

Systematics of the Caelifera (Insecta, Orthopteroidea) from the Santana Formation, Araripe Basin (Lower Cretaceous, northeast Brazil), with a description of new genera and species

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Abstract. This research presents the results of a taxonomic study of 35 specimens of fossil Caelifera from laminated limestone of the uppermost part of the Crato Member, lowest unit of the Santana Formation (Lower Cretaceous), Araripe Basin, near Santana do Cariri and Nova Olinda municipalities (Ceará State, Northeast Brazil). The group is reviewed; two new genera: *Cratolocustopsis* n. gen., *Locustrix* n. gen., and nine new species are described: *Cratocustopsis contumax* n. sp., *Zessinia petruleviciusi* n. sp., *Zessinia vikingi* n. sp., *Cratozeunerella godoi* n. sp., *Cratozeunerella nervosa* n. sp., *Cratozeunerella soaresi* n. sp., *Cratozeunerella titanella* n. sp., *Locustrix gallegoi* n. sp., *Locustrix audax* n. sp. *Cratolocustopsis cretacea* n. comb., *Cratolocustopsis araripensis* n. comb. are transferred from *Locustopsis* to *Cratolocustopsis* n. gen. *Cratozeunerella nordestina* MARTINS-NETO 1998, after supplementary material examined, is considered a junior synonym of *Cratozeunerella neotropica* MARTINS-NETO 1998. The present study increases the number of Caelifera represented in the Santana Formation, as well as in the whole South Hemisphere, to 21 species of seven genera. These are distributed in four families of grasshoppers, one of most complete and abundant assemblages of this group known of fossil record.

Key words: Caelifera, Santana Formation, Brazil, new genus, new species, Lower Cretaceous, fossil, Locustopsidae, Bouretidae, AraripeLocustidae.

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I. INTRODUCTION

The fossil record of grasshoppers is amongst the most poorly known among all insects; they are both scarce and rarely fossilized by chance. An explanation for the virtual absence of fossil representatives of this group has been proposed by BLACKITH (1973), by experiments with extant specimens. He concludes that grasshoppers are almost immediately consumed by the infauna, reduced to powder by microbes. In spite of this, the Santana Formation paleontomofauna is amongst the most

diverse in the world (likely due to peculiarities of depositional environment) with at least 23 orders of insects represented, including a wealth of grasshoppers (MARTINS-NETO 1999).

Of the Caelifera represented in the Santana Formation, the family Tridactylidae (as well as several representatives of Locustopsoidea) is also known from the Lower Cretaceous of Asia (SHAROV 1968; GOROCHOV 1992), and Australia (JELL & DUNCAN 1986). Furthermore, Caelifera known in fossil record but not represented in Brazil include eumastacoids *Taphacris turgi* LIN (LIN 1994) from the Chinese Cretaceous; *Promastax archaicus* HANDLIRSCH (1910) from the Eocene of British Columbia, Canada; *Erucius? lewisi* KEVAN & WIGHTON (1981) from the Oligocene of Montana, USA (see also LEWIS 1974; 1976); and *Paleomastacris ambarinus* PEREZ et al. (1997) from Miocene Dominican amber. Tetrigidae are also represented from Lower Cretaceous of Siberia, from Eocene Baltic amber and from Oligocene, Miocene and Eocene deposits of Europe and North America (STOROZHENKO 1997). Specimens have been reported, but not described, of the acridid subfamily Oedipodinae from the Spanish Miocene (MARTÍNEZ-DELCLÓS et al. 1991; PEÑALVER 1992-1996; PEÑALVER et al. 1996) and uncertain Acrididae from the Spanish Oligocene (ARILLO & ORTUÑO 1997) and Argentinean Paleocene (PETRULEVICIUS 1999).

A b b r e v i a t i o n s

AMNH – American Museum of Natural History, New York, USA

IGUSP – Paleontological Collection of the Instituto de Geociências da Universidade de São Paulo

MN-RJ – Paleontological Collection of the Museu Nacional, Rio de Janeiro, Brazil

SBPr – Sociedade Brasileira e Paleontropodologia, Ribeirão Preto, São Paulo, Brazil

UFCE – Universidade Federal do Ceará, Brazil.

UNG – Paleontological Collection of the Departamento de Geociências da Universidade Guarulhos, São Paulo, Brazil

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II. MATERIAL

The material comes from the Lower Cretaceous of Brazil. Type localities are: Mina Pedra Branca, Nova Olinda-Santana do Cariri road, 4 km of the municipal district of Nova Olinda and Tajuba farm, Santana do Cariri, Ceará State, Northeast of Brazil. Type stratum: laminated limestone level, Crato Member, lowermost unit of the Santana Formation, Araripe Basin. Upper Aptian/Lower Albian, Lower Cretaceous. All material described in this paper was examined by the author.

III. SYSTEMATIC PALEONTOLOGY

Order CAELIFERA

Superfamily **Locustopsoidea**

The superfamily Locustopsoidea is divided into either three or four families: Locustavidae (Triassic), Locustopsidae, known from Triassic to the Upper Cretaceous; possible descendants of Locustopsidae, Araripelocustidae from Lower Cretaceous of Brazil; and possibly the Recent family of apterous grasshoppers Tanaoceridae (GOROCHOV 2001). Of these, fossils of Locustopsidae and Araripelocustidae have been previously described from Brazil (MARTINS-NETO 1990a, 1995, 1998).

In spite of revisions of the family Locustopsidae, further discussion is necessary to include genera without heretofore clearly defined phylogenetical relationships. Presently in the literature, 12 genera are accepted as belonging to the family: *Praelocustopsis* SHAROV, 1968 (one species, Triassic of Siberia); *Triassolocusta* TILLYARD, 1922 (1 sp., Triassic of Australia); *Schwinzia* ZESSIN, 1988 (1 sp., Lower Jurassic of Germany); *Plesioschwinzia* ZESSIN, 1983 (2 spp., Lower Jurassic of Germany); *Locustopsis* HANDLIRSCH, 1906 (30 spp., Jurassic of Europe and Siberia); *Mesolocustopsis* HONG & WANG, 1990; *Pseudoacrida* LIN, 1982 (each 1 sp. from Lower Cretaceous of China), *Parapleurites* BRAUER et al., 1889 (2 spp., Middle Jurassic of Siberia); *Conocephalella* STRAND, 1936 (1 sp., Upper Jurassic of Germany); *Zessinia* MARTINS-NETO, 1998 (3 spp., Lower Cretaceous of Brazil); *Cratozeunerella* MARTINS-NETO, 1998 (3 spp., Lower Cretaceous of Brazil) and *Zeunerella* SHAROV, 1968 (1 sp., Cenomanian of Kazakhstan) (data of BRAUER et al. 1889; HANDLIRSCH 1906, 1920, 1939; COCKERELL 1915; TILLYARD 1922; MARTYNOV 1937; ZEUNER 1942; BODE 1953; SHAROV 1968; ZESSIN 1983, 1988; MARTINS-NETO 1990a, 1998; ANSORGE 1996). The presence of Locustopsidae is also confirmed in Lower Cretaceous sediments of Egypt (ANSORGE 1991), England (JARZEMBOWSKI & CORAM 1993), Montsech, Spain, (GOMES-PALEROLLA 1986).

OLSEN et al. (1978: Fig. 3C) figured a Locustopsidae specimen from the Upper Member of the Cow Branch Formation, Dan River Group (Upper Triassic North Carolina/Virginia), which they believed to be a representative of Glosselytrodea. This fore wing seems to be very similar to *Schwinzia* and *Plesioschwinzia* ZESSIN genera from the Lower Jurassic of Germany.

Family **Locustopsidae** HANDLIRSCH 1906***Cratozeunerella*** MARTINS-NETO, 1998

*1998 *Cratozeunerella* MARTINS-NETO, Rev. Española Paleont., 13(2): 135.

1999 *Cratozeunerella* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Posterior femur long and narrow, relationship W/L around 0.15. Fore wing with ScA sigmoid and four to five branches of RP, and hind wing with three to four branches of RP. Subcostal area in fore wing filled by several pectinate cross-veins.

Type species. *Cratozeunerella neotropica* MARTINS-NETO 1998, by original designation.

R e m a r k s. Similar to *Zeunerella* SHAROV, 1968, differing however by having subcostal area filled by several cross-veins (without cross-veins in *Zeunerella* SHAROV), five (exceptionally four) branches of RP in the fore-wing (three in *Zeunerella* SHAROV) and four (exceptionally three) branches of RP in the hind wing (three in *Zeunerella* SHAROV).

Cratozeunerella neotropica MARTINS-NETO 1998

Fig. 1A-E

*1998 *Cratozeunerella neotropica* MARTINS-NETO, Rev. Española Paleont., 13(2): 135-136; Fig. 2, 3A.

1998 *Cratozeunerella nordestina* MARTINS-NETO, Rev. Española Paleont., 13(2): 137, Fig. 3c, 4b. new synonymy

1999 *Cratozeunerella neotropica*, Rev. Soc. Entomol. Argent., 58(1-2): 74.

1999 *Cratozeunerella nordestina* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74, Fig. 2H.

E m e n d e d d i a g n o s i s. Fore wing 23 mm long. MA1 free. MA2 origin in MA3. RP origin little posterior to MA1. CuA2 short. MA origin posterior to CuA1+CuA2 origin. RP five-branched. Hind wing with four branches and MA1+2 origin in mid length level of wing, in the same level of the RP origin.

H o l o t y p e (Fig. 1A, B). Specimen UnG-030, housed in UnG. Type locality: Tatajuba farm.

A d d i t i o n a l m a t e r i a l (Fig. 1 C-E): UnG-031, housed in UnG. Previously designated as holotype of *C. nordestina* MARTINS-NETO 1998.

