

UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO
CENTRO DE CIÊNCIAS HUMANAS E NATURAIS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

**Systematic and Ecological aspects of fossil mayflies from the
Crato Formation, Araripe Basin (Lower Cretaceous,
Northeast Brazil)**

Arianny Pimentel Storari

Vitória, ES
Fevereiro, 2020

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Orientadora: Taissa Rodrigues Marques da Silva

Coorientador: Frederico Falcão Salles

Dissertação submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para a obtenção do grau de Mestre em Biologia Animal

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Resumo

Entre os insetos, os Ephemeroptera se destacam por sua abundância na Formação Crato, Bacia do Araripe. Neste trabalho, um espécime adulto da família Oligoneuriidae foi aqui descrito como uma nova espécie, gênero e nova subfamília. Além disso, um espécime descrito anteriormente da família Oligoneuriidae é aqui reanalisado e considerado como pertencente à família Hexagenitidae. O novo gênero preenche uma lacuna entre um ancestral da família Oligoneuriidae e o gênero *Chromarcys*. O novo táxon também demonstra que a divergência entre as subfamílias de Oligoneuriidae provavelmente ocorreu na América do Sul. Ademais, foram descritos espécimes fósseis da extinta família Hexagenitidae. Dois novos gêneros monoespecíficos foram descritos, com base em adultos, além de um espécime descrito como *Protoligoneuria limai*, e a diagnose do taxon foi revisada, além da descrição de outro espécime adultos da família Hexagenitidae, não nomeado. Ainda, nós consideramos *Cratohexagenites minor* sinônimo de *P. limai*, fornecendo novas informações morfológicas sobre a fauna de Ephemeroptera da Formação Crato. Finalmente, foi analisado um nível de mortalidade em massa de ninfas de Ephemeroptera coletadas em escavações controladas, as primeiras do tipo para a Formação Crato. As ninfas encontradas são todas pertencentes a família Hexagenitidae, demonstrando que as mesmas habitavam águas calmas de acordo com sua morfologia. As ninfas são menores que o usual, sugerindo uma coluna d'água rasa, as mesmas possuem excelente preservação e nenhuma orientação preferencial, sugerindo nenhum transporte. Portanto, concluímos que o paleolago da Formação Crato sofria uma alta evaporação sazonal causada pelo clima quente que tendia à aridez.

Palavras-chave: Ephemeroptera, Aptiano, Oligoneuriidae, Hexagenitidae, clima do Cretáceo

Abstract

Among the groups of insects, mayflies stand out in the Crato Formation, Araripe Basin. A newly discovered adult individual from the family Oligoneuriidae is here described as new species, genus and new subfamily. Also, a previously described “oligoneuriid” specimen from the same unit is here reviewed, redescribed and considered as belonging to the family Hexagenitidae. The new genus bridges an important gap between an oligoneuriid ancestor and the extant *Chromarcys*. Furthermore, demonstrate that the divergence between Oligoneuriidae clades probably occurred in South America. Additionally, we described recently collected fossil specimens of extinct family Hexagenitidae. Two new genera and species are proposed, and one specimen is described in detail and identified as *Protoligoneuria limai*, providing new information on intraspecific variability and allowed us to emend the taxon’s diagnosis. Another specimen described is considered *incertae sedis*, and presents an interesting taxonomic challenge, as it presents plesiomorphic features on the forewings. Moreover, we comment on the taxonomy of *Cratohexagenites minor* and consider it possibly synonymous with *Protoligoneuria limai*. As a supplementary material, we also present a checklist of all valid mayfly species from the Cretaceous, providing new morphological information about the Crato Formation mayfly fauna, specially the hexagenitids. Finally, we analyze a mayfly mass mortality collected at controlled excavations, the first of their kind for the Crato Formation. All mayflies found belong to the Hexagenitidae, whose morphology demonstrates that the nymphs occurred in quiet waters. The nymphs were smaller than usual, suggesting a shallow water column, with excellent preservation and no preferential orientation in the samples, suggesting lack of transport. Thus, we conclude that the Crato Formation lake experienced a seasonal high evaporation caused by the hot climate tending to aridity.

Keywords: Ephemeroptera, Aptian, Oligoneuriidae, Hexagenitidae, Cretaceous climate

General Introduction

This dissertation presents the results of a taxonomic and taphonomic study of 39 specimens of fossil insects of the order Ephemeroptera. All the material comes from the laminated limestones of the Crato Formation, the lowest unit of the Santana Group (Lower Cretaceous), Araripe Basin. The first part of this work deals with a newly discovered adult of the family Oligoneuriidae (Ephemeroptera), and a review of an previously described “oligoneuriid” specimen. The second part contains the description of three new adult Hexagenitidae specimens, a redescription of a previously Oligoneuriidae adult included now in the Hexagenitidae and a review of the diagnostic morphological characters of Brazilian representatives of the Hexagenitidae. Finally, the third part presents data of a mayfly mortality level found from an unprecedented controlled excavation, focusing specially on the paleoenvironmental aspects.

Located on the borders of the states of Ceará, Pernambuco and Piauí, Northeast Brazil, the Araripe Basin houses some of the most remarkable fossiliferous deposits in the world, notably in its Santana Group (Carvalho and Santos, 2005). The unit studied in this dissertation comprises the base of the Aptian sequence of the Araripe Basin, also known as Post-Rift Sequence I, according to Assine *et al.* (2014). The Post-Rift deposition cycles of the basin are associated with the tectonic separation mechanisms of South America and Africa, and the Santana Group comprises the layers that deposited in the stages after the division of these continents, which granted the opening and occupation of new habitats (Carvalho and Santos, 2005).

The Santana Group is stratigraphically the most complex and also the most studied within the Brazilian Cretaceous Aptian-Albian sequence, mostly for being the main Brazilian fossiliferous deposit, famous worldwide especially for the richly preserved paleoichthyofauna (Assine, 1992). Lithostratigraphically the Santana Group is composed of the Crato Formation at the base, formed by laminated limestones, the intermediate Ipubi Formation, with predominantly evaporitic sedimentation, and the overlapping Romualdo Formation (Assine *et al.*, 2014). According to Assine (1992) the development of the Santana Group sequences evolved to progressively more arid conditions, which culminated in the marine drowning of the lacustrine basin (Romualdo Formation), returning to humid conditions.

According to Neumann and Cabrera (1999), the Crato Formation, object of this study, consists mainly of six carbonate units, informally called C1 to C6. It represents a lake complex

paleoenvironment (Mabesoone and Tinoco, 1973), containing fossils of algae, plants, arthropods, mollusks, fish, amphibians, crocodylians, pterosaurs and bird feathers, all of which are usually preserved compressed (Bechly, 2007). Moreover, this geological unit preserves one of the most diverse Cretaceous entomofaunas and, among the various insect groups present, Ephemeroptera stands out (Carvalho and Santos, 2005).

The order Ephemeroptera is formed by just under 4,000 described species and has global distribution (Salles *et al.*, 2004). Biologically, this group is characterized by the long duration of the nymphal period, which presents immature aquatic stages and hemimetabolic development (Da Silva *et al.*, 2003), in contrast to a brief life in adulthood, exclusively intended to reproduce and disperse (Bispo and Crisci-Bispo, 2006). Their nymphs are one of the main groups among benthic macroinvertebrates, available in all types of freshwater aquatic environments, representing an important link in the trophic chain of water environments (Salles *et al.*, 2004). The group also exhibits a unique feature of the order, an intermediate winged stage between the nymph and the adult, called the subimago, which, unlike adults, is less active, and rests on the edges of the environments from which it emerged (Salles *et al.*, 2004). 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), and the wings, folded vertically over the abdomen when in rest (Sartori and Brittain, 2015). The hind wings are considerably smaller than the forewings and can also be entirely lost in some taxa (Kluge, 2004). The larvae of mayflies undergo numerous molts until they reach the final instar (Kluge, 2004). Extant species usually bear seven pairs of tracheal gills, which are inserted laterally on the first seven abdominal segments (Staniczek, 2007).

The Ephemeroptera are relatively well represented in the fossil record, stem group representatives of mayflies date back to the Carboniferous (Staniczek, 2007), and the first species positioned within the crown group of Ephemeroptera appear in the Lower Jurassic (Tshernova, 1967). However, notable differences from early stem group representatives of mayflies to modern Ephemeroptera can be observed. Fore and hind wings in the first fossil taxa are of the same size, the heteronomous wings first appear in the Jurassic, and all modern mayflies have significantly reduced hind wings (Willmann, 2007). Other differences concern the development of a wing tornus in modern mayflies, while the hind margin of the wing in Paleozoic stem group representatives has no sharp angle (Kluge, 2004). Generally, the size of

mayflies diminished during their evolution (Willmann, 2007). Adults of Paleozoic 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 laterocaudal direction and in modern mayflies they are fused with the mesonotum and grow parallel to the longitudinal body axis (Staniczek *et al.*, 2011). The amount of gill numbers has become reduced from nine pairs to seven (Staniczek, 2007).

According to Martins-Neto (2006) there are 15 fossil Ephemeroptera species described for the Santana Group, representing 6% of its paleoentomofauna. Undoubtedly ephemeropterans were extremely abundant in this unit, but not diverse in the number of families, according to Bechly (2007). All larval stages occur, usually preserved in dorsal or ventral aspects, mostly complete, while the attitude of adults differs greatly (to include dorsal, ventral and lateral aspects); isolated wings are also quite common (Menon and Martill, 2007). The locality of the original habitat to the lake must be related to the abundance of the Ephemeroptera (Bechly, 2007). However, a good part of the Brazilian described mayfly species were collected without any geographic or stratigraphic control, besides not being deposited in Brazil (Martins-Neto, 2006).

The description of Ephemeroptera specimens present in this dissertation, contributes to understanding the systematics and evolution of the group, and also to a better understanding of the geological history of the Araripe Basin, besides valuing the Brazilian paleontological collections.

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Chapter I - Unmasking a gap: new fossil oligoneuriid (Ephemeroptera: Insecta) from the Crato Formation (upper Aptian), Araripe Basin, NE Brazil, with comments on *Colocrus McCafferty*

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Unmasking a gap: new fossil oligoneuriid (Ephemeroptera: Insecta) from the Crato Formation (upper Aptian), Araripe Basin, NE Brazil, with comments on *Colocrus* McCafferty

Abstract

The Crato Formation (Araripe Basin) preserves one of the most diverse entomofaunas of the Cretaceous. Among the groups of insects, mayflies stand out, but among them oligoneuriids are especially rare. A newly discovered adult oligoneuriid from this unit is here described as a new genus, species and new subfamily. A phylogenetic analysis recovered the new taxon as the sister group to the species-rich and cosmopolitan Oligoneuriinae. The paratype of *Colocrus indicum*, described as an "oligoneuriid" from the same unit, is here reviewed and considered as belonging to the family Hexagenitidae. The biogeographical and taxonomic implications of this discovery and the phylogenetic position of this new taxon are discussed. This specimen bridges an important morphological gap between the Oligoneuriinae and the extant *Chromarcys*. Also, demonstrate that the divergence between Oligoneuriinae and LPU 1696 probably occurred in South America.

Key words: macroinvertebrates, systematics, brushlegged mayflies, paleontology

1. Introduction

The Crato Formation (Araripe Basin) in northeast Brazil is a geological unit that preserves one of the most diverse entomofaunas of the Cretaceous (Martins-Neto, 2005). Mayfly larvae constituted important elements of this fauna and, as they had fully aquatic lifestyles, they are more prone to be preserved as fossils than the alates (imagoes or subimagoes). This preservational bias is reflected in the strong disparity in the number of fossilized adult individuals in scientific collections, when compared to the much higher number of larvae (McCafferty, 1990). Regarding the Crato Formation, there are five named species described based on adult type material, and eleven based on larvae (Staniczek, 2007).

Among fossil mayflies, oligoneuriids are especially rare. The family is divided into three subfamilies (McCafferty, 1990; Massariol et al., 2019): Colocrurinae McCafferty, 1990; Chromarcyinae Demoulin, 1953; and Oligoneuriinae Ulmer, 1914. Colocrurinae is a subfamily

known only by fossils and comprises two species of the genus *Colocrus* McCafferty, 1990, both from the Crato Formation (*Colocrus indivicum* McCafferty, 1990 and *Colocrus magnum* Staniczek, 2007). Chromarcyinae is monotypic, represented by the extant species *Chromarcys magnifica* Navás, 1932, distributed in the Oriental Region (Hubbard and Peters, 1984). All remaining 67 species and ten genera are extant and included in the Oligoneuriinae, and exhibit a predominantly Pantropical distribution (Massariol et al., 2019; Sroka et al., 2019).

A newly discovered adult individual from the Crato Formation is here described and identified as a new genus and species. We also review the adult paratype of *Colocrus indivicum*, which is here considered as belonging to the family Hexagenitidae.

2. Institutional abbreviations

AMNH, Invertebrate Zoology Collection of the American Museum of Natural History, New York, USA

LPU, Paleontology Collection of the Regional University of Cariri (URCA), Crato, Brazil

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany

3. Material and Methods

The specimen LPU 1696 was collected in an outcrop of the Crato Formation at the Mine Antônio Finelon (S 07° 07' 22,5'' and W 39° 42' 01'') in Nova Olinda municipality, Ceará State, Brazil (Fig. 1). The material was recovered from the top level carbonate C6 (Neumann and Cabrera, 1999). More detailed geological and sedimentological information about the Crato Formation can be found in Martill et al. (2007).

This new specimen (Fig. 2) was analyzed using a binocular microscope. All drawings were made with a Wacom tablet, using the software Autodesk Version 8.6.1, and the photos were taken with a Nikon D800 digital camera. Pictures using ultraviolet light were taken using a Canon EOS Rebel T6i camera. The descriptive anatomical terminology is based on Kukalova-Peck (1983) and Kluge (2004). Pictures of AMNH 34399 (Fig. 3), the adult paratype of *Colocrus indivicum*, were made available by the American Museum of Natural History.

