

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

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## ABSTRACT

This paper reviews all previous knowledge about ephemerid nymphs from the Santana Formation (Lower Cretaceous, northeastern Brazil) involving the families Hexagenitidae, Siphonuridae 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 corradinae* 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, Siphonuridae, Oligoneuriidae, Lower Cretaceous, Brazil.

## RESUMEN

En este trabajo se revisan los conocimientos anteriores sobre ninfas de Ephemeroptera provenientes de la Formación Santana (Cretácico Inferior, nordeste de Brasil), de las familias Hexagenitidae, Siphonuridae 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 corradinae* 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 lacustrino del Miembro Crato. Además, se proponen las posibles provincias de efemerídeos y sus habitats basados sobre el material recolectado.

**Palabras clave:** Insecta, Ephemeroptera, Hexagenitidae, Siphonuridae, 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 Siphonurinae. Demoulin (1955a), in a brief note, discounted the possibility that these nymphs would really belong to the Baetidae Siphonurinae, alleging the absence of siphonuroids in Neotropical America, except for Chile. However, Demoulin (1955b) described some

siphonuroids 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 ephemeropterid 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 pars 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 oligoneuriid described by McCafferty (1990). Brito's specimens are numbered as follows (partly renumbered):

3. McCafferty's material is apparently of type A; specimen AMNH 43415 is clearly attributable to type A.

4. The gill morphology and the large and elongate gill 7 do not indicate that AMNH, DGM and Costa Lima's material are alike as supposed by McCafferty (1990, p.24) because this is a synapomorphy of all the Hexagenitidae (including Asian, European and African species).

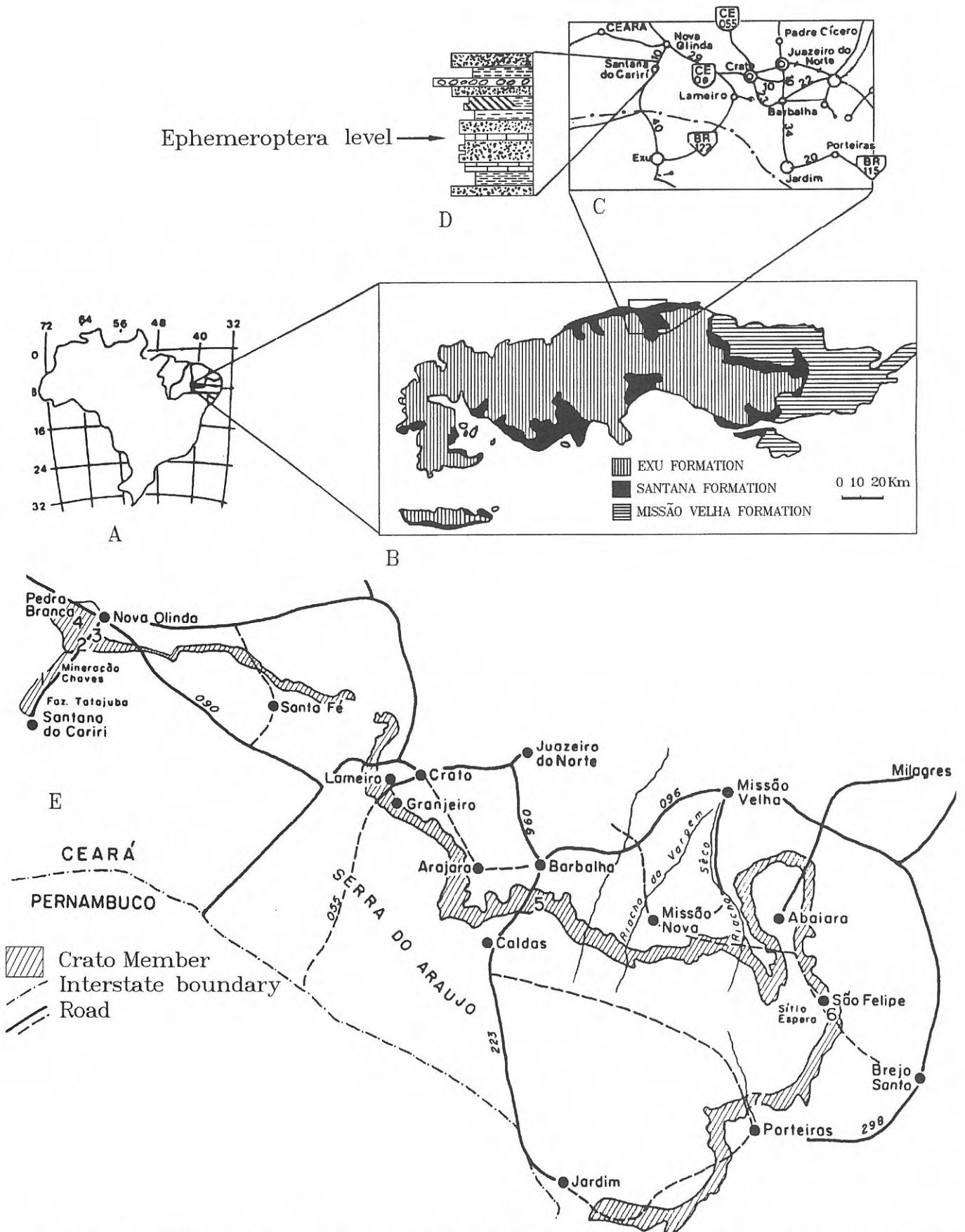
5. The name *Protoligoneuria limai* is specific for part of the McCafferty AMNH material and, at least, one specimen figured by Costa Lima in 1950. The name *Palaeobaetodes costalimai* is not a junior synonym of *Protoligoneuria limai* as supposed by McCafferty (1990), and *Palaeobaetodes* is a genus different to *Protoligoneuria*. *Palaeobaetodes costalimai* should be maintained for all specimens of Type C. I could collect at least 1.200 nymph specimens in a unique outcrop at Pedra Branca, near Santana do Cariri, an horizon which contain whole ontogenetic series ranging from 0.7 mm to 12 mm length (cerci excluded).

