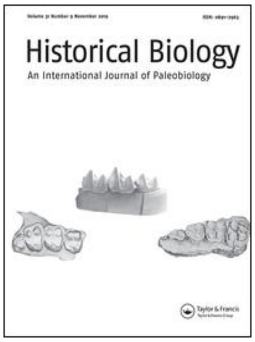

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An overview of the Hexagenitidae (Ephemeroptera) from the Crato Formation (Aptian, Lower Cretaceous) of Brazil, with the description of a new species

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ABSTRACT
Among mayflies, the Hexagenitidae is the most common family of the Cretaceous, including in the world-renowned Crato Formation (Aptian) of northeastern Brazil. However, most of the Crato mayfly fauna was described based on nymphs, which, due to their ontogenetic development, may present numerous continuous characters. As a consequence, many unclear taxa have been described, and their taxonomic position needs to be re-evaluated. We here present a checklist and revision of some previously described species from the Crato Formation and the description of new specimens. We propose a new species, *Protoligoneuria heloisae* sp. nov., based on a previously described adult erroneously referred to within Oligoneuriidae. Further adult specimens of Hexagenitidae are here described in detail, presenting new morphological data and variations that were, up to now, unknown for Hexagenitidae of the Crato Formation. Lastly, we briefly discuss the genus *Cratohexagenites*. Our new findings further add to the taxonomical and morphological diversity of the adult mayfly fauna of the Crato Formation.

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KEYWORDS
Taxonomy; aquatic insects; Araripe Basin; Neotropics

Introduction

In the fossil record of mayfly assemblages (Insecta, Ephemeroptera), the aquatic nymphal stages are dominant while fossils of the winged stages are rare (Sinitshenkova 2002; Sinitshenkova and Coram 2002), possibly due to their brief adult life span and their fragility (Grimaldi and Engel 2005). It is, however, relevant to describe adult forms, which present more potential diagnostic characters at their wings. Many nymphal characters appear to be continuous, making diagnostic characters dubious, at least for the Hexagenitidae Lameere 1917. They are a family abundant in Mesozoic assemblages, including in important Lagerstätten such as the Solnhofen beds in southern Germany (Ponomarenko 1985), the Jehol Group in northeastern China (Zhang and Zhang 2003; Huang et al. 2007), the Baissa and Khasurty localities in western Transbaikalia of Russia (Sinitshenkova 2017; Kopylov et al. 2020) and the Crato Formation in northeastern Brazil (Menon and Martill 2007) (see Tshernova 1961; Tshernova and Sinitshenkova 1974; Sinitshenkova 1975, 1989, 2002, 2017; McCafferty 1990; Carpenter 1992; Martins-Neto 1996; Lin and Huang 2001; Kluge 2004; Huang et al. 2011). So far, 21 species in 11 genera are currently considered within this family, all of them from the early Jurassic to the early late Cretaceous. Among the Cretaceous representatives, there are nine genera and 16 species (see Table S1), including the Crato Formation representatives *Protoligoneuria* Demoulin, 1955 and *Cratohexagenites* Staniczek, 2007.

The phylogenetic relationships of the Hexagenitidae are uncertain. Kluge (2004) treated Hexagenitidae as Anteritorna *incertae sedis*. Anteritorna encompasses the vast majority of mayflies diagnosed with 'tornus of forewing situated between apices of veins CuA and CuP, thus CuP usually terminates at basitornal margin of wing far from tornus'. Kluge (2004) regarded the bifurcated CuA in Hexagenitidae to be diagnostic, although not unique. Hexagenitidae also exhibits several vein loops in the CuA field, referred to by Kluge (2004) as 'Hexagenitidae triads', a highly modified wing venation unique to the family (Kluge 2004). Staniczek (2007) stated that the morphological affinities between the nymphs of Hexagenitidae and Siphlonuridae, previously pointed out by Tshernova and Sinitshenkova (1974), are plesiomorphic features. Based on gill morphology, he assumed a closer affinity within Setisura (Staniczek 2007). Finally, Willmann (2007) suggested Hexagenitidae (excl. *Cratogenitoides* Martins-Neto, 1996) as a sister taxon to the Alulata (= *Cratogenitoides* + Ephemerida) lineage, thus excluding Hexagenitidae from the crown group Ephemeroptera. Consequently, Willmann (2007) treated the unique venation of the costal field of *Cratogenitoides* and of the remaining Hexagenitidae as a plesiomorphic character. However, no other author concurred with this hypothesis.

The first mayfly known from the Crato Formation was reported by Costa-Lima (1950), a nymph he allocated in the family Baetidae Leach 1815. Demoulin (1955) described this unnamed 'Baetidae' specimen as *Protoligoneuria limai* Demoulin, 1955, and placed it in the Oligoneuriidae Ulmer, 1914. Later, Brito (1987) described a second species based on a nymph, *Paleobaetodes costalimai* Brito, 1987, and placed it in the Baetidae. McCafferty (1990) was the first author to notice that these previously described species pertained to the Hexagenitidae and synonymised *Paleobaetodes costalimai* with *Protoligoneuria limai*. McCafferty, 1990 and Martins-Neto, 1996 described additional hexagenitid species and

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genera from the Crato Formation: *Siphgondwanus occidentalis* McCafferty, 1990; *Palaeobaetodes britoi* Martins-Neto, 1996; *Cratogenites corradiniae* Martins-Neto, 1996; and *Cratogenitoides delclosi* Martins-Neto, 1996, the last one based on an adult. Finally, Staniczek (2007) synonymised all of the above species with *Protoligoneuria limai* and described a new genus, *Cratohexagenites* Staniczek, 2007, based on two species.

Here, we describe recently collected fossil specimens of Ephemeroptera from the Crato Formation, review the Hexagenitidae species from this unit by revising their diagnostic morphological characters, and provide a list of species of the order Ephemeroptera described for the Cretaceous (Table S1).