In order to determine the phylogenetic relationships of LPU 1696, a cladistic analysis was performed using morphological data from the Oligoneuriidae matrix presented by Massariol et al. (2019). Three new characters were proposed, and characters 53 (orientation of vein RP2 of

forewing in relation to RA), and 32 (insertion of gill I) were recoded in the matrix according to our interpretation (see Appendix 1 and 2). The venational nomenclature was revised after Kukalova-Peck (1983). The analysis included both larval and adult characters, with 76 binary characters in total. We also added LPU 1696 to their matrix, thus analyzing 18 ingroup taxa, representing all 12 oligoneuriid genera. Outgroup taxa were the same used by Massariol et al. (2019), from the related families Isonychiidae, Coloburiscidae, and Heptageniidae, which together with Oligoneuriidae compose the superfamily Heptagenioidea (McCafferty, 1991; Kluge, 2004). Parsimony methods were conducted using TNT 1.5 (Goloboff and Catalano, 2016) (data matrix in Appendix 2). All characters were treated as nonaddictive and unordered. A traditional search was run using the TBR algorithm (Tree Bisection Reconnection), random seed 1, branch swapping with 1000 replications, and implied weights with the default value of k (k=3). The implied weights were used because they normally increase the stability and support compared to the equal weights scheme (Goloboff et al., 2008). To estimate support of nodes, 1000 bootstrap (BT) pseudoreplicates were run, using the heuristic search algorithm.

We chose not to include data of the *Colocrus* larvae in the analysis of the combined data matrix. Since the taxon only possesses five characters to score in the matrix, it added a large amount of missing data that made many taxa unstable within branches, which could compromise the reliability of the results (Andrade et al., 2006).

Besides the analysis using the entire matrix, another one was performed using only larval characters (45 binary characters), to elucidate the phylogenetic position of *Colocrus indivicum* (once the associated adults are no longer considered conspecific, see below). The analysis followed the same protocol as detailed above.

All nomenclatural acts established herein are registered in ZooBank under LSID urn:lsid:zoobank.org:pub:EFE79A8D-18A8-4487-9748-2B80F4CF52B3.

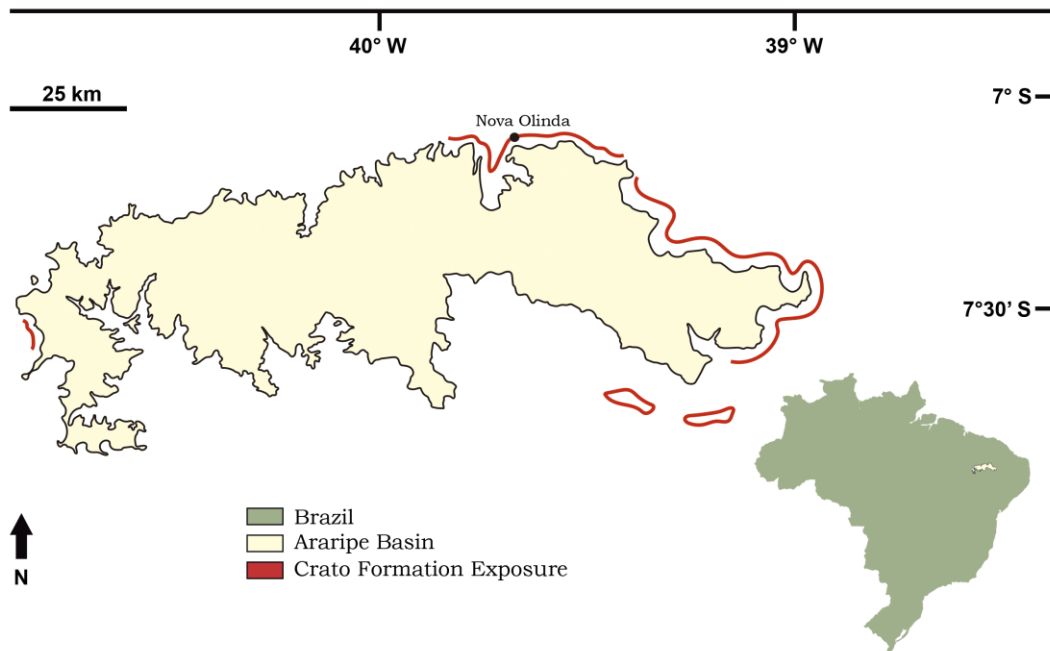


Figure 1. Locality map showing the Nova Olinda municipality where LPU 1696 was collected. Outcrops of the Crato Formation and of the Araripe Basin are also indicated.



Figure 2. LPU 1696, adult. Upper Aptian, Lower Cretaceous, Crato Formation, Araripe Basin. Nova Olinda municipality, Ceará State, Brazil. Photograph in dorsal view. Scale bar 5 mm.

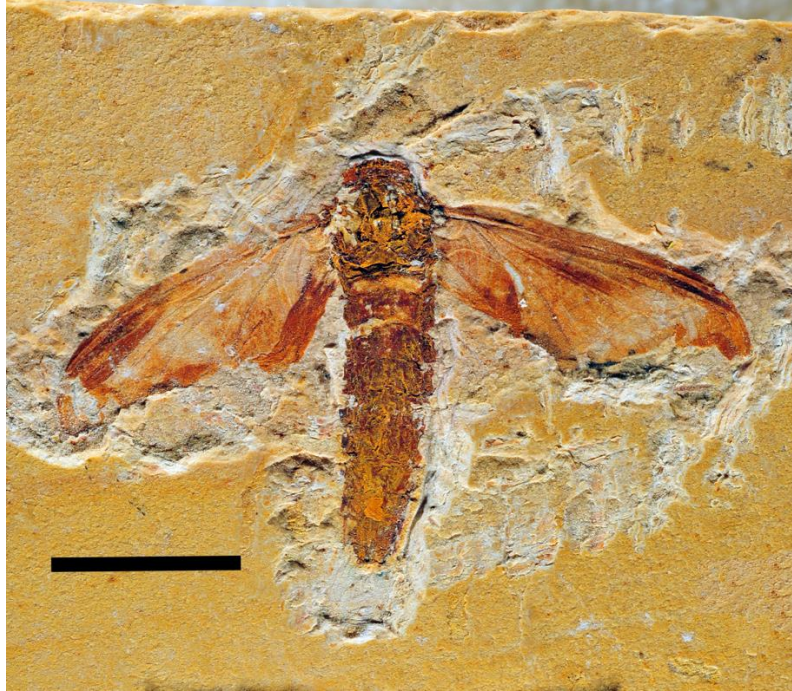


Figure 3. *Colocrus indivicum*. Paratype AMNH 34399, adult. Upper Aptian, Lower Cretaceous, Crato Formation, Araripe Basin. Ceará State, Brazil. Photograph in dorsal view. Scale bar 5 mm.

4. Results

4.1. Phylogenetic analysis

Parsimony analysis under implied weights for the combined data matrix of larval and adult characters resulted in two most parsimonious trees. The strict consensus tree is shown in Figure 4.

Oligoneuriidae was recovered as monophyletic, with bootstrap value of 80 and supported by five synapomorphies: apical angle of maxilla acute (character 7: state 0); second segment of maxillary palp much longer in relation to first (character 8: state 1); lateral margin of epimera and episterna projected laterally (character 10: state 1); both adult tarsal claws rounded (character 50: state 1); vein RP of forewing originating next to wing base (character 59: state 1). *Chromarcys* was recovered as the sister-group to all other oligoneuriids and was supported by two apomorphies: terminal filament with setae, except at the basal 1/3 (character 43: state 1); forceps with three or more apical segments (character 66: state 1). LPU 1696 + Oligoneuriinae were recovered as a monophyletic group, with bootstrap value of 82, and supported by one synapomorphy: presence of longitudinal vein gemination (pairing of longitudinal veins)

(character 55: state 1). LPU 1696 was recovered with one autapomorphy: presence of incomplete gemination (character 76: state 0). Oligoneuriinae was recovered as monophyletic, with bootstrap value of 96 and supported by three synapomorphies already found by Massariol et al. (2019), plus the absence of cubital intercalaries (character 74: state 1; new character). Relationships between its genera were not well resolved, with many taxa in polytomies. Analysis of the matrix containing only larval characters were inconclusive.

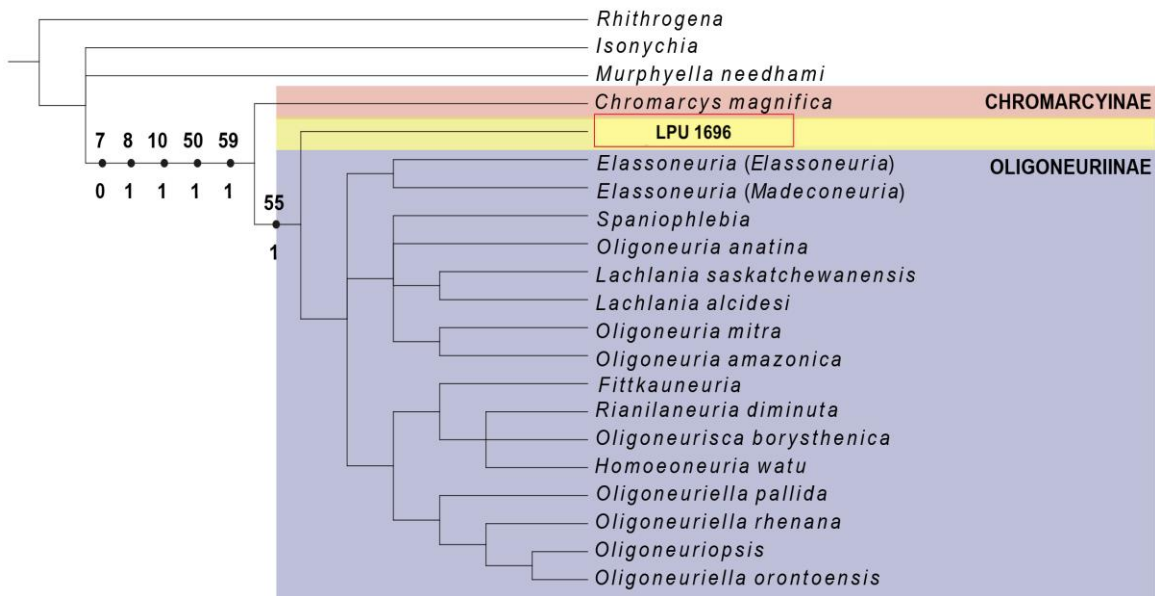


Figure 4. Strict consensus of the four most parsimonious trees, from the analysis of 77 morphological characters of Oligoneuriidae. Numbers above and below circles correspond to synapomorphies supporting these clades (characters and states, respectively).

4.2. Systematic Paleontology

Subphylum Hexapoda Latreille, 1825

Class Insecta Linnaeus, 1758

Order Ephemeroptera Hyatt & Arms, 1890

Family Oligoneuriidae Ulmer, 1914

Subfamily nov.

Branch-based definition: All species more closely related to LPU 1696 than to *Oligoneuria* and *Chromarcys*.

Genus nov.

Diagnosis: Forewing with crossveins distributed in all sectors; presence of incomplete gemination in longitudinal veins; presence of intercalary vein between MP_1 and MP_2 ; MP_2 and CuA running closely parallel for entire length; presence of intercalaries in cubital region.

sp. nov.

Holotype: Specimen no. LPU 1696, at the Paleontology Collection of the Regional University of Cariri (URCA), Crato, CE – Brazil (Fig. 2).

Type locality: Mine Antônio Finelon, Nova Olinda municipality, Ceará state, Brazil.

Referred specimen: SMNS 66623, at the Staatliches Museum für Naturkunde Stuttgart, Germany. Exact locality unknown.

Locality and horizon: Southern Ceará state, Brazil. Upper Aptian, Lower Cretaceous (Martill, 2007), Crato Formation, Santana Group, Araripe Basin.

Diagnosis: That of genus nov., monotypic.

Description: Specimen preserved in dorsal view, with both forewings articulated and spread out. Head and thorax hard to describe due to incomplete preservation. Hind wings, legs, antennae and most of the caudal filaments missing (Fig. 2).

Body length: 23mm. Forewing length: 18 mm; subtriangular; ratio of wing length to width about 2:1; crossveins present in entire wing (weak in basal sections) (Fig. 5); Sc and RA running parallel to each other; Sc and RA reaching wing apex; RP forks basally at one-fifth of wing length; RP_1 and IRP branch symmetrical at about one-quarter of distance from wing base; RP_2 branch at about one-third distance from wing apex, parallel at apex to IRP; RP_{3-4} running parallel to MA_1 ; MA fork symmetrical, distal to midlength; MP fork near base; pre-gemination of MP_1 with MA_2 distally; two intercalaries between MP_1 and MP_2 ; MP_2 and CuA curving posteriorly forming a close parallel pair for entire length; CuA_1 curving posteriorly near tornus of wing; CuA branched forming CuA_1 and CuA_2 ; CuA_2 running towards posterior wing margin; CuP not branched, curved (Fig. 5); anal veins difficult to trace. Abdomen with nine discernible segments; caudal filaments missing, with only the base of the two cerci preserved, representing 10th segment.

Comments: Staniczek (2007) mentioned a putative adult for *Colocrus magnum*. This specimen (SMNS 66623) was compared with LPU 1696 by photographs and is here referred to the sp. nov.

As Kluge (2004) pointed out, “Mayfly systematics is based on a combination of larval, subimaginal and imaginal characters; however, larvae and winged stages (subimago and imago) are so different, that their association represents a special problem”. There are several known instances of associations between larvae and adults that were latter proved to be mistaken (Kluge, 2004). Even when dealing with extant individuals, it is hard to associate larvae and imagoes based only on morphological characters, and in most situations a precise identification can be made only by rearing them (Kluge, 2004) or using DNA tools such as barcoding (Massariol and Cruz, 2015; Salles et al., 2016). There are oligoneuriid larval individuals described for the Crato Formation (the holotypes of *Colocrus indicum* McCafferty, 1990 - AMNH 43484 and *Colocrus magnum* Staniczek, 2007 - SMNS 66624). The holotype of *Colocrus magnum* has a similar size to our specimen (LPU 1696), but other than that, is not comparable, so the association of winged and larval individuals is doubtful. Therefore, we prefer to describe winged stages under separate names, as is usually accepted in paleoentomology (Sinitshenkova, 1987; 2002).