6. There is a third genus (Type B), which bears no relation to the material mentioned above, collected at Rio da Batateira, another outcrop that will be described here. The local region is characteristic for the dominant genus as will be demonstrated here. Material without a well-defined stratigraphic position is prone to the wrong interpretations and devoid of any palaeoecological significance.

7. The Ephemeroptera palaeoentomofauna from Araripe is extremely diverse and so varied, that one must be careful in the choice of types.

This paper aims to discuss the Hexagenitidae present in the Araripe palaeoentomofauna, and to discuss biostratigraphical and palaeoecological aspects of taxa belonging to the families Siphonuridae and Oligoneuriidae. This study is based upon abundant and well-preserved material (around 3.800 selected specimens) representing at least eight families, which comprise mainly nymphs (including eggs and ecdyses) together with adult forms. These fossils are associated with representatives of another 23 orders (Martins-Neto, 1991), together constituting one of the most diverse palaeoentomofaunas known in the geological record. Additionally arachnids, avian feathers, anurans and fish remains have been found. All this material was collected from the Crato Member, which is the lowest unit in the Santana Formation, Cretaceous (Late Aptian/ Early Albian) of the Araripe Basin, Northeast Brazil (see Fig.1).

Original Number			New Number		Type
DGM	6255-I	(Brito, 1987, Est.1, fig.1)	DGM	6255-I	C
DGM	6256-I	(Brito, 1987, Est.1, fig.2)	DGM	6256-I	C
DGM	6256-I	(Brito, 1987, Est.1, fig.3)	DGM	6277-I	New taxon (B type)
DGM	6256-I	(Brito, 1987, p.594, unfigured specimen)	DGM	6278-I	New taxon (not Hexagenitidae)



**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 PALAEOLOGY

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. 1950 Baetidae (Siphonurinae) Costa Lima, 418.  
 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 corradinae* 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 carena. 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 corradinae* 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<sup>o</sup> RGMN-T001, housed in the Entomology Department, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Campus de 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)**

Camptodeiform 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 (gill7) 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. Femura of all legs slightly thicker than the tibiae which are longer than femura.

**Discussion**

These nymphs are extremely similar in their general siphonurid appearance (thin legs, lamellar gills with a thickened outer margin, and a thickened rib near the posterior margin) to species of *Ephemeroptera*, as well as those of *Hexameropsis* in which the head is not preserved; thus making a detailed comparison impossible. However, the paracercus enables an immediate separation. *Cratogenites corradinae* 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 corradinae* 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. corradinae* and 0.75 for *P. limai*.

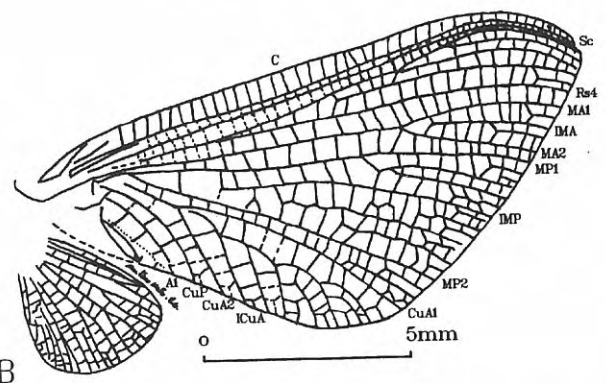
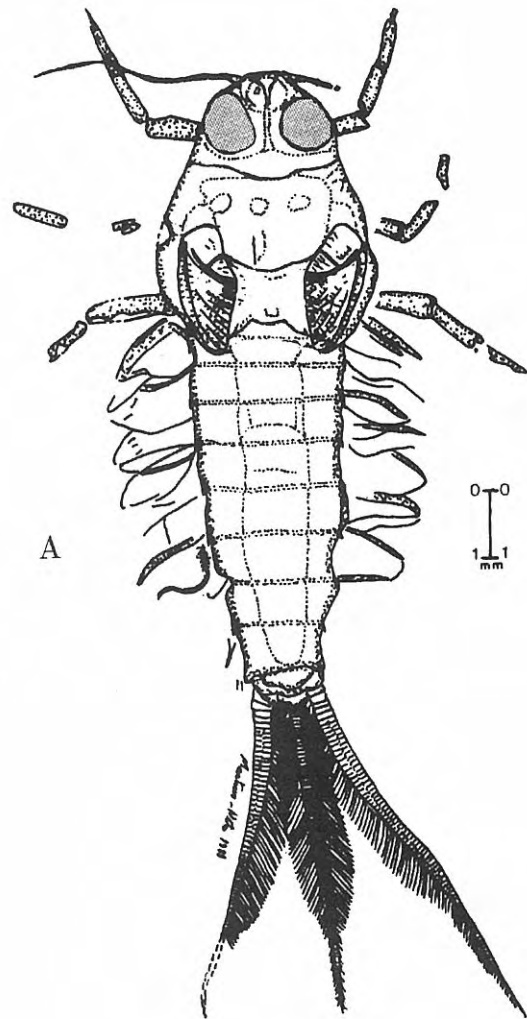
Genus *Cratogenitoides* gen. n.