Material and Methods

We describe here the new adult specimens MPSC I 763, MPSC I 1559 (from Santana do Cariri municipality, Ceará state, Brazil) and LPU 1144, and redescribe AMNH 43499 (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 examine 16 nymphs 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 and 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 Leica M250C 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 morphological terminology follows Tillyard (1932), Kukalova-Peck (1983) and Kluge (2004). Pictures of AMNH 43499 were made available by David Grimaldi and Courtney Richenbacher of the American Museum of Natural History. AHS investigated the Crato specimens first-hand at the AMNH in April 2016.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org/’. The LSID for this publication is urn:lsid:zoobank.org:pub:1578ED81-4664-4F3E-B64A-1E4807CC71FD.

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 Palaeontology Laboratory of the Regional University of Cariri (URCA), Crato, Brazil; MB, Zoology Collection of the Museum für Naturkunde, Berlin, Germany; MPSC, ‘Plácido Cidade Nuvens’ Palaeontology 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 of the University of São Paulo, São Paulo, Brazil; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Results

Systematic Palaeontology

Subphylum HEXAPODA Latreille, 1825

Class INSECTA Linnaeus, 1758

Order EPHEMEROPTERA Hyatt and Arms, 1890

Family HEXAGENITIDAE Lameere, 1917

Type genus. *Hexagenites* Scudder, 1880

Revised diagnosis. [modified from McCafferty (1990); Kluge (2004); Staniczek (2007)] *Adult*. Gemination of longitudinal veins more or less expressed, or entirely absent; CuA bifurcates in CuA_1 and CuA_2; from the bifurcation, an intercalary vein arises from CuA_1, which forms several (3–6) consecutive loops; the branch of each loop forms the next; each of these loops strongly arched; all branches of loops run towards the tornus of the wing. When present, median filament is smaller than cerci (*Ephemeropsis trisetalis* Eichwald, 1864) or vestigial, with three to five segments (*Epicharmeropsis* Huang et al., 2007). *Nymph*. Fusiform [drop-like according to Staniczek (2007)] and flattened body. Head hypognathous. Upper part of gills lamellar in shape (lower part with tracheal tuft, known only in *Protoligoneuria*); gills II–VI subequal, with more or less developed ribs; gill I predominantly smallest; gills VII enlarged in size (different proportions in each taxon); three caudal filaments, with primary swimming setae (Figure 1).

Hexagenitidae of the Crato Formation

Genus *Protoligoneuria* Demoulin, 1955

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

Revised diagnosis. [modified from Martins-Neto (1996); Staniczek (2007)] *Adult*. Length of forewing between 8 and 13 mm; forewing with numerous crossveins, including on costal field; longitudinal veins not geminated; vein RP forked at least $^1/_4$ of distance from base to margin; vein MA forked at $^2/_3$ of distance from base to margin; vein CuA forked at $^1/_3$ of distance from base to tornus; CuA field with three successive loops, with additional one to two veins distally of that last loop (Figure 2A).

Comments. Nymphal stages of *P. limai* are well documented, but presently, it is not possible to determine which of their characteristics are diagnostic at the genus or species level.

Protoligoneuria limai Demoulin, 1955

Palaeobaetodes costalimai Brito, 1987: p. 594, Figures 1–3 [description based on nymph; synonymy proposed by McCafferty (1990, p. 22)]; *Siphgondwanus occidentalis* McCafferty, 1990: p. 28, figs 9–10 [description based on nymph; synonymy proposed by Staniczek (2007, p. 172)]; *Cratogenites corradiniae* Martins-Neto, 1996: p. 180, Figures 2–3 [description based on nymph; synonymy proposed by Staniczek (2007, p. 172); *Cratogenitoides delclosi* Martins-Neto, 1996: p. 182, Figure 4 [description based on adult, synonymy proposed by Staniczek (2007, p. 172)]; *Palaeobaetodes britoi* Martins-Neto, 1996: p. 184, fig 8 [description based on nymph, synonymy proposed by Staniczek (2007, p. 172)].