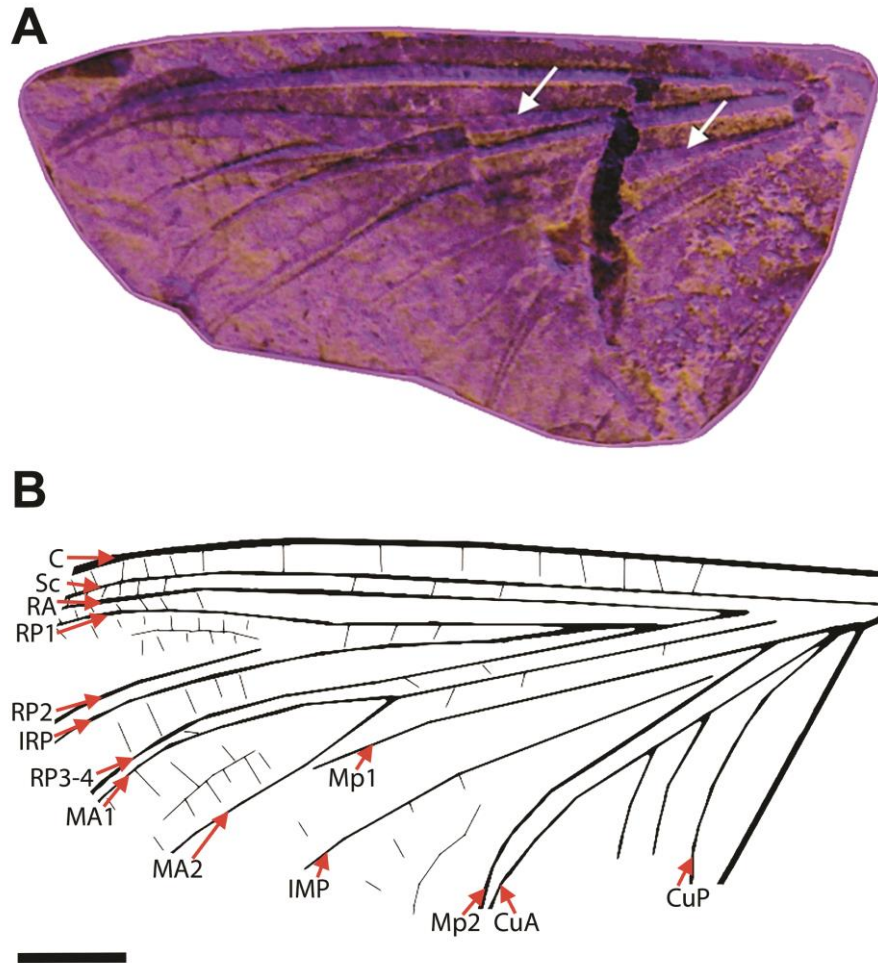


Figure 5. LPU 1696, adult. Upper Aptian, Lower Cretaceous, Crato Formation, Araripe Basin. Nova Olinda municipality, Ceará State, Brazil. A) Right forewing, photograph under ultraviolet light evidencing the crossveination. White arrows point to crossveination. B) Left forewing, interpretative drawing. Scale bar = 2 mm.

4.3. Comments on *Colocrus indicum* McCafferty, 1990

McCafferty (1990) described *Colocrus indicum* based on two specimens, one larva (holotype) and one adult (paratype), and placed the species in the family Oligoneuriidae. The paratype, AMNH 34399, was preserved with some parts of the forewing folded, giving the impression of some pre-geminated veins. However, we here revise its venational data, which clearly indicate its placement in the family Hexagenitidae, because the CuA branches with triads between CuA₁ and CuA₂ (Fig. 6). In fact, the only ephemeropterans that present such branching are the Hexagenitidae, among extinct and extant taxa. Furthermore, the relatively large

hindwings are typical of the Hexagenitidae (Staniczek, 2007). Hexagenitids, widespread during the Jurassic and Early Cretaceous, were often of large size, but the Lower Cretaceous taxa were moderate in size (Tshernova and Sinitshenkova, 1974). Hexagenitidae is the most common ephemeropteran family found in the Crato Formation (Martins-Neto, 1996; Polegatto and Zamboni, 2001), but a more detailed taxonomic review of this clade is beyond the scope of the present work.

The species *Colocrus indicum*, therefore, does not possess any adult representative. Here, we revise the diagnosis suggested by Massariol et al. (2019) for the subfamily Colocrurinae: excluding all adult characters, only one larval character is left (abdominal gill I inserted dorsally). As this character state is present in most extant Ephemeroptera including the outgroups herein analyzed (see Massariol et al., 2019), it is actually a plesiomorphy, and thus not diagnostic. More complete specimens and detailed anatomical descriptions are thus needed to better define *Colocrus* and Colocrurinae. Modern imaging techniques, such as CT scans, may help uncover features currently hidden within the limestone.

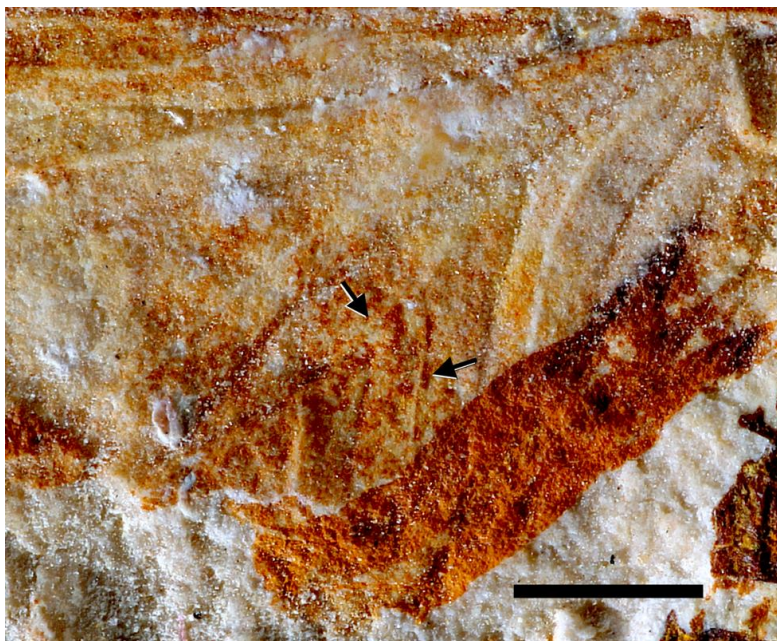


Figure 6. *Colocrus indicum*. Paratype AMNH 34399, adult. Upper Aptian, Lower Cretaceous, Crato Formation, Araripe Basin. Ceará State, Brazil. Photograph of left forewing. Black arrows point to triads between CuA₁ and CuA₂. Scale bar 1 mm.

5. Discussion

Demoulin (1971) emphasized similarities between *Chromarcys* and the Hexagenitidae, assuming a closer phylogenetic relationship between these taxa, which may explain McCafferty's (1990) dubious placement of the adult specimen (paratype) of *Colocrus indivicum* as a representative of Oligoneuriidae. However, the Hexagenitidae clearly lack the apomorphies of the Oligoneuriidae.

All analyses published so far recovered Oligoneuriidae as monophyletic (e. g. Massariol et al., 2019; McCafferty and Edmunds, 1979). Ogden and Whiting (2005) and Ogden et al. (2009) take in few Oligoneuriidae taxa, and their analyses also indicated the monophyly of the family. Following Hillis & Bull (1993), Oligoneuriidae and LPU 1696 + Oligoneuriinae were recovered in our analysis as moderately supported, while Oligoneuriinae as strongly supported.

LPU 1696 exhibits numerous venational similarities with *Chromarcys*, and differing from the Oligoneuriinae, such as forewings with numerous crossveins, some longitudinal veins of forewing not geminated, R2-5 branching toward basal fifth of forewing, and cubital sector of forewing developed (Fig. 5). Our analysis demonstrates that these characters are plesiomorphic for Oligoneuriidae, and are shared within the remaining Heptagenioidea.

The venation of LPU 1696 appears to be a mosaic between a plesiomorphic ephemeropteran wing venation, as evident in *Chromarcys*, and the highly reduced apomorphic wing with geminated longitudinal veins that is found in Oligoneuriinae. Major intercalaries except for IMP are absent in LPU 1696 as they are in Oligoneuriinae, but part of the radial and cubital area retain remnants of the plesiomorphic ephemeropteran venation, as in *Chromarcys*. A tendency towards gemination is clearly evident in LPU 1696, and is the most important evidence that this species bridges a gap in morphology between the Oligoneuriinae and other Oligoneuriidae.

The discovery of a Gondwanan species with such a combination of characters is expected. It appears that several families of Ephemeroptera have had their primary evolutionary development on the Gondwana supercontinent (Edmunds, 1972). Subsequently these southern groups have either dispersed to the temperate areas of the northern Hemisphere (Edmunds, 1979) or suffered vicariance (Massariol et al., 2019). A Gondwanan origin of the family Oligoneuriidae was suggested by Edmunds (1972; 1979), McCafferty (1999), and more recently by Massariol et al. (2019).

Massariol et al. (2019) proposed that the divergence between Oligoneuriinae and Chromarcyinae was related to the breakup of Gondwana. The initial evolution of oligoneuriids in Gondwana was complex, and clades such as *Colocrus* and LPU 1696 might have been sympatric, although more refined stratigraphic data is missing. Reasons for the divergence between major clades are unclear, but our findings give support to the hypothesis that the divergence between Oligoneuriinae + this new subfamily probably occurred in South America and that the present biogeographical distribution of *Chromarcys* can be explained by dispersal, as commented by Massariol et al. (2019). The finding of additional and well-preserved specimens may test this observation.

6. Conclusion

LPU 1696 constitutes the second fossilized adult of an oligoneuriid, and the first specimen to be described in detail, adding to current knowledge of the mayfly diversity in the Lower Cretaceous. The discovery of a new subfamily of Oligoneuriidae in the Mesozoic of South America fills important gaps in the evolutionary history of the family. From a morphological point of view, the specimens of this new taxon fill gaps between an oligoneuriid ancestor and the extant *Chromarcys*, because they present a phenotype of wing venation that combines plesiomorphic and apomorphic character states. From a biogeographical view, they demonstrate that the divergence between Oligoneuriinae + the new subfamily probably occurred in what is now South America.

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Chapter II - New Hexagenitidae mayflies (Ephemeroptera) from the Crato Formation (Aptian, Lower Cretaceous), northeastern Brazil

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New Hexagenitidae mayflies (Ephemeroptera) from the Crato Formation (Aptian, Lower Cretaceous), northeastern Brazil

Abstract

Among mayflies, the Hexagenitidae is the most common family of the Cretaceous. Although early Cretaceous mayflies are species-rich, their fossil record is dominated by nymphal stages. Here two new genera and species are described. We also describe a new adult of *Protoligoneuria* Demoulin, 1955, which allows the update of the genus' diagnosis. A new adult specimen described is classified as Hexagenitidae *incertae sedis*. Lastly, we consider *Cratohexagenites minor* Staniczek, 2007 possibly synonymous with *Protoligoneuria limai*. This work provides new insights on the taxonomic and morphological diversity of the Crato Formation mayfly fauna.

Keywords: Insecta, Palaeoptera, taxonomy, Araripe Basin, Gondwana.

1. Introduction

In early Cretaceous mayfly assemblages (Insecta, Ephemeroptera), the aquatic nymphal stages are dominant while fossils of the winged stages are rare (Sinitshenkova 2002, Sinitshenkova & Coram 2002), probably due to their brief terrestrial cycle in adulthood (Grimaldi & Engel 2005). Among families, the extinct Hexagenitidae Lameere, 1917 is the most species-rich of the Cretaceous Period (Appendix 1). In the early Cretaceous, hexagenitids were abundant in the Jehol Biota (Zhang & Zhang 2003) and are one of the most common arthropod families found in the Crato Formation (Menon & Martill 2007). So far, 11 genera and 16 valid species of this family were described from the early Jurassic to the early late Cretaceous (Zhang & Kluge 2007), including the Crato Formation representatives *Protoligoneuria* Demoulin, 1955 and *Cratohexagenites* Staniczek, 2007. Among the Cretaceous representatives there are 8 genera and 13 valid species described so far (see Appendix 1).

The phylogenetic relationships of the Hexagenitidae are uncertain. Staniczek (2007) stated that the morphological affinities between the nymphs of Hexagenitidae and Siphonuridae, previously pointed out by Tshernova & Sinitshenkova (1974), are plesiomorphic features. According to Kluge (2004), Hexagenitidae is included in Anteritorna, a group that encompasses the vast majority of mayflies and whose diagnostic characters are: "tornus of forewing situated

between apices of veins CuA and CuP, thus CuP usually terminates at basitomal margin of wing far from tornus". Kluge (2004) regarded the bifurcated CuA in Hexagenitidae to be diagnostic, although not unique. Hexagenitids also exhibit several triads in the CuA field, an extremely modified wing venation unique of the family (Kluge 2004).

The first mayfly known from the Crato Formation was reported by Costa-Lima (1950), a nymph he allocated in the family Baetidae. In 1955, Demoulin described this unnamed "Baetidae" specimen as the new species *Protoligoneuria limai*, and positioned it in the Oligoneuriidae. Posteriorly, Brito (1987) described a second species, *Paleobaetodes costalimai*, and placed it in the Baetidae. McCafferty (1990) was the first author to notice that these previously described species pertained to the Hexagenitidae, and synonymized *Paleobaetodes costalimai* with *Protoligoneuria limai*. McCafferty (1990) and Martins-Neto (1996) described additional hexagenitid species and genera from the Crato Formation: *Siphondwanus occidentalis* McCafferty, 1990; *Palaeobaetodes britoi* Martins-Neto, 1996; *Cratogenites corradinae* Martins-Neto, 1996, and *Cratogenitoides delclosi* Martins-Neto, 1996. Posteriorly, Staniczek (2007) synonymized all of the above species with *Protoligoneuria limai*, and described a new genus, *Cratohexagenites*, based on two species.

Here, we provide a list of valid species of the order Ephemeroptera described for the Cretaceous (Appendix 1), describe recently collected fossil specimens of Ephemeroptera from the Crato Formation, and review the Hexagenitidae species from this unit by revising their diagnostic morphological characters.

2. Institutional abbreviations

AMNH, Invertebrate Zoology Collection of the American Museum of Natural History, New York, USA

CD, Vulcano collection, São Paulo, Brazil

LPU, Collection of the Paleontology Laboratory of the Regional University of Cariri (URCA), Crato, Brazil

MB, Zoology Collection of the Museum für Naturkunde, Berlin, Germany

MPSC, 'Plácido Cidade Nuvens' Paleontology Museum of the Regional University of Cariri (URCA), Santana do Cariri, Brazil

MSF, Ms-fossil, Sulzbachtal, Germany

MURJ, Collection Masayuki Murata, Kyoto, Japan

RGMN, Martins-Neto Collection, at Museu de Zoologia da USP, São Paulo, Brazil

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany

3. Material and Methods

A species checklist of valid Cretaceous species of mayflies was made through an extensive bibliographic search using data platforms such as Google Scholar, Georef, Scielo, Paleobiology Database, and Ephemeroptera of the World with the keywords: Ephemeroptera, Cretaceous, fossil, paleontology, mayfly, Mesozoic, and Cretaceous.

