# A revision of the orders Blattaria, Mantodea and Orthoptera (Insecta) from the Lower Cretaceous Crato Formation of Northeast Brazil

### Dissertation

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### Abstract

This study presents the results of a systematic research on 108 specimens of fossil insects including the order "Blattaria", Mantodea and Orthoptera originating from laminated limestone from the Lower Cretaceous Crato Formation of Northeast Brazil. The exceptionally well preserved and articulated material allows for the morphology not only of the forewings, but also (to a large extent) of the hind wings to be analyzed. The originally described groups are emended with new data and supplemented with drawings and photographs. Altogether, 16 genera including 37 species are described in this study. Of these, 13 species are as of yet unnamed. Furthermore, the descriptions of the following taxa have been revised: *Ponopterix* maxima Bechly, 2007 (family Umenocoleidae Chen et Tian, 1973), Araripeblatta Mendes, 2000 (family Araripeblattidae Martins-Neto et al., 2010), Mesoblattina limai Pinto & Purper, 1986 (family Blattellidae Karny, 1908), Bouretia Martins-Neto, 2001 (family Bouretidae Martins-Neto, 2001) and Family Araripelocustidae Martins-Neto, 1995. This study furthermore includes the first description of the following taxa: The first Chaeteessa Burmeister, 1838 (Family Chaeteessidae Handlirsch, 1920; Mantodea) in the Crato Formation, the first Tettigoniidae Krauss, 1902 in the Crato Formation (as well as being the first description in the Cretaceous as a whole) and the first descriptions of Haglidae Handlirsch, 1906 (with two new species) and Prophalangopseidae Kirby, 1906 (with one new species) in the Crato Formation (both of these families belong to the Superfamily Hagloidea Handlirsch, 1906). Additionally, new data concerning the morphology, taphonomy and taxonomic diversity of the studied taxa are given and discussed.

Keywords: Fossil insects, Blattaria, Mantodea, Orthoptera, Ensifera, Caelifera, Mesozoic, Lower Cretaceous, Crato Formation, Brazil.

### Zusammenfassung

In der vorliegenden Arbeit werden die Ergebnisse der systematischen Untersuchung von 108 Exemplaren fossiler Insekten aus den Ordnungen "Blattaria", Mantodea und Orthoptera der unterkretazischen Crato-Formation im Nordosten Brasiliens vorgestellt. Das in den Plattenkalken sehr gut und teilweise komplett erhaltene Material ermöglicht die morphologische Analyse außer der regulären Vorderflügel auch die zahlreicher Hinterflügel. Die Originalbeschreibungen der bekannten Gruppen werden durch neue Zeichnungen, Fotos und zusätzliche Angaben ergänzt und erweitert. Ingesamt werden 37 Arten aus 16 Gattungen beschrieben, darunter 13 bisher noch unbenannte Arten. Weiterhin werden die folgenden Taxa revidiert: Ponopterix maxima Bechly 2007 (Familie Umenocoleidae Chen et Tian, 1973), Araripeblatta Mendes, 2000 (Familie Araripeblattidae Martins-Neto et al., 2010), Mesoblattina limai Pinto & Purper 1986 (Familie Blattellidae Karny, 1908), Bouretia Martins-Neto, Martins-Neto, 2001 (Familie Bouretidae 2001) und die Araripelocustidae Martins-Neto, 1995. Außerdem werden die folgenden Taxa erstmals für die Crato-Formation dokumentiert: Chaeteessa Burmeister, 1838 (Familie Chaeteessidae Handlirsch, 1920; Mantodea), Tettigoniidae Krauss, 1902 (Erstnachweis für die Kreidezeit) sowie zwei Arten der Familie Haglidae Handlirsch, 1906 und eine der Familie Prophalangopseidae Kirby, 1906 (beide gehören zur Überfamilie Hagloidea Handlirsch, 1906). Zusätzlich werden neue Ergebnisse zur morphometrischen und taphonomischen Analyse und taxonomischen Vielfalt dargestellt und diskutiert.

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### 1. Introduction

### 1.1. Cretaceous insects

Insects are very diverse in their taxonomy, morphology and ecology. Insects are also very important in most terrestrial ecosystems and also strongly influence human activity in issues pertaining to health agriculture and culture. The origin of insects about 400 million years ago represents an important event in the history of the Earth. The origin of insect wings in the middle Carboniferous and complex metamorphisms (Holometabola) in the Late Carboniferous significantly influenced the biota and diversity on land. According to an estimation from Grimaldi & Engel (2005), about a total of 5 million species of insect are alive today. Of them, only about 1 million species are known to science and named. Considering the history of Earth as a whole, approximately 100 million insect species have existed in the past and present. A variety of insect fossils have been documented. More than twenty thousand fossil species have been discovered and described (Willmann, 2003). The oldest fossil insect is represented by a springtail (Collembola) from the Lower Devonian. Knowledge concerning fossil insects is important for the interpretation of ecological dispersal, palaeobiogeography through time and furthermore provides the basis for reconstructing phylogenetic relationships.

In the Cretaceous, global floral patterns underwent major changes related to the origin and radiation of the angiosperms. Because insects are intimately associated with plants, this event significantly affected the evolution of various insect taxa. Many researchers assert that this event is the main reason for a significant fauna change of insects in the middle Cretaceous about 100 million years ago. This may also be the reason for the fact that most of the recent families of insects first appeared in Cretaceous. On the contrary, the global mass extinction event at the end of Cretaceous (about 65 million years ago) only had a minor or regional effect on insects (Grimaldi & Engel, 2005).

Until the late 1960s, records of Cretaceous insect fauna were rare. The lack of fossil insects from the Cretaceous is even "One of the most unfortunate gaps in our knowledge of insect phylogeny (Willi Hennig, 1969)". Since then, numerous Cretaceous insects have been discovered around the worldand in various Cretaceous amber sites from Lebanon, Siberia, Myanmar, Spain, France, Canada and the USA (Bechly, 2007b). One of the most prominent Cretaceous fossil sites is the Crato Formation of Brazil. No other location has insect fossils with comparable numbers, diversity and quality of preservative. Within the two species of the genus *Cratoelcana* Martins-Neo, 1991 alone, thousands of specimens have been collected. Similarly, abundant specimens of cockroaches (Blattaria) have been described due to the excellent preservation (Martins-Neto, 2006; Martins-Neto & Gallego, 2006).

The following relative abundances of arthropods from the Crato Formation have been described (Bechly 1998a, Menon & Martill 2007): Ephemeroptera 7%, Odonata 2%, Blattaria 26%, Orthoptera 27%, Hemiptera 23%, Neuroptera 4%, Coleoptera 3%, Hymenoptera 2% and Diptera 2%, all other > 1% (n = 3651). Blattaria plus Orthoptera thus dominate in the collections thus far. Since materials has only available for the 30 years, the study of fossil insects from the Crato Formation is still at its infancy. The objective of this study is to focus on the morphological and taxonomic research of insects from the Blattaria (roaches and

cockroaches) and Orthoptera (grasshoppers, crickets and locusts) and to make inference with respect to taphonomy, histology, diversity and systematics

### 1.2. Crato Formation

### 1.2.1. Introduction

The Crato Formation takes its name from the University town of Crato, Ceará, situated in the north central part of the Chapada do Araripe, a large plateau in north-eastern Brazil (fig. 1). Its outcrop forms a narrow strip along the flanks of the plateau and is also present as a few isolated outliers to the south of the plateau. The Crato Formation is mined commercially for cement manufacturing and paving stones and is thus of considerable economic importance to the region, providing both raw materials and employment (Martill & Bechly, 2007).

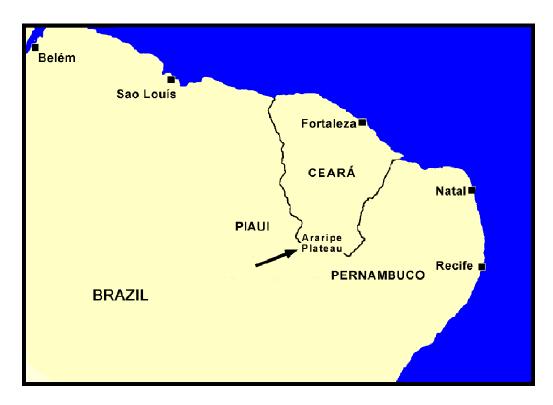


Fig. 1. Location of the Araripe Plateau. (from Bechly, unpublished)

The Crato Formation limestones are famous for its wealth of fossils, including the flora with both gymnosperm and angiosperm, invertebrate fauna with Chilopoda, Arachnida, Crustacea and Insect and the vertebrate fauna including fish, anurans, turtles, lizards, crocodiles, pterosaurs and birds. Among these fossils, insects dominate both in abundance and taxonomic diversity, notable the terrestrial adult orthopterans, hemipterans, ephemeropterans and odonatans (Menon & Martill, 2007). The Crato Formation has the most diverse fossil assemblage of any non-marine Cretaceous locality in Gondwana, and perhaps Laurasia as well (Martill et al., 2007).

The first fossil insects from the Crato Formation were briefly noted by Costa Lima (1950), who figured several larval ephemeroptera from the limestone near Santa Fé in the

municipality of Crato. Fossil insects from the now famous fossiliferous outcrops around Nova Olinda were not reported, however, until late 1980s. Since the beginning of the 1980s, the extraction of limestone for building and paving stone from the outcrops of the Crato Formation have extensively exposed the lowermost limestones and has brought to light huge numbers of fossils, especially fish, insects and plants (Martill & Heimhofer, 2007).

### 1.2.2. Geology & stratigraphy

The insect fossil described in this dissertation originate from the Nova Olinda Member of the Crato Formation. The Nova Olinda Member is the lowermost member of the Crato Formation which itself belongs to the Araripe Group (fig. 2). The age of the Araripe Group is Aptian (see fig. 3). The Crato Formation is situated in the north central part of the Chapada do Araripe, north-eastern Brazil, (ca. 7 to 8 degrees south and 39 to 41 degrees west). This location is a consequence of a long process of continental drift. During the Aptian, the Crato Formation lay much further south than its present location (fig. 4) and was situated between 10 to 15 degrees south of the palaeo-equator within the tropics (Skelton, 2003). The exact timing of the separation of South America and Africa is still controversial (Martill, 2007).

GROUP	FORMATION	MEMBER	LITHOLOGY
	IPUBI		Mainly gypsum
		CASA DE PEDRA	Heterolithic - including black shales and muddy ssts
		JAMACARU	Laminated lst
ARARIPE	CRATO	CALDAS  (Barbalha Mbr of Martill & Wilby 1993)	Heterolithic - including silty mudstones, silts and fine to medium ssts. Some thin laminated lsts
		NOVA OLINDA  Transition beds -	Laminated lst
	BATATEIRAS		

Fig. 2. Stratigraphic scheme employed for the Crato Formation; 1st, limestone; Mbr, member; sst, sandstone (after Martill & Heimhofer, 2007).

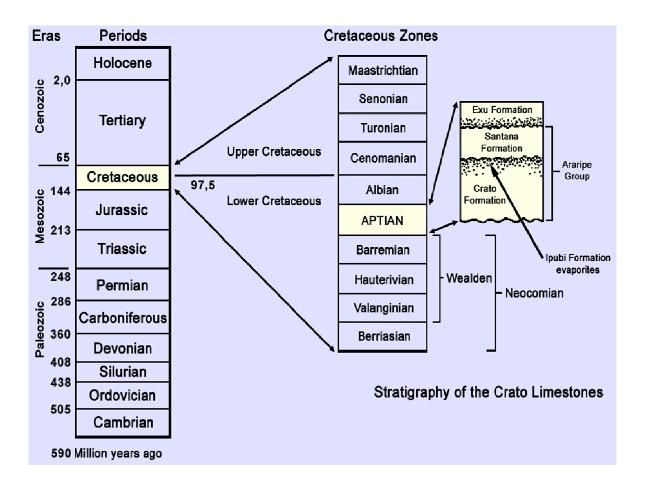
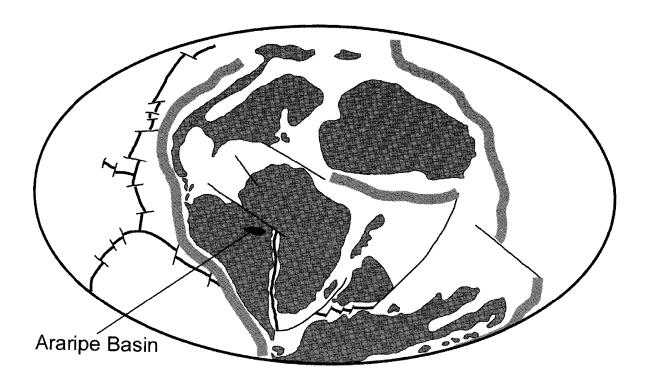


Fig. 3. Stratigraphy of the Crato Limestones (from Bechly, unpublished).



**Fig. 4.** Palaeogeographic reconstruction of the Early Cretaceous world with the location of the Araripe Basin indicated (after Martill, 2007).

### 1.2.3. Palaeoenvironment

The knowledge of the palaeoenvironment of the Nova Olinda Member is still insufficiently known and its depositional environment is problematic (Martill & Bechly 2007). Ponte and Appi (1990) suggested that a freshwater lake was present which was limited to the Araripe Basin. Estimations of water depth range between shallow (Maisey, 1990) to relatively deep (Martill and Loveridge, 2006). Similarly, the salinity of the water is also controversial ranging from fresh water (Maisey, 1990, 1996), to brackish (Bechly, 1998b; Neumann et al., 2003) to hypersaline (Martill and Wilby, 1993) conditions. Thus different terms have been used to describe the body of water where the organisms were deposited ranging from a lake to a salt water lagoon (e.g Martill, 1993) (fig.5).

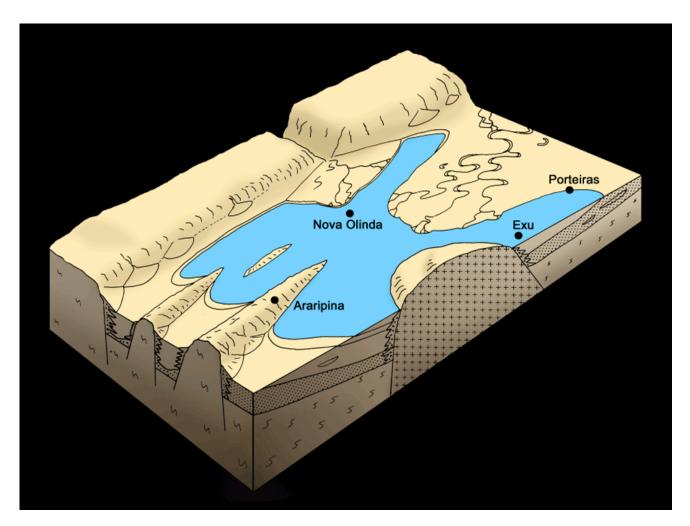


Fig. 5. Reconstruction of the Crato lake/lagoon (after Martill, 1993 redrawn by Bechly).

### 2. Material and methods

### 2.1. Material from the Crato Formation

The drawings in the present dissertation were made from dry specimens directly from the fossil surface using a camera lucida attached to a Wild M5 and a Leica MZ125 stereo microscope. The results were digitized by scanning with a Canon CanoScan 4400F flatbed scanner. Fossils were photographed with a Leica DFC490 digital macro camera on a Leica Z16-Apo microscope with Synchroscopy Auto-Montage<sup>TM</sup> software. All figures have been subsequently edited with the Adobe Photoshop<sup>TM</sup> CS3 imaging software.

Some fossils have been further prepared during this study. If the plate and counter plate of a fossil were available, raw drawings of both sides were made and combined for the final fossil illustrations. If the wings are at rest and folded, the veins of different layers are analyzed and reconstructed (see below). For convenience, comparison of all wings were shown in right (or both) views. If the right and left side of the wings varied in the same individual, this is discussed in the text.

The nomenclature for fore- and hind wings is based on Carpenter (1992), as modified of Mantodea by Nel & Roy (1996); Tettigoniidae by Sharov (1968) and Locustopseidae by Martins-Neto (2003): C, costa; CA, costa anterior; CP, costa posterior; ScA, subcosta anterior; ScP, subcosta posterior; RA, radius anterior; RP(=RS), radius posterior; MA, media anterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; AA, anal anterior; AP, anal posterior JA, jugal anterior and JP, jugal posterior.

The insect fossils of Crato Formation are abundant and its collections are distributed worldwide in museums as well as private and commercial collections. Up to now, there are several statistical analysis of insect diversity from this formation especially concerning specific taxonomic units. In this study, the diversity of Blattaria and Orthoptera (plus a few specimens of Mantodea) are interpreted from the two investigated Crato collections, one is the large scale collection from the MSF, Fossils Worldwide, Sulzbachtal, Germany containing of 2394 specimens and the others is from the Staatliches Naturkunde Museum Stuttgart, Germany containing of 105 individuals. The latter, however, includes much rarer and representative species. It also forms the base of the systematic analysis of this study (see tables 2-3 and figs. 187-192).

All material is deposited in the Staatliches Museum für Naturkunde Stuttgart, Germany. Material from the MSF, Fossils Worldwide, Sulzbachtal, Germany collection was used for compiling morphological data for statistical analysis.

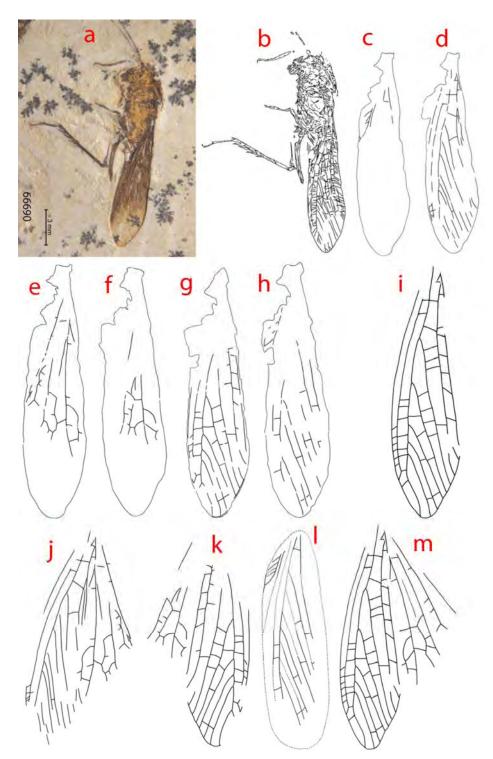
### 2.2. Multilayer analyses

Almost all the winged-insect (Pterygota) fold or overlap their wings at rest with different variations. Insects belonging to the Neoptera only fold the hind wing. Dragonflies and butterflies fold their right- and left wings in an upright position. Cockroaches, beetles and wasps fold their fore- and hind wings together. Mantids, grasshoppers and lacewings, for example, fold all four wings. A large portion of fossil insects thus have their wings in a folded or overlapping condition. In this dissertation, these fossil wings are "unfolded" providing for an improvement for morphological research. This is especially true for those insects in which the forewings are not heavily sclerotized allowing the recognition of the various folds of the hind wings within the same specimen. The directions and thickness of the wing veins can be identified making use of different lighting conditions (preferably slightly dark and from a sideway view vertical to the veins). With some patience, even each single layer of the folded wings can be identified. In this study, up to six layers were analyzed and finally joined together in an illustration. A similar approach has also been used in some earlier research. Sharov (1968) mentions using this method, but without displaying any specific examples. Zessin (1983, 1987, 1988) also made some nearly complete reconstruction of fossil insects (Elcanidae and Locustopsidae) using this method.

The "folded/overlapped" fossils analyzed in this study are several Blattaria (mostly hind wings), four specimens of Hagloidea, eight specimens of Elcanidae, five specimens of Locustopseidae and two specimens of Bouretidae. Three detailed examples of this method are presented as follows:

### Example 1 (fig. 6), SMNS 66690: Cratoelcana damianii Martins-Neto, 1991

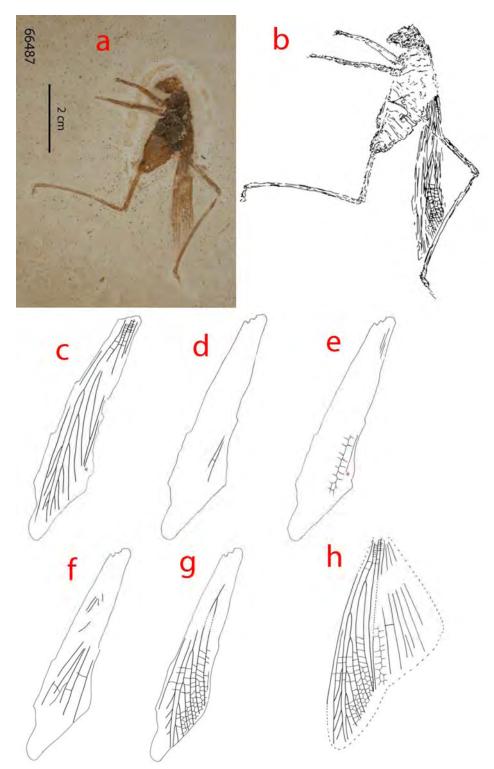
The analysis of Elcanidae is difficult, because the fore- and hind wing are very similar to one other. All wing branches are in fact parallel and there are no distinct differences between them.



**Fig. 6.** Cratoelcana damianii SMNS 66690. **a**, **b**: the complete specimen with folded wings; **c-h**: six layers of wing members arranged from top to bottom, **c**: left forewing; **d**: left hind wing; **e**: left hind wing anal area; **f**: right hind wing anal area; **g**: right hind wing; **h**: reconstructed right forewing; **i**: hind wing without anal area; **j**: left hind wing; **k**: right hind wing; **l**: forewing; **m**: hind wing.

## Example 2 (fig.7), SMNS 66487: Bouretia elegans Martins-Neto, 2001

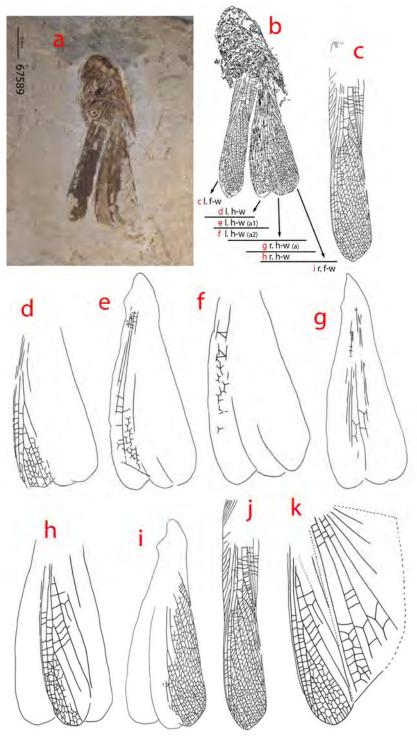
This specimen has practically no more forewings, only two hind wings are present overlapping one other. Furthermore, the A-fold of the wings are also folded.



**Fig. 7.** Bouretia elegans SMNS 66487. **a**, **b**: the whole folded wings; **c**-**g**: five layers from top to bottom, **c**: left hind wing; **d**: anal veins; **e**: left hind wing anal area; **f**: right hind wing anal area; **g**: right hind wing; **h**: reconstructed hind wing.

### Example 3 (fig.8), SMNS 67589: New genus & species

If the wings are folded or overlapped "irregularly", it can be easier to discern the venation of the wings, since the veins are not regularly arranged and thus the layers can be more easily distinguished.

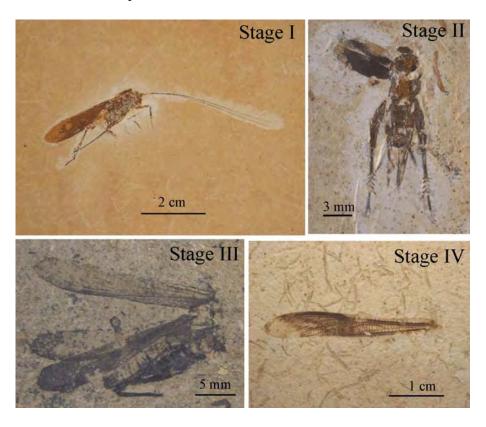


**Fig. 8.** Locustopsoidea. New genus & species SMNS 67589. **a**, **b**: the whole folded wings; **c**: left forewing; **d**-**i**: the irregular folded wings from top to bottom; **d**: left hind wing; **e**: left hind wing anal area; **f**: left hind wing anal area; **g**: right hind wing anal area; **h**: right hind wing; **i**: right forewing; **j**: reconstructed forewing; **k**: reconstructed hind wing.

### 2.3. Taphonomic analyses

Taphonomy studies the transition from organic matter from the biosphere into the geological record. Traditionally, most taphonomic studies are based on shelled animals including molluscs, brachiopods and trilobites. Not all concepts appropriate for these organisms, however, are applicable to insects. The taphonomic analyses of insects are in any case still in the early phase. Up to now there have been some taphonomic studies of insects, for example McCobb *et al.* (1998), Martins-Neto & Gallego (2006), Menon & Martill (2007) and Martins-Neto & Tassi (2009).

The taphonomy of the studied insects was analyzed following the subdivision of Martins-Neto & Gallego (2006). The fossil insect specimens can thus be placed into four taphonomic stages (fig.9) before total fragmentation. These stages are defined as follows (Martins-Neto & Gallego, 2006): Stage I, antenna preserved whereby the missing, apparently damaged parts can be preserved in the counterpart. This is a collecting problem and not a problem of preservation. Stage II is characterized by the partial loss of appendages (*e.g.*, antenna and legs). In Stage III, all appendages are lost, the head is missing and the body begins to decay process. Stage IV shows isolated wings or other body parts (for example, isolated legs). This followed by the total fragmentation of the body and the wings which represent the most durable parts of the insect.



**Fig. 9.** Four stages of preservation stages (I, II, III and IV) of studied insects from the Crato Formation. The sample species of Stage I: *Cratoelcana zessini* (SMNS 66500); Stage II: *Araripegryllus spinosus* (SMNS 67579); Stage III: *Cratozeunerella godoii* (SMNS 67588); Stage IV: *Zessinia vikingi* (SMNS 66692). See text for explanations.

### 3. Systematic palaeontology

### 3.1. "Blattaria": cockroaches and roachoids

Fossil cockroaches and roachoids are often abundant and especially common in the Crato Formation. About 4000 Recent species of cockroaches plus about 1000 fossil roachoid species have been described (Vršanský, 2005b).

Morphological characters, according to Bechly, 2007a: Living cockroaches are usually small to large insects with long filiform antennae. They possess hypognathous chewing mouthparts with well-developed mandibles. The compound eyes are large and two lateral ocelli present. Usually they have two pairs of wings, but some are secondarily wingless. The forewings are heavily sclerotized as tegmina and are much more slender than the broad hind wings, which have a large anal fan. In the forewings vein CuP is strongly curved and delimits a rounded anal field. The abdominal cerci are relatively long with numerous segments and the female ovipositor is reduced in modern cockroaches, but is still present in fossil roachoids that seem to belong to stem group Dictyoptera rather than the crown group Blattria. All living cockroaches lay large pods of eggs called oothecae. Development is paurometabolous with a gradual development from larva to imago.

Blattaria in the crato Formation, according to Bechly, 2007a: Fossil cockroaches were first described from this locality by Pinto and Purper (1986) and Pinto (1989). Even though many hundreds of specimens have been discovered already, such that cockroaches are one of the most abundant fossils in the Nova Olinda Member, only a few species have been formally described. About 26 % (960 from a sample of 3651 fossil insects) of the many thousands of Crato insects discovered are cockroaches and roachoids. According to Vršanský (2004), among the hundreds specimens only seven different species are present, dominated by Blattellidae (60 %), with subdominant extinct family Blattulidae (25%), as well as the extinct family Umenocoleidae (15%) and a single species of the extinct family Mesoblattinidae. Even though there may be a few more species, this is a relatively small diversity of species compared to the thousands of specimens collected.

### 3.1.1. Family: †Cratovitismidae Bechly, 2007

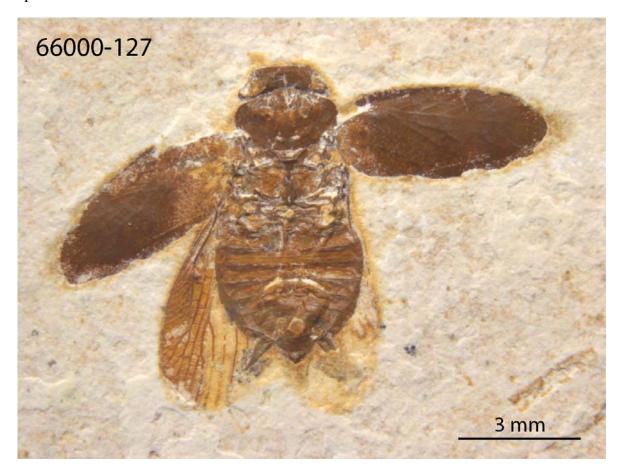
Original diagnosis, according to Bechly, 2007a: like Vitismidae intermediate between Blattulidae and Umenocoleidae; with strongly sclerotized forewings, pterostigmata in the hind wings, transverse head (different to Vitismidae) with relatively short antennae, and a short ovipositor; but with curved CuP in the broader forewings, a more dense venation in hind wings, and a disk-like pronotum (differences to most Umenocoleidae).

Genus: Cratovitisma Bechly, 2007

Original diagnosis: same as type species, since monotypic.

Species: *Cratovitisma oldreadi* Bechly, 2007 (figs. 10-11)

# Specimen **SMNS 66000-127**



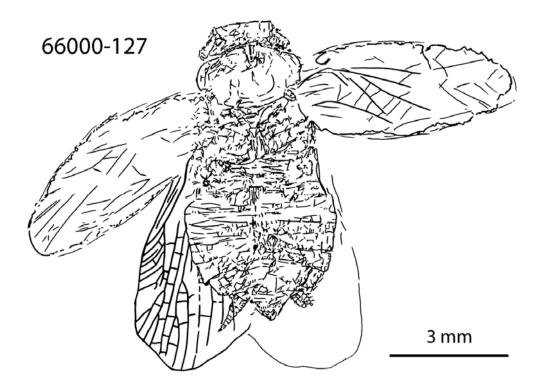


Fig. 10. Cratovitisma oldreadi Bechly, 2007, Habitus.

# 66000-127 2 mm

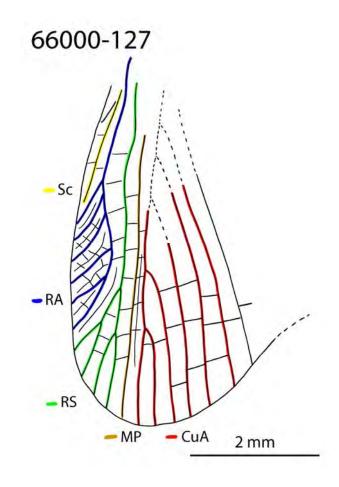


Fig.11. Cratovitisma oldreadi Bechly, 2007, Fore & Hind wings.

Original diagnosis and description, according to Bechly, 2007a: It has a body length of 6.9 mm and a forewing length of 5.3 mm. As in *Vitisma*, the forewings are broader than in *Ponopterix* (max. 2 mm wide), strongly sclerotized, but with vestiges of the wing veins still well visible. The vein CuP seems to be strongly curved and delimits a typical roachoid anal field in the forewings. The hind wing venation is very much like in *Vitisma*, thus more dense than in *Ponopterix*, but of similar pattern and with pterostigma. The head is transverse as in Umenocoleidae (different from *Vitisma*) and the antennae are also similar to Umenocoleidae, thus shorter than the body. The pronotum is flat and disk-like as in *Vitisma* and true cockroaches, very different from *Ponopterix* and *Umenocoleus*. A protruding ovipositor seems to be present, but is somewhat less conspicuous than in *Ponopterix* (similar to Blattulidae). Comment: The transverse head seems to place this new genus and species closer to Umenocoleidae than *Vitisma*, so that a new family would be justified.

New description: Forewing, Sc bifurcated, Radius with eight branched, M with five to six branched, CuA similar with Genus *Ponopterix* to have a single terminal fork, CuP strongly curved and delimits a typical roachoid anal field. Hind wing, Sc alone and less than half of whole wing length, RA with six branched, RS with a total of four branches and similar to *Ponopterix axelrodi*, MP alone and CuA with probably seven branched (or six CuA plus one CuP). The ovipositor from this single specimen is 0.6 mm long (about 7.89% of body length), is tendentious shorter than that in Umenocoleoideas both species in the crato Formation, also clearly shorter than that in *Elisama brevis* (=americana) (Blattulidae).

### Superfamily: †Umenocoleoidea Chen & Tian, 1973

According to Vršanský, 2003a: Monophyletic lineage with 3 possible families known (Umenocoleidae, and possibly Anaplectidae and Oulopterigidae): Umenocoleidae are known since the lowermost Cretaceous of Siberia. The probably extant representatives of the lineage are some species currently placed within Oulopterigidae and Anaplectidae which inhabit tropical regions worldwide (e.g., *Melyroidea*).

Original Diagnosis, according to Vršanský, 2003a: Small (under 20 mm), beetle-like cockroaches with more or less globular head (eventually orthognathous); pronotum with paranota reduces; with legs eventually short and strong. The most characteristic are heavily sclerotised forewings with reduced venation and with the presence of cup-like cells called "bunky". Species are most probably diurnal with similar flight activity of both males and females, with sexual dimorphism not much pronounced.

### 3.1.2. Family: **Umenocoleidae** Chen & Tian, 1973

Original Diagnosis, according to Vršanský, 2003a: Head more or less globular, antenna with wide segments and very long setae in transversal rows; pronotum mostly short and narrow, with reduced paranota; forewing heavily elytrised, with cup-like cells called "bunky" and reduced venation; hindwing venation generally of early polyphagoid groundplan (simplified venation with CuA without tertiary branches, CuP simple, A1 curved, with short branches), but with reduced venation of R (with few branches – possibly with pterostigma), M branched. Cerci with numerous long hair; females with short external ovipositor.

Genus: *Ponopterix* Vršanský & Grimaldi, 1999 (in Vršanský 1999a)

Original Diagnosis, according to Vršanský, 2003a: Forewing is pale with dark maculas and distinct venation, heavily sclerotised. Hind wing with rich R and pterostigma (plesiomorphies). Head large, with large eyes.

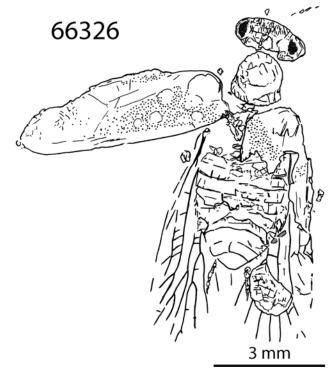
Species: *Ponopterix axelrodi* Vršanský & Grimaldi, 1999 (in Vršanský 1999a) (figs. 12-19).

Original Description, according to Vršanský, 2003a: Body 5-7 mm long. Head spherical, 1.8 to 3 mm wide. Antenna 7.1 to 8.3 mm long, the first three segments elongate, the others very short. Elytra 4.9 to 9.1 mm, usually about 6.5 mm long, 1.7 to 2.8 mm wide. Radius rich (up to 10 branches), M and Cu variable but usually with single terminal fork. Anal veins numerous (visible in some individuals). Hind wing: pterostigma present, R1 richly branched. Legs cursorial, heavily mounted with spurs. Forelegs similar to legs of early mantises, tibia 0.88-1.27mm, tarsus 1.5mm long; mid leg tibia 1.85mm long, bearing 8 spurs; tarsus 1.74mm long; hind leg tibia 2.7mm long, with 8 spurs; tarsus 2.3mm long. Tarsi 5-segmented. Terminalia: Female with external ovipositor at least 0.67-0.9mm long. Male with distinct styli and with phallomere of a primitive type. Cerci placed closer to each other than in the female. Cercus about 1.5mm long, with 11-13 segments.

New Description: Body 6.4 to 8.0 mm long. Forewing 5.1 to 6.3 mm long and 1.7 to 2.1 mm wide. Hind wing 5.2 to 6.3 mm long, is almost the same length as the forewing. Hind wing: Sc alone, shorter than half of the whole wing length, RA with four branched, RS with two stem branches and that is two to four terminal branches totally, MP with two to three branched, CuA with six branched, CuP alone. Ovipositor is about 0.67 to 0.9 mm long, approximately is 10% - 12.12% of body length.

Specimen SMNS 66326: Male. Hind wing well preserved





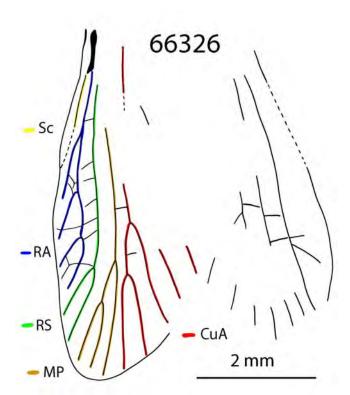


Fig. 12. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Habitus & Hind wings.

Specimen **SMNS 66329**: Female. Ventral side. Compound eyes well preserved. Abdominal segments clearly.

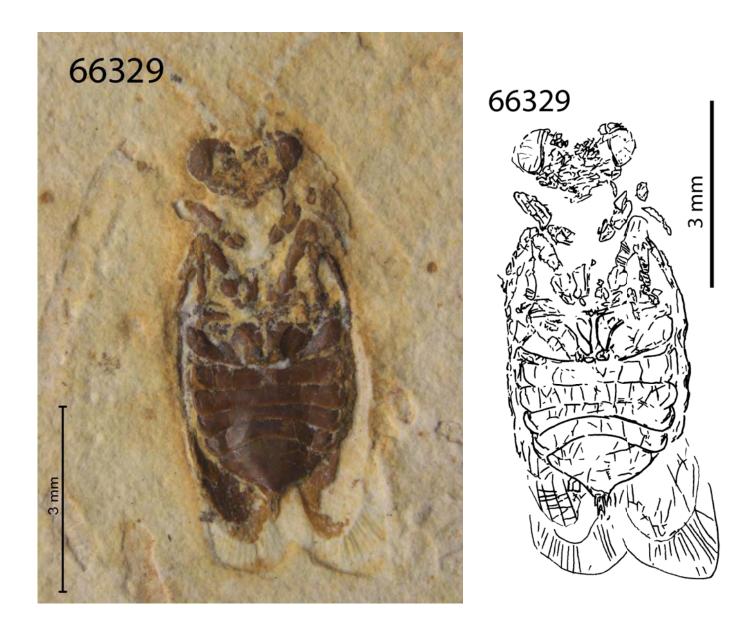


Fig. 13. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Habitus, ventral view.

Specimen SMNS 66334: Probably male. Hind wing only partly visible.

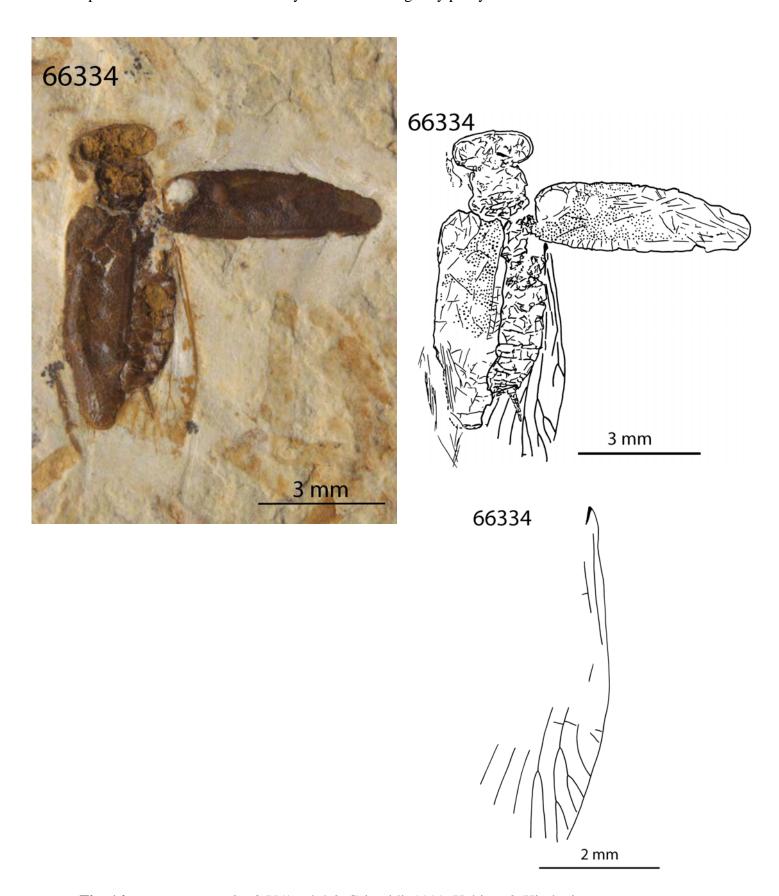


Fig. 14. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Habitus & Hind wing.

Specimen SMNS 66335: Female. Ventral side. Abdomen swelled.



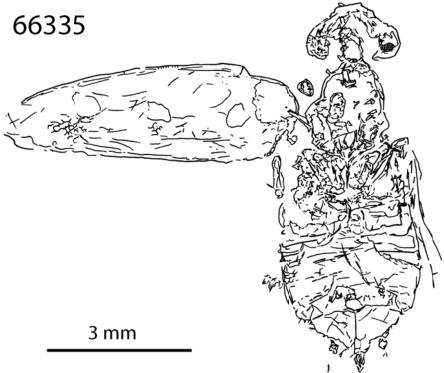


Fig. 15. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Habitus, ventral view.

Specimen SMNS 66336: Male. Forewing venation visible, but varied between right and left side. Comment: Specimen SMNS 66336 has a relative large body size, measured 8.0 mm long, it could belong to the species *Ponopterix maxima* too. On account of the relative narrower head, shorter forewing (6 mm long) and the hind wing RA with four-branched and RS with two stem-branches, here categorizes this specimen as species *Ponopterix axelrodi*.

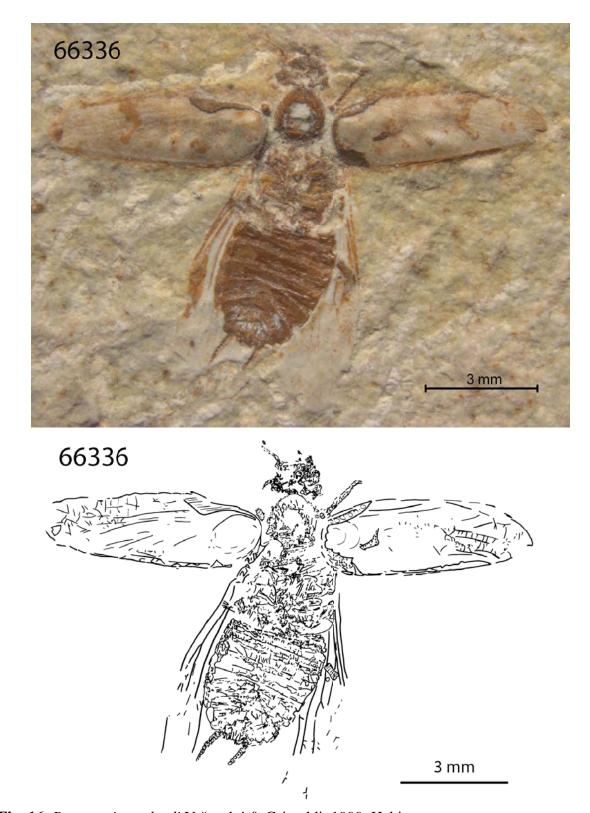


Fig. 16. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Habitus.

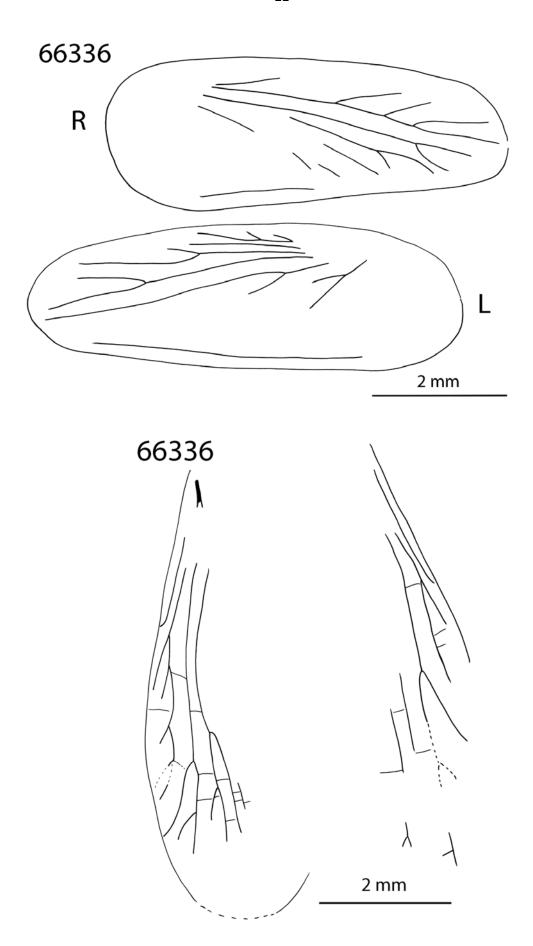
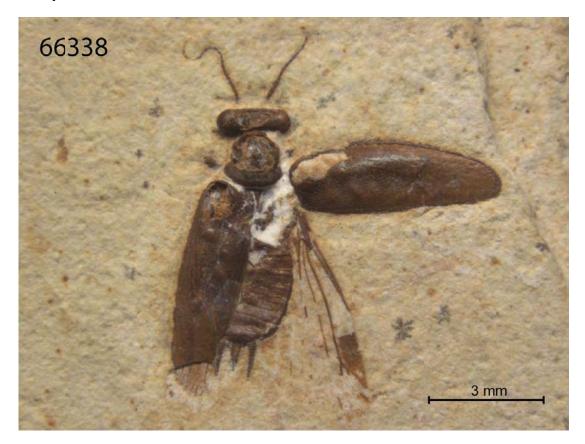
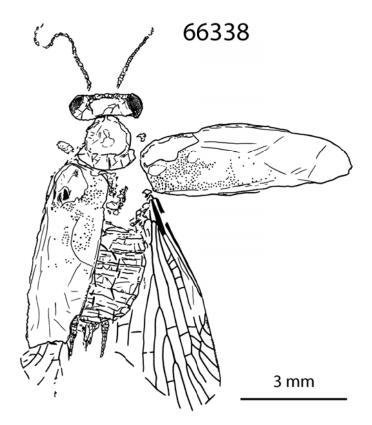


Fig. 17. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Fore & Hind wings.

Specimen **SMNS 66338**: Female. Hind wing fast preserved completely. Cerci and ovipositor clearly visible.





**Fig. 18.** *Ponopterix axelrodi* Vršanský & Grimaldi, 1999, Habitus.

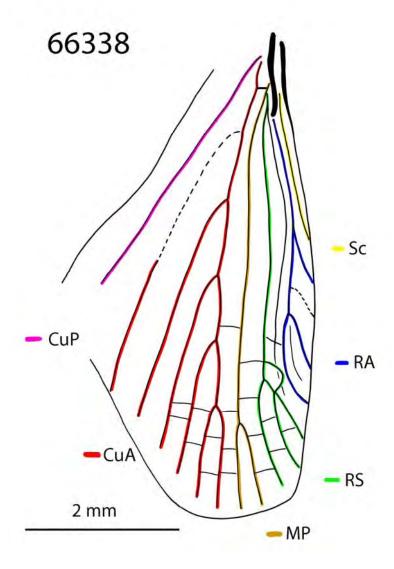


Fig. 19. Ponopterix axelrodi Vršanský & Grimaldi, 1999, Hind wing.

Discussion: *Ponopterix axelrodi* differs from *Ponopterix maxima* Bechly, 2007 by the smaller body size and by hind wing with different RP pattern (in *P. maxima* RP with sequential branches one after another and in *P. axelrodi* RP with two stem-branches and each one may have more terminal branches). However, according to this study those two ones could be indeed belong to the same species. More detail comparison and discussion see fig. 192, p. 223.

Species: *Ponopterix maxima* Bechly, 2007 (figs. 20-37)

Original Diagnosis, according to Bechly, 2007a: Body length 7.5 to 12.5 mm; forewing length 6.5 to 10.5 mm; head broader than in previous species, especially between the compound eyes; pronotum comparatively larger and broader and saddle-shaped; otherwise very similar to *P. axelrodi*, therefore very probably belonging to the same genus.

New Description: Antenna at least 6 mm long and about half of body length. Body 8.4 to 11.2 mm long. Forewing 6.4 to 9.3 mm long and 1.9 to 2.7 mm wide, Sc alone, Radius with four to eight branched, usually four to six (seven- and eight branched only by one specimen), M and

Cu variable but usually with single terminal fork, Anal veins numerous, general all venations more or less straight; Hind wing about the same length as the forewing, Sc alone and less than half of the whole wing length, RA with two to four branched, RP with three to five branched, MP with two branched, CuA with five branched and CuP alone. Leg has five- segments tarsi with claws, first segment elongated, 2<sup>th</sup> 3<sup>th</sup> and 5<sup>th</sup> segments about the same length and the 4<sup>th</sup> segment extremely short. Female with external ovipositor at least 0.8-1.3 mm long, about 7.84%-12.26% of body length. Cersus in roaches form, 12 to 16 segments.

Specimen SMNS 66323: Male. Length of the antenna is about ½ of the body length. Large compound eyes. Hind wing only partly visible.

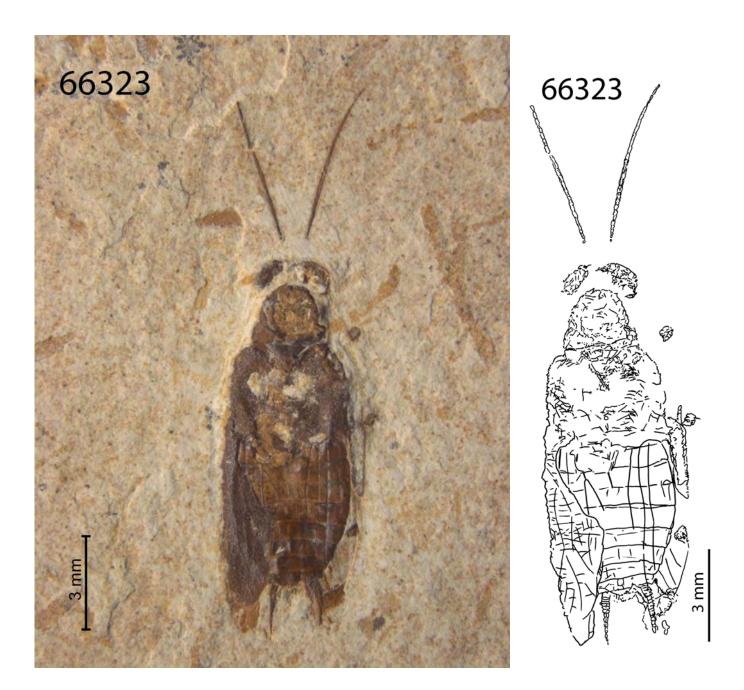
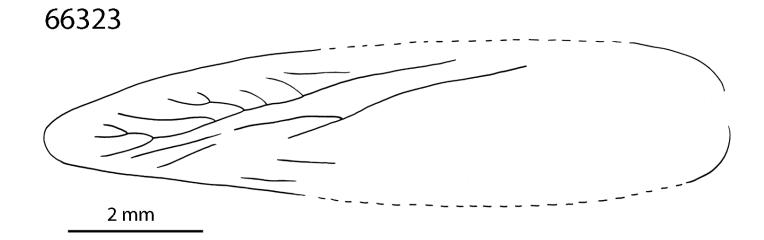


Fig. 20. Ponopterix maxima Bechly, 2007, Habitus.



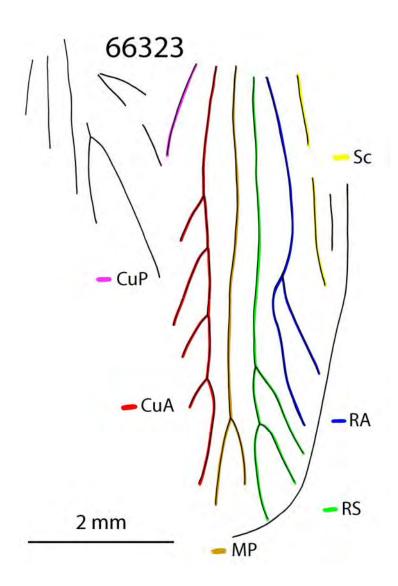
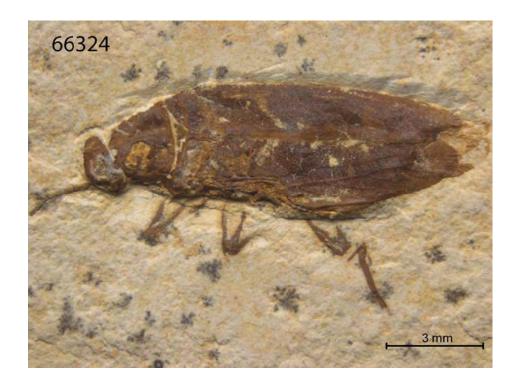


Fig. 21. Ponopterix maxima Bechly, 2007, Fore & Hind wings.

Specimen SMNS 66324: Lateral side. Femur of three legs well preserved.



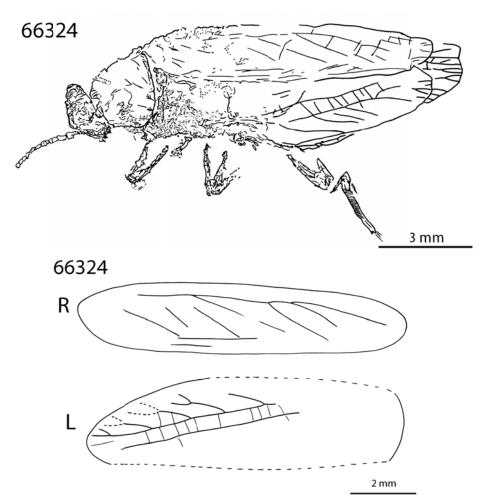
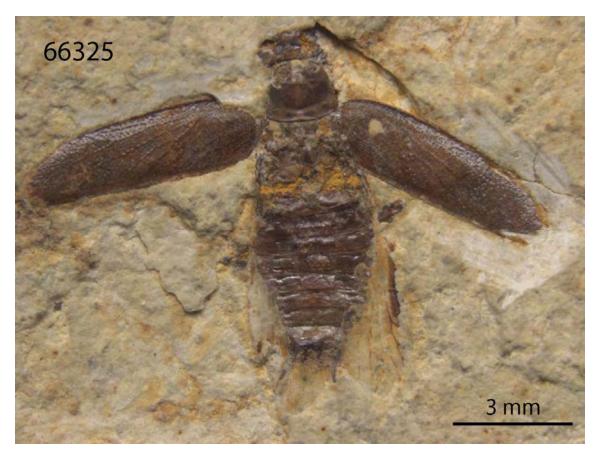


Fig. 22. Ponopterix maxima Bechly, 2007, Habitus & Forewings.

Specimen **SMNS 66325**: Male. Venation of both forewings clearly preserved. Hind wing with pterostigma and large part of venation identifiable.



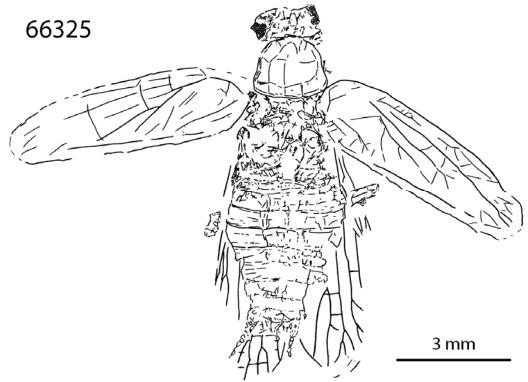
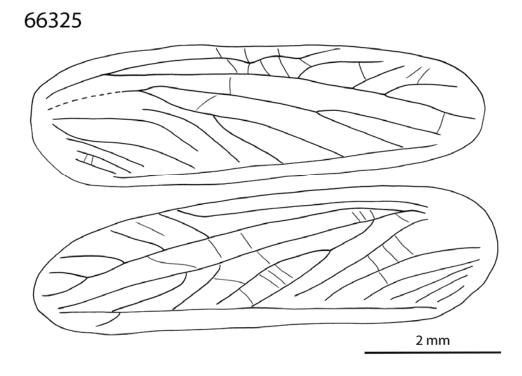


Fig. 23. Ponopterix maxima Bechly, 2007, Habitus.



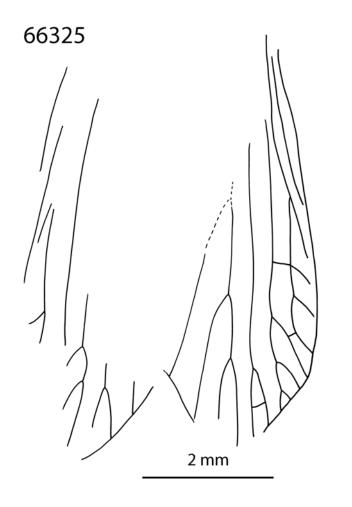


Fig. 24. Ponopterix maxima Bechly, 2007, Fore & Hind wings.

Specimen **SMNS 66327**: Female. Legs well preserved, tarsus with five segments, first segment elongated,  $2^{th}$   $3^{th}$  and  $5^{th}$  segment about the same length,  $4^{th}$  segment extremely short. Abdomen swelled.

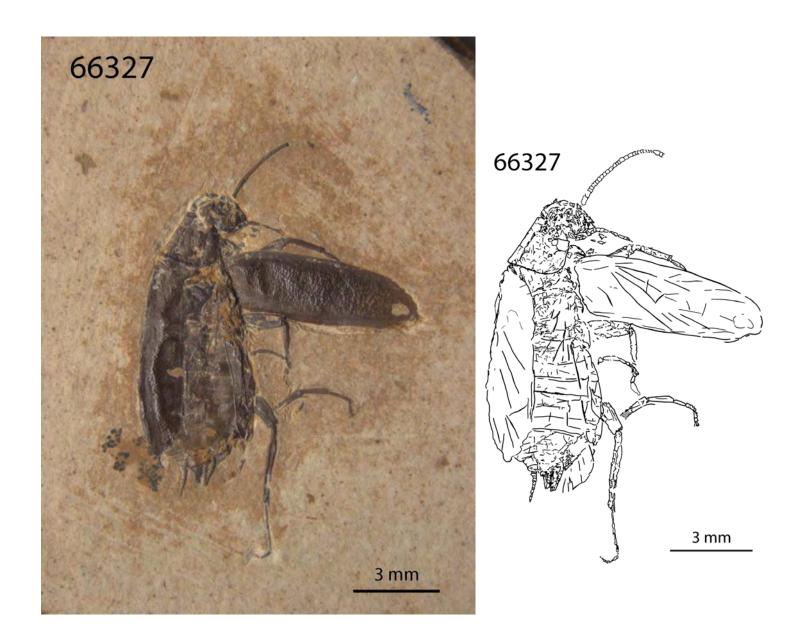


Fig. 25. Ponopterix maxima Bechly, 2007, Habitus.