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

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

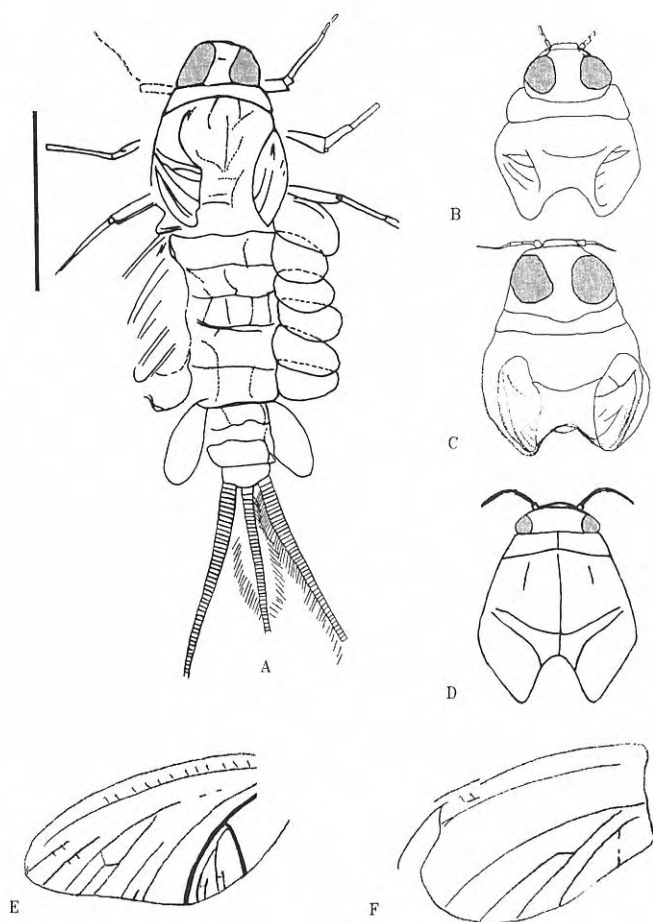
**Diagnosis**

Imago: Wing venation moderately developed;



**Figure 2.** A) *Cratogenites corradinae* sp. n., holotype, mature nymph; B) *Cratogenitoides delclosi* gen. n., sp. n., fore and hind wing of the imago; holotype.

forewing triangular; costal margin of wing longer than anal; longitudinal veins in apical half slightly curved (only Sc, Rs1 and Rs2 more curved); cubital area has four sharply curved loop-like veins, each with intermediate oblique veins.



**Figure 3.** A,E) *Palaeobaetodes costalimai* Brito: A) additional material of mature nymph; E) alar rudiments in detail. B-D) head and thorax morphology of Hexagenitidae nymphs from Santana Formation for comparison: B) *Palaeobaetodes britoi* sp. n., drawing of specimen RGMN-T006; C) *Cratogenites corradinae* sp. n., drawing of holotype; D) *Protoligoneuria limai* Demoulin, redrawn after McCafferty, 1990, fig.1 (pars). F) detail of alar rudiments of *Palaeobaetodes britoi* sp. n., drawing of holotype. Scale bar 1 mm.

### Discussion

This form is classified as Hexagenitidae based upon the following characteristics: four sharply curved loop-like veins; median fork normal; MA1 and MA2 uniformly diverging.

#### *Cratogenitoides delclosi* sp. n. Pl. I, fig. 4; Fig. 2B

**Derivatio nominis:** In honour of Dr. Xavier Martinez Del Clós from Universitat Central de Barcelona for his many contributions to palaeoentomology.

**Holotype:** Martins-Neto Collection n° RGMN-T002, 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.** The same as *C. corradinae*.

### 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

Imago forewing (Fig.2B) triangular; costal margin slightly curved; apical margin longer than anal margin; longitudinal veins slightly curved in apical half; costal area relatively wide, narrowing toward tip, with pectinated crossveins; geminations of wing very masked; Sc long, apically very curved; R1 subparallel to Sc; four branches from the radial sector; MA quite straight in the middle part of the wing, distally branched to approximately 1/3 from the apex, at the same level of Rs2 origin; MA1 and MA2 uniformly diverging; MP1 and MP2 diverge at an angle of approximately 30; Cu forks at 1/3 of the base of the wing; CuA1 end at apical margin extremity and CuA2 ends at middle part of the anal margin. Between CuA1 and CuA2, in the cubital area, there are four loop-shaped forks, each with a secondary vein.

Cross veins very numerous throughout wing, including the cubital area. Hindwing very small (2.7 mm).

