NEW MAYFLIES (INSECTA, EPHEMEROPTERA) FROM THE SANTANA FORMATION (LOWER CRETACEOUS), ARARIPE BASIN, NORTHEASTERN BRAZIL

Rafael Gioia MARTINS-NETO

Departamento de Geologia, Fisica e Matematica, Faculdade de Filosofia, Ciencias e Letras, Universidade de Sao Paulo, Campus de Ribeirao Preto. Av. Bandeirantes, 3900, 14040-901 Ribeirao Preto, SP - Brasil.


ABSTRACT

This paper reviews all previous knowledge about ephemerid nymphs from the Santana Formation (Lower Cretaceous, northeastern Brazil) involving the families Hexagenitidae, Siphlonuridae and Oligoneuriidae, represented by nymphs and adult forms. They occur associated with representatives of at least five other ephemerid families, as well as twenty three other insect orders. This is one of the richest and most diverse insect fauna known in the geological record. Five new taxa are proposed, viz. Cratogenites corradiniae gen. n., sp. n., Cratogenitoides delclosi gen. n., sp. n., Palaeobaetodes britoi sp. n., Costalimella nordestina gen. n., sp. n., and Cratoligoneuriella leonardii gen. n., sp. n. The genera Protoligoneuria Demoulin and Palaeobaetodes Brito are reviewed. The palaeontological significance of ephemerid nymphs in the lacustrine complex at Crato Member is discussed, and possible ephemerid provinces are proposed, as well as habitats, as deduced from the material collected.

Keywords: Insecta, Ephemeroptera, Hexagenitidae, Siphlonuridae, Oligoneuriidae, Lower Cretaceous, Brazil.

RESUMEN

En este trabajo se revisan los conocimientos anteriores sobre ninfas de Ephemeroptera provenientes de la Formacion Santana (Cretácico Inferior, nordeste de Brasil), de las familias Hexagenitidae, Siphlonuridae y Oligoneuriidae, representadas tanto por ninfas como por formas adultas. Ellas se presentan asociadas con representantes de por lo menos otras cinco familias de Ephemeroptera, además de otros veintitrés órdenes de insectos; una de las más ricas y diversificadas faunas de insectos de las que se tiene conocimiento en el registro geológico. Son propuestos cinco nuevos taxones: Cratogenites corradiniae gen. n., sp. n.; Cratogenitoides delclosi gen. n., sp. n.; Palaeobaetodes britoi sp. n.; Costalimella nordestina gen. n., sp. n., y Cratoligoneuriella leonardii gen. n., sp. n.; y se revisan los géneros Protoligoneuria Demoulin y Palaeobaetodes Brito. Se discuten las implicaciones paleontológicas de las ninfas de efemerídeos en el complejo lacustro del Miembro Crato. Además, se proponen las posibles provincias de efemerídeos y sus hábitats basados sobre el material recolectado.

Palabras clave: Insecta, Ephemeroptera, Hexagenitidae, Siphlonuridae, Oligoneuriidae, Cretácico Inferior, Brasil.

INTRODUCTION

Costa Lima (1950) commented briefly upon three fossil ephemerid nymphs from Santa Rosa farm, near Crato, Ceará, identifying them as Baetidae, probably Siphlonurinae. Demoulin (1955a), in a brief note, discounted the possibility that these nymphs would really belong to the Baetidae Siphlonurinae, alleging the absence of siphlonuroids in Neotropical America, except for Chile. However, Demoulin (1955b) described some siphlonuroids from Brazil. Demoulin (1955a) also stated that the paracercus of these nymphs is very short and that they should, therefore, be included in the Family Oligoneuriidae Ulmer. On the basis of photographs in Costa Lima (1950), he proposed a new genus and species: Protoligoneuria limai. However, the attribution is rather dubious in view of the imperfect preservation of the paracercus. This form was mentioned by Chernova (1970), but all subsequent papers ignored it. However, the material analysed by Costa Lima (1950) is deposited
in Vulcano collection, and is, therefore, available for study (specimen CD 6616).