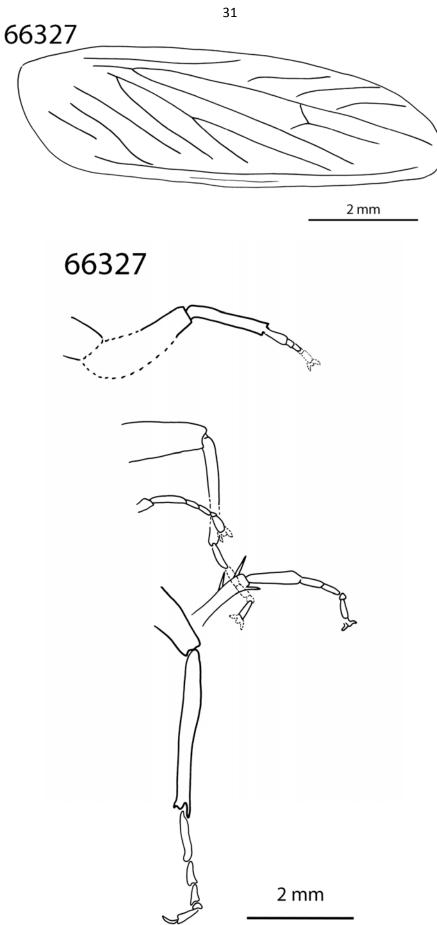


Fig. 26. Ponopterix maxima Bechly, 2007, Forewing & Legs.

Specimen **SMNS 66328**: Female. The venations of both forewings clear visible. Ovipositor and circus well preserved.

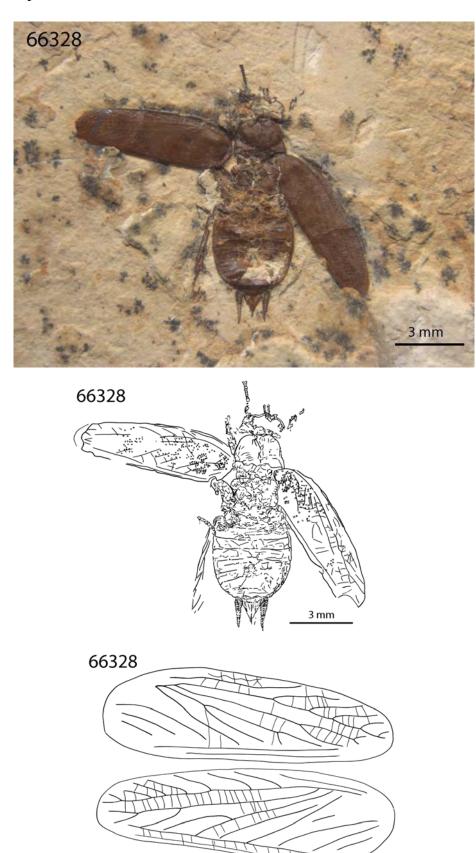


Fig. 27. Ponopterix maxima Bechly, 2007, Habitus & Forewings.

Specimen **SMNS 66330**: Female, ventral side. Legs well preserved especially in femur and coxa part.

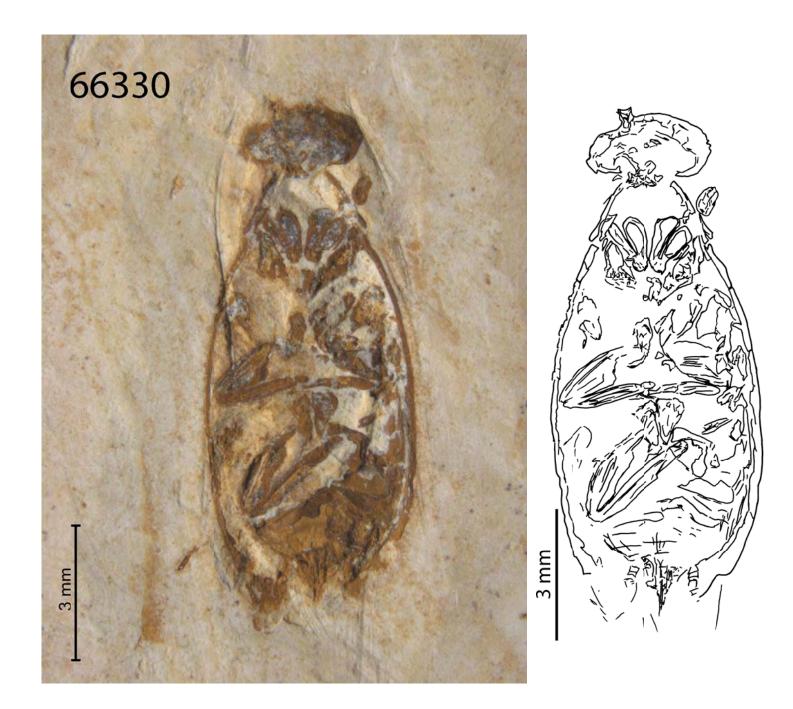
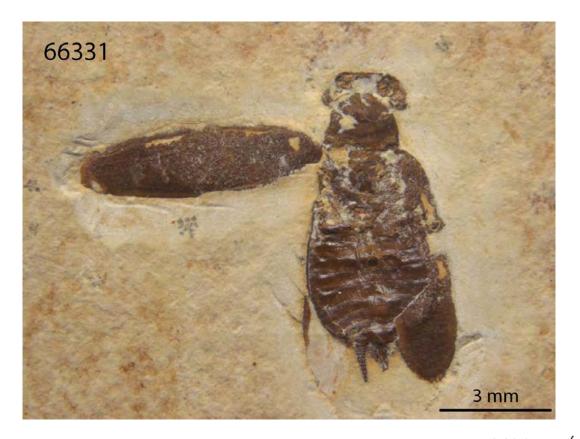


Fig. 28. Ponopterix maxima Bechly, 2007, Habitus, ventral view.

Specimen **SMNS 66331**: Female. Forewing heavily sclerotised, venation reduced. Hind wing partly preserved.



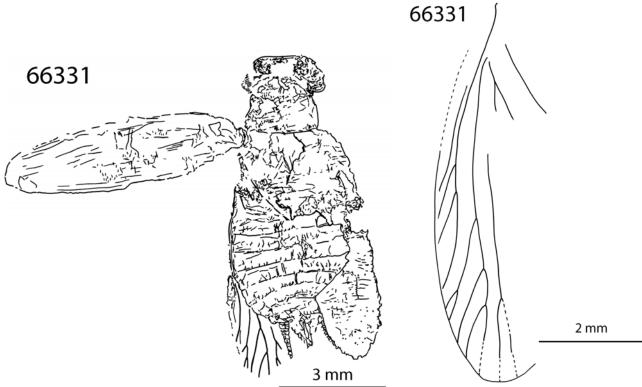


Fig. 29. Ponopterix maxima Bechly, 2007, Habitus & Hind wing.

Specimen **SMNS 66332**: Material holotype. Compound eyes well preserved. The venations of forewings clear visible.

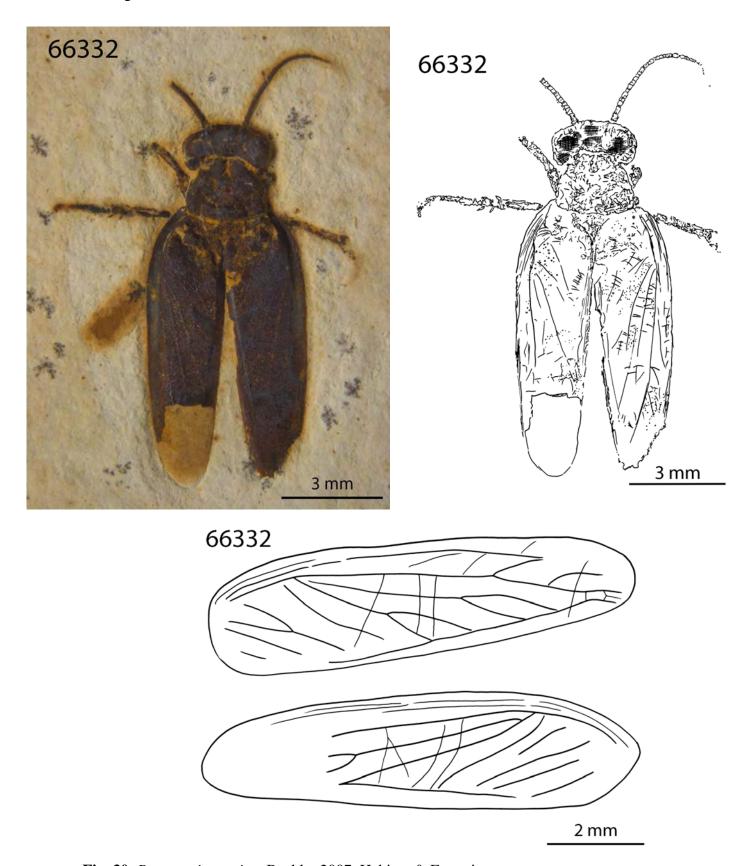
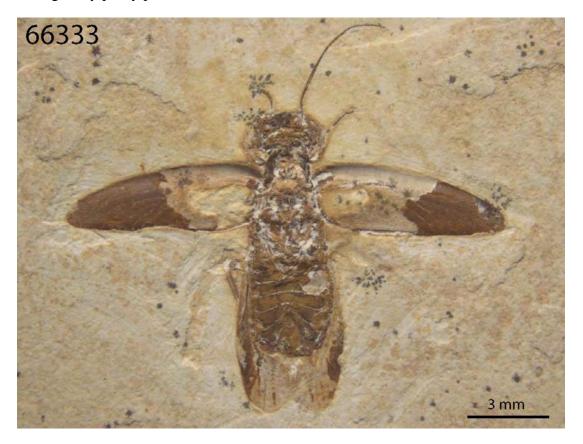


Fig. 30. Ponopterix maxima Bechly, 2007, Habitus & Forewings.

Specimen SMNS 66333: Female. Head broader than the other specimens. Fore and hind wings only partly preserved.



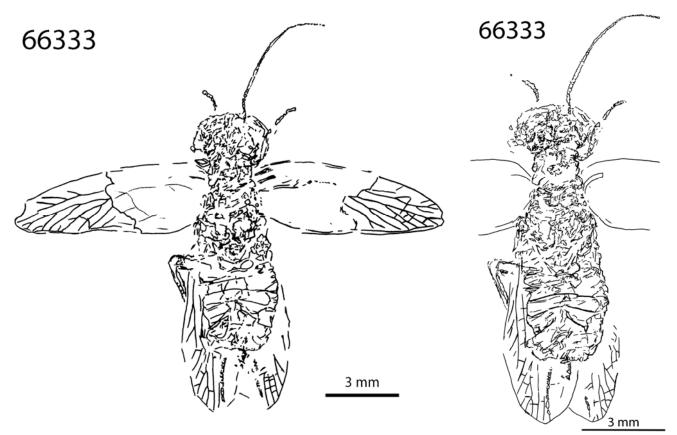


Fig. 31. Ponopterix maxima Bechly, 2007, Habitus.

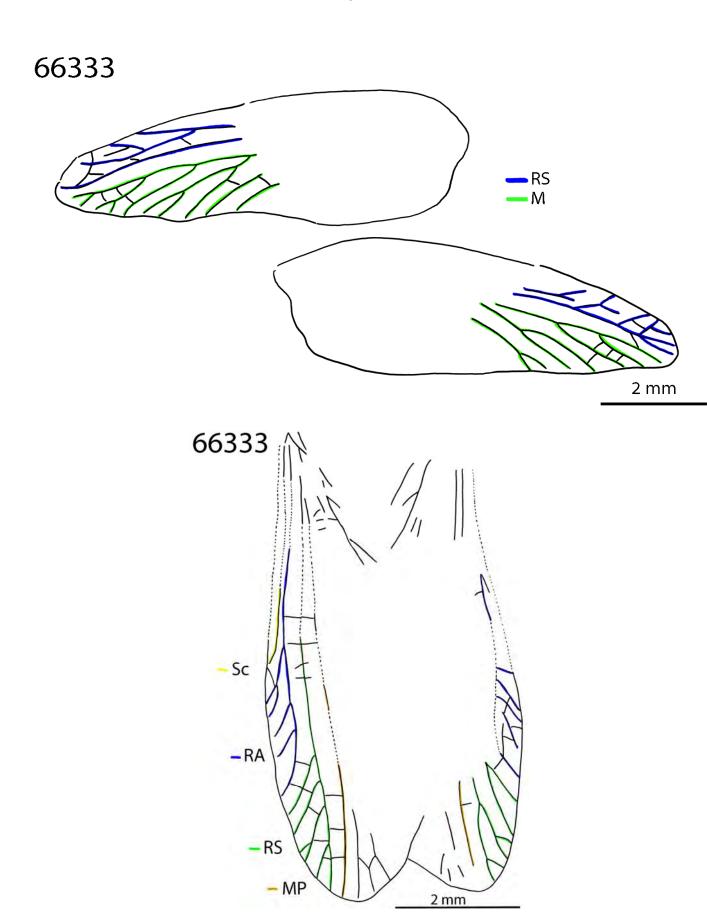
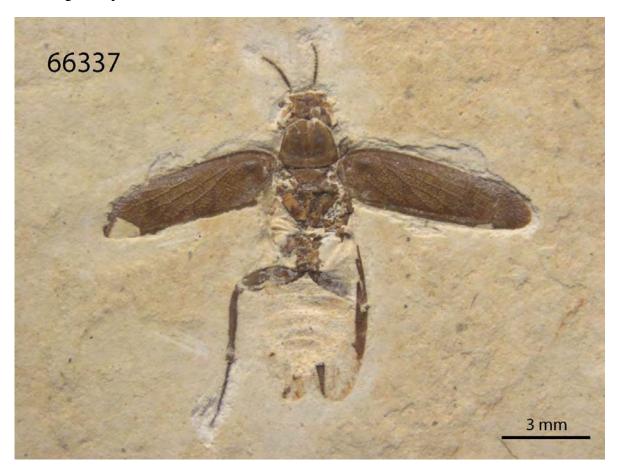


Fig. 32. Ponopterix maxima Bechly, 2007, Fore & Hind wings.

Specimen **SMNS 66337**: Male. Venation of forewings clearly visible. Hind leg well preserved, including coxa part.



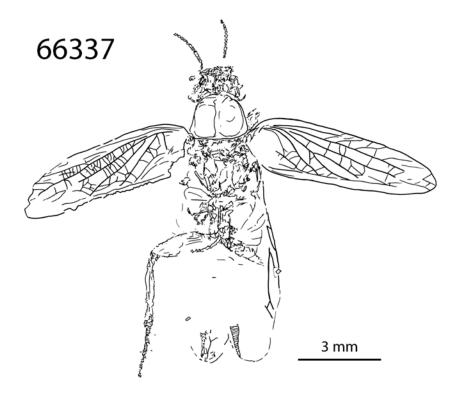


Fig. 33. Ponopterix maxima Bechly, 2007, Habitus.

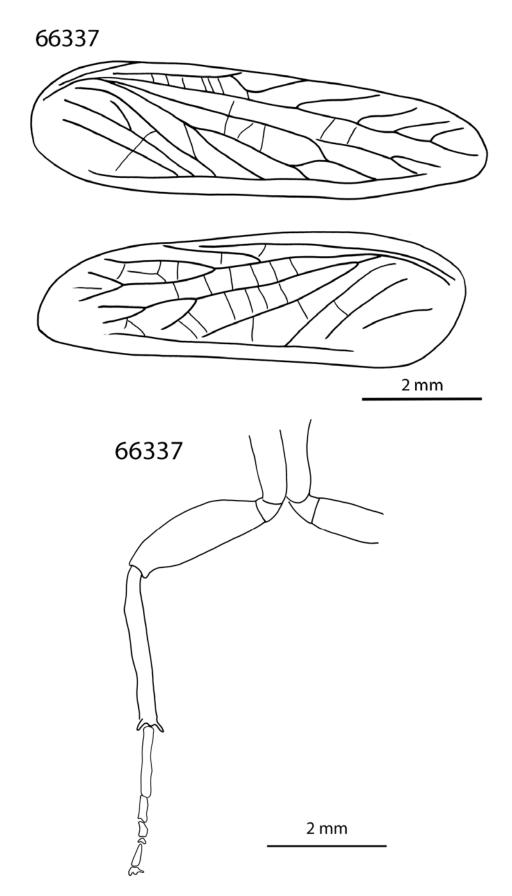
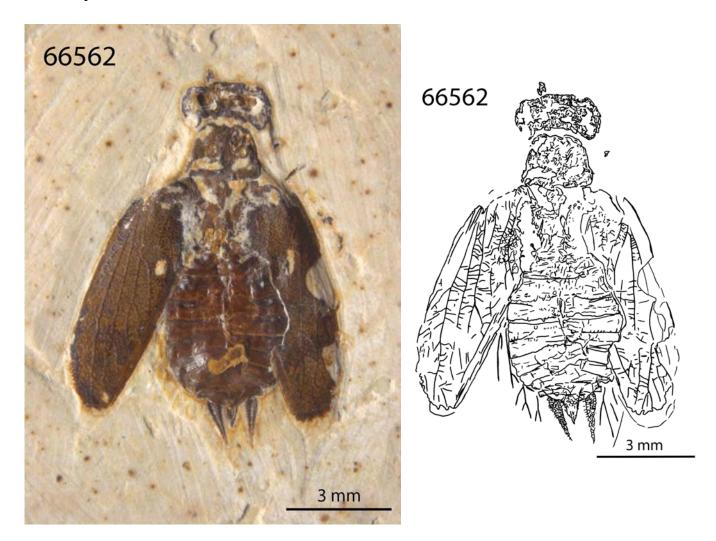


Fig. 34. Ponopterix maxima Bechly, 2007, Forewings & Hind legs.

Specimen **SMNS 66562**: Female. Forewing clearly. Abdomen swelled. Circus and ovipositor well preserved.



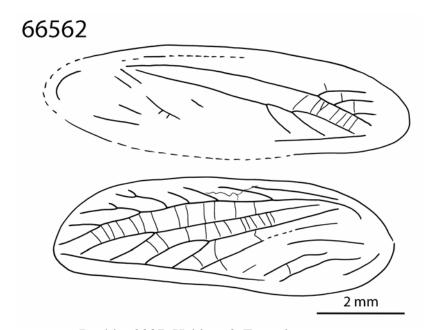


Fig. 35. Ponopterix maxima Bechly, 2007, Habitus & Forewings.

Specimen **SMNS 67574**: Probably male, lateral side. Mouthpart well preserved, maxillary palps and labia palps visible.



Fig. 36. Ponopterix maxima Bechly, 2007, Habitus, lateral view.

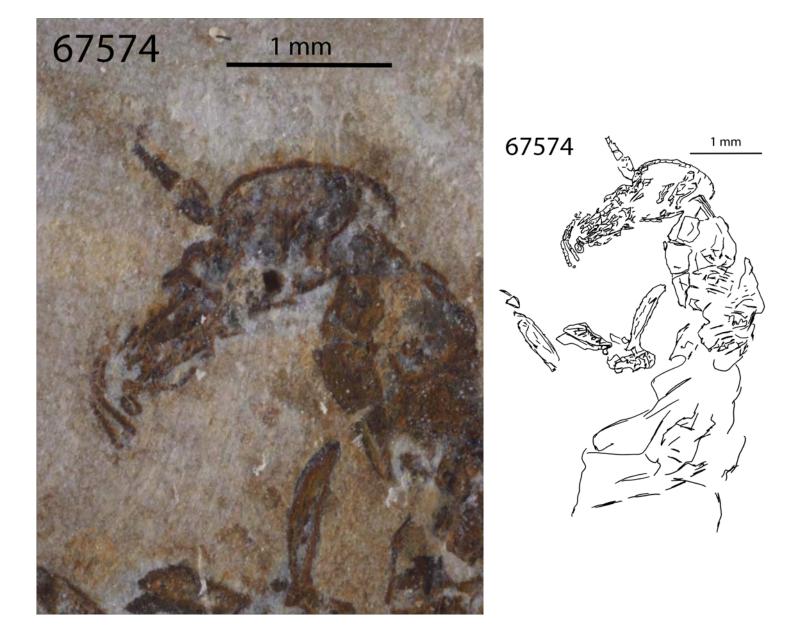


Fig. 37. Ponopterix maxima Bechly, 2007, Head & Mouthpart, lateral view.

Discussion: *Ponopterix maxima* differs from *Ponopterix axelrodi* by larger body size and by hind wing with slightly different RP pattern (in *P. maxima* RP with sequential branches one after another and in *P. axelrodi* RP with two stem-branches and each one may have more terminal branches, though this variety is actually not significant).

Remark: On the basis of the similarity of fore- and hind wings between *Ponopterix axelrodi* and *P. maxima* and the variety of body size of this two species uninterrupted (see fig. 192, page 223), it is possible that those two ones indeed belong to the same species.

Superfamily: Polyphagoidea Princis, 1960

## 3.1.3. Family: †Blattulidae Vishniakova, 1982

The family originated in the Late Triassic and they presented dominant cockroach family in many sites ranging from the Early Jurassic to the Early Cretaceous for more than 100-million years. The more surprising is its low generic diversity- only 13 genera are known through its long history (Vršanský, 2005a; Vršanský *et al.*, 2002; Wang *et al.*, 2007a). According to Vršanský (2004) about 25% of the fossil roaches from this locality belong to the extinct family Blattulidae, with two genera and species (*Elisama brevis* (=americana) and a further undescribed genus and species). This family could either belong to the stemgroup of Dictyoptera (Grimaldi & Engel, 2005) or might be related to Polyphagidae (Vršanský, 1999b). Vršanský (2003) described structural similarities of the external ovipositor in Blattulidae and Umenocoleidae.

Genus: Elisama Giebel, 1856

Species: *Elisama brevis* Mendes, 2000 (figs. 42-63)

Synonym: *Elisama americana* Vršanský, 2002; *Araripeblatta brevis* Mendes, 2000 (see Vršanský, 2002; Martins-Neto *et al.*, 2010)

Original diagnosis and discussion of *Araripeblatta brevis* Mendes, 2000, according to Martins-Neto *et al.*, 2010: Diagnosis. Small-sized blattopteran with tegmen length around 9 mm. Females with recurrent ovipositor. Contact points of first R branch with the anterior wing border of MA origin (oMa), and contact of CuP with the posterior wing border are arranged in one line (e.g. fig. 38) slightly transverse to the wing long axis. M and R fused close to the tegmen base. Paired small spines on the left fore tibia (in ventral view), and not paired long spines in the right fore tibia (in ventral view). Discussion: the family Araripeblattidae differs from Blattulidae Vischniakova, 1982, the closest family, by having RA, oMA, and CuP transversely aligned. In Blattulidae tegmen, the secondary branches of RP and MA are restricted to the apical area, above the middle of the apex. A line between the contact of RA with the anterior wing border and the point of contact of CuP with the posterior wing border are nearly perpendicular arranged to the wing long axis. The point of M bifurcation (oMA) is situated slightly backward of this line (see Martins-Neto *et al.*, 2005).

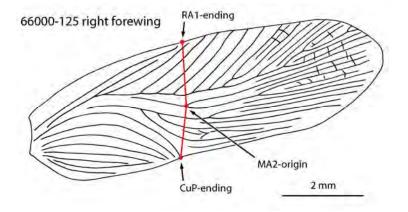
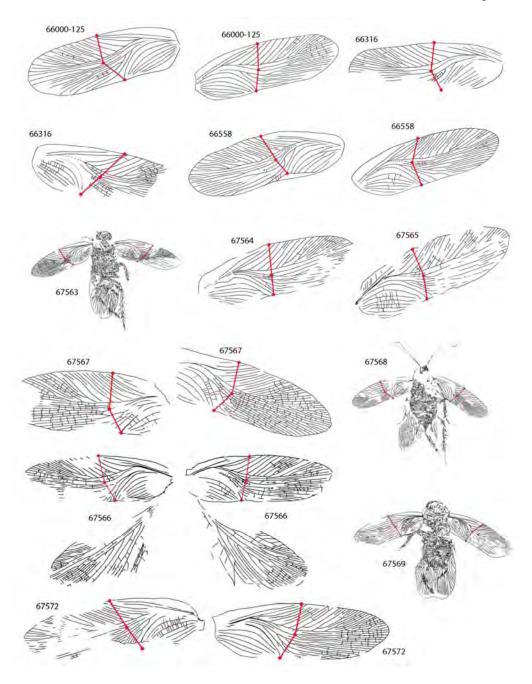
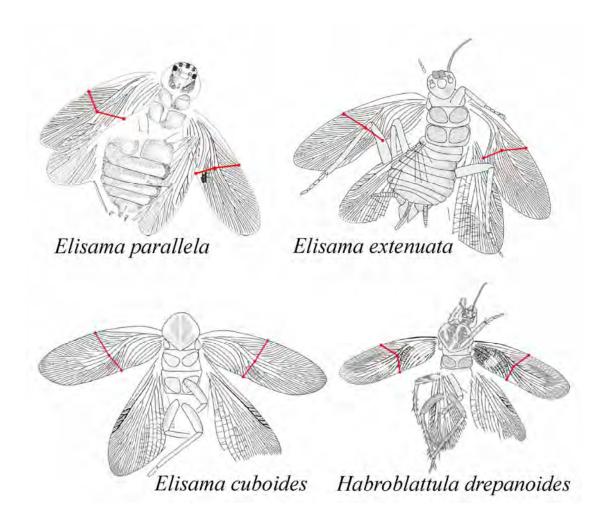


Fig. 38. The line RA1-ending, MA2-origin and CuP-ending, an example from this study.

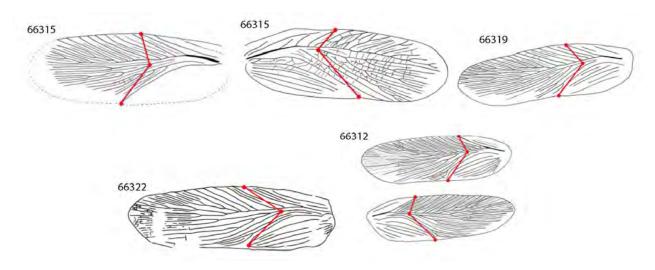
New Discussion: The main difference between the two families Araripeblattidae and Blattullidae (see above and Martins-Neto *et al.*, 2010), does not apply to this study. Than the lines from RA1-ending, MA2-origin and CuP-ending of *Araripeblatta brevis* variant, both intraspecific (even between right and left forewings in the same specimen) and interspecific (fig. 39), there are no significant different between *Araripeblatta brevis* Mendes, 2000 and Blattulidae, that is, *Elisama tsaganica* Vršanský, 2002, *E. parallela* Vršanský, 2003, *E. extenuata* Ren, 1995, *E. cuboides* Wang, Ren et Liang, 2007 and *Habroblattula drepanoides* Wang, Liang et Ren, 2007 (fig. 40). *Araripeblatta brevis* is here considered a junior synonym of *Elisama brevis* and belong to family Blattulidae. Indeed his RA1-oMA2-CuP lines are clear different but between Blattulidae and "*Mesoblattina*" *limai* (Blattellidae) (fig. 41).



**Fig. 39.** The lines RA1-ending, MA2-origin & CuP-ending of *Elisama brevis*, Mendes, 2000, Family Blattulidae. Not to the same scale.



**Fig. 40.** The lines RA1-ending, MA2-origin & CuP-ending of *Elisama parallela* Vršanský, 2003; *E. extenuate* Ren, 1995; *E. cuboides* Wnag, Ren et Liang, 2007 and *Habroblattula drepanoides* Wang, Liang et Ren, 2007. Family Blattulidae. (After Vršanský, 2003b; Wang *et al* 2007a & b. redrawn here) Not to the same scale.



**Fig. 41.** The lines RA-ending, MA2-origin & CuP-ending of (*Mesoblattina*) *limai* Pinto & Purper, 1986, Family Blattellida. Not to the same scale.

Original diagnosis of *Elisama americana*, according to Vršanský, 2002: The ground plan of both wings of a general polyphagoid (blattulid- vitismid) appearance, but with very strong veins. Body length 6.5-8.5 mm; antennae about as long as the body; head with very large and globular compound eyes; width of pronotum is 146% of head width; pronotum is broadest in the middle, thus with about equal anterior and posterior halves; forewing length 7.5-10.2 mm; forewing venation with an extremely curved CuP and anal veins that reach the hind margin; forewings sometimes preserved with a distinctly band color pattern.

Original description of *Elisama americana*, according to Vršanský, 2002: Small size roaches. Head more or less globular, with large eyes. Forewing length about 8 mm. Wing fore margin arcuate basally, almost straight farther. Costa area as wide as subcosta area. Sc very short, not reaching the apical third of a wing. R with indicated but not fully expressed Rs, with about ten branches. M with three-four branches, CuA branched. CuP arching, clavus rather large. Intercalaries pale compared to strong main veins. Hind wing R with three branches, RS with six; M with three; CuA with four-six simple branches. Intercalaries of similar character found in the forewing. Foreleg with coxa (0.9 mm) free and very long, femur (1.4 mm) approximately 1.3 times as long as tibia (1.24 mm). Terminalia with two pairs of two-segmented and multi-segmented styli, and cerci composed of at least nine segments with numerous sensillae (ampullae of large sensilla chaetica) present.

New description: Antenna about the same length as body. Body length between 7.9-9.5 mm. Head wide and longer than the pronotum. Head with very large and globular compound eyes, probably three ocelli (SMNS 66558) reside in the forehead between the compound eyes. Pronotum is about 1.5 times width as the head, approximately round shape, except in the hind part sharp gradually. Forewing 8-10 mm long and 2.4-3 mm wide. Sometimes slightly sclerotized. It is possible that the degree of sclerotization accompany with colored band pattern disappear. RA+RS with total of 13-16 branches, instead of ten. M with three-four branches. CuA with four-six branches, rarely seven (SMNS67572 right side). Hind wing about the same length as the forewing and is 8.5-9.8 mm long. Sometimes in anterior margin, that is RA area, slightly sclerotized, or that is pterostigma. Sc alone, reaching to a little less than ½ of the anterior margin of the whole wing length. RA with four-five branches, instead of three, RS with six-seven branches. MP with three branches. CuA in principle with six branches, rarely seven (SMNS 67566 left side), CuP should be alone and probably reaching the end of the wing. Body 7.8-9.1 mm long. Legs presented long and strong spines. Tarsus has probably all five segments. Abdomen is in female tendentious much rounded than in male, in male more elongate. Cerci in roaches form, 12-18 segments. Ovipositor convex and sharp, with sheath, 0.8-1.5 mm long (about 10.13-16.67% of body length). Terminalia with indeed unsegmented styles.

Specimen **SMNS 66000-125**: Male. Eye big, place by the side of the head and area inbetween is large. Pronotum is about 1.5 times wide as head, nearly rounded, except in the hind part sharp gradually.



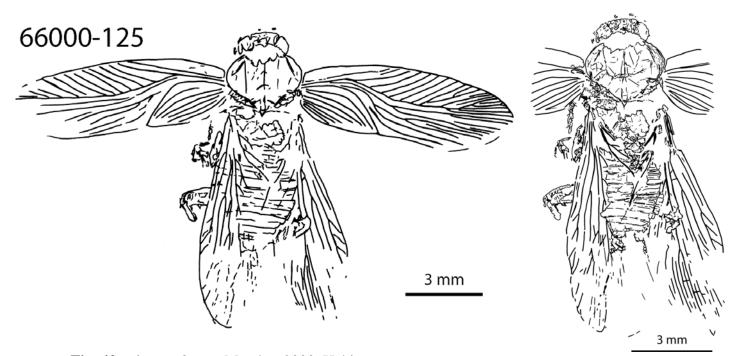


Fig. 42. Elisama brevis Mendes, 2000, Habitus.

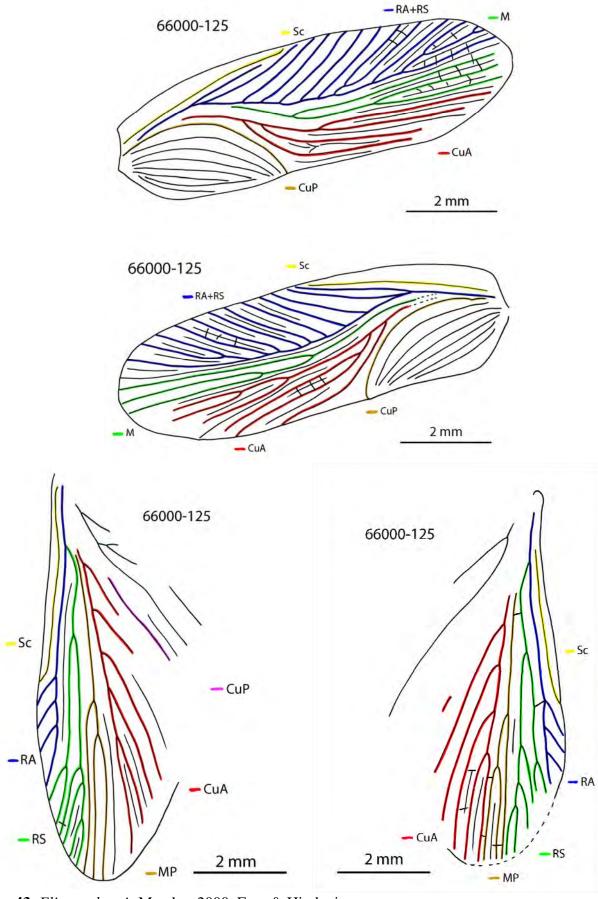
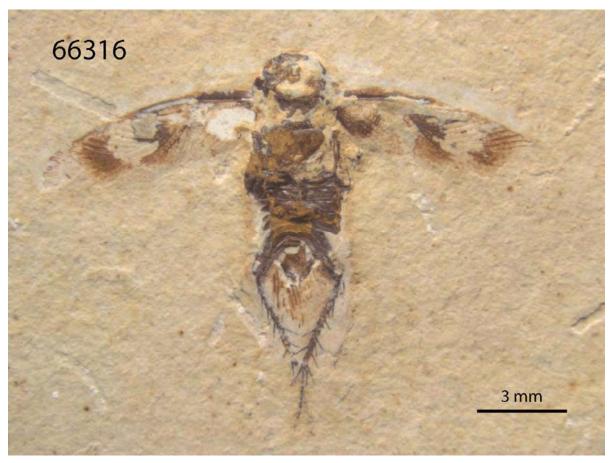


Fig. 43. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen SMNS 66316: Female. Forewing preserved with a distinctly band color pattern.



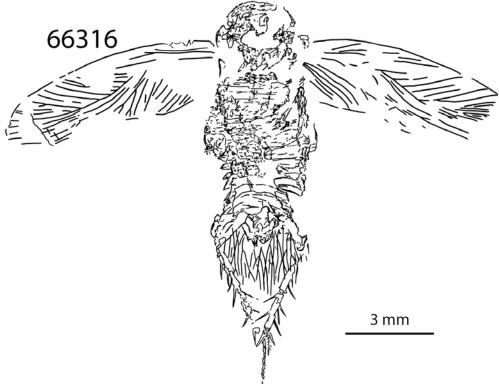
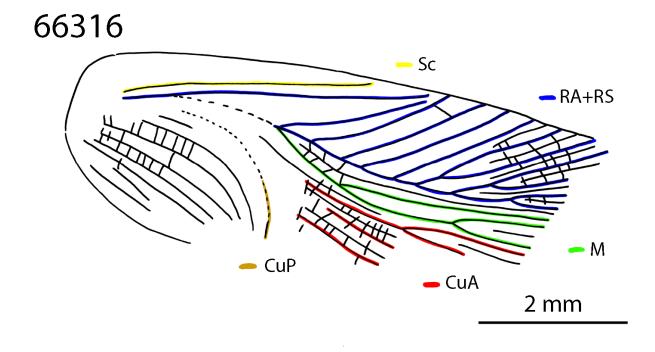


Fig. 44. Elisama brevis Mendes, 2000, Habitus.



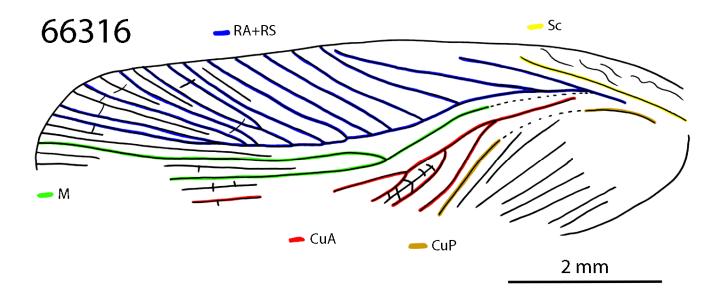
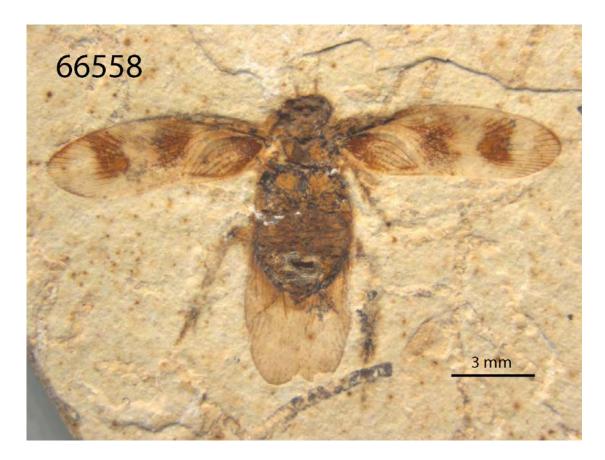


Fig. 45. Elisama brevis Mendes, 2000, Forewings.

Specimen SMNS 66558: Male, ventral view. Head probably three ocelli existed between two compound eyes in the forehead side. Forewing preserved with a distinctly banded color pattern. Foreleg tibia is about the same length as tarsus.



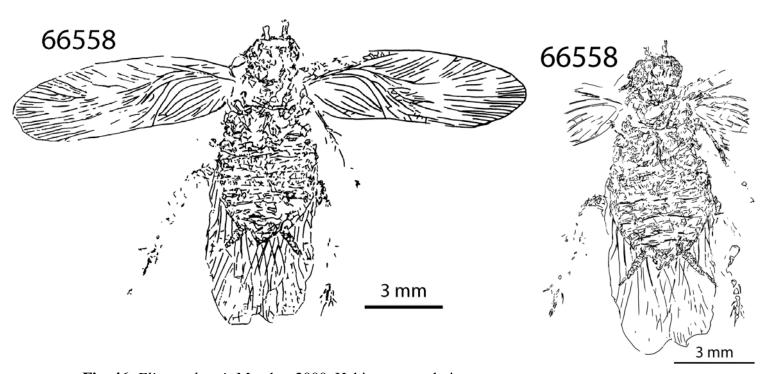


Fig. 46. Elisama brevis Mendes, 2000, Habitus, ventral view.

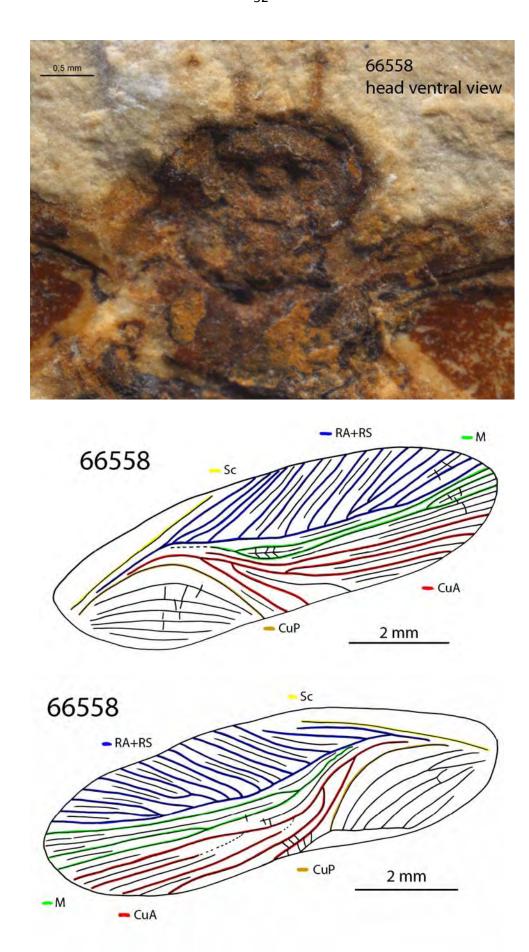
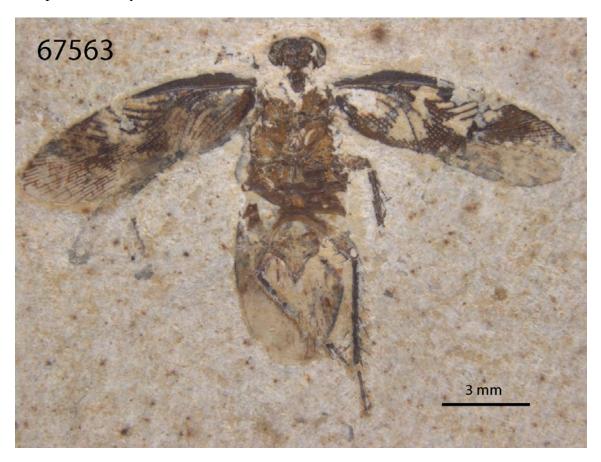


Fig. 47. Elisama brevis Mendes, 2000, Head & Forewings.

Specimen **SMNS 67563**: Female. Forewings sclerotized. Hind leg has long and strong spines. Ovipositor clearly.



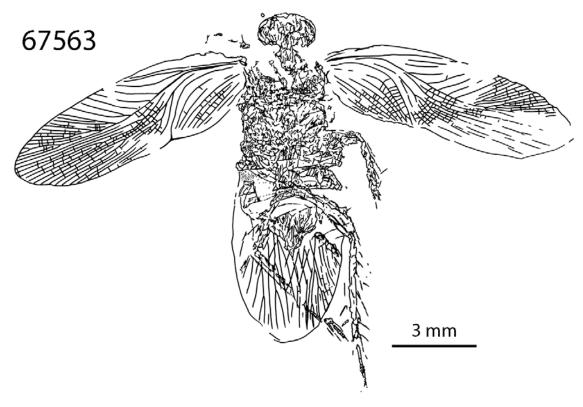
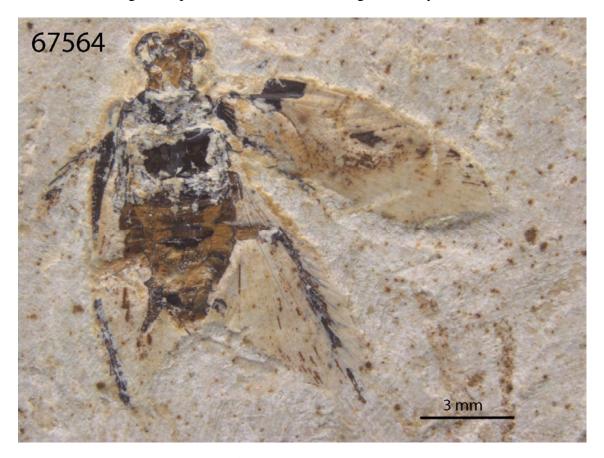


Fig. 48. Elisama brevis Mendes, 2000, Habitus.

Specimen **SMNS 67564**: Female. Large compound eyes well preserved. Fore and hind legs tibia with several long, thin spines. Terminaila with unsegmented styli.



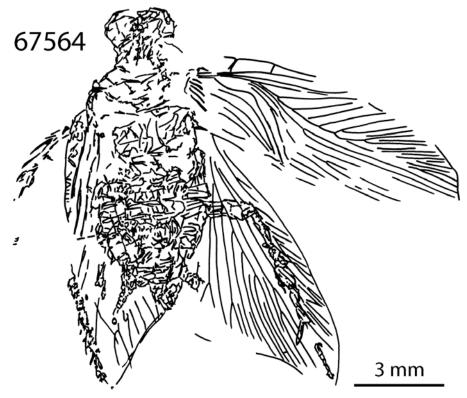
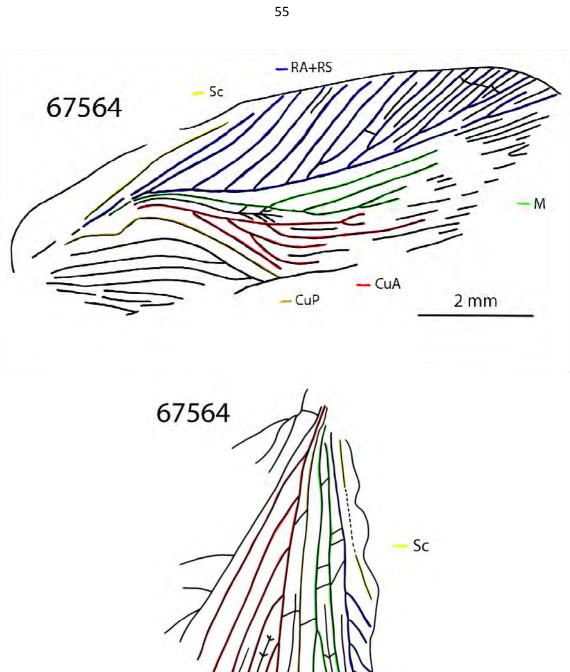


Fig. 49. Elisama brevis Mendes, 2000, Habitus.



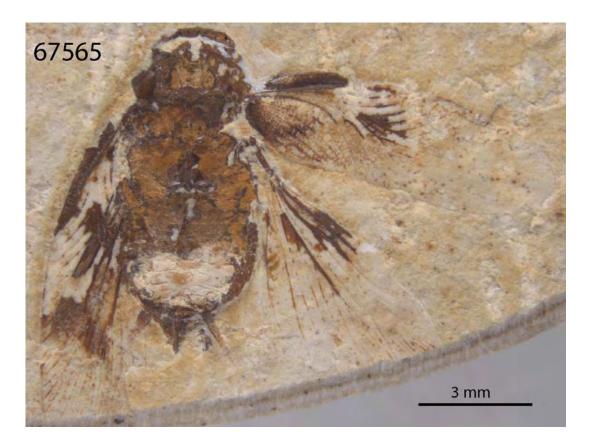
- RA

-RS

2 mm

Fig. 50. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen **SMNS 67565**: Female. Pronotum sclerotized, nearly rounded and about 1.5 times long as head width. Forewing sclerotized. Abdomen rounded. Ovipositor short, well preserved.



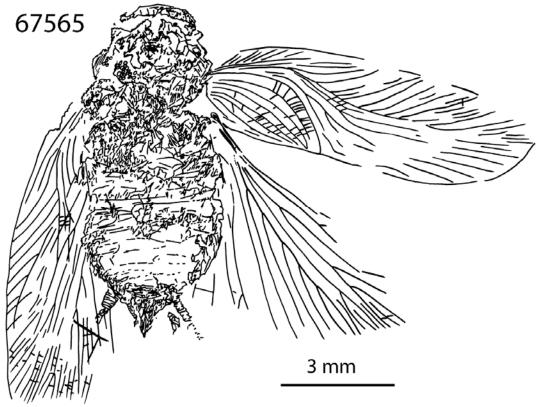


Fig. 51. Elisama brevis Mendes, 2000, Habitus.

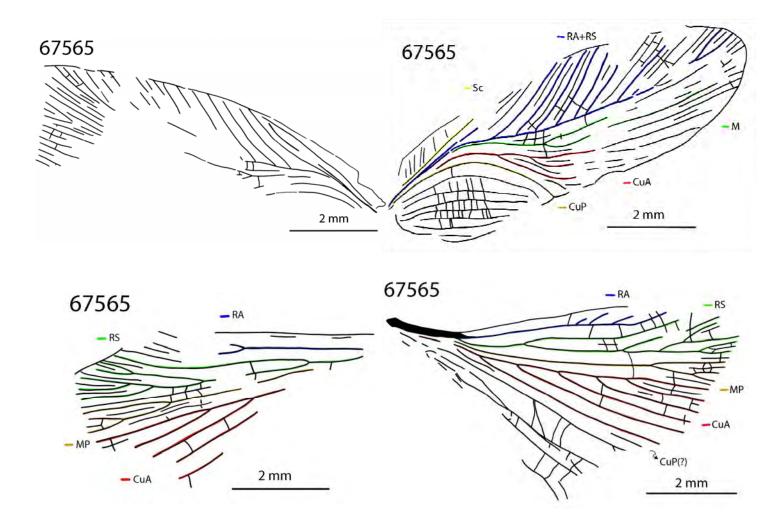
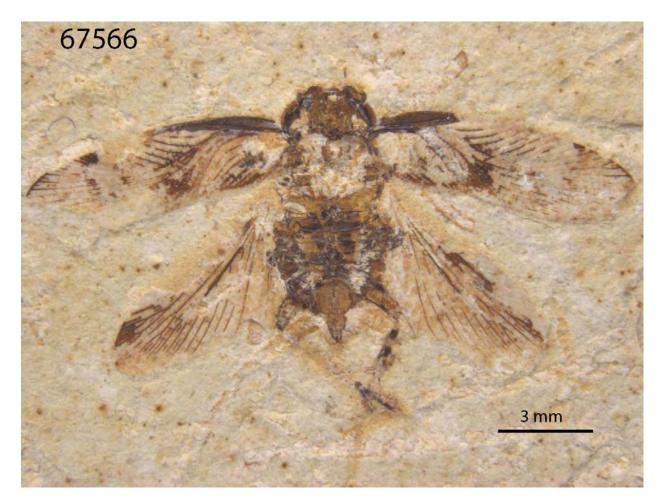


Fig. 52. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen SMNS 67566: Female, with the complete and unfold fore and hind wings.



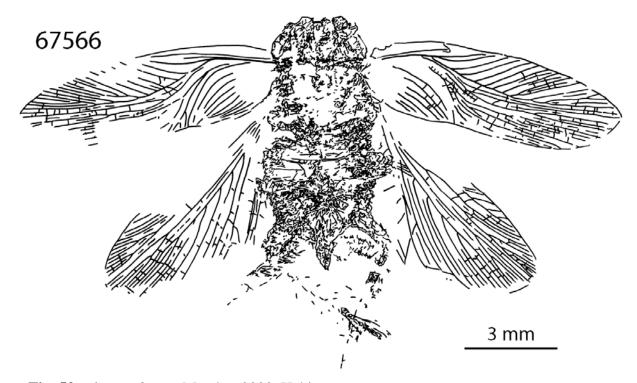


Fig. 53. Elisama brevis Mendes, 2000, Habitus.

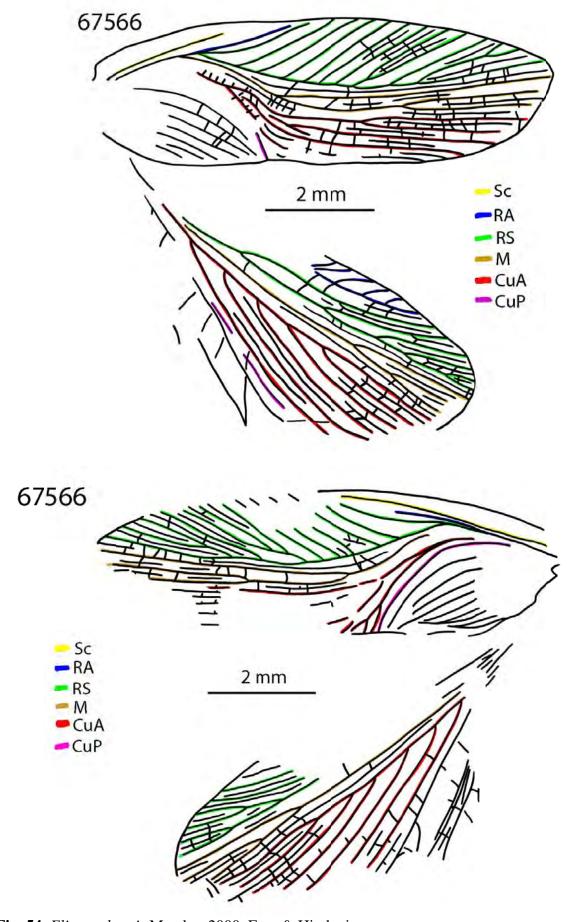
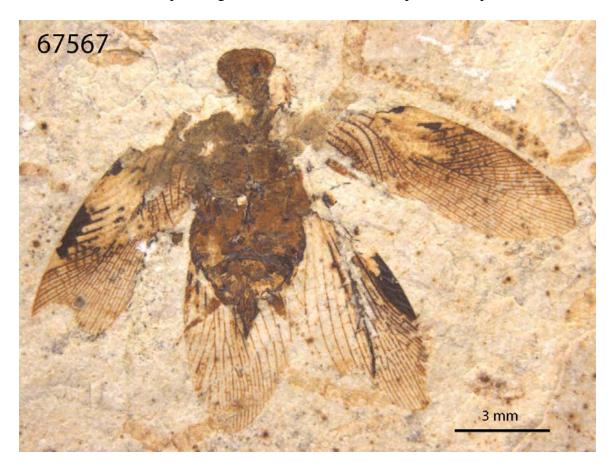


Fig. 54. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen **SMNS 67567**: Female. Hind wing in the anterior margin, that is RA area, sclerotized, or that is pterostigma. Abdomen rounded. Ovipositor sharp.



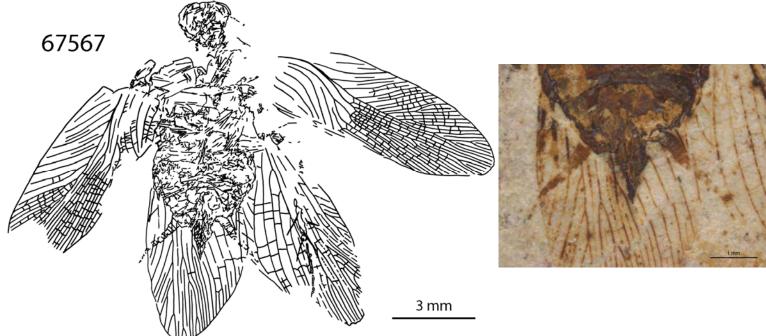


Fig. 55. Elisama brevis Mendes, 2000, Habitus & Ovipositor.

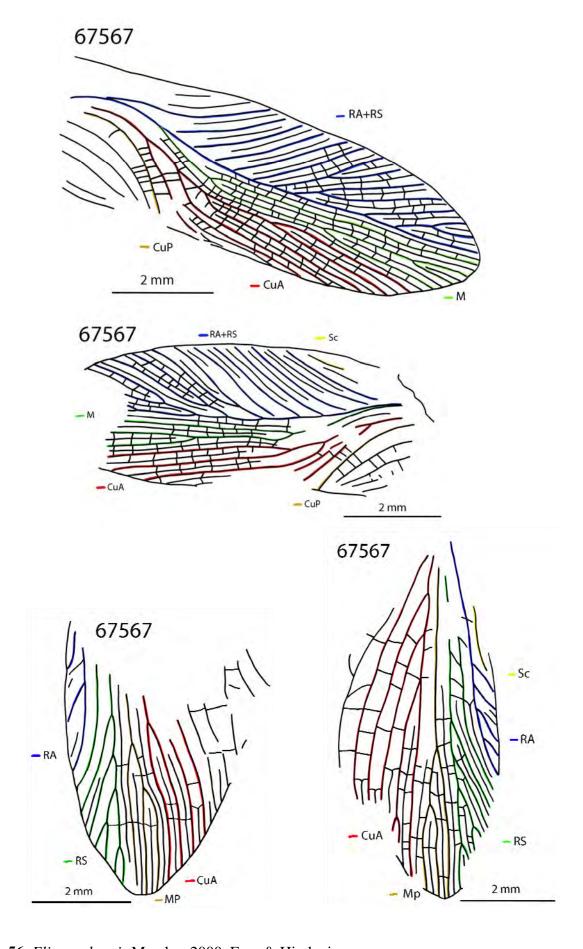
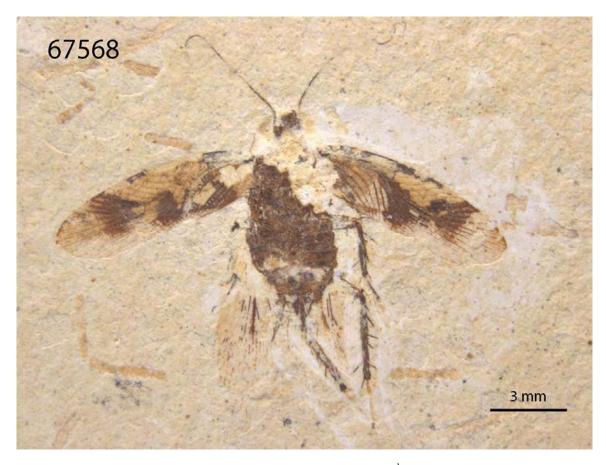


Fig. 56. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen **SMNS 67568**: Female. Antenna about the same length as the body. Mid and hind legs tibia with several long, strong spines.



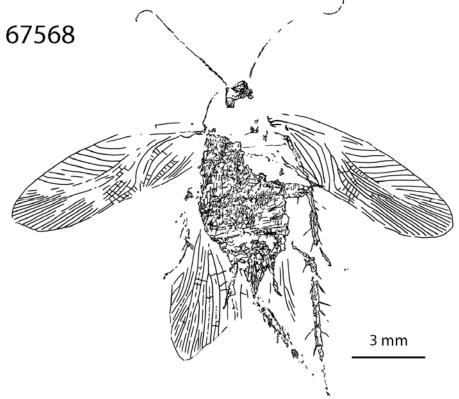


Fig. 57. Elisama brevis Mendes, 2000, Habitus.

Specimen **SMNS 67569**: Female. Pronotum is about 1.5 times wide as the head, nearly rounded, except in the hind point sharp. Mid leg femur with several short spines.