Holotype. Nymph CD 6616

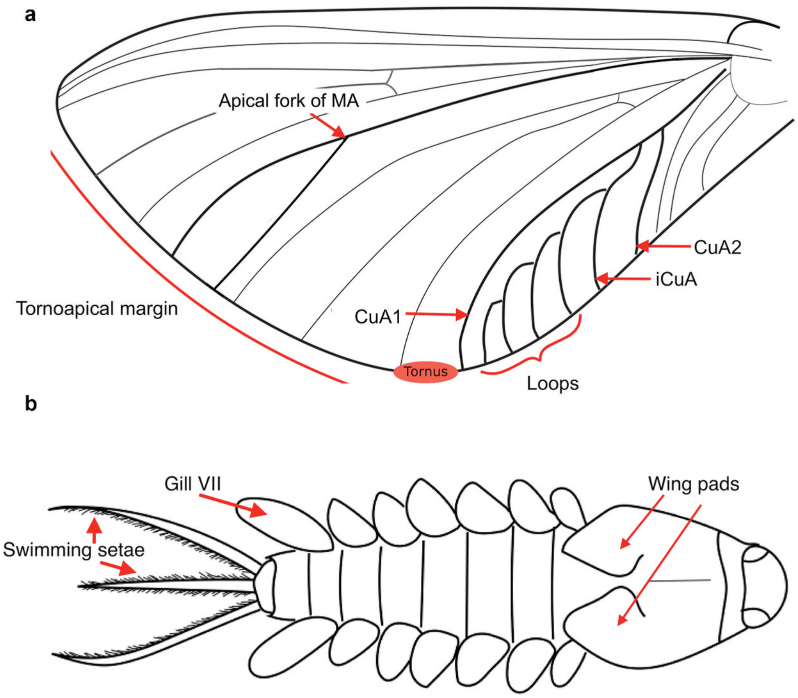

Figure 1. Major diagnostic characters of the Hexagenitidae. (A) Hexagenitidae forewing, interpretative drawing with major diagnostic characters and structures highlighted. The drawing evidences the tornoapical margin of the forewing, which is the outer, or hind-distal, margin of forewing; the tornus, which is situated close to apices of veins CuA, and CuP terminating at basitomal margin of wing far from tornus, as in the representatives of Anteritorna, such as Hexagenitidae (in contrast to Posteritorna, in which the tornus is situated behind the apex of CuP); the apical fork of MA close to half of the wing; the vein CuA bifurcated into CuA1 and CuA2; an intercalary iCuA arises from CuA1 and CuA2 forming loops, which represents a unique apomorphy of Hexagenitidae (Kluge 2004; Staniczek 2007). (B) Hexagenitidae nymph, interpretative drawing with major diagnostic characters and structures highlighted, evidencing the primary swimming setae of the caudal filaments that are dense in Hexagenitidae; the enlarged gill VII (in contrast to other gills), unique of Hexagenitidae; and the wing pads partially fused medially as in recent species of Setisura (Kluge 2004; Staniczek 2007). Crossveins, antennae and legs omitted for clarity. Drawing not based on any particular genus or species.

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

Revised diagnosis. [based on Martins-Neto (1996); Staniczek (2007)] *Adult*. Forewing with MP forked at $^1/_6$ of distance from base to margin; loops of same length (Figure 2A). Hind wing length between $^1/_3$ and $^1/_4$ of forewing length. *Nymph*. Body length of mature specimens up to 16 mm. Abdomen with posterolateral spine on segment IX (Figure 2B). All gills consisting of a lamellar upper part and a lower tracheal tuft; in gill VII anterior branch of anal rib markedly thin, curved and pointed apically, gill VII with upper portion larger than preceding gills and with a second longitudinal rib on the posterior half. Caudal filaments are half of the body length, with primary swimming setae; cerci slightly longer than median filament.

Protoligoneuria heloisae sp. nov.

= *Colocrus indivicum* McCafferty, 1990: p. 195: 31, figs 17, 19 [*partim*]

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Derivation of name. Specific epithet *in memoriam* of Paula Heloísa Santana Resende, a young Brazilian biologist who was dedicated to the study of fossils from the Araripe Basin.

Holotype. Adult AMNH 43499, formerly described as a paratype of *Colocrus indivicum* McCafferty, 1990 (Figure 3). Although Brazilian legislation requires that type specimens are curated at Brazilian institutions, this specimen has already been formally described and referred to as type material in the literature three decades ago.

Locality. Southern Ceará state, Brazil

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

Diagnosis. Adult. Forewing with MP forked at $^1/_4$ of distance from base to margin; three successive loops between CuA_1 and CuA_2, the first loop largest. Hind wings almost half the length of forewings. *Nymph*. So far unknown.

Generalities. Specimen preserved in dorsal view, with both forewings articulated and spread out. Legs, antennae, and caudal filaments missing. The forewings of this specimen are mostly twisted between the veins C and MP1, and such conformation gives a somehow geminated aspect in some parts of the veins (see Comments). Hind wings present but venation not discernible.

Description. Body length: 13.2 mm. Head almost as wide as pronotum; eyes small, situated dorsolaterally; distance between eyes more than the width of one eye. Pterothorax length four times that of head. Forewing length: 11 mm; subtriangular; relation of wing length to width about 2:1; costal brace strongly arched; crossveins present in all wing fields; Sc and RA straight, parallel to each other reaching wing apex; numerous intercalaries between RP and anal fields; vein RP forked at $^1/_4$ of distance from base to margin; 3–4 intercalaries between RP_1 and RP_2; RP_2 forks at middle length; vein MA forked at $^2/_3$ of distance from base to margin; vein MP forked at $^1/_5$ of distance from base to margin; MP_2 and CuA_1 forming almost parallel pair for entire length; vein CuA forked at $^1/_3$ of distance from base to tornus; CuA_1 straight; three successive loops between CuA_1 and CuA_2, with at least one intercalary between each loop, the third loop largest; CuP curved, parallel to CuA_1 basally and to CuA_2 distally; presence of two anal veins (A_1 and A_2). Hind wings approximately 5 mm long; venation not discernible. Abdomen length three times that of pterothorax, and same width as thorax; with nine segments preserved; caudal filaments missing.

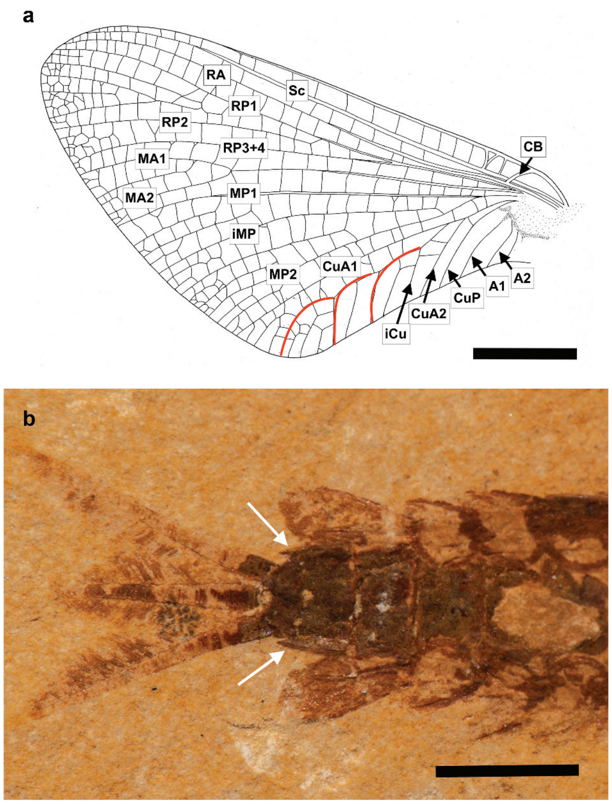

Figure 2. *Protoligoneuria limai*. (A) SMNS 66635, adult, forewing, interpretative drawing of venation. Three successive loops on the CuA field marked in red. Scale bar 2 mm. (B) MPSC I 2515, nymph in ventral view. White arrows point to posterolateral spines on segment IX. Scale bar 2 mm.