We describe the new adult specimens MPSC I 763, MPSC I 1559 (from Santana do Cariri municipality, Ceará state, Brazil) and LPU 1144, and redescribe AMNH 34399 (both without exact locality information), all from the Crato Formation. The new specimens have been collected by mine workers and therefore without stratigraphic control.

We also examined 16 nymph specimens collected in an outcrop of the Crato Formation at the Mine Antônio Finelon (S 07° 07' 22.5'' and W 39° 42' 01'') in Nova Olinda municipality, Ceará State, Brazil. The material was recovered from the top level carbonate C6 (Neumann & Cabrera 1999), which is the main and most important carbonate lithofacies of the Crato Formation. Macroscopically, the C6 limestones mostly present fine granulation and are laminated with alternation of beige and brown colour layers, sometimes presenting a bluish colour (Cabral *et al.* 2019).

The new specimens were analysed using a binocular microscope. All drawings were made with a Wacom tablet, using the software Autodesk Version 8.6.1, and the photos were taken with a Nikon D800 digital camera. The descriptive anatomical terminology follows Kukalova-Peck (1983), Kluge (2004) and Tillyard (1932). Pictures of AMNH 34399 were made available by the American Museum of Natural History.

4. Results

Subphylum HEXAPODA Latreille, 1825

Class INSECTA Linnaeus, 1758

Order EPHEMEROPTERA Hyatt & Arms, 1890

Family HEXAGENITIDAE Lameere, 1917

Type genus. *Hexagenites* Scudder, 1880

Diagnosis (modified from McCafferty 1990; Kluge 2004; Staniczek 2007; Zhang & Kluge 2007). **Adult.** On forewing vein MA vein bifurcate apically; CuA bifurcates in CuA₁ and CuA₂; from the CuA bifurcation a vein "iCu" arises, which forms several (3–6) triads following one another; the anterior branch of each triad forms the next triad; each of these triads have the anterior branch strongly arched; all branches of these triads run toward the tornus of the wing. When median filament present, is smaller than cerci (*Ephemeroptera trisetalis* Eichwald, 1864) or vestigial (*Epicharmeropsis* Huang, Ren & Shih, 2007). **Nymph.** Siphonuroid minnow-like appearance: Head spherical and oval in dorsal view, and hypognathous. Relatively short thorax and long abdomen. Upper part of gills lamellar in shape (lower part known only in *Protoligoneuria*); gills I–VI subequal; gills VII different than others (or enlarged in size - different proportions for each taxon; or with more developed anal rib - see *Shantous lacustris* Zhang & Kluge, 2007); three caudal filaments (Figure 1).

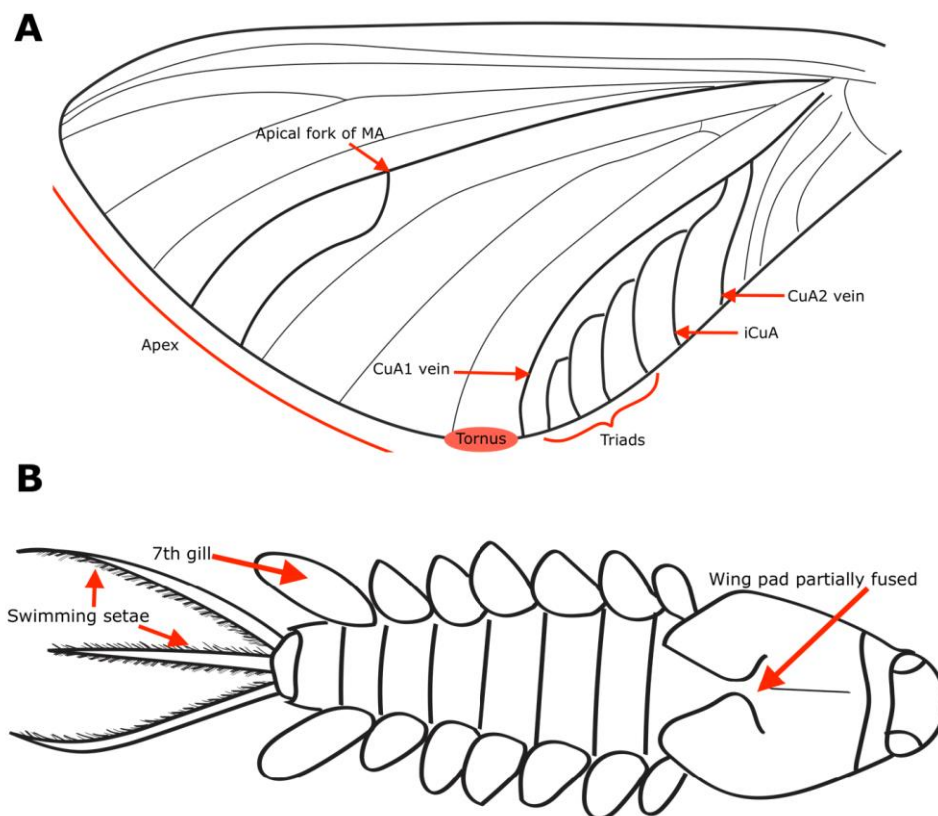


Figure 1. A) Hexagenitidae forewing interpretative drawing with major diagnostic characters and structures evidenced. B) Hexagenitidae nymph interpretative drawing with major diagnostic

characters and structures evidenced. Antennae and legs omitted for clarity.

4.1 *Crato Formation Hexagenitidae*

Genus PROTOLIGONEURIA Demoulin, 1955 p. 271

Palaeobaetodes Brito, 1987 p. 594; *Siphgondwanus* McCafferty, 1990 p. 28; *Cratogenites* Martins-Neto, 1996 p. 180; *Cratogenitoides* Martins-Neto, 1996 p. 181.

Type species. *Protoligoneuria limai* Demoulin, 1955

Emended diagnosis (modified from Staniczek 2007). Adult. Length of forewing between 8–13 mm; forewing with numerous crossveins, including on costal field; vein RP forked one-quarter distance from base of vein to margin; fork of vein MA in three-quarter distance from base of vein to margin; vein MP forked one-sixth distance from base of wing to margin; vein CuA forked one-third distance from base of wing to tornus; CuA field with four successive 'hexagenitid triads'; A₁ with common short stem with A₂. Hind wing one-quarter the size of forewing; costal process absent; RS, MA and MP apically forked. **Nymph.** Body length of mature specimens up to 16 mm. Abdomen with posterolateral spine on segment IX. All gills consisting of a lamellar upper part and a lower gill tuft; costal rib present on upper lamella of all gills; upper portion of gill VII with a second longitudinal rib on the posterior half; gills VII larger than others. Caudal filaments are half of the body size, with primary swimming setae; cerci slightly longer than median filament.

Protoligoneuria limai Demoulin, 1955 p. 271

Palaeobaetodes costalimai Brito, 1987 p. 594; *Siphgondwanus occidentalis* McCafferty, 1990 p. 28; *Cratogenites corradinae* Martins-Neto, 1996 p. 180; *Cratogenitoides delclosi* Martins-Neto, 1996 p. 182; *Palaeobaetodes britoi* Martins-Neto, 1996 p. 184.

Holotype. nymph CD 6616

Diagnosis. That of genus *Protoligoneuria*, monospecific.

Protoligoneuria sp.

Material. adult MPSC I 763 (Figure 2)

Locality. Santana do Cariri municipality, Ceará state, Brazil

Age and horizon. Lower Cretaceous, Upper Aptian (Martill 2007), Crato Formation, Santana Group, Araripe Basin

Generalities. Specimen preserved in dorsal view, with both forewings spread out. Thorax hard to describe due to incomplete preservation, left hind leg missing. Sexual characters not discernible, but possibly female due to apparent presence of numerous eggs preserved in the abdomen. Forewings preserved wrinkled, with right forewing damaged in apical part, and left forewing damaged in cubital area. Hind wings not preserved (Figure 2).

Description. Body length 12 mm. Head short, as broad as thorax; compound eyes 1 mm wide, separated by 0.5 mm dorsally; right antenna about 2 mm long. Forelegs well developed, about 5 mm long; 2 mm long right hind leg as preserved. Forewing length: 12 mm; relation of wing length to width about 3:1; crossveins preserved only in costal field and wing apex; most longitudinal veins (Sc, RA, RP, MA and MP) with common point of origin, probably due to the folded base of forewing; fork of vein MA at three-quarter distance from base of vein to margin; CuP arched; remaining veins difficult to trace. Abdomen with all segments visible, cerci 11 mm long.

Comments. MPSC I 763 is very similar to *Protoligoneuria limai* in the shape and venation of forewings. Forewings have almost the same size as the holotype of *Cratogenitodes delclosi*, which was synonymized and considered a putative winged specimen of *Protoligoneuria limai* by Staniczek (2007). *Cratogenitoides delclosi* has 13 mm long forewings, but in the diagnosis of adults of *Protoligoneuria limai* given by Staniczek (2007), the forewing length is presented as 18–20 mm. We could not find in the literature any individual associated with *Protoligoneuria limai* with such forewing sizes, considering there are only two putative winged specimens described, and that the second specimen (SMNS 66635) has a forewing length of 8 mm. Therefore, either the author has mistaken the wing size range associated with this taxon, or has analysed a specimen with such size but did not cite it. If that is the case, there is an even larger variation in size of adult representatives of *Protoligoneuria limai*, which is not usual among extant mayflies (Malmqvist, 2000). MPSC I 763 probably represents *Protoligoneuria limai*, but due to the preservation of forewing, specially the CuA field that is missing, the precise identification is not possible.

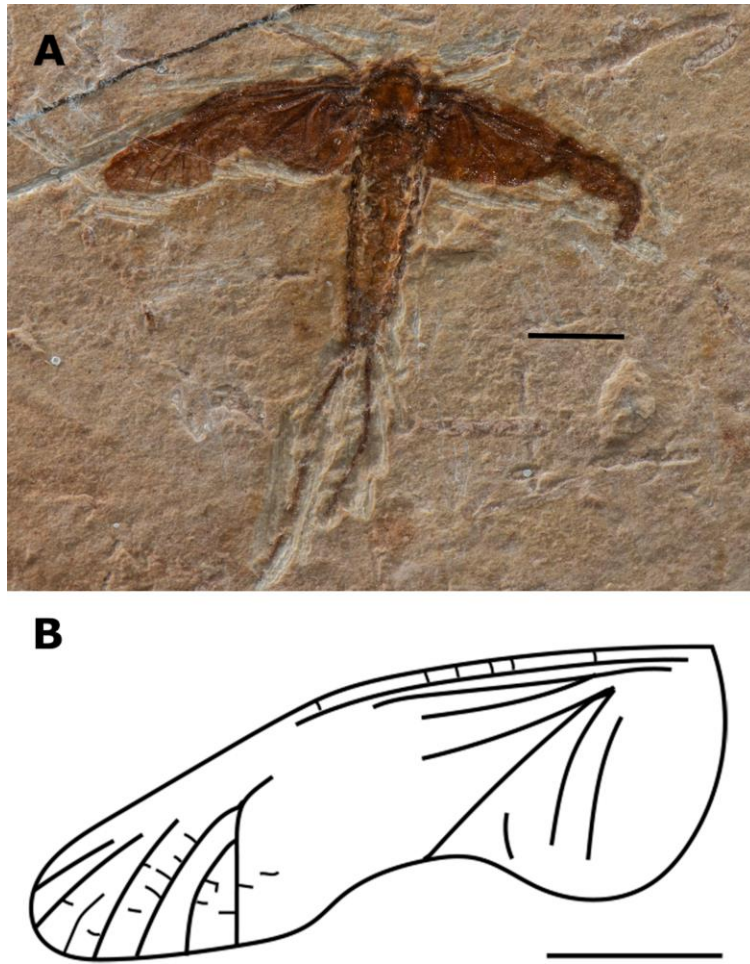


Figure 2. A) MPSC I 763, photograph. Scale bar 4 mm. B) MPSC I 763, left forewing, interpretative drawing. Scale bar 2 mm.

Genus CRATOHEXAGENITES Staniczek, 2007

Type species. *Cratohexagenites longicercus* Staniczek, 2007

Emended diagnosis (modified from Staniczek 2007). **Nymph.** Gill VII around one-third the length of body. Three caudal filaments almost as long as body length; median filament slightly shorter.

Comments. One of the characters used to differentiate *Cratohexagenites* and *Protoligoneuria* is the size and shape of the gill VII (Staniczek 2007), which would be bigger and apically truncate in *Cratohexagenites*, and smaller and apically rounded in *Protoligoneuria*. However, mayflies' gills could have their shape modified during fossilization, so we consider the gill shape a dubious character. The body shape was also used to distinguish both genera, with *Cratohexagenites*

described as having broader drop-like shape (Staniczek 2007), but we did not observe a strong visual difference between the holotype of *Cratohexagenites longicercus* and *Protoligoneuria* concerning this characteristic.

Cratohexagenites longicercus Staniczek, 2007

Holotype. nymph holotype MURJ 447; nymph paratype MB.I.2026; putative adult MSF O46.

Diagnosis (modified from Staniczek 2007). Nymph. Body length of about 27 mm. Length of gill VII 11 mm; close to half the length of body. Length of cerci 28 mm, length of median filament 24 mm. **Adult.** Putative adult with body length of 23.5 mm corresponds to the large size of the nymphal holotype.

Comments. The caudal filaments of *Cratohexagenites longicercus* are notably longer than those found in *Protoligoneuria limai*, being a diagnostic character. But we noticed a problem concerning the collection number of the paratype of *Cratohexagenites longicercus*, which is the same as the holotype of *Cratohexagenites minor*. Although both could be preserved at the same slab of limestone, an explanation has not been stated in the original description.

Cratohexagenites minor Staniczek, 2007

Holotype. nymph holotype MB.I.2026.

Diagnosis (from Staniczek 2007). Nymph. Estimated body length of 16.5 mm. Length of gill VII is about 2.4 mm; around one-seventh the length of body. Length of caudal filaments about 6 mm.