_Palaeobaetodes costalimai_ Brito, 1987 is another ephemerid taxon described by Brito (1987). Specimen DGM 6255-I, a poorly preserved nymph housed in the palaeontological collection of the Departamento Nacional da Produção Mineral (DNPM), Rio de Janeiro, has been designated as the holotype. Three other specimens, housed in the same institution under the same number DGM 6256-I, are described as paratypes. McCafferty (1990) described additional material unfortunately kept abroad, and alleged that Costa Lima's specimens belong to the same taxon as Brito's specimens. He proposed _Protoligoneuria limai_ McCafferty for this material and described some additional new taxa. His treatment is regarded as confusing.

There is presently no doubt that both Costa Lima's specimens and par of Brito's are Hexagenitidae. The same applies to the McCafferty's material described under _Protoligoneuria limai_. However, they do not belong to the same genus (see below).

The material mentioned above belongs to at least three different nymph taxa, which are named here in open nomenclature, type A, type B and type C. All belong to the Hexagenitidae:

- **Type A**: head triangular; width circa three times the length; eyes small, occupying nearly 35% of total head area; antenna length nearly 60% of the head width.
- **Type B**: head trapezoidal; width circa one-and-half times the length; eyes large, occupying nearly 75% of total head area; antenna two times longer than head width.
- **Type C**: head elliptical; width circa two times longer than length; eyes normal, occupying near 50% of total head area; antenna a little smaller than head width.

The following remarks should be made:

1. Costa Lima's material is only partially lost. He presented one of the three specimens to his colleague Maria Aparecida Vulcano, who allowed the present writer to examine it. This specimen can be referred to type A. The other two specimens are lost.

2. Brito's material is heterogeneous. The holotype and one of the three paratypes are of type C, the third specimen is of type B and the fourth specimen is not a Hexagenitidae but belongs to the Oligoneuriidae; it bears no relation to the oligoneurid described by McCafferty (1990). Brito's specimens are numbered as follows (partly renumbered):

<table>
<thead>
<tr>
<th>Original Number</th>
<th>New Number</th>
<th>Type</th>
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<tr>
<td>DGM 6255-I</td>
<td>DGM 6255-I</td>
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<tr>
<td>DGM 6256-I</td>
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<td>DGM 6256-I</td>
<td>DGM 6277-I</td>
<td>New taxon (B type)</td>
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<td>DGM 6256-I</td>
<td>DGM 6278-I</td>
<td>New taxon (not Hexagenitidae)</td>
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Figure 1.  A) Geographical situation; B) Araripe Basin geological map; C) local position; D) Stratigraphic column at Santana do Cariri and position of the collected specimens; E) Outcrops of Crato Member 1, 2, 3 and 4 respectively, Fazenda Tatajuba, Mineração Chaves, Mina Pedra Branca abd Fazenda Santa Rosa.
SYSTEMATIC PALAEONTOLOGY

Family Hexagenitidae Lameere, 1917

Diagnosis (after Chernova, 1967b)
Very large to medium size mayflies. Venation profuse. CuA bifid on forewing, with a branch extending from the fork and giving rise to a series of regularly looped curved veins to the posterior wing margin. The nymph has seven pairs of isolated, leaf-shaped gills along the sides of the abdomen; large and elongate gill7; the sides of the abdominal segments bear caudal projecting process; caudal setae densely arranged, with long hairs.

Discussion
The Family Hexagenitidae Lameere was proposed for the genus Hexagenites Scudder, 1880, described from the remains of imago wings from the Upper Jurassic of Solnhofen, Germany. Later on, new forms were proposed, new occurrences recorded and taxonomic aspects discussed (Handlirsch, 1906-1908; Cockerell, 1924, 1927; Ping, 1928; Carpenter, 1932; Demoulin, 1953a, b, 1954, 1956, 1967, 1970, 1971; Chernova, 1958, 1967a, b, 1970, Chernova & Sinitshenkova, 1974; Sinitshenkova, 1976; Hennig, 1981). Nowadays, only two genera are accepted, viz. Hexagenites, from western Europe and Ephemeropsis Eichwald, 1864, from Transbaikalia, Mongolia and northern China. Forms proposed in previous papers were considered Late Jurassic, but it is now accepted that Ephemeropsis remains do occur in the Lower Cretaceous (Sinitshenkova, 1975).