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 43499, 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 importantly, we observed that the CuA branches with loops between CuA_1 and CuA_2. This revised venational data clearly indicate its placement in the family Hexagenitidae, as already pointed out by Storari et al. (2020). Furthermore, the relatively large hind wings are also typical of the Hexagenitidae (Staniczek 2007).

The fossilisation of the forewings of AMNH 43499 presents some interesting peculiarities. At first glance, there seems to be a unique intercalary vein posterior to MA, but as two consecutive positive veins in a mayfly wing are impossible, this particular vein must, in fact, represent MP_1 that became positive during fossilisation (Figure 3A). Also, there are some peculiar features, such as the asymmetry of the MA fork, which is not unusual in mayflies, but particularly in this specimen could be the result of the twisted wing; and the bending of the veins between C and MP_1 (e.g. the angles of bends at −45° at the RP field veins). These angles are not congruent with the usual mayfly wing venation (see Kluge (2004): Index of characters; Wings p. 380). These apparently twisted veins are probably the result of wing damage (e.g. during moulting from subimago to imago). McCafferty's (1990) conclusion about placement within *Colocrus* may have been influenced by this twisted wing.

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

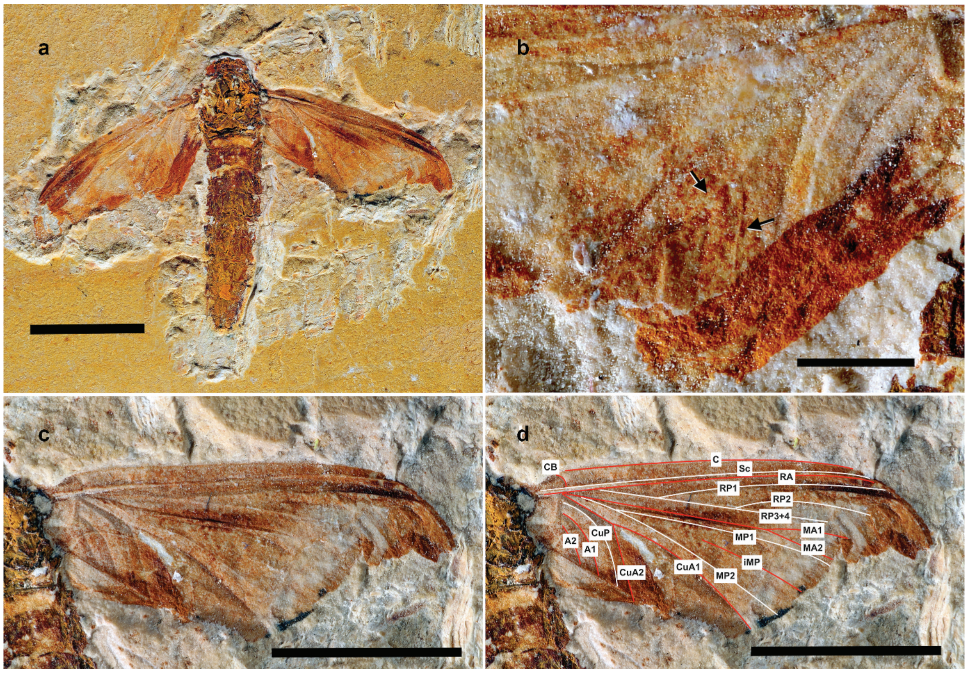

Figure 3. *Protoligoneuria heloisae* sp. nov. Holotype. AMNH 43499. (A) Photograph of the specimen in dorsal view. Scale bar 5 mm. (B) Detail of left forewing. Black arrows point to loops between CuA_1 and CuA_2. Scale bar 2 mm. (C) Photograph of right forewing without drawing of venation. Scale bar 5 mm. (D) Photograph of right forewing with an interpretative drawing of venation (red lines denote positive veins and white lines denote negative veins, CB is costal brace). Scale bar 5 mm.

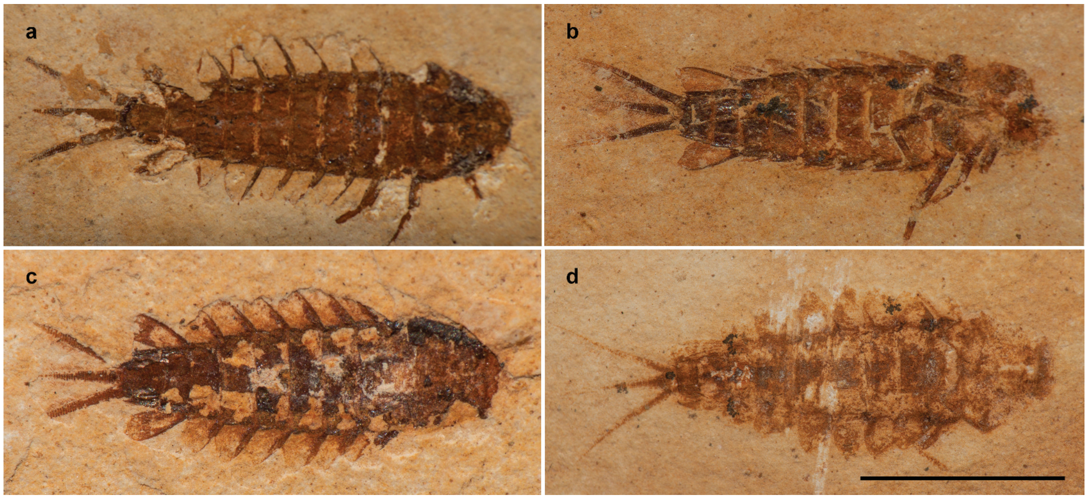

Figure 4. *Protoligoneuria limai* nymphs. Specimens in which the gills I–VI present different shapes, probably modified during fossilisation. (A) MPSC I 2526; (B) MPSC I 2525; (C) MPSC I 2529; (D) MPSC I 2522. All specimens to the same scale. Scale bar 5 mm.