### Discussion

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

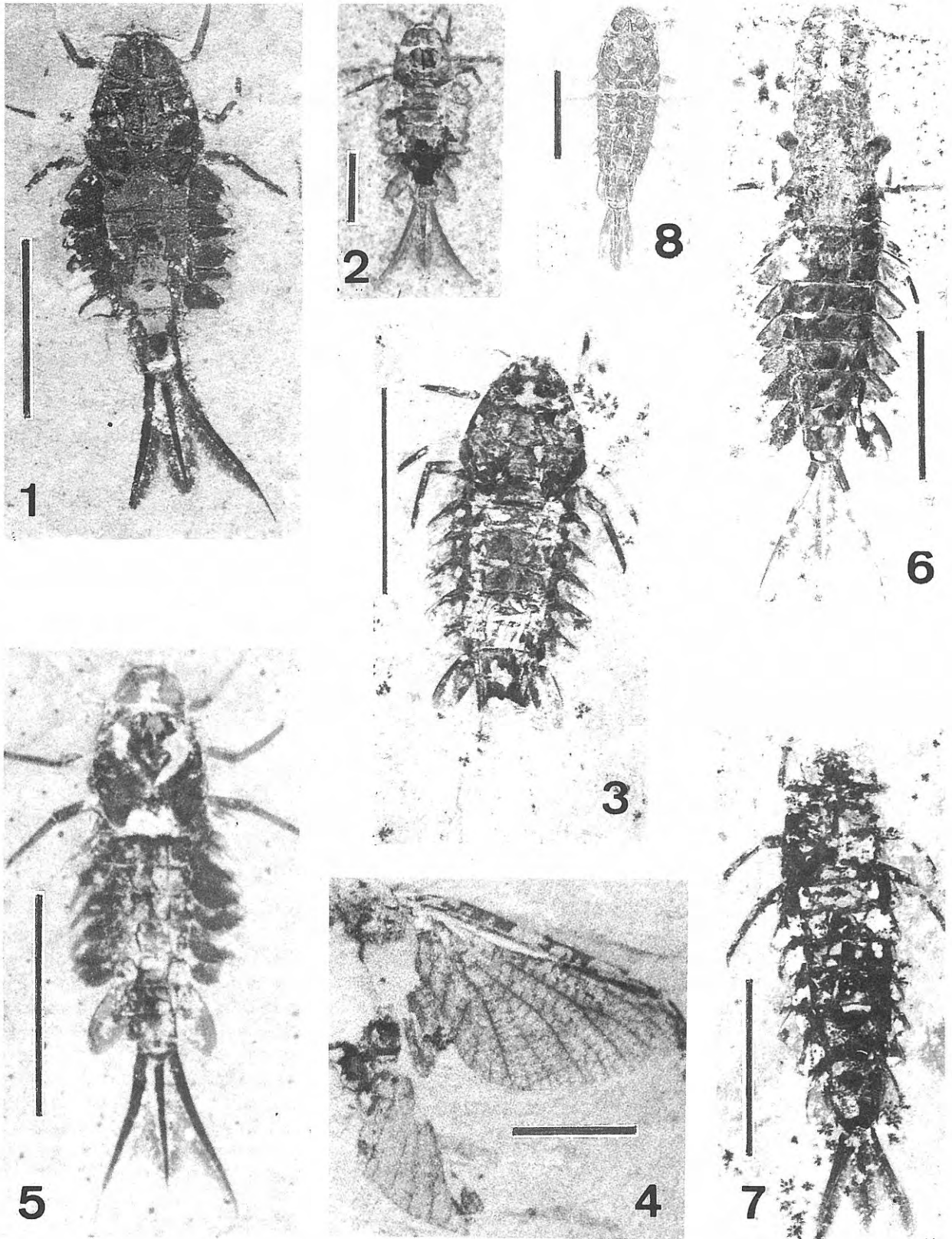
p.\* 1987 *Palaeobaetodes* Brito, fig. 1-3.

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 corradinae* sp. n. 1) holotype RGMN-T001, mature nymph. 2-3) unnumbered additional nymphs.  
 4 *Cratogenitoides delclosi* sp. n., holotype RGMN-T002, fore and hind of the imago.

- 5-7 *Palaeobaetodes costalimai* Brito, unnumbered additional specimens (nymphs). 6) partial exuvia.  
 8 *Palaeobaetodes 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. \* 1987 *Palaeobaetodes costalimai* Brito, fig. 1-3.p. 1990 *Protoligoneuria limai* Demoulin; McCafferty, 22.**Holotype:** DGM 6255-I. Housed in Departamento Nacional da Produção Mineral - DNPM, Rio de Janeiro.**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 (innitial stages) to 12 mm long (mature stages).

**Decription**

(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. Gills1-6 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 nº 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 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).

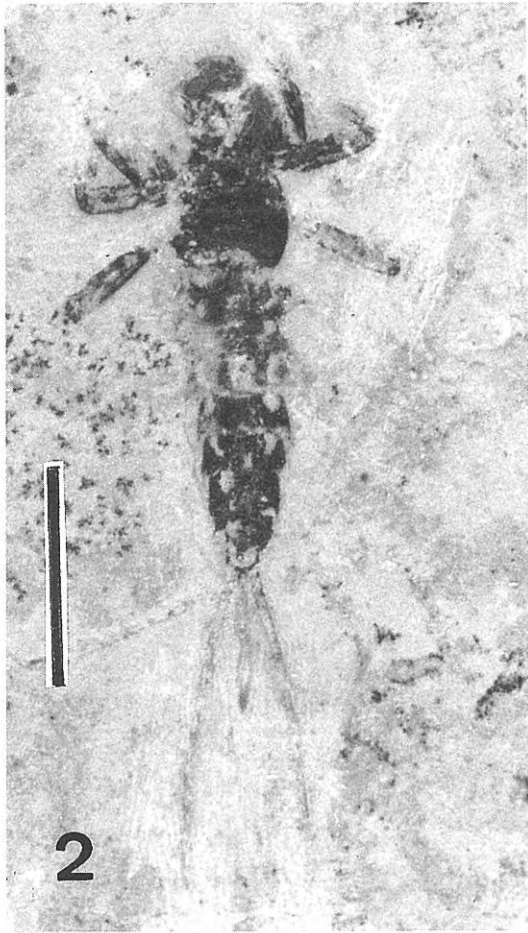
**Discussion**

This species can be distinguished from *P. costalimai* by the Gill7/ Gill6 ratio: 2:1. Gills1-6 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 **Siphonuridae** Ulmer, 1920Genus *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.