Both nymph and imago have been identified for the genus Ephemeropsis (see Chernova, 1967b), but no nymph has been found for Hexagenites. A third form, Hexameropsis Chernova & Sinitshenkova, 1974 (also Hubbard, 1987), has been described from the Lower Cretaceous of Ukraine and Algeria, as well as from Mongolia (Ponomarenko & Popov, 1980). Sinitshenkova (1985, 1986, 1989) includes two genera in this family, viz. Siberiogenites (1985, nymphs) and Mongologenites (1986, adult and nymphs).

Composition
Ephemeropsis Eichwald, from the Lower Cretaceous of Transbaikalia, Mongolia and N China; Hexagenites Scudder, from the Upper Jurassic of western Europe; Hexameropsis Chernova & Sinitshenkova, from the Lower Cretaceous of the Ukraine, North Africa and Mongolia; Siberiogenites and Mongologenites from the Early Cretaceous of Mongolia; Protoligoneuria Demoulin and Palaeobaetodes Brito from the Early Cretaceous of Brazil.

Genus Protoligoneuria Demoulin, 1955
p.* 1955a Protoligoneuria Demoulin, 271.
p. 1990 Protoligoneuria Demoulin; McCafferty, 22-26.

Type-species: Protoligoneuria limai Demoulin, 1955.

Emended diagnosis
Nymph. Apart from the characters listed by McCafferty (1990), a triangular head is noted; width circa three times the length; the small eyes occupy around 35% of the head area; antenna length around 60% of the head width.

Discussion
The emended diagnosis is necessary because in the original description (Demoulin, 1955a), as well as a later one (McCafferty, 1990), the head/eyes proportion is not given.

Known species. Only the type-species.

Genus Cratogenites gen. n.

Type-species: Cratogenites corradiniae sp. n. by present designation.

Derivatio nominis: Crato, regional unit and genites from Hexagenitidae.

Diagnosis
Nymph: Head trapezoidal; posterior margin length circa one and a half times the anterior margin length; eyes large, occupying nearly 75% of total head area; antenna length two times the head width. Femur of all legs slightly thicker than tibiae; tibiae larger than femora. Outer thickened margins of gills with a longitudinal carina. Paracercus two thirds of the cerci length.

Discussion
This genus is separated from Protoligoneuria Demoulin on the shape and proportions of head and eyes: head trapezoidal and eyes large in Cratogenites, head triangular and eyes small in Protoligoneuria.

Cratogenites corradiniae sp. n.
Pl. I, figs. 1-3; Figs. 2A, 3C

Derivatio nominis: In honour of Mrs Urania Gusmão Corradini, São Paulo.

Holotype: (Nymph). Martins-Neto Collection n° RGMN-T001, housed in the Entomology Department, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Campus of Ribeirão Preto - FFCL/USP-RP (Pl. I, fig. 2).

Additional material: Around 25 unnumbered specimens, collected at Fazenda Tatajuba.

Locus and stratum-typicum
Outcrop in the Fazenda Tatajuba, Santana do Cariri, Ceará. 15 m thickness. Holotype collected at 4 m from the base of outcrop. Laminated limestone of the Crato Member, the lower unit of Santana Formation, Araripe Basin: Lower Cretaceous. Upper Aptian/Lower Albian.
Diagnosis. As for the genus.

Dimensions of holotype (mm)

- Body length, 10; paracercus, 4; cerci, 6; total length, 16;
- maximal width of head, 2; maximal width of thorax, 3.5;
- antenna, 4.2.

Description (nymph)

Campodeiform nymph of small to medium size preserved in dorsal view. Head trapezoidal, compound eyes large, rounded; no ocelli; antenna long, two times the head width, multisegmented with scapus larger than subsequent segments. Pronotum twice as wide as long. Anterior wing rudiments in accordance with the Hexagenitidae pattern. Posterior wing rudiments not exceeding 1/3 of the anterior wing length. Abdomen with ten segments; first segments at least five times wider than long, but becoming only twice wider, and only a little wider than long in the last segments. The abdomen bears seven pairs of leaf-shaped gills with a thickened outer margin and a rib near the posterior margin. Length of branchial plate exceeds the length of the corresponding abdominal segment. The last gill (gill 7) is large and elongate. Heavily pubescent caudal filaments. Paracercus two thirds the length of cerci, which are thickened basally, multisegmented, and narrowing towards the tip. Cerci pubescent only on the inner margin; paracercus pubescent on the inner margin as well as on the outer margin. Legs weak. Femur of all legs slightly thicker than the tibiae which are longer than femur.