D e s c r i p t i o n. As in MARTINS-NETO (1998a)

R e m a r k s. After examination of the holotype of *C. nordestina* MARTINS-NETO and more preparation in the area of CuA, the presence of the extra branch was verified, what makes this specimen undistinguishable from *C. neotropica* MARTINS-NETO; therefore a new synonymy is proposed herein.

***Cratozeunerella amedegnatoi* MARTINS-NETO 1998**

*1998 *Cratozeunerella amedegnatoi* MARTINS-NETO, Rev. Española Paleont., 13(2): 136-137, Fig. 3b, 4a

1999 *Cratozeunerella amedegnatoi* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74, Fig. 2G.

E m e n d e d d i a g n o s i s. Fore wing 25 mm long. MA1 free. MA2 origin in MA3. RP origin a little posterior to MA1 origin. CuA2 long. MA origin anterior to CuA1+2 origin. RP five-branched. Hind wing four-branched and RP origin posterior to MA1+2 origin.

H o l o t y p e. Specimen CD-I-127, housed in Desirée collection; MN-RJ. Type locality unknown, probably near Santana do Cariri.

D e s c r i p t i o n. As in MARTINS-NETO 1998a.

***Cratozeunerella godoi* n. sp.**

Figs 1G; 2A, F-G; 8A, E

D i a g n o s i s (based on holotype). Fore wing 23 mm long. MA3 free. MA2 origin in MA1. RP origin at same level as MA1+2 origin. CuA1+2 origin anterior to MA3 origin.

E t y m o l o g y. In honour of the paleontologist Vinícius Moreno DE GODOI (FFCLRP-USP).

H o l o t y p e. Specimen RGMN-T125 (Figs 1G, 8A), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. Specimen AMNH-43868 (Figs 2A, F-G; 8E): now in the collection of SBPr. Type locality: uncertain Santana Formation.

D e s c r i p t i o n (holotype, Fig. 1G). Fore wing 23 mm long. ScA long, sigmoid, reaching costal margin about 1/3 of base of wing. ScP long, with ScP1 relatively far from end of ScA. Area between ScP and RA narrow. RP origin at mid length level of wing. Area between RA and RP notably narrow. RP with four preserved branches. MA3 free, MA2 origin in MA1. CuA1+2 origin at level of RP origin. MA3 origin anterior to RP origin. Origin of branch more proximal of RP relatively far from MA1+2 origin. AMNH-43868: body (Fig. 2A) notably short, robust, 15 mm long. Small, narrow head, same width as pronotum. Pronotum relatively great, seliform. Abdomen short and robust. Fore wing 17 mm long (Fig. 2F). RP origin at same level as mid length of wing. Area between RA and RP notably narrow. RP with three branches, relatively long. MA3 free, MA2 origin in MA1. MA1+2 origin anterior to RP origin. CA1+2 far from RP3 origin. CuA1+2 origin posterior

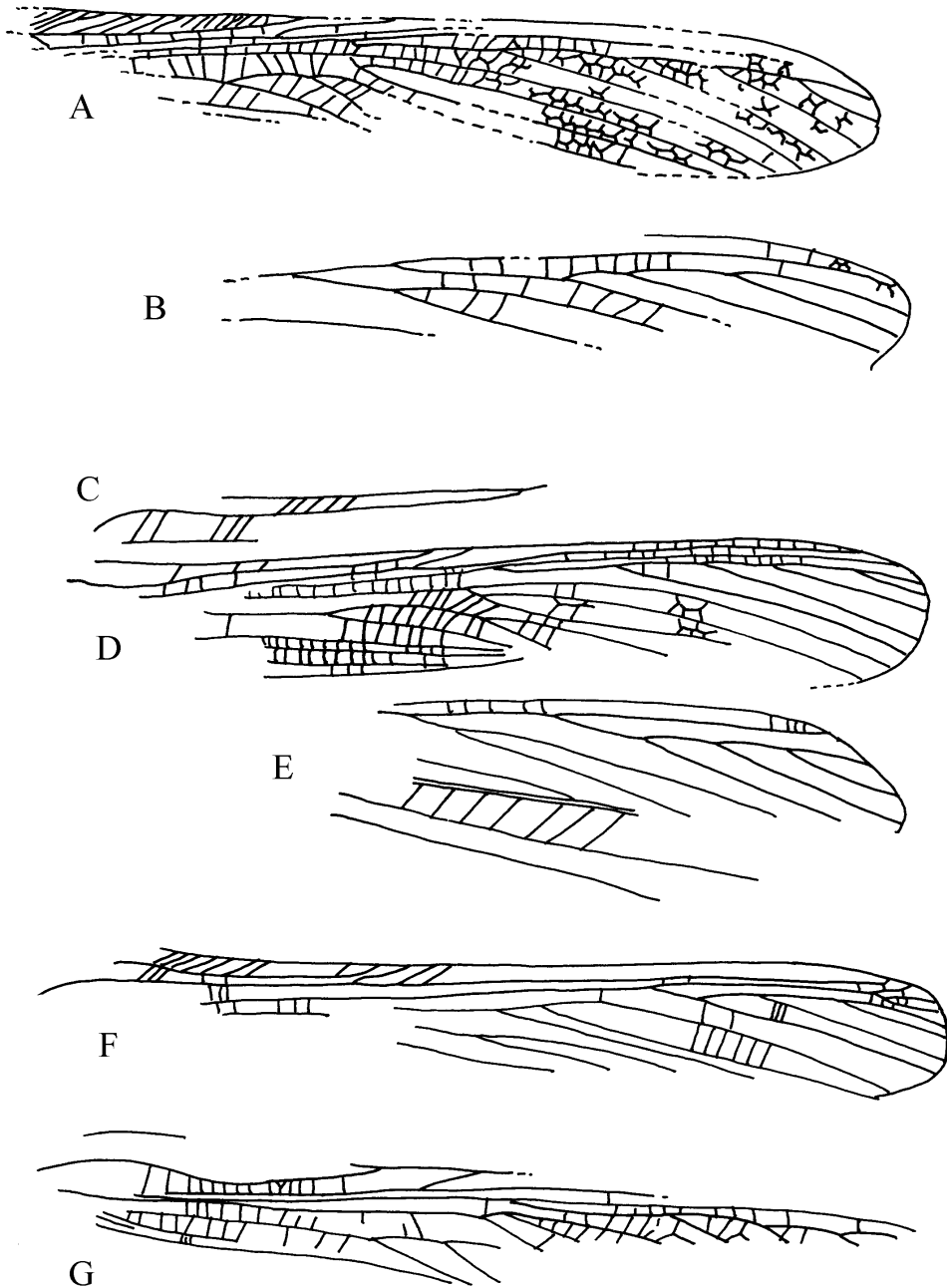


Fig. 1. A-B. *Cratozeunerella neotropica* MARTINS-NETO, 1998, holotype UnG-03: fore wing (A) and hind wing (B); C-E. *Cratozeunerella neotropica* MARTINS-NETO, 1998, specimen UnG-031: fore wing, detail of the subcostal area (C), fore wing (D) and hind wing (E); F. *Cratozeunerella nervosa* n. sp., fore wing of holotype RGMN-T126; G. *Cratozeunerella godoi* n. sp., fore wing of holotype RGMN-T125.

of MA3 origin. Hind wing (Fig. 2G) with RP originating three branches, relatively long and RP origin far from wing base, about 1/3 apical of area. M1 and M2 long, with M2 converging to M1.

D i s c u s s i o n. *Cratozeunerella godoi* n. sp. differs from all described species of the genus *Locustopsis* by sigmoid ScA; differs from *Zeunerella arborea* SHAROV 1968 by having more branches of RP and from *Cratozeunerella neotropica* MARTINS-NETO and *Cratozeunerella amedegnato* MARTINS-NETO by having MA3 free in the fore wing.

GOMES-PALEROLLA (1986: Fig. 45) presents a Locustopsidae specimen, where the hind wing has three branches of RP and similar morphology to one of the species described above, mistakenly interpreted by this author in a previous work as a neuropteran wing. ANSORGE (1991) mentions that the specimen belongs correctly in the family Locustopsidae, suggesting that it is a species of the genus *Zeunerella* SHAROV, 1968. This material very probably belongs to the genus *Cratozeunerella* MARTINS-NETO, 1998, as the costal and subcostal area is wide; it is narrow in *Zeunerella*.

Cratozeunerella nervosa n. sp.

Figs 1F; 9H

D i a g n o s i s. Fore wing 18 mm long. MA3 free. MA2 origin in MA1. RA distally branched. Reduced RP area. RP origin posterior to origin of MA1+2. CuA1+2 origin anterior to MA3 origin.

E t y m o l o g y. Alluding to the great number of supplemental veins in the wings of this species.

H o l o t y p e. Specimen RGMN-T126 (Figs 1F; 9H), housed in MARTINS-NETO Collection, SBPr. Type locality. Mina Pedra Branca.

D e s c r i p t i o n (holotype, Fig. 1F). Fore wing 18 mm long. ScA long, sigmoid, reaching Costal margin about 1/3 from wing base. ScP long, with ScP1 close to end of ScA. Area between ScP and RA narrow. RA distally branched. RP origin far from wing base, about 1/3 of apical margin, with four branches. MA3 free, MA2 origin in MA1. MA1+2 origin very anterior to RP origin. CuA1 long.

R e m a r k s. Similar to *C. godoi* n. sp. in having MA3 free. It differs, however, from all previously described and known species of this genus by its smaller length, by RA distally branched, and RP origin very close to the apical area.

Cratozeunerella soaresi n. sp.

Figs 3C-F, H; 8B-D

D i a g n o s i s. Characteristics of genus. Fore wing between 30 and 32 mm long. Hind wing with four branches of RP, RP1+2 relatively long. MA1 convergent to RP4 and MA2 convergent to M1.

E t y m o l o g y. In honour of Prof. Olavo SOARES, retired of UFPR.

H o l o t y p e. Specimen RGMN-T118 (Figs 3C-D, H; 8B), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. CD-I-124 (Fig. 8C, part, and D, counterpart), Desirée collection, MN-RJ (Fig. 3E, F). Same locality and stratum as in holotype.