In *Hexagenites*, the forewings are quite bigger (16–23 mm), MA forks symmetrically, and CuA is strongly curved in apical half with four curved loops, so this specimen cannot be included in this genus. In *Hexameropsis*, the forewing has additional intercalary veins in the MA and MP fields, and MA forks slightly asymmetrically; the hind wing is less than half the length of the forewing and has numerous small intercalaries in cubital and MP fields; and MA and MP of hind wing are forked more proximally, all unlike AMNH 43499.

Mongologenites has forewing 18 mm long, relatively narrow, with MP forked proximally; the hind wings are bigger than half the size of the forewing, all differing from AMNH 43499. Specimens of *Epicharmeropsis* have large size (forewing length: 35–43 mm), vein CuA forked at $\frac{1}{4}$ of distance from base to tornus, curved CuA_1, intercalaries between MP_2 and CuA_1, four to six curved loops in cubital field, and crossveins connecting CuA_2 to CuP, unlike in AMNH 43499. In *Ephemeropsis*, there are crossveins connecting CuA_2 to CuP, and four to five loops in the cubital field, differing from AMNH 43499. Furthermore, all specimens of *Ephemeropsis* are much bigger (35–45 mm) than AMNH 43499.

AMNH 43499 matches *Protoligoneuria*, as apparent in the emended diagnosis, in the length of forewing; the conformation of crossveins; point of bifurcation of RP, MA and CuA veins; and also in the number of loops in the cubital field. It differs from *P. limai* mainly in the length of hind wings: whereas *P. limai* possesses a hind wing of around $\frac{1}{3}$–$\frac{1}{4}$ the size of the forewing, the hind wing length of AMNH 43499 is about half the length of the forewing. Also, in AMNH 43499 the MP vein forks more apically than in *P. limai* and the three loops in the cubital fields are not equal in length as in *P. limai*. Therefore, there is evidence that this specimen should be placed as new species in the genus *Protoligoneuria*.

Genus *Cratohexagenites* Staniczek, 2007

Type species. *Cratohexagenites longicercus* Staniczek, 2007

Diagnosis. [from Staniczek (2007)] *Nymph*. Body broader than *Protoligoneuria* (drop-like shape); gill VII larger than gills I–VI, and of trapezoidal shape with angular instead of rounded hind margin; anterior branch of anal rib of gill lamella VII markedly large, straight and rounded apically.

Comments. The characters used to establish *Cratohexagenites* were the size and shape of gill VII (Staniczek 2007) that are larger and truncate at their posterior margins in *Cratohexagenites*, and smaller and apically rounded in *Protoligoneuria*. This last characteristic, however, should be investigated given the possible variation in shape due to taphonomical modifications demonstrated by new specimens of *Protoligoneuria limai*. MPSC I 2526 shows gills I–VI with subtriangular shape (Figure 4A); MPSC I 2525 presents slender gills I–VI and gill VII with a subtriangular shape (Figure 4B); MPSC I 2529 has a more typical *Protoligoneuria* pattern of gills I–VII, which are oval, instead of subtriangular (Figure 4C); and MPSC I 2522 presents more rounded gills I–VI and slender gill VII (Figure 4D), so we consider the gill shape a variable character. Additionally, these specimens demonstrate that intraspecific gill size variation is larger than previously expected (Figure 4). The body shape was also used to distinguish both genera, with *Cratohexagenites* described as having a broader drop-like shape (Staniczek 2007), but more precise conclusions about the systematic position of both genera need additional investigation of the nymphal type specimens of *C. longicercus* and *P. limai*.

Cratohexagenites longicercus Staniczek, 2007

Material examined. Nymph holotype MURJ 447; nymph paratype MB.I.2026; putative adult MSF O46.

Revised diagnosis. [modified from Staniczek (2007)] *Nymph*. Body length about 27 mm. Length of gill about $\frac{1}{5}$ the length of body. Length of cerci 28 mm, length of median filament 24 mm. *Adult*. Putative adult with body length 23.5 mm, corresponding to the size of the holotype.

Comments. The caudal filaments of *Cratohexagenites longicercus* are of the same length as the body, being notably longer than in *Protoligoneuria limai*.

Cratohexagenites minor Staniczek, 2007

Material examined. Nymph holotype MB.I.2026.

Diagnosis. [from Staniczek (2007)] *Nymph*. Estimated body length 16.5 mm, maximum width of body 6.1 mm. Length of gill VII is about 2.4 mm.

Comments. Staniczek (2007) described *Cratohexagenites minor* based on a nymph with an enlarged gill VII of trapezoidal shape, differing from *C. longicercus*, the type species of the genus, by having smaller body, gill VII, and caudal filaments. *Cratohexagenites minor* is only known from one specimen, whose body shape is reported as different from *Protoligoneuria* by being more trapezoid, but part of the head is apparently missing, giving the specimen a drop-like shape aspect.

We have analysed and measured 16 nymphs of *Protoligoneuria limai* from the Crato Formation, measuring between 6 and 12 mm in body length. All of them present the body shape of 'siphlonuroid minnow-like appearance' assigned for *Protoligoneuria* (Staniczek 2007), and some of the nymphs also have gill sizes that would correspond to *C. 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 *C. minor*. The holotype of *C. 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 (Table 1). Some specimens have the gill VII even longer than the holotype of *C. minor*, but combined with the body shape diagnostic of *Protoligoneuria*, so the gill VII size of *C. minor* is within the expected variation of *P. limai*. The body 16.5 mm long and caudal filaments close to half the length of the body of *C. minor* are also within the expected size variation of *P. limai*. This demonstrates that some of the early proposed features need to be revised, and new characters should be proposed based on reinvestigation of types of all taxa belonging to *Protoligoneuria* and *Cratohexagenites*.