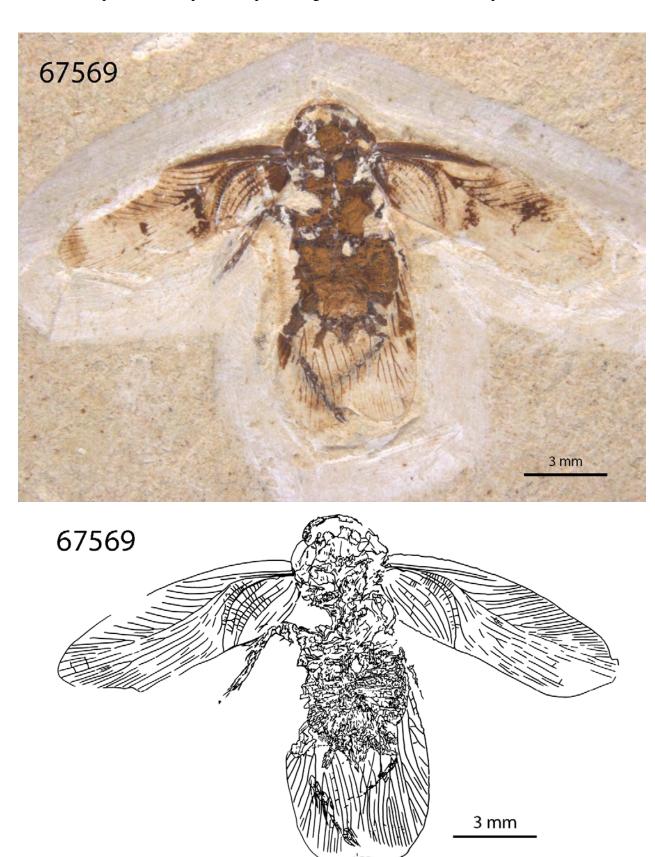
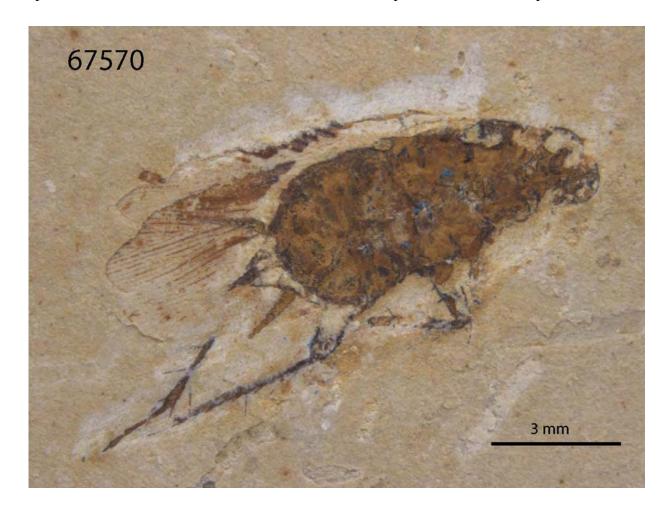


Fig. 58. Elisama brevis Mendes, 2000, Habitus.

Specimen SMNS 67570: Female. Abdomen swelled. Ovipositor and cerci well preserved.



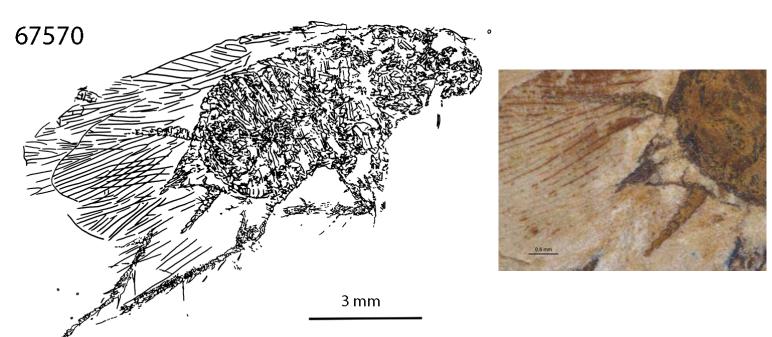


Fig. 59. Elisama brevis Mendes, 2000, Habitus & Ovipositor.

Specimen SMNS 67571: Female. Abdomen rounded. Cerci with numerous sensilla.





Fig. 60. Elisama brevis Mendes, 2000, Habitus.

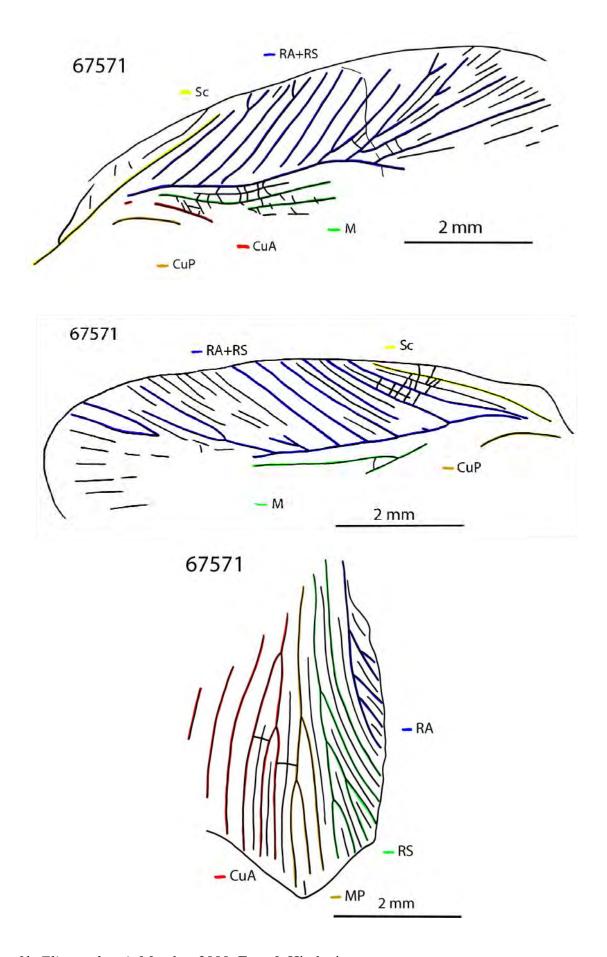
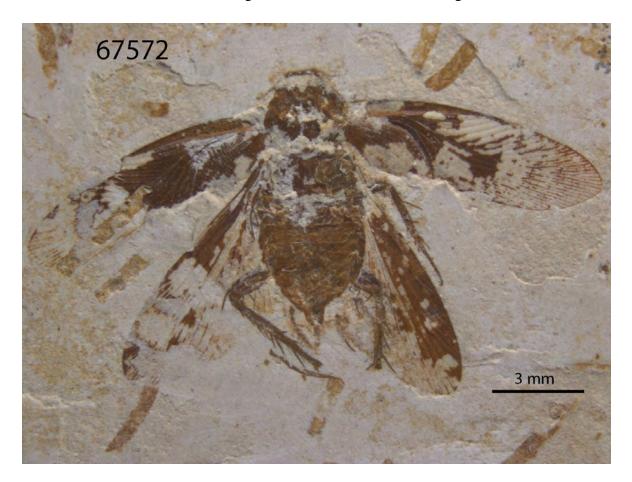


Fig. 61. Elisama brevis Mendes, 2000, Fore & Hind wings.

Specimen **SMNS 67572**: Female, with the complete and unfold fore and hind wings. Full length mid leg is preserved, tarsus with five segments with pretarsus, the length are probably 0.9, 0.6, 0.2, 0.2 and 0.3 mm, five segments with total of 1.8 mm long.



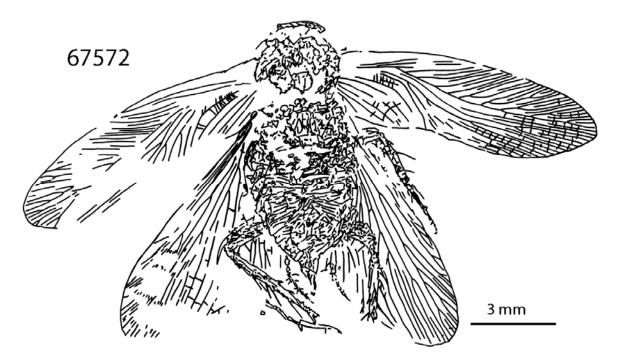


Fig. 62. Elisama brevis Mendes, 2000, Habitus.

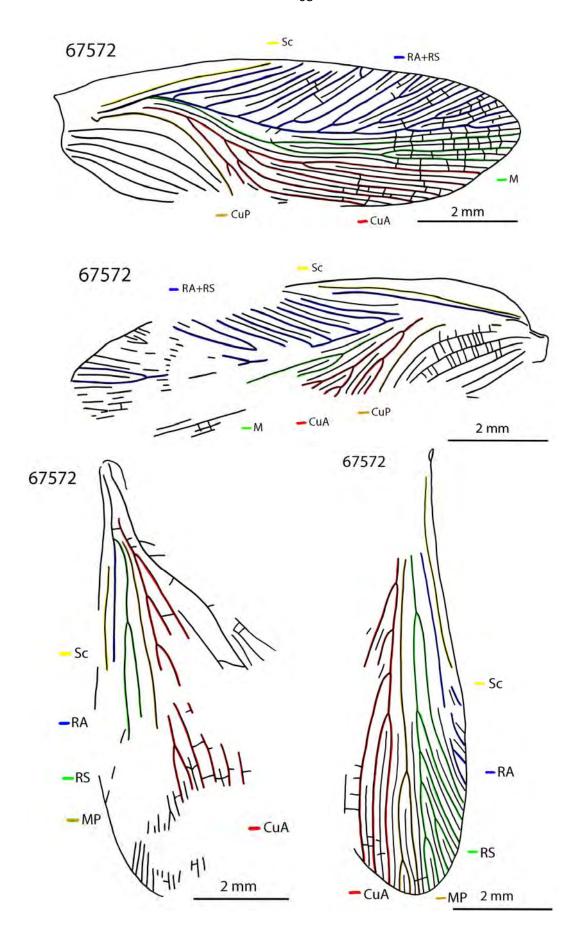


Fig. 63. Elisama brevis Mendes, 2000, Fore & Hind wings.

Discussion: *Elisama brevis* (=americana) differs from (*Mesoblattina*) *limai* by smaller body size. Similar to another species of Blattulidae (*Ocelloblattula* Anisyutkin *et* Gorochov, gen.) by head with probably three ocelli reside in the forehead between the compound eyes (Anisyutkin & Gorochov, 2008). The ovipositor of *E. brevis* (=americana) (about 10.13-16.67% of body length) is tendentious convexer than that in Umenocoleoideas both species in the Crato Formation (by *P. axelrodi*: 10-12.12% and by *P. maxima*:7.84-12.26%), and till clearly longer than that in *Cratovistima sp. nov.* (SMNS 66000-127 by 7.89%).

Genus: (probably) Elisama Giebel, 1856

Species: undescribed (Unknown Species A) (figs. 64-66)

Specimen **SMNS** 67573: One pair complete and nearly unfolded hind wing. Forewing detail unknown and is about 12 mm long and 4.2 mm wide. Hind wing 12 mm long.

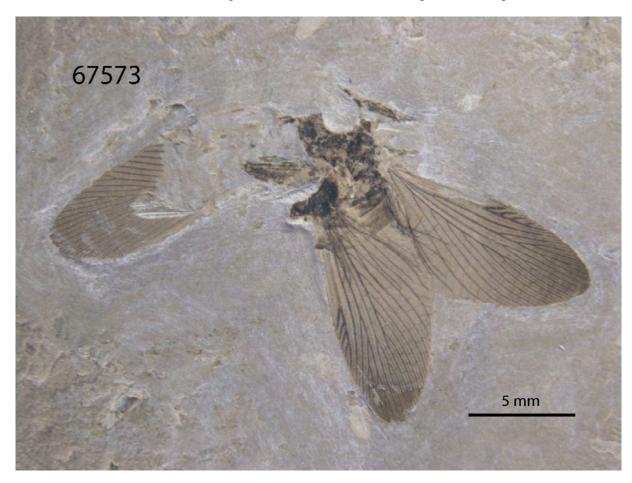


Fig. 64. Unknown Species cockroach A, Fore & Hind wings.

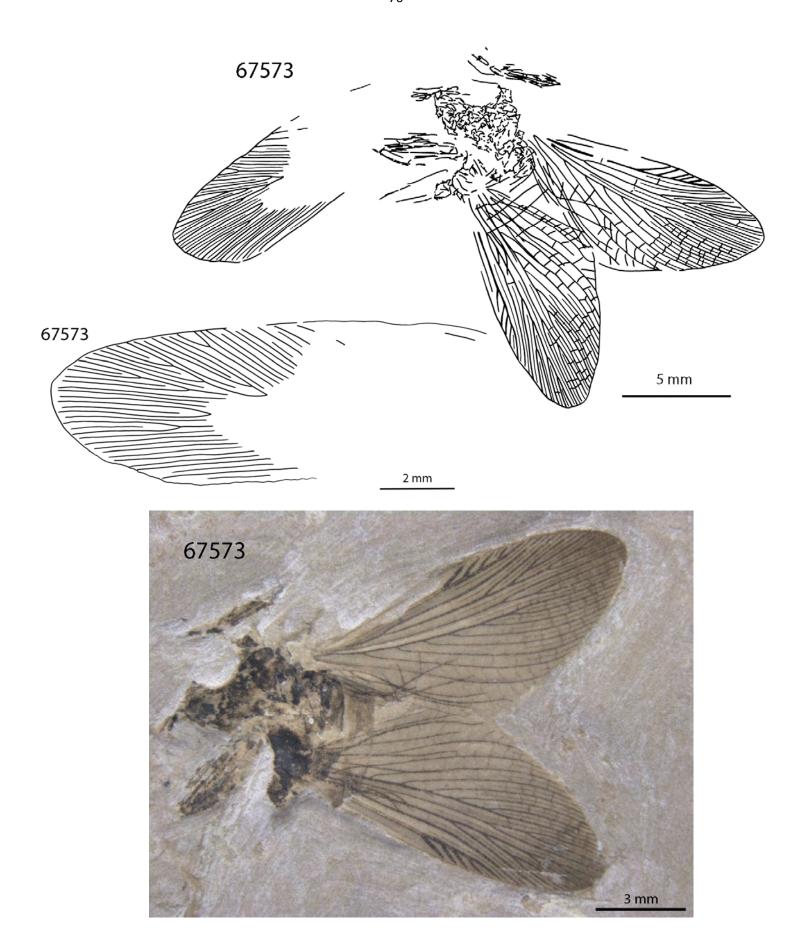


Fig. 65. Unknown Species cockroach A, Fore & Hind wings detail.

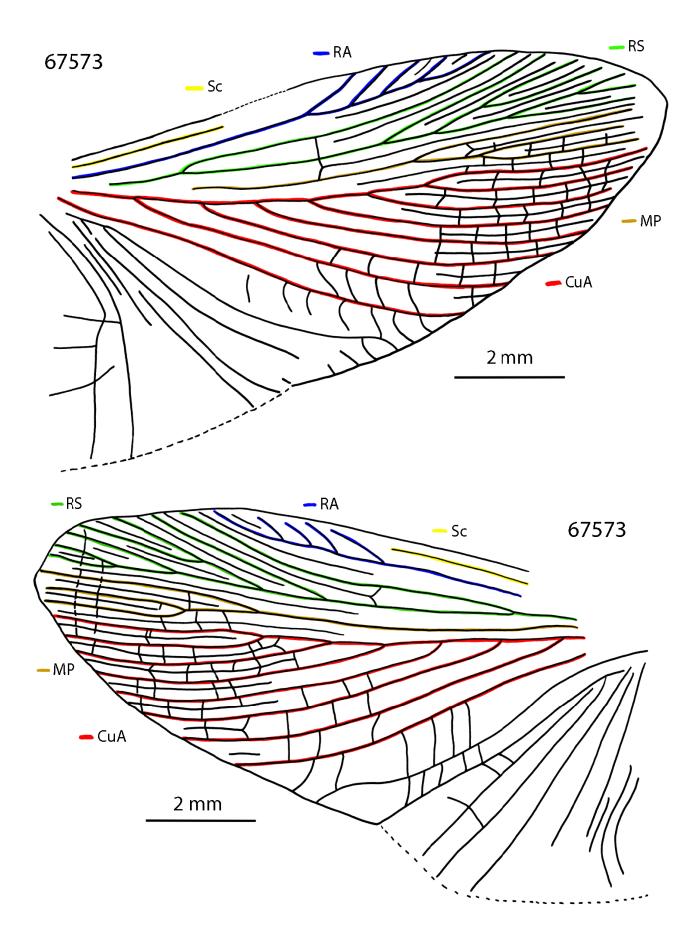


Fig. 66. Unknown Species cockroach A, Right & Left Hind wings detail.

Description: Hind wing 12 mm long, Sc alone, reaching less than ½ length of the anterior margin, RA with five branches, RS with seven branches, MP with three branches, CuA with eight branches, CuP alone and A1 with about four (to five) branches. According to Vršanský (pers. comm.) this specimen representative of the family Blattulidae, probably a species of *Elisama*, but not belong to *Elisama americana* (=brevis), very similar is also hind wing of attached *Kridla*.

Discussion: Hind wing, except with probably slightly larger size otherwise very similar to *Elisama parallela* Vršanský, 2003 by venations (in *E. parallela*: Sc alone, R+RA four to seven, MP three to five, CuA six to eight branches); differs from *Elisama tsaganica* Vršanský, 2002 (=*Ctenoblattina tsaganica* Vršanský, 1999) by hind wing larger size and similar in most parts of venations (in *E. tsaganica* hind wing 8-9 mm long and Sc simple, RA three to seven, RS three to seven, MP two to four, CuA four to seven, CuP simple and A1 two to four branches). This two morphological difference between *E. parallela* and *E. tsaganica* are rather sexual dimorphism present in Blattulidae (Vršanský, 2003b).

Remark: SMNS 67573 is much close to *Elisama parallela* both in size and form. Generally the hind wing is larger than another species of genus *Elisama*. Detail summary as below:

Differs from Kridla stastia Vršanský, 2005 by hind wing clearly larger size (in K. stastia 8.1 mm long) and wing venation (in K. stastia: Sc alone, RA seven, RS four, MP two, CuA six and CuP simple branches) (Vršanský, 2005a). Differs from Elisama fragmentaria Vršanský, 2005 by hind wing larger size (in E. fragmentaria ca. 10-11 mm long) and with generally more branches (in E. fragmentaria Sc simple, RA five, RS two to three, MP two and CuA about six branches) (Vršanský, 2005c). Differs from Elisama brevis (=americana) Vršanský, 2002 by hind wing larger size (in E. americana 8.5-10 mm long) and wing venations (in E. americana Sc alone, RA four to five, RS six to seven, MP three and CuA six branches). And compare with the Material from Liaoning, China. Differs from Habroblattula drepanoides Wang, Liang et Ren, 2007 by hind wing slightly larger size (in *H. drepanoides* 10 to 11 mm long) and wing venation (in H. drepanoides Sc simple, RA five to six, RS nine to eleven, MP two to five and CuA six to nine branches) (Wang et al., 2007a). Elisama extenuata Ren, 1995 by hind wing 7-8 mm long and Sc simple, RA four to six, RS four to seven, MP three to four and CuA five to six branches (Wang et al., 2007b). Elisama cuboides Wang, Ren et Liang, 2007 by hind wing 10 mm long and Sc simple, RA six, RS seven, MP six and CuA seven branches (Wang et al., 2007b). Macaroblattula ellipsoids Wang, Ren et Liang, 2007 by hind wing 10.5 mm long and Sc simple, RA four to five, RS six to eight, MP six and CuA six to eight branches (Wang et al., 2007b).

Superfamily: Blattoidea

3.1.4. Family: Blattellidae Karny, 1908

Blattellidae is the largest family of living cockroaches, comprising more than 1740 species and about 209 genus (Roth, 1991). Transition between the Jurassic and Cretaceous is characterized by the change in the dominance order of families, and by appearance of extant families in the fossil record. Caloblattinidae have been replaced by Blattellidae, Mesoblattinidae and, to a lesser extent, by Blattulidae as the dominant families (Vršanský *et al.*, 2002). The Blattellidae is the dominant family in the Santana roach assemblage, representing about 60% of the cockroaches. Two species (one undescribed) of two undescribed genera include (*Mesoblattina*) *limai* (Vršanský, 2004).

Genus: undescribed

According to Vršanský (pers. comm.) the species (*Mesoblattina*) *limai* is currently not attributed to any genus, as it is apparently another genus and family. But based on the morphological characteristics of forewing, which is identical with *Piniblattella vitimica* and other species in this genus. It is possibly, the species belong to the genus *Piniblattella*.

Piniblattella gen. Vršanský, 1997

Type species. *Piniblattella vitimica* Vršanský, 1997 (=*Mesoblattina vitimica* Vishniakova, 1964)

Original description of genus, according to Vršanský, 1997: Head structure similar to that of *Symploce*; eyes large, ellipsoidal in lateral view. Body cuticle poorly sclerotised (like in the living *Blattella germanica*), probably brownish. Outer valvulae in females present, male abdominal terga VII, VIII with glandular area sclerotised, convex. Forewing extending beyond apex of abdomen, elliptical; Sc simple or terminally forked; CuA branches meeting posterior wing margin. Medial stem rich, branched with 12 to 23 veinlets; Radius without distinct R1. Hind wing (known for type species only) with CuA secondarily branched; A1 terminally forked, 6 posteriormost veins folding fan like at rest. R1 distinct and RS with apical forked ramifications. Legs cursorial, strong; coxae large, subcontiguous medially, mid and hind pairs separated by keel; femora and tibiae carinated, fore tibia very short.

Species: (Mesoblattina) limai Pinto & Purper, 1986 (figs. 67-74)

Original diagnosis, according to Pinto & Purper, 1986: Body 13.15 mm long; head wide, pronotum subcircular, tegmen 12.80 mm long, 1.36 mm wide; costa area short; Sc bifurcated; R with 8 to 11 branches some furcated. MA and CuA free; anal veins simple; intercalated veins and few cross-veins present.

Emended diagnosis, according to Bechly, 2007a: Body length 11-14 mm; antenna about as long as body; pronotum subcircular, very broad (about 200-233% of head width) with very broad lateral lobes; forewing venation typically blattellid with Sc bifurcated, R 8-11 branches (some of them bifurcated), MA and CuA free and branched, several anal veins simple and

ending on CuP, intercalary veins and crossveins present (not as few as mentioned in the original description).

New description: Pronotum subcircular, hind margin relative straight, about twice the width as the head, fore margin of pronotum reaches nearly the same length as the top of head. Head with two large compound eyes, with two ocelli in the forehead. Thorax with coxa in roaches form, mid-and hind leg tarsus about 4/5 length of tibia, tarsus with five segments. Forewing: 10.3-13 mm long and 3.5-4.2 mm wide, Sc typically blattellid with bifurcated, RA+Rs with 15-23 branches totally, M with six-nine branches (except SMNS 66315 left side with five), CuA with two branches (except SMNS 66315 left side with four). Hind wing: about 12-13 mm long, detail unknown. Cerci in typical roaches form and about 14 segments. Terminalia with unsegmented styli.

Specimen **SMNS 66312**: Ventral side. Head with two well preserved compound eyes, near the scape and in the fore head side exist two ocelli, mouthparts well preserved. Pronotum about twice of the width as the head. Thorax with coxa in roaches form. Terminalia near cerci with one pair styli, unsegmented.

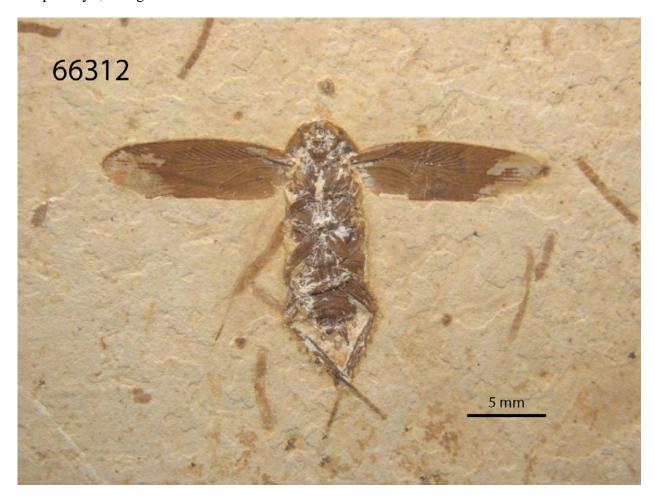


Fig. 67. (Mesoblattina) limai Pinto & Purper, 1986, Habitus, ventral view.

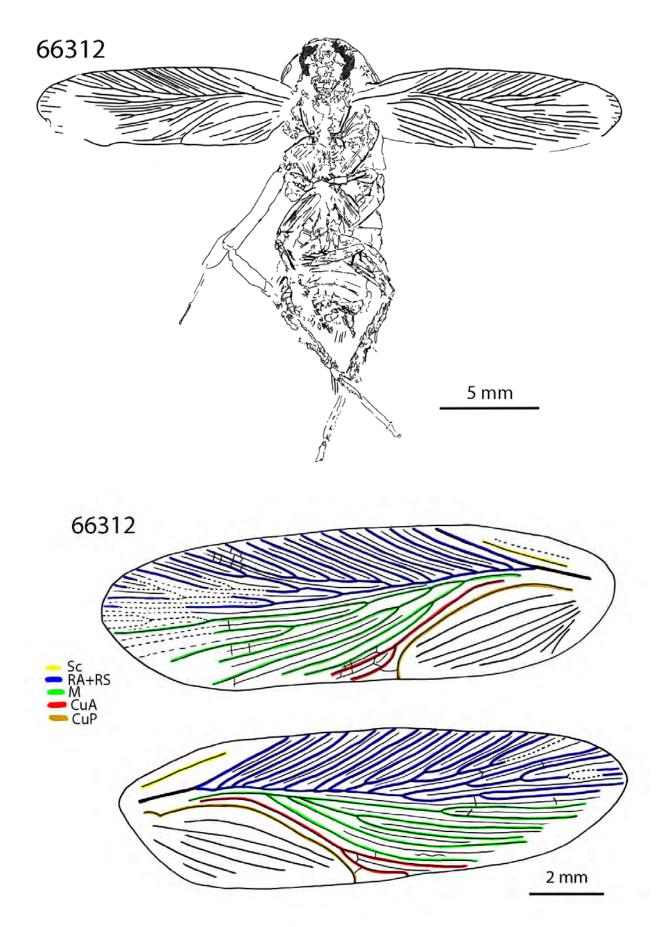


Fig. 68. (Mesoblattina) limai Pinto & Purper, 1986, Habitus & Forewings.

Specimen **SMNS 66314**: Antenna shorter than body length. Mid- and hind leg tarsus long and well preserved.

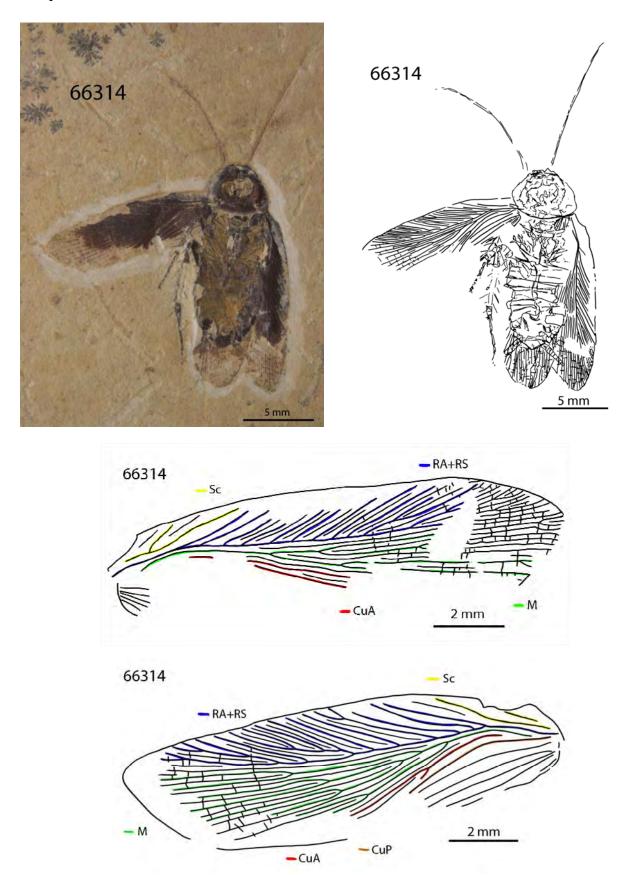
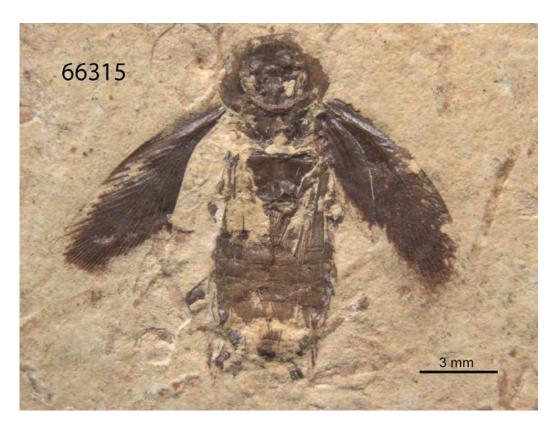


Fig. 69. (Mesoblattina) limai Pinto & Purper, 1986, Habitus & Forewings.

Specimen **SMNS 66315**: The venation between left and right forewings clearly different, especially in M and CuA. In the right side, CuA with two- and M with totally nine branches, that is more in "normal" form. In the left side, the CuA with four- and M with "only" five branches, is rather unusual. Left side is also a little smaller (9 mm long, 3 mm wide) than the right side (10.3 mm long, 3.5 mm wide) and the "normal" size. It is possibly, that the left side is still in nymph phase, but the sclerotization in both sides is quite equal.



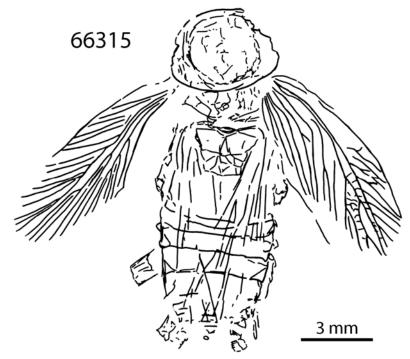
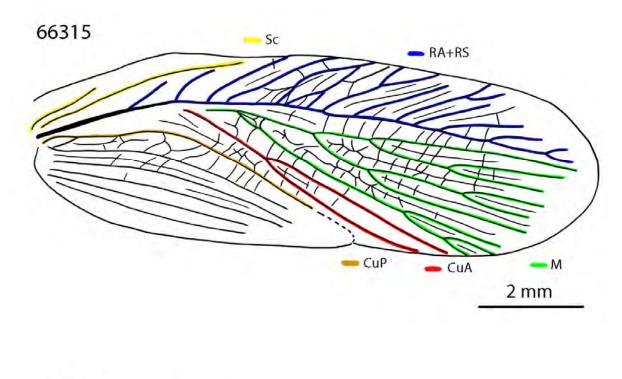
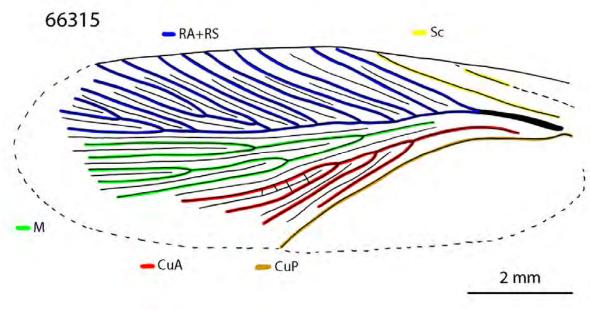


Fig. 70. (Mesoblattina) limai Pinto & Purper, 1986, Habitus.





**Fig. 71.** (*Mesoblattina*) *limai* Pinto & Purper, 1986, Forewings; variation between right- & left forewings from the same individual.

Specimen **SMNS 66319**: Pronotum about double width as head. Its fore margin is almost the same length as the head.

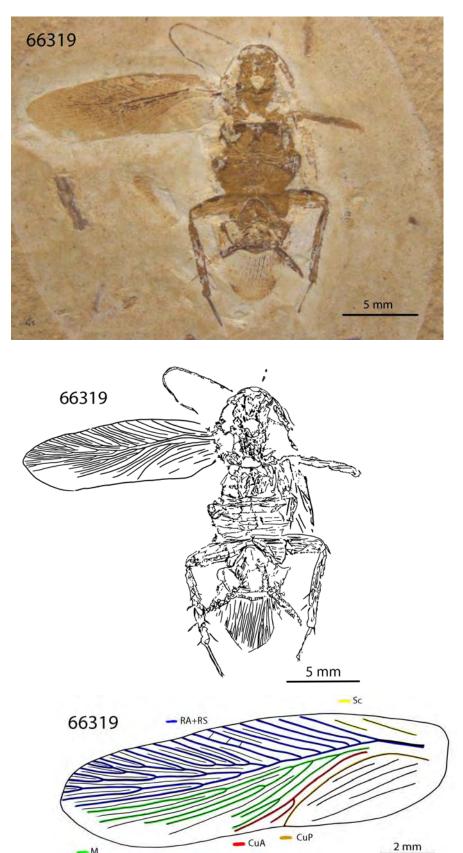
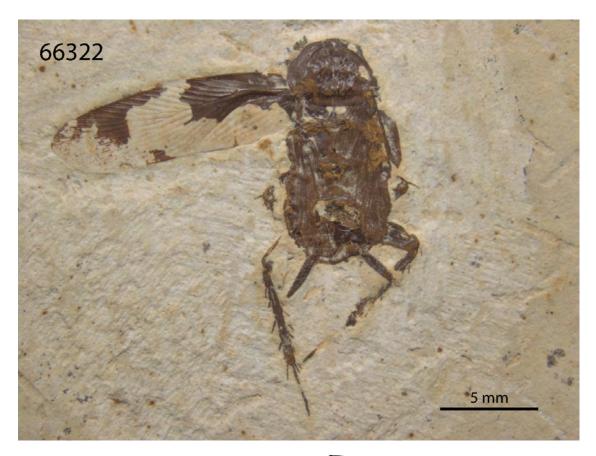


Fig. 72. (Mesoblattina) limai Pinto & Purper, 1986, Habitus & Forewings.

Specimen **SMNS 66322**: Hind leg tibia with several spines. Terminalia with one pair well preserved cerci, 14 segments.



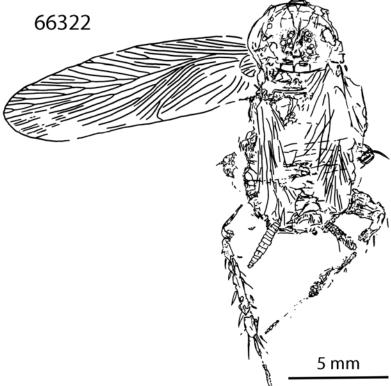


Fig. 73. (Mesoblattina) limai Pinto & Purper, 1986, Habitus.

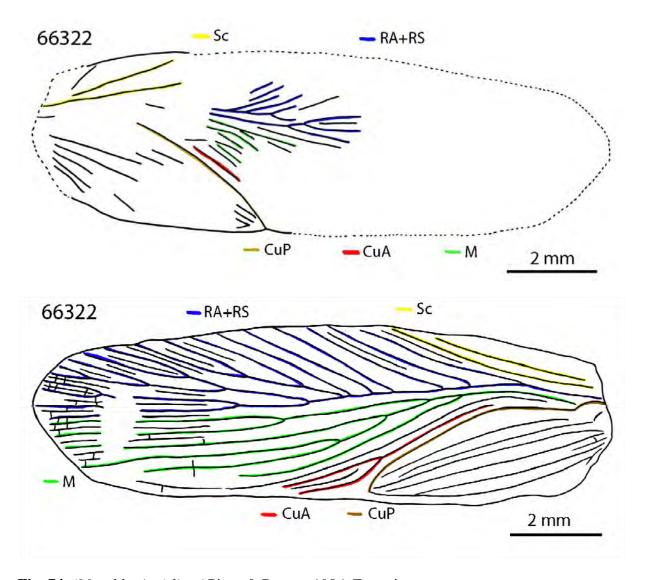


Fig. 74. (Mesoblattina) limai Pinto & Purper, 1986, Forewings.

Discussion: Differs from *Piniblattella vitimica* Vršanský, 1997 by generally smaller size (in *P. vitimica* forewing, 13.5 to 15.5 mm long and 4 to 4.9 mm wide; hind wing 15.2 mm long); by forewing M with more branches (in *P. vitimica* two to five) and CuA with only two main branches (in *P. vitimica* CuA with two main branches and one to seven veinlets).

## **Unnamed new genus and species B** (figs. 75-85)

Original diagnosis, according to Bechly, 2007a: Body length 18.3-27.0 mm; antennae distinctly longer than body (31 mm in a specimen with 25 mm body length); pronotum very large with 215-233% of head width and with very broad lateral lobes; pronotum broadest in the middle of the posterior half; forewing venation typically blattellid.

New description: Antenna shorter than double of body length. Body length 17.8-25 mm. The top of head slightly protrude from the fore margin of pronotum. Pronotum broad, approximately oval shape, posterior half much wider and hind margin relative straight. Forewing: 16-21 mm long and 4.8-6.2 mm wide, Sc with two major branches, each one sometime has several (two-four) terminal branches, RA+RS with 18-20 branches totally, M with 8-12 major branches, some branches with more terminal branches, CuA with three-five

branches, A-veins fused often especially in the base part. Hind wing is about the same length as forewing and is 16-19.5 mm long. Hind leg tarsus is about ¾ of the length of the tibia and with five or four (SMNS 66000-116, 66317; see figs. 76, 81, 84) segments, the first segment is longest and about half of the length of the whole tarsus. Segments continue to be shorter from the second to the fourth tarsal segment, the fifth segment is elongated again, with two claws and pretarsus. Cerci in roaches form, with 14-17 segments. It is possible that the female is generally larger than the male.

Specimen **SMNS 66000-116**: Body size relatively smaller than the other specimens of this species. Pronotum broad and well preserved. The terminalia is male external genitalia partly presented, there is some hook-like structure visible. Unusually hind leg tarsus, left side with five- but right side with four segments (fig. 76). Right side tarsus (totally 4.7 mm) is shorter than left side (totally 5.1 mm). Comparatively from the length of each segment, the "third" segment should be lost by right side. This "four segments tarsus-" pattern is not rare, in specimen SMNS 66317 (fig. 81) both side of hind leg tarsus with only four segments.

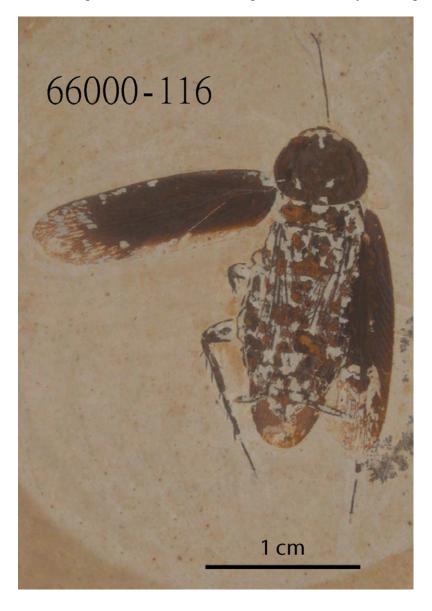


Fig. 75. Unnamed species cockroach B, Habitus.

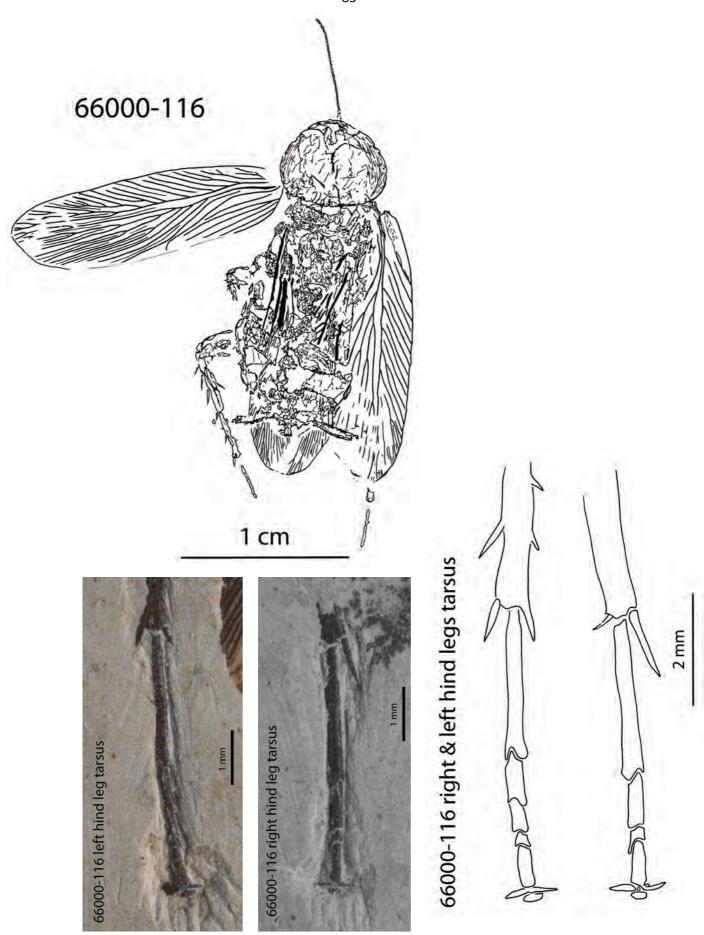
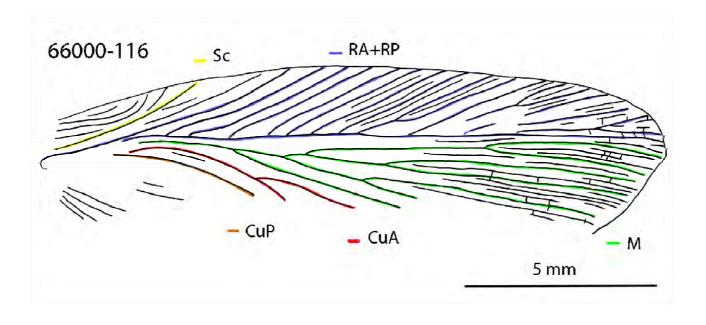


Fig. 76. Unnamed species cockroach B, Habitus & Hind legs tarsus.



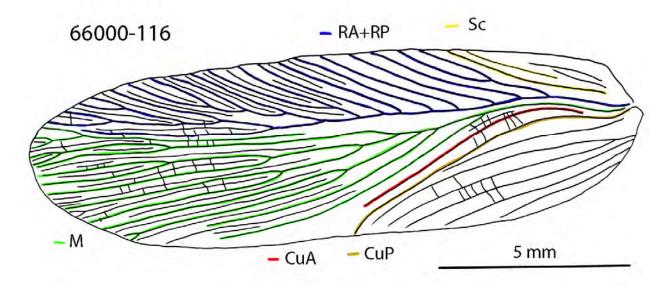


Fig. 77. Unnamed species cockroach B, Forewings.

Specimen **SMNS 66310**: Body size large. Antenna (41 mm long) is about shorter than double of body length (25 mm). Cerci well preserved, about 17 segments.

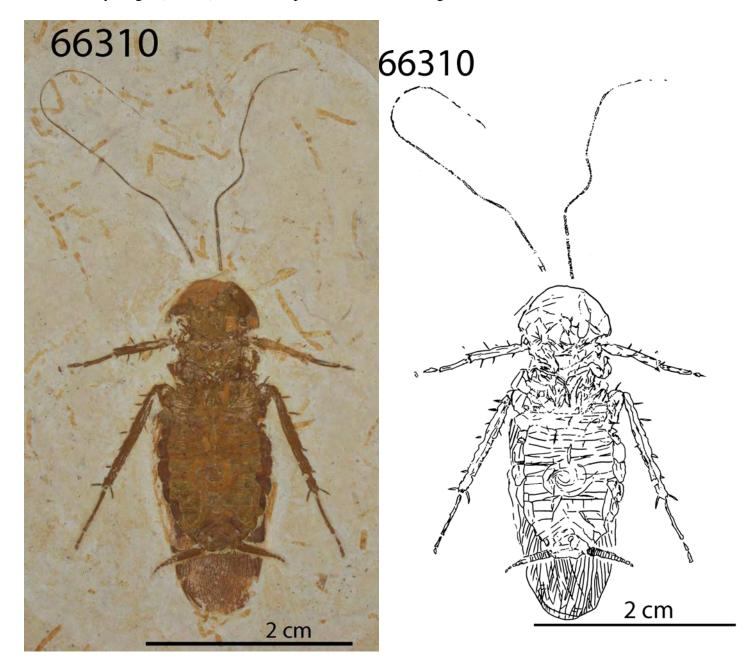


Fig. 78. Unnamed species cockroach B, Habitus.

Specimen SMNS 66313: Mid and hind leg tarsus with five segments.

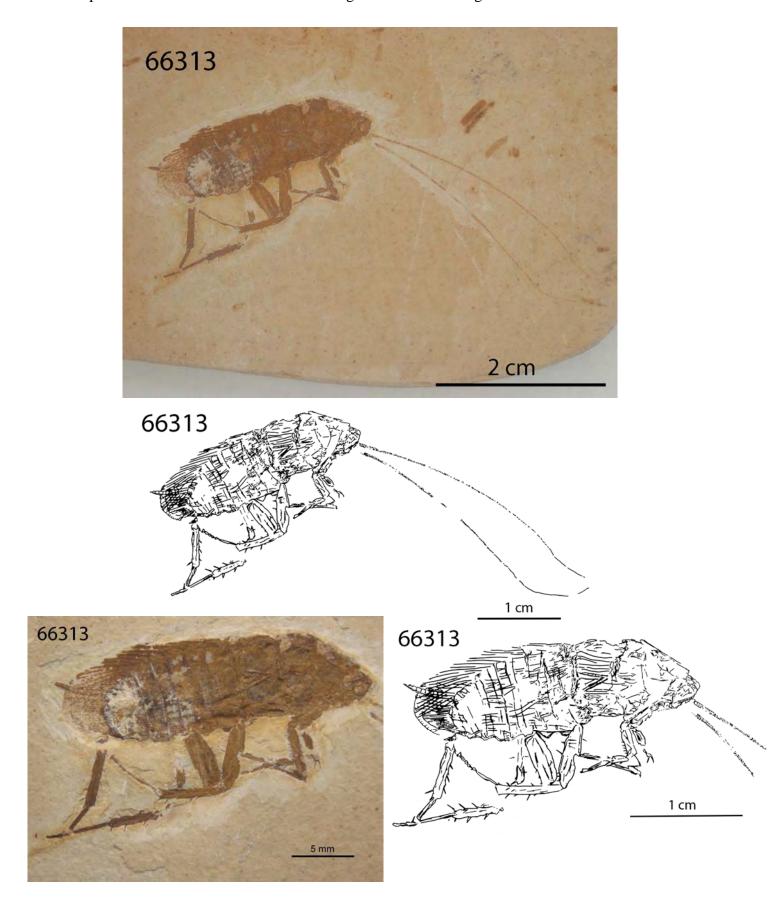
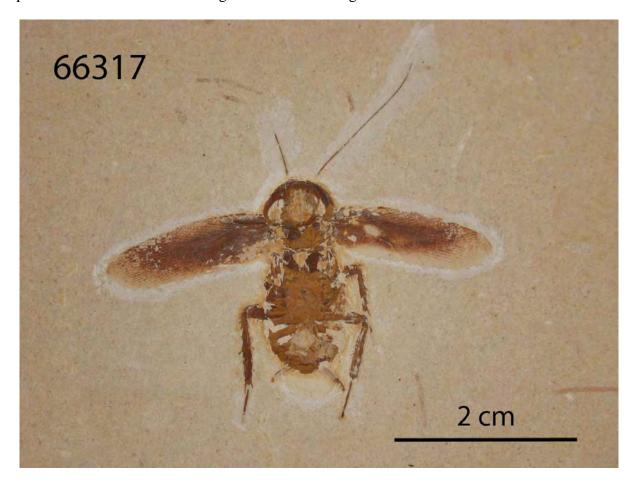


Fig. 79. Unnamed species cockroach B, Habitus.

Specimen SMNS 66317: Hind leg tarsus with four segments



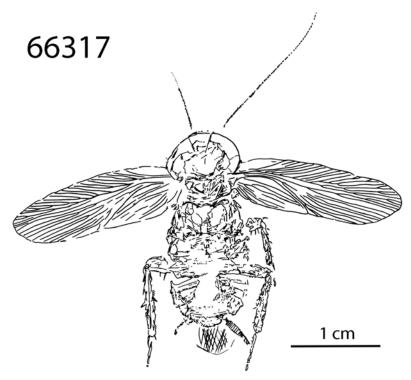


Fig. 80. Unnamed species cockroach B, Habitus.

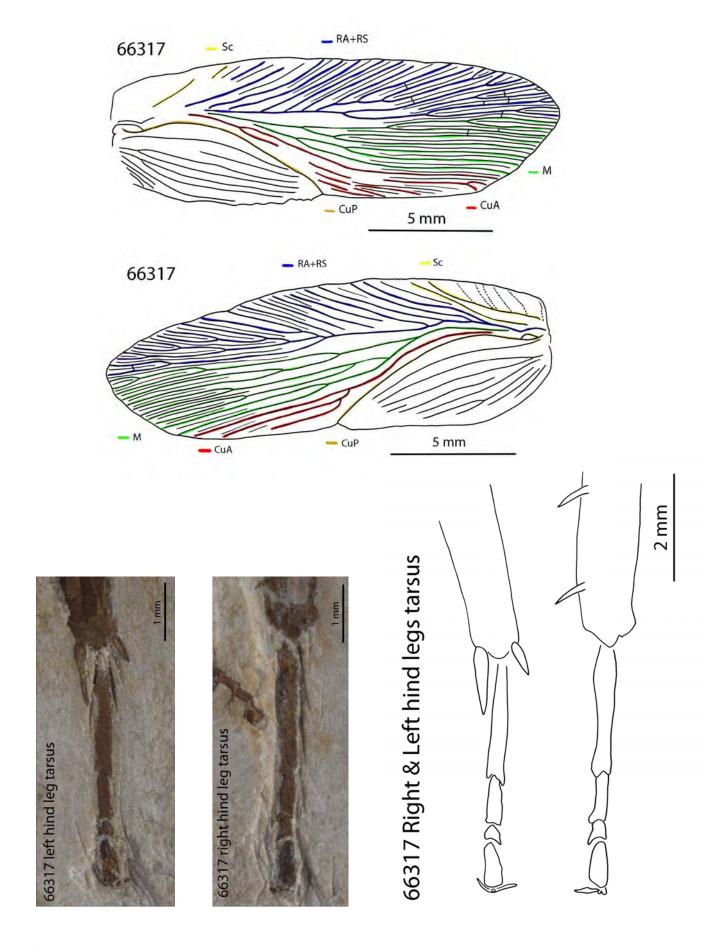


Fig. 81. Unnamed species cockroach B, Forewings & Hind legs tarsus.

Specimen SMNS 66318: Forewing Sc with several branches. Abdomen swelled.

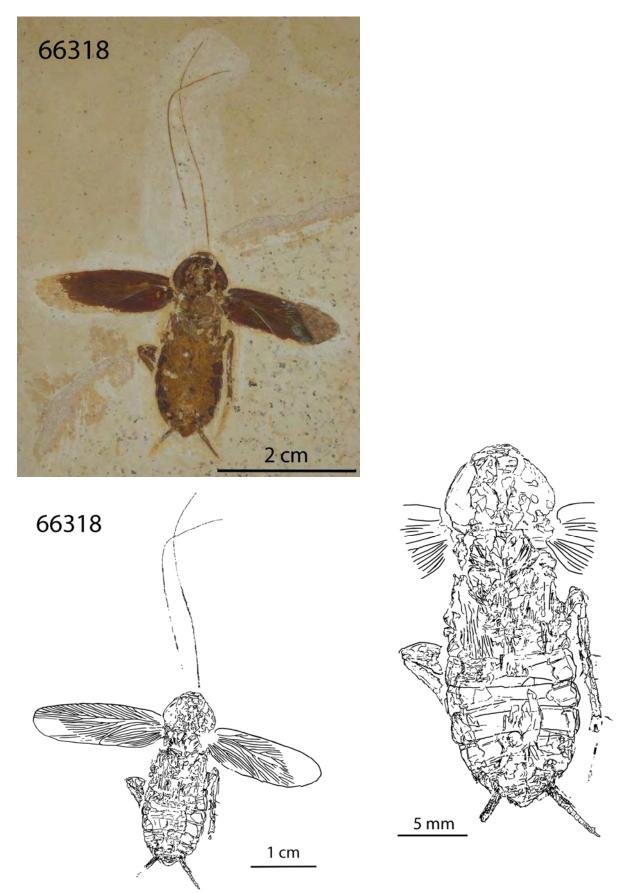
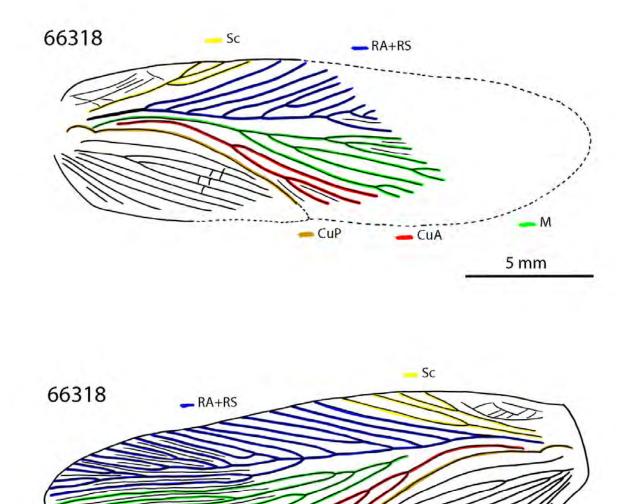


Fig. 82. Unnamed species cockroach B, Habitus & Body part.



- CuP

5 mm

Fig. 83. Unnamed species cockroach B, Forewings.

**—**CuA

Specimen **SMNS 66320**: Forewing Sc with two major branches, the Sc2 has further terminal branches. Hide wing is only partly preserved.

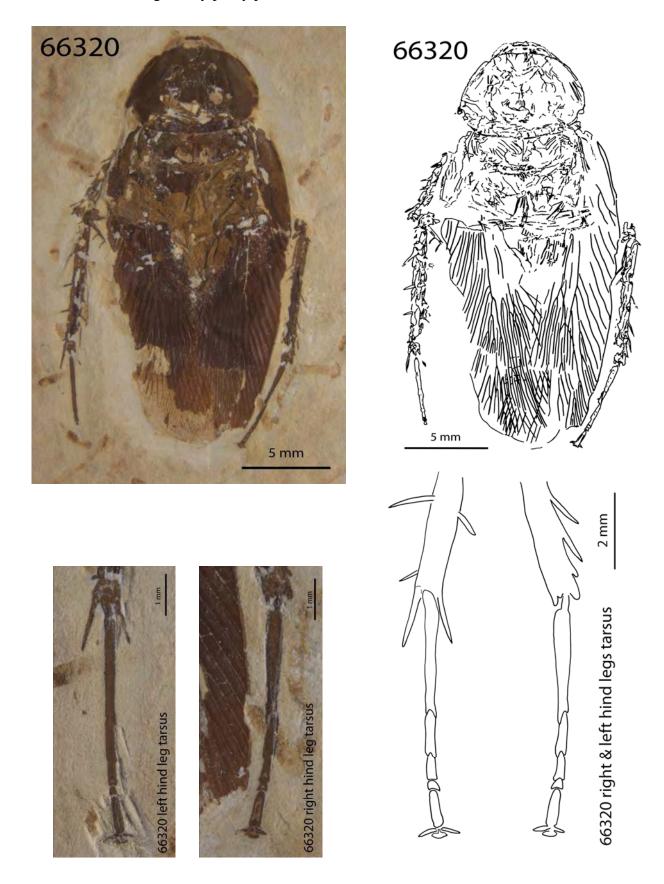


Fig. 84. Unnamed species cockroach B, Habitus & Hind legs tarsus.

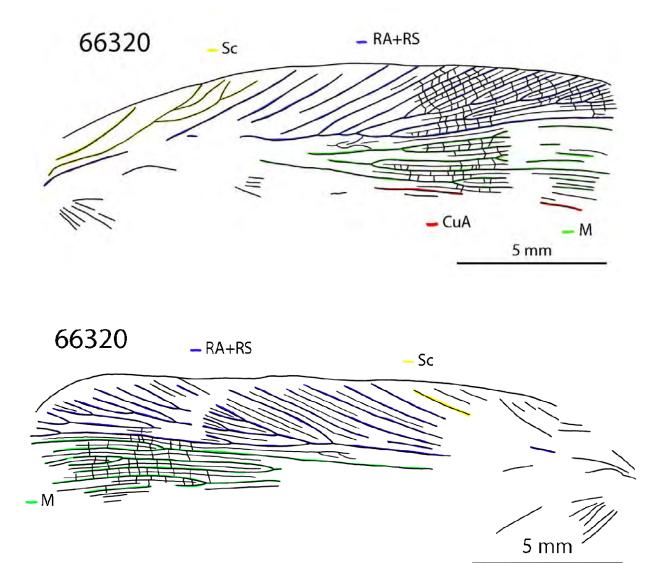


Fig. 85. Unnamed species cockroach B, Forewings.

Discussion: Similar to the (*Mesoblattina*) *limai* Pinto & Purper, 1986, except for the distinctly larger size. Differs from (*M.*) *limai* in forewing by the CuA three-five branches (in *M. limai* the CuA is coincidentally only two branches), and the A-veins fused often.

Family: uncertain

## Unnamed new genus and species C (figs. 86-91)

Original diagnosis, according to Bechly, 2007a: Body length about 8.7-9.5 mm; shape of body longish oval; antennae about as long as body; pronotum much broader than head (width 3.0-3.7 mm, thus 180-195% of head width), posteriorly broader than anteriorly, but with narrower lateral lobes than the new blattellid species mentioned above; forewing venation unknown, but with a broad costa margin; cerci with about 10 segments.