D e s c r i p t i o n (holotype, Fig. 3C-D, H). Body elongate, 29.5 mm long. Head oblique and relatively narrow (Fig. 3D). Eyes relatively big. Pronotum trapezoidal, with anterior margin convex, without ornamentation, laterally short, and exhibiting protuberance in proximal extremity. Prolonged abdomen, narrowed abruptly at subgenital valve level. Hind member with prolonged femur 16.2 mm long (Fig. 3H); distal extremity very narrow, without spiniform projections; inferior and posterior lobes similar in size. Hind wing (Fig. 3C) 30 mm long and 4 mm wide. RP with four

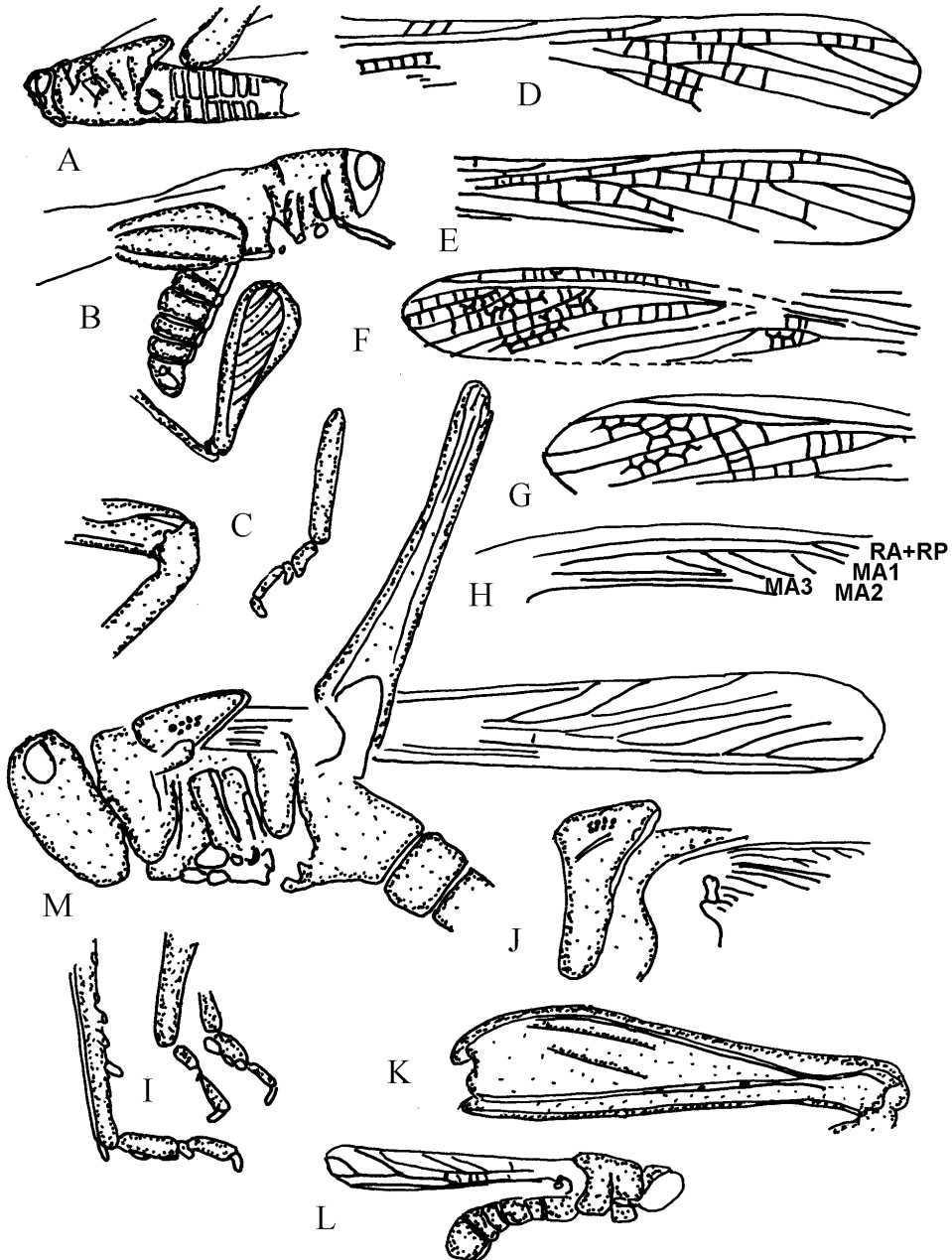


Fig. 2. A, F-G: *Cratozeunerella godoii* n. sp., specimen AMNH-43868: detail of body (A), fore wing (F), and hind wing (G); B. *Zessinia caririensis* MARTINS-NETO 1990, specimen RGMN-T124, general aspect; C, H-K: *Zessinia* sp., specimen RGMN-T114: details of tibio-femoral joint and anterior tarsus (C); details of fore wing (H); details of middle and posterior tarsus (I); details of pronotum (J); details of posterior femur (K); D. *Locustrix audax* n. sp., holotype RGMN-T129, schematic drawing of fore wing; E, L: *Locustrix gallegoi* n. sp., holotype RGMN-T128: fore wing (E), general aspect (L); M. *Cratozeunerella titanella* n. sp., holotype RGMN-T127, general aspect.

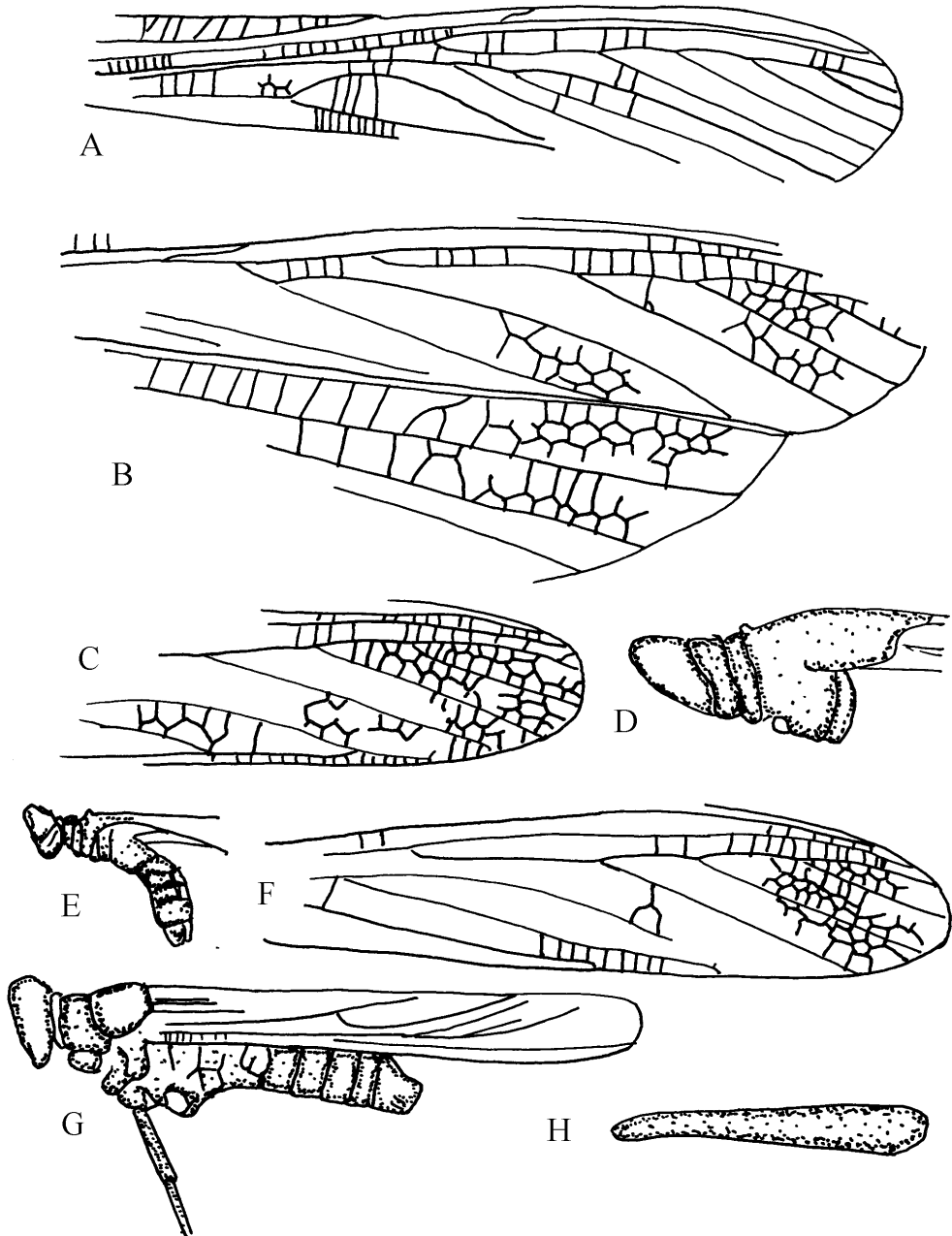


Fig. 3. A. *Zessinia caririensis* MARTINS-NETO 1990, specimen RGMN-T122; B. *Zessinia vikingi* n. sp., specimen RGMN-T123: detail of hind wing; C-F, H: *Cratozeumerella soaresi* n. sp., holotype RGMN-T118: details of hind wing (C), details of pronotum (D), details of hind femur (H); E, F: *Cratozeumerella soaresi* n. sp., specimen CD-I-124: general aspect (E), details of hind wing (F); G. *Zessinia petruleviciusi* n. sp., general aspect of holotype RGMN-T116.

branches, RP1+2 relatively long. MA1+2 long with MA1 convergent to RP4 and MA2 convergent to MA1, distally fused.

D i s c u s s i o n. Differs from all previously described and known species by the larger size (between 30 and 32 mm), RP1+2 larger, MA1 convergent to RP4 and MA2 convergent to MA1.