Plate II

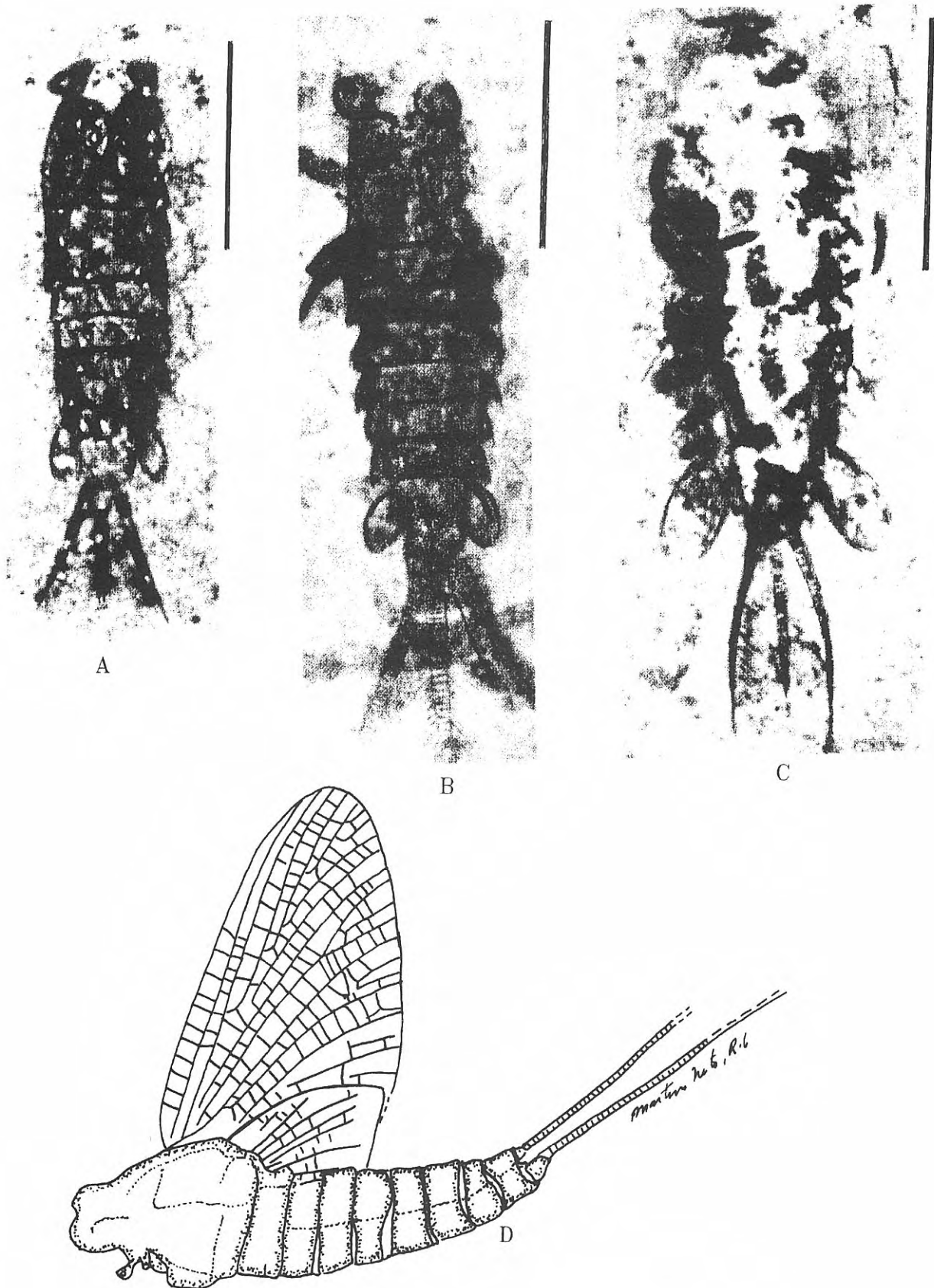


1 *Costalimella nordestina* sp. n., holotype RGMN-T004, relatively complete imago.

