Zamboni, 2001**
(Fig. 3)

2006b *Costalimella zucchini* Martins-Neto, p. 196

2007 *Costalimella zucchini* Zamboni, 2001, Staniczek, p. 184

2018 *Costalimella zucchini* 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 RSa_2' - $iRSa_2$ - RSa_2 . MA branched in apical half of wing, close to the origin of RSa_1 , 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.

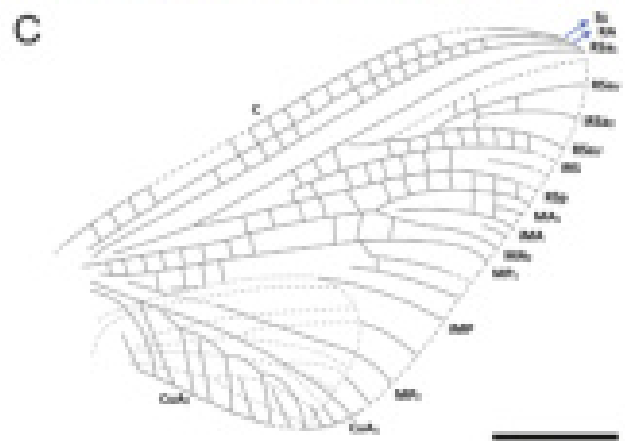
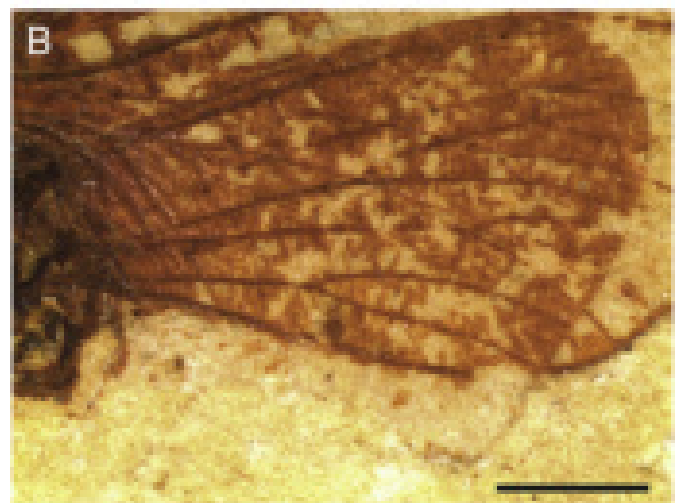


Fig. 3. *Costalimella zucchini* (holotype), LP/UFC CRT1276. (A) Photograph of lateral view. (B) Detail of the cubital field of the forewing; Scale bar, 1.0 mm. (C) Fore and hind wing drawing. Scale bars: 2 mm.

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 basitornal (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 subparallel; Sc and RA with semi-equal space

between them; Sc not shortened. No conspicuous gemination 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 $RSa_1-iRSa-RSa_2$; RSa_2 formed triad $RSa_2'-iRSa_2-RSa_2''$; RSp non-branched. MA length 7.0 mm; MA branched in apical half of wing, close to the origin of RSa_1 , at about three-quarters of MA length (MA fork at 5.0 mm from MA base); MA_1 and MA_2 uniformly diverging; iMA equidistant to MA_1 and MA_2 . The distance between the forks RS and MA is approximately 3.0 mm. MP basally branched, with very short common stem; MP_1 and MP_2 slightly curved in their apical half; iMP equidistant to MP_1 and MP_2 ; intercalary vein in the area between MP_1-iMP and $iMP-MP_2$. MP_2 and CuA veins are straight at their bases. CuA vein basally bifurcated to CuA_1 and CuA_2 , from the bifurcation a vein iCu formed three successive 'hexagenitid' triads, whose branches extend to the basiternal margin of wing; anterior branch of each triad is arched and forms next triad; CuP not branched, subparalleling CuA basally and CuA_2 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* Demoulin, 1955**

1996 *Cratogenites corradinae* Martins-Neto, p. 180–181

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

Referred material. LPRP/USP 0583 - holotype of *Cratogenites corradinae* (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 Tatajuba, 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), siphonuroid 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 ommatidia. 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); rectangular 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-equal 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. Segmented 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 ephemeropterans worldwide and some extant mayfly taxa with fossil representatives have revealed a unique set of wing characters (i.e., MP_2 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 MP_2 and CuA veins, for instance, are straight at their bases, as opposed to those of Fimbriatotergeriidae (Kluge, 2004), the MP_2 and CuA veins of which are arched at their bases, as shown by the Australiphemeridae, Euthyplociidae, Ephemeridae, Polymitarciidae, and Potamantidae (Martins-Neto and Caldas, 1990; McCafferty, 1990) of that stratigraphic unit.