Discussion

These nymphs are extremely similar in their general siphlonurid appearance (thin legs, lamellar gills with a thickened outer margin, and a thickened rib near the posterior margin) to species of Ephemeropsis, as well as those ofHexameropsis in which the head is not preserved; thus making a detailed comparison impossible. However, the paracercus enables an immediate separation. Cratogenites corradianiae is very similar in general appearance to Protoligoneuria limai of the same region, but differs in several details: head configuration (trapezoidal in shape), eyes (greater), antenna (greater) and proportions body length/cerci length; cerci / paracercus; eyes/head; antenna/head, etc. The more distinctive characters are found in the head and eye morphology, and the antenna length. In Cratogenites corradianiae the ratio cerci/body length is 0.6; in Protoligoneuria limai, 0.3 to 0.4. The ratio paracercus / cerci is 0.66 for C. corradianiae and 0.75 for P. limai.

Genus Cratogenitoides gen. n.

Type-species: Cratogenitoides delclosi sp. n. by present designation.

Derivatio nominis: Crato, regional unit and genitoides, near Hexagenites.

Diagnosis

Imago: Wing venation moderately developed; forewing triangular; costal margin of wing longer than anal; longitudinal veins in apical half slightly curved (only Sc, R1 and Rs2 more curved); cubital area has four sharply curved loop-like veins, each with intermediate oblique veins.

Figure 2. A) Cratogenites corradianiae sp. n., holotype, mature nymph; B) Cratogenitoides delclosi gen. n., sp. n., fore and hind wing of the imago; holotype.
Locus and stratum-typicum. The same as *C. corradiniae*.

**Diagnosis**

As for the genus. Imago forewing: costal area wide; MA forks at the same level of Rs1+Rs3 fork.

**Dimensions**

Forewing: 13 mm long, 8 mm of maximal width. Hindwing: 3.7 mm long, 3.3 mm of maximal width.

**Description**

This form is distinguished from *Hexagenites weyenberghii* Scudder, 1880 and allied forms from the Upper Jurassic by the presence of numerous transverse veins in the cubital area (as in *Ephemeropsis* species), by the wide costal area in the Araripe form and by its smaller size. It differs from *Hexameropsis* species in having MA1 and MA2 diverging uniformly. Undoubtedly, the structure of its venation is similar to that of other known species of Hexagenitidae, as well as being similar to that of *Ephemeropsis* and *Hexameropsis*. *Cratogenitoides delclosi* is the first true imago Hexagenitidae present in the Araripe fauna having the typical four sharply curved loop-like veins. This synapomorphy is shared with all Hexagenitidae.

**Genus Palaeobaetodes Brito, 1987**

p.* 1987 *Palaeobaetodes* Brito, fig. 1-3.

p. 1990 *Protoligoneuria* Demoulin; McCafferty, 22.

**Type-species:** *Palaeobaetodes costalimai* Brito, 1987.

**Diagnosis**

Nymph: Head elliptical; head width circa two times the head length; large eyes occupying around 50% of the head area; antenna length nearly the width of the head.
1-3 *Cratogenites corradiniae* sp. n. 1) holotype RGMN-T001, mature nymph. 2-3) unnumbered additional nymphs.

4 *Cratogenitoides deleclusi* sp. n., holotype RGMN-T002, fore and hind of the imago.

5-7 *Palaeobdactodes costalimai* Brito, unnumbered additional specimens (nymphs). 6) partial exuvia.

8 *Palaeobdactodes britoi* sp. n., holotype, RGMN-T003 nymph.

Scale bar 5mm.
Palaeobaetodes costalimai Brito, 1987
Pl. I, figs. 5-7; Fig. 3A, E; 4A, B; 5A, C
p. 1990 Protoligoneuria limai Demoulin; McCafferty, 22.


Paratype: DGM 6256-I. Housed in the same institution.