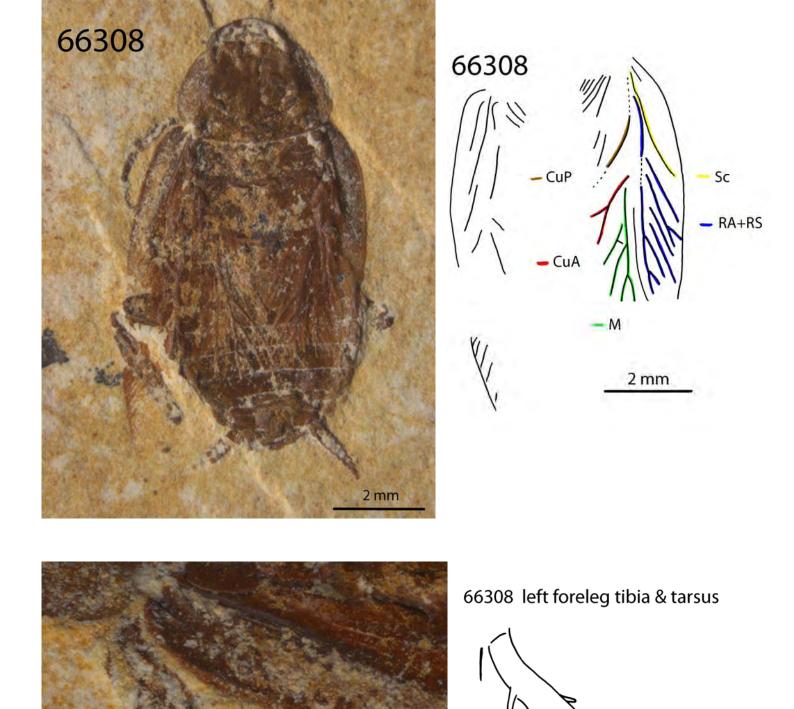
New description: Antenna a little longer than body length. Body about 8.7-11.9 mm long. The top of head slightly protrude from the fore margin of pronotum. The hind margin of pronotum is relative straight. Forewing, costa margin broad, Sc probably bifurcated, Sc1 extra short and except the base part not very distinct. Hind wing Mp at least three branches, CuA at least five branches. For- mid- and hind legs in similar pattern, that is, tibia always slightly longer than femur, tarsus with five segments and all together about 70-86% of tibia length, the first segment is longest, about a half of the whole tarsal length, the second segment is the second longest, third and forth segment shorter, the fifth segment elongated again and with claws and pretarsus. Cerci in roaches form, 13-14 segments. Treminalia with unsegmented styli.

Specimen **SMNS 66308**: Antenna slightly longer than the body length. Fore- and hind wings overlap and only partly identifiable, that is: forewing Sc with two branches, CuA at least two branches, hind wing Mp at least three branches, CuA at least five branches. Foreleg tarsus well preserved. Cerci in typical roaches form, 14 segments.





Fig. 86. Unnamed species cockroach C, Habitus.



1 mm

Fig. 87. Unnamed species cockroach C, Habitus, Forewings & Foreleg.

66308 left foreleg tibia & tarsus

Specimen **SMNS 66309**: Forewing probably much thin, only the base part slightly sclerotized. Hind leg well preserved.

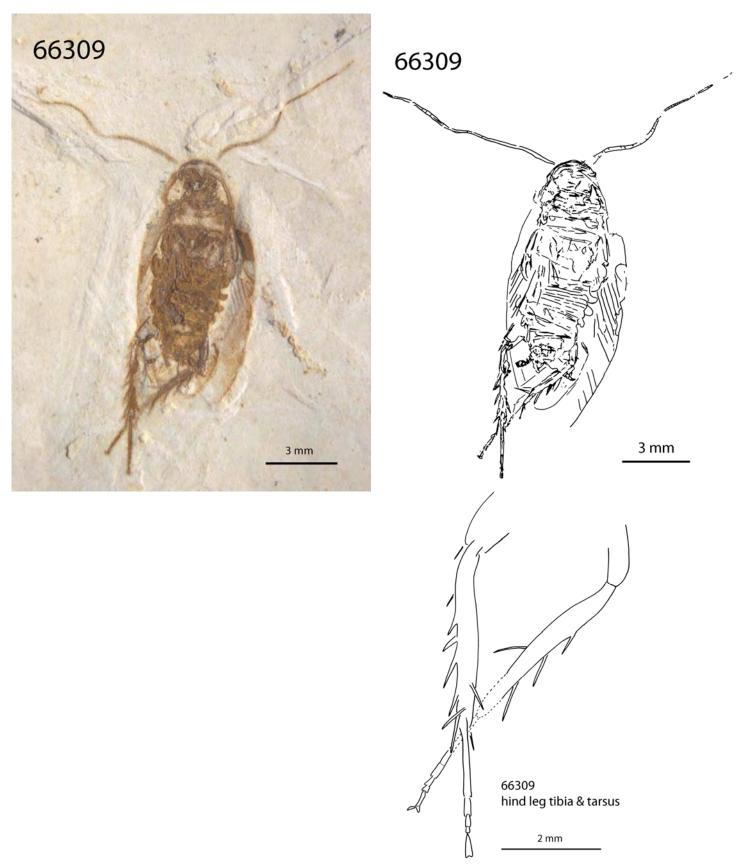


Fig. 88. Unnamed species cockroach C, Habitus & Hind legs.

Specimen SMNS 66311: Hind leg well preserved. Treminalia with unsegmented styli.

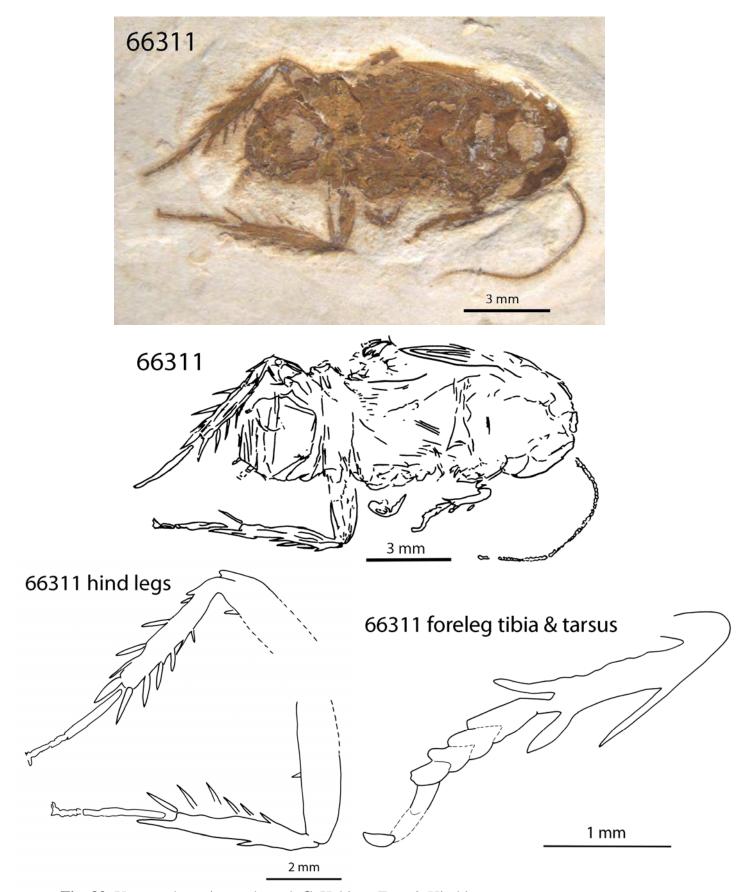


Fig. 89. Unnamed species cockroach C, Habitus, Fore & Hind legs.

Specimen **SMNS 66321**: Ventral side. Head with a pair of large compound eyes. Mouth parts, including labrum, maxillary- and labial palp partly visible. In thorax, the coxal and the trochanters was well preserved.

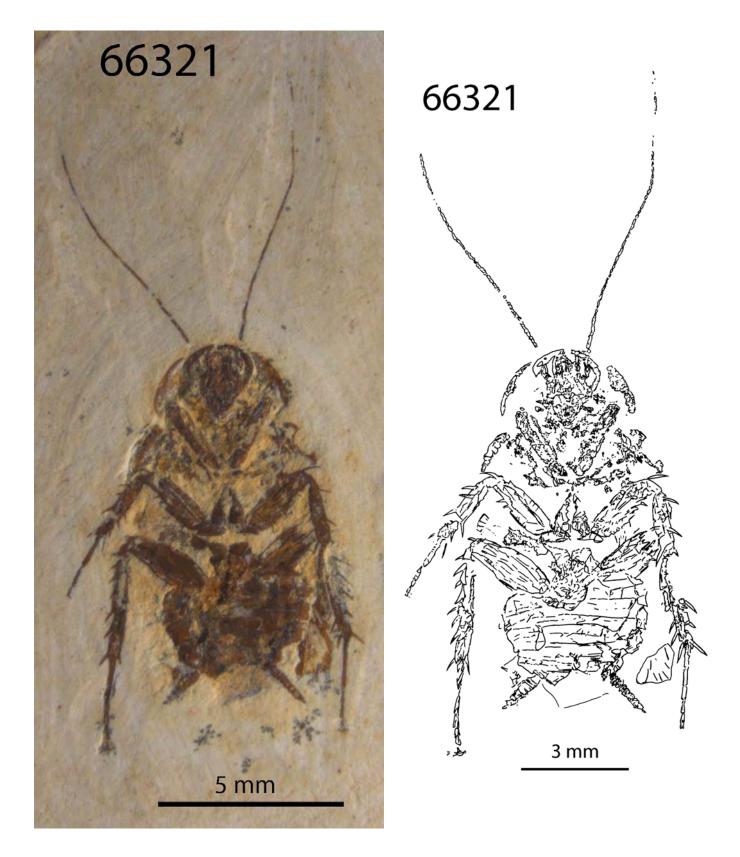


Fig. 90. Unnamed species cockroach C, Habitus.

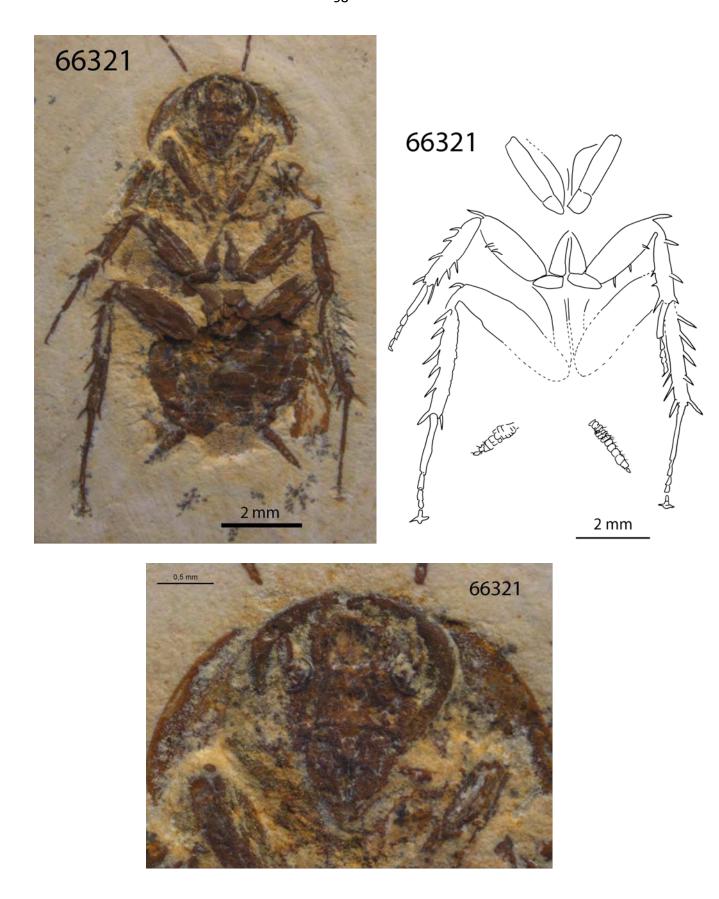


Fig. 91. Unnamed species cockroach C, Legs & Head ventral view.

Discussion: Because of deficient in forewing characters is the comparison with another taxon still difficult.

## 3.2. Order: Mantodea Burmeister, 1838

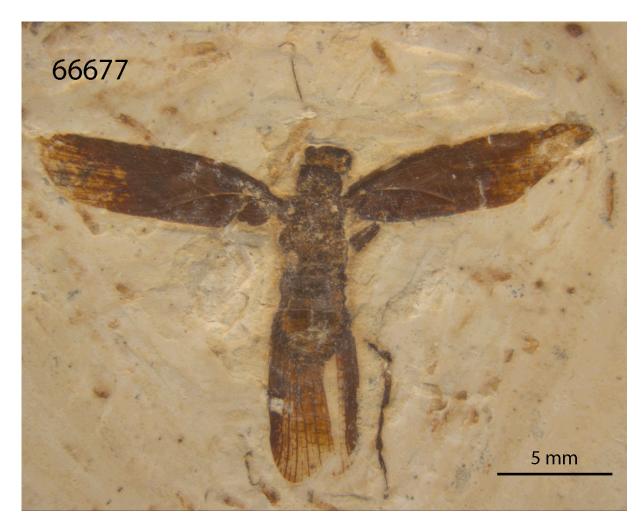
The traditional classification of mantises is by Beier (1968), who recognized eight families: the "bases" mantises, comprising five families (Chaeteessidae, Mantoididae, Metallyticidae, Amorphoscelidae and Eremiaphilidae); Superfamily Mantoidea, comprising three families (Empusidae, Hymenopodidae and Mantidae) and 95% of the recent species in the order, radiated in the early Cenozoic to produce the exuberance of forms seen today (Beier, 1968; Grimaldi, 2003; Grimaldi & Engel, 2005).

Mantodea are very rare in the fossil record. Gratshev & Zherikhin (1993) counted less than two dozen fossil mantids described thus far (included 11 taxa and 10 of them compression from the early to late Cretaceous of Eurasia, some 135-90 Ma) and add that nearly all the taxa need revision (Gratshev & Zherikhin, 1993; Nel & Roy, 1996; Grimaldi, 2007). Grimaldi (2003, 2007) counted approximately only 25 described species, of them 17 species-level taxa of Cretaceous Mantodea, and only about 10 Cenozoic ones are known, though the available Cenozoic specimens are not as well studied and their diversity is much greater. The phylogenetic pattern thus indicates that mantises evolved in the late Jurassic, had their basal diversification in the Cretaceous, and explosively diversified (as the Mantoidea) in the Cenozoic (Grimaldi, 2007).

Meanwhile the Crato Formation has yielded two species of mantises. One is obscured and not named specimen SMNS 66528 (fig. 92) and the second species is based on a spectacular series (holotype specimen AMNH 1957, and paratypes SMNS 66677, SMNS 66680, SMNS 66678, SMNS 66679 and SMNS 66519; figs 93-95) of the primitive mantis, *Santanmantis axelrodi* Grimaldi, 2003 (Bechly *et al.*, 2001; Grimaldi, 2003, 2007; Grimaldi & Engel, 2005).



**Fig. 92.** Unnamed species mantis SMNS 66528, fore- and hind wings unknown.



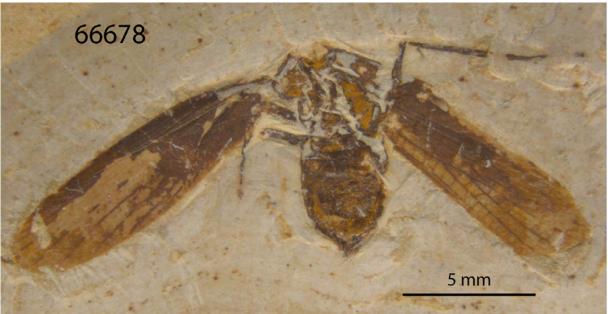


Fig. 93. Santanmantis axelrodi Grimaldi, 2003, SMNS 66677, 66678.



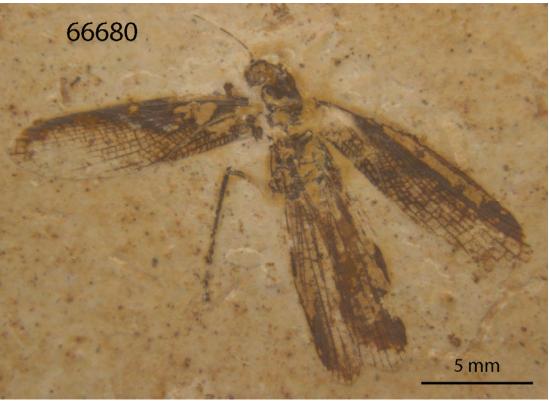
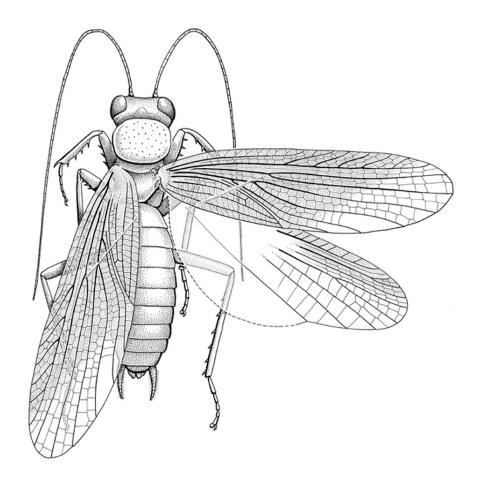


Fig. 94. Santanmantis axelrodi Grimaldi, 2003, SMNS 66679, 66680.



**Fig. 95.** Life restoration of *Santanmantis axelrodi* Grimaldi, 2003. Forewing length 12.5 mm. After Engel & Grimaldi (2005).

## 3.2.1. Family: Chaeteessidae Handlirsch, 1920 sensu Gratshev & Zherikhin, 1993

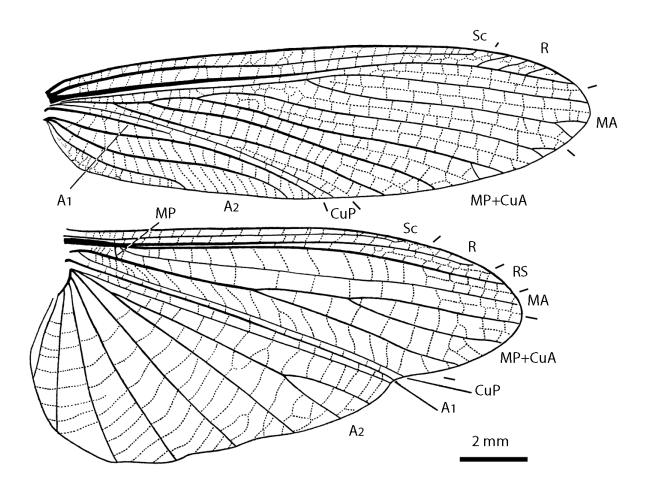
The family seems to be paraphyletic, because all features common for its genera clearly symplesiomorphic (Gratshev & Zherikhin, 1993; Grimaldi, 1997).

Original Diagnosis, according to Gratshev & Zherikhin, 1993: Small or medium-sized mantids with cylindrical body. Head freely movable, without excrescence; antennae long, filiform. Prothorax short, without lateral expansion. Forewings fully developed; costa field narrow, not widened basally; intercalary veins present, at least between some longitudinal veins; Sc usually moderately long, multibranched; R almost always multibranched apically; RS indistinguishable; M with two or three branches, M5 indistinguishable among transverse veins; CuA at least four-branched; clavus large, distinctly separated. Hind wings fully developed, without color patterns; R usually with short apical branches; RS long, simple; M two or three branched, M5 slightly oblique, transverse; anterior branch of A2 distinct; anal region moderately large. Fore femora narrow, with two ventral rows of rigid setae; fore tibiae without terminal hook, with two rows of rigid setae, setae of apical pair larger than others, symmetrical; tarsal articulation between them. Mid and hind legs without projections, tarsi five-segmented. Abdomen without projections; cerci long, multisegmented, not widened apically.

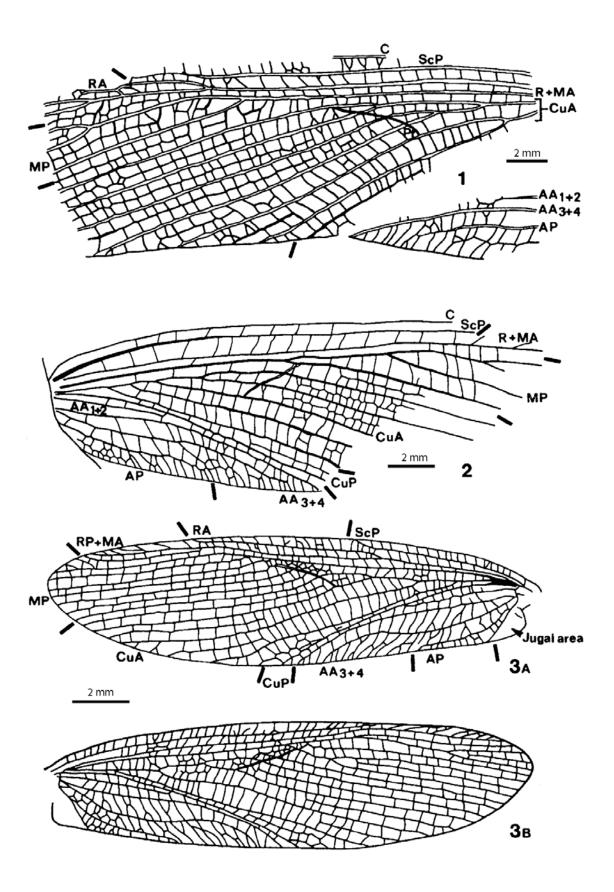
Composition: *Chaeteessa* Burmeister, 1838 (Recent, South America), *Lithophotina* Cockerell, 1908 *see* Sharov, 1962 (Oligocene, North America), *Arvernineura* Piton, 1940 *see* Nel & Roy, 1996 (Paleocene, West Europe), *Cretophotina* Gratshev & Zherikhin, 1993 (Cretaceous, Asia), *Vitimophotina* Gratshev & Zherikhin, 1993 (Lower Cretaceous, Siberia), *Kazakhophotina* Gratshev & Zherikhin, 1993 (Upper Cretaceous, Turonian), *Megaphotina* Gratshev & Zherikhin, 1993 (Oligocene, Russia) and a species within uncertain genus for nymph in Upper Cretaceous amber from Siberia *Chaeteessites minutissimus* Gratshev & Zherikhin, 1993.

# Genus: Chaeteessa Burmeister, 1838

Morphological character: pronotum short, has a unique arrangement of thick, dark foreleg spines, virtually forming a basket and primitively lacks a feature found in all living mantises (Grimaldi & Engel, 2005). The genus *Chaeteessa* has only five recent neotropical (South America) species: *C. caudata* Saussure, 1871; *C. filata* Burmeister, 1838 (fig. 96); *C. nana* Jantsch, 1995; *C. nigromarginata* Salazar, 2004 and *C. valida* Perty, 1833 (fig. 97) (Rondón *et al.*, 2007). The only one fossil description so far is an adult of Miocene amber from the Dominican Republic (Grimaldi, 2003).



**Fig. 96.** Fore- and Hind Wings of *Chaeteessa filata* Burmeister, 1838. (After Smart, 1956, with changed designations of the veins from Sharov, 1962)



**Fig. 97. 1** & **2**: Wings of *Arvernineura insignis* Piton, 1940, France, Palaeocene; **3**: *Chaeteessa valida* (Perty, 1833), Recent specimen, female. **A**-left forewing, **B**-right forewing. (After Nel & Roy, 1996)

Unknown new Species **D** (figs. 98-99)

Specimen **SMNS 67583**: Antenna 31 mm long and more than 110 segments. Forewing 23 mm long and 6 mm wide.



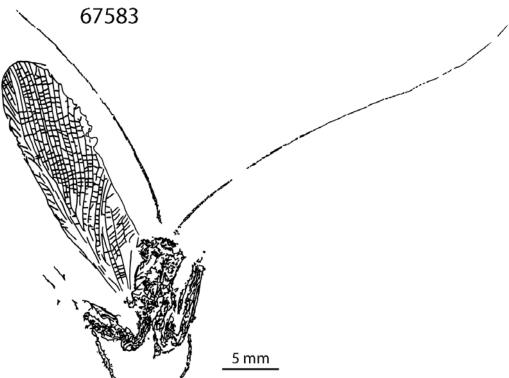
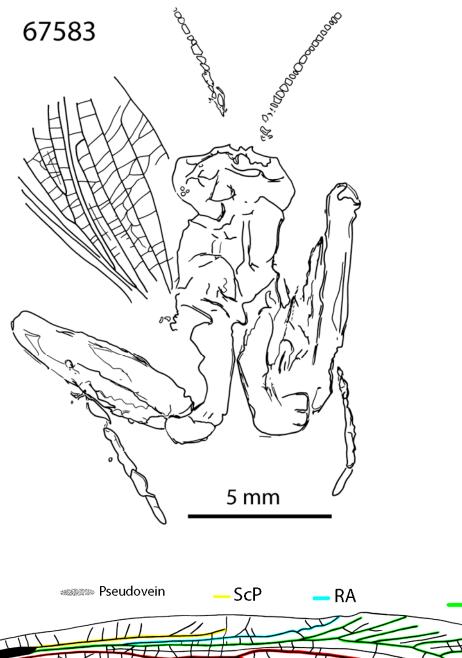


Fig. 98. Unnamed Species mantis D, Habitus.



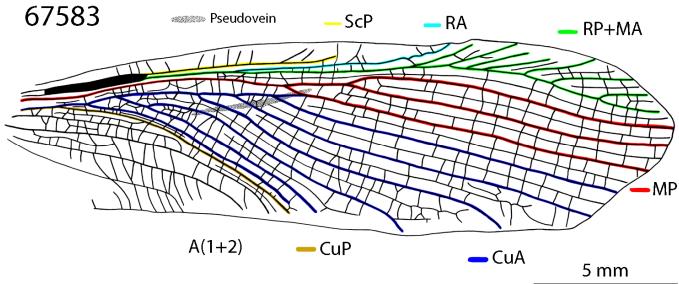


Fig. 99. Unnamed Species mantis D, Body part & Forewing.

Diagnosis: Forewing very similar to the *Chaeteessa valida* (Perty, 1833), differs only by RP+MA and CuA more branched.

Description: Antenna 31 mm long and more than 110 segments. Head is wider than the thorax from dorsal view and with big eyes. Pronotum short. Raptorial Foreleg could be more or less identify, coxa long, femur robust and tarsus segments elongate. Forewing oval formal, 23 mm long and 6 mm wide. Sc about ½ of whole wing length, Sc area much narrower than costa area. RA long and origin in about anterior 1/3 level of wing. RP+MA with eight branches. MP with three branches. CuA with six branches. It is possible, that the first branch of CuA fused with MP3. CuP is adjacent and parallel with CuA6. A with at least three (possible four) branches.

Discussion: Forewing very similar to the *Chaeteessa valida* (Perty, 1833) (fig. 97.3), differs only by RP+MA and CuA more branched and by the origin of CuP much closer to CuA6 (in *C. valida* and *C. filata* the origin of CuP is much deeper). Forewing differs from *C. filata* Burmeister, 1838 and *Lithophotina floccose* Cockerell, 1908 by having the long RA. The forewing size of this specimen is larger than *C. valida* (about 17.3 mm long) and *C. filata* (about 17 mm long).

#### 3.3. Order: **Orthoptera** Olivier, 1789

Well known for their remarkable stridulation and jumping abilities, the Orthoptera constitute the most diverse group of Polyneoptera, comprising approximately 22.500 living species (Grimaldi & Engel, 2005). The monophyly of Orthoptera is well established and supported by both morphological and molecular data (see Hennig, 1981; Flook & Rowell, 1997, 1998; Flook *et al.*, 1999; Gorochov & Rasnitsyn, 2002; Grimaldi & Engel, 2005; Heads & Martins-Neto, 2007). The order is defined by several distinctive morphological apomorphies including large saltatorial (jumping) hind legs with a robust, muscular femur and straightened femorotibial articulation, the lateral development of the pronotum to form a cryptopleuron (the orthopteran "saddle") and a reversal in the orientation of nymphal wing pads during development (Heads & Martins-Neto, 2007). Traditionally, the Orthoptera are divided into two monophyletic subgroups: the Ensifera (crickets, katydids and their allies) and the Caelifera (grasshoppers and locusts).

The Orthoptera fauna of the Crato Formation is of worldwide importance, being one of the most diverse and well-preserved Mesozoic assemblages known (Martins-Neto, 1991b, c, 2003; Rasnitsyn & Quicke, 2002; Grimaldi & Engel, 2005; Heads & Martins-Neto, 2007). Among the fossils from the Crato Formation the Orthoptera are the most abundant element with about 27 % of all fossil insects discovered (Heads & Martins-Neto, 2007). Both suborders are represented and have been extensively documented by Martins-Neto (1987–2009).

## 3.3.1. Suborder: Ensifera Chopard, 1920

The Ensifera is the more "ancient" of the two orthopteran suborders, with putative forms recorded from as early as the Late Permian (Béthoux & Nel, 2002). Monophyly of Ensifera has been supported by most recent phylogenetic studies and is based primarily on the long flagellate antennae (Flook & Rowell, 1997, 1998; Desutter-Grandcolas, 2003). Tympanal (auditory) organs, when present, located on foreleg tibiae; stridulatory structures (if present) on the overlapping, horizontal part of the forewings in resting position; ovipositor, when present, swordshaped (Carpenter, 1992). According to Heads & Martins-Neto (2007), the ten extant families are distributed in superfamilies: Stenopelmatoidea, comprising the families Gryllacrididae (leaf-rolling crickets, tree crickets), Raphidophoridae (camel crickets, cave sand-treader crickets), Schizodactylidae (splay-footed crickets Anostostomatidae (king crickets and wetas) and Stenopelmatidae (Jerusalem crickets); Tettigonioidea, comprising only Tettigoniidae (katydids and bush crickets); Hagloidea comprising the relict Haglidae (hump-winged crickets); and Grylloidea, comprised of Gryllidae (true crickets), Myrmecophilidae (ant crickets) and Gryllotalpidae (mole crickets). Of these superfamilies, only Grylloidea and Hagloidea are known from the Crato Formation. Grylloidea dominate the ensiferan assemblage in terms of diversity and are represented by Gryllidae and Gryllotalpidae along with the extinct Baissogryllidae. Hagloidea are represented earlier by the problematic 'family' Prophalangopsidae and plus some new descriptions in this study. (data of Martins-Neto 1991b,c; Heads & Martins-Neto, 2007)

## Superfamily: Grylloidea Laicharting, 1781

Grylloidea dominate the ensiferan assemblage in terms of diversity and are represented (in Transbaikalia, West Mongolia and Brazil) by three families: Gryllidae (Gryllospeculinae) and Gryllotalpidae along with the extinct Baissogryllidae (three subfamilies) (Gorochov & Rasnitsyn, 2002; Heads & Martins-Neto, 2007).

# 3.3.1.1. Family: †Baissogryllidae Gorochov, 1985

Original Diagnosis, according to Gorochov, 1985: Elytra with very slightly diverging Sc and CuA. Lanceolate cell fairly small, not forming part of intercalary triangle, which is probably formed by the same elements as in the Protogryllidae. One branch of CuA2 characteristically curved, bordering broadened area (speculum) that is intersected by several cross veins arranged more-or-less parallel to diagonal vein. Bases of CuP, 1A and 2A, as in the Protogryllidae, closely spaced and almost equally curved. Differs from Protogryllidae and Gryllotalpidae in having true speculum.

The extinct grylloid family Baissogryllidae is represented by twenty species in ten genera in the Crato Formation: *Caririgryllus* Martins-Neto, 1991 with five species; *Cearagrylloides* Martins-Neto, 2009 with three female species; *Cearagryllus* Martins-Neto, 1991 with three male species; *Santanagryllus* Martins-Neto, 1991 and *Castillogryllus* Martins-Neto, 1991 each with a single species; *Notocearagryllus* Martins-Neto, 1998 and *Olindagryllus* Martins-Neto, 1998 each with two species; *Allocearagryllus* Martins-Neto, 2009, *Cryptocearagryllus* Martins-Neto, 2009 and *Paracearagryllus* Martins-Neto, 2009 each with a single species. (data of Martins-Neto, 1991b,c, 1998b; Heads & Martins-Neto, 2007; Martins-Neto & Tassi, 2009)

## Subfamily: Cearagryllinae Marins-Neto, 2009

Original Diagnosis, according to Martins-Neto & Tassi, 2009: Male tegmen with trapezoidal to square-rounded speculum and two specular veins (sp1 and sp2). Diagonal vein strongly deflected to CuA. Presence of the d-am veinlet connecting the anterior margin of the speculum to d2. Area between the anterolateral margin of the speculum and CuP at the chords filled with several perpendicular cross-veins. Females with robust body and long setiform ovipositor; cerci smaller than the ovipositor.

Genera included. *Cearagryllus* Martins-Neto, 1991; *Santanagryllus* Martins-Neto, 1991; *Notocearagryllus* Martins-Neto, 1998; *Allocearagryllus* Martins-Neto, 2009; *Cryptocearagryllus* Martins-Neto, 2009, and possibly *Anglogryllus* Gorochov *et al.*, 2006 (male); *Cearagrylloides* Martins-Neto, 2009 and *Paracearagryllus* Martins-Neto, 2009 (females).

## Genus: Cearagryllus Martins-Neto, 1991

Species included (male): *Cearagryllus monstruosus* Martins-Neto, 1991 (the type species); *Cearagryllus gorochovi* Martins-Neto, 1991 and *Cearagryllus robustus* Martins-Neto, 1991.

Original Diagnosis, according to Martins-Neto, 1991c: Medium to large size cricket. Head general large. Body robust. Hind leg elongated and forewing 15 to 35 mm long. Male has large stridulatory organ, speculum round, in between with two lateral veins paralleled with costa margin. "Harp (veins)" long, bend and relatively close to each other. Female with forewing elongated, costa area large and with secondary branches that are paralleled with each other, more lateral branches formed in a polygon net-complex, different in size and form. Ovipositor long, lance form, varied in length.

Species: *Cearagryllus robustus* Martins-Neto, 1991 (figs. 100-101)

Original Diagnosis, according to Martins-Neto, 1991c: Forewing similar to *Cearagryllus monstruosus*, but the "harp (veins)" oblique to CuA, about 22 mm long and 6 mm wide. Speculum round, the anterior margin is always broader than posterior margin, with two straight lateral veins: sp1, longer than sp2, parallel to anal margin. Body robust, abdomen mostly larger than thorax.

Original Description, according to Martins-Neto, 1991c: Forewing about 22 mm long and 6 mm wide in the level of the speculum. Apical margin round and bent to terminal zone. Costa area filled at least 11 cross-veins. In lanceolate cell (=RA) filled with five cross-veins. Speculum round, with anterior margin twice the length of the posterior one; anterolateral margin longer than the posterolateral one. The speculum has two straight cross-veins, sp1 and sp2, both parallel to anal margin. Between the speculum and the anal margin of the wing is four extra cross-veins cs1 to cs4, which are about the same length and form. "Harp"-complex filled at least three cross veins, proximate and oblique to CuA. Apical area filled with secondary Cu, that is parallel and always in the same broad in between. CuP bended in the base. Thorax relatively short, abdomen robust and exceptional round. Hind leg elongated, femur slender, tibia shorter than femur.

Specimen **SMNS 67580**: Male. Body 21 mm long and up to 7 mm wide. Forewing about 25 mm long. Hind wing 28 mm long.

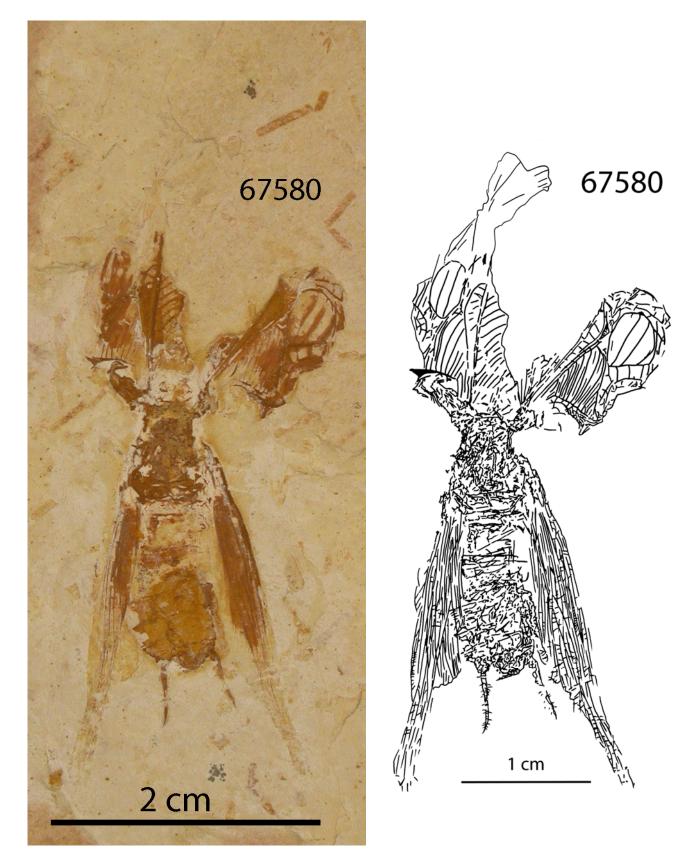
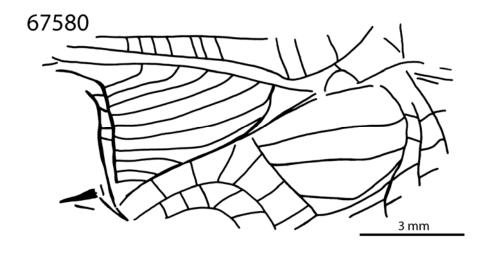


Fig. 100. Cearagryllus robustus Martins-Neto, 1991, Habitus.



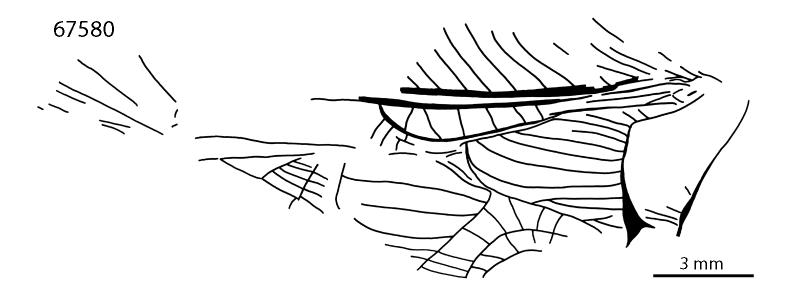


Fig. 101. Cearagryllus robustus Martins-Neto, 1991, Forewings.

New Description: Forewing the branches of Sc long and slanting. The lanceolate cell (=RA) small, its tip reached about the level posterior rand of speculum. In the lanceolate cell presented several cross veins. Speculum with two cross veins, horizontal. The posterior margin of speculum rounded, anterior margin straight, anterior margin a little longer than posterior one, boundary of the posterolateral and anterolateral margins well defined. Harpcomplex filled about 13 veins. Cerci relatively short.

Discussion: Differs from *Cearagryllus monstruosus* by "harp (veins)" oblique to CuA (in *C. monstruosus* parallel). The thorax of *C. robustus* is rather robust and have a longer posterior margin of speculum.

Species: *Cearagryllus gorochovi* Martins-Neto, 1991 (figs. 102-103)

Original Diagnosis, according to Martins-Neto, 1991c: Forewing 17 mm long flipped. Speculum round, with two cross veins, soft wavy. Body especially elongated.

Original Description, according to Martins-Neto, 1991c: Forewing 17 mm long flipped. Costa margin bend. Sc mildly bended. Costa area relatively narrow, the maximal width presented in the mid part of wing, filled at least 14 cross veins. R long, bent, deviated from Sc. Area between Sc and R was filled at least five cross veins, short and perpendicular. CuA deviated from R. Speculum round, with two straight cross veins more or less parallel and mild bent, both parallel to the posterior\* margin of speculum [here should means lateral margin]; sp2 slightly longer than sp1; d (that is the "bone" of Harp) straight, transversal until to speculum. "Harp"-complex is composed of four long and one mostly short veins, which based with CuP; h2 (that is the "string" of harp) bent in base part and proximal close with d, h3, h4 and h5 progressive shorter, less bent and the distance in between always narrower, all veins more or less parallel to other. Base of CuP soft wavy. Body: head globular, thorax elongated, abdomen robust and exceptional round. Cerci relatively short.

Specimen SMNS 67581: Male. Forewing at least 24 mm long.

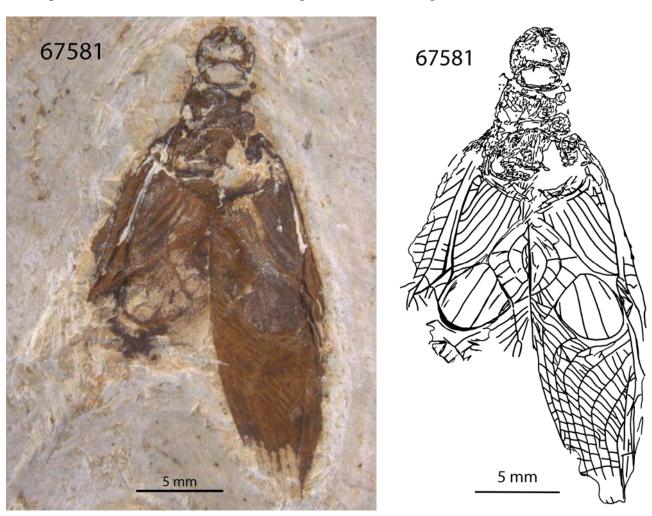


Fig. 102. Cearagryllus gorochovi Martins-Neto, 1991, Habitus.

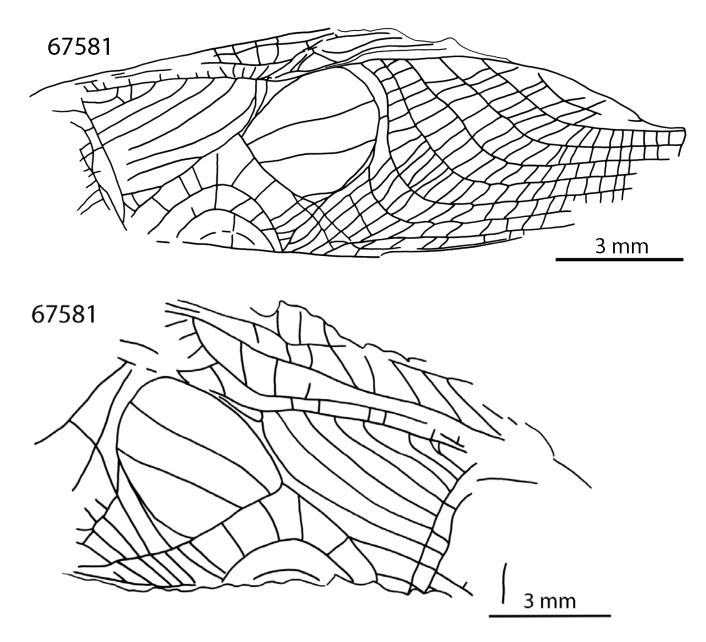


Fig. 103. Cearagryllus gorochovi Martins-Neto, 1991, Forewings.

New Description: Head globular, with diameter 3.5 mm. Eye big, round and located at the side of the head. Forewing oval, the branches of Sc slanting. The lanceolate cell (=RA) small, its tip reached about the level posterior rand of speculum. In the lanceolate cell presented several cross veins. Speculum round, located near the center of wing and in it with two cross veins, nearly horizontal. The posterolateral margin of speculum rounded, anterolateral margin straight, boundary of the posterolateral and anterolateral margins indistinct, only the boundary anterior margins well defined. Harp-complex filled about nine veins.

Discussion: Differs from all other species in the genus Cearagryllus in having a much rounded speculum and elongated body.

Genus: *Cearagrylloides* Martins-Neto, 2009 (=*Cearagryllus* Martins-Neto, 1991)

Type species: Cearagryllus perforatorius Martins-Neto, 1991, designated 2009.

Original Diagnosis, according to Martins-Neto & Tassi, 2009: Female. Robust cearagryllids with relatively small head. Forewing length equal to the body length; ovipositor long and setiform, longer than the forewing/body length.

Species: *Cearagrylloides perforatorius* Martins-Neto, 2009 (=*Cearagryllus perforatorius* Martins-Neto, 1991) (figs. 104-105)

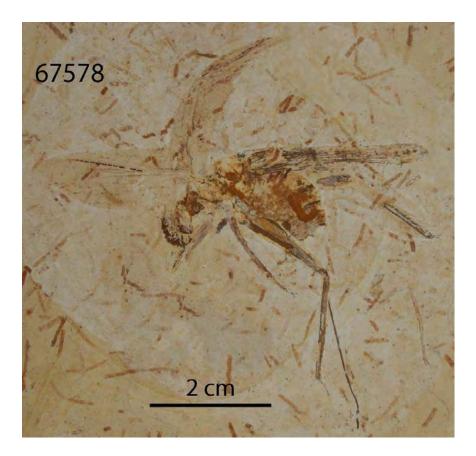
Original Diagnosis of *Cearagryllus perforatorius*, according to Martins-Neto, 1991c: Female. Body larger than 25 mm long, robust, head large and ovipositor longer than the body length, lance form; cerci relatively short. Hind leg elongated. Forewing in female form, slightly longer than the body length.

Original Description of *Cearagryllus perforatorius*, according to Martins-Neto, 1991c: Body: Head large, dorsal round, lateral elongated and limited. Eye large. Body robust. Abdomen swell, exceptional plump. Hind leg elongated, femur slender, tibia long, slightly shorter than the femur, indented, the first tarsal segment elongated. Forewing: long, about the body length. Costa area large, reaching about half of whole wing length, narrowing towards the apex, filled by long slanting cross-veins, this secondary and vertical across veins forming a polygon net. Sc long, sigmoid. R long, more or less parallel to Sc and relatively close to each other. Specimen DGM-6281-I: CuA long, sigmoid, has divided the whole wing into two parts, with the same size, origin until to the peak six secondary branches. The branches bend in the base and horizontal in apical, parallel each other. CuP long, origin near the base of wing. 1A relatively long, more or less parallel to CuP.

Emended Diagnosis, according to Martins-Neto & Tassi, 2009: Females with robust body, varying from 29 to 32 mm length; forewing length varying from 28 to 32 mm; ovipositor length varying from 32 to 36 mm. Ovipositor 1.1 times longer than the body and/or the forewing length. Relatively large and dorsally rounded head. Forewing about three times longer than wide; ScP sigmoid, distally converging towards the costa margin and notably thickened basally; R parallel to ScP. MP two-branched; around nine MP2 secondary branches. r-m present, connecting R to MA.

Original Description, according to Martins-Neto & Tassi, 2009: (supplementary material RGMN-506) Body and forewing length 32 mm. Ovipositor length as preserved 32 mm (total length ca. 36 mm). Fore tibia smooth with a relatively long apical spur. Forewing three times longer than wide, with wide costa area, narrowing towards the apex, filled by rather long cross-veins and accessory veinlets forming a mosaic of heterogeneous cells. ScP sigmoid, thickened at its base, converging towards the costa margin around a quarter wing-length from the apex. R parallel to ScP. M three-branched. Presence of r-m connecting R to MA, situated at the mid length of the wing. At least nine MP2 secondary branches, all connected by cross-veins, forming a mosaic of heterogeneous cells.

Specimen **SMNS 67578:** Body 32 mm long and up to 9 mm wide. Forewing 29 mm long, sharp in the tip. Ovipositor 31 mm long.



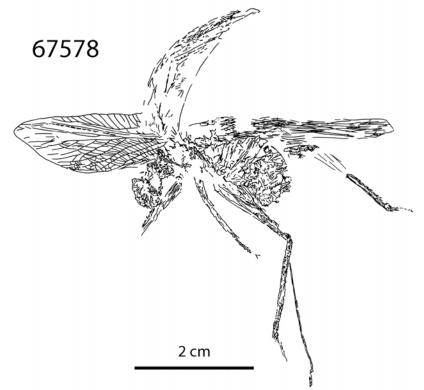


Fig. 104. Cearagrylloides perforatorius Martins-Neto, 2009, Habitus.

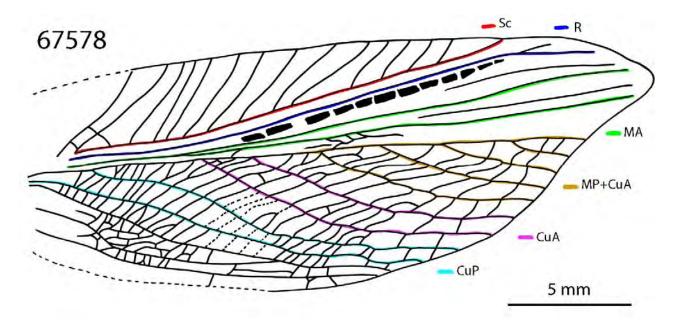


Fig. 105. Cearagrylloides perforatorius Martins-Neto, 2009, Forewing.

New Description: Hind leg femur slender, 19 mm long and up to 3.5 mm thick, tibia thin and about the same length with femur, with long spines and at least two apical spurs. Forewing in typical female crickets form. That is the Sc and R curved, the stem of MP+CuA1 straight and horizontal. MP, CuA, CuP and A parallel. One special character of this species is the presence of pigment in between R and MA. The divided point of MA1 and MA2 is deep near the base. MP, CuA, CuP and A altogether is 12-branched.

Discussion: Differs from the other female species of the genus by the length of ovipositor. In *C. microcephalus* the ovipositor is one time and a half longer than the body. In *C. poliacanthus* the ovipositor is about 2/3 of the body length. In *C. previstus* the ovipositor is a little longer than the body. And *C. previstus* is smaller in body size (body 20 mm, forewing 25 mm and ovipositor 24 mm long).

Species: *Cearagrylloides microcephalus* Martins-Neto, 2009 (=*Cearagryllus microcephalus* Martins-Neto, 1991) (figs. 106-107)

Original Diagnosis of *Cearagryllus microcephalus*, according to Martins-Neto, 1991c: Similar to *Cearagryllus perforatorius*, but with the ovipositor longer than the body length and small head, not reach the half big of the thorax.

Original Description of *Cearagryllus microcephalus*, according to Martins-Neto, 1991c: Head notably small and limited. Body robust, swell. Abdomen exceptionally round. Ovipositor extreme elongated, about one and a half length of the body length, slightly bent and lance from.

Emended Diagnosis, according to Martins-Neto & Tassi, 2009: Females with robust body, varying from 24 to 26 mm length; forewing length varying from 24 to 28 mm; ovipositor length around 38 mm. Ovipositor 1.6 times longer than the body and/or the forewing length.

Head notably small, laterally elongated. ScP straight, not thickened; R parallel to ScP. MP unbranched; around six MP2 secondary branched. r-m indistinct.

Original Discussion, according to Martins-Neto & Tassi, 2009: In addition to the original characters assigned to the species (smaller body and head, longer ovipositor), the forewing provided other important characters. In *C. perforatorius* ScP is sigmoid, distally divergent and basally thickened, in contrast to *C. microcephalus*, which exhibits a straight ScP, not thickened. Additionally, MA has typically three anterior secondary branches, not present in *C. microcephalus*. Another minor difference is a smaller number of MP secondary branches.

Specimen **SMNS 67577:** Head 5 mm long and 2.5 mm wide. Body 25.5 mm long and 9 mm wide. Forewing oval, 32 mm long and 11 mm wide. Ovipositor 36 mm long.

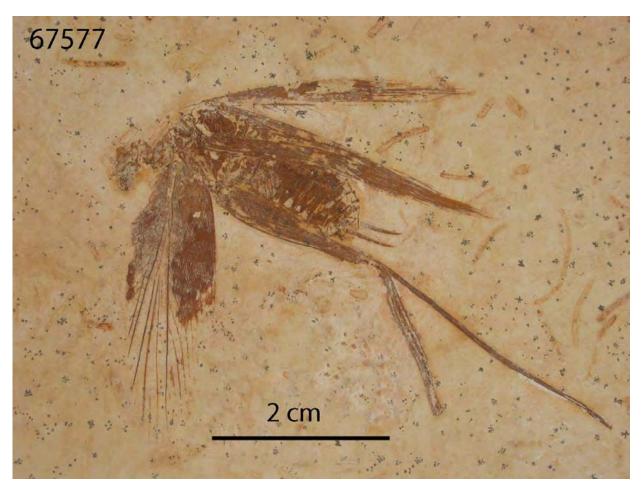


Fig. 106. Cearagrylloides microcephalus Martins-Neto, 2009, Habitus.

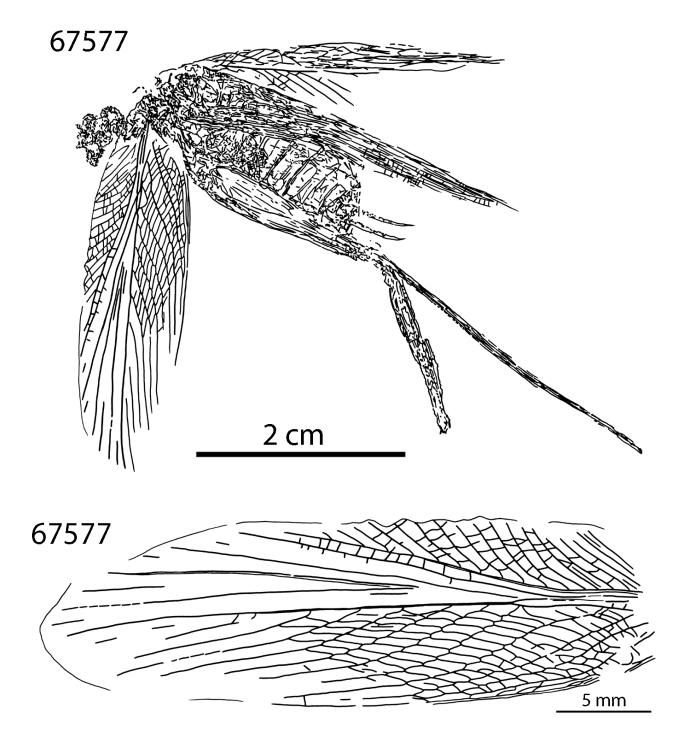


Fig. 107. Cearagrylloides microcephalus Martins-Neto, 2009, Habitus & Forewing.

New Description: Hind leg femur slender, 18 mm long and up to 3.5 mm thick, tibia about the same length as the femur and presents several short spines in the 1/3 of distal end. Forewing oval, probably relatively thin, since it is folded on the right side of this specimen. Forewing is in typical female crickets form. That is the Sc, R and MA1 curved, the stem of MP+CuA1 straight and horizontal, MP, CuA, CuP and A parallel. Specially is the distance between MA1, MA2 and MA3 broad. MP, CuA, CuP and A altogether is 15-branched. Cerci short, sharp and 6.5 mm long.

Discussion: Differs from the original Description of Martins-Neto, 2009 by forewing with generally more branches and ScP still sigmoid (instead of straight), it is on the contrary similar to *C. perforatorius*. Differs from the other female species of the genus by the notably smaller head and the longer ovipositor. In *C. perforatorius* and *C. previstus* the ovipositor is about the same length as the body. In *C. poliacanthus* the ovipositor is about 2/3 of the body length.

Subfamily: Sharategiinae Gorochov, 1992

Gorochov (1985, 1992a, 1995) proposes three subfamilies for the family Baissogryllidae: Baissogryllinae, which is not represented in the Brazilian Lower Cretaceous, Sharategiinae (Gorochov, 1992a) and Bontzaganiinae (Gorochov, 1992b). Sharategiinae for the genera *Sharategia* (Gorochov, 1992a), *Neosharategia* (Gorochov, 1992a), *Mongologryllus* (Gorochov, 1985). In the Brazilian Lower Cretaceous are represented the following Sharategiinae one genus *Caririgryllus* (Martins-Neto, 1991c) and five species: *Caririgryllus elongatus* (Martins-Neto, 1991c), *Caririgryllus pilosus* (Martins-Neto, 1991c), *Caririgryllus mesai* (Martins-Neto, 1991c) and *Caririgryllus brachypterus* (Martins-Neto, 2002b).

Genus: Caririgryllus Martins-Neto, 1991

Type species: Caririgryllus elongatus, Martins-Neto, 1991.

Original Diagnosis, according to Martins-Neto, 1991c: Head big, the width is equal to the length, antenna is two times of the body length; body rather robust. Limb of tibia relatively short, surface expanded; hind leg tibia has two short apical spurs that are similar in size. Forewing elongated, nearly ellipse, male contains stridulatory apparatus; speculum big, square, with single trans-vein, mild bent; harp-complex reduced in the number of veins (three to four), relatively far from speculum. Female has ovipositor setiforme, mostly shorter than cerci; forewing in typical form of female cricket, with much vertical veins and shaped the square cells, which are equally in size and form.

Species: Caririgryllus brachypterus (=brevipterus) Martins-Neto, 2002 (fig. 108)

Original Diagnosis, according to Martins-Neto, 2002b: Female tegmen of 6 mm in length with RA and RP quite straight, parallel to the costa margin. Space between the secondary branches of CuP forming mosaics of heterogeneous cells.

Original Description, according to Martins-Neto, 2002b: Female tegmen with 6 mm in length, oval elongated in shape. Costa area relatively narrow filled by nine transversal cross-veins. RA parallel and close to RP, quite straight, attained the apical margin close to the boundary of the costa margin. CuP slightly divergent of CuA, reaches the apical margin above the apex. Few secondary branches of CuP (three preserved), and great cross-vein forming a heterogeneous mosaic cells.

Specimen **SMNS 66687**: This specimen is not complete, in the absence of forewing, identification is rather difficult. Because of the size of body and body parts, it could belong to the species *Caririgryllus brachypterus* Martins-Neto, 2002.

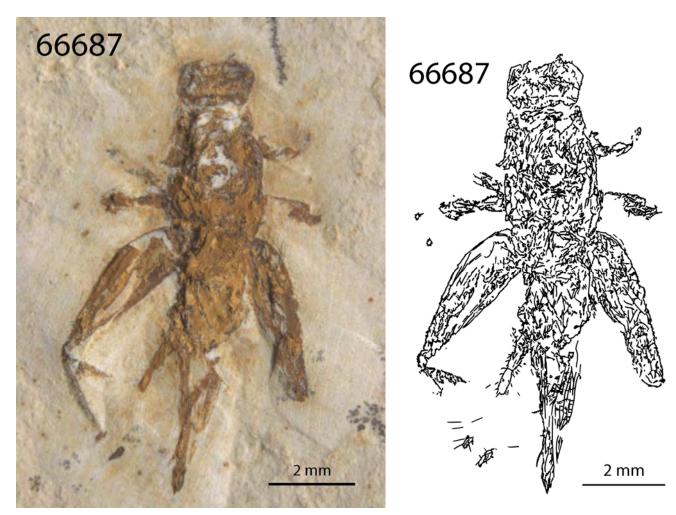


Fig. 108. Caririgryllus brachypterus Martins-Neto, 2002, Habitus.

New Description: Small size female cricket. Head notably big, 1 mm long and 1,6 mm wide. Eye medium size, round and located at the side of the head. Antenna base presented. Thorax elongated, 3 mm long and 2.2 mm wide. Hind wing 8 mm long in folded form. Abdomen small and slender, 3 mm long. Hind leg femur robust, 4.2 mm long and up to 1.2 mm thick, a long spur probably presents at the base of tibia. Ovipositor long, relative thick, lance form, 3.8 mm long. Cerci 3.8 mm long, about the same length as the ovipositor.