***Cratozeunerella titanella* n. sp.**

Figs 2M, 4D; 7E, F

D i a g n o s i s. Characteristics of genus. Fore wing c. 40 mm long. RP origin anterior to MA3 origin.

E t y m o l o g y. From Latin “titan”, alluding to the great size of the species.

H o l o t y p e. Specimen RGMN-T127 (Figs 2M; 7F), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. RGMN-T120 (Figs. 4D; 7E); same institution, locality and stratum as in the holotype.

D e s c r i p t i o n (holotype, Fig. 2M). Body elongated, 39.5 mm long, head oblique, relatively elongated. Eyes relatively small. Antennae inserted below level of eyes. Pronotum seliform, laterally short, ornamented with homogeneous granulation. Thorax robust. Abdomen long and narrow, with last segment not much wider than basal ones. Subgenital plate elongated. Posterior member with femur very long, 26.2 mm long, notably narrow in its distal half; distal extremity without spiniform projections and inferior lobe little smaller than superior one. Fore wing 40 mm long. ScA origin close to base of wing. ScP, RA and RP parallel. Origin of RP1, although not preserved, is far before to origin of MA3 and also anterior to CuA1 origin. MA3 free. MA2 origin in MA1. MA3 origin anterior to CuA1 origin. Branch more proximal of RP far ahead MA1+2 origin. CuP long, straight, parallel and very close to anal margin.

R e m a r k s. Differs from all previously described species of the genus by its great size, and by the origin of RP more anterior to the origin of MA3, and to the origin of CuA1.

***Cratolocustopsis*, n. gen.**

D i a g n o s i s. Fore wing with MP+CuA two-branched. Hind femur relatively short and robust (W/L ratio ranges 0.20-0.35).

Type species. *Locustopsis cretacea* MARTINS-NETO 1990a, by present designation.

E t y m o l o g y. Alluding to the Cretaceous and genus *Locustopsis*. Gender: feminine.

***Cratolocustopsis cretacea* n. comb.**

Fig. 6A

*1990 *Locustopsis cretacea* MARTINS-NETO, Atas I Simp. Bacia do Araripe e Bacias Interiores do Nordeste: 279-280, Fig. 1. Est. IA.

1998 *Locustopsis cretacea* MARTINS-NETO, Rev. Española Paleont., 13(2): 134.

1999 *Locustopsis cretacea* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Fore wing 21 mm long. RP four-branched. RP origin after MA1+2 origin. CuA1+2 origin circa 1/3 of wing base.

H o l o t y p e: specimen GP/1T-1671, housed in IGUSP. Type locality: outcrop of the Tatjuba farm. Paratype: specimen GP/1T-1618, same locality, stratum and institution.

D e s c r i p t i o n. As in MARTINS-NETO 1990a.

R e m a r k s. *Cratolocustopsis cretacea* n. comb. differs from “*Locustopsis*” *magnifica* HANDLIRSCH. and “*Locustopsis*” *gracilis* ZEUNER, the closest species (probably attributable to the

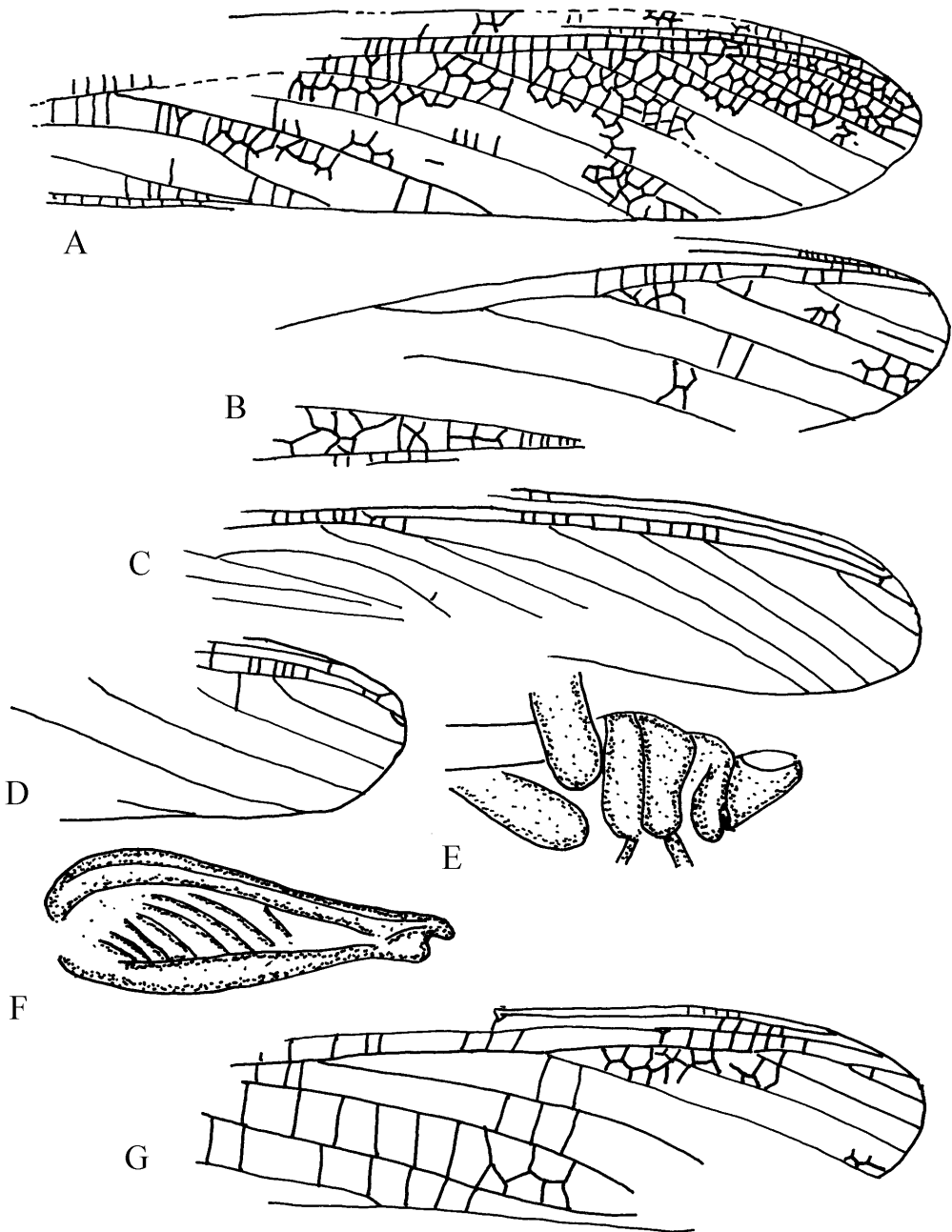


Fig. 4. A-B: *Zessinia vikingi* n. sp., holotype RGMN-T119: fore wing (A), hind wing (B); C, E: *Zessinia vikingi* n. sp., specimen RGMN-T121: fore wing (C), detail of general aspect of body (E); D: *Cratozeumerella titanella* n. sp., specimen RGMN-T120, apical details of hind wing; F: *Zessinia caririensis* MARTINS-NETO 1990, specimen RGMN-T124, detail of hind femur; G: *Zessinia vikingi* n. sp., specimen CD-I-001, details of hind wing.

genus *Cratolocustopsis*), by having RP four-branched in the fore wing (three-branched in “*L.*” *gracilis* and five-branched in “*L.*” *magnifica*), and by the RP origin (beyond the MA1+2 origin in *C. cretacea* n. sp., before in “*L.*” *gracilis* as well as in “*L.*” *magnifica*). Additionally *C. cretacea* n. comb. has a longer fore wing and the CuA1+2 origin is closer to the wing base.

***Cratolocustopsis araripensis* n. comb.**

Fig. 6F

*1990 *Locustopsis araripensis* MARTINS-NETO, Atas I Simp. Bacia do Araripe e Bacias Interiores do Nordeste: 280-283, Fig. 2A. Est. IB.

1998 *Locustopsis araripensis* MARTINS-NETO Rev. Española Paleont., 13(2): 134.

1999 *Locustopsis araripensis* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Similar to *Cratolocustopsis gracilis* n. comb. by having fore wing with RP three-branched, and a similar size (17 mm in *C. araripensis* n. sp), differing, however in CuA1+2 origin: close to MA3 origin in *C. gracilis*, closer to wing base in *C. araripensis* n. comb.

H o l o t y p e. Specimen GP/1T-1672; housed in IGUSP. Type locality: outcrop of the Tajuba farm.

D e s c r i p t i o n. As in MARTINS-NETO 1990a.

***Cratolocustopsis contumax* n. sp.**

Figs 6B-E, G; 8F

D i a g n o s i s. Characteristics of genus. Fore wing 18 mm in long. Hind wing with four branches of RP. CuP sigmoid. Hind tarsi with first article with distal spiniform projection and tubercle-like structure at base.

E t y m o l o g y. Latin form of “contumaz”.

H o l o t y p e. Specimen RGMN-T113, housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

D e s c r i p t i o n (holotype, Fig. 6B-E, G). Body relatively short and robust, 15.4 mm long (Fig. 6B). Large head, subvertical, subconical. Relatively large eyes placed at vertex; clypeus relatively wide. Pronotum seliform, short. Short abdomen. Subgenital plate pronounced. Hind member with femur long and narrow, 10.2 mm long, with spiniform projection on distal extremity (Fig. 6D, E). Posterior superior and inferior lobe of similar size. Tibia long and narrow, with spines only starting from distal extremity; a pair of short apical spurs. Tarsus with three articles: first longer and robust, exhibiting a pair of distal projections, proximal tubercle-like (Fig. 6E); second article is shortest; third long and narrow; small terminal claws. Hind wing (Fig. 6G) 18 mm long and 2.8 mm wide. Area between RA and RP relatively wide. RP with four branches, RP2 being very small. MA1+2 relatively short and divergent. MA2 larger than MA1. RP origin anterior to MA1+2 origin. CuP sigmoid. Anal fan wide. Cross-veins forming a mosaic of large cells.