Comments. Staniczek (2007) described *Cratohexagenites minor* based on a nymph with an enlarged gill VII of trapezoidal shape, differing from the type species (*Cratohexagenites longicercus*) by having its body, gill VII and caudal filaments smaller. *Cratohexagenites minor* is known only from one specimen, whose body shape is reported as different from *Protoligoneuria*, being more trapezoid, but part of the head is missing, giving the specimen a drop-like shape aspect. The characters used to erect *Cratohexagenites minor* were the size and format of the gill VII, which we consider dubious. Besides the variation in shape that this structure could assume due to taphonomical reasons, intraspecific size variation is larger in *Protoligoneuria limai* than previously expected. We have analysed and measured 16 nymphs of this species from the Crato Formation, measuring between 6 and 12 mm in length. All of them present the body shape

('siphonuroid minnow-like appearance' of Staniczek 2007) assigned for *Protoligoneuria*, and some of the nymphs have also gill sizes that would correspond to *Cratohexagenites minor*. We calculated the proportion between their body length to their gill VII length and found a high variation, with seven nymphs with smaller proportions than those found in *Cratohexagenites minor*. The holotype of *Cratohexagenites minor* (MB.I.2026) has a body/gill VII length proportion of 6.8 (estimated body size: 16.5 mm, and gill VII size: 2.4 mm). We found even smaller proportions than that (see Table 1). Some specimens have the gill VII even longer than those of the holotype of *Cratohexagenites minor*, but combined with the body shape diagnostic of *Protoligoneuria*. So, the gill VII size of *Cratohexagenites minor* is within the expected variation of *Protoligoneuria limai*. The body and caudal filaments of *Cratohexagenites minor* are also within the expected size variation of *Protoligoneuria limai*. Given that, *Cratohexagenites minor* could be synonymous with *Protoligoneuria limai*, but as we did not examine the holotype first-hand, at this time we refrain from a formal synonymization.

Table 1. Specimens in which the body/length proportions were calculated. In grey are the specimens whose body/7th gill proportion was smaller than in *Cratohexagenites minor*.

Specimen	body length (mm)	7th gill length (mm)	proportion
MPSC 2532	10	2	5
MPSC 2533	11	2	5,5
MPSC 2524	11	2	5,5
MPSC 2529	6	1	6
MPSC 2503	6	1	6
MPSC 2512	6	1	6
MPSC 2526	12	2	6
MPSC 2525	10	1,5	6,7
MPSC 2516	10	1,5	6,7
MPSC 2515	12	1,8	6,7
MB.I.2026	16,5 (estimated)	2,4	6,8
MPSC 2513	7	1	7
MPSC 2504	7	1	7
MPSC 2514	8	1	8
MPSC 2507	9	1	9

MPSC 2522	12	1,3	9,2
MPSC 2509	11	1	11

Genus nov.

Diagnosis. Adult. Forewing length: 11 mm; multiple intercalaries between RP_1 and RP_2 , curved towards median apical margin of wing (at approximately -45 degrees); intercalaries visible only between RP_1 and RP_2 ; RP_{3+4} straight until it curves at about one-sixth distance from apex; fork of vein MA asymmetrical and at four-fifths distance from base of vein to margin; fork of vein MP asymmetrical and at one-fifth distance from base of vein to margin; MP_1 running almost parallel to MA until it diverges from MA at about middle length; CuA_1 quite straight; three triads in the CuA field, the third widest; no intercalaries between the triads.

sp. nov.

Holotype. adult AMNH 34399, formerly described as the paratype of *Colocrus indivicum* McCafferty, 1990 (Figure 3)

Locality. southern Ceará state, Brazil

Age and horizon. Upper Aptian, Lower Cretaceous (Martill 2007), Crato Formation, Santana Group, Araripe Basin.

Diagnosis. That of genus nov., since monospecific.

Generalities. Specimen preserved in dorsal view, with both forewings articulated and spread out. Legs, antennae, and caudal filaments missing. Hind wings present but venation not discernible.

Redescription. Body length: 13.2 mm. Head almost as wide as pronotum; small eyes situated dorsolaterally; distance between eyes more than the length of one eye. Pterothorax length four times that of the head. Forewing length: 11 mm; subtriangular; relation of wing length to width about 2:1; crossveins present in all wing fields, not profuse; Sc and RA straight, parallel to each other reaching wing apex; vein RP forked one-quarter distance from base of vein to margin; multiple intercalaries between RP_1 and RP_2 curved towards median apical margin of wing (at approximately -45 degrees); RP_2 forks at middle length, curved in same direction of the RP intercalaries; RP_{3+4} straight until it curves at about one-sixth distance from apex; fork of vein MA asymmetrical and at four-fifths distance from base of vein to margin; MP_1 running parallel

to MA until it diverges from MA at about middle length; fork of vein MP asymmetrical and at one-fifth distance from base of vein to margin; MP₂ and CuA₁ forming almost parallel pair for entire length; vein CuA forked one-third distance from base of wing to tornus; CuA₁ straight; three successive triads between CuA₁ and CuA₂ (visible on the left forewing - see Figure 4B), the third triad longest; with no intercalaries between triads; CuP curved, parallel to CuA₁ basally and to CuA₂ distally; presence of two anal veins (A₁ and A₂). Hind wings length: 5 mm; venation not discernible. Abdomen length three times that of pterothorax, and same width as thorax; with nine segments preserved; caudal filaments missing.

Comments. McCafferty (1990) described *Colocrus indivicum* based on two specimens, a nymph (holotype) and an adult (paratype), and placed them in the family Oligoneuriidae. The paratype, AMNH 34399, was preserved with some parts of the forewing folded, and the Sc and RA veins, for instance, gave the impression of being geminated. But, when analysed closely, we noticed that they are separated at the wing apex. More important, we observed that the CuA branches with triads between CuA₁ and CuA₂. This revised venational data clearly indicate its placement in the family Hexagenitidae. Furthermore, the relatively large hind wings are also typical of the Hexagenitidae, except in the genus *Protoligoneuria* (Staniczek 2007).

In AMNH 34399 there seems to be a unique intercalary vein, posterior to MA, but, since it is impossible to exist two consecutive positive veins in a mayfly wing, this particular vein must be in fact the MP₁ that became positive during fossilization (Figure 3A).

Apart from the two Hexagenitidae genera known from the Crato Formation (*Protoligoneuria* and *Cratohexagenites*), there are other five with adult representatives: *Hexagenites*, from the Upper Jurassic of Germany, *Ephemeropsis* Eichwald, 1864, from the Upper Jurassic of Transbaikalia and Mongolia, *Hexameropsis* Tshernova & Sinitshenkova, 1974, from the Lower and 'mid' Cretaceous of Ukraine and Algeria, *Mongologenites* Sinitshenkova, 1986, from the Lower Cretaceous of Mongolia, and *Epicharmeropsis*, from the Lower Cretaceous of China (Staniczek 2007; Lin *et al.* 2018).

AMNH 34399 can be excluded from *Protoligoneuria* because of the following characters: the crossveins are not profuse; the Sc and RA veins are straight; the vein MA forks more apically at four-fifths distance from base of vein to margin; absence of intercalaries between MP₂ and CuA₁; there are three triads between CuA₁ and CuA₂; absence of crossveins between CuA₂ and CuP and presence of larger hind wings.

In *Hexagenites*, the forewings are quite bigger (16–23 mm), the MA forks symmetrical, and the CuA is strongly curved in apical half with four curved loop-like triads, so this specimen can't be included in this genus. In *Hexameropsis* there are intercalary veins situated between iMP and MP₁ and iMP and MP₂, the CuA vein is curved and the size of the hind wing is less than half the length of the forewing, unlike in AMNH 34399. *Mongologenites* has six curved loop-like triads in the cubital field, forewing of 18 mm long, and the hind wings are bigger than half the size of forewing, also differing from AMNH 34399. Specimens of *Epicharmeropsis* have large size (forewing length: 35–43 mm), vein CuA forked at one-quarter distance between wing base and tornus, curved CuA₁, intercalaries between MP₂ and CuA₁, four to six curved loop-like triads in cubital field, and crossveins connecting CuA₂ to CuP, unlike AMNH 34399. In *Ephemeropsis* the Sc vein is apically curved, the CuA₁ is strongly curved, also with crossveins connecting CuA₂ to Cup, and there are four to five triads in the CuA field, differing from AMNH 34399. Furthermore, all specimens of *Ephemeropsis* are way bigger (35–45 mm) than AMNH 34399. The unique combination of characters found in AMNH 34399 indicates that the specimen represents a new genus and species of Hexagenitidae.



Figure 3. AMNH 34399, adult. A) AMNH 34399, photograph of right forewing, interpretative drawing of venation (red lines are the positive veins and white lines are the negative veins). Scale bar 5 mm. B) AMNH 34399, close photograph of left forewing. Black arrows point to

triads between CuA₁ and CuA₂. Scale bar 2 mm. C) AMNH 34399, photograph of right forewing without drawing of venation.

Genus nov.

Diagnosis. Adult. Forewing: 9 mm. vein RP forked one-fifth distance from base of vein to margin; fork of vein MA symmetrical and close to two-third distance from base of vein to margin; CuA with three curved loop-like triads of equal sizes, with intercalaries between triads; hind wings size of one-third the size of forewings.

sp. nov.

Holotype. adult LPU 1144 (Figure 4)

Locality. southern Ceará state, Brazil

Age and horizon. Lower Cretaceous, Upper Aptian (Martill 2007), Crato Formation, Santana Group, Araripe Basin

Diagnosis. Adult. That of genus nov., since monospecific.

Generalities. Specimen preserved in left lateral view with both forewings overlapping. Hind wings partially superimposing forewings and covering some cubital and anal veins. Head, thorax and abdomen preserved. Antennae, legs and caudal filaments missing (Figure 4A).

Description. Body length: 12 mm. Eyes situated dorsolaterally. Thorax robust; pterothorax length four times that of head. Forewing length: 9 mm; subtriangular; relation of wing length to width about 2:1; numerous crossveins in all sectors of wing; Sc and RA parallel, apically curved; vein RP forked one-fifth distance from base of vein to margin; RP₂ forks close to middle length; RP₃₊₄ parallel to MA; intercalaries in all RP fields; fork of vein MA symmetrical and close to two-third distance from base of vein to margin, almost at middle length; fork of vein MP symmetrical and at one-eighth distance from base of wing to margin; vein CuA forked one-quarter distance from base of wing to tornus; CuA₁ straight (Figure 4B); intercalaries between MP₂ and CuA₁; three successive triads visible between CuA₁ and CuA₂; intercalaries between triads present (Figure 4C); MP₂, CuA and CuP origins at the same point; CuP curved. Hind wing length: 3.5 mm; subtriangular; RA forks at middle length; RP and MA unforked, originating at the same point; MP unforked, quite straight; remaining veins of hind wing difficult to trace. The abdomen length is 2.5 times bigger than pterothorax; nine abdominal segments preserved.

Comments. LPU 1144 can be excluded from *Protoligoneuria* mostly because its CuA presents three triads instead of four, and its MA forks close to middle length of the wing, not at three-quarter distance from base of vein to margin, as in *Protoligoneuria limai*. Also in *Protoligoneuria* the vein RP forks at one-quarter distance from base of vein to margin, and the hind wings size are one-quarter the size of forewings, unlike in LPU 1144. Moreover, LPU 1144 can be excluded from *Ephemeropsis* and *Epicharmeropsis* due to its forewing size of 9 mm, more than four times smaller than in *Ephemeropsis* (35–43 mm) and *Epicharmeropsis* (34–38 mm). The hind wing is less than half the length of the forewing, unlike in *Ephemeropsis* and *Epicharmeropsis* in which the hind wings are half as long as forewings, besides other venational characters.

The specimen LPU 1144 shares some characters with the genera *Hexameropsis* and the new genus presented here: the three curved loop-like triads in cubital field (unlike other genera that have four to six triads), their moderate size (forewing length: 6.9–23 mm) and forewing length less than two times that of hind wings (Lin *et al.* 2018). However, we chose not to associate this specimen to AMNH 34399 or *Hexameropsis*. Even though the genus *Hexameropsis* has already been found at an Algerian basin (*Hexameropsis africana* Sintshenkova, 1975), which were also part of Gondwanaland, these deposits were far apart geographically and mayflies have low dispersion ability (Malmqvist, 1999). They are also separated temporally: *Hexameropsis africana* is from the Hauterivian (~133–129 Ma) and LPU 1144 from the Aptian (~125–113 Ma). Regarding AMNH 34399, even though these two taxa are from the same geological unit (Crato Formation), they have different hind wing sizes (half the size of forewing in AMNH 34399 and one-third the size in LPU 1144), and in LPU 1144 the crossveins on the forewing are profuse, the Sc and RA veins are apically curved, the vein RP forks at one-fifth distance from base of vein to margin, the MA forks almost at middle length, and intercalaries are present between MP₂ and CuA₁, unlike in AMNH 34399.

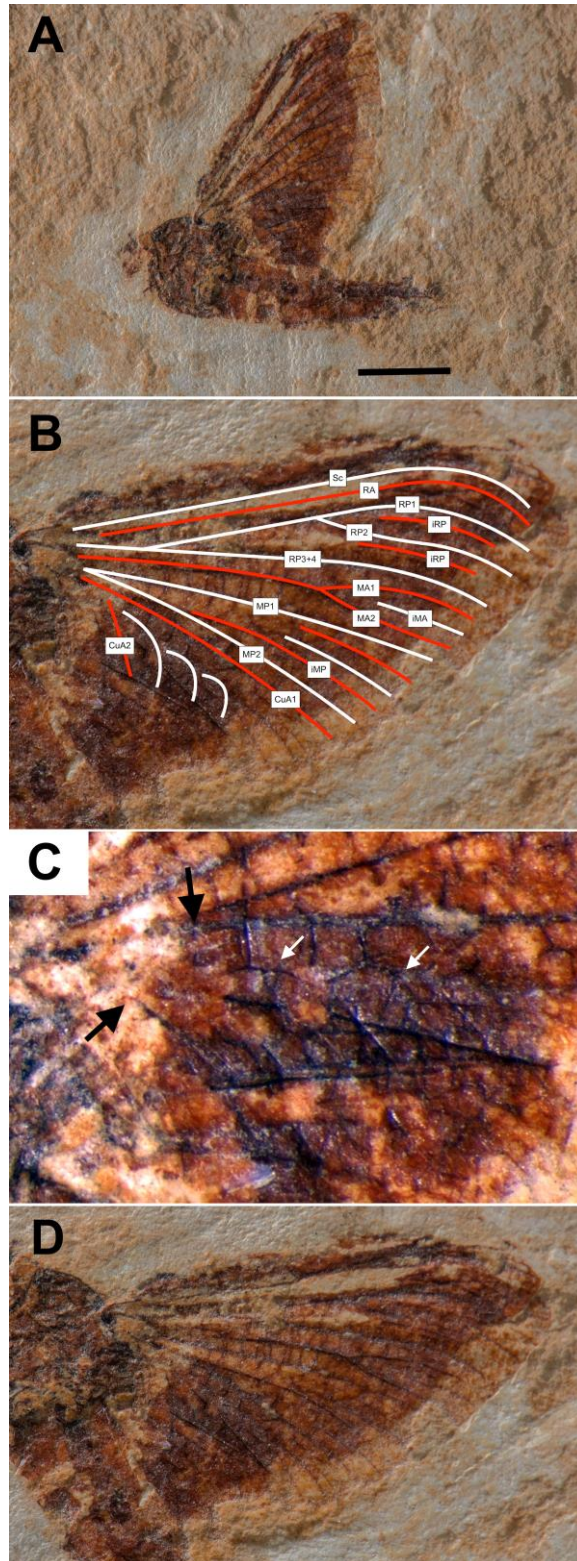


Figure 4. LPU 1144, adult. A) LPU 1144, photograph. Scale bar 3 mm. B) LPU 1144, left forewing interpretative drawing of venation (red lines are the positive veins and white lines are

the negative veins). C) LPU 1144, photograph of left forewing. Black arrows point to CuA₁ and CuA₂. White arrows point to triads between CuA₁ and CuA₂. D) LPU 1144, photograph of left forewing without drawing of venation.