Additional material: Around 1.200 specimens collected from Rio da Batateira, Crato municipality, at the level I; specimens unnumbered.

Nymph diagnosis
As for the genus. Gill7/ Gill6 ratio 1.5:1.

Dimensions (nymphs only)
From 5 mm (innital stages) to 12 mm long (mature stages).

Description
(Fig. 3A). Nymph: Head elliptical, compound eyes large, rounded, occupying around 50% of the head area; antenna length similar to the head width. Head width a little wider than anterior margin of the pronotum which is trapezoidal in mature stages, and subsquare in the immature stages. Abdominal segments with rounded anterior angles, slightly convex lateral margins, and lacking denticles. Gill7-6 similar in width and of smaller length than the width of the respective abdominal segments. Gill7 one and a half times longer than preceding ones with the same length of the respective abdominal segment width. Thickened trachea on oval branchial plates situated distinctly closer to the outer margin in all plates. Paracercus just a little smaller than the cerci which are as long as the body length. These proportions are maintained in all the specimens examined.

Remarks
This species bears no relation to Protoligoneuria limai as suggested by McCafferty (1990), with the exception of the elongated Gill7 (Hexagenitidae synapomorphy and not Protoligoneuria autapomorphy). P. costalimai differs from Protoligoneuria limai in several morphological details: head elliptical (triangular in P. limai), large eyes occupying around 50% of the head area (eyes are smaller, occupying around 35% of the head area in P. limai) and an antenna length in excess of the head width (around 60% of head width in P. limai).

Palaeobaetodes britoi sp. n.
Pl. I, fig. 8; Fig. 3B: 5B

Derivatio nominis: Named after Prof. Ignacio Machado Brito who is the author of the preliminary description of some Araripe nymphs.

Holotype: Martins-Neto Collection n° RGMN-T003, housed in the Entomology Department, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Campus de Ribeirão Preto - FFCL/USP-RP.

Additional material: Around 850 unnumbered specimens, collected from level III.

Locus and stratum-typicum
Holotype and additional material. Outcrop at Rio da Batateira, near Crato township, Ceará, at level III. Laminated limestone of Crato Member, lower unit of Santana Formation, Araripe Basin. Lower Cretaceous. Upper Aptian/Lower Albian.

Diagnosis
As for the genus. Nymph Gill7/ Gill6 ratio 2:1.

Dimensions
This species reaches lengths from 7 mm to a little over 13 mm when fully developed.

Description (based on 850 specimens)
Nymph: Head (Fig. 3B) elliptical, compound eyes large, rounded, occupying about 50% of the head area; antenna about 2 mm long. Head width narrower than the anterior margin of the pronotum which partially encloses the head laterally. Abdominal segments (Fig. 5B) with rounded anterior angles, slightly convex lateral margins, and without denticles. Gills, Gill 1-6 similar in width and length, but smaller in width than the respective abdominal segments. Gill 7 twice longer than the preceding ones, an larger in width than the respective abdominal segments. Thickened trachea on oval branchial plates situated distinctly closer to the outer margin on all plates. Paracercus in mature nymphs (around 4 mm) just a little smaller than the cerci (around 6 mm) which are smaller than the body length (around 13 mm).

Discussion
This species can be distinguished from P. costalimai by the Gill7/ Gill6 ratio: 2:1. Gill1-6 are very small when compared to the respective abdominal segment widths, and Gill7 is longer than the respective abdominal segment width. This is an apomorphy shared with Mongologenites laqueatus Sinitchenkova, 1986, from the Lower Cretaceous of Mongolia, which differs however in the shape of both head and abdominal segments (generic distinctions). With respect to the gill morphology (1-6), Palaeobaetodes costalimai is similar to the Hexameropsis, perhaps this is homoplasy rather than apomorphy (morphoecological aspects only).

Family Siphlonuridae Ulmer, 1920
Genus Costalimella gen. n.

Type-species: Costalimella nordestina sp. n. by present designation.

Derivatio nominis: In honour of Costa Lima who first recognised a fossil ephemerid from Brazil.
1 *Costalimella nordestina* sp. n., holotype RGMN-T004, relatively complete imago.