Discussion: Since its big head and notably small body size, it could be belong to the species *Caririgryllus brachypterus*. As the body 6 mm and hind wing 8 mm long, in comparison, the forewing size is 6 mm in *C. brachypterus*, 9 mm in *C. mesai*, 14 mm in *C. arthaudi*, 15 to 16 mm in *C. pilosus* and 14 to 17 mm in *C. elongatus*. Specimen SMNS 66687 differs from *C. mesai* by both smaller body and ovipositor size (in *C. mesai* the body 12.5 mm and the ovipositor 6.2 mm long). Specimen SMNS 66687 differs from SMNS 66510 by the notably big head.

#### 3.3.1.2. Family: Gryllidae Latreille, 1802 sensu Gorochov, 1985

Diagnosis, according to Gorochov, 1985: (for forms with fully developed elytra) Elytrum with very slightly diverging, parallel, or converging Sc and CuA. Lanceolate cell small, often indistinct, forming part of intercalary triangle. Speculum well developed, except in forms with reduced and feminized venation, intersected by one or several cross veins, whose posterior parts form large angle with diagonal vein and are connected not to posterior branch of CuA2, but to cross vein bordering speculum. Speculum sometimes without cross veins. Bases of CuP, 1A and 2A may be more-or-less similarly curved, or 2A may be almost straight. Gryllidae differs from all other families of Grylloidea in having the lanceolate cell form part of the intercalary triangle and in the presence of a speculum with characteristic arrangement of cross veins.

Gryllidae constitute the principal family of the Grylloidea with more than 350 extant genera encompassing over 3000 species distributed world-wide (Rentz & Su, 2003). Most classifications presently recognised about seven subfamilies. The true crickets are represented in the Crato Formation by twelve species distributed in four genera: *Araripegryllus* Martins-Neto, 1987 with seven species; *Cratogryllus* Martins-Neto, 1991 with three species; *Brontogryllus* Martins-Neto, 1991 and *Nanoararipegryllus* Martins-Neto, 2002 each with one species. (Martins-Neto, 1991a,b,c, 2002b; Heads & Martins-Neto, 2007)

# Subfamily: Gryllospeculinae Gorochov, 1985

Original Diagnosis, according to Gorochov, 1985: Elytra with slightly diverging Sc and CuA. Lanceolate cell clearly not entirely separated from its base, as it is in other subfamilies of the Gryllidae. Bases of CuP, 1A and 2A similarly curved. The Gryllospeculinae are represented by three genera in Mongolia and four genera in the Crato Formation. This subfamily differs from others of the Gryllidae in the more-or-less similarly curved bases of CuP, 1A and 2A in the stridulation apparatus.

Genus: Araripegryllus Martins-Neto, 1987

Type species: Araripegryllus camposae Martins-Neto, 1987

Original Diagnosis, according to Martins-Neto, 1991c: Head relatively big, globular, width much longer than length; antenna begin in the middle of head, scape robust. Pronotum rectangular, ranged from slightly to much broader than the head. Abdomen robust, cerci long, as the body length. Foreleg robust, tibia with three strong apical spurs, the insides are much longer than outsides; tarsus with first segment extremely long and the second one in "hearts"-form. Forewing between 5 to 25 mm long and 10 mm wide flipped, triangular formed, the base is much broader than the apical field. Male has stridulatory apparatus: speculum oval, with two more or less parallel slanting veins. CuP in base part straight, chord pronounced bent. Lanceolate cell not entirely separated from its base, reduced in cross veins. Female has ovipositor long, shorter than cerci, lance form. Forewing in typical female pattern crickets, Sc and R rather parallel and limited in a definite area, filled with less than 15 branches. The secondary branches parallel with each other, bent in the base and straight in the apical region. Strongly cross veins formulated the polygonal cells, which heterogeneous in size and form.

Species: *Araripegryllus nanus* Martins-Neto, 1991 (fig. 109)

Original Diagnosis, according to Martin-Neto, 1991c: Forewing 8 mm long and 4 mm wide flipped. Speculum similar to *Araripegryllus camposae*, but with the cross veins much closer to each other, the speculum is divided in three parts, in-between areas are relatively equally. Harp-"strings" rather parallel each other, without divergent. "File"-complex bend.

Original Description, according to Martins-Neto, 1991c: Body. Specimen CV-2061, head relatively small, width is twice as long as the length, gena small. Pronotum slightly longer and wider than the head, in rectangular form; meso- and metanotum robust, much broader than both pronotum and abdomen. The abdomen cylindrical, with cerci. Specimen RGMN-1664, generally similar to Specimen CV-2061: Eye relatively small and round. Hind leg femur robust, tibia shorter than femur, smooth, internal side has one long apical spine, which is nearly 1/3 of the length of first tarsus segment, and in external side two short ones. The first segment of tarsus elongated and robust.

Specimen **SMNS 66484** is not very complete, the forewing could not be identify. It should be a male belong to Araripegryllus. It is similar to *Araripegryllus nanus* Martins-Neto, 1991 on account of the size of the body and body parts, but clearly smaller than *A. marianoi* Martins-Neto, 1991 and also smaller than *A. camposae* Martins-Neto 1987.



Fig. 109.1. Araripegryllus nanus Martins-Neto, 1991, Habitus.



Fig. 109.2. Araripegryllus nanus Martins-Neto, 1991, Habitus.

New Description: Compound eye big, oval. Forewing very broad in base. Hind leg tibia (5 mm) only about 2/3 of the length as femur (7 mm). Cerci short and hirsute.

Species: Araripegryllus femininus Martins-Neto, 1991 (fig. 110)

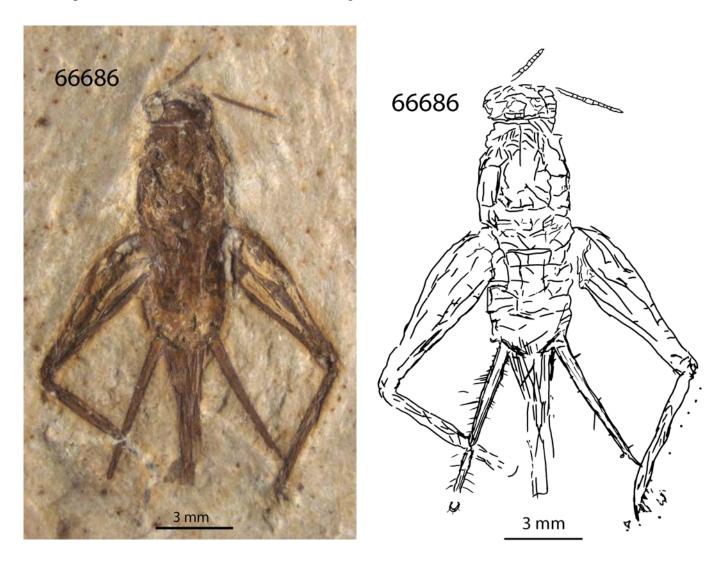
Original Diagnosis, according to Martins-Neto, 1991c: Hind leg tibia smooth, with a long apical spur in internal side and two short ones in external side. Forewing with Sc and R nearly horizontal, reaching to the apical margin of the anterior area.

Original Discussion, according to Martins-Neto, 1991c: There are some evidences for it, that this species *Araripegryllus femininus* could be the female species of *Araripegryllus camposae*.

Original Description, according to Martins-Neto, 1991c: Body: Head relatively big, globular, without ocelli, width is twice as long as the length. Antenna long, filiform, multi segments, longer than the body length (about 1½ times), insert in the middle of head; scape robust, larger than the others segments. Eyes broad laterally, relatively big and projecting. Pronotum rectangle, ranged from slightly to much broader than the head. Mesonotum robust, broader than both pro- and metanotum. Abdomen robust, more slender than mesonotum, with the sharp end semi-sphere. Cerci extremely long, nearly as long as the body length, thick in the base, slender progressively. Ovipositor long, about 2/3 length of the cerci, lance form. Hind wing long, hidden the anterior 1/3 length of cerci. Hind leg is adapted for jumping: femur robust, tibia slightly shorter than femur, smooth, with three apical spurs, the internal one extremely long, reaching nearly half of the length of the first tarsi segment. Tarsus long, the first segment elongated, the second segment in a "heart" form, the third segment about 1/3 of length first segments. Forewing: Costa margin nearly straight, apical margin round and anal margin bent. Triangular forming, with maximal width in the base. Costa area broad in the base, narrow in the apex, filled at least 20 cross veins. Sc long, almost horizontal, end part

touch the apical margin. R long, relatively proximity to Sc, nearly parallel, in between filled at least 18 short cross veins. CuA long, almost horizontal, from it origin six to eight secondary branches, all branches horizontal, parallel and rarely the same with each other. This diagonal branches formed the polygon cells, heterogeneous in size and form, together in a net form. CuP slightly sigmoid, reaching the anal margin at the half of the whole length. 1A long, sigmoid, more or less parallel to CuP in the whole length, convergent first and then distant. 2A and 3A rather parallel to anal margin, convergent with each other.

Specimen **SMNS 66686** body 11 mm long and 3.5 mm wide. Hind wing 14.5 mm in maximal length. Hind leg femur robust 7.5mm long and up to 2.3 mm thick, tibia 5.5 mm long. Ovipositor at least 4.5 mm and cerci 7 mm long.



**Fig. 110.** Araripegryllus femininus Martins-Neto, 1991, Habitus.

New Description: Head big, slightly broader than the pronotum [by original Description: Pronotum more or less broader than head]. Eye big, round and located at the side of the head. Hind wing long, hidden almost the whole length of cerci. [by original Description: hidden only the front 1/3 length] Or as it were, in the folding shape the tip of hind wing reached almost the tip of cerci.

Discussion: Differs from another female species *Araripegryllus* (*A. megacephalus*, *A. spinosus* and *A. serrilhatus*) by hind leg tibia smooth, with a long inner apical spur and two outer smaller ones.

Remark: Specimen SMNS 66686 has a broader (than pronotum) head, it is much similar to *Araripegryllus serrilhatus*. But because of thorax, slender abdomen, more robust hind leg femur and the characteristics of hind leg tibia, clearly, this specimen should belong to *A. femininus* but not to *A. serrilhatus*. Therefore by the male species of *Araripegryllus* (*A. camposae*, *A. nanus*) [but *A. marianoi* unknown] the head are narrower than thorax, by female species except *A. spinosus* narrower, the other three (*A. femininus*, *A. serrilhatus* and *A. megacephalus*), the head is (at least slightly) broader than prontum.

Species: Araripegryllus spinosus Martins-Neto, 1991 (fig. 111-112)

Original Diagnosis, according to Martins-Neto, 1991c: Similar to *Araripegryllus femininus* but in hind leg tibia with several spines and at least four apical ones. Forewing with Sc and R curved, reaching the costa margin at about 1/3 length from apex.

Original Description, according to Martins-Neto, 1991c: Forewing: Sc and R relatively short, curved, especially deviated from the CuA, reaching the costa margin at a little after the middle point of whole length. M more or less parallel with R. Body: Hind leg tibia has three to five long spines, all concentrated in the distal 1/3 part. With one long inner apical spur and at least three (probably four) outer smaller ones. Other detail similar to *A. femininus*.

Specimen **SMNS 66483**: This specimen is not very complete. It is similar to *A. spinosus* on account of body size and the hind leg tibia. Complex eye big, oval. Mid leg tarsus with four segments. Hind leg tarsus with three segments.

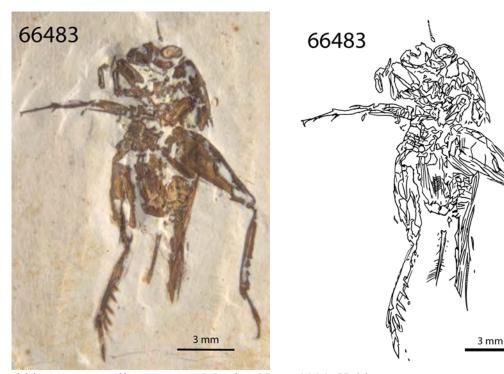


Fig. 111. Araripegryllus spinosus Martins-Neto, 1991, Habitus.

Specimen **SMNS 67579**: Well presented especially in forewing and hind leg. Body 11 mm long and 3.5 mm wide. Forewing oval, 7 mm long and 3.8 mm wide.

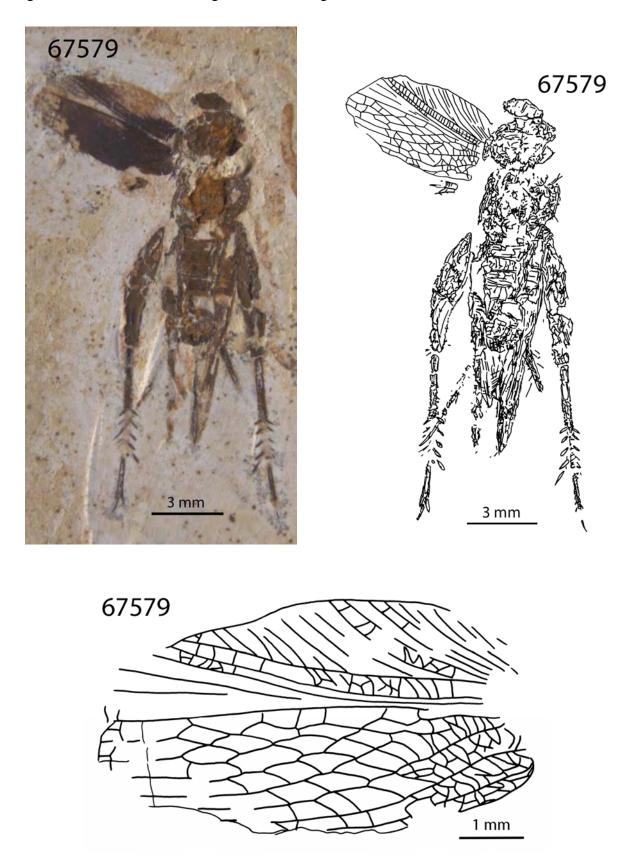


Fig. 112. Araripegryllus spinosus Martins-Neto, 1991, Habitus & Forewing.

New Description: Head small and especially flat. Only 12 segments of the antenna is preserved. Forewing oval, ScP and RA curved. Hind wing in folding shape, its tip reached the tip of ovipositor. Mid leg femur longer than tibia, tarsus with four segments. Hind leg femur robust 6 mm long and up to 2 mm thick, tibia with at least four pair spurs and one long apical spine, concentrated in the distal 1/3 part, tarsus with three segment, first segment with two apical spurs. Abdomen round, almost the same width as the thorax. Ovipositor is long, lance form. Cerci even slightly longer than ovipositor.

Discussion: Differs from another female species *Araripegryllus* (*A. femininus* and *A. serrilhatus*) by hind leg tibia with several spines and at least four apical ones. In *A. megacephalus* Martins-Neto, 1991 the hind leg tibia with several spines too, but diffused in the distal half part (by *A. spinosus* concentrate only in the distal 1/3 part). And *A. megacephalus* is larger

Species: Araripegryllus serrilhatus Martins-Neto, 1991 (fig. 113)

Original Diagnosis, according to Martins-Neto, 1991c: Similar to *Araripegryllus femininus*, but the hind leg tibia is serrated and with a long apical spur; tarsal serrated.

Original Description, according to Martins-Neto, 1991c: Head relatively big, slightly broader than pronotum, globular, without ocelli, beak small. Antenna long, filiform, multi segments, insert in the center between eyes. Eye big, projected in the lateral side of head. Pronotum rectangle, anterior side much slender than posterior side. Abdomen robust, broader than both pro- and mesonotum, round. Cerci extremely long, nearly as long as the body length. Ovipositor about the length as cerci. Hind legs are adapted to jumping, after all slim: femur relatively thin, tibia rather shorter than femur, serrated, with only one long apical spur, about 2/3 of the first tarsal segment length. Tarsi long, about 1/3 of the tibia length, serrated. Forewing still unknown.

New Description: Antenna about double the length of body, is 25 mm long and more than 210 segments. Hind wing in folding shape, its tip reached more than the half length of ovipositor. Mid leg femur longer than tibia and tarsus with four segments. Hind leg tarsus with three segments, first segment long, serrated and with a long apical spur too. This spur is even longer than the second tarsal segment. Ovipositor long, lance form. Cerci thick and about 1.5 times longer than the ovipositor.

Discussion: Differs from another female species *Araripegryllus* (*A. megacephalus*, *A. spinosus* and *A. femininus*) by hind leg tibia serrated and with a long apical spur.

Specimen **SMNS 66485:** Body 12 mm long and up to 4.5 mm wide. Antenna at least 25 mm long. Hind leg femur robust, 8 mm long and up to 2 mm thick. Ovipositor 8 mm and cerci 13 mm long.

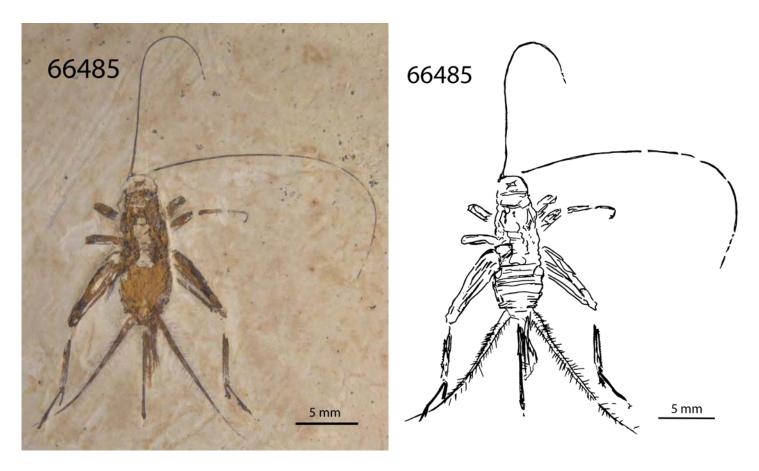


Fig. 113. Araripegryllus serrilhatus Martins-Neto, 1991, Habitus.

Species: Araripegryllus megacephalus Martins-Neto, 1991 (figs. 114-116)

Original Diagnosis, according to Martins-Neto, 1991c: Posture enormous, head particularly big, beak partly visible; antenna inserted into the lateral margin of beak; scape robust, round; eye relatively small, projecting and located at the lateral side of head. Ovipositor is small in circumference, lance form. Hind leg tibia has long spines and short apical spurs.

Original Description, according to Martins-Neto, 1991c: Head big, width is nearly as long as length, peak raised. Eye small, lateral-standing, nearly round. Scape robust, round, insert into the lateral of beak. Antenna preserved partly, filiform, multi segments. Pronotum rectangle, nearly so broad as head. Meso- and metanotum relatively short. Abdomen robust, cylindrical to extremely round. Cerci preserved partly. Ovipositor is around 2/3 of body length, lance form. Fore- and mid leg only few preserved: femur rather robust. Hind leg enormous, femur

robust, tibia slightly shorter than femur and with strong spurs and apical spine. Tarsi with first segment elongate and rather robust.

New Description: Body 17.5 to 20 mm long and about 6 mm wide. Head notably big, width (5mm) is longer than length (3 mm) [by original Description: width is nearly as length], slightly broader than the pronotum. Antenna is as long as or longer than the body, with about 200 segments. Hind wing in folding shape measured about 17 to 23 mm long. Fore and mid leg femur robust and slightly longer than tibia. Hind leg femur robust 13 mm long and up to 3.8 mm thick, tibia with long spines, dispersed mostly in the distal half part of the tibia, tarsus three segments, the first segment (2.5 mm) elongated and about half of the length as the whole tarsi (5 mm). This first tarsal segment is with a pair of long apical spur, which is about half the length of the second tarsal segment. Abdomen round, longer and thicker than thorax. Ovipositor is long, lance-form and about half of the body length. Cerci (13.5 mm) about  $1\frac{1}{2}$  longer than the ovipositor (8 mm).

Specimen **SMNS 66488**: Body 18 mm long, antenna more than 24 mm long, hind wing 17 mm long, ovipositor 8 mm long and cerci at least 13.5 mm long.

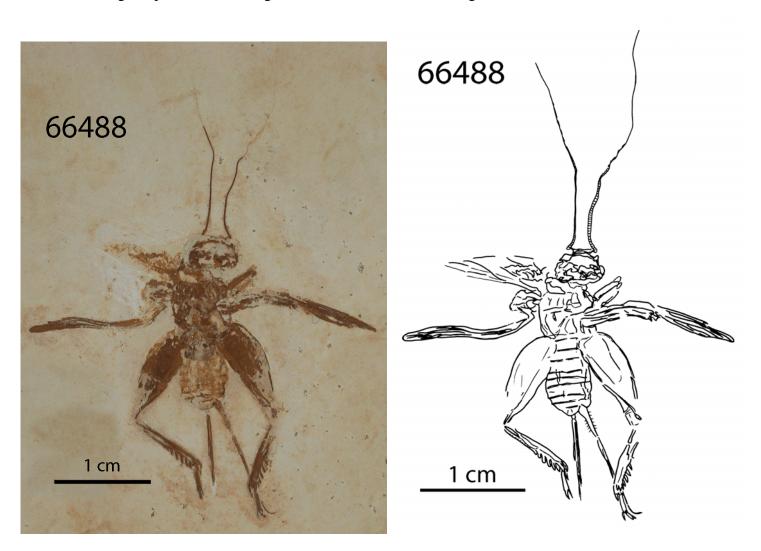


Fig. 114. Araripegryllus megacephalus Martins-Neto, 1991, Habitus.

Specimen **SMNS 66505**: Body 20 mm long, antenna more than 20 mm long, with about 200 segments and ovipositor 9 mm long. Hind leg well preserved inclusive of three tarsus segments.

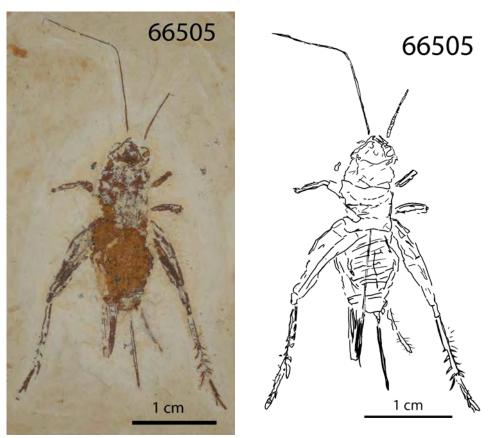


Fig. 115. Araripegryllus megacephalus Martins-Neto, 1991, Habitus.

Specimen **SMNS 66508**: Body 17.5 mm long and ovipositor 9 mm long. Hind wing in folding shape, its tip reached the tip of ovipositor and measured about 22 mm long.

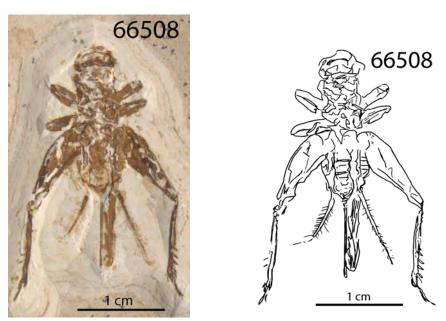


Fig. 116. Araripegryllus megacephalus Martins-Neto, 1991, Habitus.

Discussion: Differs from another female species *Araripegryllus* (*A. femininus* and *A. serrilhatus*) by hind leg tibia with long spines and at least one apical spur. In *A. spinosus* the hind leg tibia also with several spines, but more concentrated only in the distal 1/3 portion. And *A. spinosus* is smaller, body 9 to 12 mm long.

Family: (probably) Gryllidae

Unknown Genus and Species: **E** (figs. 117-118)

Specimen **SMNS 66510**: This specimen is not complete, the forewing could not be identify. Remarkably small body size and extremely long antenna.

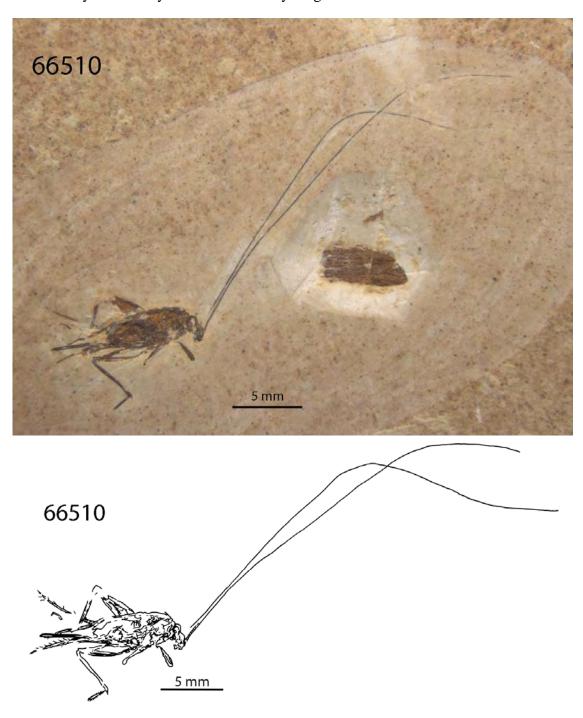
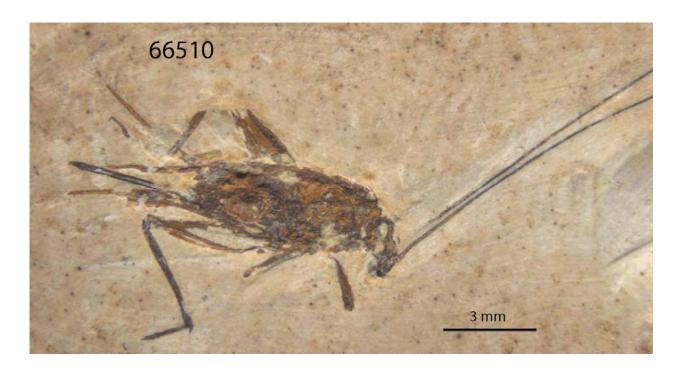


Fig. 117. Unknown species crickets E, Habitus.



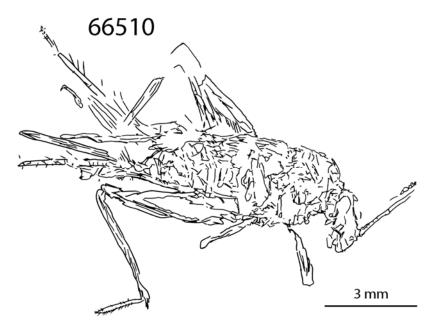


Fig. 118. Unknown species crickets E, Body part detail.

Description: Small size female cricket. Head small, 2 mm long and 1 mm wide. Eye big, oval and located at the middle part of the head. Antenna 33 mm long with more than 300 segments, about five times of the body length. Body rather oval, 6.5 mm long and 2.6 mm wide. Hind wing 8 mm long in folded form. Fore- and mid leg tibia narrow, smooth. Hind leg femur robust, 5 mm long and up to 0.8 mm thick, tibia about the same length of the femur, smooth on the surface and with long apical spur. Tarsus with three segments. The first segment relatively long and covered with short setae, the second and the third segments smooth. Ovipositor long, relatively thick, lance form, 4 mm long. Cerci 6 mm long, about the same length as the body.

Discussion: Since its notably small body size, it is on average smaller than all the genera of described cricket (in the Crato Formation) only out of *Caririgryllus*. But this specimen differs from *Caririgryllus* by the smaller head and the longer antenna (in *Caririgryllus* the antenna is two times of the body length). However, from the body size it could be similar to species *Caririgryllus brachypterus* Martins-Neto, 2002. As the body 6.5 mm and hind wing 8 mm long, in comparison, the forewing size is 6 mm in *C. brachypterus*, 9 mm in *C. mesai*, 14 mm in *C. arthaudi*, 15 to 16 mm in *C. pilosus* and 14 to 17 mm in *C. elongatus*. Specimen SMNS 66510 differs from *C. brachypterus* (an example represented by specimen SMNS 66687) by the smaller head and the longer antenna. SMNS 66510 differs from *C. mesai* by smaller body and ovipositor size (in *C. mesai* the body 12.5 mm and the ovipositor 6.2 mm long).

#### Superfamily: **Gryllotalpoidea** sensu Vickery, 1977

Vickery (1997) placed the single family Gryllotalpidae under superfamily Gryllotalpoidea, but most authors placed this family still under superfamily Grylloidea. (Gorochov & Rasnitsyn, 2002; Grimaldi & Engel, 2005; Groll & Günther, 2003; Heads & Martins-Neto, 2007)

## 3.3.1.3. Family: **Gryllotalpidae** sensu Vickery, 1977

Original Description, according to Vickery, 1977: Distribution, world-wide. Habitat, subterranean. Large, heavy-bodied two ocelli only; pronotum much longer than broad, forming a strongly convex dorsal shield; body densely setose; prothoracic legs short, robust, apical tibial spurs modified as dactylar processes for digging; stridulating mechanism of male lacking a mirror; disc of tegmen with a large triangular cell, apical field reduced. The difference in general characters between the crickets and mole crickets is rather great and is consistent, a valid reason for considering them as belonging in different superfamilies.

Other morphological characters include: hind leg not differentiated as jumping-leg and ovipositor totally reduced. Gryllotalpidae are world-wide about 65 species and known from three monotypic genera in the Crato Formation: Archaeogryllotalpoides ornatus Martins-Neto, 1991; Palaeoscapteriscops cretacea Martins-Neto, 1991; and Cratotetraspinus fossorius Martins-Neto, 1995. (Groll & Günther, 2003; Heads & Martins-Neto, 2007; Martins-Neto, 1991c)

#### Genus: Cratotetraspinus (=Tetraspinus) Martins-Neto, 1995

According to Gorochov (2001) the genus *Cratotetraspinus* (Martins-Neto 1995b, 1997) is a very primitive representative of Gryllotalpidae. This monotypic genus is evidently a representative of some new subfamily ancestral for all known fossil and recent Gryllotalpidae. It is remarkable because of the structure of its body and especially its legs, which have an intermediate condition between Protogryllidae (similar to recent Gryllidae in general appearance) and Cenozoic Gryllotalpidae. This find shows how morphological changes could arise as an adaptation to a digging mode of life, leading from Protogryllidae to recent Gryllotalpidae.

Type species: Cratotetraspinus fossorius Martins-Neto, 1995

Original Diagnosis, according to Martins-Neto, 1995b: Media size. Foreleg with robust femur and tibia adapted to burrowing: mid leg with three tibial apical spurs: hind leg robust with tibia armoured with four long fixed spines and a tibial spur; tarsal with the first segment armoured with an apical spur.

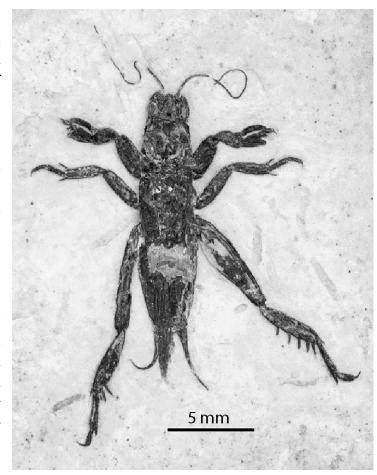
Original Discussion, according to Martins-Neto, 1995b: Differs from all the described species of the ensifera, recent and fossil, by the hind leg tibia armoured with four long fixed spines. Foreleg the same as mid leg, differs from another gryllotalpidae by exceptionally robust femur and elongated equally (short in gryllotalpidae).

Species: Cratotetraspinus fossorius Martins-Neto, 1995 (figs. 119-122)

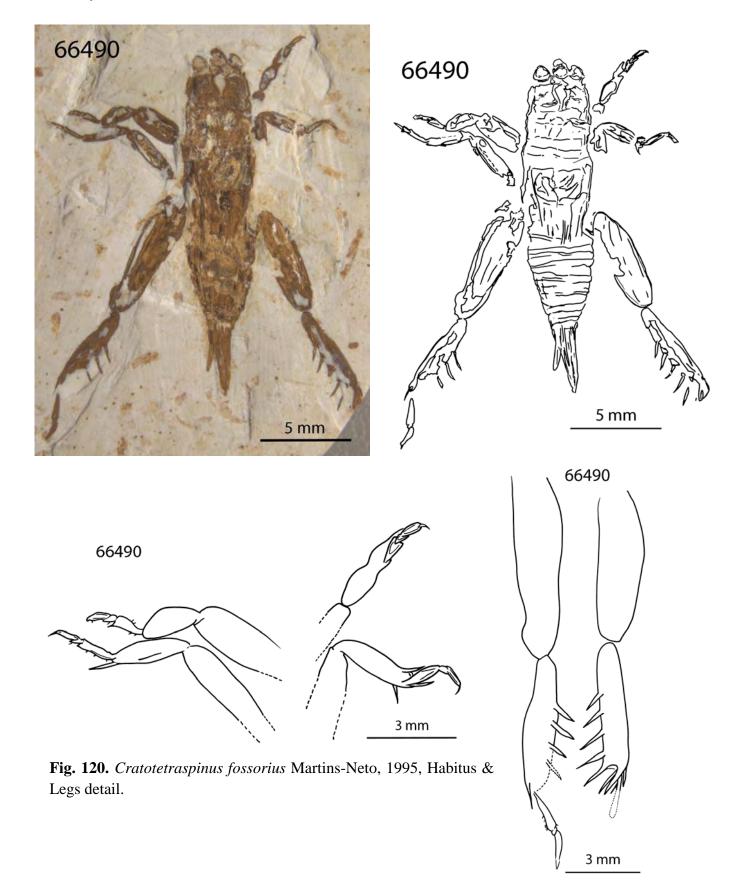
Original Description, according to Martins-Neto, 1995b: Body relatively robust, head globular, scape robust, insert below the eye; antenna long, filiform. Abdomen cylindrical. Forewing only poorly preserved. Foreleg especially robust and adapted for burrowing: femur short, robust; tibia much reduced and with fixed robust spines; tarsal strongly reduced. Mid leg tibia broad and with three mighty apical spines; tarsal much reduced. Hind leg adapted for jumping, femur robust and elongated; tibia about 2/3 of the femur length, relatively broad and armoured with four long fixed spines: the first and the second are in similar size; the third slightly shorter and the fourth much shorter and robust. Tarsus with three segments: the first segment much enlarged, elongated and with a mighty apical spine; the second one is much shorter and broad, in triangular form; the third segment is little longer than the second one and sharp. Few hirsute on the second segment only.

New Description: Body 15 to 16.5 mm long and 4 to 4.5 mm wide. Eye big, round and projected from the anterior side of head. Body elongated, with a strong thorax and a circa similar size abdomen. Fore, mid- and hind leg tarsal in the same pattern, that is, three tarsus segments with claw, the second segment notably short. Hind leg tibia with four to five long fixed spines and several (maybe up to four) apical spurs. Cerci middle length.

**Fig. 119.** *Cratotetraspinus fossorius* Martins-Neto, 1995, A well preserved specimen, particularly by the enlarged foreleg tarsus and hind leg spines. (SMNK PAL 5477, Staatliches Museum für Naturkunde, Karlsruhe, Germany) (After Heads & Martins-Neto, 2007).



Specimen **SMNS 66490**: Body 15 mm long and 4 mm wide. Hind wing in folding shape measured about 12 mm long. Foreleg tibia robust, with at least two strong apical spurs, tarsus three-segments with claw, the second segment notably short. Mid leg tibia with three apical spurs, tarsus three-segments with claw, the second segment notably short. Hind leg tibia with five long fixed spines and four to five apical spurs, tarsus three-segments, the second one notably short, the third one with claw.



Specimen **SMNS 66496**: Body 16.2 mm long and 4 mm wide. Hind leg tibia with four long fixed spines and apical spur.



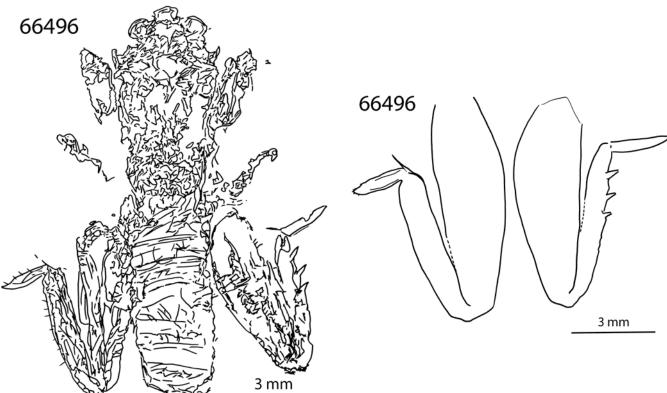
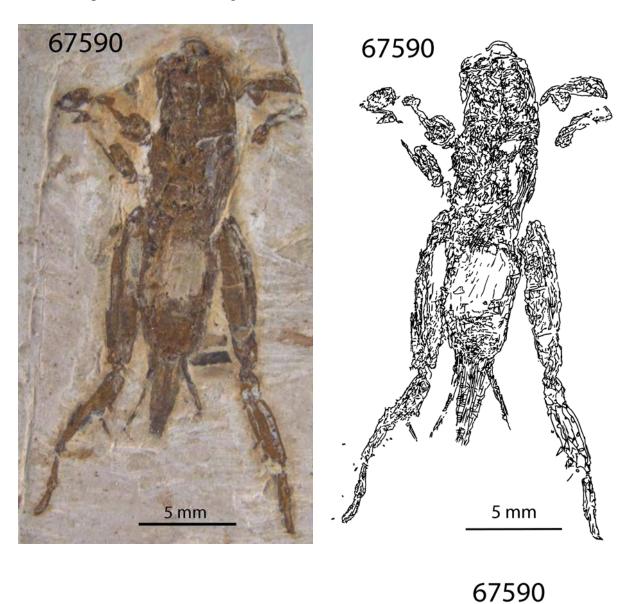
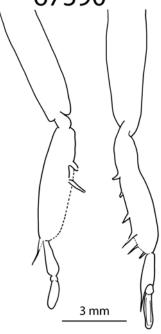


Fig. 121. Cratotetraspinus fossorius Martins-Neto, 1995, Habitus & Hind legs detail.

Specimen **SMNS 67590**: Body 16.5 mm long and 4.5 mm wide. Hind wing in folding shape measured about 18 mm long. Hind leg tibia with five long fixed spines and a apical spur, tarsus three-segments, first segment with a long apical spur, second segment notably short. Cerci well preserved, middle length.



**Fig. 122.** Cratotetraspinus fossorius Martins-Neto, 1995, Habitus & Hind legs detail.

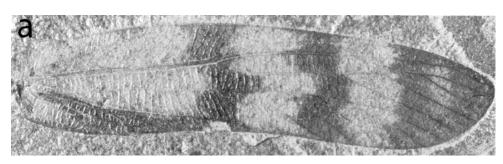


#### Superfamily: **Tettigonioidea** Zeuner, 1935

Tettigonioidea consists of the familiar katydids and bush crickets and, with about 6000 species, is the most diverse lineage of Ensifera. Presently, the superfamily consists of only the nominate family and several subfamilies that are sometimes given family rank. Tettigoniids are large insects occurring throughout the world. Many tettigoniids are arboreal or live in bushes and are remarkably cryptic, typically mimicking leaves, but also mimicking lichens and mosses (Grimaldi & Engel, 2005). According to Gorochov, 1995 the superfamily Tettigonioidea consists of one fossil, Haglotettigoniidae and one recent, Tettigoniidae families. The oldest Tettigonioidea (Haglotettigoniidae) are found in Transbaikalia, Glushkovo Formation whose age can be Early Cretaceous as well (Gorochov & Rasnitsyn, 2002). Morphological characters: medium to very large size (15-120 mm), tarsi with four segments, ovipositor from three pair genitalia valves, auditory organs commonly present and situated in the base of the fore tibia, tegmina well sclerotized and their apices folded together at rest, rare complete reduced, stridulatory structures commonly well developed and asymmetric (Carpenter, 1992; Groll & Günther, 2003).

# 3.3.1.4. Family: **Tettigoniidae** Krauss, 1902

The most ancient Tettigoniidae, *Pseudotettigonia* Zeuner, 1937 (=*Tettigonia amoena* Henriksen, 1929) (fig. 123) were found in the Eocene (Sharov, 1968; Carpenter, 1992). The venation of this species *P. amoena* is closely related to that of *Tettavus fenestratus*. A comparison of the venation of this two species clearly shows that the Tettigoniidae are descendants of the Tettavidae (Sharov, 1968). It has been suggested, however, that a mimetic species *Triassophyllum leopardii* Papier *et al.*, 1997 from France, which shows similarities especially to the subfamily Pseudophyllinae, is an indirect indication that the family Tettigoniidae can be dated back to the Mesozoic (Triassis: lower Anisian) (Papier *et al.*, 1997).



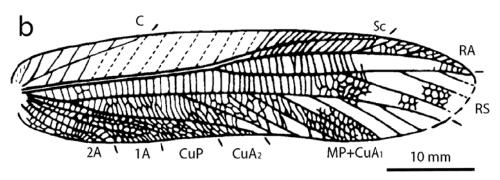
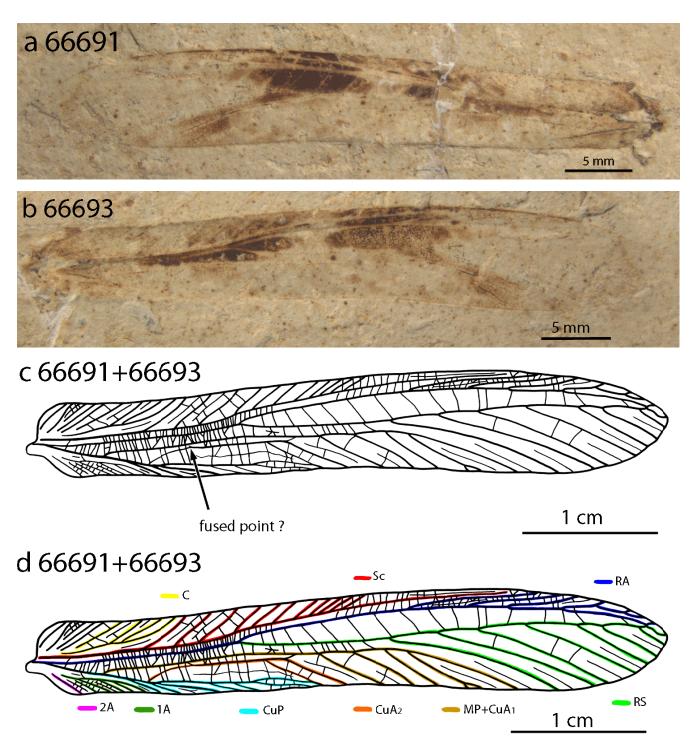


Fig. 123. a: Tettigonia amoena Henriksen, 1929. Forewing of female. Length 60 mm. Fur Museum, Denmark. (After Larsson, 1975) **b**: Pseudotettigonia Zeuner, 1937 (= (Pseudo)Tettigonia amoena Henriksen, 1929), forewing, Brithsh Museum (Nat. Hist.) No.I.36702, Paleogene, Western Europe. (After

Sharov, 1968)

# Specimen **SMNS 66691**+ **SMNS 66693** (Unknown new Species **F**) (fig. 124)

Reconstruction of a female left forewing from plate and its counter plate of a fossil, 46 mm long, 7 mm wide [by male, stridulatory structures commonly well developed; right tegmen with a membranous area between CuP and branches of CuA; left tegmen with a similar structure, but CuP larger and serrulate (Carpenter, 1992)]. This is the first description of Tettigoniidae in the Crato Formation or rather Cretaceous.



**Fig. 124.** Unknown new species katydids **F**, **a** & **b**: plate and counter plate. **c**: the stem of CuA2 and MP+CuA1 is probably fused. **d**: reconstructed Forewing.

Diagnosis: Similar to *Pseudotettigonia* Zeuner, 1937, but differs by the base of (MP+CuA1)+CuA2 and CuP fused in a single stem (in *Pseudotettigonia* still has two stems).

Description: Female forewing, medium size and narrow, 46 mm long and 7 mm wide. Costa short and the width between C and anterior margin wide. Sc long, slightly sigmoid, parallel with RA and adjacent to each other. RA with five branches. RS origin in the anterior 1/3 length of the whole wing. RA and RS parallel and the width between is wide, and fused the both again at the terminal end. RS with eight branches. MP+CuA1 with five branches. The stems of MP+CuA1 and CuA2 are parallel and adjacent with each other, probably fused (with a fused point?). CuA2 with two branches. CuP with seven branches. 1A with five (or six) branches, 2A alone.

Discussion: Differs from *Pseudotettigonia* by the smaller forewing size (in *P. amoena* forewing about 63 mm long and 14 mm wide), fused in base stems of MP+CuA1, CuA2 in ones and CuP and generally more vein-branched.

#### Superfamily: Hagloidea Handlirsch, 1906

The superfamily Hagloidea contains a single modern family with two subfamilies that seem to intermingle traits of the Tettigonioidea and Grylloidea. Hagloids were much more diverse in the past, extending at least into the Triassic, apparently diminishing in diversity through the Cretaceous (Grimaldi & Engel, 2005). Hagloidea are represented in the Crato Formation by only one monotypic genus and species *Prezotophlebia helbae* Martins-Neto, 2007. The two attributed to the Hagloidea species *Kevania araripensis* Martins-Neto, 1991 and *Cratohaglopsis santanaensis* Martins-Neto, 1991, both transferred newly to the Stenopelmatoidea (Martins-Neto, 1991c, 2007; Heads & Martins-Neto, 2007;). Though the assignment of *Prezotophlebia helbae* in Hagloidea may be erroneous.

### 3.3.1.5. Family: †**Haglidae** Handlirsch, 1906 sensu Gorochov, 1988

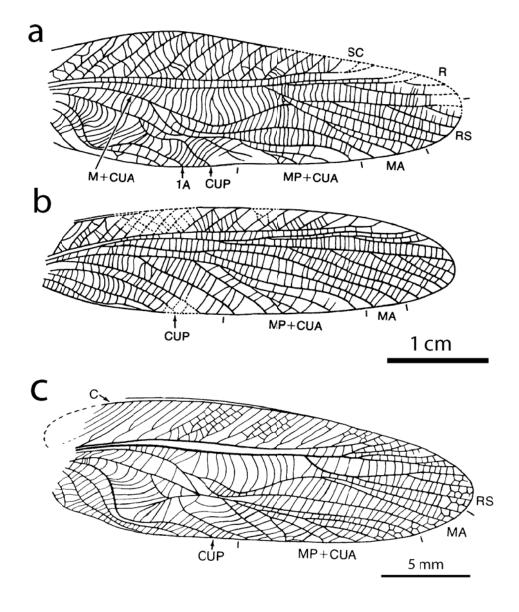
Related to Oedischiidae but with the venation of the wings conspicuously different in males and females; forewing of males with a more or less elaborate stridulatory organ. Hind wing known in only a few species; venation as in Oedischiidae but with an enlarged anal area in some specialized genera. This family was very large and diverse during the early half of the Mesozoic (Carpenter, 1992). The latest Haglidae is in late Jurassic: a single subfamily Cyrtophyllitinae first appearing in Triassic (Gorochov & Rasnitsyn, 2002), therefore the two new descriptions of this studies could be the latest Haglidae up to now.

Original Diagnosis and Composition, according to Gorochov, 1988: Male elytra with branches of Sc not intersected by developed false Costa vein, with lanceolate field widening in middle or proximal part of elytrum. Stridulating vein little inclined, bordering short basal field; crossveins, diagonal vein and CuA2 located mostly in proximal half of elytrum. Crossveins distinctly separate from basal part; MA2 branching proximally or distally to most convex part of lanceolate field. Seven subfamilies, of which five are from Lower and Middle Jurassic, and two are Triassic.

Subfamily: Haglinae Handlirsch, 1906 sensu Gorochov, 1988

Original Diagnosis and Composition, according to Gorochov, 1988: Male elytra with lanceolate field not closed or, in primitive forms, closed by rudimentary proximal part of 1MA1; 2MA1 close to RS; RS with many branches; MA2 branching proximally to most convex part of lanceolate field. Proximal and distal parts of CuA2 clearly displaced to each other; between distal part of CuA2 and diagonal vein no corner angular veins or only one such vein; venation not parallel. Sixteen Triassic genera and two Jurassic genera: *Hagla* Giebel, 1856 and *Liassophyllum* Zeuner, 1935; Lower Jurassic, England.

Type genus: *Hagla* Giebel, 1856 (fig. 125)



**Fig. 125.** Family Haglidae: **a** & **b**, *Hagla* Giebel, 1856, Forewing of a, male and b, female (Zeuner, 1939), Jurassic, England; **c**, *Archihagla* Sharov, 1968, Forewing of male, Lower Triassic, USSR, Kirghiz. (After Sharov, 1968; Carpenter, 1992)

Specimen SMNS 66501 (Unknown new Species G) (fig. 126)



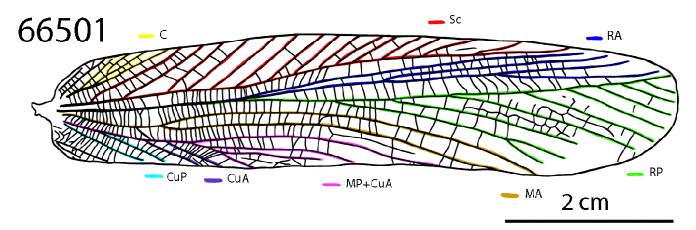


Fig. 126. Unknown new species *Hagla* G, Forewing.

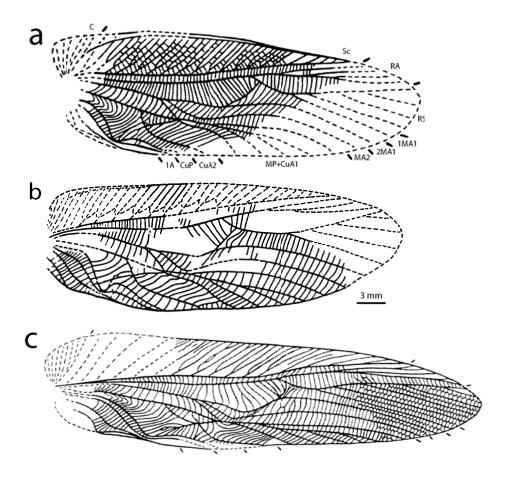
Diagnosis: Female forewing. Notably large in size, 74 mm long and up to 17 mm wide. Similar to the genus *Hagla* Giebel, 1856, but differs at the origin of RA1 in the anterior 1/3 length of whole wing and reaching to the origin of the RP, RP with nine-branches (by Hagla with five to six), the origin of the stem of MA was already separated from the base of the stem of R (by Hagla the stem of MA and the base of the stem of R was still fused), the origin of MA2 and the origin of the MP+CuA are much anterior to the wing base, and the width between the stem of MP+CuA and anal margin is much narrower, only about ½ of wing width (by *Hagla* about 1/2).

Description: Large size female forewing. Costa short, with four branches. Sc slightly sigmoid in the posterior half. RA four branches. RP1 straight and terminal bended to the anterior margin. RP with nine branches, RP9 with two terminal branches. MA sigmoid, MA1 and MA2 parallel. The MP, CuA, CuP and A are in typical Hagla female pattern but the area is much smaller.

Discussion: The difference with *Hagla* is rather clearly, in the origin of RA1 is much anterior in the whole wing, RP with more branches, the origin of the stem of MA was already separated from the base of the stem of R and the width between the stem of MP+CuA and anal margin much narrower. It is possibly that this specimen SMNS 66501 could be described as a new genus. However Hagloid females could not be determined reliably to genus by wing structure, except when identified as conspecific to males (Gorochov, 1996; pp. 440).

## Subfamily: Cyrtophyllitinae Zeuner, 1935 sensu Gorochov, 1988 (fig. 127)

Original Diagnosis and Composition, according to Gorochov, 1988: Male elytrum with long oblique vein closing lanceolate field at apex; 2MA1, RC, MP + CuA1, MA2 and cross venation between CuP and CuA2 as in Voliopinae; CuA2 with proximal and distal parts not displaced relative to each other; first short and not gently inclined to longitudinal axis of elytrum; venation not parallel. Two genera: *Archaboilus* Martynov, 1937, Lower and Middle Jurassic, central Asia and Siberia, and *Cyrtophyllites* Oppenheim, 1888, Upper Jurassic, Western Europe.



**Fig. 127.** Cyrtophyllitinae. **a:** *Archaboilus shurabicus* Martynov. Lower Jurassic, Middle Asia, without scale. (After Sharov, 1968; Gorochov, 2003); **b.** *Archaboilus martynovi* Gorochov, 1988, Kirgiz SSR, Sogyuty locality; Lower Jurassic. (After Gorochov, 1988); **c.** *Voliopus ancestralis* Gorochov, 1986. (Subfamily: Voliopinae Gorochov, 1986) Triassic, Middle Asia, without scale. (After Gorochov, 2003)

Genus and Species: incertae sedis

Specimen SMNS, without number (New Species **H**) (figs. 128-130)

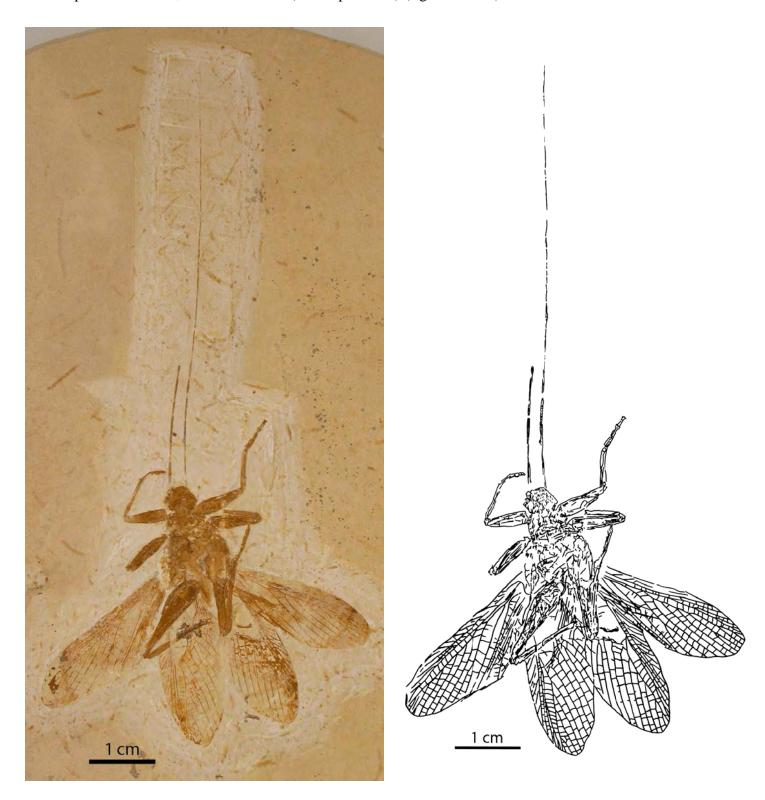
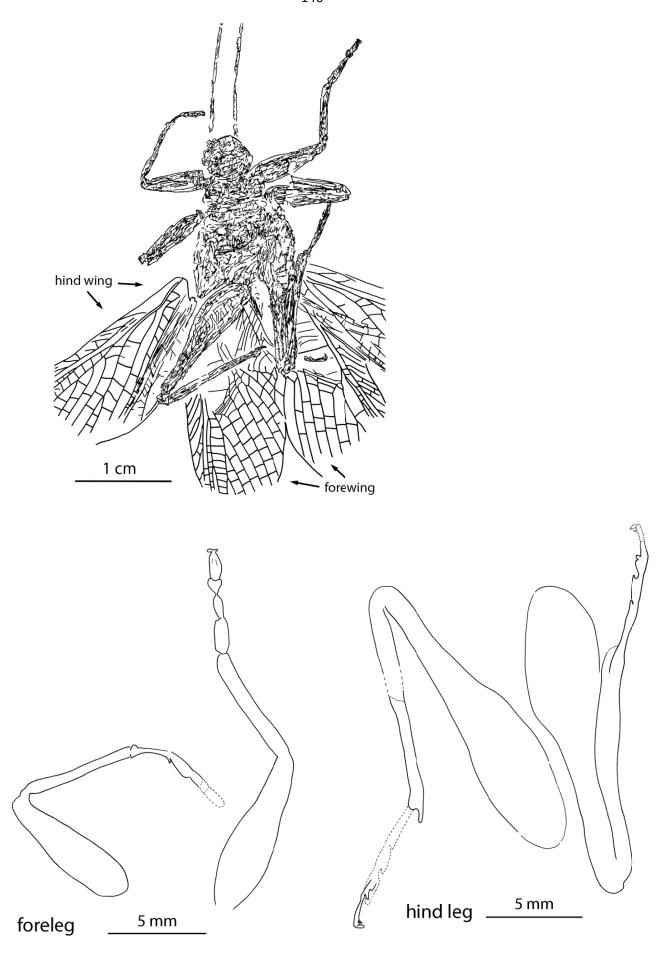


Fig. 128. Unknown new species Haglidae H, SMNS without number, Habitus.



 $\textbf{Fig. 129.} \ \ \textbf{Unknown new species Haglidae $H$, SMNS without number, Body part \& Legs.}$ 

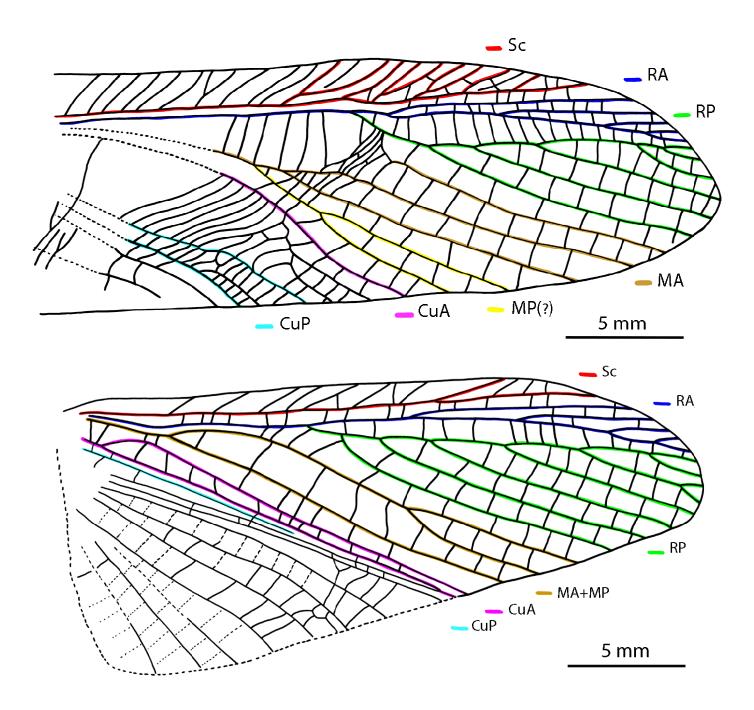


Fig. 130. Unknown new species Haglidae H, SMNS without number, Fore & Hind wings.