Table 1. Body/ gill VII length proportions in selected specimens. In grey are the specimens with body/gill VII proportion smaller than in *Cratohexagenites minor.*

Specimen	body length (mm)	gill VII 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

*holotype of *Cratohexagenites minor*.

Hexagenitidae *incertae sedis*

Material examined. Adult LPU 1144 (Figure 5)

Locality. Southern Ceará state, Brazil

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

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. Small fragment of left hind femur preserved. Antennae, caudal filaments and remaining legs missing (Figure 5A).

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; RP forked at $^1/_5$ of distance from base to margin; RP_2 forks close to middle length; RP_{3+4} parallel to MA; intercalaries in all RP fields; MA forked symmetrically and close to $^2/_3$ of distance from base to margin, almost at middle length; fork of MP symmetrical at $^1/_8$ of distance from base to margin; two strong intercalaries between MP_1 and iMP; CuA forked at $^1/_4$ of distance from base to tornus; CuA_1 straight (Figure 5B); intercalaries between MP_2 and CuA_1; three successive loops visible between CuA_1 and CuA_2; intercalaries between loops present (Figure 5C); MP_2, CuA and CuP origins at the same point; CuP curved. Hind wing length: 3.5 mm; subtriangular. Abdomen 2.5 times longer than pterothorax; at least nine abdominal segments preserved.

Comments. LPU 1144 can be excluded from *Protoligoneuria* because its MA forks close to the middle length of the wing and not at a $^2/_3$ distance from base to margin. Also, in *Protoligoneuria*, the RP forks at $^1/_4$ of the distance from base to margin, unlike in LPU 1144. Moreover, LPU 1144 can be excluded from *Ephemeropsis* and *Epicharmeropsis* due to its forewing size of 9 mm, almost four times smaller (*Ephemeropsis*: 35–43 mm; *Epicharmeropsis*: 34–38 mm), and because the hind wing is less than half the length of the forewing, which is half as long as the forewing in these genera, besides other venational characters.

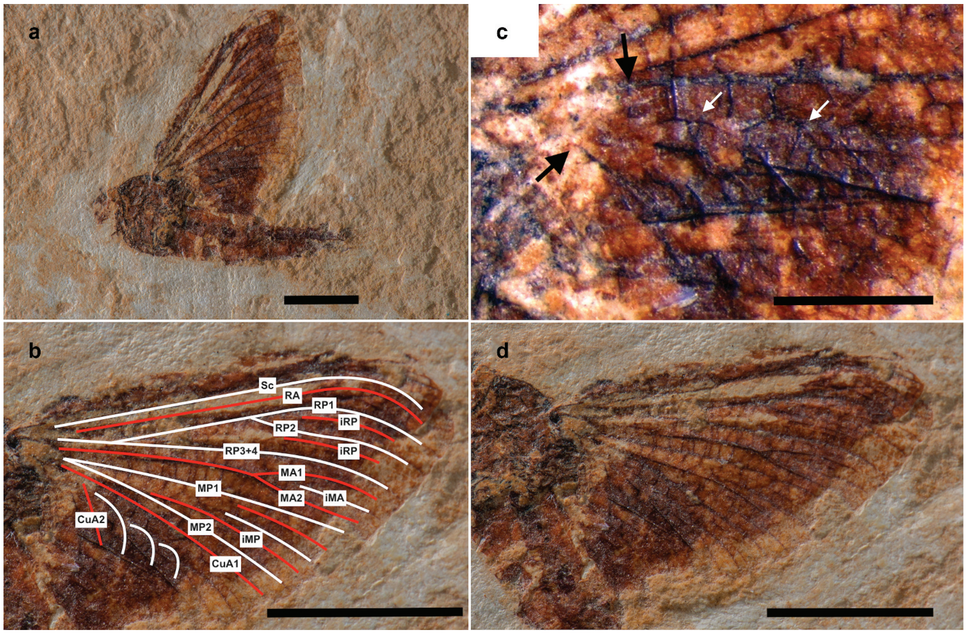

Figure 5. Hexagenitidae *incertae sedis*, LPU 1144, adult. (A) Photograph. Scale bar 3 mm. (B) Left forewing with an interpretative drawing of venation (red lines denote positive veins and white lines denote negative veins). Scale bar 4 mm. (C) Detail of left forewing. Black arrows point to CuA_1 and CuA_2. White arrows point to loops between CuA_1 and CuA_2. Scale bar 1 mm. (D) Photograph of left forewing without drawing of venation. Scale bar 4 mm.

The specimen LPU 1144 shares some characters with the genus *Hexameropsis*, as their moderate size (forewing length: 6.9–23 mm) and forewing length less than two times that of the hind wing. However, it is unlikely that this specimen pertains to *Hexameropsis* because the latter has an asymmetry of the MA and because they were separated geographically and temporally (Table S1).

Overall, LPU 1144 has similarities with *Costalimella* Martins-Neto, 1996, described in the Siphlonuridae. The first described species was *Costalimella nordestina* Martins-Neto, 1996 and later *Costalimella zucchii* Zamboni, 2001 was described. In 2007, Staniczek (2007) regarded the taxon as Ephemeroptera *incertae sedis*. The size of the forewings and the proportions of the hind wings of LPU 1144 are close to those of *C. zucchii*, as are other venational details such as the bifurcation of the RP, MA and MP, as well as on the presence of two strong intercalaries between MP_1 and iMP. It is possible that *C. zucchii* also possesses cubital loops, typical of the Hexagenitidae. Unfortunately, the cubital field of the known *Costalimella* specimens seems, based on pictures, to be poorly preserved. LPU 1144, therefore, could represent a specimen of that genus, but we chose not to associate this specimen without reinvestigation of the type.