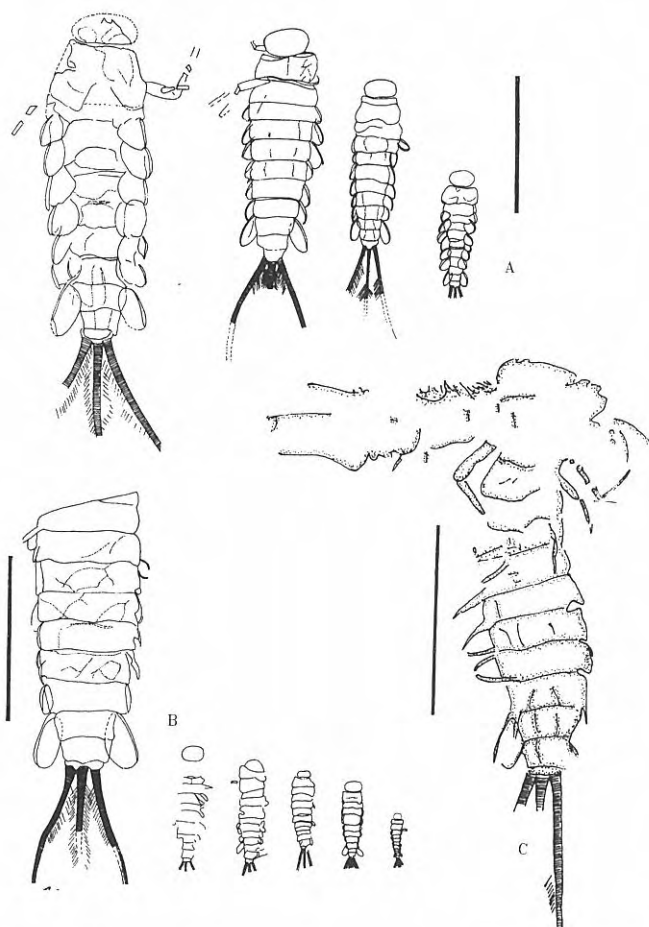
2-3 *Cratoligoneuriella leonardii* sp. n., holotype RGMN-T005. 2) general view of nymph. 3) detail of the

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.



**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 siphonurid 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*.

### Discussion

Very similar to *Stackelbergisca* Chernova from the Jurassic of Transbaikalia, but differing in the MA1, MA2 and IMA morphology (shorter) and in its minuscule size (6 mm long). This form is very different to the other Araripe siphonurids, including *Siphgondwanus* McCafferty, 1990 (a nymph). *Costalimella* is distinguished from *Proameletus* Sinitshenkova, 1976, and *Siphgondwanus* McCafferty, 1990, mainly by the short branches of MA in the imago forewing of the species from Araripe. It differs from *Olgisca* Demoulin, 1970 (Jurassic of Solnhofen), by the presence of intercalary

veins between Rs1 and Rs2 on the forewing.

### *Costalimella nordestina* sp. n.

Pl. II, fig. 1; Fig. 4D

**Derivatio nominis:** From nordeste (northeast).

**Holotype:** Martins-Neto Collection n° 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.

### Description

Imago forewing relatively narrow, triangular with fairly sharp tip. Sc long, reaching the apical margin; costal area relatively broad at base, narrowing towards the tip, filled up by numerous crossveins, Rs origin in the middle region of wing, giving rise to five ultimate branches; presence of a long intercalary vein between Rs1 and Rs2; Rs5 long, originating near the wing base; MA long, nearly straight, branching near the posterior margin where it gives rise to two symmetric branches; presence of an intercalary vein (IMA) between the two branches of MA (MA1 and MA2); MP long, slightly curved apically, and branching near the wing base; a long intercalary vein (IMP) present between the two branches of MP (MP1 and MP2); Cu partially preserved. Numerous crossveins in whole wing. Hindwing partially superimposed upon forewing and covering almost the entire anal and cubito-anal veins. Head poorly preserved. Thorax robust and abdomen with clear segmentation. Caudal filaments partially preserved. Members and antenna not preserved.

### Discussion

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

Although Jell & Duncan (1986) figured and described a diverse fauna of Ephemeroptera Siphonuridae (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

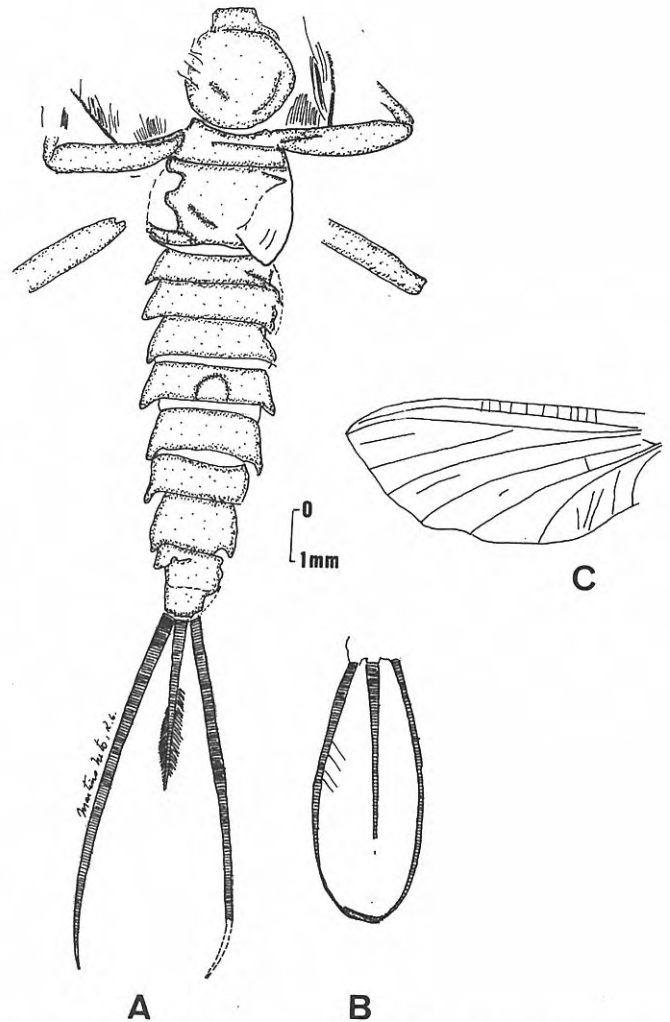
Nymph (mm): Body length, 12; maximal width, 2.8; cerci, 8; paracercus, 3.5; total length, 20; anterior femur length 2.5, posterior femur length, 3.