D i s c u s s i o n. Similar to *C. araripensis* n. comb. in general morphologic aspects (body shape, tibiae with spines and length). *C. contumax* n. sp. differs by smaller eyes (large and prominent in *C. araripensis* n. comb.), subgenital plate larger, presence of spines only starting from distal half of hind tibia (in whole tibia of *C. araripensis* n. comb.) and the presence of a tubercle at base of posterior tarsus. From all previously described species of the genus, *C. contumax* n. sp. differs by sigmoid CuP.

Zessinia MARTINS-NETO, 1990

E m e n d e d d i a g n o s i s. MP+CuA1 strongly curved, sigmoid. Posterior femur, when preserved, is relatively short and robust, with W/L about 0.35. Fore and hind wing with four to six branches of RP.

Type species. *Zessinia pulcherrima* MARTINS-NETO 1990, by original designation (MARTINS-NETO 1990a).

Zessinia pulcherrima MARTINS-NETO 1990

Fig. 5B

*1990 *Zessinia pulcherrima* MARTINS-NETO, Atas I Simp. Bacia do Araripe e Bacias Interiores do Nordeste: 282, Fig. 3A. Est.. IC;

1998 *Zessinia pulcherrima* MARTINS-NETO, Rev. Española Paleont., 13(2): 134.

1999 *Zessinia pulcherrima* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Characteristics of genus. Fore wing 26 mm in length. RP origin at the same level of MA fork. MA1 free. MA3 origin in MA2. Annals with complex venation pattern with successive coalitions.

H o l o t y p e. Specimen GP/1T-1666; housed in IGUSP. Type locality. Outcrop of the Tajuba farm.

D e s c r i p t i o n. As in MARTINS-NETO 1990a.

Zessinia caririensis MARTINS-NETO 1990

Fig. 2B, 3A; 4F, 5A, E; 7A; 8G; 9B, E

*1990 *Zessinia caririensis* MARTINS-NETO, Atas I Simp. Bacia do Araripe e Bacias Interiores do Nordeste: 283-284, Fig. 3B. Est.. ID.

1998 *Zessinia caririensis* MARTINS-NETO, Rev. Española Paleont., 13(2): 134.

1999 *Zessinia caririensis* MARTINS-NETO, 1999, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Fore wing 27 mm long. RP origin beyond mid length of wing, at level of MA

H o l o t y p e. Specimen GP/1T-1667 (Fig. 5A), housed in IGUSP. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. RGMN-T115 (Figs 5E; 8G), RGMN-T122 (Figs 3A; 9E), RGMN-124 (Figs 2B; 4F; 7A) and RGMN-130 (9B). Locality and stratum as in the holotype; housed in MARTINS-NETO Collection; SBPr.

D e s c r i p t i o n (RGMN-T115, Fig. 5E). Fore wing long and narrow, 27 mm long. Subcostal area wide at base, filled by long cross veins. C long. Area between RA and ScP relatively narrow and filled by pectinated cross veins. RP origin beyond mid length of wing, at level of MA fork, which is long, quite parallel to the RA, until close to its bifurcation. MA3 free. MA2 origin in MA1. MP+CuA1 notably bent, distally sigmoid, converging with MA3. Additional material: RGMN-T122 (Figs 3A; 9E). Fore wing (Fig. 3A) 26 mm long and 4.5 mm wide. Costal area relatively narrow. ScA long, reaching costal margin in mid length level of wing. ScP long, parallel to costal margin, reaching apical margin close to apex. Area between ScA and ScP wider than between ScP and RA. RP origin posterior to ScA end, in mid length level of wing. RP with five branches. MA3 free, MA2 origin in MA1. MA1+2 origin between RP origin and RP5 origin. MA3 origin posterior to RP origin. MP+CuA1 notably bent and almost distally fused to CuA2. Hind wing with RP four-branched. RGMN-T124 (Figs 2B, 4F): body relatively short, 22 mm long. Small head, same width as pronotum. Pronotum seliform, short. Short abdomen. Hind member with long and robust femur, 11 mm long, 3 mm wide (Fig. 2F). Posterior lobe smaller than anterior one. Hind tibia long

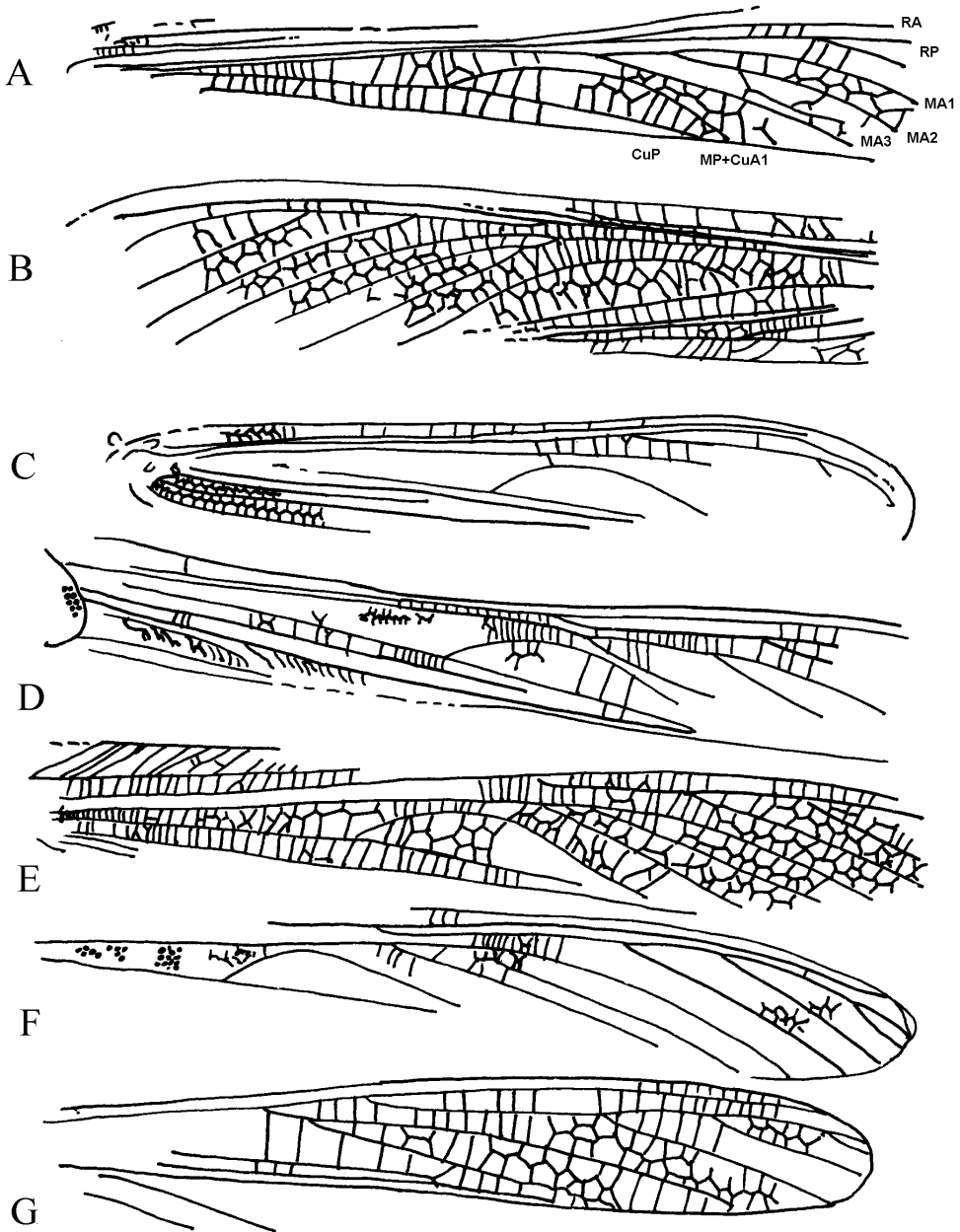


Fig. 5. A. *Zessinia caririensis* MARTINS-NETO 1990, fore wing of holotype GP/IT-1667; B. *Zessinia pulcherrima* MARTINS-NETO 1990, fore wing of holotype GP/IT-1666; C. *Zessinia reticulata* MARTINS-NETO 1990, fore wing of holotype GP/IT-1668; D. *Zessinia petruleviciusi* n. sp., holotype RGMN-T116, schematic drawing of fore wing; E. *Zessinia caririensis* MARTINS-NETO 1990, fore wing of specimen RGMN-T115; F-G: *Zessinia petruleviciusi* n. sp., specimen RGMN-T117: fore wing (F) and hind wing (G).

and narrow, without spines, at least in proximal third preserved. Hind wing 25 mm long, with similar venation to the holotype. RGMN-T130 (8B): body relatively short and robust, 15 mm long. Pronotum seliform, short, notably elongated, ornamented with homogeneous granulation on entire surface. Abdomen short. Hind member with elongated and robust femur. Inferior lobe smaller than superior one. Posterior tibia long and narrow, with robust spines starting from distal extremity; at least a short apical spur preserved. Tarsus with three tarsomeres, first a little longer than third, exhibiting tubercles in posterior margin; second article shortest, almost vestigial; small terminal claws. Fore wing macropterous, partially covering thorax.

Zessinia reticulata MARTINS-NETO 1990

Fig. 5C

*1990 *Zessinia reticulata* MARTINS-NETO, Atas I Simp. Bacia do Araripe e Bacias Interiores do Nordeste: 284-285, Fig. 3C. Est. IE.

1998 *Zessinia reticulata* MARTINS-NETO, Rev. Española Paleont., 13(2): 134.

1999 *Zessinia reticulata* MARTINS-NETO, Rev. Soc. Entomol. Argent., 58(1-2): 74.