Diagnosis: Male fore and hind wings typically haglidae. Forewing similar to *Archaboilus*, with the lanceolate field (that is between stems of RA and MA) enlarged, rounded and its apex with thick crossveins. Branches from RP to CuP (especially MP+CuA1) rather straight and parallel. The width between CuA and CuP1 expand.

Description: Antenna 66 mm long and more than 200 segments, about twice of the length of the forewing length. Forewing: about 33 mm long and 10 mm wide, Sc parallel with anterior margin and with slanting branches. RA with five branches. RP with six branches. The width between anterior RA and RP is wider, gradual narrower toward the posterior end. MA with three branches. The area between stems of R and M develop to a round lanceolate field, with

parallel branches in it. MP probably fused with MA and with two branches. The base area of MP, CuA and CuP is not well preserved thus the stridulatory organ is not clear. The width between CuA and CuP1 expand, with more dense, parallel and sigmoid branches in between. Hind wing: 30 mm long and up to 9 mm wide, Sc elongate. RA with five branches. RP with seven branches. MA curved in the base part and with two terminal branches. MP alone. CuA with two branches, CuA1 strongly curved in the base part. CuP short, reaching only 2/3 of the wing. [And there are some slight differences between left and right hind wings of this specimen, in the right hind wing, RP3 is alone and RP4 has two terminal branches. In left hind wing, RP3 has two short terminal branches and RP4 is alone (Fig. here as left side).] Body: Head round, broader than the prothorax. Thorax short. Foreleg tarsus with four segments and claws. Hind leg femur robust, tarsus with four segments, the first segment elongate, the forth segment with claws.

Discussion: Forewing similar to *Archaboilus* (subfamily: Cyrtophyllitinae) by the ground pattern and lanceolate field. Differs from *A. shurabicus* Martynov, 1937 and *A. martynovi* Gorochov, 1988 by Sc-area narrower, MA1 origin direct from the middle point of the lanceolate field [this character is similar to *Voliopus ancestralis* Gorochov, 1986b (Subfamily Voliopinae Gorochov, 1986b, Triassic, Middle Asia)], branches from RP to CuP, especially MP+CuA1 rather straight and parallel (in *A. shurabicus*, *A. martynovi* and other Haglidae species the MP+CuA1 generally bent strongly) and the width between CuA and CuP1 expand.

Remark: Because of the similarity to the genus *Archaboilus*, it is possible, that this specimen also belongs to the Subfamily Cyrtophyllitinae Zeuner, 1935.

### 3.3.1.6. Family: **Prophalangopsidae** Kirby, 1906; sensu Gorochov, 2003

Prophalangopsidae consists of five fossil and one Recent subfamilies: 1. Protaboilinae Gorochov, 1988, one genus (Lower Jurassic; Middle Asia), 2. Aboilinae Martynov, 1925, 19 genera and 46 species (Lower Jurassic-Upper Cretaceous; Siberia, Kazakhstan, Kirgyzstan, Mongolia, China, Japan, Germany), 3. Chifengiinae Hong, 1982, five genera (Upper Jurassic-Lower Cretaceous; Siberia, China), 4. Termitidiinae Zeuner, 1939, one genus (Lower Cretaceous; England), 5. Tettohaglinae Gorochov, 2003, one genus (Lower Cretaceous; Siberia) and one Recent subfamily, Prophalangopsinae Kirby, 1906 (India, China) (Gorochov, 2003; Gu *et al.*, 2009). During Early Cretaceous, Prophalangopsidae continued its radiation, all the subfamilies arising in this period, being distributed in China, Japan, Russia, Central Asia, Europe, England, and Brazil (Gorochov & Rasnitsyn 2002; Gu *et al.*, 2010). However the record in Brazil has been revised (Martins-Neto, 2007) (more detail see Discussion, page. 227) and the specimens of this study is the first description of Prophalangopsidae in the Crato Formation and even South America.

Original diagnosis and description, according to Gorochov, 2003: Prophalangopsidae is the youngest family of the superfamily Hagloidea. The origin of Prophalangopsidae from the Triassic-Early Cretaceous family Haglidae is possibly connected with distinct improvement of flying function of hind wings and with decrease of importance of stridulatory apparatus. The improvement of hind wings consists of widening of their anal part and of appearance of rather long additional (secondary) longitudinal vein obliquely connecting MP+CuA1 with CuA2.

The widened hind wings of Prophalangopsidae need a larger space under tegmina during the rest position. The tegmina raise themselves a little in this position, and the characteristic fold appears between the proximal part of their costa area (contacting the body) and other parts of tegmina (embracing hind wings). Along this fold, the new longitudinal vein from transverse veinlets between branches of Sc (false C) appears. These characters of hind wing and tegmina are most important for distinguishing the Prophalangopsidae and their descendants from other Hagloidea.

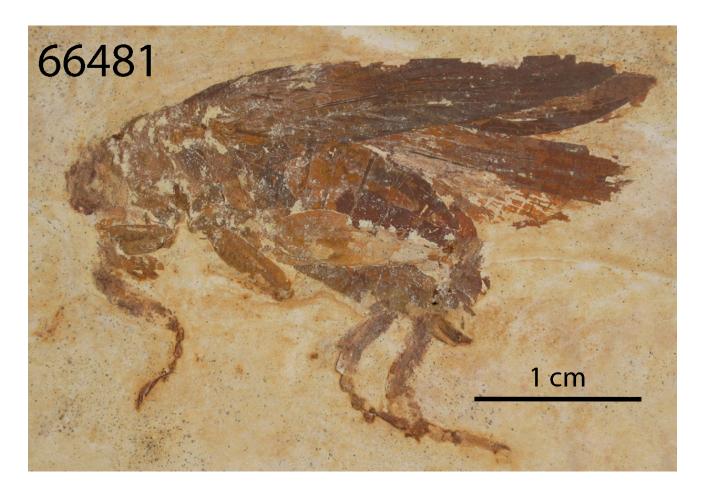
Subfamily and genus: incertae sedis

Unknown new Species I (figs. 131-136)

Diagnosis: Forewing narrow and the top sharp, pre-costa area large and round. Radial few branched, that is RA with three and RP with only two branches. Hind wing Radial few branched, RA with only two and RP with three branches.

Description: Small size. Antenna are a little shorter than body length and more than 100 segments. Head flat and wide. Eye small, oval and located at the central of the head. Forewing 24-31 mm long and up to 3-5.5 mm wide, narrow, broad in the base and peak in the terminal. Pre-costa area large, the costa margin curve strongly. "False Costa" clear and straight, parallel with Sc. The width between "false C" and Sc wide. Sc with eight branches, the width between Sc-branches are quite equal and broad. RA with three branches. RP with two branches, RP1 with two terminal branches. MA by female with two- and by male with three branches (or one more inter-vein?). The connect vein between stem of MA and MP+CuA is extremely short. CA2 and CuP adjacent and slightly sigmoid. Hind wing Costa short, the width between anterior margin and C in the middle part is wide. Sc alone. RA with two branches. RP with three branches. M sigmoid. The apices of hind wing folded together at rest. Body: Thorax narrow and flat. Fore- and mid leg tibia thick and with several spines. Fore-, mid- and hind leg tarsus all in the same pattern, that is, tarsus with five segments, the length of each segment from the first till fourth segment are short and about equal length, the fifth segment elongated and with claws. Abdomen oval, ovipositor short.

Specimen **SMNS 66481**: Female. Forewing small and narrow, broad in the base and peak in the terminal, 31 mm long and up to 5.5 mm wide. Pre-costa area large, the costa margin is strongly curved. "False Costa" clearly and straight, parallel with Sc. The width between "false C" and Sc is wide. Sc with eight branches, the width between Sc-branches quite equal and wide. RA with three branches. RP with two branches. MA with two branches. The connect vein between stem of MA and MP+CuA is extremely short. CA2 and CuP adjacent and slightly sigmoid. Body: Thorax narrow and flat. Foreleg tibia thick, tarsus with five segments, the fifth segment elongate and with claws. Hind leg tarsus the same with foreleg, five segments, the fifth segment elongate and with claws. Abdomen oval, ovipositor short.



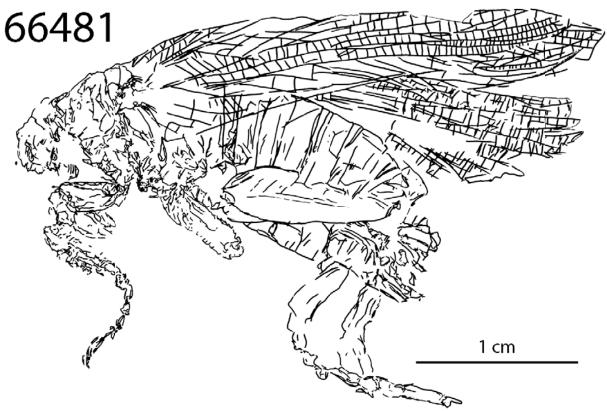
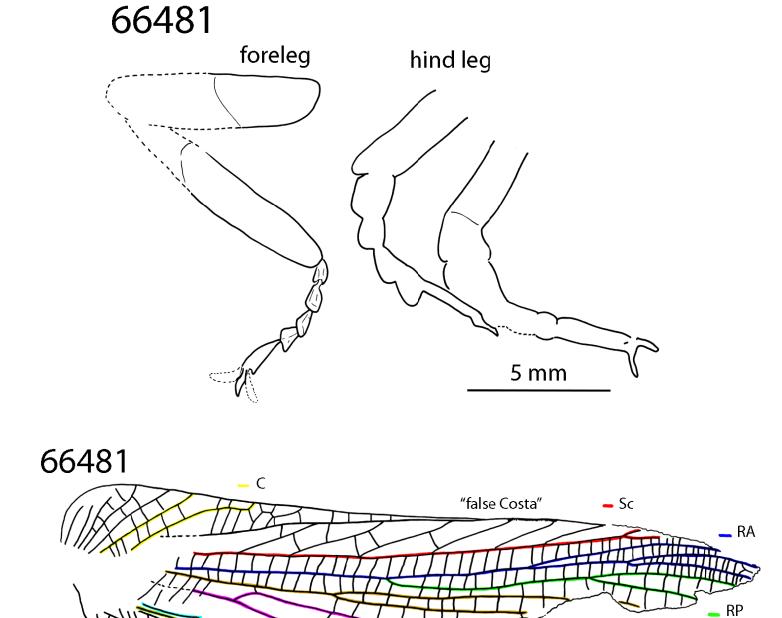


Fig. 131. Unknown new species Prophalangopsidae I, Habitus.



- MP+CuA

<u>-</u>МА

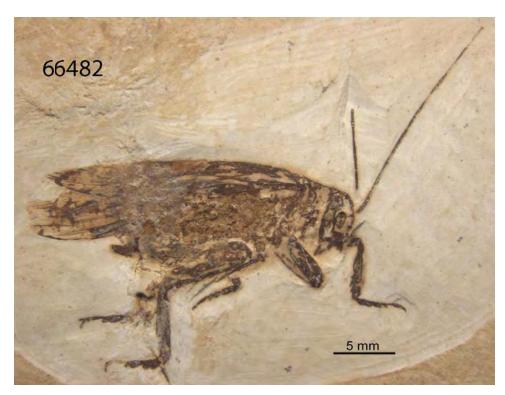
5 mm

Fig. 132. Unknown new species Prophalangopsidae I, Legs & Forewing.

CuP

CuA2

Specimen SMNS 66482: Female. Antenna long, a little shorter than the body length and more than 100 segments. Head flat and wide. Eye small, oval and located at the central of the head. Thorax narrow and flat. Foreleg tibia thick and with several spines. Fore-, mid- and hind leg tarsus well preserved, all in the same pattern, that is, tarsus with five segments, the length of each of segment from first till fourth segment are short and about equal length, the fifth segment elongated and with claws. Abdomen oval and ovipositor short. Forewing 24 mm long and up to 3 mm wide, narrow, broad in the base and peak in the terminal. Only a few veins of fore and hind wing in the peak part were preserved.



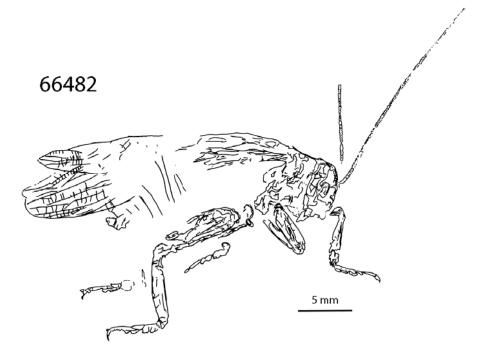


Fig. 133. Unknown new species Prophalangopsidae I, Habitus.

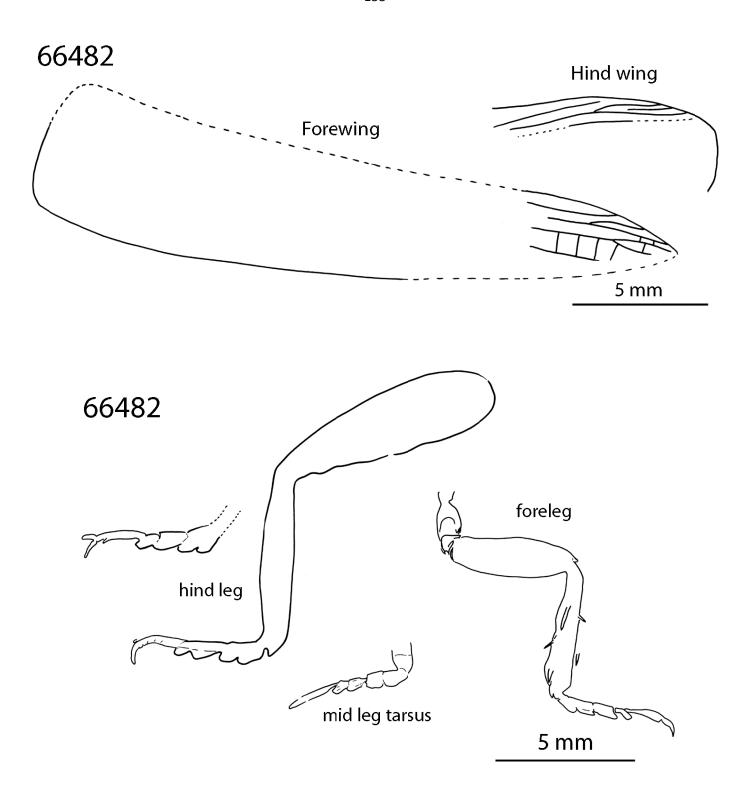


Fig. 134. Unknown new species Prophalangopsidae I, Fore-, Hind wings & Legs.

Specimen SMNS 67582: Probably male. Forewing small and narrow, about 29 mm long. Sc with at least eight branches. RA with three branches. RP with two branches, RP1 with two short terminal branches. MA with three branches and MA2 and MA3 fused together (alternatively MA with two branches and an inter-vein (or a fold?) between R and M extra; is rather here improbable). MP, CuA, CuP and A veins were not preserved. Hind wing Costa short, the width between fore margin and C in the middle part wide. Sc alone. RA with two branches. RP with three branches. M sigmoid. Particularly is, it presented several (2?) short flexion lines between RA and RP, this line is from the base of RP until to the apex of wing and the field RA+RP folded together at rest. Body: Mid leg tibia thick and with several spines, tarsus with five segments, the fifth segment elongate and with claw. Hind leg tibia thin and smooth, tarsus with five segments, the fifth segment elongate and with claw. Abdomen round, terminalia without ovipositor, at least no evidence about it.

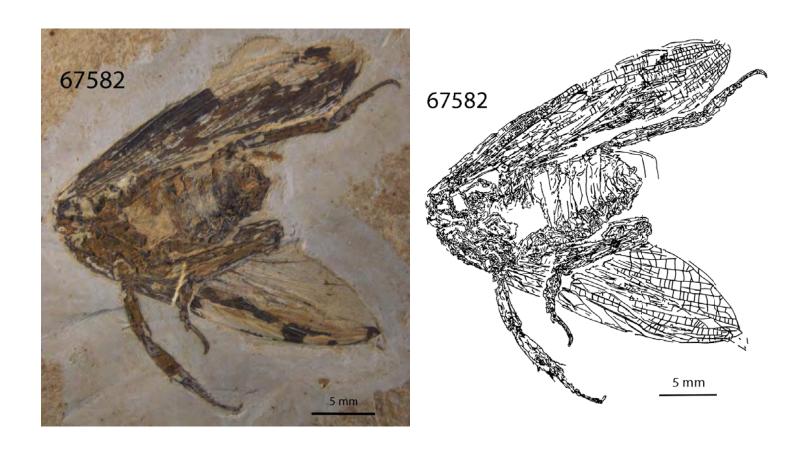


Fig. 135. Unknown new species Prophalangopsidae I, Habitus.

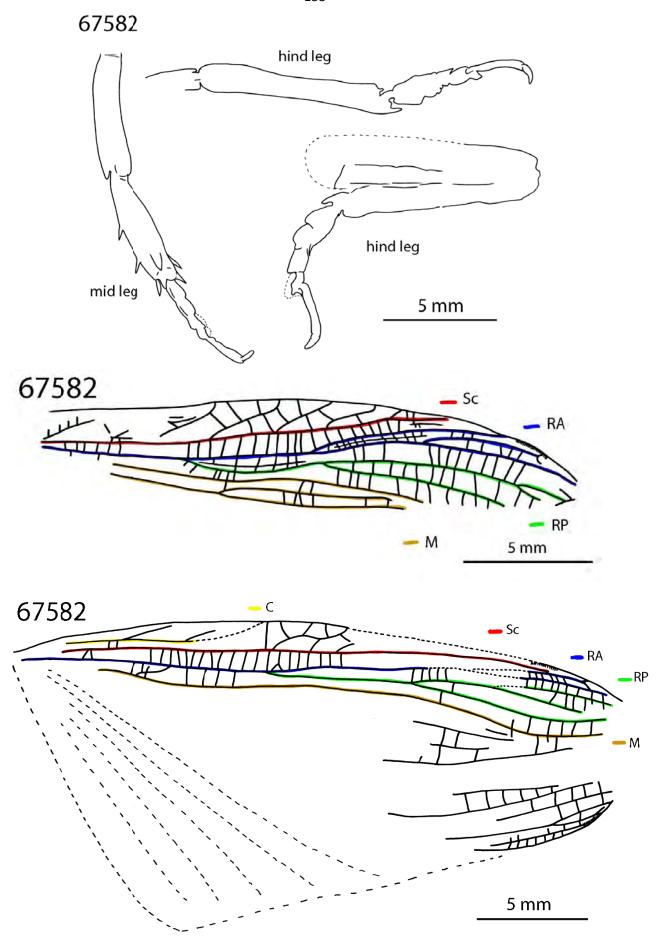
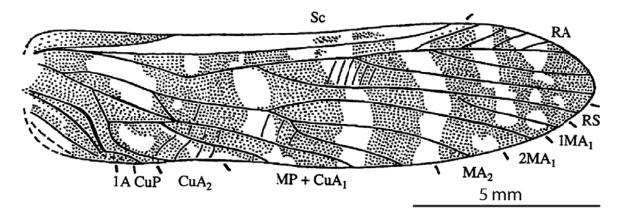


Fig. 136. Unknown new species Prophalangopsidae I, Fore-, Hind wings & Legs.

Remark: Specimen SMNS 66481, SMNS 66482 and SMNS 67582 are principally similar, both in size and habitus. Specimen SMNS 66481 is about the same size as SMNS 67582 and both are a little larger than SMNS 66482. Forewing the "false C", Sc, RA and RP coincides each other by SMNS 66481 and SMNS 67582, only the MA in SMNS 67582 has one more branch, could be a inter sexual difference. Terminal RA and RP-branches of fore and hind wing are coincided by all three specimens. Body in fore- mid- and hind leg, all the tarsus with five segments.

Discussion: Differs from almost all the genera of Prophalangopsidae by the forewing RA and RP few branched, that is RA with three and RP with only two branches. Similar only by the genus *Karatailus* Gorochov, 1996 (Subfamily Aboilinae Martynov, 1925; Upper Jurassic; Kazakhstan) (fig. 137) as well with the two-RS(+1MA1) branched (Gorochov, 1996, 2003). Differs from *Karatailus micropterus* by RA with three branches (in *K. micropterus* RA with seven branches) and pre-costa area large.



**Fig. 137.** *Karatailus micropterus* Gorochov, 1996 (Subfamily: Aboilinae Martynov, 1925) Male, holotype. (After Gorochov, 1996)

Superfamily: Elcanoidea Handlirsch, 1906 sensu Peñalver & Grimaldi, 2010

According to Peñalver & Grimaldi (2010), Elcanoidea included two families, Elcanidae and the paraphyletic Permelcanidae. Both families possessed some common features: long, slender forewings with the costa and posterior margins roughly parallel and frequently slightly concave; Rs and M joined near the middle of the wing by a short, basal segment of Rs; and the main trunks of R and Rs parallel or nearly so for much of their length, with a series of 3–10 or more parallel, oblique M veins arising ventrally from Rs. Wings of both families were frequently infuscate along some veins, and did not possess stridulatory structures. The phylogenetic position of the Elcanoidea (Elcanidae plus Permelcanidae) is unsettled. In one scheme, this clade is the sister group to the Caelifera (grasshoppers and locusts), even though elcanoids retain the plesiomorphically long, flagellate antenna found in Ensifera (Béthoux & Nel, 2002; Grimaldi & Engel, 2005). In another scheme (Gorochov & Rasnitsyn, 2002), Elcanoidea and Permoraphidoidea are hypothesized to be the sister group to all other Orthoptera, which is a position traditionally believed to be held by the Oedischioidea.

#### 3.3.1.7. Family: †Elcanidae Handlirsch, 1906 sensu Zessin, 1987

Type genus: Elcana Giebel, 1856

According to the study of Zessin (1987, 1988) is leaded to a drastic reduction of the number of species in this monophyletic group from 120 to 26 and are placed into the Elcanidae the following five genera: Promartynovia Tillyard, 1937 (=Permelcana Sharov, =Proelcana Sharov) (five species; Lower Perm; North America & Russia), Meselcana Sharov, 1968 (one species; Triassic; Middle Asia), *Parelcana* Handlirsch, 1906 (three species; Lias; Europe), Elcana Giebel, 1856 (=Archelcana Sharov) (16 species; Jurassic; Europe & Asia) and Baisselcana Sharov, 1968 (one species; Lower Cretaceous; Siberia). Since then were some new genera described as follows: Eubaisselcana Gorochov, 1986a (Lower Cretaceous; Mongolia), Synelcana Zessin, 1988 (Early Jurassic; Europe), Probaisselcana Gorochov, 1989 (Upper Jurassic; Kazakhstan), Sibelcana Gorochov, 1990 (Late Jurassic or Early Cretaceous; Siberia), Cratoelcana Martins-Neto, 1991 (Lower Cretaceous; Brazil), Minelcana Gorochov et al., 2006 [this genus included species Bittacus dubius Giebel, 1856 (Lower Cretaceous; southern England) and possibly Cratoelcana damianii Martins-Neto, 1991 (Lower Cretaceous; Brazil)], one amber species Longioculus Poinar et al., 2007 (Early Cretaceous; Myanmar), one amber nymphal species Burmelcana Peñalver & Grimaldi, 2010 (Early Cretaceous; Myanmar) and three amber nymphal species *Hispanelcana* Peñalver & Grimaldi, 2010 (Early Cretaceous; northern Spain) (data: Zessin, 1987, 1988; Martins-Neto, 1991c, 1992, 1995b; Gorochov et al., 2006; Poinar et al., 2007; Peñalver & Grimaldi, 2010).

Original Diagnosis, according to Zessin, 1987: Forewing membranous. Anterior- and posterior margin slightly curved, commonly in the middle part of wing mutually arched. In the base of anterior margin without prominent curve. Costa-field narrow and long, Costa-P with short branches. ScA reach about ¼ of wing length, the stems of Costa-P and ScA almost parallel and adjacent with each other. ScP with comb-like branches in distal area, not reach to the tip of wing, commonly only to the middle. RA distal with comb-like branches. Between RA and RP with nearly vertical branches, parallel with each others. RP in the beginning as a

short slanting branch, that resembles to a cross-vein and commonly connected with MA by a short stretch. The stem of MA and RP in one vein, the branches of MA and RP come from the comb-like complex and follow backwards. MP connected with CuA, with one or more branches. CuP come close to AA narrowly, formed a slender pre-anal field. AP with two or three branches. Anal field not reaches to middle wing length. Cross-vein relative few, shaped no true reticulation. Most lively pigmented specially in distal wing area, formed the characteristic pattern. Hind wing ScA short. ScP, RA, RP, MA and their branches similar to the forewing. MP like forewing connected with CuA1. CuA2, CuP and AA moved closer and parallel. Anal- and jugal field together about the width of wing and by the Paleozoic Elcanidae more than middle of wing, by the Mesozoic one reached near to the apex. Antenna long and filiform. Hind leg tibia with sharp spine, by some Mesozoic species has width leaf-shape appendage. Hind leg femur robust. Ovipositor long, about the length of abdomen.

The family Elcanidae was divided into two subfamilies: Elcaninae Handlirsch, 1906 (=Baisselcaninae Gorochov, 1986) and Archelcaninae Gorochov *et al.*, 2006 (Gorochov, 1986a; Gorochov *et al.*, 2006). According to Gorochov *et al.* (2006): The subfamily Archelcaninae differs from Elcaninae in the more or less widened area between tegminal RA and RS, the free (rather than fused together) distal parts of tegminal CuA2, CuP, and 1A, and probably the larger spines of the hind tibiae. Archelcaninae include four genera: Early Jurassic *Parelcana* Handlirsch, 1906 and *Synelcana* Zessin, 1988; Early and Middle Jurassic *Archelcana* Sharov, 1968 and Late Jurassic or Early Cretaceous *Sibelcana* Gorochov, 1990. The numerous species of Archelcaninae included in *Elcana* by earlier authors (Handlirsch, 1906; Sharov, 1968; Zessin, 1987) are in need of generic revision.

Subfamily: **Elcaninae** Handlirsch, 1906 (=Baisselcaninae Gorochov, 1986) *sensu* Gorochov *et al.*, 2006

According to Gorochov *et al.*, 2006: This subfamily is characterized by the more or less narrowed area between tegminal RA and RS, the fused (with each other) distal parts of CuA2, CuP, and 1A or only CuP and 1A, and possibly the rather small spines of the hind tibiae. Elcaninae include five genera: Late Jurassic and Early Cretaceous *Probaisselcana* Gorochov, 1989; Early Cretaceous *Panorpidium* Westwood, 1854 (*Elcana* Giebel, 1856; *Baisselcana* Sharov, 1968), *Eubaisselcana* Gorochov, 1986, *Cratoelcana* Martins-Neto, 1991, and *Minelcana* Gorochov *et al.*, 2006.

Genus: Cratoelcana Martins-Neto, 1991

Original diagnosis, according to Martins-Neto, 1991c: the genus Cratoelcana is similar to the genus *Elcana*, but differs by larger area of the costa-zone in the base of the forewing, more secondary RP branch, the slanting veins without radial field and longer CuA, reaching quasi the hind rand of wing apex. Male: the forewing is much sharper in apex, with more secondary RP branches, head slender and relatively big, scape robust. Female: with long ovipositor, saber form, almost as long as the body length. Forewing much rounded in apex and has less secondary RP branches. Head much wider, eye relatively smaller, scape smaller. Both male and female have long antenna, filiform, much longer than the forewing. Hind leg femur robust,

tibia with less than six long spines. Tarsus long, about 2/3 length of the tibia, the first segment different in length, about half of the length of tibia. Tibia is about 12 to 26 mm long.

Species: *Cratoelcana zessini* Martins-Neto, 1991 (figs. 138-146)

Original diagnosis, according to Martins-Neto, 1991c: Body length between 28 and 37 mm. Forewing length between 22 and 26 mm and with more secondary RP branches, female has 8 and male has 12.

New diagnosis: Female ovipositor is generally thin and long, slightly bended. (In *C. damianii* the ovipositor is broader and shorter.)

Original description, according to Martins-Neto, 1991c: Female, forewing long, length is about five times shorter than the width; fore rand straight, base part relatively curve, apex sharp and round. Costa area big in the wing base, with branch, slightly bend. Sc relatively curve, reaching to the anterior middle point of the fore rand. RA elongate and bend, distance between RA and ScP is narrow. RP1 elongate and bend, parallel with RA. The distance between radial branches is basically the same, the apex area relative narrow. RP with 8 secondary branches, rarely with between-vein, all branches parallel and reaching to the rand of apex. MA1 origin close to the level where Sc ends. MA2, MP+CuA1 and CuA2 long and parallel. Base part of CuP is sigmoid. Male, Forewing similar with female, more narrow, apex sharper and with 12 RP branches, which is more than female. Body, male and female abdomen short, eye relatively big and round, antenna filiform, longer than the forewing, scape robust especially in male. Female is generally larger, head oval, relatively longer and eye smaller than males. Ovipositor elongate, saber form and longer than the body. Male head oval, scape robust like the females. Hind leg femur long and robust, tibia thin and elongate, with less than six mighty and long spines. Tarsus with three segments, first segment very long, almost half of the length as tibia, second segment is about half of the length of the first segment, third segment short.

New description: The length of the antenna is longer than twice the length of the body, scape similarly robust in both sex. Body size is probably larger than as known; forewing 41 mm and total body 50 mm long. Forewing of some individual with RP2 and RP3 with further branches and sigmoid. Hind wing shorter than the forewing and in the similar pattern with forewing, that is the RA and RP1parallel and the stem of RP branches, MA, MP and Cu are secondary connected with RP1. Specially is the Sc short and parallel with RA, the distance between Sc and the fore rand narrow, RP seven-branches. Fore- and mid leg are in the similar pattern, femur is about the same length as tibia, tarsus three segments with claw, the first segment is longer than the third segment and the second one clearly short. Hind leg femur robust, the tibia is about the same length as the femur and with maximal eight long, mighty and leaf-form spines, tarsus two segments with claw, instead of three, the first segment long and with an apical spur, the second segment about half length as the first one.

Specimen **SMNS 66492**: Male, body and wing notably large, forewing 41mm and body totally 50 mm long, clearly larger than the specimen *Cratoelcana zessini* (forewing 22.0 to 31.2 mm and body totally 27.8 to 36.8 mm (Martins-Neto, 1992)). Head oval, eye large. Thorax wide, saddle form. Hind wing is similar with the forewing in pattern, RA and RP1

parallel and adjacent, RP with seven-branches, less than forewing. Hind leg femur robust, 16 mm long and up to 5 mm wide, tibia about the same length as femur and with at least eight mighty spines.

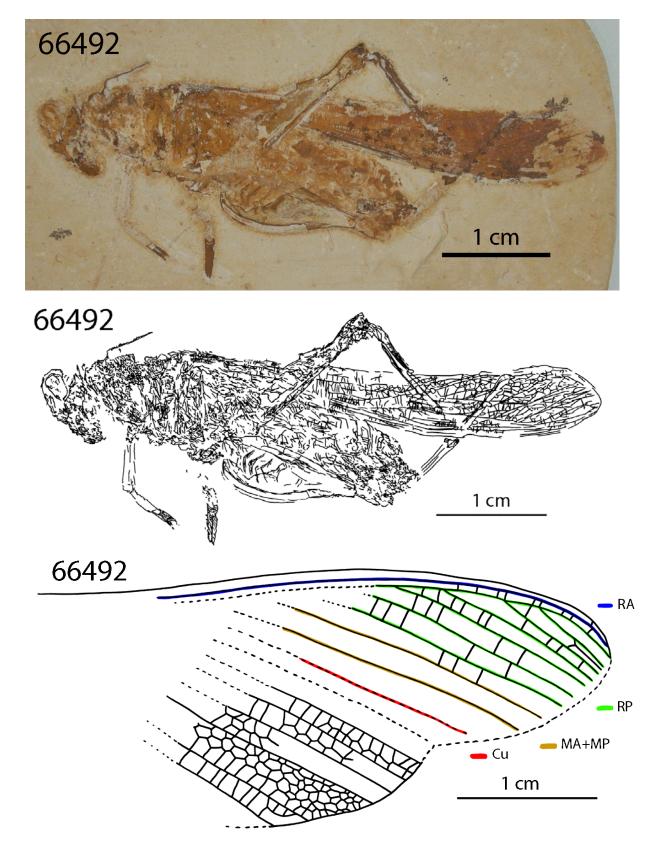
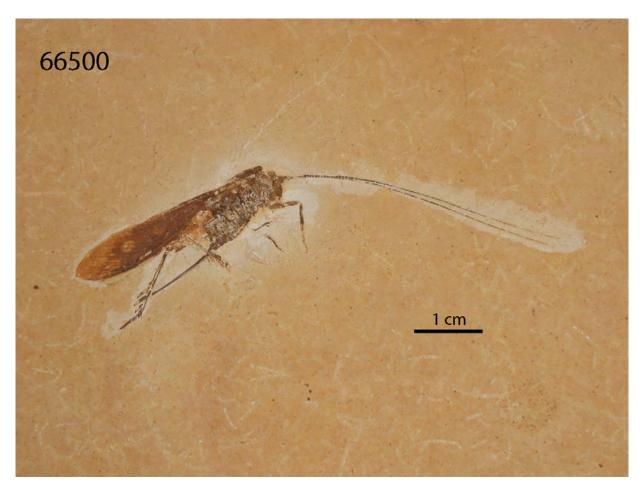


Fig. 138. Cratoelcana zessini Martins-Neto, 1991, Habitus & Hind wing.

Specimen SMNS 66500: Female, the length of the antenna is about one and a half length of the totally body length. Forewing, the distance between ScP and fore rand broad, RP with elfbranches. Hind wing with similar pattern but probably fewer RP branch. Fore- and mid leg in similar pattern, femur is about the same length as tibia, tarsus three segments with claw, the second segment clearly short. Hind leg femur robust, tibia is about the same length as the femur and with at least four long, mighty spines, leaf form. Ovipositor relative thin, slightly bend.



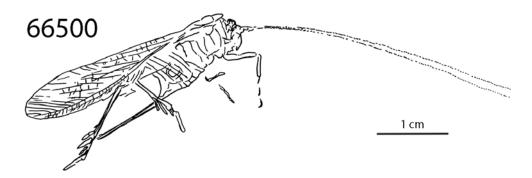
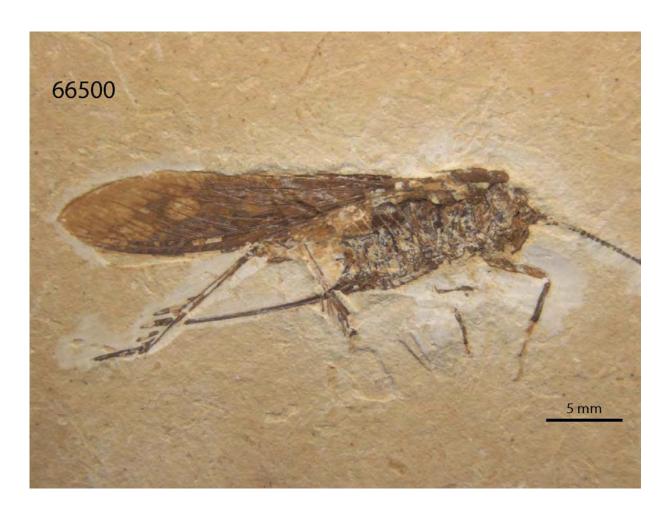


Fig. 139. Cratoelcana zessini Martins-Neto, 1991, Habitus.



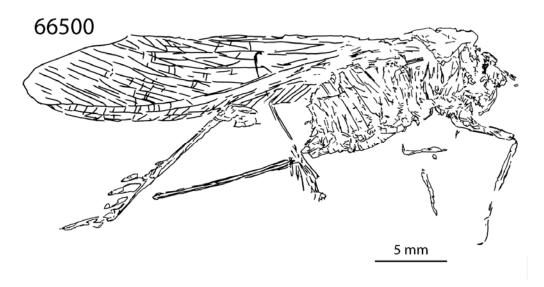


Fig. 140. Cratoelcana zessini Martins-Neto, 1991, Body parts.

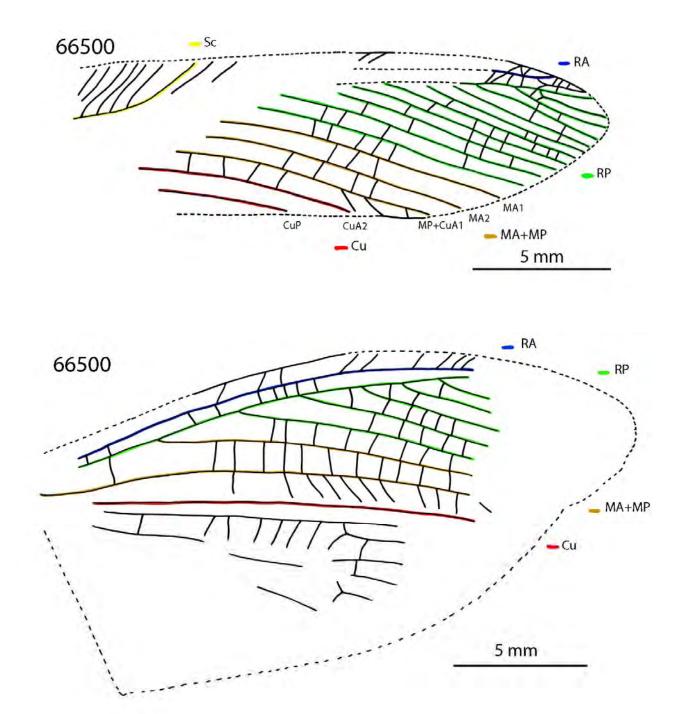


Fig. 141. Cratoelcana zessini Martins-Neto, 1991, Fore & Hind wings.

Specimen SMNS 66566: Female, the length of the antenna is longer than twice of the body length and more than 180 segments, scape robust. Eye big and round. Mouthpart partial visible, labrum sharp, maxillary palpus and labial palpus several segments. Thorax wide, saddle form. Fore- and mid led in the same pattern, femur is about the same length as tibia, tarsus three segments with claw, the first segment longer than the third segment and the second segment clearly short. Hind leg femur robust, tibia with at least four long, mighty spines, leaf form, tarsus two segments with claw, first segment long and with an apical spur, the second segment about half of the length as the first one.

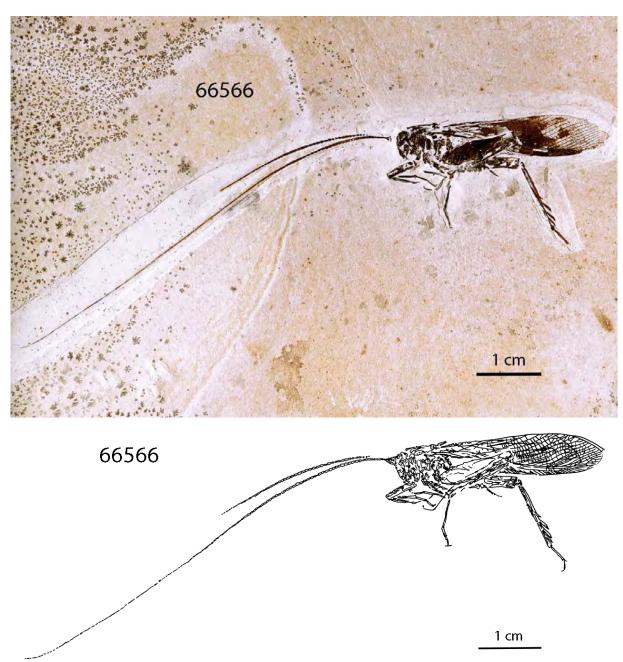
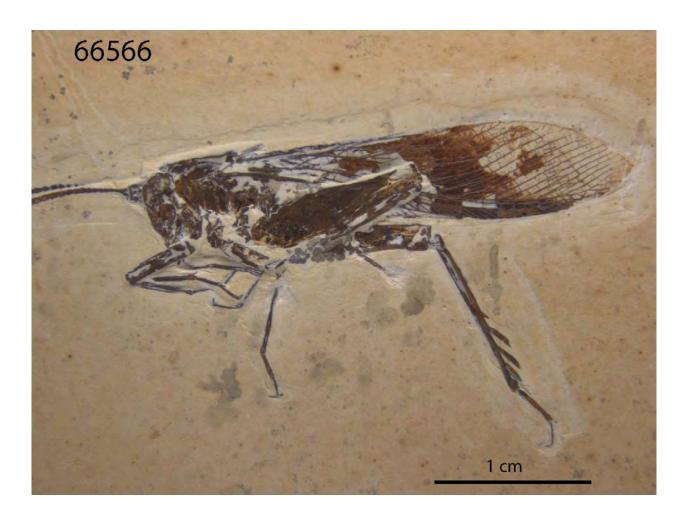


Fig. 142. Cratoelcana zessini Martins-Neto, 1991, Habitus.



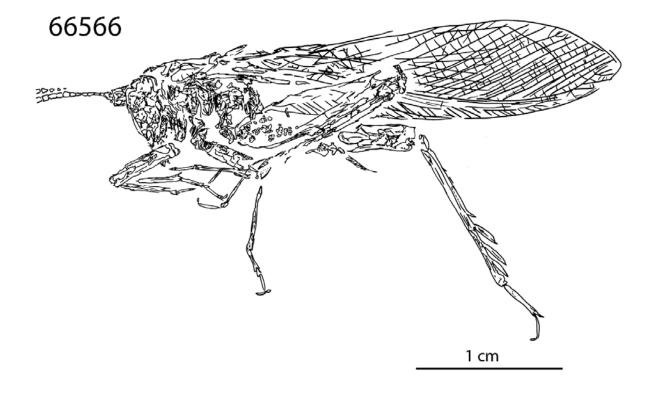


Fig. 143. Cratoelcana zessini Martins-Neto, 1991, Body parts.





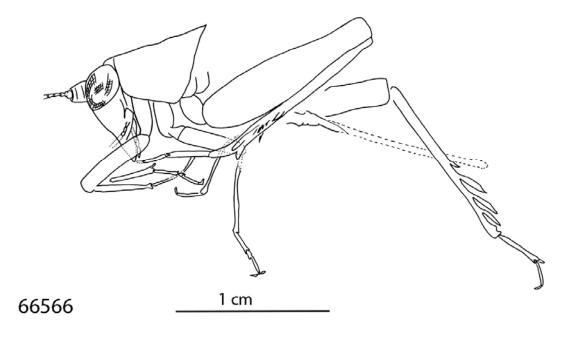


Fig. 144. Cratoelcana zessini Martins-Neto, 1991, Legs detail.

Specimen **SMNS 67584**: probably Male. Forewing, the distance between ScP and fore rand broad, RP2 with three-branches, RP3 and RP4 sigmoid, RP 14-branches. Hind wing almost complete and unfold, ScP short and parallel with fore rand and RA, RP2 slanting and the end touch with RP3, RP eight branches, MP and Cu lead to MA.

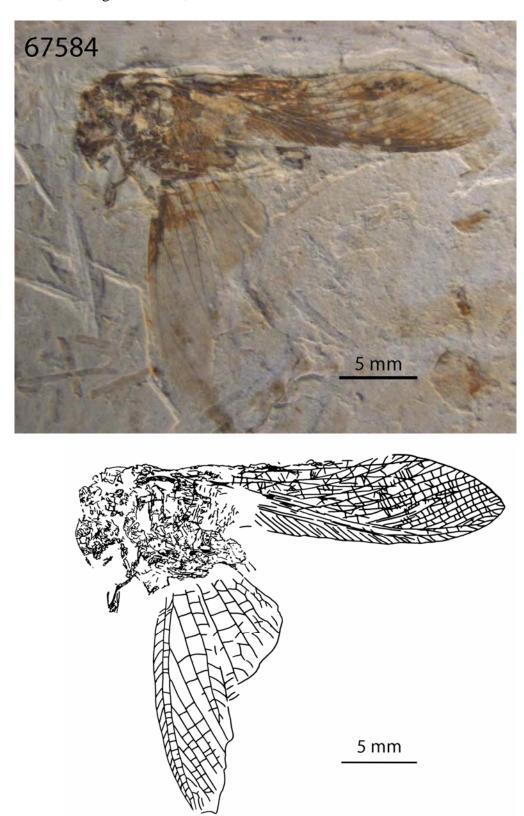


Fig. 145. Cratoelcana zessini Martins-Neto, 1991, Habitus.

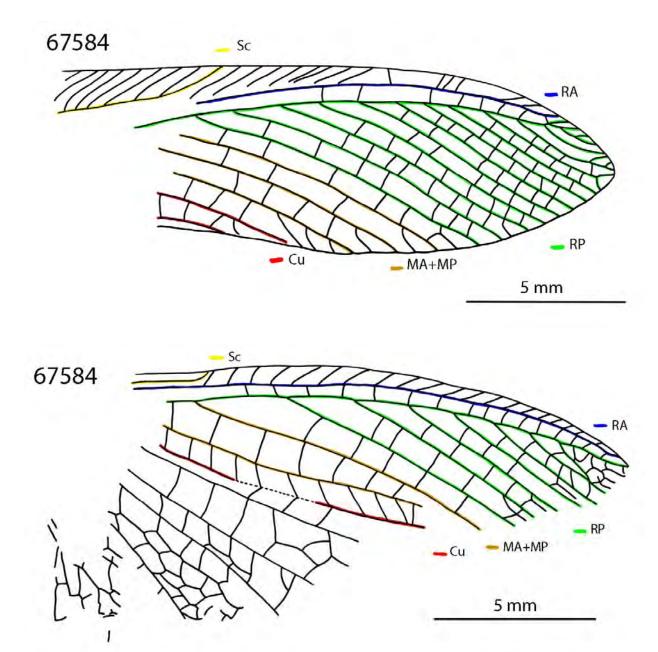


Fig. 146. Cratoelcana zessini Martins-Neto, 1991, Fore & Hind wings.

Discussion: *Cratoelcana zessini* Martins-Neto, 1991 differs from Cratoelcana damianii Martins-Neto, 1991 by the larger body and forewing size, (*C. zessini*: body mostly 28-37 mm, forewing mostly 22-26 mm long; *C. damianii*: body 12-16 mm, forewing 9-14 mm long.), by the more RP branches in for- and hind wing (*C. zessini*: RP in forewing, female eightbranches and male 12-branches; in hind wing, male seven to eight branches; *C. damianii*: RP in forewing, female four-branches and male six-branches; in hind wing, female five-branches.) and by the thin and relative longer ovipositor.

Species: Cratoelcana damianii Martins-Neto, 1991 (figs. 147-154)

Original diagnosis, according to Martins-Neto, 1991c: Body between 12 and 16 mm length. Forewing between 9 and 14 mm length and with less secondary RP branches, female has 4 and male 6.

New diagnosis: Female ovipositor is broad, shorter and bend. (In *C. zessini* the ovipositor is thinner and a little longer.)

Original description, according to Martins-Neto, 1991c: Female, forewing elongate, generally similar with *C. znssini*, except in having fewer RP branches. Male, forewing similar with female, apex sharper. Body similar to *C. zessini* but smaller.

New description: Female, the length of the antenna is longer than twice the length of the wing, scape robust. Hind wing generally similar to *C. zessini*, except in having fewer RP branches. Body similar to *C. zessini* but smaller. Cerci short.

Specimen SMNS 66491: Female, the length of the antenna is longer than twice the length of the wing, scape robust. Forewing RA and RP1 parallel, stems in the base half part of wing adjacent with each other, RP five branches. Hind wing RP five branches. Foreleg femur longer than tibia, tarsus three segment with claw, first segment long, second segment clearly short, third segment is about 2/3 length of the first segment. Hind leg femur robust, tibia slightly shorter than femur and with at least four long, leaf form spines, tarsus two segments with claw, the second segment is about half length as the first segment. Ovipositor longer than the body, a little bent. Cerci short and hairy.

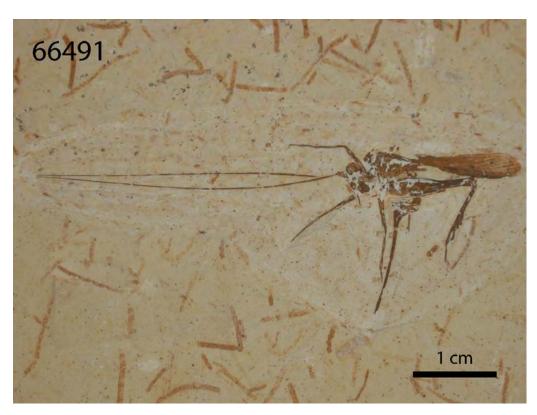


Fig. 147. Cratoelcana damianii Martins-Neto, 1991, Habitus.

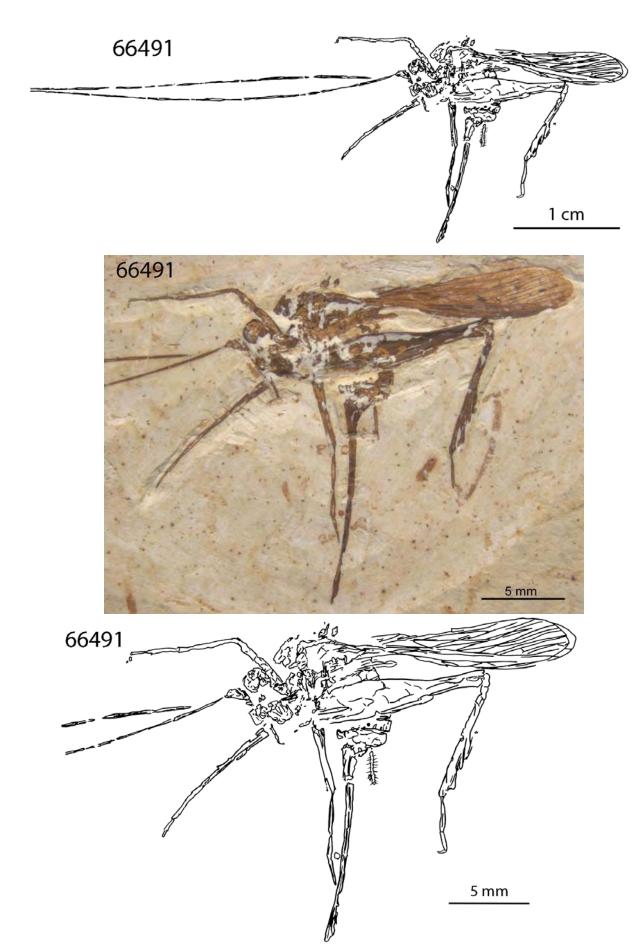


Fig. 148. Cratoelcana damianii Martins-Neto, 1991, Habitus & Body part.

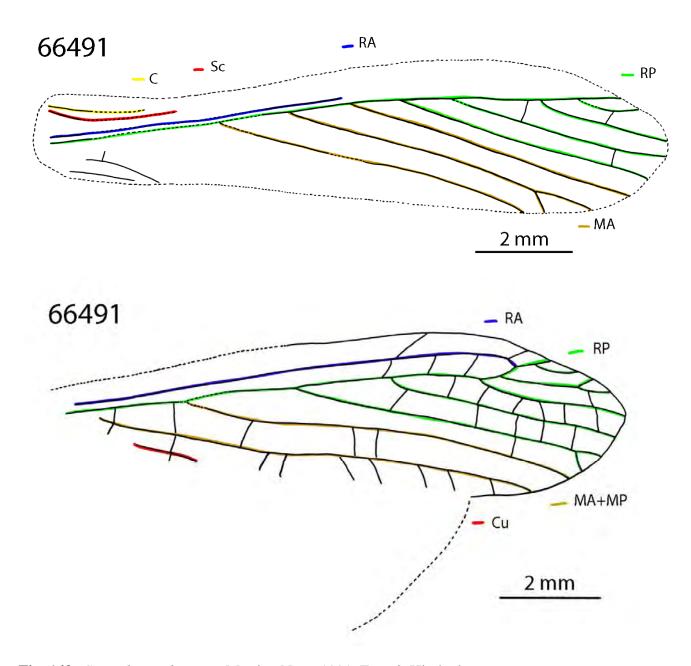
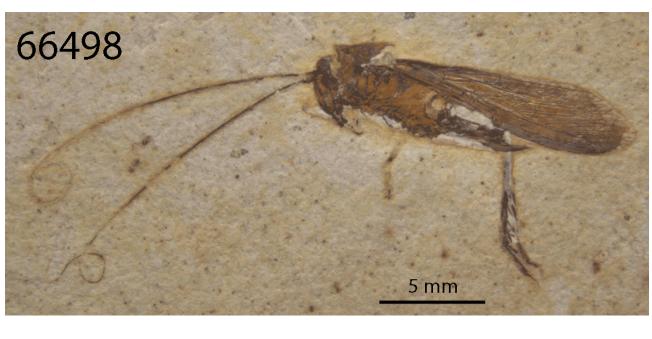


Fig. 149. Cratoelcana damianii Martins-Neto, 1991, Fore & Hind wings.

Specimen SMNS 66498: Female, the length of the antenna about twice of the wing length. Head flat, mouthpart partial visible with several segments. Thorax wide, saddle form. Forewing, ScP long, reaching almost the middle point of the whole wing, RA and RP1 parallel and slight sigmoid. RP six branches. The ends of MA1 and MA2 join together, end part of MP with four branches. Hind wing, RP five branches. Hind leg femur robust and slightly longer than tibia, tibia with several long spines, tarsus two segments, first segment with apical spur, second segment about half of the length as the first segment. Ovipositor thick, saber form.



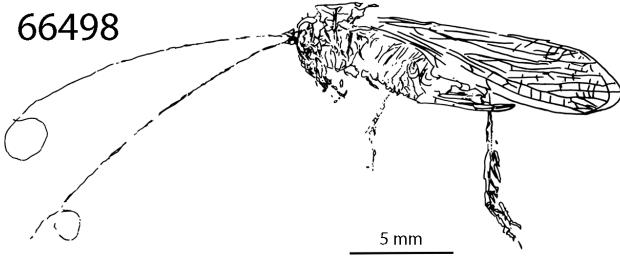
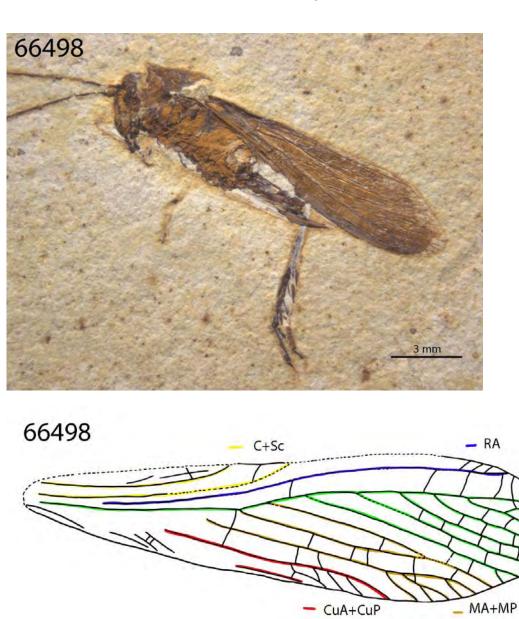


Fig. 150. Cratoelcana damianii Martins-Neto, 1991, Habitus.



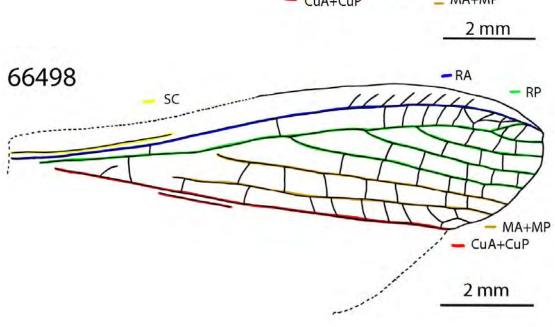


Fig. 151. Cratoelcana damianii Martins-Neto, 1991, Body part, Fore & Hind wings.

Specimen **SMNS 66690**: Female, the length of the antenna is longer than total body length. Forewing, ScA short and the distance between ScA and the fore rand wide. Hind wing, RP1 sigmoid, RP five branches. Foreleg tarsus three segments with claw, first segment about the same length as the third segment, second segment clearly short. Hind leg tibia with at least four long spines, tarsus two segments with claw, first segment long, second segment about 2/3 length as the first one. Ovipositor thick, saber form.

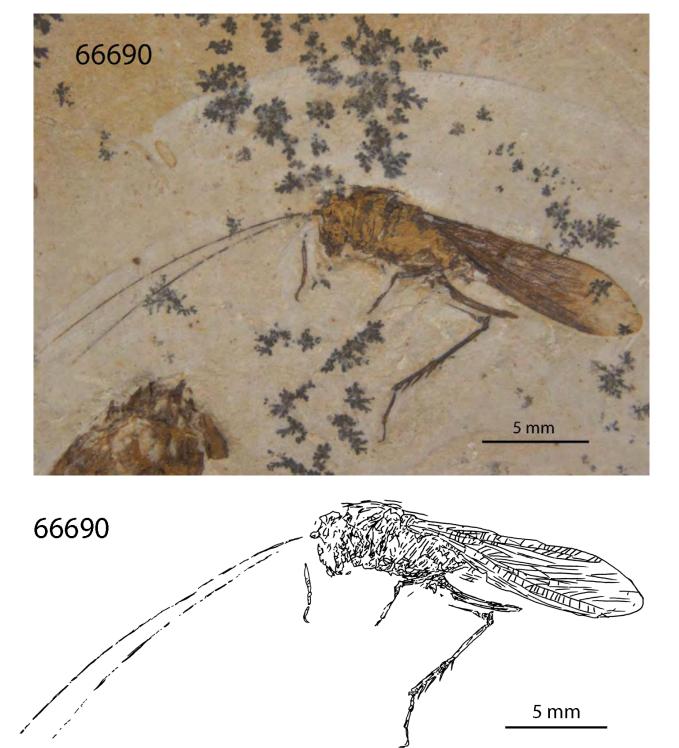
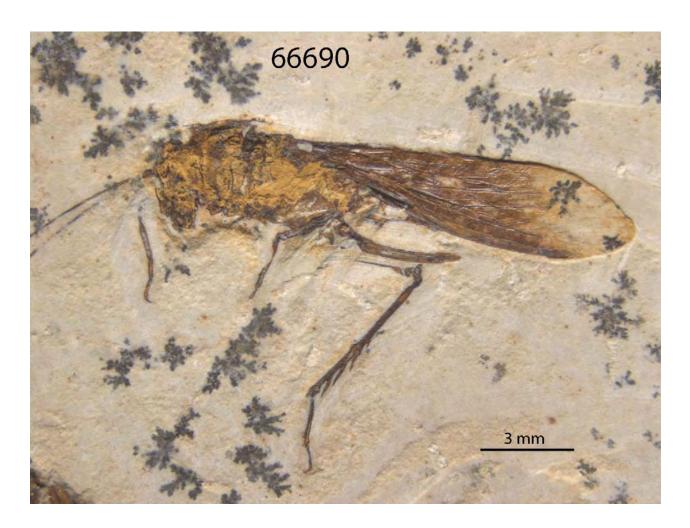


Fig. 152. Cratoelcana damianii Martins-Neto, 1991, Habitus.