### 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 middle 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,



**Figure 6.** A-B) *Cratoligoneuriella leonardii* sp. n., drawing of holotype: A) general view of the nymph. B) specimen DGM 6278-I, caudal filaments. C) Oligoneuriidae gen. et sp. indet, isolated imago forewing.

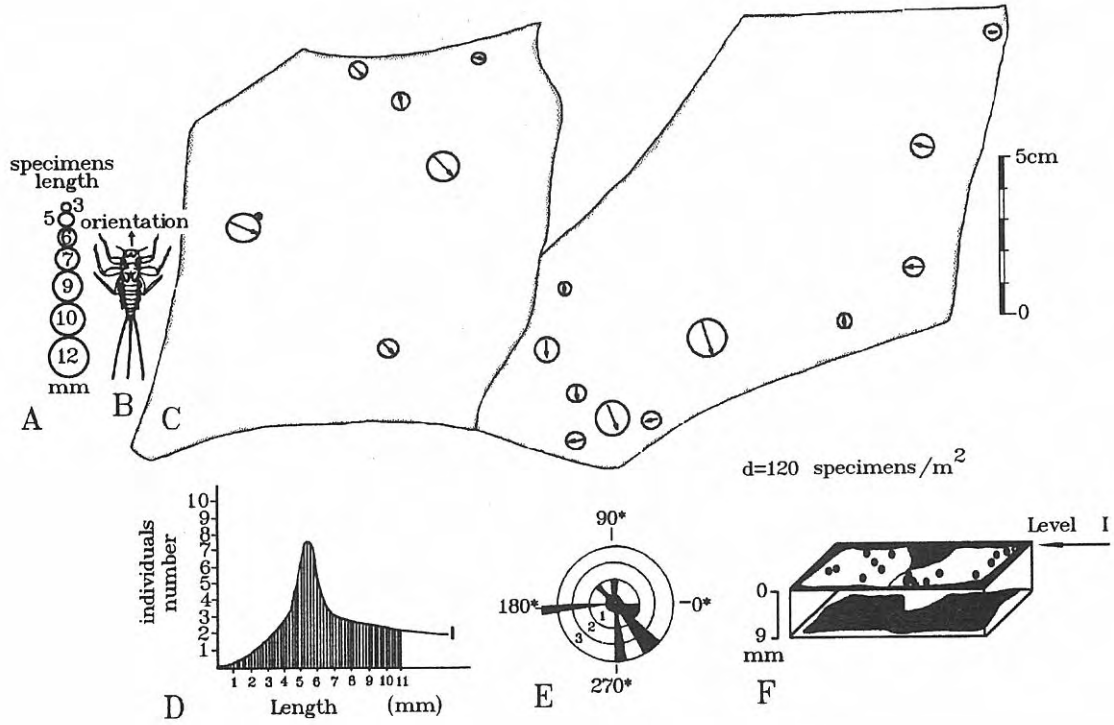
resembles that of extant *Homoeoneuria* and *Oligoneurisca* of the Neotropics. However, it differs by the possession of long femora (these are relatively short in the extant species).