Hexagenitidae incertae sedis

Material. adult MPSC I 1559 (Figure 5)

Locality. Santana do Cariri municipality, Ceará state, Brazil

Age and horizon. Lower Cretaceous, Upper Aptian (Martill 2007), Crato Formation, Santana Group, Araripe Basin

Generalities. Specimen preserved in dorsal view, with both forewings spread out. Basal part of the fore and hind wings not preserved. Caudal filaments preserved, the left one incomplete. Right hind wing absent. Both antennae and right fore leg also preserved (Figure 5A).

Description. Body length: 10 mm. Head narrower than pronotum; compound eyes situated dorsolaterally; eyes widely separated on meson of head by a length approximately equal to the maximum width of an eye; antennae about 1 mm long. Reduced pronotum; mesonotum length three times that of head; with a wide Y shaped impression; metanotum length one-third that of mesonotum; pterothorax length four times that of head (Figure 5C). Forelegs 4 mm long. Forewing length: 8 mm; oval, relation of wing length to width about 3:1; with distal portion only slightly broader than the basal portion; basal connection of veins not discernible; crossveins preserved in several areas of forewing, not profuse; Sc and RA parallel, strongly curved apically; vein RP forked one-third distance from base of wing to margin; RP₂ forks at two-third distance from base of wing to margin; one intercalary between RP₂ and RP₃₊₄; RP₃₊₄ parallel to MA₁; fork of vein MA symmetrical, and at three-quarter distance from base of wing to margin; fork of vein MP asymmetrical; iMP closest to MP₂ (Figure 5B); intercalary veins between MP₂ and CuA; CuA forked (visible only in left forewing); cubital field and anal veins not visible. Hind wing apparently round, half the size of forewing, with longitudinal veins quite straight. Abdomen length of 2.5 times the length of pterothorax; abdomen of same width of thorax up until segment IV; nine abdominal segments visible; segments II–IV short, of subequal length; segments VI and VII enlarged, with segment VII being the longest; posterolateral spines visible on segments IV and V; two 15 mm long cerci, without median filament.

Comments. MPSC I 1559 is similar to adults of *Protoligoneuria limai* in size and shares the RP fork at one-quarter distance from base of vein to margin. However, it is distinguished from *P. limai* in its more apically forking of MA and in its hind wing size, which is half of the size of the forewing, while in *P. limai* the hind wings are smaller (one-quarter the size of the forewing). The specimen also possesses a peculiar character, a wide Y shaped impression on mesothorax. The impression could represent a mesonotal suture strongly stretched backwards medially (non parallel) (Figure 5C). A non-parallel suture between pronotum and mesonotum is also present in the genus *Epicharmeropsis*. Also like in *Epicharmeropsis* the broad hind wings are more or less half as long as the forewing, and the relation of wing length and width is similar too. But the suture we observe is not clear, and could also represent the impression of the thoracic sternum. Thus, we chose not to erect a new taxon for this individual. Furthermore, in MPSC 1559 the triads between CuA aren't visible because the CuA field is not preserved, and they are important generic diagnostic characters. The basal parts of the fore and hind wings are also not preserved, hampering the observation of the fork of some veins, such as the MP and CuA.

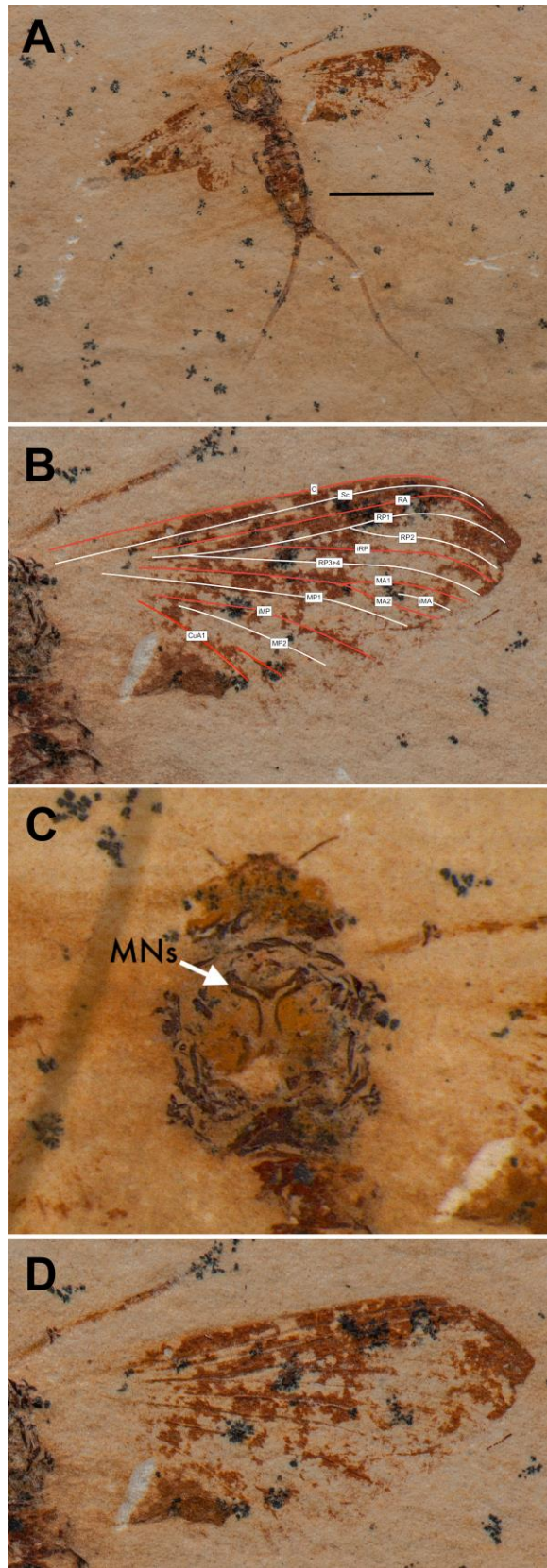


Figure 5. A) MPSC I 1559, photograph. Scale bar 5 mm. B) MPSC I 1559, right forewing

interpretative drawing (red lines are the positive veins and white lines are the negative veins). C) MPSC I 1559, thorax photograph, evidencing mesonotal suture (MNs). D) MPSC I 1559, photograph of right forewing without drawing of venation.

5. Conclusions

Considering there were only two putative winged specimens described for *Protoligoneuria limai* (RGMN-T002 and SMNS 66635), the description of the specimen MPSC I 763 provides new information about the taxon. We recorded a different size variation than previously noticed for the putative adults of *P. limai*, besides also including in the diagnosis the presence of abdominal spines in the nymphs.

The putative adult of *Cratohexagenites longicercus* was associated to the type nymphs based on size (Staniczek 2007), but other than that these stages are not comparable in terms of morphology. We recommend to describe winged stages under separate names. The association, however, is not impossible for palaeontologists to infer, in case of finding the adult in the same assemblage and stratigraphic level as the nymphs (Sinitshenkova 2002) if species richness is low, like the association of *Hexameropsis* larvae and adults made by Sinitshenkova (1975).

We regard *Cratohexagenites minor* as a possible synonym of *Protoligoneuria limai* based on pictures and the original descriptions of both taxa. However, as we did not analyse the type specimens first-hand, it is difficult to make further interpretations on their morphology.

The relatively large hind wings of AMNH 34399 and MPSC I 1559, which are half the length of forewings, and also the numerous intercalary veins in their forewings, are plesiomorphic features within mayflies (Kluge 2004). AMNH 34399 also possesses a costal brace, another plesiomorphic character (Staniczek *et al.* 2011). Therefore, those taxa are worthy of further investigation.

Lastly, we modified some taxa diagnoses by removing characters here considered non-diagnostic, and redundant information that could confuse the reader, like venational features widespread in Ephemeroptera. Besides the geological aspect, the material described above is of interest for the systematic and phylogeny of the order Ephemeroptera.

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Chapter III - Mass mortality events of autochthonous faunas caused by episodic aridity in a Lower Cretaceous Gondwanan Lagerstätte

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Mass mortality events of autochthonous faunas caused by episodic aridity in a Lower Cretaceous Gondwanan Lagerstätte

Abstract

Here we provide the first taphonomic analysis of specimens collected in a mayfly mass mortality from controlled excavations, the first of their kind for that unit. The excavations were conducted in Nova Olinda municipality, Ceará State, Brazil. A layer collected at 285 cm from the top of the Formation presented evidence of one mass mortality event, with 40 mayfly larvae recovered. The only other autochthonous taxon observed was the gonorynchiform fish *Dastilbe*. The larvae were smaller than usual, suggesting a shallow water column, with excellent preservation and no preferential orientation in the samples, suggesting lack of transport. The *Dastilbe* individuals are also relatively small, complete and without preferential orientation. All mayflies belong to the Hexagenitidae, whose morphology demonstrates that the larvae occurred in quiet waters. Subjacent layers to that of the mortality level presented crystals and pseudomorphs of halite, so we hypothesize that the larvae could have died as a result of increasing draught and salinity. We also recovered in the same layer allochthonous taxa indicative of drier weather conditions, and conclude that the Crato Formation lake experienced a seasonal high evaporation caused by the hot climate tending to aridity.

Key words: Ephemeroptera, mayfly, Crato Formation, climate

2. Material and Methods

2.1. Geological setting

The Araripe Basin is located in the northeastern region of Brazil and presents outcrops in three different states: southwestern Ceará, northwestern Pernambuco, and eastern Piauí (Saraiva *et al.*, 2007). Among the Cretaceous deposits, the Santana Group is a depositional sequence associated with the South Atlantic opening. This sequence comprises, from bottom to top, the Barbalha, Crato, Ipubi, and Romualdo Formations (Assine *et al.*, 2007). From these, the Crato Formation represents a stratigraphic sequence of lacustrine deposits with predominance of carbonates and is constituted by six units named, from bottom to top, C1 to C6, interleaved by sandstones, siltstones and shales (Neumann and Cabrera, 1999). These six carbonate packages can be found from the municipality of Santana do Cariri until near Porteiras, both in Ceará, in a

series of laminated limestone outcrops on the Araripe Plateau, where they are commonly located in commercial quarries or in river margins (Viana and Neumann, 2002). More detailed geological and sedimentological information about the Crato Formation can be found in Martill *et al.* (2007).

2.2. Methods

Controlled excavations were conducted by the group of paleontologists of the Regional University of Cariri (URCA) in an outcrop of the Crato Formation at the Mine Antônio Finelon (S 07° 07' 22,5'' and W 39° 42' 01'') in Nova Olinda municipality, Ceará State, Brazil (Figure 1). The surface of the quarry was divided into 5.0 m² x 2.0 m² quadrats and was excavated until the base of the Formation (in total, three meters in depth). A sequence number was attributed on a field form for all collected fossils, and the following information was assessed: place of collection (distance from the top of the excavation); type of fossil (to the least inclusive taxonomic group possible); integrity (complete, incomplete or fragment); preservation type (compressed, impression or 3D); fossil length (cm); fossil width (cm); fossil orientation (azimuth) and other observations of interest (such as sedimentological). The collected fossils were deposited in the Paleontological Collection of URCA (LPU) in Crato municipality, and in the Paleontology Museum Plácido Cidade Nuvens (MPPCN) in Santana do Cariri municipality, both in Ceará State, Brazil.

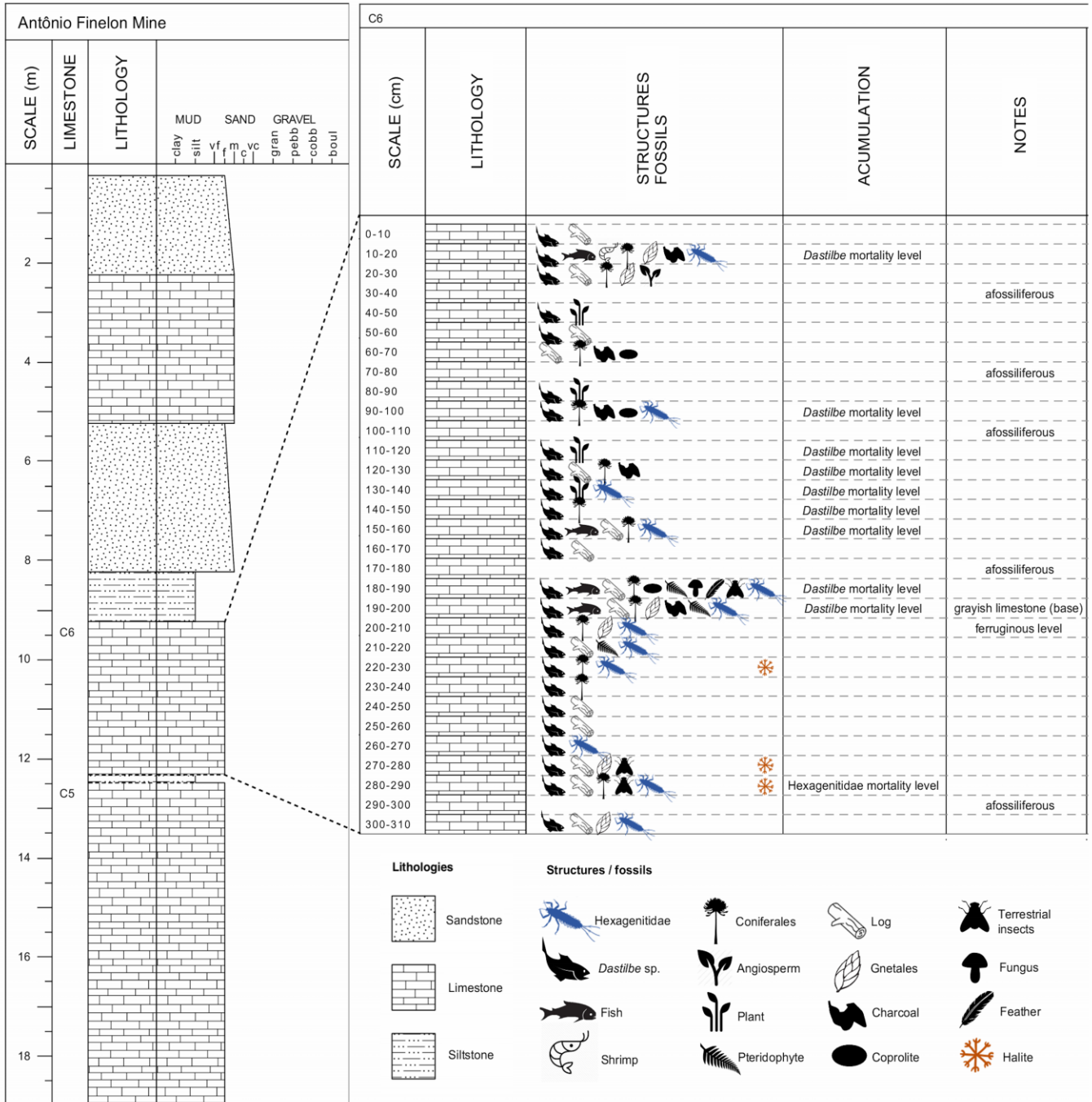


Figure 1. Excavation profile of the Mine Antônio Finelon, Nova Olinda municipality, Ceará State, Brazil. The fossil assemblage from the excavated level C6 in right.