E m e n d e d d i a g n o s i s. Fore wing 21 mm long. RP origin anterior to level of MA fork. Anal area ornamented microreticulate.

H o l o t y p e. Specimen GP/1T-1668; housed in IGUSP. Type locality: outcrop of the Tajuba farm.

D e s c r i p t i o n. As in MARTINS-NETO (1990a).

Zessinia petruleviciusi n. sp.

Figs 3G, 5D, F, G; 7B-C; 8H

D i a g n o s i s. Fore wing 26 mm long. RP origin anterior to level of MA fork. MA3 free. MA2 origin in MA1. Origin of MA1+2 close to RP4 origin.

E t y m o l o g y. In honour to the paleoentomologist Dr. Julian Fernando PETRULEVICIUS, Museo de La Plata, Argentina.

H o l o t y p e. Specimen RGMN-T116, housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. RGMN-T117 (Figs 5F, G; 7B-C). Same locality. stratum and destination as in holotype.

D e s c r i p t i o n (Holotype, Figs 3G, 5D). Body relatively short and lanky, 22 mm long (Fig. 3G). Head relatively small, subvertical and subconical. Pronotum seliform, short, notably reduced laterally, ornamented with homogeneous granulation on entire surface. Abdomen short, with segments partially preserved. Fore wing (Fig. 5D) long and narrow 26 mm long and 4 mm wide. Long C. Area between RA and ScP relatively narrow and filled with pectinated cross veins. RP origin beyond mid length of wing, anterior to MA fork, which is long, parallel to RA until close to its bifurcation. MA3 free. MA2 origin in MA1. MA1+2 relatively long. MP+CuA1 notably bent, converging for MA3. AA long, straight, parallel to CuP. Cross-veins with microreticulate pattern at base of wing.

Additional material (Fig. 5F, G): fore wing (Fig. 5F) long and narrow, 26 mm long and 4 mm wide. Long RA, more parallel to costal margin, reaching apical area close to apex. Origin of RP beyond mid length of wing, a little anterior to MA fork which is long, quite parallel to RA, until close to its bifurcation. RP with four branches, RP1+2 relatively short. RP4 origin far from M1+2 origin. MA3 free. MA2 origin in MA1. MP+CuA1 notably bent. CuP very long, convergent for MA3. Cross veins exhibiting a microreticulate pattern in base of wing. Hind wing long (Fig. 5G). RP with four branches, RP1+2 being smallest. MA1+2 very long, MA1 little longer than M2. MA origin anterior to RP origin, anterior to mid length of wing.

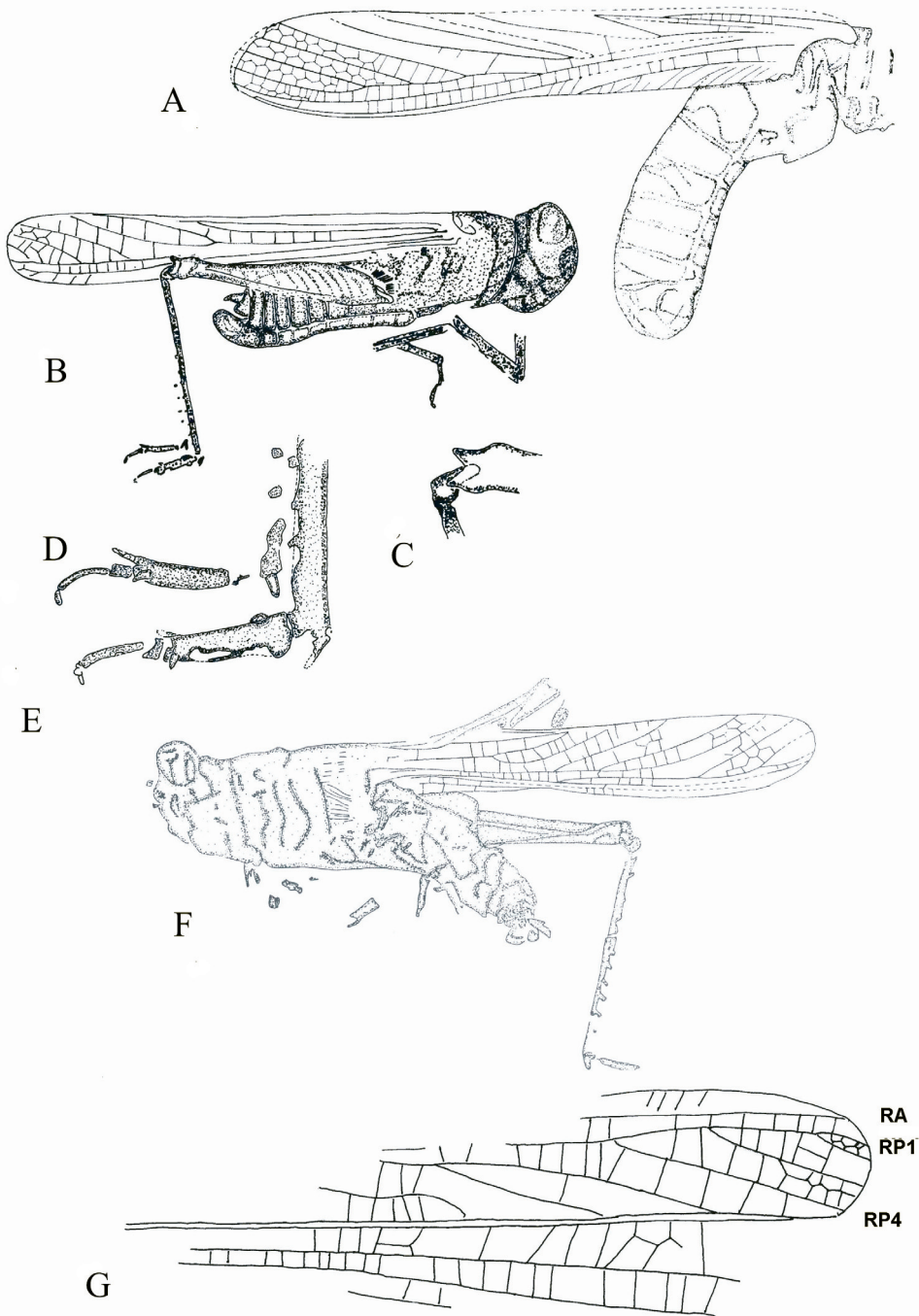


Fig. 6. A. *Cratocustopsis cretacea* n. comb., holotype GP/1T-1671; B-E, G: *Cratocustopsis contumax* n. sp., holotype RGMN-T113: general aspect (fold of hind wing omitted) (B); details of tibio-femoral joint (C); details of posterior tarsus (D, E); details of hind wing (with interpretation of wing fold) (G); F. *Cratocustopsis araripensis* n. comb., schematic drawing of holotype GP/1T-1672.

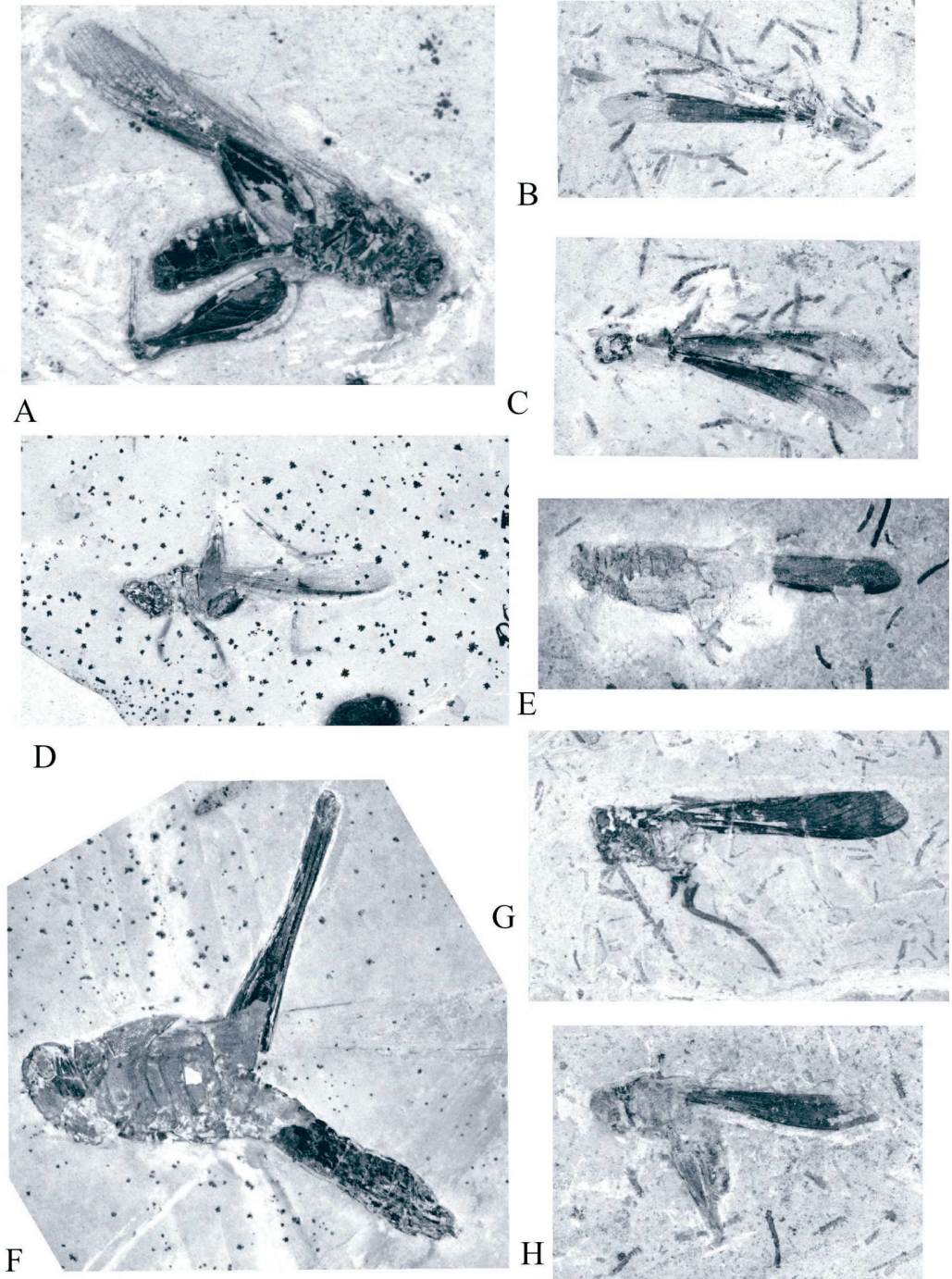


Fig. 7. A. *Zessinia caririensis* MARTINS-NETO 1990, specimen RGMN-T124; B-C: *Zessinia petruleviciusi* n. sp., specimen RGMN-T117, part (B), and counterpart (C); D. *Zessinia vikingi* n. sp., specimen RGMN-T121; E. *Cratozeumerella titanella* n. sp., specimen RGMN-T120; F. *Cratozeumerella titanella* n. sp., holotype RGMN-T127; G. *Zessinia vikingi* n. sp., holotype RGMN-T119; H. *Zessinia vikingi* n. sp., specimen RGMN-T123.