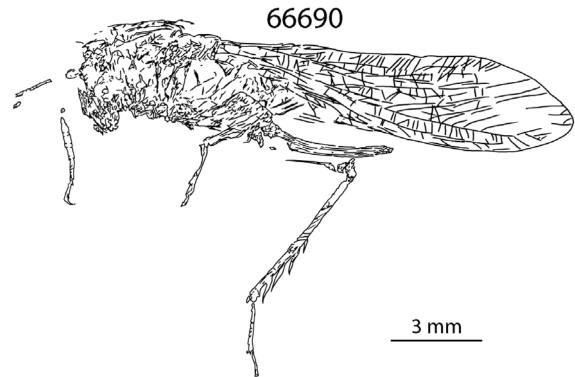


Fig. 153. Cratoelcana damianii Martins-Neto, 1991, Body part.

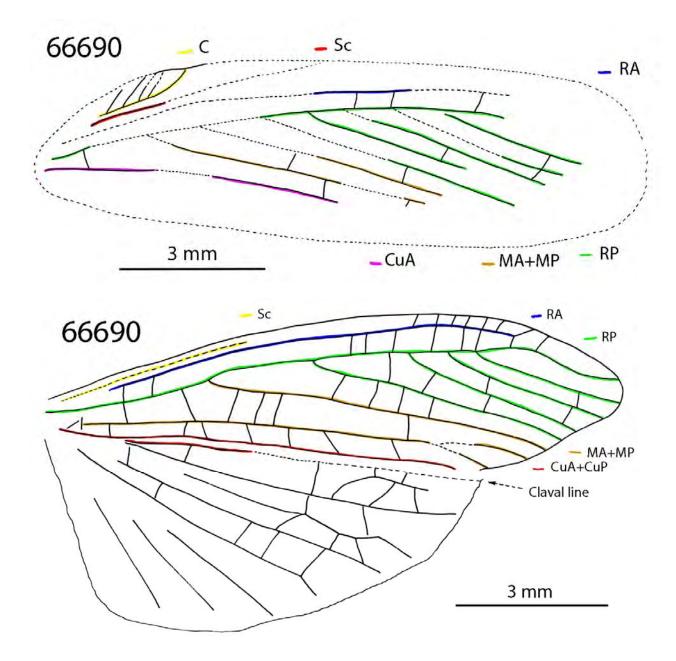
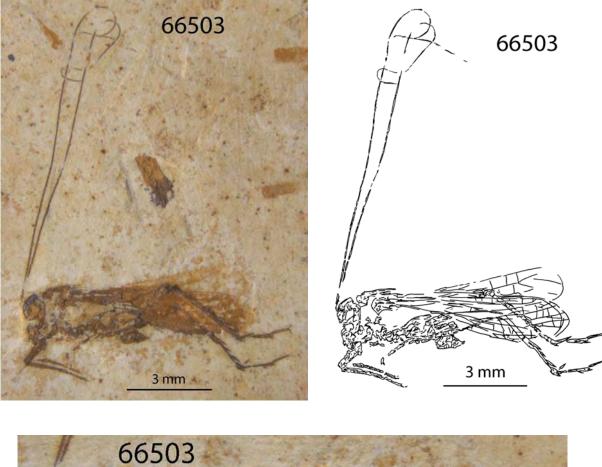


Fig. 154. Cratoelcana damianii Martins-Neto, 1991, Fore & Hind wings.

Discussion: *Cratoelcana damianii* Martins-Neto, 1991 differs from *Cratoelcana zessini* Martins-Neto, 1991 by the smaller body and forewing size, (*C. zessini*: body mostly 28-37 mm, forewing mostly 22-26 mm long; *C. damianii*: body 12-16 mm, forewing 9-14 mm long.), by the fewer RP branches in for- and hind wing (*C. zessini*: RP in forewing, female eight-branches and male 12-branches; in hind wing, male seven to eight branches; *C. damianii*: RP in forewing, female four-branches and male six-branches; in hind wing, female five-branches.) and by the thick and relatively shorter ovipositor.

Species: unknown (New Species J) (figs. 155, 156)

Specimen **SMNS** 66503: Male, notably in small size, body 4 mm and forewing 7 mm long, the length of the antenna is longer than twice of the wing length, head round, eye notably big. Fore and hind wing in generally pattern of Elcanidae. Forewing RP five branches and hind wing RP four branches. Foreleg femur a little shorter than tibia, tarsus three segments with claw. Hind leg femur robust, longer than tibia, tibia with at least five long spines, tarsus two segments with claws, first segment long and with spines, the second segment shorter.



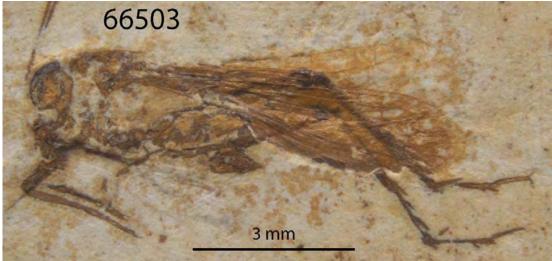


Fig. 155. Unknown species Elcanidae J, Habitus & Body part.

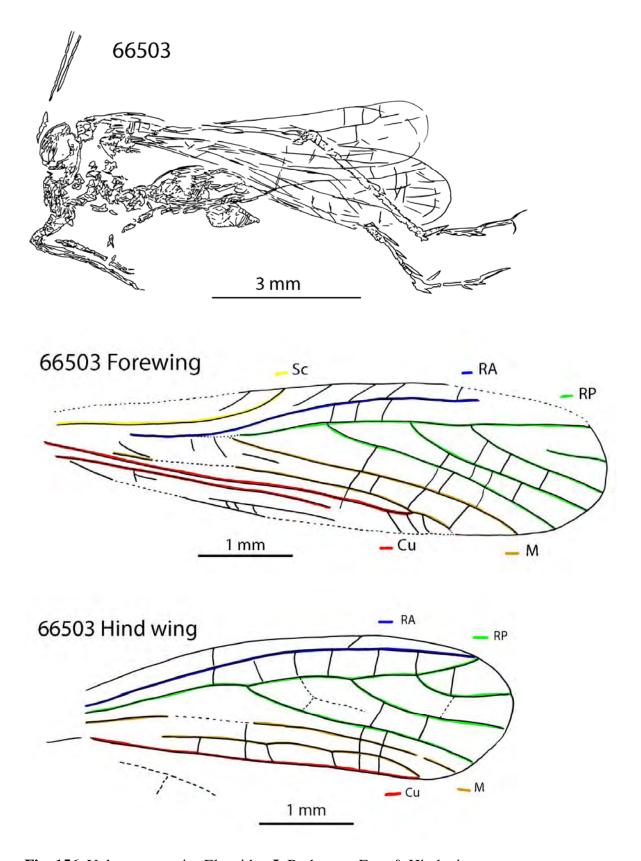


Fig. 156. Unknown species Elcanidae J, Body part, Fore & Hind wings.

Discussion: Specimen SMNS 66503 similar to *Cratoelcana damianii* Martins-Neto, 1991 by the wings and fore- and hind leg forms, but differs clearly by the notably big head and eyes and by smaller body size and less RP branches in fore- and hind wings.

### 3.3.2. Suborder: Caelifera Ander, 1936

Morphological characters, according to Carpenter, 1992: Antennae shorter than body, with not more than 30 segments; tympanal organs, when present, on first abdominal segments; stridulatory mechanism diverse (rarely absent), hind tibia or femora commonly scraped across ridges on abdomen or forewings; ovipositor, when present, typically short.

The earliest true caeliferans are recorded from the Triassic and are thought to be derived from and elcanid-like stem group (Béthoux & Nel, 2002; Grimaldi & Engel, 2005). Monophyly of Caelifera is well supported by the reduced antennae and complete reduction of the ovipositor (Flook *et al.*, 2000; Grimaldi & Engel, 2005). The caeliferan fauna of the Crato Formation is dominated by extinct elcanid and "locustopsoid" forms. Of the extant superfamilies only Eumastacoidea (represented by Proscopiidae) and Tridactyloidea are recorded with certainty (represented by Tridactylidae), though Bouretidae may in fact represent stem group Tetrigidae (Heads & Martins-Neto, 2007).

### Superfamily: Locustopsoidea Handlirsch, 1906

This Superfamily is known from the beginning of the Triassic to the present; it includes the most primitive Caelifera with equally developed fore and hind wings (if present). The forewings are narrow in the middle and broadest near the apex. The costa ends before the beginning of RS; RS always bears a comb of branches. The valves of the ovipositor are long and serrated (Sharov, 1968). The Superfamily contains either three or four families: Locustavidae Sharov, 1968 (Triassic); Locustopseidae Handlirsch, 1906 (known from Triassic to the Upper Cretaceous); possible descendants of Locustopseidae, Araripelocustidae from Lower Cretaceous of Brazil; and possibly the Recent family of apterous grasshoppers Tanaoceridae (Martins-Neto, 2003; Gorochov *et al.*, 2006).

#### 3.3.2.1. Family: †Locustopseidae Handlirsch, 1906

Extinct family (Triassic through Cretaceous), related to Acrididae. Forewing slender, commonly twice as long as body, typically broader distally than proximally; apex rounded; crossveins not so numerous as in Acrididae. Stridulatory apparatus apparently absent. Diagnosis: forewing, MA with three long and parallel branches, origin about in the same level of the beginning of the RS; MP+CuA1 bent strongly. Hind wing as in Acrididae; M anastomosed with R basally. (Carpenter, 1992; Zessin, 1983).

Presently in literature, 14 genera are accepted as belonging to the family: *Locutopsis* Handlirsch, 1906 (=*Brodiana* Zeuner, 1942) (30 species, Jurassic of Europe and Siberia); *Conocephalella* Strand, 1926 (1 sp., Upper Jurassic of Germany); *Parapleurites* Brauer, Redtenbacher, & Ganglbauer, 1889 (2 spp., Middle Jurassic of Siberia); *Praelocustopsis* Sharov, 1968 (1 sp., Triassic of Siberia); *Schwinzia* Zessin, 1983 (1 sp., Lower Jurassic of Germany); *Plesioschwinzia* Zessin, 1988 (2 spp., Lower Jurassic of Germany); *Triassolocusta* Tillyard, 1922 (1 sp., Triassic of Australia); *Zeunerella* Sharv, 1968 (1 sp., Cenomanian of Kazakhstan); *Mesolocustopsis* Hong & Wang, 1990; *Pseudoacrida* Lin, 1982 (each 1 sp. From Lower Cretaceous of China) and plus more four in Crato existed genus: *Cratozeunerella* Martins-Neto, 1998 (6 spp.); *Cratolocustopsis* Martins-Neto, 2003 (3 spp.); *Zessinia* Martins-

Neto, 1990 (5 spp.) and *Locustrix* Martins-Neto, 2003 (2 spp.). (data of Sharov, 1968; Zessin, 1983, 1988; Carpenter, 1992; Martins-Neto, 1990a, 1998a, 2003; Heads & Martins-Neto, 2007) The presence of Locustopseidae is also confirmed in Lower Cretaceous sediments of Egypt (Ansorge, 1991), England (Jarzembowski & Coram, 1997), Montsech, Spain (Gomez-Pallerola, 1986).

Genus: Zessinia Martins-Neto, 1990

Original Diagnosis and Discussion, according to Martins-Neto, 1990a: Forewing with long C. Rs branches not ending in the anterior margin, with variable origin. MP+CuA with MP+CuA1 very curved converging to MP+CuA. Anals with complex pattern of venation with successives fusions. Intense number of braided cross-veins. The genus *Zessinia* similar to *Zeunerella* Sharov, 1968 in C, Rs and MA2 origin. However the typical MP+CuA morphology and the complex system of the annals venation pattern distinguish the genus *Zessinia* of all know genera.

Emended Diagnosis, according to Martins-Neto, 2003: MP+CuA1 strongly curved, sigmoid. Posterior femur is relatively short and robust (W/L about 0.35). Fore and hind wing with four to six branches of RP.

Species: **Zessinia vikingi** Martins-Neto, 2003 (fig. 157)

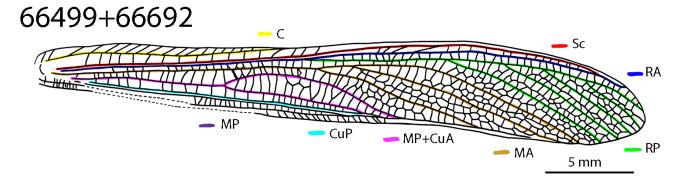
Original Diagnosis, according to Martins-Neto, 2003: characteristics of genus. Forewing from 29 to 32 mm long and 6 mm wide. RP origin posterior to MA fork. MA3 free. MA2 origin in MA1. MA3 far from MA1+2. Hind wing with RP five-branched.

Original Description, according to Martins-Neto, 2003: Forewing 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 forewing, with RP five-branched.

Specimens SMNS 66499+66692: Forewing 34.5 mm long and up to 5 mm wide.







**Fig. 157.** Zessinia vikingi Martins-Neto, 2003, Forewing (drawing supplemented with counter plate).

New Description: Forewing long and narrow. Costa is a little less than 1/3 of the whole wing length and reaching almost to the origin of RP. Stems of Sc and RA in the anterior half of the wing are adjacent with each other, almost fused. RP origin of at mid length level of wing and slightly anterior to the MA3 origin.

Discussion: Specimens SMNS 66499+66692 differs from *Zessinia caririensis* Martins-Neto, 1990 by larger forewing size and by fused stem of Sc and RA in the basis of the anterior half of the wings. Specimen SMNS 66499+66692 is very similar to *Zessinia vikingi* Martins-Neto, 2003, both in form and size, but differs by RP origin slightly anterior to the MA3 origin (in *Z. vikingi* M3 origin slightly anterior to RP origin), in any case the both origins are quite at the same level. It is possible that both belong to the same species.

Genus: Cratozeunerella Martins-Neto, 1998

Original Diagnosis, according to Martins-Neto, 1998a: Similar to *Zeunerella* Sharov, 1968 in possessing C long, reaching almost the origin of RP. Branches of RP not reaching anterior margin. MA2 originating on the base of the posterior branch of MA1. Base of CuA and CuA2 in the form of a single curved vein, the distal third of which branches anteriorly into a bifurcated MP+CuA1. *Cratozeunerella* differs from *Zeunerella* in the precosta area between Costa-margin and Costa, being basally narrower than in its distal part and ScA in *Zeunerella*, but broader and with the subcosta field with cross-veins in *Cratozeuberella*.

Emended Diagnosis, according to Martins-Neto, 2003: Posterior femur long and narrow (W/L about 0.15). Forewing with C sigmoid and four to five branches of RP, and hind wing with three to four branches of RP. Subcosta area in forewing filled by several pectinate cross-veins. Similar to *Zeunerella*, differing however by having subcosta area filled by several cross-veins (without cross-veins in *Zeunerella*), forewing five (exceptionally four) branches of RP (three in *Zeunerella*).

Species: undescription (New Species **K**) (figs. 158-159)

Specimen **SMNS 67586**: Forewing circa 34 mm long and 4.5 mm wide, hind wing 24 mm long.

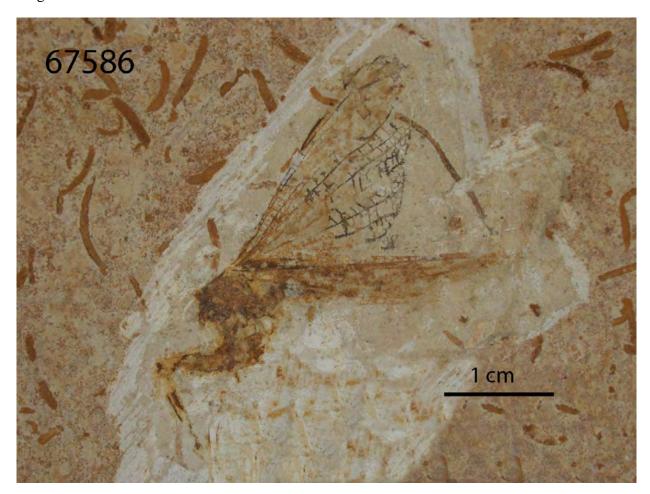


Fig. 158. Unknown new species Locustopseidae K, Habitus.

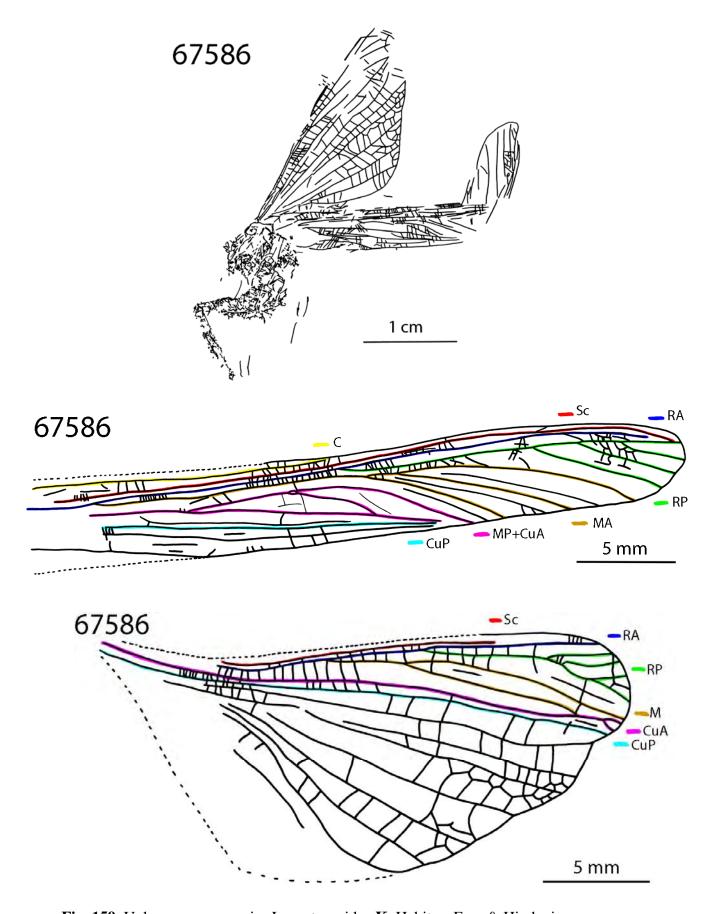


Fig. 159. Unknown new species Locustopseidae K, Habitus, Fore & Hind wings.

Diagnosis: Similar to *Cratozeunerella*. Forewing C straight, Sc alone and MP+CuA with three branches. Hind wing RP sigmoid strongly.

Description: Forewing long and narrow. Costa is half of the whole wing length and reaching almost to the origin of RP. Sc long and without branch. Sc, RA and RP1 parallel. Origin of RP is a little anterior to the MA3 origin. RP four-branched, straight. MA three-branched, MA3 free, MA2 origin in MA1. MP+CuA three-branched, CuA2 origin in CuA1 and the ending touched with CuA3. Hind wing: The tip of the hind wings are rounded. RP four-branched, sigmoid. M two-branched, M2 ending touched with CuA. CuA and CuP both alone and parallel.

Discussion: Specimen SMNS 67586 differs from genus Zeunerella Sharov, 1968 in forewing C straightly, RP in fore- and hind wing with four branches. By Cratozeunerella differs from all locustopseidae having Sc of the forewing with only one branch (Martins-Neot, 1998a). But here by SMNS 67586 the Sc is alone, without branch (at least no evidence about it). SMNS 67586 differs from Cratozeunerella soaresi Martins-Neto, 2003 by a smaller hind wing 24 mm long (in C. soaresi 30 mm), RP branched sigmoid and M2 ending in CuA. SMNS 67586 differs from Cratozeunerella titanella Martins-Neto, 2003 by forewing origin of RP, which is a little anterior to M3 origin and far after to CuA1 origin (in C. titanella the origin of RP1 is far before to origin of MA3 and also anterior to CuA1 origin). In addition, MA3 origin is distinctly posterior to CuA1 origin (in C. titanella MA3 origin anterior to CuA1 origin). Hind wing four RP-branching sigmoid (in C. titanella straight). SMNS 67586 differs from Cratozeunerella neotropica Martins-Neto, 1998 and from Cratozeunerella amedegnatoi Martins-Neto, 1998 by MA3 free (in C. neotropica and C. amedegnatoi is MA1 free). SMNS 67586 differs from Cratozeunerella godoii Martins-Neto, 2003 and from Cratozeunerella nervosa Martins-Neto, 2003 by larger forewing size. SMNS 67586 differs from Cratolocustopsis Martins-Neto, 2003 by larger forewing size.

Remark: This species (Specimen SMNS 67586) is similar to *Cratozeunerella* but differs from all six described species. If the Sc of the forewing was really alone (without branches), then it should be described as a new genus; or the Sc was actually branched, but invisible in the fossil.

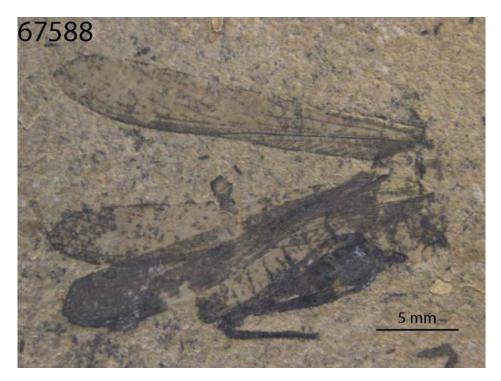
Species: *Cratozeunerella godoii* Martins-Neto, 2003 (figs. 160, 161)

Original Diagnosis, according to Martins-Neto, 2003: Forewing 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.

Original Description, according to Martins-Neto, 2003: Forewing 23 mm long. Costa long, sigmoid, reaching costa margin about 1/3 of base of wing. Sc long, with Sc1 relatively far from end of Costa. Area between Sc 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. Body notably short, robust, 15 mm long. Small, narrow head, same width as pronotum. Pronotum relatively great, seliform. Abdomen short and robust. Hind wing 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. *Cratozeunerella godoii* differs from all described species of the genus *Locustopsis* by sigmoid Costa.

Specimen **SMMS 67588**: Body approximately 20 mm long. Forewing 24 mm long and up to 4 mm wide. Hind wing 25 mm long.



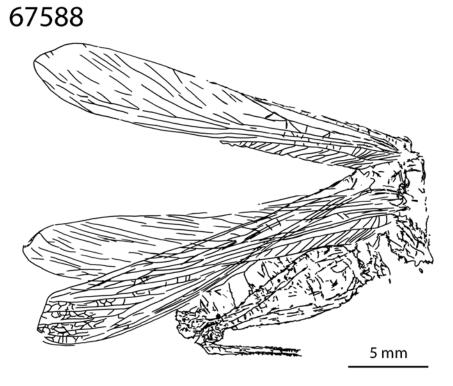


Fig. 160. Cratozeunerella godoii Martins-Neto, 2003, Habitus.

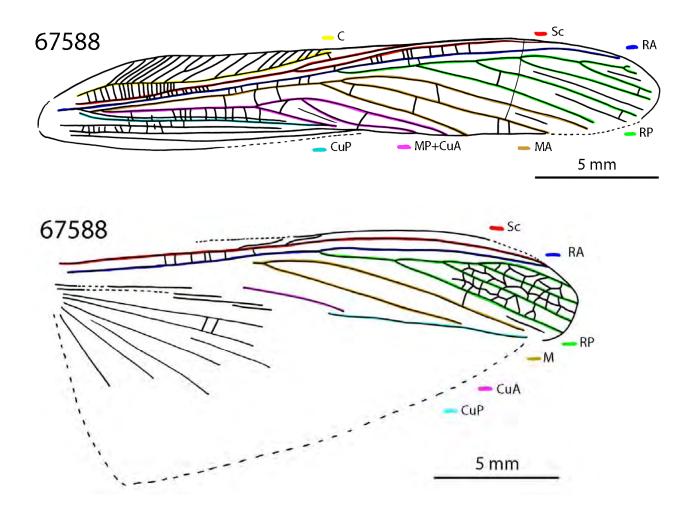


Fig. 161. Cratozeunerella godoii Martins-Neto, 2003, reconstructed Fore & Hind wings.

New Description: Forewing long and narrow. Costa sigmoid, about half of the whole wing length (probably more than 1/3) and reaching almost to the origin of RP. RP origin in the same level than the M1+2 origin. RP six-branched (instead of four), straight, RP1 notably short. CuA1+2 origin is anterior to M3 origin. CuP alone and ending in CuA3. Hind wing Sc has at least two extra branches or oblique cross veins respectively. RP four-branched (instead of three), straight. M two-branched. CuA and CuP possible both alone. Body: hind leg femur robust 11.5 mm long and up to 3.5 mm thick, tibia smooth.

Discussion: Specimen SMNS 67588 differs from specimen RGMN-T125 Martins-Neto, 2003 in forewing having a longer Costa, about half of the whole wing length (in GRMN-T-125 about 1/3). Sc1 origin is anterior to the end of Costa. RP is six-branched, instead of four. Differs from specimen AMNH-43868 Martins-Neto 2003 by hind wing RP four-branched (in AMNH-43868 three).

### 3.3.2.2. Family: †Bouretidae Martins-Neto, 2001

Bouretidae is a monotypic family erected by Martins-Neto, 2001 for *Bouretia elegans*. Known only from a single poorly preserved specimen, the relationship of *Bouretia* are uncertain. Martins-Neto (2001, 2003) placed Bouretidae within Locustopseidea. In other's opinion (Heads & Martins-Neto, 2007), there is little evidence to support this assignment and *Bouretia* shares several features in common with Tetrigidae (Tetrigoidea), including two-segmented pro- and mesothoracic tarsi, robust legs and an enlarged pronotum partly enclosing the abdomen. These features, along with the comparatively small size of *Bouretia* (body length of approximately 30 mm) suggest a relationship with Tetrigidae. However, both specimens from this study presented hind wings, in which the RA are clearly terminal branched. This could be an evidence to suggest a relationship with Haglidae.

Original Diagnosis, according to Martins-Neto, 2001: Big-sized locustopsoids, about 40 mm long, macropterous, having an enlarged pronotus which partly encloses the abdomen. Femora robust. Posterior tarsi three-segmented as long as two-thirds of the tibia length. Anterior and middle tarsi two-segmented.

Genus: Bouretia Martins-Neto, 2001

Original Diagnosis, according to Martins-Neto, 2001: Family characters. Pronotum robust, dome-like, enclosing the whole thorax and partially the abdomen. Anterior and middle tibia relatively robust. Posterior tarsi with the first segment longer than the second and third together. Anterior and middle tarsi with the first segment as long as the second one.

Species: *Bouretia elegans* Martins-Neto, 2001 (figs. 162-165)

Original Diagnosis: As for the genus.

Original Description, according to Martins-Neto, 2001: Macropterous with forewing 42 mm long. Head relatively large with rounded vertex. At least eighteen preserved antenna segments. Scapus longer and wider than the flagellar segments, inserted in the middle part of the head, below the eyes. Pronotum dome-like, relatively long and with a granular surface. Abdomen 18 mm long and 7 mm wide. Posterior femur robust, 19.5 mm long. Posterior tibia 14.5 mm long, smooth and relatively narrow having at least a little apical spur. First tarsal segment very long (5.5 mm). Second and third are 2.5 mm long. Anterior and middle legs as robust as posterior although smaller. Anterior femur 12.5 mm long. Anterior tibia 8 mm long and tarsi 6 mm long (each segment 3 mm long). Femora robustness ratio (width/length) 0.2+/-0.05.

New Diagnosis: Head hypognathous. Abdomen cylindrical to conical. Fore- and mid leg are stated as above, that is the tibias are relatively robust. Hind leg elongated, not only femur but also tibia. But the tarsi segments are not particularly long. Forewing only indistinct reconstructed, probably narrow, tendentious all the veins parallel and adjacent with each other. Hind wing especially is in RA with four extra terminal branches.

New Description: Forewing costa is half of the whole wing length. RP probably simple, with a few branches. M probably two-branched. Hind wing Sc alone and reaching the apex of wing, the distance between Sc and RA is broad, in between with four RA extra terminal-branches. RP five-branched, M two-branched, the origin of M2 is clearly anterior to the origin of RP.

Specimen **SMNS 66487**: Head hypognathous, 8 mm long, big eye located at the tip of the head, mouthparts sharp. Wing circa 46.5 mm long. Body (thorax plus abdomen) 28 mm long and up to 10.5 mm wide. Mid leg femur 10 mm long, tibia 6 mm long, first tarsal segment 4.5 mm long. Hind leg femur 28 mm long, tibia elongate, smooth, narrow, without spine and 27 mm long, first tarsal segment 3 mm long, second tarsal segment about 2.5 mm long. Forewing absent. Hind wing well reconstructed.

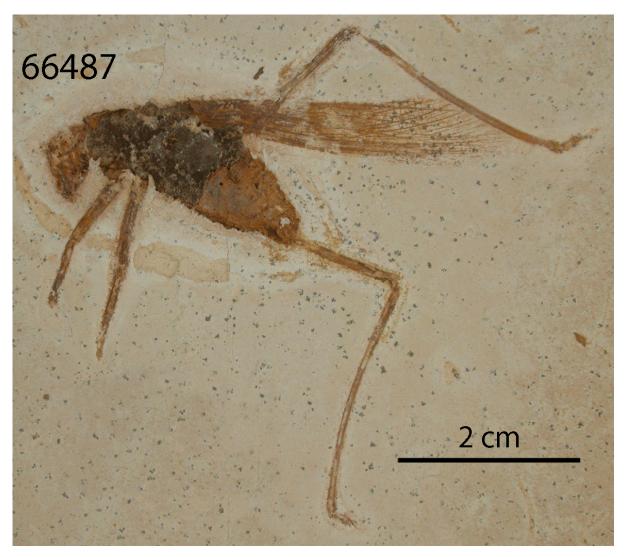


Fig. 162. Bouretia elegans Martins-Neto, 2001, Habitus.

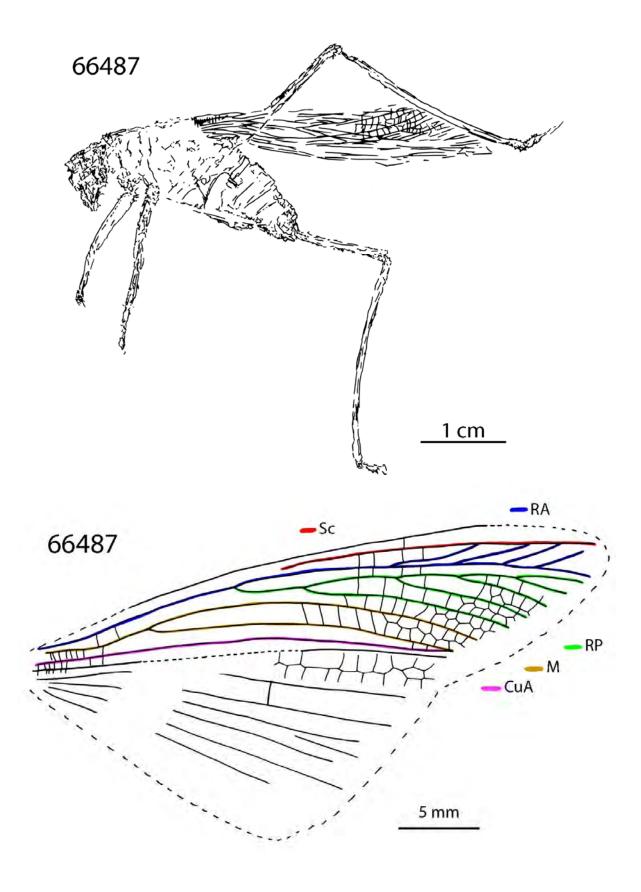


Fig. 163. Bouretia elegans Martins-Neto, 2001, Habitus & Forewing.

Specimen **SMNS 67585**: Head hypognathous, 6.5 mm long and 3 mm wide, big eye located at the tip of the head, mouthparts sharp. Wing circa 41 mm long. Thorax 10 mm long and up to 7 mm wide. Mid leg femur 10 mm long, tibia 4.3 mm long, first tarsal segment 2.3 mm long. Tibia and tarsus part with few spines. Hind leg femur 21 mm long, and up to 2.8 mm thick. Forewing only indistinct reconstructed.



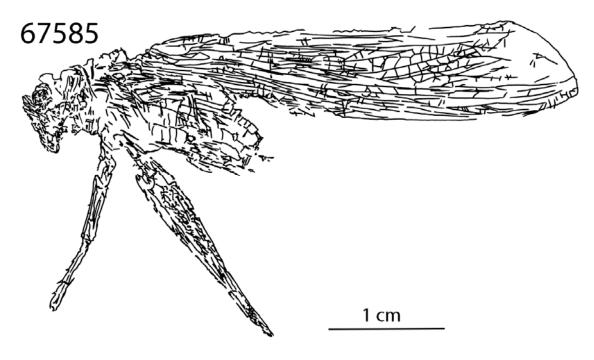


Fig. 164. Bouretia elegans Martins-Neto, 2001, Habitus.

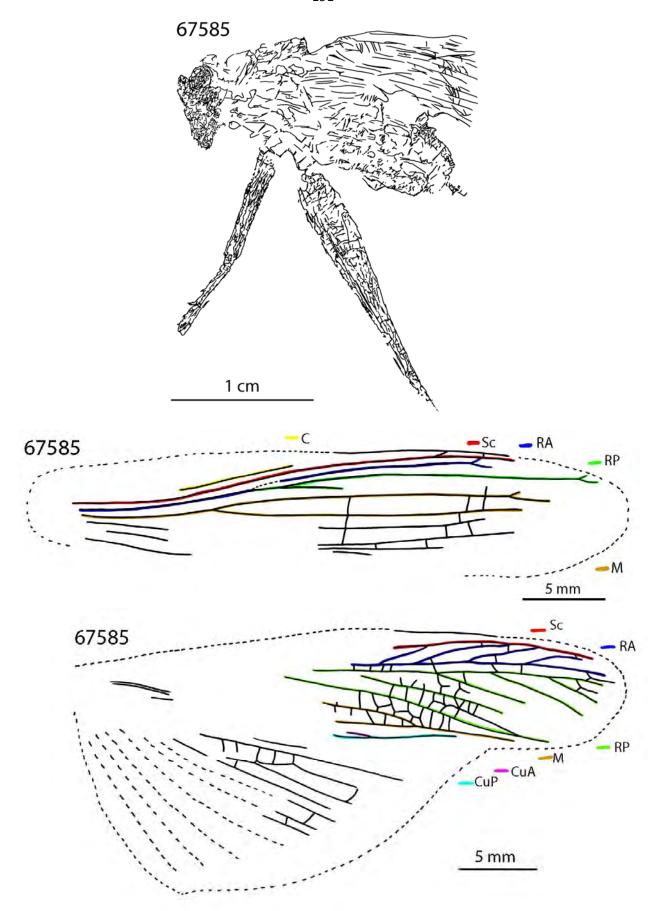


Fig. 165. Bouretia elegans Martins-Neto, 2001, Body part, Fore & Hind wings.

Discussion: Specimen SMNS 66487, SMNS 67585 and *Bouretia elegans* Martins-Neto, 2001 Specimen CD-90-I are similar in body form but not in size. In both specimens SMNS 66487 and 67585 the enlarged pronotus is not visible, the hind wings of the two specimens are principly the same. Specimen SMNS 66487 differs from *Bouretia elegans* Martins-Neto, 2001 Specimen CD-90-I by the hind leg. The tibia of SMNS 66487 is clearly elongated and the first tarsal segment is short as usual. The model proposed by Martins-Neto (2001), which the length of first tarsal segment is longer than the combined length of the second and third (or the combined length of three tarsal segments is as long as 2/3 of tibia length), does not apply to this case.

Remark: Because in forewing all the veins tend to be parallel and next to each other, in particular the RA of the hind wing with terminal branches it can be suggested that *Bouretia* is related to Haglidae.

## 3.3.2.3. Family: †Araripelocustidae Martins-Neto, 1995

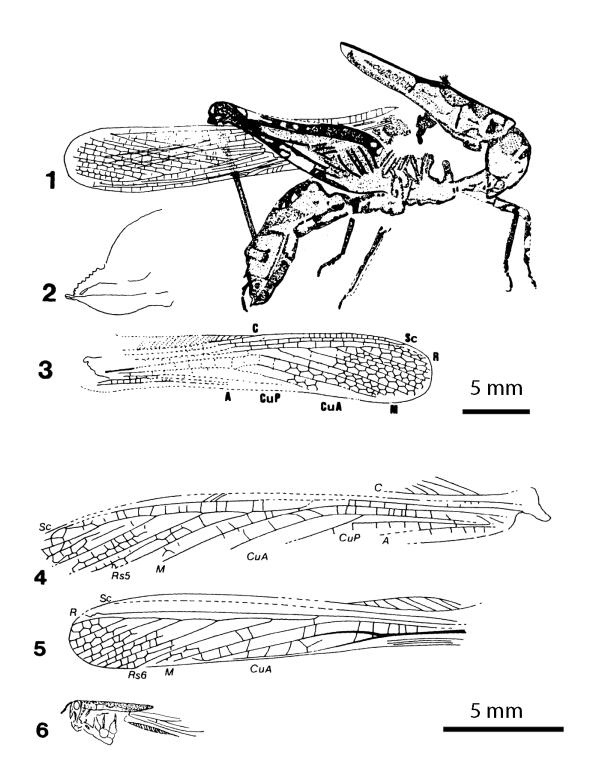
The extinct Araripelocustidae includes two species within the genus *Araripelocusta* Martins-Neo, 1995: the type species *Araripelocusta longinota* and a second smaller species *Araripelocusta brevis*. The family is characterised by the very robust metathoracic femora and by the distinctive, strongly sclerotised posterior expansion of the pronotum and cryptopleuron to form a shield-like structure which, when the animal was at rest, would have covered the entire meso- and metathoraces as well as the base of the wings and possibly the first few abdominal segments (Heads & Martins-Neto, 2007). Three specimens are described in this study, SMNS 66509, an *Araripelocusta longinota* Martins-Neto, 1995, SMNS 67587 and SMNS 67589. The two new species have the robust pronotum which is noted above. However, because of the wing morphology, they should not belong to the genus *Araripelocusta*, but a new taxa that is closer to genus *Cratozeunerella*. The strongly sclerotised posterior expansion of the pronotum could be a convergence.

Original Diagnosis, according to Martins-Neto, 1995a: Proposed to median to greatsized grasshoppers, macropterous, having a very enlarged pronotus, which encloses the whole thorax and abdomen base; hind leg femur robust, with the basal lobe shorter than upper; forewing with MA unbranched and MP+CuA two-branched.

Subfamily: Araripelocustinae Martins-Neto, 1995

Genus: Araripelocusta Martins-Neto, 1995 (fig. 166)

Original Diagnosis, according to Martins-Neto, 1995a: Characteristic of the family. Female: stridulatory apparatus absent, tibia smooth and ovipositor indented.



**Fig. 166.** Araripelocusta. **1-4**: Araripelocusta longinota Martins-Neto, 1995. **1**: Lateral view; **2**: Ovipositor; **3**: Forewing; **4**: Forewing detail. **5-6**: Araripelocusta brevis Martins-Neto, 1995. **5**: Forewing detail; **6**: Lateral view, without scale. (After Martins-Neto, 1995)

Species: Araripelocusta longinota Martins-Neto, 1995 (figs. 167, 168)

Original Diagnosis, according to Martins-Neto, 1995a: Head half-ball shape. Pronotum till the base of hind leg, femur long. The maximal width of hind leg femur is wider than the length of foreleg tibia. Forewing 26.5 mm long and 5 mm wide.

Original Description, according to Martins-Neto, 1995a: Body: Head half-ball shape with a relatively round eye. Pronotum elongated strongly, cover the whole thorax plus the base of the abdomen. Abdomen cylindrical and narrower than thorax, ovipositor indented. Tarsus three segments; tibia always the same width, narrow and smooth; hind leg femur robust, especially with the basal lobe shorter than the upper lobe. Forewing: long and narrow, costa long and reach approximately to the mid length of costa margin. Sc long, bend slightly and reach to the apex wings. R long and parallel with Sc. Rs five branched, M alone, no branched, bend and the full length is probably from anal margin till apex margin. CuA two branched, CuA1 longer than CuA2, CuP and anal veins are presented only near the base of margin. Body 25.8 mm long, forewing 26.7 mm long and 5 mm wide, pronotum 13.7 mm long, hind leg femur 14.7 mm long and 4.7 mm wide.

Specimen **SMNS 66509**: Body approximately 22 mm long. Hind leg femur 11 mm long and up to 4 mm thick. Forewing 26 mm long and 4.5 mm wide. Hind wing not very complete, probably the same length as forewing.





Fig. 167. Araripelocusta longinota Martins-Neto, 1995, Habitus.

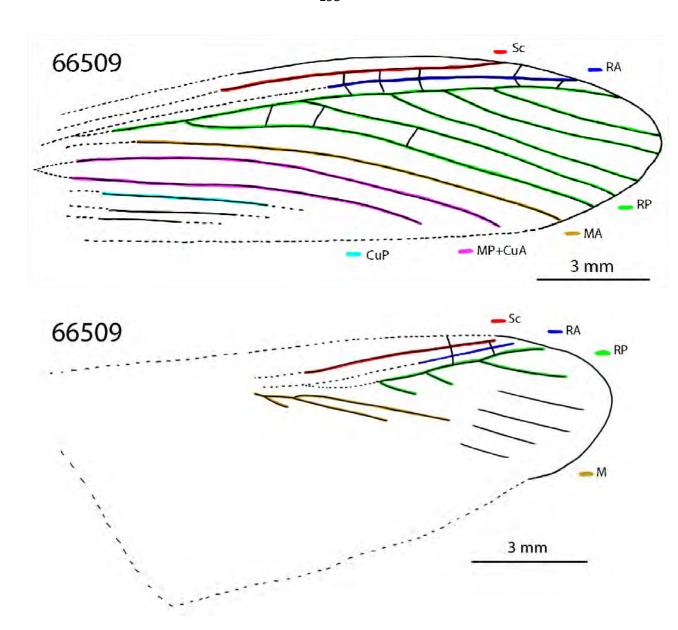


Fig. 168. Araripelocusta longinota Martins-Neto, 1995, Fore & Hind wings.

New Description: Forewing, RP six-branched. Hind wing not very complete, RP four-branched, M three-branched, M3 free and M2 origin in M1.

Discussion: Specimen SMNS 66509 Araripelocusta sp. differs from the described species of the Araripelocusta longinota Martins-Neto, 1995 by forewing RP six-branched (in A. longinota five). Both (SMNS 66509 and Araripelocusta longinota) are similar in whole size. SMNS 66509 Araripelocusta sp. differs from the described species of the Araripelocusta brevis Martins-Neto, 1995 by the larger size, but both SMNS 66509 and Araripelocusta brevis are similar in forewing form, especially in six-branched RP.

## Two new species

**New Species L** (figs. 169, 170)

Specimen **SMNS** 67587: Body 19 mm long, forewing 21 mm long and 3 mm wide, hind wing circa 19 mm long. The specimen displays strongly sclerotised pronotum, which could be a

characteristic feature of the family Araripelocustidae Martins-Neto, 1995. But the morphological characters of forewing clearly differs from *Araripelocusta* and on the contrary very similar with *Cratozeunerella*, especially *C. neotropica* (see fig. 171). Together with specimen SMNS 67589, they should be described as a new taxa with two new species closer to *Cratozeunerella* but not *Araripelocusta*. The strongly sclerotised pronotum seen here may be a convergence.

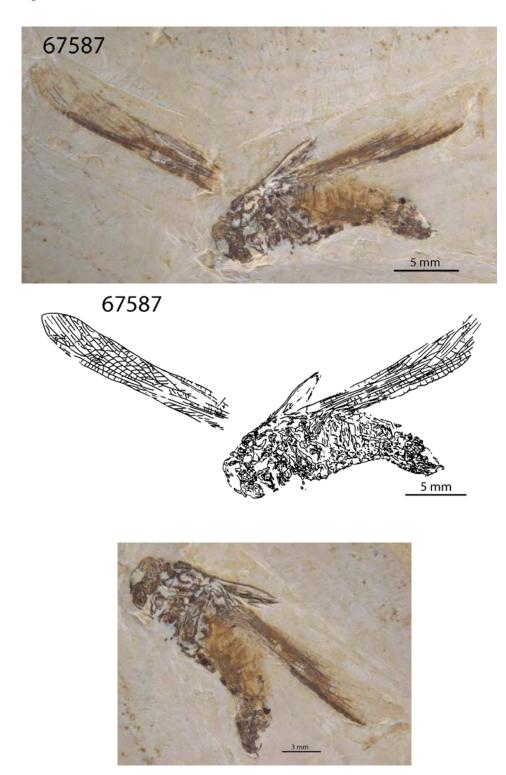
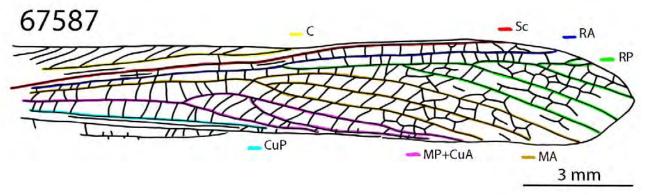


Fig. 169. Unknown new species Araripelocustidae L, Habitus.





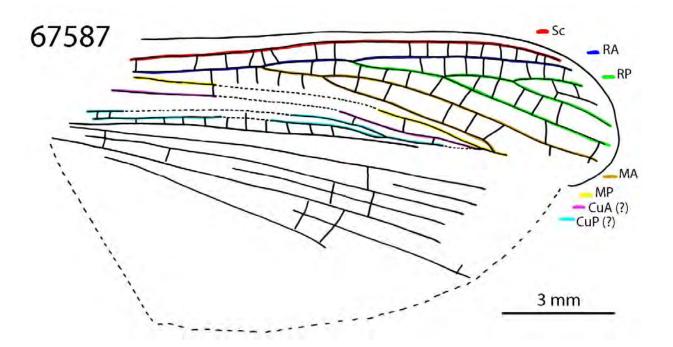
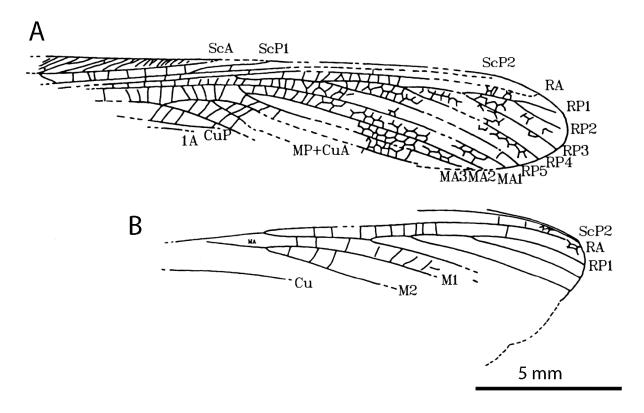


Fig. 170. Unknown new species Araripelocustidae L, Fore & Hind wings.

Diagnosis: With a vey enlarged pronotum, which encloses the whole thorax and the abdomen base. Both fore- and hind wing similar to genus *Cratozeunerella* Martins-Neto, 1998, especially *C. neotropica*, that is forewing MA three-branched, M1 free, MP+CuA three-branched, CuP2 short and in the hind wing the stem of MA originated from the anterior 1/3 length of RA.

Description: Head big, compound eye oval. Forewing long, slightly narrower in the middle. Costa reaches less than half of the margin of the wing. Sc long, un-branched. The distance between Sc and margin of wing narrow. RP origined at mid length level of the wing. RP five-branched, RP1 extreme short. MA three-branched, MA1 free, MA2 origin in MA3. MA3 origin anterior to the RP origin. MP+CuA three-branched CuA2 short and origin in CuA1, CuA3 free. CuA3 origin anterior to the MA3 origin. CuP alone. Hind wing: RP with three branches. MA origin in mid length of RA and with two-branched. MA2 origin anterior to the RP origin.

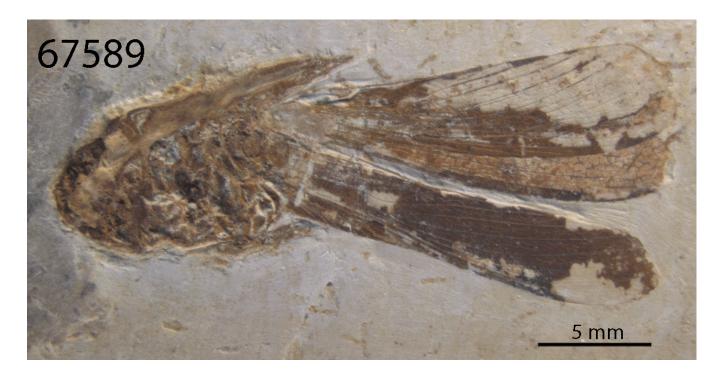
Discussion: Specimen SMNS 67587 clearly differs from the described genus of the *Araripelocusta* by forewing MA three-branched (in *Araripelocusta*, only one) and MP+CuA three-branched (in *Araripelocusta*, two). Specimen SMNS 67587 is similar to *Cratozeunerella neotropica* (fig. 171) by forewing size, and most part of the for- and hind wing, slightly differs by forewing Sc alone (in *Cratozeunerella* generally branched), CuA2 origin is at the same level with MA3 origin (in *C. neotropica* CuA2 origin anterior to the MA3 origin). By hind wing RP three-branched (in *C. neotropica* four). Specimen SMNS 67587 is similar to SMNS 67589 in body size. Differs by forewing Sc alone (in SMNS 67589 with three extra branches), RP five-branched (in SMNS 67589 four). Hind wing RP three-branched (in SMNS 67589 probably only one).



**Fig. 171.** *Cratozeunerella neotropica* Martins-Neto, 1998, holotype, **A**: Forewing & **B**: Hind wing. (After Martins-Neto, 1998)

# **New Species M** (figs. 172, 173)

Specimen **SMNS 67589**: Head plus thorax is at least 12 mm long. Forewing 22 mm long and 4 mm wide, hind wing 20 mm long. The specimen is similar to SMNS 67587, that is having a strongly sclerotised pronotum just like the ones in family Araripelocustidae Martins-Neto, 1995 but with the forewing in form of genus *Cratozeunerella* Martins-Neto, 1998. especially *C. neotropica*.



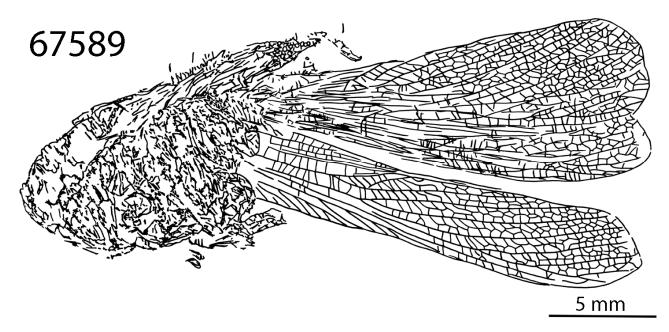
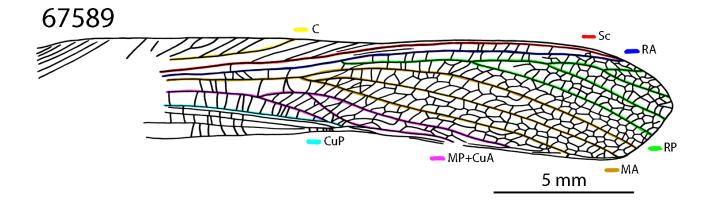


Fig. 172. Unknown new species Araripelocustidae M, Habitus.



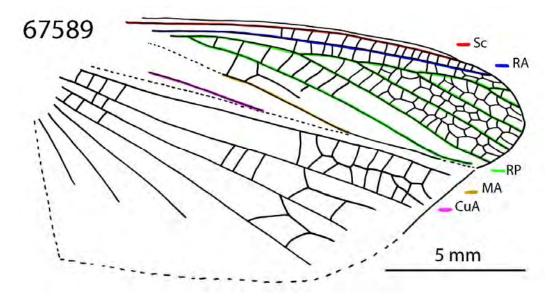


Fig. 173. Unknown new species Araripelocustidae M, Fore & Hind wings.

Diagnosis: Similar to SMNS 67587 with a very large pronotum. Forewing similar to that in *Cratozeunerella neotropica* and SMNS 67587 but not the hind wing. Hind wing RP with sixbranched.

Description: Forewing long, slightly narrower in the middle. Costa reaches a little bit less than half of the anterior margin of the wing. Sc long, with three extra branches. The distance between Sc and margin of wing narrow. RP origined at mid length level of the wing. RP four-branched. MA1 free, MA2 origined in MA3. MA3 origin is anterior to the RP origin. MP+CuA three branched, CuA2 short, CuA3 free. CuA3 origin is anterior to the MA3 origin. CuP alone. Hind wing: RP with six branches, RP1 notably short. MA and CuA have both count at least one.

Discussion: Specimen SMNS 67589 clearly differs from the described genus of the *Araripelocusta* by forewing RP four-branched (in *A. longinota* five), MA three-branched (in *Araripelocusta* only one) and MP+CuA three-branched (in *Araripelocusta* two). Specimen SMNS 67589 similar to *Cratozeunerella neotropica* (see fig. 171) in forewing size, forewing Sc with three extra branches (in *Cratozeunerella* generally branched). Differs by RP origin posterior to MA3 origin (in *C. neotropica* this two origins at the same level), CuA2 origin slightly posterior to MA3 origin (in *C. neotropica* CuA2 origin clearly anterior to MA3

origin). By hind wing RP six-branched (in *C. neotropica* four). SMNS 67589 similar with SMNS 67587 in body and wing size. Differs by forewing RA with three extra branches (in SMNS 67587 un-branched), by RP four-branched (in SMNS 67587 five). Hind wing RP six-branched (in SMNS 67587 three), MA probably only one (in SMNS 67587 two).

## Superfamily: **Tridactyloidea** sensu Heads, 2009

According to Heads (2009), the superfamily Tridactyloidea comprises three families: Tridactylidae Blanchard, 1845, Ripipterygidae Ander, 1939 and Cylindrachetidae Giglio-Tos, 1914. The Ripipterygidae (commonly misspelled as "Rhipipterygidae") are very closely related to Tridactylidae and have at times been considered a subfamily of the latter. They are nevertheless distinct from the tridactylids in having elongate mesotibia with parallel or nearparallel margins and males with one-segmented cerci. Cylindrachetidae consists of nine peculiar species commonly known as sand gropers (Grimaldi & Engel, 2005). Cylindrachetids are a peculiar group of fossorial insects known only from Patagonia, Australia and New Guinea. According to Heads (2009), Monophyly of Tridactyloidea is supported by a number of morphological characters: [1] the prosternum connected directly to the pronotum by means of a precoxal bridge; [2] protarsus with two tarsomeres, inserted on the inner surface of the protibia; [3] mesotarsus with two tarsomeres; [4] metatarsus always reduced to only one tarsomere; [5] arolia entirely absent; [6] abdomen with nine fully sclerotised sterna in both sexes, the ninth forming a simple subgenital plate lacking styli; [7] abdominal repugnatorial glands; and [8] male paraproct with distinctive sclerotised hooks. Tridactyloidea are an ancient group, though fossil representatives are extremely rare. The earliest definitive tridactyloids are known from the Early Cretaceous of Central Asia (Transbaikalia and Mongolia), Brazil and southern England (Sharov, 1968; Martins-Neto, 1990b; Gorochov, 1992c; Gorochov et al., 2006) though the precise relationships of these primitive taxa remains uncertain. Moreover, it is still unclear as to whether the Cretaceous genera represent stemgroup Tridactylidae sensu stricto or are the stem-group to a clade comprising Tridactylidae and Ripipterygidae.

## 3.3.2.4. Family: **Tridactylidae** Brullé, 1835 sensu Heads, 2009

According to Heads (2010), the Tridactylidae are the most diverse of the three tridactyloid families comprising 16 genera and around 140 valid species. Commonly referred to as pygmy mole crickets due to their superficial resemblance to true grylloids, tridactylids and the closely related ripipterygids, are characterised by their small size (usually less than 15 mm long), disproportionately large metafemora and long, slender metatibiae.

Original Diagnosis, according to Heads, 2009: Tridactylidae are distinguished from the Cylindrachetidae by their saltatorial metathoracic legs with markedly enlarged femora and long, slender tibiae. As stated previously, Tridactylidae are most closely related to Ripipterygidae, but can be distinguished from the latter by the male cerci two-segmented. The family is characterised by their very small size (a feature shared with Ripipterygidae) and significantly reduced tegminal venation comprising between two and four longitudinal veins. Members of the family are generally a glossy black and white with occassional brown/off-

white patches and usually have fossorial prothoracic legs, often with a number of dactylar processes present on the protibia.

In the Crato Formation, Tridactylidae are known from two species in the genus *Cratodactylus* Martins-Neto, 1990: the type species *Cratodactylus ferreirai* and *Cratodactylus kellneri* (Heads & Martins-Neto, 2007; Martins-Neto, 1990b, 1999, 2003).

Genus: Cratodactylus Martins-Neto, 1990

Type species. Cratodactylus ferreirai Martins-Neto, 1990

Original Diagnosis, according to Martins-Neto, 1990b: Medium-sized tridactylid 7 to 14 mm long; antenna moniliform; forewing reduced and hind wing elongated, outstrip the length of abdomen. Foreleg by tibia expanded for digging to adapt; hind leg tibia narrow and elongated, without lamella, only in apical site presented some short spurs; hind leg tarsi reduced, single segment. Discussion: differs from *Monodactylus* Sharov, 1968 (and *Monodactyloides*, Sharov) (Lower Cretaceous amber in Baisa, Transbaikalia) by relatively large size, smaller forewing and for leg for digging to adapt. Differs from all the other genus by hind wing long and absence of lamella in tibias.

Species: Cratodactylus ferreirai Martins-Neto, 1990 (figs. 174, 175)

Original Diagnosis, according to Martins-Neto, 1990b: Eye relatively small, round and placed at the tip of the head. Thorax length is half of the body length. Foreleg tibia without spurs.