3.Results

A layer collected at 285 cm from the top of the Formation, belonging to top level carbonate C6 (sensu Neumann and Cabrera, 1999) and composed by yellowish limestone,

presented evidence of at least one mass mortality event, with 40 mayfly larvae recovered in 5.0 x 2.0 m². Its over and underlying layers, at 274.5 and 288 cm respectively, presented halite crystals and pseudomorphs. The only other autochthonous taxon observed at the 285 cm level were 18 specimens of the gonorynchiform fish *Dastilbe*.

All mayfly larvae from that level belong to the extinct family Hexagenitidae and could be identified as *Protoligoneuria limai* due to the diagnostic enlarged seventh gill (Staniczek, 2007). Martins-Neto (1996) classified *Protoligoneuria* larvae into ontogenetic categories, with specimens with body length between 0.1 and 1 cm as young, and larvae up to 1.2 – 1.6 cm as mature larvae. The body length of the specimens recovered from this level is consistent with the former (Table 1). These larvae have excellent preservation with all specimens complete. In addition, there is no preferential orientation in the samples suggesting lack of transport. For comparison purposes, the *Dastilbe* individuals from the same level are also smaller than those found in other levels: while they can reach up to 21 cm in length (Brito, 2007), at the layer 285 cm the largest one measures 5 cm, with most of them measuring only 1.5 cm. They are also complete and without preferential orientation (chaotic disposition).

Most of the layers in which Ephemeroptera larvae were found during the controlled excavations presented few individuals, such as one or two. Eighteen larvae were recovered from a layer at 180.4 cm from the top of the Formation, but all its individuals had preferential orientation, so this aggregation was probably caused by transport. Also, the number of preserved specimens at this layer was much smaller than that of layer 285 cm.

Individuals belonging to allochthonous taxa that were recovered at the 285 cm layer include plants (complete *Brachyphyllum obesum* leaves, one *Araucaria* sp. seed, an incomplete *Ginkgo* sp. leaf, *Duartenia araripensis* trunk, and incomplete *Pseudofrenelopsis* sp. branch) and terrestrial insects (an incomplete Orthoptera individual, a complete Hemiptera individual, and a complete Blattaria wing) (Figure 1), all of them also without preferential orientation.

Table 1. Hexagenitidae larvae measurements at the mortality level (layer 285 cm).

Length (cm)	Width (cm)
0.8	0.3
0.8	0.3
0.8	0.3
0.8	0.2

0.8	0.3
0.8	0.3
1.0	0.4
1.0	0.4
0.6	0.2
0.6	0.2
1.0	0.4
1.0	0.4
0.8	0.3
1.0	0.4
1.0	0.5
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
0.4	0.2
0.4	0.2
0.5	0.2
0.5	0.3
0.5	0.3
0.5	0.3
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4
1.0	0.4

1.0

0.4

1.0

0.4

4. Discussion

There is compelling morphological and taphonomic evidence that hexagenitid larvae were well-adapted to standing waters. Their larvae have a minnow-like body with posterolateral abdominal processes, lamellar gills with a thickened outer margin and a thickened rib near the posterior margin, slender weak legs, short claws, and strongly pubescent swimming caudal filaments (McCafferty, 1990; Meshkova, 1961), besides heads that are spherical and oval in dorsal view, and hypognathous in lateral view (Polegatto and Zamboni, 2001). Overall, they are very similar to the general appearance of the extant family Siphonuridae (McCafferty, 1990). The Siphonuridae (known as primitive minnow mayflies) inhabits all kind of aquatic habitats, like lakes, ponds, rivers, swamps and streams vegetation, they reach up to 20 mm, and are considered to be highly tolerant to water quality changes (Bouchard, 2004).

Minnow-like swimming caudal filaments, as occur in hexagenitids, are associated with quiet-water habitats, and the siphonurid-like short claws are associated with either quiet waters or habitats with solid rather than fine substrates (McCafferty, 1990). Meshkova (1961) concluded that the presence of leaf-shaped gills, weak legs (not adapted for burrowing), and strongly pubescent caudal filaments of the larvae of *Ephemeropsis* indicated that they had inhabited undisturbed waters, and in fact, all other hexagenitids from Laurasia have been considered lacustrine (Sinitshenkova, 1984). Martins-Neto (1996) described the habitat of several species of Hexagenitidae as consisting of silty and sandy bottoms with running and shallow water, or stagnant shallow water within vegetated lakes. McCafferty (1990) and Tshernova (1970) hypothesized quiet waters as a habitat for *Protoligoneuria limai* because of its larval swimming adaptations. Polegatto and Zamboni (2001) considered that Hexagenitidae larvae have the typical generalized body-form associated with a facultative diet, such as in extant Siphonuridae (Domínguez *et al.*, 2006). It is therefore likely that the Crato Formation hexagenitids occurred in quiet waters.

Individuals found at layer 285 cm are characterized by excellent preservation with relatively intact specimens. Any type of transport would have consequences regarding the completeness of morphological elements (Martill *et al.*, 2007). Moreover, there is no preferential

orientation in the samples, therefore any transport involving currents or waves is discarded. Braz (2012), studying impressions of the Crato Formation angiospermic phytoflora, observed that most of the fossils were poorly fragmented, and concluded that the deposition occurred in a shallow lake environment with little or no transport. Without the action of water transport, the large accumulation verified by us was probably not random but episodic, and such quality of preservation demands a minimum transport distance (Archibald and Makarkin, 2005), agreeing with the hypothesis of an autochthonous fauna.

Based on the fossils found in layer 285 cm, the Hexagenitidae were the only taxon of autochthonous arthropods that managed to survive longer during times of environmental stresses. These larvae are smaller compared to those found in other levels, suggesting an episode when the water column was so low that they could not molt to reach larval maturity. Possibly, younger individuals could support lower water levels due to their small sizes, as in the early stages their body is only 0.1 cm (Staniczek, 2007). Furthermore, Kluge (2004) points out that mayflies that develop in warmer waters are smaller than those that live in colder waters. The smaller sizes of the *Dastilbe* individuals found in layer 285 cm are also consistent with an episode of a shallower water column.

Over and underlying layers of the mortality level presented crystals and pseudomorphs of halite (NaCl), which form due to the dissolution of a primary salt precipitate (Martill *et al.*, 2007) and indicate that, with the decrease of the water volume, the salinity of the lake increased and salts precipitated (Williams, 1999). Macro-invertebrates are considered to be sensitive indicators of water quality (Clarke and Hering, 2006) and their use as an indicator of water quality has long been recognized as effective (Williams *et al.*, 1991). Many studies have shown that there is a wide variation in the salinity tolerances of different macro-invertebrate taxa (Lancaster and Scudder, 1987; Metzeling, 1993; Berezina, 2003; Kefford *et al.*, 2004). Extant species of mayfly are generally halophobic and only a few species are reported to tolerate elevated salt concentrations as present in brackish water (Chadwick *et al.*, 2002). Even small increases in salinity will result in the loss of sensitive species (James *et al.*, 2003) and can lead to the gain of salt tolerant biota (Nielsen *et al.*, 2003). Although many taxa may be able to survive at elevated salt concentrations, chronic exposure to increased salinity may significantly reduce the recruitment and growth of juveniles, as well as the reproductive capability of the taxa (Hart *et*

al., 2003; Nielsen *et al.*, 2003). Thus, we hypothesize that the larvae recovered at level 285 cm could have died as a result of increasing salinity levels.

Gymnosperms constitute the dominant and most diverse group of plants in the Crato paleoflora, especially the Coniferales (Mohr *et al.*, 2007). At layer 285 cm, the following Coniferales are recognized: *Brachyphyllum obesum* Heer, 1875, *Pseudofrenelopsis* sp., *Duartenia araripensis* Mohr *et al.*, 2012, and *Araucaria* sp. They possess xerophytic characters, such as reduced and compressed leaves in *Brachyphyllum obesum* and *Pseudofrenelopsis* (Kunzmann *et al.*, 2004), as well as thick cuticles, papillae, stomata immersed in the epidermis, and the twisted cauline growth in *Duartenia araripensis* (Mohr *et al.*, 2012). Their preferred habitat would be coastal, riparian or marshy sandy regions of saline or brackish water bodies (Bernardes-De-Oliveira *et al.*, 2013). The presence of *Araucaria* is also related to drier weather conditions (Kershaw and Wagstaff, 2001). These adaptations to a semi-arid to arid climate support the proposed scenario of significant evaporation at the Crato paleolake.

5. Conclusions

Being part of the autochthonous fauna of the Crato Formation, data collected from mayfly fossils, along with paleoclimatic, sedimentological and biological observation, can be used to better understand the paleoenvironmental context of this unit.

According to Martins-Neto (1996; 2006), at least one group of insects experienced mass mortality episodes in the Crato paleolake: Hexagenitidae larvae. There is compelling evidence to consider the assemblage at layer 285 cm as such. The paleoenvironment of the Crato paleolake was subject to constant shifts in salinity, water depth, and degree of oxygenation, causing stress on the aquatic animals. This likely seasonal phenomenon of high evaporation was probably caused by the hot climate tending to aridity.

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General Conclusion

Fossilized mayfly larvae are abundant in several deposits formed in terrestrial aquatic palaeoecosystems, but adult forms are considerably more difficult to be found. In Chapter one, we presented the description of new genus, species and subfamily of the Oligoneuriidae, being the second adult record of the Oligoneuriidae extinct representatives. The taxon's positioning was based on phylogenetic and morphological analysis. The new taxon presents a phenotype of wing venation that combines plesiomorphic and apomorphic character states of Oligoneuriidae representatives, and also demonstrates that the divergence between Oligoneuriidae clades probably occurred in what is now South America.

In the Chapter two, we describe three new adult specimens and redescribe an overlooked one, all from the Crato Formation Lagerstätte of Brazil and pertaining to the Hexagenitidae, a family that was dominant during the Cretaceous. All specimens are almost complete and present the outstanding preservation typical of the Crato Formation. The finding of Crato Formation mayflies with ephemeropteran plesiomorphic characters demonstrate that there are still greatly morphological aspects about the extinct mayfly's clades worthy of study, notably at the Crato Formation. Recommendations to future researchers working with taxonomical aspects of fossil mayflies were also made. Finally, in Chapter three, relying on the morphological and taphonomic information provided by the larvae mass burial, we better understand climatic issues about the environment of the Crato Formation.

Appendix

Appendix 1 of Chapter 1. Morphological characters and their states coded for this phylogenetic analysis (from Massariol *et al.*, 2019, except where noticed).

- 1) Antenna, position: (0) dorsal; (1) frontal
- 2) Antenna, apical antennomeres, processes: (0) absent, (1) present
- 3) Anterior projection: (0) absent, (1) present
- 4) Eye, side, indent: (0) absent, (1) present
- 5) Eye, side, indent, amount: (0) one, (1) two
- 6) Labrum, anterior margin, spines: (0) absent, (1) present
- 7) Maxilla, apical angle, shape: (0) acute, (1) broad
- 8) Maxilla, maxillary palp, second segment length in relation to first: (0) subequal,
(1) much longer
- 9) Labium, accessory gills: (0) absent, (1) present
- 10) Epimera and episterna, lateral margin extension: (0) not projected laterally, (1)
projected laterally
- 11) Epimera and episterna, projection, shape: (0) rounded, (1) acute
- 12) Mid and hind coxae, shape: (0) cylindrical, (1) flattened
- 13) Mid and hind coxae, dorsal projection: (0) absent, (1) present
- 14) Fore femur, outer margin, fine, long, simple setae: (0) absent, (1) present
- 15) Fore femur, outer margin, fine, long, simple setae, position: (0) up to half the
length, (1) exceeding
- 16) Mid and hind femora, outer margin, fine, long, simple setae: (0) absent, (1)
present
- 17) Mid and hind femora, outer margin, fine, long, simple setae, position:(0) up to
half the length, (1) exceeding
- 18) Mid and hind femora, inner margin, setae, protuberances at base: (0) absent, (1)
present
- 19) Mid and hind femora, inner margin, setae, protuberances at base, development:
(0) barely, (1) strongly