Material examined. adult MPSC I 1559 (Figure 6)

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 foreleg preserved (Figure 6A).

Description. Body length: 10 mm. Head narrower than pronotum; compound eyes situated dorsolaterally; eyes widely separated by a length approximately equal to the maximum width of an eye; antennae about 1 mm long. Narrow pronotum; mesonotum length three times that of head; with a wide Y-shaped impression (V-shaped mesonotal suture [MNs] and relatively wide median longitudinal suture [MLs]; proximal end of lateroparapsidal suture [LPs] is visible from both sides); metanotum length $^{1}/_{3}$ that of mesonotum; pterothorax length four times that of head (Figure 6C). 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 at $^{1}/_{3}$ of distance from base to margin; vein RP_2 forked at $^{2}/_{3}$ of distance from base to margin; one intercalary between RP_2 and RP_{3+4}; RP_{3+4} parallel to MA_1; fork of vein MA slightly symmetrical, and at $^{3}/_{4}$ of distance from base to margin; iMP closest to MP_2 (Figure 6B); intercalary veins between MP_2 and CuA; CuA forked (visible only in left forewing); cubital field and anal veins not visible. Hind wing apparently round, half the length of forewing, with longitudinal veins quite straight. Abdomen length 2.5 times the length of pterothorax; thorax of same width as abdominal segments I–IV; nine abdominal segments visible; segments II–IV short, of subequal length; segments VI and VII enlarged, with segment VII the longest; posterolateral spines visible on segments IV and V; two 15-mm-long cerci, vestigial median filament.

Comments. MPSC I 1559 is similar to adults of *Protoligoneuria* in size and in the RP fork at $^{1}/_{4}$ of the distance from base to margin. However, it is distinguished from *Protoligoneuria* in its more apically forked MA. 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 6C), as in the genus *Epicharmeropsis* (Huang et al. 2007, p. 43–45, 47, Figures 2A, 3A, 4B and 7B). Also, like in *Epicharmeropsis*, the broad hind wings are more or less half as long as the forewings, and the relation of wing length to width is also similar. But the suture we observe is not clear and could also represent the impression of the thoracic sternum. Furthermore, in MPSC 1559, the cubital field is not preserved, so the cubital loops, which are important generic diagnostic characters, are not visible.

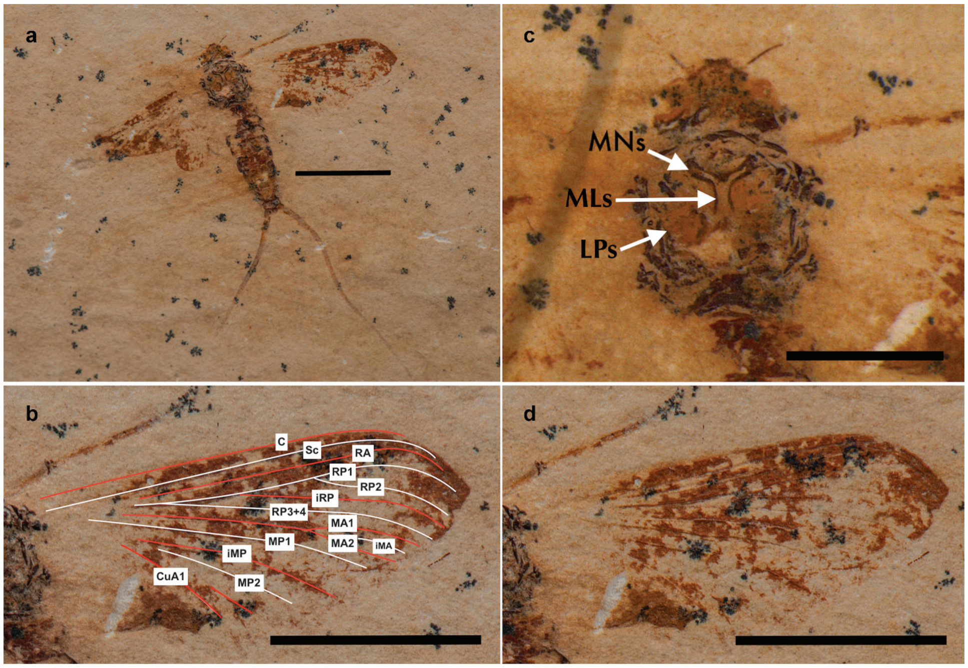

Figure 6. Hexagenitidae *incertae sedis*, MPSC I 1559. (A) Photograph. Scale bar 5 mm. (B) Right forewing interpretative drawing (red lines denote positive veins, and white lines denote negative veins). Scale bar 4 mm. (C) Thorax photograph, evidencing possible mesonotal suture (MNs), lateroparapsidal suture (LPs) and median longitudinal suture (MLs). Scale bar 2 mm. (D) Photograph of right forewing without drawing of venation. Scale bar 4 mm.