2-3 *Cratoligoneuriella leonardii* sp. n., holotype RGMN-T005. 2) general view of nymph. 3) detail of the forefemur filtering hairs.

4 *Protoligoneuria limai* Demoulin, additional unnumbered specimen.

Scale bar 5mm, except details (x12).

Figure 4. A-B) *Palaeobaetodes costalimai* Brito: A) holotype, DGM-6255-I, reproduced from Brito, 1987, fig.1; B) paratype, DGM-6256-I, reproduced from Brito, 1987, fig.2. C) *Cratogenites?* sp., DGM-6277-I, reproduced from Brito, 1987, fig.3. D) *Costalimella nordestina* sp. n., drawing of holotype. Scale bar 5mm.
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**Figure 5.** A) Ontogenetical series of *Palaeobaetodes costalimai* Brito, collected at the Rio da Batateira outcrop. B) Ontogenetical series of *Palaeobaetodes britoi* sp. n., collected from the same outcrop. C) Exuvia of *Palaeobaetodes costalimai* Brito, from the same outcrop. Scale bar 5 mm.

**Diagnosis**

*Imago:* Small siphlonurid with a relatively narrow forewing, with a triangular and fairly sharp tip. Similar to *Stackelbergisca* Chernova, 1967, in several aspects of the forewing venation: median fork of RS situated at the base of the bifurcation of MA; IMA equidistant from MA1 and MA2; all three MP veins long, differing however in the MA1, MA2 and IMA being branches shorter than in *Stackelbergisca.*

**Description**

*Imago:* Forewing 6 mm long, at 2.5 mm maximum width. Body length 7 mm; cerci, 6 mm as preserved.

*Holotype:* Martins-Neto Collection no. RGMN-T004, housed in the Entomology Department, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Campus de Ribeirão Preto - FFCL/USP-RP. Only the holotype is known.

**Locus and stratum-typicum**

Outcrop in the Fazenda Tatajuba, Santana do Cariri, Ceará. 15 m bed thickness, and collected at 4 m from base of outcrop. Laminated limestone of Crato Member, lower unit of Santana Formation, Araripe Basin. Lower Cretaceous. Upper Aptian/Lower Albian.

**Diagnosis**

As for the genus.

**Dimensions**

Forewing 6 mm long, at 2.5 mm maximum width. Body length 7 mm; cerci, 6 mm as preserved.

**Discussion**

Apart the generic characters, *Costalimella nordestina* differs from all known fossil siphlonurid species by its small size (6 mm).

Although Jell & Duncan (1986) figured and described a diverse fauna of Ephemeroptera Siphlonuridae (nymphs only) from Koonwarra, Lower Cretaceous of Australia, there is no comparison with this Araripe taxon.

**Family Oligoneuriidae** Ulmer, 1914

**Genus** *Cratoligoneuriella* gen. n.

**Derivatio nominis:** Crato, local unit name and oligoneuriella from Oligoneura, an extant ephemerid.
Type-species: Cratoligoneuriella leonardii gen. n. et sp. n., by present designation.

Diagnosis
Nymph: medium-sized oligoneuriid (body length about 12 mm) with thickened and rather long femora (about 3 mm), densely pubescent with long and pectinated hairs, having a sclerotic process in the middle length of the anterior femur. Head rounded, smaller than the thorax; cerci twice as long as paracercus.

Discussion
This new genus is split off from Colocrus McCafferty, 1990, described from the same region, and distinguished by the distinctive morphology of the filtering hairs of the forelegs (having no sclerotic process in the anterior femur).

Cratoligoneuriella leonardii sp. n.
Pl. II, figs. 2, 3; Fig. 6 p. 1987 Palaeobaetodes costalimai Brito, 594.

Derivatio nominis: Named after Dr. Giuseppe Leonardi, for his great contribution to Brazilian palaeontology.

Holotype: Martins-Neto Collection n° RGMN-T005, housed in the Entomology Department, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Campus de Ribeirão Preto - FFCL/USP-RP. (Pl. II, figs. 2, 3).

Paratype: DGM 6278-I, formerly DGM 6256-I, in part. (Fig.6) housed in the Departamento Nacional da Produção Mineral, DNPM, Rio de Janeiro. Only the holotype and paratype are known.