- 20) Fore tibia and tarsus, fusion: (0) fused, (1) not fused
- 21) Fore tibia, anterior surface, row of setae: (0) absent, (1) present
- 22) Fore tibia, anterior surface, row of setae, position: (0) restricted to apex, (1) along entire length
- 23) Mid and hind tibiae, inner margin, long, simple setae: (0) absent, (1) present
- 24) Mid and hind tibiae, inner margin, spine-like setae: (0) absent, (1) present
- 25) Mid and hind tarsal claw, shape: (0) slender, (1) robust
- 26) Abdominal terga, posterior margin, spines: (0) absent, (1) present
- 27) Abdominal terga, lateral margins, setae: (0) absent, (1) present
- 28) Abdominal terga, lateral margins, setae, type: (0) simple, (1) spine-like
- 29) Abdominal sterna, tuft of long setae: (0) absent, (1) present
- 30) Abdomen, posterolateral projection, segment distribution: (0) I-IV to IX, (1) VIII to IX
- 31) Abdominal sterna, segment I, finger-like process: (0) absent, (1) present
- 32) Gill I, insertion: (0) dorsal, (1) ventral
- 33) Gill I, outer lamella: (0) absent, (1) present
- 34) Gill I, outer lamella, development: (0) vestigial, (1) well developed
- 35) Gill IV, outer lamella, symmetry: (0) symmetric, (1) asymmetric
- 36) Gill IV, outer lamella, dorsal surface and margins, spines: (0) absent, (1) present
- 37) Gill IV, outer lamella, length in relation to width: (0) about 5x, (1) about 2x
- 38) Gill IV, outer lamella, inner margin, long simple-setae: (0) absent, (1) present
- 39) Gill IV, inner lamella: (0) absent, (1) present
- 40) Gill IV, inner lamella, development in relation to outer lamella: (0) poor-developed (reaching half of total length of outer lamella), (1) well-developed (same length or longer than outer lamella)
- 41) Terminal filament: (0) absent, (1) present
- 42) Terminal filament, length in relation to length of cerci: (0) shorter (reaching half of length of cerci), (1) reaching at least 3/4 of length of cercus
- 43) Terminal filament, setae distribution: (0) almost along entire length, (1) along entire length, except in the basal 1/3

- 44) Caudal filaments, setae, amount: (0) abundant (covered with primary swimming setae in most segments), (1) rare (setae absent in most segment, only a few segments with scarce setae)
- 45) Caudal filaments, spine-like setae: (0) absent, (1) present
- 46) Male eye, continuity: (0) contiguous, (1) not contiguous
- 47) Plumidia: (0) absent, (1) present
- 48) Plumidia, length in relation to metanotum: (0) short (not reaching median length of abdominal segment I), (1) long (reaching median length of abdominal segment I)
- 49) Middle leg, coxae development: (0) not developed (around 1/5 of length of forefemur), (1) developed (at least 1/2 of forefemur)
- 50) Tarsal claws, shape: (0) at least one acute, (1) both rounded
- 51) Forewing, vein RP2: (0) absent, (1) present
- 52) Forewing vein RP2, origin in relation to length of forewing: (0) before basal third, (1) after basal third
- 53) Forewing, vein RP2, orientation in relation to RA: (0) parallel, (1) divergent
- 54) Forewing, IRP vein: (0) absent, (1) present
- 55) Forewing, longitudinal veins, gemination: (0) absent, (1) present
- 56) Forewing, vein IMP: (0) absent, (1) present
- 57) Forewing, vein IMP, translucency: (0) complete, (1) spectral
- 58) Forewing, vein MA, origin of bifurcation in relation to length of wing: (0) after basal third, (1) next to base
- 59) Forewing, vein RP, origin of bifurcation in relation to length of wing: (0) after basal quarter, (1) next to base
- 60) Forewing, complete crossveins present between veins, distribution: (0) all sectors, (1) restrict to 2 costal, subcostal, radial or median anterior (MA) sectors
- 61) Forewing, spectral crossveins: (0) absent, (1) present
- 62) Forewing, cubito-anal sector: (0) developed, (1) reduced
- 63) Forceps: (0) absent, (1) present 2
- 64) Forceps, pedestal of gonostyli: (0) absent, (1) present 1
- 65) Forceps, apical segments, division: (0) single, (1) divided
- 66) Forceps, apical segments, amount: (0) two, (1) three or more

- 67) Styliiger plate, posterior margin, paired projection: (0) absent, (1) present
- 68) Penis, inner and outer lobe, fusion: (0) fused, (1) not fused
- 69) Penis, inner and outer lobe, articulation: (0) articulated, (1) free
- 70) Penis lobe, inner lobe: (0) membranous, (1) semi-membranous 4
- 71) Penis lobe, proximal sclerotized process: (0) absent, (1) present 1
- 72) Penis lobe, proximal sclerotized process, shape: (0) pointed, (1) saddle 1
- 73) Female, abdomen, posterolateral projection in the segment IX: (0) absent, (1)

present

- 74) Forewing, cubital intercalaries: (0) present, (1) absent (**new**)
- 75) Forewing, vein IMA: (0) present, (1) absent (**new**)
- 76) Forewing, longitudinal veins, gemination (0) incomplete, (1) complete (**new**)

Appendix 2 of Chapter 1. Matrix of morphological characters and states used for the phylogenetic analyses of Oligoneuriidae. Ready for use in TNT (hendata format).

xread

76 22

Murphyella_needhami

0010?01000?1111110?10?01110?0?0011??1?1111?1110?00110101000000111000??0?100?

Isonychia

100??01010?1010100?111011011?000?????????0??1100?00110101000000111000??0?000?

Rhithrogena

100??01000?1011110?10?01110??10011110111000000?0?111101000000111000??0??10?

LPU_1696

??1????111111001000????????????000

Colocrus_indivicum

????????????????????????????????11?0?011??1??

Chromarcys_magnifica

00111001111110?110?10?01101000001101101110100??01111101001000111100??0?00?

Oligoneuria_amazonica

011110011111110111010?0110100001100010111100011001101111111101100?11000?1111

Oligoneuria_mitra

011110011111110111010?01101000011000101111000110011011111111111100?11000?1111
Oligoneuria_anatina

0111100111111111111110?1110100001110010111110011001101111111111101011000?1111
Lachlania_alcidesi

01110001111110?111010?0110100001110010110??101100111111011101100?11010?0111
Lachlania_saskatchewanensis

011??0011111?0?0???10?0110??0001110?10??0??0?1??01111111011101100?11010??111
Spaniophlebia

0011100111111111111110?1110100001??0?10110??1011001101111011111100?01010?1111
Fittkauneuria

1010?00110?110?100?10?01100?01010?11110?10000111011011110111010??01??0??111
Homoeoneuria_watu

1010?10110?0011110?0??10000?11110?00010?1100000?110??010?111010??01100?1111
Elassoneuria_madeconeuria

1010?001110110?0???10?0111110001111101010001011010??011101111101011000?1111
Elassoneuria_ellasoneuria

1010?0011101110100?10?01111100011011101010001111010??011101111101001010??111
Oligoneuriella_rhenana

0010?001110110?100?11001100?0001110110111000011101101110?111?11010011111?111
Oligoneuriella_pallida

0010?001110110?100?11101100?00011101101111000?110?101110?111011010011111?111
Oligoneuriella_orontoensis

0010??011101110110?11001100?0001110?10111?000?1?????????????????1011011110?111
Oligoneuriopsis

1010?0011101110110?10?01100?0001110110111100111101101110?111?110110111101111
Oligoneurisca_borysthenica

1110?101?0?0010110?0??10000?11011111111110000??11101110?1110110100??0??111
Rianilaneuria_diminuta

??00?11101110?11111100?01110?0111

Appendix 1 of Chapter 2. Table of Valid species of Ephemeroptera from the Cretaceous. Hexagenitidae in dark grey. Brazilian species in light gray.

Family	Species	Holotype provenance	Holotype
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			ontogenetic stage
Ametropodidae	<i>Palaeometropus cassus</i> Sinitshenkova, 2000	Raritan Formation (USA)	adult
Australiphemeridae	<i>Borephemera goldmani</i> Sinitshenkova, 2000	Raritan Formation (USA)	adult
Australiphemeridae	<i>Nanophemera myanmarensis</i> McCafferty and Santiago-Blay, 2008	Burmese amber (Myanmar)	adult
Baetidae	<i>Myanmarella rossi</i> Sinitshenkova, 2000	Burmese amber (Myanmar)	adult
Baetidae	<i>Palaeocloeon taimyricum</i> Kluge, 1997	Taimyr amber (Russia)	adult
Baetidae	<i>Vetuformosa buckleyi</i> Poinar, 2011	Burmese amber (Myanmar)	adult
Baetiscidae	<i>Cretomitarcys luzzii</i> Sinitshenkova, 2000	Raritan Formation (USA)	adult
Baetiscidae	<i>Protobaetisca bechlyi</i> Staniczek, 2007	Crato Formation (Brazil)	nymph
Epeoromimidae	<i>Epeoromimus infractus</i> Sinitshenkova, 1989	Tsagantsab Formation (Mongolia)	nymph
Ephemeridae	<i>Australiephemera revelata</i> McCafferty, 1990	Crato Formation (Brazil)	adult
Ephemeridae	<i>Cratonympha microcelata</i> Martins- Neto and Caldas, 1990	Crato Formation (Brazil)	nymph
Ephemeridae	<i>Microphemera neotropica</i> McCafferty, 1990	Crato Formation (Brazil)	adult
Euthyplociidae	<i>Pristiplocia rupestris</i> McCafferty, 1990	Crato Formation (Brazil)	nymph
Heptageniidae	<i>Amerogenia macrops</i> Sinitshenkova, 2000	Raritan Formation (USA)	adult
Hexagenitidae	<i>Baikalogenites firmus</i> Sinitshenkova, 2017	Transbaikalia (Russia)	nymph
Hexagenitidae	<i>Caenoephemera shangyuanensis</i> Lin and Huang, 2001	Yixian Formation (China)	nymph
Hexagenitidae	<i>Cratohexagenites longicercus</i>	Crato Formation	nymph

	Staniczek, 2007	(Brazil)	
Hexagenitidae	<i>Cratohexagenites minor</i> Staniczek, 2007	Crato Formation (Brazil)	nymph
Hexagenitidae	<i>Ephemeropsis martynovae</i> Tshernova, 1961	Zaza Formation (Russia)	adult
Hexagenitidae	<i>Ephemeropsis trisetalis</i> Eichwald, 1864	Turga Formation (Russia)	nymph
Hexagenitidae	<i>Epicharmeropsis hexavenulosus</i> Huang et al., 2007	Yixian Formation (China)	adult
Hexagenitidae	<i>Epicharmeropsis quadrivenulosus</i> Huang et al., 2007	Yixian Formation (China)	adult
Hexagenitidae	<i>Hexameropsis africana</i> Sinitshenkova, 1975	Algeria	nymph
Hexagenitidae	<i>Hexameropsis elongatus</i> Lin et al., 2018	Burmese amber (Myanmar)	adult
Hexagenitidae	<i>Hexameropsis selini</i> Tshernova and Sinitshenkova, 1974	Ukraine	adult
Hexagenitidae	<i>Mongologenites laqueatus</i> Sinitshenkova, 1986	Gurvan-Eren Formation (Mongolia)	nymph
Hexagenitidae	<i>Protoligoneuria limai</i> Demoulin, 1955	Crato Formation (Brazil)	nymph
Leptophlebiidae	<i>Aureophlebia sinitshenkovae</i> Sinitshenkova, 2000	Raritan Formation (USA)	adult
Leptophlebiidae	<i>Clavineta brevinodia</i> Huang et al., 2011	Yixian Formation (China)	nymph
Leptophlebiidae	<i>Clavineta citima</i> Huang et al., 2011	Doronino Formation (Russia)	nymph
Leptophlebiidae	<i>Clavineta excavata</i> Huang et al., 2011	Yixian Formation (China)	nymph
Leptophlebiidae	<i>Clavineta transbaikalia</i> Sinitshenkova, 2000	Doronino Formation (Russia)	nymph
Leptophlebiidae	<i>Furvoneta khasurtensis</i> Sinitshenkova, 2017	Transbaikalia (Russia)	nymph
Mesonetidae	<i>Mesoneta deusta</i> Sinitshenkova, 2000	Doronino Formation	nymph

		(Russia)	
Oligoneuriidae	<i>Colocrus indicum</i> McCafferty, 1990	Crato Formation (Brazil)	nymph
Oligoneuriidae	<i>Colocrus magnum</i> Staniczek, 2007	Crato Formation (Brazil)	nymph
Palaeoanthidae	<i>Palaeoanthus minutus</i> Kluge, 1993	Kheta Formation (Russia)	adult
Palaeoanthidae	<i>Palaeoanthus orthostylus</i> Kluge, 1993	Kheta Formation (Russia)	adult
Palingeniidae	<i>Mesopalingea lerida</i> Whalley and Jarzembowski, 1985	La Pedrera de Rúbies Formation (Spain)	nymph
Polymitarcyidae ?	<i>Caririnympha mandibulata</i> Martins-Neto and Caldas, 1990	Crato Formation (Brazil)	nymph
Potamanthidae ?	<i>Olindinella gracilis</i> Martins-Neto and Caldas, 1990	Crato Formation (Brazil)	nymph
Prosopistomatidae	<i>Proximicorneus rectivenius</i> Lin, Shih, Zhao and Ren 2018	Burmese amber (Myanmar)	adult
Siphonuridae	<i>Albisca tracheata</i> Sinitshenkova, 1989	Tsagantsab Formation (Mongolia)	nymph
Siphonuridae	<i>Australurus plexus</i> Jell and Duncan, 1986	Koonwarra fossil beds (Australia)	nymph
Siphonuridae	<i>Cretoneta acmoptera</i> Kluge, 1993	Kheta Formation (Russia)	adult
Siphonuridae	<i>Cretoneta zherichini</i> Tshernova, 1971	Kheta Formation (Russia)	adult
Siphonuridae	<i>Dulcimanna sculptor</i> Jell and Duncan, 1986	Koonwarra fossil beds (Australia)	nymph
Siphonuridae	<i>Mesobaetis amplectus</i> Sinitshenkova, 2000	Doronino Formation (Russia)	nymph
Siphonuridae	<i>Mesobaetis crispa</i> Sinitshenkova, 2017	Transbaikalia (Russia)	nymph
Siphonuridae	<i>Proameletus branchiatus</i> Sinitshenkova, 2017	Transbaikalia (Russia)	nymph
Siphonuridae	<i>Promirara cephalota</i> Jell and	Koonwarra fossil beds	nymph

	Duncan, 1986	(Australia)	
Siphonuridae	<i>Siphangarus rotundus</i> Sinitshenkova, 2000	Doronino Formation (Russia)	nymph
Torephemeridae	<i>Torephemera longipes</i> Sinitshenkova, 1989	Tsagantsab Formation (Mongolia)	nymph
<i>incertae sedis</i>	<i>Caririphemera marquesi</i> Zamboni, 2001	Crato Formation (Brazil)	nymph
<i>incertae sedis</i>	<i>Costalimella nordestina</i> Martins- Neto, 1996	Crato Formation (Brazil)	adult
<i>incertae sedis</i>	<i>Costalimella zuechii</i> Zamboni, 2001	Crato Formation (Brazil)	adult