### Oligoneuriidae gen. et sp. indet.

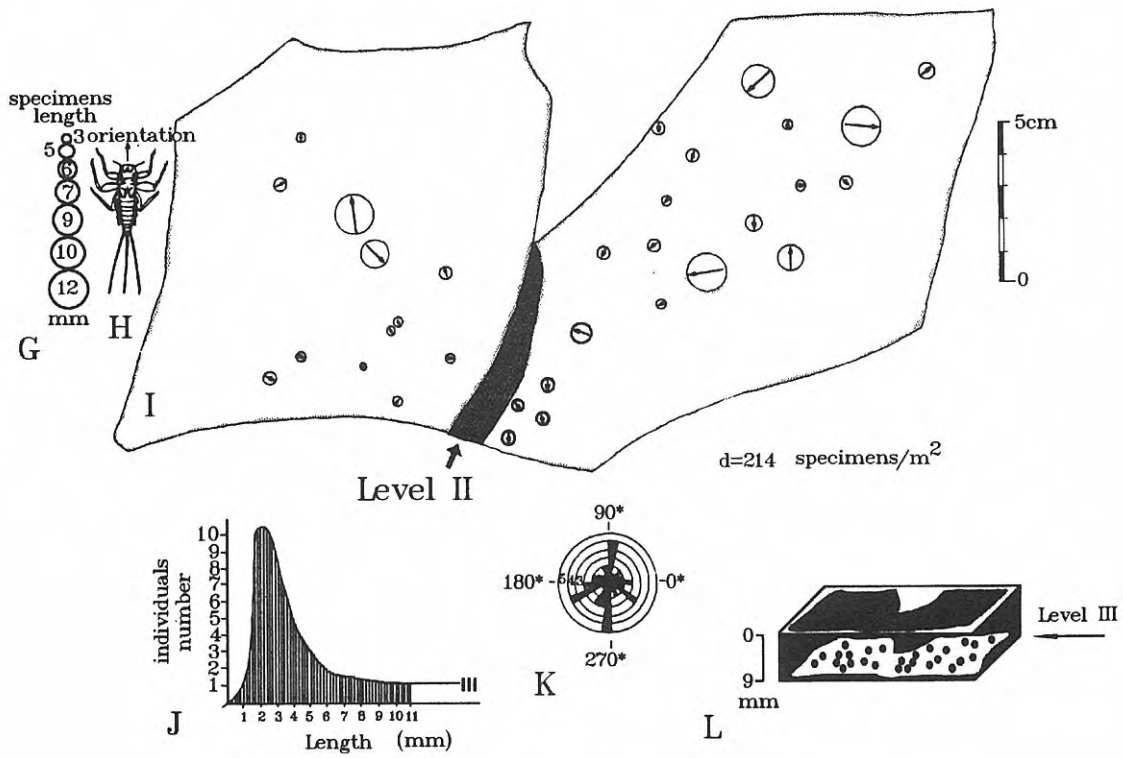
Fig. 6C

### 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.

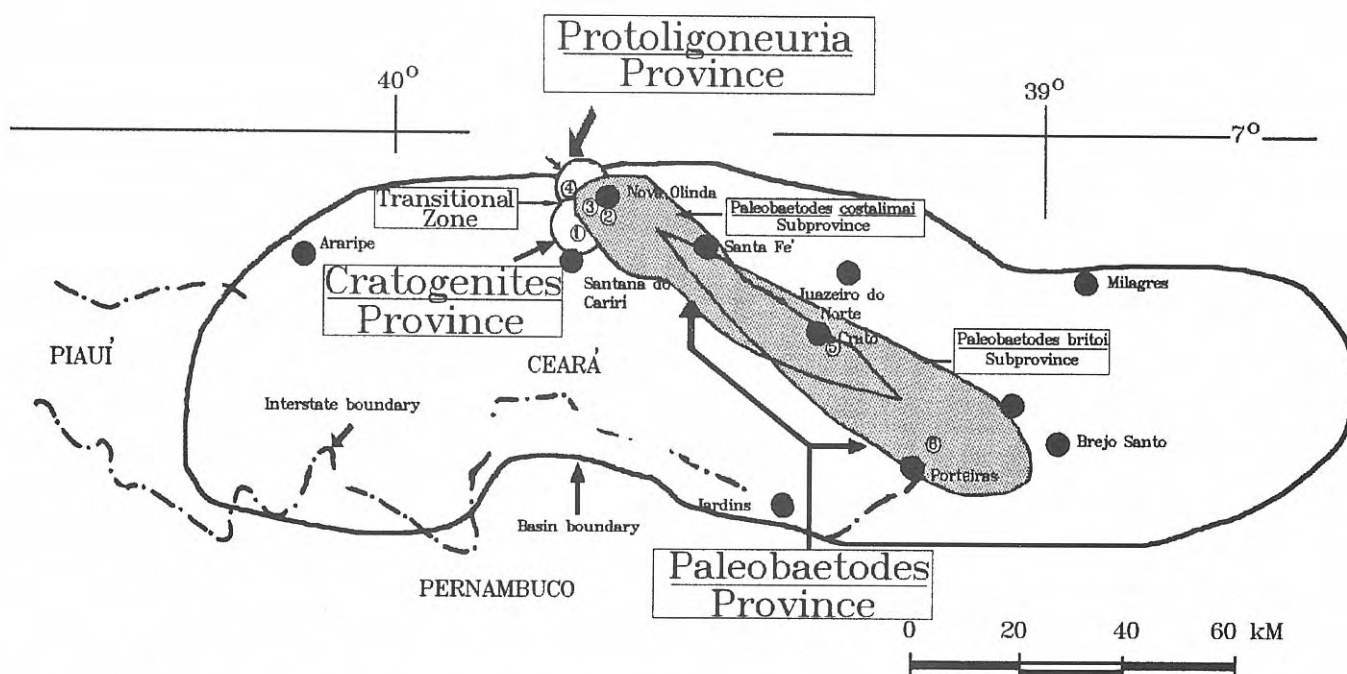


LEVEL I



LEVEL III

**Figure 7.** Distribution of Ephemeroptera nymphs of the genus *Palaeobaetodes* from Rio da Bateira 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.



**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

Ephemerid 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 corradinae* (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: *Carirynympha 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: *Palaeobaetodes costalimai* (Hexagenitidae), including ontogenetical series.

Rare: *Palaeobaetodes 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 corradinae* (Hexagenitidae).

4. Riacho do Salgado, Fazenda Santa Rosa, near Pousada Santa Fé.

Rare: *Protoligoneuria limai* (Hexagenitidae).

5. Rio da Batateira, Lameiro, near Crato. Outcrop bordering the river.

Dominant: *Palaeobaetodes britoi* (Hexagenitidae), including ontogenetical series.

Abundant: *Palaeobaetodes costalimai* (Hexagenitidae), including ontogenetical series.

6. Sítio Massapê, Mina dos Rosados. Base of the Serra de São Felipe, 6.5 km from Porteiras.

Rare: *Palaeobaetodes 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 uncompact and showing the absence of transport or only minimal transport.

3. In this outcrop, one sample of 350 cm<sup>2</sup> with 9 mm of thickness shows the following characteristics:

a) Level or horizon I (upper) has an average density of 120 individuals/m<sup>2</sup> 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/m<sup>2</sup> 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 neuropteran 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 palaeontofauna, 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 region 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, paleofauna and paleoflora.

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

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