A close affinity with Hexagenitidae, the most common ephemeropterans 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 *Protobaetisca bechlyi* also lacks support due to marked differences in wing venation. In Baetiscidae and in others phylogenetically closed taxa, as Cretomitarciidae (Sinitschenkova, 2000a) and Prosopistomatidae (Lin et al., 2017), with fossils respectively from the New Jersey and Myanmar amber, the wing tornus is placed posterior to A_1 . 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 Siphonuridae by lacking CuA attached to the hind margin of forewing by a series of veinlets, often forking or sinuating (Edmunds et al., 1976). In fact, we concur with Staniczek (2007), who questioned the occurrence of siphonurids in the Crato Formation. Unlike siphonurid from the Jurassic of Russia (Tshernova, 1967), *Astraeoptera cretacica* sp. nov. lacks the 'siphonuroid' forewing, with an exceptionally long and narrow cubital field (Zhou and Peters, 2003).

Finally, the lack of basally detached IMA, MA_2 , IMP, and MP_2 veins in the forewing prevents the nesting of *Astraeoptera cretacica* sp. nov. within Baetidae, some imagoes of which are known from the Cretaceous Tainmyr and Burmese amber (Kluge, 1997; Poinar, 2011).

Astraeoptera cretacica sp. nov. shares with Ametropodidae, Heptageniidae, Leptophlebiidae, and Metretropodidae forewings with 1–2 pairs of intercalaries between CuA and CuP (Edmunds et al., 1976). However, its assignment to Ametropodidae or Heptageniidae is hampered by differences in the MP sector. In ametropodids, MP_2 detaches basally, whereas MP_1 and MP_2 have a common branch in *Astraeoptera cretacica* sp. nov. In heptageniids,

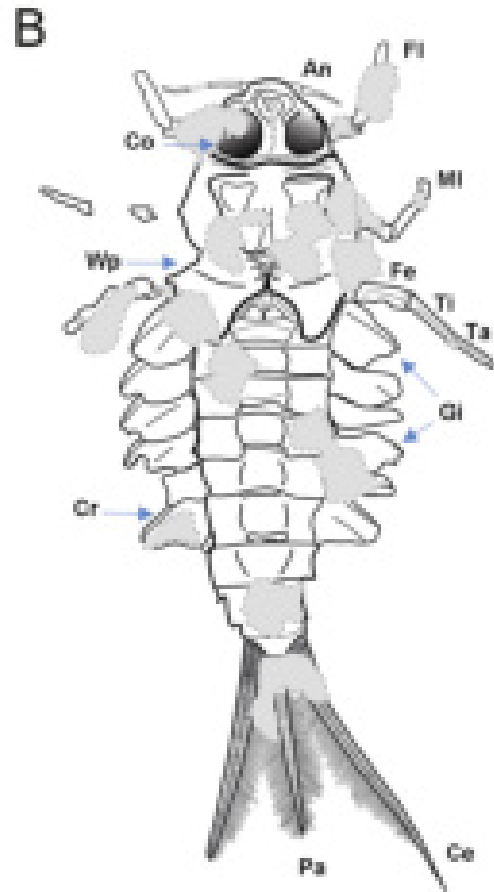


Fig. 4. *Cratogenites corradinae* (holotype), LPRP/USP 0583 (junior synonym of *Protoligoneuria limai*). (A) Photograph in dorsal view. (B) Drawing. (C) Detail of the left antenna. Captions: An, Antenna; Ce, Cerci; Co, Compound eyes; Cr, Costal rib; Fe, Femur; Fl, Fore leg; Gi, Gills; Ml, Middle leg; Pa, Paracercus; Ta, Tarsus; Ti, Tibia; Wp, Wing pad. Scale bar (A): 5 mm, (C): 1 mm.

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 Leptophlebiidae is also problematic, because the typical leptophlebiid characters cannot be assessed in *Astraeoptera cretacica* 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 cretacica* 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 tibioapatellar suture, furcasternal protuberances, paracercus, tarsi and wings), which is not present in the new species. Given the comparisons presented above, the available evidence does not allow assigning *Astraeoptera cretacica* 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 corradinae*

Siphonuridae 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 siphonurids in the Crato Formation is unexpected, because most extant genera of this family are found in cold climates of higher latitudes, including Holartic areas, Australia, New Zealand, and southern South America (Edmunds et al., 1976).

Martins-Neto (1996) described *Cratogenites corradinae* (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 corradinae* based on head shape, eyes and antennae sizes. However, Staniczek (2007) pointed out that, although the figure published in Martins-Neto (1996) shows elongated antennae, 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 corradinae* 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). Antennae of 2.0 mm have been reported for *Palaeobaetodes costalimai* Brito, 1987 (Martins-Neto, 1996), also a junior synonym of *Protoligoneuria limai*. Therefore, the antenna length in *Cratogenites corradinae* does not allow distinguishing it from *Protoligoneuria limai*, confirming their synonymy.

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 Mesonetidae and Siphonuridae (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 cretacica* 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 corradinae* 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.

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