Locus and stratum-typicum: As for Costalimella nordestina.

Diagnosis
As for the genus.

Dimensions of the holotype
Nymph (mm): Body length, 12; maximal width, 2.8; cerci, 8: paracercus, 3.5; total length, 20; anterior femur length 2.5, posterior femur length, 3.

Description
Nymph (Fig.6): head rounded with its margin projecting forwards; prothorax short, wider than the head; metathorax wider than pro- and mesothorax; wing rudiments not crossing the first abdominal segment; abdomen 7 mm long, narrow with projecting posterior angle of segments on the sides; cerci 8 mm long, multisegmented, twice as long as paracercus, pubescent on inner margin (paracercus pubescent on both inner and outer margins); femora around 3 mm long, relatively broad; fore femur with long filtering hairs, the midle part of which possesses a long (about 2 mm) sclerotic process containing a tuft of long setae (varying from 1 to 1.4 mm).

Discussion
The form of the abdomen, which is long and narrow, resembles that of extant Homoeoneuria and Oligoneurtica of the Neotropics. However, it differs by the possession of long femora (these are relatively short in the extant species).

Oligoneuriidae gen. et sp. indet.
Fig. 6C

Description
Imago isolated forewing triangular with reduced cross-veins. Costal area relatively narrow with few cross-veins. Sc long, curved in apical part. R1 long with at least three secondary branches, the third arising from the middle part of R1. MA long, slightly curved, ending on the middle part of the anal margin; CuA long, apparently unbranched, slightly curved, connected to MA by a relatively long cross-vein (ma-cua) arising at 1/3 the distance from the origin of MA.CuP curved, diverging from CuA near the wing base, and ending on the first 1/3 of anal margin. Anal veins partially preserved.
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LEVEL I

Figure 7. Distribution of Ephemeroptera nymphs of the genus *Palaeobaetodes* from Rio da Batateira outcrop: Level I: A) size of the specimens in mm; B) specimen orientation on the slab; C) slab figuring the specimens in the position, size and orientation as collected; D) mortality curve (hachured zone) in the band analysed: E) graph of current orientation pattern; F) studied level. Level III: G, H, I, J, K, L respectively as for A, B, C, D, E, F.

LEVEL III
Figure 8. Possible ephemerid provinces and its habitats in the lacustrine complex at Crato Member. 1-6 respectively the studied outcrops (see text).

PALAEONTOLOGICAL SIGNIFICANCE OF EPHEMERID NYMPHS IN THE LACUSTRINE COMPLEX AT CRATO MEMBER

Outcrops
  Ephemeropteran material (nymphs only) was collected from the following localities (Dominant, over 50%; Rare, 10 to 30%; Very Rare, less than 10%):  
  1. Fazenda Tatajuba - access by road, arriving from the head office of the Sítio Pedra Branca (Mineração Chaves).  
    Dominant: Cratogenites corradiniae (Hexagenitidae).  
    Rare: Paleobaetodes costalimai (Hexagenitidae).  
    Very Rare: Cratonympha microcelata Martins-Neto & Caldas, 1990 (Ephemeridae).  
    Very Rare: Olindinella gracilis Martins-Neto & Caldas, 1990 (Potamanthidae).  
    Very Rare: Caririnympha mandibulata Martins-Neto & Caldas, 1990 (Polymitarcidae).  
    Very Rare: Cratoligoneuriella leonardii (Oligoneuriidae).  
  2. Mina Pedra Branca (Mineração Chaves), 4 km from Nova Olinda. 12 m bed thickness. Two horizons: 5 and 6 m from base of outcrop.  
    Dominant: Paleobaetodes costalimai (Hexagenitidae), including ontogenetical series.  
    Rare: Paleobaetodes britoi (Hexagenitidae).  
  3. Outcrop bordering the road linking Nova Olinda to Santana do Cariri, 12.5 km from the former. Ephemeroptera level at 1 m from the base of outcrop.  
    Dominant: Paleobaetodes costalimai (Hexagenitidae).  
    Rare: Protoligoneuria limai (Hexagenitidae).  
    Rare: Cratogenites corradiniae (Hexagenitidae).  
  4. Riacho do Salgado, Fazenda Santa Rosa, near Pousada Santa Fé.  
    Rare: Protoligoneuria limai (Hexagenitidae).  
    Dominant: Paleobaetodes britoi (Hexagenitidae), including ontogenetical series.  
    Abundant: Paleobaetodes costalimai (Hexagenitidae), including ontogenetical series.  
  6. Sítio Massapê, Mina dos Rosados. Base of the Serra de São Felipe, 6.5 km from Porteiras.  
    Rare: Paleobaetodes costalimai (Hexagenitidae).  