D i s c u s s i o n. Similar to *Zessinia caririensis* MARTINS-NETO in having MA3 free. *Z. petruleviciusi* n. sp. differs from all species included in the genus by having RP origin anterior to MA fork (at the same level in *Z. pulcherrima* MARTINS-NETO, *Z. caririensis* MARTINS-NETO and *Z. reticulata* MARTINS-NETO).

***Zessinia vikingi* n. sp.**

Figs 3B, 4A, B, C, E, G; 7D, G, H; 9A, C

D i a g n o s i s. Characteristics of genus. Fore wing from 29 to 32 mm long and 6 mm wide. RP origin posterior to MA fork. MA3 free. MA2 origin in MA1. MA3 far from MA1+2. Hind wing with RP five-branched.

E t y m o l o g y. Alluding to the legendary Vikings, Scandinavian warriors from the past.

H o l o t y p e. Specimen RGMN-T119 (Figs 4A, B; 7G), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

A d d i t i o n a l m a t e r i a l. RGMN-T123 (Figs 3B; 7H), 121 (Figs 4C; 4E; 7D), 131 (9C), all from the same locality and housed in the same institution as holotype, and CD-001-I (Figs 4G; 9A), from uncertain locality, Santana Formation; housed in Desirée collection, MN-RJ.

D e s c r i p t i o n (RGMN-T119, Figs 4C; 7G). Fore wing (Fig. 4C) 29 mm long and 6 mm wide. ScP long, reaching apical area. RA long, parallel to ScP, reaching apical area close to apex. RP origin of at mid length level of wing. RP with five branches, relatively long and parallel to each other. MA3 free, MA2 origin in MA1. MA1+2 origin posterior to RP origin, and M3 origin anterior to RP origin. MP+CuA1 notably bent, sigmoid. CuP long, oblique to anal margin and distally convergent to CuA2. Intense cross veins forming mosaics of cells in entire area of wing. Hind wing of similar morphology to fore wing, with RP five-branched.

Additional material RGMN-T123 (Fig. 7H). Hind wing (Fig. 3B) 26 mm long and 4.5 mm wide. RP with four branches, growing in length of RP1 up to RP4. RP4 origin far from RP origin. MA1 and MA2 very long. MA1+2 origin little anterior to end of ScA1. Wide anal fan with inter-anal areas very wide. Profuse transverse cross veins, forming great polygonal cells in all areas of wing and of anal fan. RGMN-131 (Fig. 9C). Body relatively short and robust. Pronotum seliform, short, notably elongated laterally, ornamented with homogeneous granulation on entire surface. Abdomen short. Hind member with femur elongated and robust. Inferior lobe smaller than superior. Posterior tibia long, narrow, with robust spines, starting from distal extremity; at least a short apical spur preserved. Tarsus with three articles, first little longer than third, exhibiting tubercles in its posterior margin; second article shortest, almost vestigial; small terminal claws. CD-001 (Fig. 9A): fore wing (Fig. 4G) 37 mm long and 6 mm wide. ScA1 very prolonged, reaching Costal margin at limit of apical area. Area between Costal margin and ScP very narrow. RA long, reaching apical area close to apex. Area between ScP and RA very narrow. RP long, originating five perpendicular branches, all reaching apical margin and parallel to each other. RP5 origin very posterior of to MA1 origin. RP origin posterior to MA1 origin. MA2 and MA3 convergent distally.

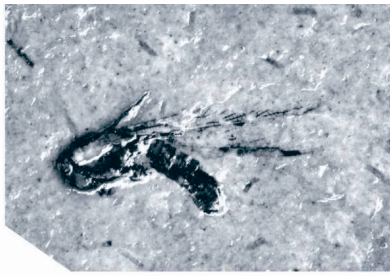
R e m a r k s. Similar to "*Locustopsis*" *africanus* ANSORGE 1991 from the Lower Cretaceous of Egypt in general aspect of the venation of the fore wing; differs by having a extra branch of RP.

***Zessinia* sp.**

Figs 2C, H-K; 9D

M a t e r i a l. Specimen RGMN-T114, housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

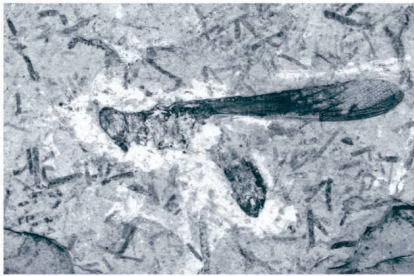
D e s c r i p t i o n (Fig. 9D). Nymph. Head not preserved. Body relatively short and robust, 15 mm long. Pronotum seliform (Fig. 2J), short, notably elongated laterally, ornamented with homogeneous granulation on entire surface. Abdomen short. Hind member with elongated and ro-



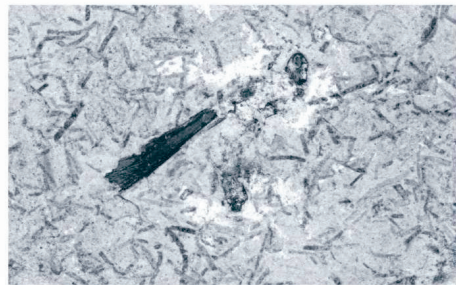
A



B



C



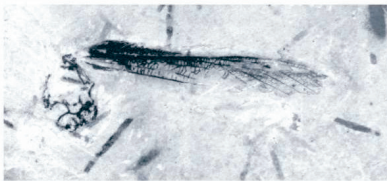
D



E



F



G



H

Fig. 8. A. *Cratozeunerella godoii* n. sp., holotype RGMN-T125; B. *Cratozeunerella soaresi* n. sp., holotype RGMN-T118; C-D: *Cratozeunerella soaresi* n. sp., specimen CD-I-124, part (C) and counterpart (D); E. *Cratozeunerella godoii* n. sp., specimen AMNH-43868; F. *Cratolocustopsis contumax* n. sp., holotype RGMN-T113; G. *Zessinia caririensis* MARTINS-NETO, 1990, specimen RGMN-T115; H. *Zessinia petruleviciusi* n. sp., holotype RGMN-T116.