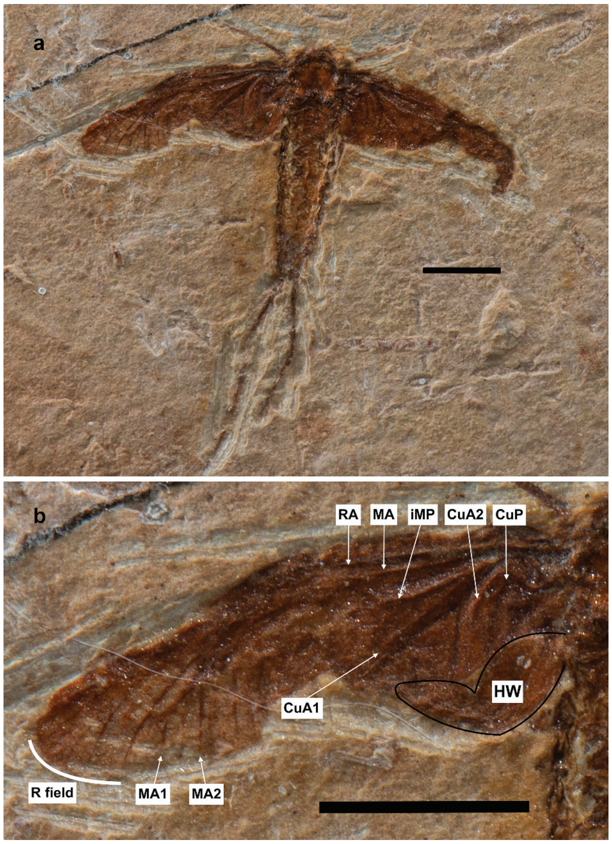

Figure 7. Hexagenitidae *incertae sedis*, MPSC I 763. (A) Photograph. Scale bar 4 mm. (B) Left forewing venation. HW is hind wing. Scale bar 4 mm.

The basal parts of the fore and hind wings are also not preserved, so forks of MP and CuA are not visible. Thus, we chose not to erect a new taxon for this specimen.

Material examined. Adult MPSC I 763 (Figure 7)

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 poor preservation, basal part of left hind femur preserved. Sexual characters not discernible but probably female due to the apparent presence of numerous eggs preserved in the abdomen. Forewings preserved wrinkled, with right forewing twisted in apical part, and damaged in cubital field. Hind wings poorly preserved (Figure 7B).

Description. Body length 12 mm. Head relatively wide, as broad as anterior part of pronotum; compound eyes approximately 1 mm wide, separated by 0.5 mm gap; right antenna about 2 mm long. Forelegs well developed, about 5 mm long, visible part of both femur about 1.8 mm and visible part of one preserved tibia about 2.1 mm; 2-mm-long right hind leg as preserved. Forewing length: 12 mm; crossveins poorly preserved but present in almost all sectors of wing (R-sector; between RP and MP; MP-sector; between CuA$_1$ and MP$_2$); most longitudinal veins (Sc, RA, RP, MA and MP) with a common point of origin, probably due to the folded base of forewing; MA forked at $^3/_4$ of distance from base to margin; at least two proximal loops are visible in the field between CuA$_1$ and CuA$_2$; CuP arched; remaining veins difficult to trace. Hind wing closely attached to cubital and anal field (Figure 7B). Abdomen with all segments preserved, cerci 11 mm long.

Comments. MPSC I 763 is very similar to *Protoligoneuria* in forewings shape and venation. Forewings have almost the same size as the holotype of *Cratogenitodes delclosi*, which was synonymised and considered as a putative winged specimen of *Protoligoneuria limai* by Staniczek (2007). *Cratogenitodes delclosi* has 13 mm long forewings, but in the diagnosis of adults of *P. limai* given by Staniczek (2007), the forewing length is measured as 18–20 mm. However, this measurement most probably refers to the total wingspan of SMNS specimen 66635, as it has a forewing length of 11 mm. Otherwise, there is only one other putative winged specimen described (RGMN-T002). MPSC I 763 could probably represent *Protoligoneuria*, but due to the poor preservation of forewing, especially the CuA field, precise identification is not possible.

Conclusions

Considering there were only two putative winged specimens described for *Protoligoneuria limai* (RGMN-T002 and SMNS 66635), the description of *Protoligoneuria heloisae* sp. nov. provides new information about the genus that now is no longer monospecific. We also recorded a different size variation than previously noticed for putative adults of *P. limai*, demonstrating that this frequently found species has larger intraspecific variation than formerly assumed. We also documented, for the first time, the presence of abdominal spines in the nymphs of the species, which are likely diagnostic.

The putative adult of *Cratohexagenites longicercus* was associated with the nymphs based on size (Staniczek 2007), but other than that, these stages may not be comparable in terms of morphology (Storari et al. 2020). As further evidence for higher species richness among the mayflies of the Crato Formation emerges, we recommend describing 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* nymphs and adults made by Sinitshenkova (1975). Finally, the association of life stages can also be achieved by the observation of nymphal wing pads' venation. However, the surfaces of the wing pads are often poorly preserved or lost.

Hexagenitidae is a highly abundant autochthonous group of the Crato Formation, forming a monospecific assemblage of *P. limai* (similar to *Ephemeropsis trisetalis* in the Jehol Biota [Pan et al. 2014]), and has even been recently reported as forming a mass mortality event (Storari et al. 2021). Earlier studies have probably inflated hexagenitid diversity through the description of several taxa that are, nowadays, considered synonymous. Later works (e.g. Staniczek 2007) have reviewed these species and suggested the presence of one dominant species, *P. limai*. However, the finding of new species is not unlikely. Unfortunately, all the mayfly type specimens described so far were collected without stratigraphic control, so we do not know how much of the observed morphological variations are intraspecific or how they are related to geographical or temporal divergences (Pinheiro and Rodrigues 2017). Given that in the Crato mayfly fauna, there are numerous specimens with unclear taxonomic affiliations, we chose to maintain some uncertain specimens as Hexagenitidae *incertae sedis* to avoid the risk of increasing the number of dubious taxa until more specimens are described. A thorough review that includes first-hand investigation of type specimens is crucial, including the whereabouts of the types of the late Martins-Neto's private collections. Such review is paramount to clarify the current taxonomy of the

Crato mayfly fauna.

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Disclosure statement

The authors declare no competing interests.

Author contributions

APS, FFS, AAFS and TR conceived the study; APS and TR administrated the project; AAFS carried out the fieldwork and administrated the data collection; APS, RJG, FFS and AHS investigated and validated the data; APS wrote the manuscript; APS, RJG, FFS, AAFS, AHS and TR discussed the results and revised the manuscript.

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