Characteristics of the locality 5  
  The most comprehensive collection comes from locality 5, having the following characteristics:  
  1. The Ephemeroptera nymphs are found at certain horizons, without preferred orientation. These horizons occur at certain intervals (cyclic), with only a few millimeters thickness in between.  
  2. The specimens are complete and articulated, tridimensional, relatively uncompacted and showing the absence of transport or only minimal transport.  
  3. In this outcrop, one sample of 350 cm² with 9 mm of thickness shows the following characteristics:  
    a) Level or horizon I (upper) has an average density of 120 individuals/m² with a high incidence of more mature nymphs with preferred orientation (Fig.7).  
    b) Level or horizon III (lower) has an average density of 214 individuals/m² with mainly young individuals, which show no preferred orientation (chaotic disposition).
Conclusions (only based on nymphs)

1. The high mortality tax among mature nymphs, gradually starts as a low mortality tax among young stages. This suggests that the water body was falling from level III to I. A plausible explanation might be that the young could support water body levels lower than the mature nymphs because they bulk together. Besides, the area of their bodies in the initial nymphal stages are near 1 mm long, whereas in the mature stages they could reach 10 to 12 mm, i.e., ten times larger. If so, this phenomena was observed also in locality 2.

2. Tiny dead individuals would be more easily reoriented than the adults which needed water body levels in excess of its own thickness for reorientation.

3. The water bodies probably split into smaller lakes; by this time decreasing cycles of water level would lead to cryptic levels for the biota, bringing periodic or cyclic mass mortality.

Other palaeontological evidence suggesting occasionally rather low water levels has been reported by Martins-Neto (1990), with neopteran species (relatively abundant in the Crato Member) preserved together with sediment imprints. A print of this type associated with the insect which made it would need a very low water level, cryptic to the life of the aquatic palaeontomofauna, as is the case for the Ephemeroptera nymphs. There is no relation to microbial-algal events in this case, because the bottom of the Araripe sublakes are anoxic as is shown by sedimentological analysis (Silva, 1983).

4. When water level decreased the lakes would have become more and more stagnant and the bottom more and more anoxic, so accelerating mass mortality. This would explain the excellent preservation. This explanation is supported by several sedimentological studies that demonstrate an anoxic environment at the lake bottom (Mabesoone & Tinoco, 1973; Silva, 1983).

POSSIBLE EPHEMERID PROVINCES AND ITS HABITATS IN THE LACUSTRINE COMPLEX AT CRATO MEMBER

Based on the collected material the following ephemerid provinces may be suggested (see Fig.8):

1. Palaeobaetodes Province. Occupying initially the whole Araripe Basin. Later on the Palaeobaetodes CostaLimai Subprovince emerged (occupying the west part of the basin) and the Palaeobaetodes britoi Subprovince (occupying the eastern part of the basin). Probable palaeoenvironment: shallow and stagnant vegetated lakes in which the nymphs swam freely. This interpretation is supported by the local sedimentology, palaeofauna and palaeoflora.

2. Protoligoneuria Subprovince, occupying the northwestern part of the basin (including localities 3 and 4), with very shallow water; interpretation supported by the local sedimentology, palaeofauna and palaeoflora.

3. Cratogenites Subprovince, occupying the southwestern part of the basin (including localities 1, 2 and 3) with very shallow water; interpretation supported by sedimentology, palaeofauna and palaeoflora.

4. Transitional zone between the Subprovinces Protoligoneuria and Cratogenites, in which the lakes had sandy and muddy bottoms (ideal for Ephemeroptera, Potamanthidae and Polymitarcyidae) as well as local running water (ideal for Oligoneuriidae); interpretation supported by sedimentology, palaeofauna and palaeoflora.

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