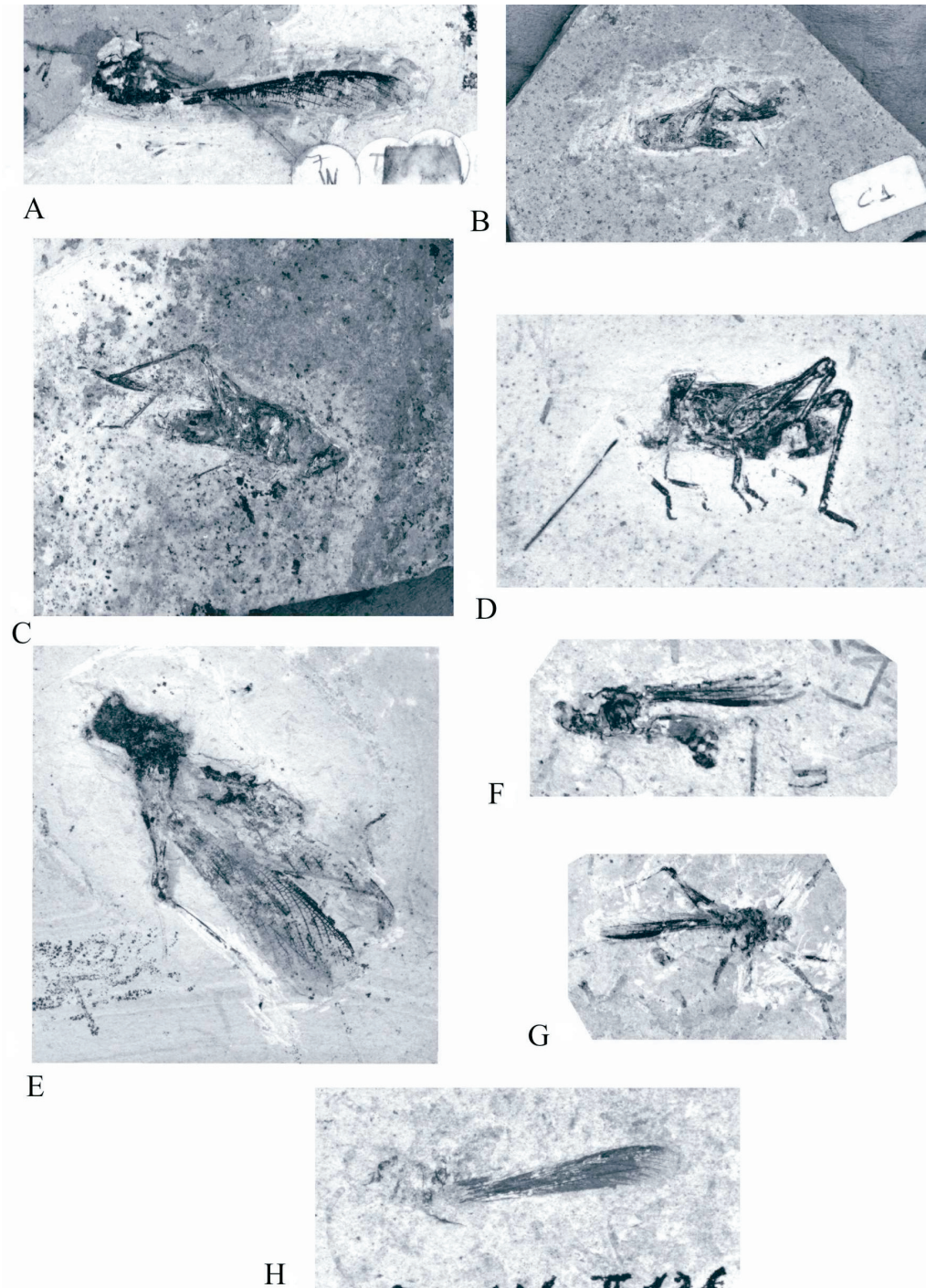


Fig. 9. A. *Zessinia vikingi* n. sp., specimen CD-I-001; B. *Zessinia caririensis* n. sp., specimen RGMN-T130; C. *Zessinia vikingi* n. sp., specimen RGMN-T131; D. *Zessinia* sp., specimen RGMN-T114; E. *Zessinia caririensis* n. sp., specimen RGMN-T122; F. *Locustrix gallegoi* n. sp., holotype RGMN-T128; G. *Locustrix audax* n. sp., holotype RGMN-T129; H. *Cratozeumerella nervosa* n. sp., holotype RGMN-T126.

bust femur, measuring 13 mm long and 3mm wide (Fig. 2K). Inferior lobe smaller than superior. Posterior tibia long and narrow, with robust spines starting from distal extremity; at least a short apical spine preserved. Tarsus with three articles, first little longer than third, exhibiting tubercles in its posterior margin (Fig. 2I); second article shortest, almost vestigial; small terminal claws. Fore wing micropterous, partially covering thorax (Fig. 2H). RP origin posterior to M1+2 origin. MA3 free. CuP long and straight, parallel to anal margin.

***Locustrix* n. gen.**

D i a g n o s i s. ScP short. MA two-branched; MP+CuA two-branched. Fore and hind wing with RP three-branched.

Type species: *Locustrix gallegoi* n. sp., by present designation.

E t y m o l o g y. Locust conjunction, common designation of grasshoppers, and *trix*, alluding to the three branches of the radial sector. Gender: neutrum.

***Locustrix gallegoi* n. sp.**

Figs 2E, L; 9F

D i a g n o s i s. Fore wing 15 mm long. MA1+2 origin anterior to RP origin.

E t y m o l o g y. In honor to Dr. Oscar Florencio GALLEGO (Universidad del Nordeste, Corrientes, Argentina), in acknowledgement of his contribution to Argentinian paleontology.

H o l o t y p e. Specimen RGMN-T128 (Fig. 2E, L), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

D e s c r i p t i o n (holotype, Fig. 2E, L). Body (Fig. 2L) long and narrow, 13 mm long. Head relatively large. Robust thorax, with pronotum relatively large, seliform, entirely covering thorax. Abdomen long and narrow, narrower basally than distally. Fore wing (Fig. 2E) 15 mm long. ScA relatively long and ScP relatively short, reaching costal margin little beyond mid length of wing, anterior to RP origin. RA long, quite parallel to costal margin, reaching apical margin close to apex. RP short, three relatively long branches. MA with two branches, both similar in length. MA1+2 origin anterior to RP origin. MP+CuA with two branches of similar length, not curved at base. CuP long, straight, convergent to CuA2.

***Locustrix audax* n. sp.**

Figs 2D; 9G

D i a g n o s i s. Fore wing 16 mm long. MA1+2 posterior to RP origin.

E t y m o l o g y. Latin for audacious.

H o l o t y p e. Specimen RGMN-T129 (Figs 2D; 9G), housed in MARTINS-NETO Collection; SBPr. Type locality: Mina Pedra Branca.

D e s c r i p t i o n (holotype, Fig. 2D). Fore wing 16 mm long. ScA relatively long, ScP relatively short, reaching costal margin after mid length of wing and posterior to RP origin. RA long, quite parallel to Costal margin, reaching apical margin close to apex. RP short, with three branches relatively long. MA with two branches, similar in length. MA1+2 origin posterior to RP origin. CuA with two branches of similar length.

R e m a r k s. Differs from *Locustrix gallegoi* n. sp. by longer ScP, reaching Costal margin posterior to RP origin (anterior in *L. gallegoi* n. sp.) and MA1+2 origin posterior to RP origin (anterior in *L. gallegoi* n. sp.)

Family **Bouretidae** MARTINS-NETO 2001**Bouretia** MARTINS-NETO, 2001

Type species. *Bouretia elegans* MARTINS-NETO 2001.

Bouretia elegans MARTINS-NETO 2001

*2001 *Bouretia elegans* MARTINS-NETO, Acta Geol. Leopoldensia, 24(52/53): 117-118, Pl. II; Fig. 2C.

D i a g n o s i s a n d d e s c r i p t i o n. As in MARTINS-NETO 2001.

H o l o t y p e. Specimen CD-90-I, housed in Desirée collection, housed in MN-RJ. Type locality: location uncertain, probably close to Santana do Cariri.

Family **Araripelocustidae** MARTINS-NETO 1995Subfamily **Araripelocustinae** MARTINS-NETO 1995**Araripelocusta** MARTINS-NETO 1995

Type species. *Araripelocusta longinota* MARTINS-NETO 1995, by original designation.

Araripelocusta longinota MARTINS-NETO 1995

*1995 *Araripelocusta longinota* MARTINS-NETO 1995, Revta. Bras. Entomol. 39(2): 312-315, Figs. 1-4, 7-12.

1999 *Araripelocusta longinota* MARTINS-NETO 1999, Revta. Soc. Entomol. Argent., 58(1-2): 74.

D i a g n o s i s a n d d e s c r i p t i o n. As in MARTINS-NETO 1995.

H o l o t y p e. Specimen CV-1572, housed in Vulcano private collection, São Paulo. Type locality: outcrop of the Tatajuba farm. Paratype. CV-906, same locality and collection.

Araripelocusta brevis MARTINS-NETO 1995

*1995 *Araripelocusta brevis* MARTINS-NETO, Revta. Bras. Entomol. 39(2): 315, Figs. 5, 6, 13.

1999 *Araripelocusta brevis* MARTINS-NETO, Revta. Soc. Entomol. Argent., 58(1-2): 74.

D i a g n o s i s a n d d e s c r i p t i o n. As in MARTINS-NETO 1995.

H o l o t y p e. Specimen CV-1777, housed in Vulcano private collection, São Paulo. Type locality: outcrop of the Tatajuba farm.

Family **Tridactylidae** BRUNNER 1882**Cratodactylus** MARTINS-NETO, 1990

Type species. *Cratodactylus ferreirai* MARTINS-NETO 1990, by original designation (MARTINS-NETO 1990b).

Cratodactylus ferreirai MARTINS-NETO 1990

*1990 *Cratodactylus ferreirai* MARTINS-NETO, An. Acad. bras. Ci., 62(1): 53-55; Est. ID, Fig.1.

1999 *Cratodactylus ferreirai* MARTINS-NETO, Revta. Soc. Entomol. Argent., 58(1-2): 74.

D i a g n o s i s a n d d e s c r i p t i o n. As in MARTINS-NETO 1990b.

H o l o t y p e. Specimen GP/1T-1649, housed in IGUSP. Type locality: outcrop of the Tatajuba farm. Paratypes: GP/1T-1650, GP/1T-1651, housed in the same Institution as Holotype; AMA-I-034, housed in the UFCE collection; CV-2436, CV-2352, CV-2353, CV-2359 and CV-2438, housed in the Vulcano collection, São Paulo.

Cratodactylus kellneri MARTINS-NETO 1990

*1990 *Cratodactylus kellneri* MARTINS-NETO, An. Acad. bras. Ci., 62(1): 53-56; Est. IB, Fig. 2.

1999 *Cratodactylus kellneri* MARTINS-NETO, Revta. Soc. Entomol. Argent., 58(1-2): 74.

D i a g n o s i s a n d d e s c r i p t i o n. As in MARTINS-NETO 1990b.

H o l o t y p e. Specimen GP/1T-1652, housed in IGUSP. Type locality: outcrop of the Tajuba farm.

Paratypes: CV-1010, CV-2037, CV-2039 and CV-2520, housed in the Vulcano Collection, São Paulo; same locality.

IV. FINAL CONSIDERATIONS

The present study raises the number of the represented Caelifera in the Santana Formation, as well as in the whole Southern hemisphere, to twenty one species of seven genera, distributed in four families of grasshoppers, one of the most complete and abundant assemblages known in the fossil record.

Two new genera, nine new species, and two new combinations of grasshoppers of the family Locustopsidae are proposed and described for the Santana Formation, enlarging the knowledge considerably on the group. Of the other families of Caelifera represented in the Santana Formation, Tridactylidae also possesses representatives in Asia (SHAROV 1968; GOROCHOV 1992) and in Australia (JELL & DUNCAN 1986), Araripe locustidae with the genus *Araripe locusta* MARTINS-NETO 1995) and Bouretidae with the genus *Bouretia* MARTINS-NETO 2001 according to present knowledge is seems to be endemic to the Lower Cretaceous of Brazil. Eumastacidae described from Asia, Central America, United States and Canada indicate a distribution until now restricted to Laurasia, have seen the virtual absence of the group in South American Mesozoic.

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