Original Description, according to Martins-Neto, 1990b: Specimen holotype GP/1T-1649, head relatively ascent, eye remarkably, round, projecting and placed at the tip of the head. Pronotum relatively short. Mesothorax robust, wider than pronotum, salient to a hump form. Abdomen elongated, peak round, with segments much broad and relatively long. Hind wing long and narrow, longer than the body. The margins of anal and costa almost parallel and apex sharp, with little long veins. Hind leg femur robust, quasi the same length as abdomen; anterior margin of the femur filled with tubers and granules. Hind leg tibia long and narrow, slightly longer than the femur, with a pair of apical spine. Tarsal single-segment. Specimen CV-2438, mid leg femur long and smooth, tibia elongated and with the distal part narrower, tarsus two-segments. Head triangular and antenna presented seven segments. Cerci relatively long. Specimen CV-2359, forewing covers only the base of the abdomen. Specimen CV-2436, foreleg coxa round, robust. Forewing with Sc and R clearly, slanting. Abdomen robust, cerci long.

New Description: Forewing short, covering only the anterior 2/3 of the abdomen. The venation simple, A-Zone rich. Hind wing longer than the abdomen. Foreleg short, in the base zone of tibia tuberous, with joint and purtrusion. Mid leg elongate, tibia robust and smooth, tarsus two-segment, first segment short, second one elongate and with claw. Hind leg femur robust, about the same length as the abdomen. Ovipositor long and straight. Cerci long, about the same length as ovipositor.

Specimen **SMNS 66489**: Thorax wide. Foreleg in the base zone of tibia tuberous, with joint and purtrusion. Forewing short, covering only the anterior 2/3 of the abdomen. The venation simple, A-Zone rich. Hind wing long, reaching the end of abdomen.

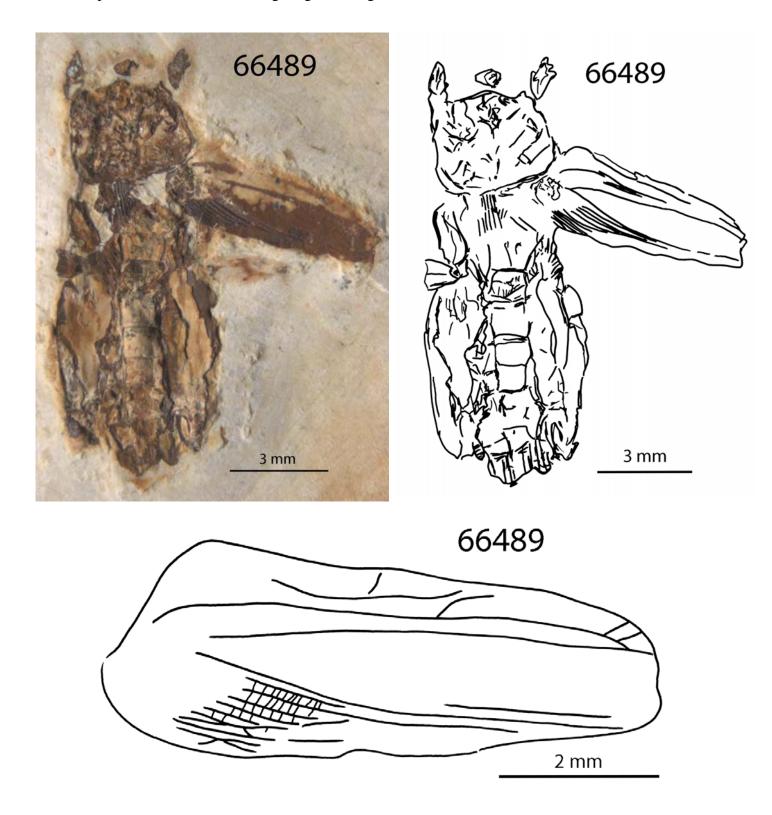
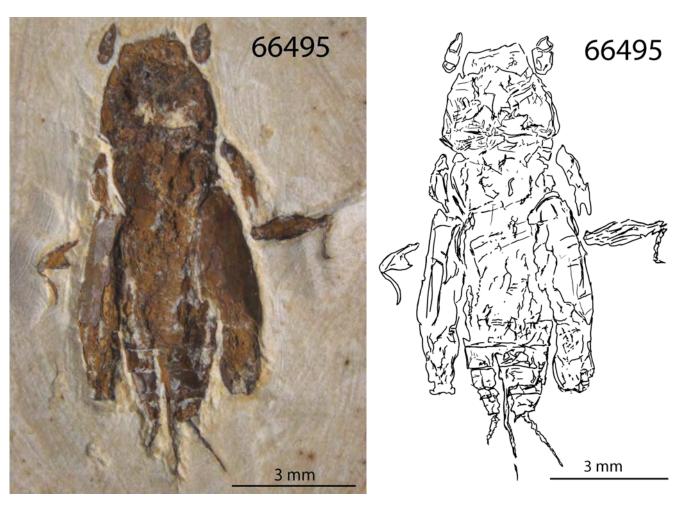


Fig. 174. Cratodactylus ferreirai Martins-Neto, 1990, Habitus & Forewing.

Specimen **SMNS 66495**: Thorax wide. Mid leg long, tibia robust and smooth, tarsus two-segment, first segment short, second one elongate and with claw. Ovipositor long, about the same length as cerci.



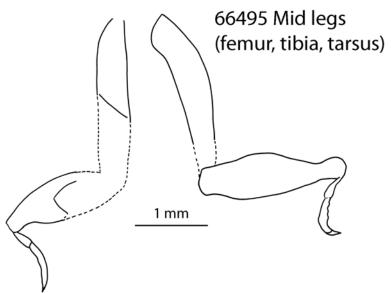


Fig. 175. Cratodactylus ferreirai Martins-Neto, 1990, Habitus & Mid legs detail.

Discussion: *Cratodactylus ferreirai* Martins-Neto, 1990 differs from *Monodactylus* Sharov, 1968 by the shorter forewing with a simpler venation (in *Monodactylus dolichopterus* the forewing long, their apex reaching end of abdomen). *Cratodactylus ferreirai* differs from *Cratodactylus kellneri* Martins-Neto, 1990 by the size and form of eye (*C. kellneri* has a big, elongate eye, placed in the middle part of the head), by the longer thorax (in *C. ferreirai* the thorax length is about half of the body length and in *C. kellneri* is about 1/3 to ½) and by the foreleg tibia without spurs (in *C. kellneri* with several spurs).

Species: Cratodactylus kellneri Martins-Neto, 1990 (figs. 176-178)

Original Diagnosis, according to Martins-Neto, 1990b: Body 7 to 11 mm long. Eye big, elongate and placed in the middle part of the head. Thorax length is 1/3 to ¼ of the body length. Anterior tibia with several spurs.

Original Description, according to Martins-Neto, 1990b: Specimen holotype GP/1T-1652, head relatively small, with the remarkable eye, oblong in lateral and quasi in a triangular form, placed in the middle part of the head. Pronotum in saddle form. Mesothorax robust, much broader than the prothorax. Abdomen elongated, peak round, with segments much broader and relatively long. Hind wing long and narrow, longer than the body. Hind leg femur robust, longer than the abdomen but without tuber and granule; tibia long and narrow, partly with spurs; tarsal short, single-segment. Foreleg femur robust, tibia smooth and much narrow than femur. Specimen CV-1010, antenna moniliform, less than nine segments. Foreleg tibia robust, with long and enormous spurs for digging to adapt. Specimen CV-2520, antenna has ten segments, head triangular.

New Description: Antenna has nine segments and probably is the complete length. Forewing short, hind wing longer than the abdomen. Foreleg stocky, tibia smooth [robust and with several spurs(Martins-Neto 1990b)], tarsus two-segment, first segment shorter than the second one. Mid leg elongate, tibia robust and smooth, tarsus two-segment with claw. Hind leg femur robust, clearly longer than the abdomen. Ovipositor long, robust and straight. Cerci short with thick spurs.

Specimen **SMNS 66494**: Antenna short, at least five segments. Foreleg stocky, tibia smooth [robust and with several spurs (Martins-Neto, 1990b)], tarsus two-segment, first segment shorter than the second one. Hind leg femur robust, clearly longer than the abdomen. Ovipositor robust.

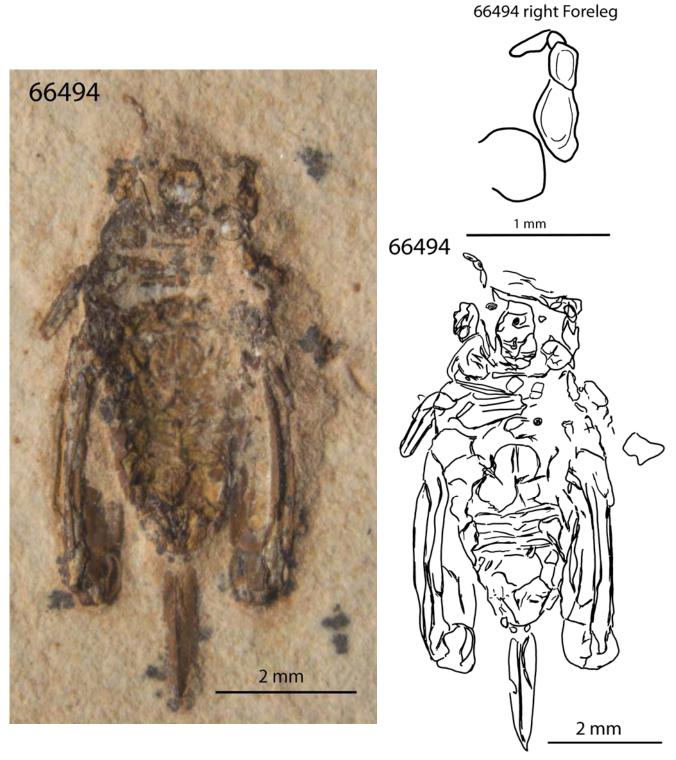


Fig. 176. Cratodactylus kellneri Martins-Neto, 1990, Habitus & Foreleg detail.

Specimen **SMNS 66688**: Antenna short and with nine segments, probably the total length. Hind wing long, reach the end of abdomen. Mid leg elongate, tibia robust and smooth, tarsus two-segment, first segment short, second one elongate with claw. Ovipositor long. Cerci short and with thick spurs.

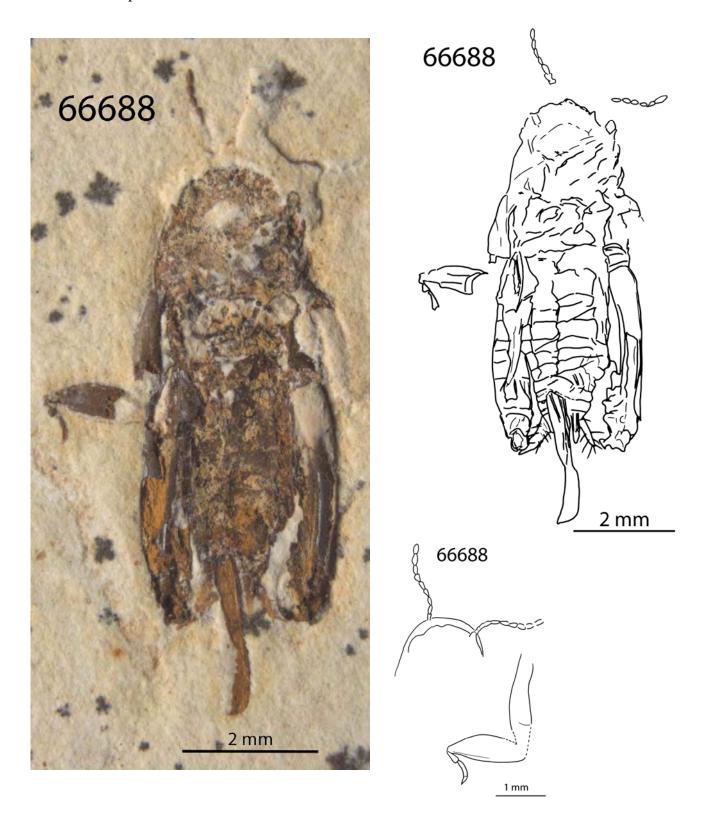


Fig. 177. Cratodactylus kellneri Martins-Neto, 1990, Habitus, Antenna & Mid leg detail.

Specimen **SMNS 66689**: Hind leg femur robust and clearly longer than abdomen. Ovipositor robust, straight.

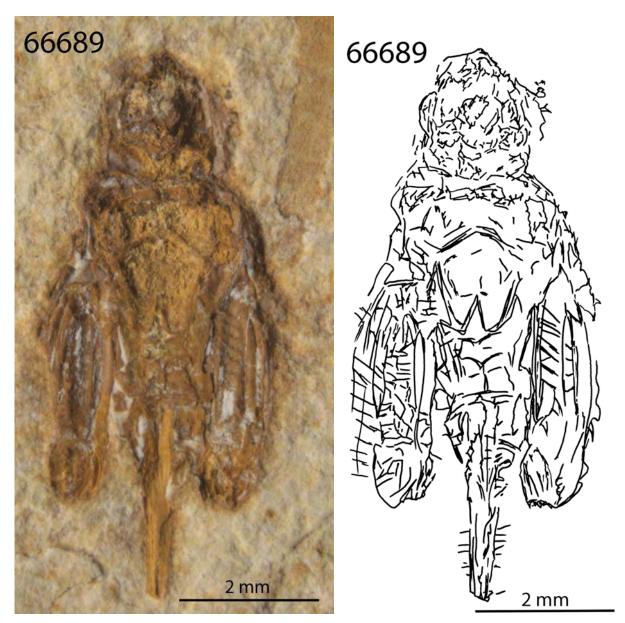


Fig. 178. Cratodactylus kellneri Martins-Neto, 1990, Habitus.

Discussion: *Cratodactylus kellneri* Martins-Neto, 1990 differs from *Cratodactylus ferreirai* by the size and form of eye (*C. ferreirai* has a small, round eye, placed at the tip of the head), by the shorter thorax (in *C. ferreirai* the thorax length is about half of the body length and in *C. kellneri* is about 1/3 to ½) and by the foreleg tibia with several spurs (in *C. ferreirai* without spurs).

Species: unknown (New Species N) (fig. 179)

Diagnosis: Specimen **SMNS** 66493, body size notably small, body 4 mm long, total length including hind wind 5.5 mm. Thorax length is about 1/3 of the body length.

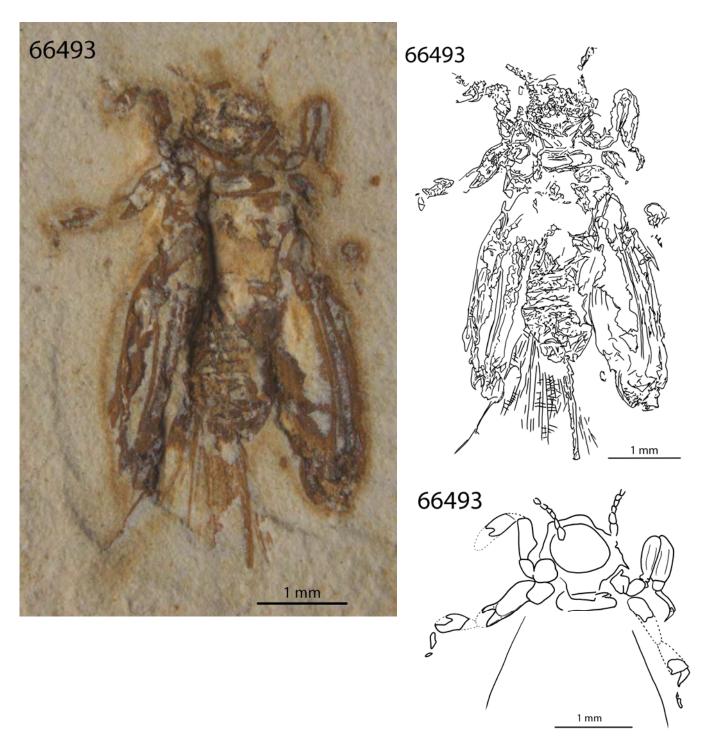


Fig. 179. Unknown new species pygmy mole cricket N, Habitus & reconstructed Body part.

Description: Antenna moniliform, short, at least six segments. Eye small, round and located in the middle part of the head. Head small, round and placed under the pronotum. Thorax length is about 1/3 of the body length. Foreleg elongate, trochantin and coxa round, femur and tibia

cover smooth and circa the same length, tibia swelled, tarsus two-segment with claw, second segment narrow and longer than the first one, no evidence about pretarsus. Mid leg thick, the tip of femur has two large peaks, tibia smooth, tarsus elongate, probably with two-segment. Hind leg femur notably robust, clearly longer than the abdomen. Hind wing longer than hind leg femur and abdomen, tip reaching the end of ovipositor. Abdomen small and round. Ovipositor relative thin and long, lance form.

Discussion: Specimen SMNS 66493 similar to *Cratodactylus kellneri* Martins-Neto, 1990 by the antenna, the head and the length of thorax. Differs by the smaller body size, elongated foreleg, notably robust hind leg femur and thin ovipositor.

Genus: Cratodactylus Martins-Neto, 1990 (?)

Species: unknown (New Species O) (fig. 180)

Diagnosis: Specimen **SMNS 66504**, body size notably small, body 4 mm long. Antenna 2.3 mm long, more than half of the body length. Thorax length is about 1/3 of the body length.

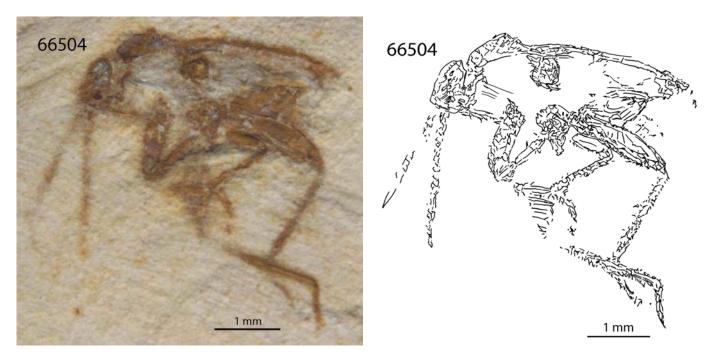


Fig. 180. Unknown new species pygmy mole cricket O, Habitus.

Description: Antenna elongate, more than half of the body length. Eye big, round and located in the middle part of the head. Head oval and small. Thorax length is about 1/3 of the body length. Foreleg elongate, femur a little bit longer than the tibia. Mid leg femur longer than tibia. Hind leg for jumping, femur about the same length than tibia, tarsal elongate, one-segment.

Discussion: Similar to *Cratodactylus* gen. Martins-Neto, 1990 by the length of thorax and the hind leg one-segment tarsal. Differs by the notably elongated antenna, smaller body size, and the elongated foreleg.

#### **Problematic**

The following specimens are mostly poorly preserved and only deficiently to identify.

Specimen **SMNS 66497**: Similar to Araripelocustidae in having the very robust hind leg femur and the strongly sclerotised posterior expansion of the pronotum. Body approximately 16 mm long. Forewing 22 mm long and 4.7 mm wide, RP preserved (at least) three branched. Hind leg tibia smooth and has a robust apical spur, tarsal with three (or four) segments, fist segment elongate (2.5 mm) more than half of total tarsus length (4mm).

Discussion: Specimen SMNS 66497 from body size is similar to SMNS 67589 in forewing 22 mm long and 4 mm wide, comparatively with *Araripelocusta longinota* body 25.8 mm and forewing 26.7 mm long, SMNS 67587 body 19 mm and forewing 21 mm long, *Araripelocusta brevis* body about 15 mm and forewing 18.2 mm long.

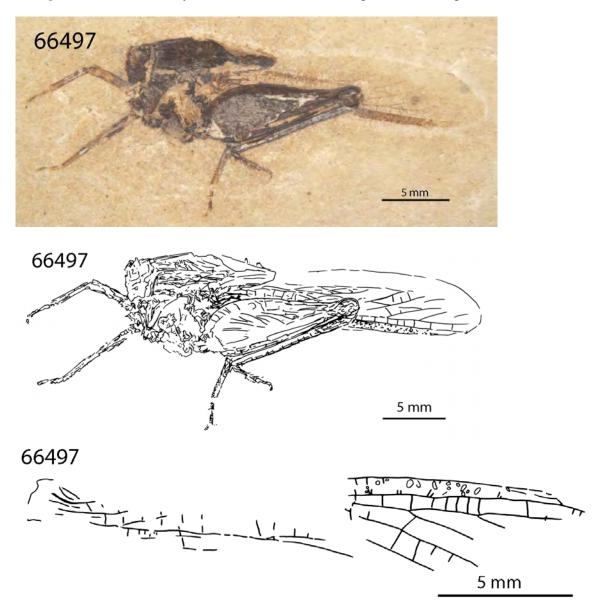


Fig. 181. Unknown species Locustopseidae P, Habitus & Forewing.

Specimens **SMNS** 67575 + **SMNS** 67576: Similar to Araripelocustidae in having the strongly sclerotised posterior expansion of the pronotum. Fore- and hind wing at rest 24 mm long and 4 mm wide. Body size and general habitus similar to SMNS 67587 (see figs. 169, 170).

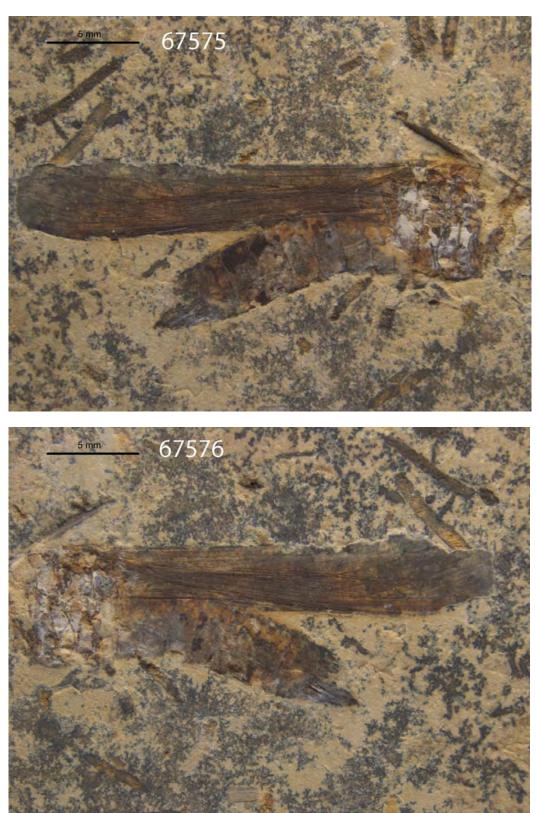


Fig. 182. Unknown species Locustopseidae Q, Habitus with counter plate.

Specimen **SMNS 66479**: Remarkably by the large size. Antenna 18 mm long. Body 27 mm long. Ovipositor 35 mm long. Head relative large. Hind wing measured at rest about 36 mm long. Foreleg tarsus with three segments, first segment (3 mm) elongate, more than half of total tarsal length (5.5mm). Hind leg femur thin and elongate, tibia has short spines and an apical spur, tarsus three segments, first segment (4.7 mm) elongate, more than half of total tarsal length (7.2 mm). Ovipositor longer than body length, lance form.



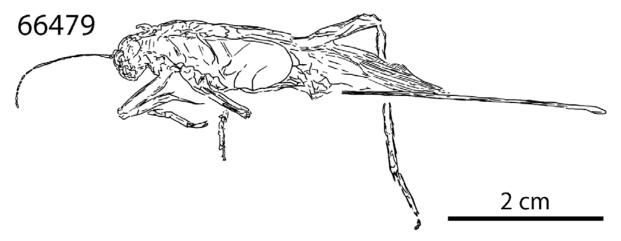


Fig. 182. Unknown species Ensiferan R, Habitus.

Specimen **SMNS 66480**: Remarkably by the large size. Antenna 38 mm long. Body 35 mm long. Forewing similar to the male of Grylloidea. Hind wing measured at rest about 35 mm long. Fore-, mid- and hind legs general robust. Hind leg tarsus with three segments, first segment (3.5 mm) longer than the second (1.8 mm) and the third (2.5 mm) segments. Cerci can be probably identify and short (3 mm).

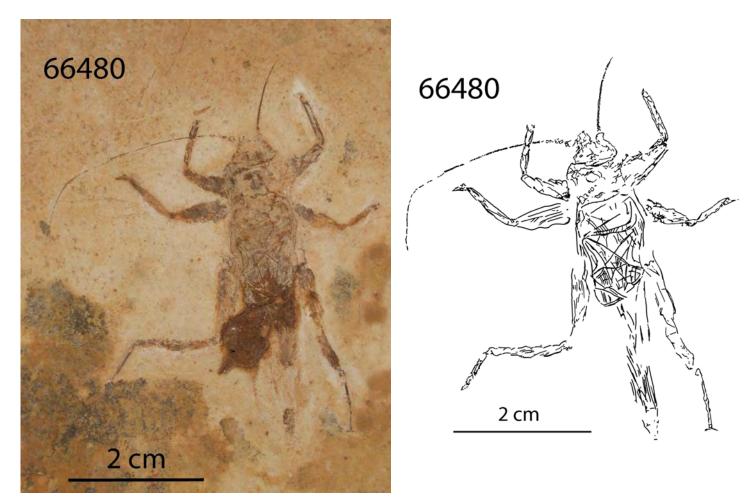
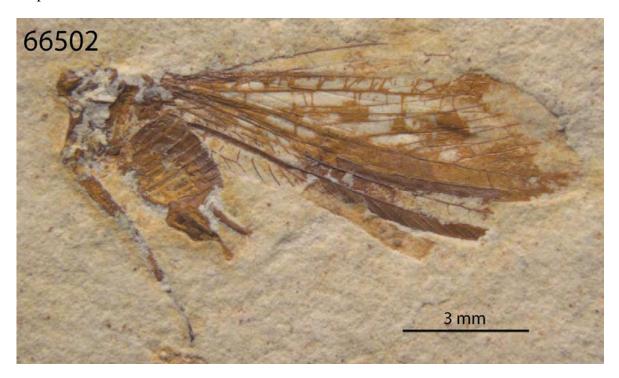


Fig. 183. Unknown species Ensiferan S, Habitus.

Specimen **SMNS 66502**: Remarkably by the for- and hind wings clearly larger than the body. Forewing about 10 mm long and 3 mm wide. Hind wing 11 mm long. Hind wing similar to Elcanidae but forewing rather peculiar. Hind leg not as jumping-leg differentiated and ovipositor robust.



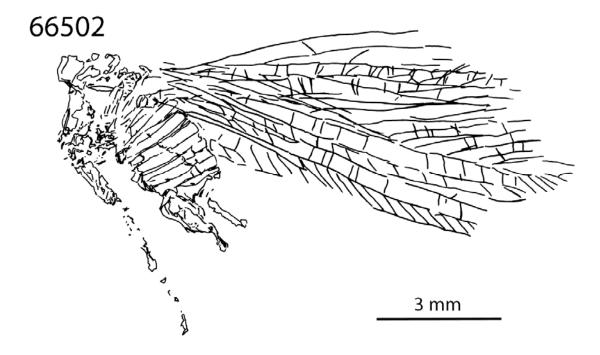


Fig. 184. Unknown species Ensiferan (?) T, Habitus.

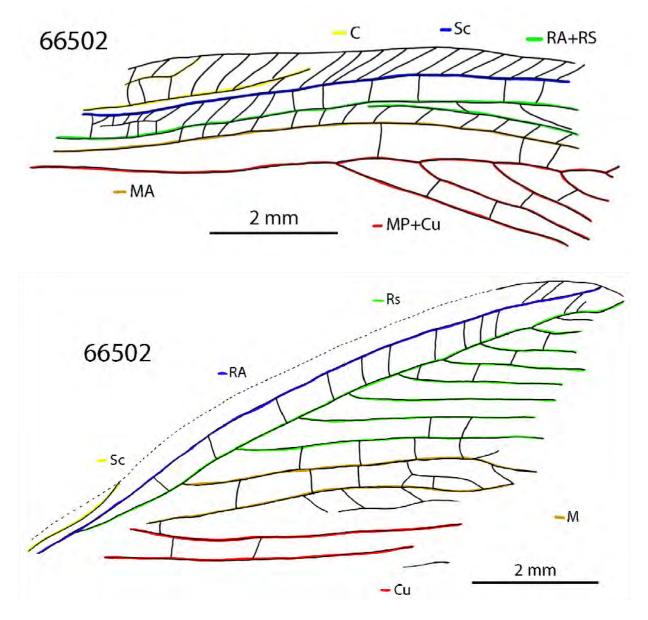


Fig. 185. Unknown species Ensiferan (?) T, Fore & Hind wings.

#### 4. Discussion

# 4.1. Taphonomy

The presence of the four taphonomic stages of Martins-Neto & Gallego (2006) are compiled in Table 1. The insect fossils of the Crato Formation appear to show a size independent preservation with specimens of all sizes showing different preservation stages. The specimens of this study are typical for museum collection with preferences for rare, well preserved and representative samples. This is reflected by the fact that about 85% of the specimens belong to Stage I and Stage II (see table 1). This is in contrast to the results of Martins-Neto (2002a), Martins-Neto & Gallego (2006) and Martins-Neto & Tassi (2009) gathered from large scale field data showing that different genera show various preservation states.

**Table. 1.** Statistic of the four fossil preservation stages by families (n=105 individuals). For preservation stages see figure 9.

	Stage I	Stage II	Stage III	Stage IV
Blattaria				
Cratovitismidae	1			
Umenocoleidae	14	4		
Blattulidae	10	3		1
Blattellidae	13	2		
Mantodea	3	1	2	
Orthoptera				
Baissogryllidae	1	2	2	
Gryllidae	7	2		
Gryllotalpidae	3			
Tettigoniidae				1
Haglidae	1			1
Prophalangopsidae	1	2		
Elcanidae	7		2	
Locustopseidae		1	2	1
Bouretidae		2		
Araripelocustidae			4	
Tridactylidae	4	3		
unknown Taxon	2			

### 4.2. Histology

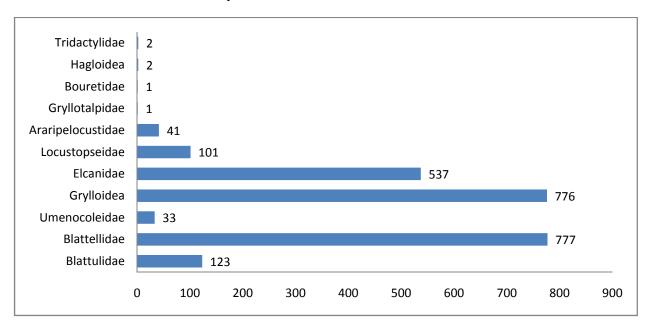
Some insect fossils show detail histological structures, for example mouth part, compound eyes, single eyes (ocelli: for example SMNS 66558) and even muscle tissue. The muscle tissue can be identified especially in the large sized specimen in this study, for example in the thorax area of cockroaches (SMNS 66000-116, 66310, 66317, 66318, 66320). This muscle tissue is present as fine fragments in a fiber like structure adhering to the cuticle. For similar records of muscle tissue of a plant bug (Heteroptera) from the Crato Formation, see Grimaldi & Engel (2005, fig. 2.10, pp. 48).

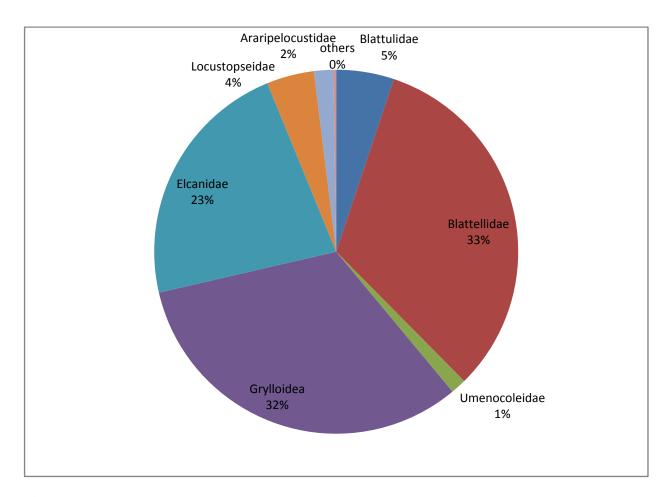
## 4.3. Diversity

The insect fossils of Crato Formation are abundant and its collections are distributed worldwide in museums as well as private and commercial collections. An analysis of the taxonomic diversity using these collections is thus difficult. Up to now, there are several statistical analysis of diversity concerning specific taxonomic units, for example that of arthropods by Bechly (1998a), insects by Menon & Martill (2007), cockroaches by Vršanský (2004), Elcanidae by Martins-Neto (1992) and Ensifera by Martins-Neto (1995b). In this study, the diversity of "Blattaria" and Orthoptera (plus a few specimen of Mantodea) is interpreted from the two investigated collections, one is the large collection from the MSF, Fossils Worldwide, Sulzbachtal, Germany collection containing 2394 specimens, the others is from the Staatliches Museum für Naturkunde, Stuttgart, Germany containing 105 individuals. The latter collection, however, includes much rarer and representative species. It also forms the base of the systematic analysis of this study (see tables 2-3 and figs. 186-191).

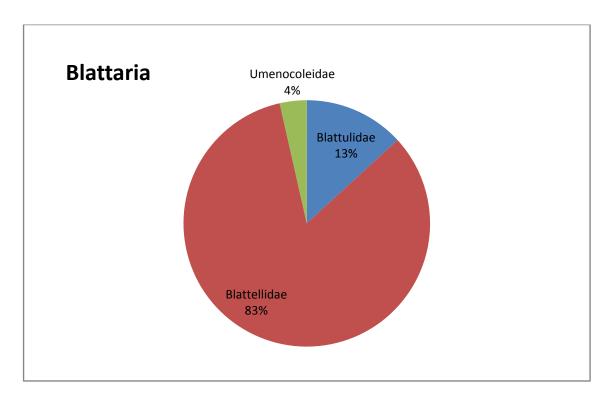
The result of this study shows that the dominant family of the order "Blattaria" in the Crato Formation is clearly the family Blattellidae with about 83% of the cockroaches. This result is similar to that of Vršanský (2004) who showed a value of 60%. This study shows a surprisingly low number of members of the family Umenocoleidae (only 4%) which may be a collecting bias. The collection in American Museum of Natural History, New York shows the Umenocoleidae being represented by 15% of all roaches (Vršanský, 2004). The order Orthoptera shows a dominance of the superfamily Grylloidea (including two families Baissogryllidae and Gryllidae) and the family Elcanidae, which together comprise about 90% of all the Orthoptera. The other 10% belong to the suborder Caelifera which includes he families Locustopseidae and Araripelocustidae. The families Gryllotalpidae, Hagloidea, Bouretidae, and Tridactylidae are extremely rare.

**Table 2.** Crato Formation insect diversity of orders Blattaria and Orthoptera. Diversity by families. Specimens numbers within each group (n=2394). Collection of MSF, Fossils Worldwide, Sulzbachtal, Germany.

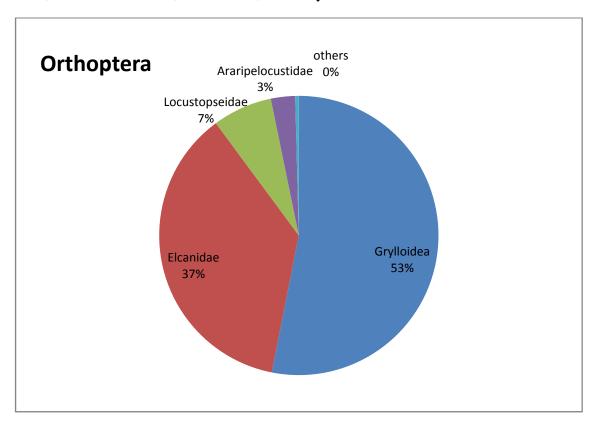




**Fig. 186.** Crato Formation insect diversity of orders Blattaria and Orthoptera. Diversity by families. Percentages represent the number of individuals within each group (n=2394). Collection of MSF, Fossils Worldwide, Sulzbachtal, Germany.

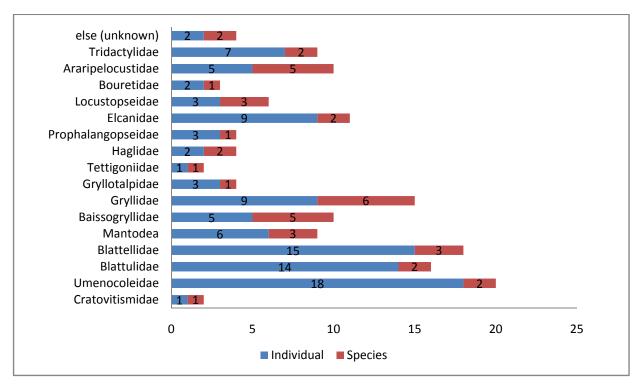


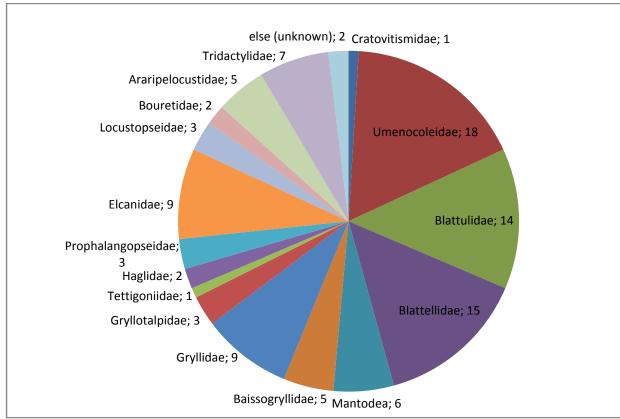
**Fig. 187.** Crato Formation insect diversity of order Blattaria. Diversity by families. Percentages represent the number of individuals within each group (n=933). Collection of MSF, Fossils Worldwide, Sulzbachtal, Germany.



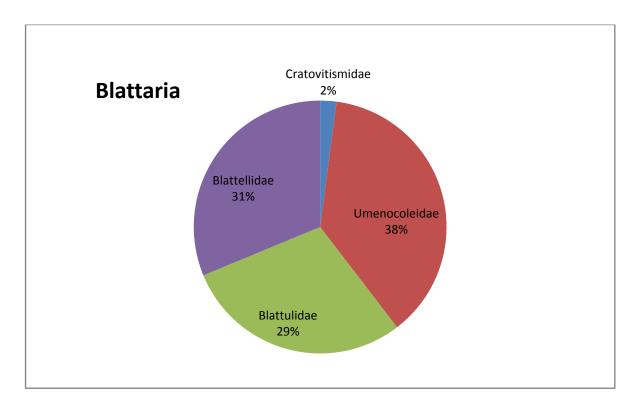
**Fig. 188.** Crato Formation insect diversity of order Orthoptera. Diversity by families. Percentages represent the number of individuals within each group (n=1461). Collection of MSF, Fossils worldwide, Sulzbachtal, Germany.

**Table 3.** Crato Formation insect diversity of orders Blattaria, Mantodea and Orthoptera. Diversity by families. Individuals & Species numbers within each group (n=105). Collection of Staatliches Museum für Naturkunde Stuttgart, Germany.

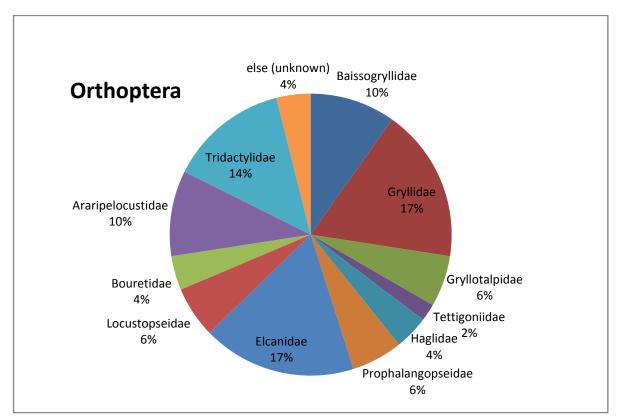




**Fig. 189.** Crato Formation insect diversity of orders Blattaria, Mantodea and Orthoptera. Diversity by families. Individuals numbers within each group (n=105). Collection of Staatliches Museum für Naturkunde Stuttgart, Germany.



**Fig. 190.** Crato Formation insect diversity of order Blattaria. Diversity by families. Percentages represent the number of individuals within each group (n=48). Collection of Staatliches Museum für Naturkunde Stuttgart, Germany.



**Fig. 191.** Crato Formation insect diversity of order Orthoptera. Diversity by families. Percentages represent the number of individuals within each group (n=51). Collection of Staatliches Museum für Naturkunde Stuttgart, Germany.

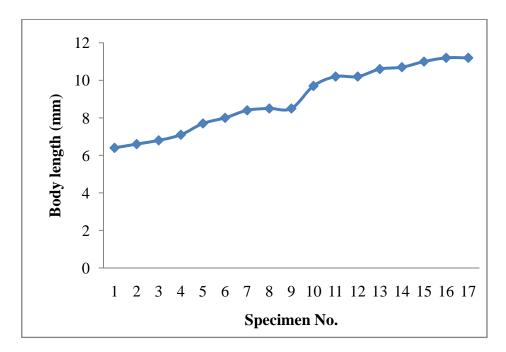
### 4.4. Systematics

The morphological details of these taxa were discussed in chapter 3. The systematic palaeontology of newly described taxa is as follows.

## "Blattaria"

#### Umenocoleidae:

There are two species of Umenocoleidae in the Crato Formation, *Ponopterix axelrodi* Vršanský & Grimaldi, 1999 and *Ponopterix maxima* Bechly, 2007. The main difference between this two species should be their body size. According to this study, however, there is a continuous size distribution in the studied specimens of this genus (see figure 192). The fore and hind wings between these two species are also not significantly different with respect to morphology. The length of the ovipositor compared to that of the body length is also quiet similar (in *P. axelrodi* about 10% - 12.12% and in *P. maxima* about 7.84%-12.26%). It is possible that those two ones indeed belong to the same species.



**Fig. 192.** Body length of two species, *Ponopterix axelrodi*: 6.4-8.0 mm long and *Ponopterix maxima*: 8.4-11.2 mm long. The body size distribution in the studied specimens of this genus is rather continuous.

#### Blattulidae:

The main difference between family Araripeblattidae Martins-Neto, 2010 and their closest family Blattulidae Vischniakova, 1982 (see Matins-Neto *et al.*, 2010 or pp. 44 of this study) does not apply to the specimens in this study. Comparing the lines from RA1-ending, MA2-origin and CuP-ending of *Araripeblatta brevis* Mendes, 2000 variants, both intraspecific (even between the right and the left forewings of the same specimen) and interspecific, there are no significant differences between *Araripeblatta brevis* and family Blattulidae (see figures

39-40 for more detail). *Araripeblatta brevis* is thus considered here to be a junior synonym of *Elisama brevis* and belongs to family Blattulidae. Indeed, these RA1-oMA2-CuP lines are clearly different from that in families- Blattulidae and Blattellidae ("*Mesoblattina*" *limai*) (see fig. 41). The characteristics of this line RA-oMA-CuP could be considered, although variation is generally great.

An unknown species, specimen SMNS 67573 (see figs. 64-66) is described: the complete hind wings specimen shows a typically cockroaches form and belongs to genus *Elisama* (Blattulidae) but not *Elisama brevis* (=americana) Mendes, 2000, so far, the only species of family Blattulidae in the Crato Formation. Generally, specimen SMNS 67573 is larger than another species of *Elisama* and much similar to *Elisama parallela* Vršanský, 2003.

#### Blattellidae:

According to Vršanský (pers. comm.) the species (*Mesoblattina*) *limai* Pinto & Purper, 1986 (see figs. 67-74) is currently not attributed to any genus, as it is apparently another genus and family. Based on the morphological characteristics of forewing, which is identical with *Piniblattella vitimica* and other species in this genus, it is possible that the species belongs to the genus *Piniblattella*.

There are two unnamed new genera and species of Blattaria in this study. Species B included six specimens SMNS 66000-116, 66310, 66313, 66317, 66318 and 66320 (see figs. 75-85). This species is with remarkable large body size and probably belongs to the family Blattellidae. Species C included four specimens SMNS 66308, 66309, 66311 and 66321 (see figs. 86-91), its body relatively small and round, few sclerotized forewing and the veins not sufficient known.

Some characters are present in the same individual but differ in exact morphology in the left and right sides of the insects, for example in the left and right wings and tarsus segments. Slight difference between the left and right wings take place in most insect groups. The most clear differences are present in Recent cockroaches and mantis taxa (pers. observation). Specimen SMNS 66315 *Mesoblattina limai* (Blattellidae) in this study has a clearly different left and right forewings (see fig. 71). This "deformity" takes place not only in wings, but also in the tarsus. Specimen SMNS 66000-116 has five segments tarsus in the left hind leg, but only four segments in the right hind leg (see fig. 76). In comparison specimen SMNS 66317 of the same species shows four segments tarsus in both hind legs (see fig. 81). In the "Blattaria", the tarsus should consist of be five segments (see fig. 84) or in case with four segments after regeneration (Bohn, 2003). Probably this is a common feature of fossil Blattaria in the Crato Formation as this was seen in two (or rather three legs) of a total of six specimens.

# Mantodea

Specimen SMNS 67583 shows a typical mantid forewing and raptorial forelegs (see figs. 98, 99). It is the first description of the genus *Chaeteessa* (Mantodea) in the Crato Formation and the oldest fossil record of the primitive mantid family Chaeteessidae. This specimen is very similar to the *Chaeteessa valida* (Perty, 1833) and certainly belongs to a new species.

## **Orthoptera**

### Gryllidae

SMNS 66510 has the typical jumping hind leg of crickets and is notably by small body size and its long antenna, forewing unknown (see figs. 117, 118). Comparing with others especially the similar body size cricket species in the Crato Formation, it is generally different and therefore this specimen should belong to a new species of family Gryllidae.

# Tettigoniidae

Specimen 66691 and its counter plate 66693 (see fig. 124) is the first Cretaceous Tettigoniidae, to be discovered and described. This only forewing specimen is similar but clearly different to most ancient species currently known of Tettigoniidae, *Pseudotettigonia* Zeuner, 1937 (=*Tettigonia amoena* Henriksen, 1929) from the Eocene. It should belong to a new Cretaceous species.

## Haglidae

Two new species were described and is practically the first Haglidae discovered in the Crato Formation. [The only single description of the Haglidae in the Crato Formation up to now is the *Prezotophlebia helbae* Martins-Neto, 2007 (Martins-Neto, 2007). This poorly preserved specimen shows however no significant characters of the family Haglidae and perhaps better reserved until more complete material is studied.] Specimen SMNS 66501 is a single female forewing, notably large in size and similar to genus *Hagla* (see fig. 126). The other specimen (SMNS without number) is a very complete male fossil. Forewing similar to *Archaboilus* (subfamily: Cyrtophyllitinae) and hind wing typically Haglidae (see figs. 128-130). It should be described as a new genus and species.

## Prophalangopsidae

A new species with three specimens SMNS 66481, 66482, 67582 were described (see figs. 131-136). Particularly by the forewing with simply (three branched-) RA and (two branched-) RP. Its similarity is only to the genus *Karatailus* (Aboilinae) as well as the simple RP branched. It should be described as a new genus and species. The fossils record of Prophalangopsidae is limited to Europe, Asia and New Zealand (Gorochov & Rasnitsyn 2002; Lin *et al.*, 2008; Gu *et al.*, 2010). The two species *Kevania araripensis* Martins-Neto, 1991 and *Cratohaglopsis santanaensis* Martins-Neto, 1991, that originally interpreted as Prophalangopsidae, was transferred newly to the subfamily Euclydesinae, within family Mimnermidae (Martins-Neto, 2007). Another Triassic fossil record from South America, genus *Notopamphagopsis* Cabrera, 1928 (sp. *N. bolivari* Cabrera, 1928) was originally interpreted as Prophalangopsidae by Zeuner (1939) and then transferred to the family Haglidae by Sharov (1968). Therefore the new species of this study is the first description of Prophalangopsidae in South America.

#### Elcanidae

Up to now there are two species of Elcanidae in the Crato Formation, *Cratoelcana zessini* Martins-Neto, 1991 and the smaller size *Cratoelcana damianii* Martins-Neto, 1991. However the specimen SMNS 66503 has a notably small body size and simple wing venations (see figs. 155, 156). Although this specimen is only poorly preserved, it is possible that this one belongs to a new Elcanidae species.

## Locustopseidae

A new species is described in this study. The specimen SMNS 67586 has a fore- and well preserved hind wings (see figs. 158, 159). This species is similar to *Cratozeunerella* but differs from all its six described species. It could be belong to a new species of this genus.

#### Bouretidae

Up to now, only a single poorly preserved specimen was published (Martins-Neto, 2001). Both specimens of species *Bouretia elegans* Martins-Neto, 2001 from this study SMNS 66487 & 67585 presented hind wings, in which the RA are clearly terminal branched (see figs. 162-165). This could be an evidence to suggest a relationship with Haglidae instead of Locustopseidae.

### Araripelocustidae

The extinct family Araripelocustidae includes two species within the genus *Araripelocusta* Martins-Neto, 1995, were founded mainly on "Locustopsoidea" with strongly sclerotised posterior expansion of the pronotum. However, two specimens of this study SMNS 67587 & 67589 have this robust pronotum but their fore- and hind wings are clearly similar to that in genus *Cratozeunerella* (especially *C. neotropica*) instead of *Araripelocusta* (see figs. 169-173). Thus, those two specimens should be described as two new species closer to *Cratozeunerella* but not *Araripelocusta*. The strongly sclerotised pronotum seen here may be a convergence.

#### **5. Conclusions**

Well preserved insect material from the Crato Formation was studied from a large collection of the Staatliches Museum für Naturkunde Stuttgart, Germany. This study concentrates on insect wing morphology in great details allowing for multi-layered folded wings to be separated into their specific components. This study especially considers the hind wings, both with respect to their morphology and their relation to the forewings. Furthermore, intraspecific variations are considered. The collection from Sulzbachtal was also referred to for diversity comparisons.

Up to now, the systematic discussion of fossil insects was based mainly on the morphology of the forewings. The morphological variation of hind wings are less pronounced than that of the forewings. Furthermore the collection of fossil hind wings is, in fact, rarer than that of forewings. The discussion of the morphology of hind wings is, however, still needed. Intraspecific variations should be considered if more than one specimen of the same species is available. The characters (including wing venations) are not static, but variable.

Altogether, 16 genera including 37 species were described in this study. Of these, 13 species are as of yet unnamed. Furthermore, the descriptions of the following taxa have been revised: *Ponopterix maxima* Bechly, 2007 (family Umenocoleidae Chen et Tian, 1973), *Araripeblatta* Mendes, 2000 (family Araripeblattidae Martins-Neto *et al.*, 2010), *Mesoblattina limai* Pinto & Purper, 1986 (family Blattellidae Karny, 1908), *Bouretia* Martins-Neto, 2001 (family Bouretidae Martins-Neto, 2001) and Family Araripelocustidae Martins-Neto, 1995. This study furthermore includes the first description of the following taxa: The first *Chaeteessa* Burmeister, 1838 (Family Chaeteessidae Handlirsch, 1920; Mantodea) in the Crato Formation, the first Tettigoniidae Krauss, 1902 in the Crato Formation (or rather Cretaceous) and the first (three spp.) of Haglidae Handlirsch, 1906 and Prophalangopsidae Kirby, 1906 (both belonging to the Superfamily Hagloidea Handlirsch, 1906) in the Crato Formation. Based on these results, some questions can be asked particularly concerning the origin of the Tettigoniidae (which is the most diverse lineage of extant Ensifera), the extinction of the Haglidae (abundant in the Jurassic) and the existence of the family Prophalangopsidae in South America.

This study is based on first hand observations of original material. On this basis of this, some original descriptions have been revised. More studies on more poorly preserved taxa as well as comparison to other Cretaceous localities are needed along with detailed phylogenetic and cladistic analyses.

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Appendix I Body size of Blattaria

Body size: mm long(wide)	A 4	D - d - 1 4b	Head	Forewing	hind Wing	Pronotum	Meso/ Metathorax	Foreleg; fem (tib) (tar)		Lind I from (42h) (4)	Abdomen	Ovipositor	Cerci	C4-1:
long(wide)	Antenna	Body length	неаа	Forewing	wing	Pronotum	Metatnorax	Foreleg; tem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci	Styll
Cratovitismidae														
Cratovitisma oldreadi														
66000-127		7.6	0.6 (2.3)	5.8 (2.4)	6.2	1.5 (2.6)	1.4 (3)				3.6 (3.7)	0.6	1.1	
Umenocoleidae														
Ponopterix axelrodi														
66326		7.1	0.9 (2)	5.7 (1.9)	5.8	1.5 (1.4)	1.7 (2.3)				3.1 (2.6)		0.7	
66329	1.5	6.4	1.1 (2)	5.1 (-)	5.2	0.8? (-)	1.2? (2.7)				3.2 (3)	>0.4		
66334		6.8	1 (1.9)	5.3 (1.7)	5.3	1.3 (1.4)	1.4 (1.8)				3.4 (2.1)		0.8	
66335		7.7	1.3 (1.9)	6.3 (2)		1.4 (1.3)	1.2 (2.2)				3 (3)	>0.5		
66336		8	0.8 (1.5)	6 (2.1)	6.5	1.4 (1.4)	2 (2.3)				3.7 (3)		1.1	
66338	3	6.6	0.7 (2.1)	6 (2.1)	6.3	1.6 (1.6)	1.5 (2)				3 (2.7)	0.8	1.1	
Ponopterix maxima														
66323	6	11.2	1 (2.5)	8.7 (1.9)		2.1 (2.5)	3 (2.6)				5.5 (3.9)		1.8	
66324	2.4	11	1 (1.9)	9.3 (2.3)		2.1 (2.6)								
66325		8.5	0.8 (1.7)	6.4 (1.9)	6.5	1.6 (1.8)	1.8 (2.8)				4.5 (3.2)		1.5	
66327	4	10.7	1.4 (2)	7.1 (2.4)		1.9 (2)	2 (3)	2.5 (1.5) (-)	2.5 (2) (-)	3 (2.8) (0.9)0.5)0.4)0.2)0.5)	5.5 (3.7)	1	1.1	
66328	1.5	10.2	1 (1.9)	7.5 (2.3)	7.4	2 (2.4)	1.7 (3)				4.8 (3.7)	1.1	1.5	

Appendix I Body size of Blattaria

Body saize:mm long(wide)	A4	Body length	Head	Forewing	hind Wing	Pronotum	Meso/ Metathorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci	C4-1:
long(wide)	Antenna	Body length	Head	Forewing	wing	Pronotum	Metatnorax	Foreieg; 1em (tib) (tar)	mid Leg; tem (ub) (tar)	nind Leg; tem (ub) (tar)	Abdomen	Ovipositor	Cerci	Styll
Ponopterix maxima														
66330		11.2	1.5 (2.8)			2 (2.9)	2.5 (-)		1.8 (1.8) (-)	2.3 (2.8) (-)	5 (-)	1.2		
66331		8.4	0.8 (2.3)	7 (1.9)	7	1.5 (2.1)	1.8 (2.5)				4 (3.6)	0.9	1.2	
66332	3.5		1.1 (2.7)	8.6 (2.4)		2 (2.5)		X (1.4) (-)	X (2) (-)					
66333	5.4	10.6	1.6 (2.9)	7.8 (2.7)	7.6	2 (2.2)	2.5 (2.7)				4.6 (3.4)	1.3	1.9	
66337	1.7	9.7	1 (1.8)	7.1 (2.1)	7.7	1.7 (2.1)	2.5 (2.8)			2.5 (2.8) (0.6)0.5)0.4)0.2)0.5)	4.9 (-)		1.2	
66562		10.2	1.1 (2.6)	7.6 (2.4)		1.7 (2.2)	1.9 (2.8)				4.8 (3.7)	0.8	1.5	
67574	0.7	8.5	1.1 (-)			1.6 (-)	2.9 (-)				4.2 (-)		1.1	
Blattulidae														
Elisama brevis														
66000-125		8.5	x(2)	8.8 (2.8)	8.5	2.3 (3)	1.2 (2.7)			2 (3.8)	4.2 (3)		2	
66316		8.2	x(2)	8 (2.4)		1.8 (3)	1.5 (2.7)			2 (3.5) (2.6totally)	3.2 (3.8)	1		
66558		7.9	2.2 (2)	8.9 (2.7)	8.5	2.3 (3)	1.2 (2.8)	1.4 (1.3) (>0.8)		2.7 (3.5) (>1.2totally)	3.8 (3.8)	0.8	1.6	
67563		8.5	2 (2)	9 (2.8)	9	2 (-)	1.2 (3.2)		1.9 (2.1)	3.5 (3.8) (1)0.6)	3.6 (3.8)	1.1		
67564		9.5	2.2 (1.8)	9.5 (3)	9.5	2.4 (3.2)	1.3 (3)			3 (4.5) (1)	4.2 (3.8)	1	2	1
67565		8.8	x(2)	8.8 (2.5)		2.5 (3)	1.8 (2.8)				3.5 (3.8)	1.3	1.8	
67566		8.2	x(2)	8.8 (2.8)	8.8	2.2 (3)	1.5 (3.2)			3.2 (3.8) (1)	3.4 (3.6)	1		
67567		9.2	1.7 (1.8)	10 (2.8)	9.8	2.5 (2.7)	1.5 (3)			2.5 (4) (1.3)0.6)0.2)0.2)	4 (3.7)	1.3	2	

# Appendix I Body size of Blattaria

Body size: mm long(wide)	Antenna	Body length	Head	Forewing	hind Wing	Pronotum	Meso/ Metathorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomon	Ovipositor	Cerci	Ctyli
long(wide)	Anteinia	Body length	Heau	Forewing	wing	Fionotum	Metathorax	roreleg; tem (ub) (tar)	iniu Leg; tem (tib) (tar)	mind Leg; tem (tib) (tar)	Abdomen	Ovipositor	Cerci	Styll
Elisama brevis														
67568	7	8.8	1.7 (1)	8.8 (2.6)	9	2.5 (3)	1.2 (2.8)		2.8 (2.3) (1)(0.6)	3 (3.3) (1)0.7)0.2)0.2)	3.4 (3.6)	1.4	2.5	
67569		9	X(2.2)	9.2 (2.9)	9.4	2.5 (3.4)	1.8 (3.2)		2 (3.5)	3 (3.6)	3.4 (4)	1.2	>1	
67570		9	1.3 (2)	9.1 (2.6)	9	2.8 (3?)	1.4 (3?)		2.8 (2.5)	3 (3.5) (1)0.7)0.2)	3.4 (3.5)	1.3	2	
67571		8.3	1.8 (2)	9.2 (3)	9.2	2.2 (3)	1.8 (2.8)				3 (3.5)	1	2.1	
67572		9	X(1.8)	9 (2.8)	9	2.5 (3)	1.6 (3)		2.8 (2.4) (0.9)0.6)0.2)0.2)0.3)	3 (4)	4 (3.9)	1.5	2.2	
Blattellidae														
(Mesoblttina) limai														
66312		14	2.9(2.7)	12.8(3.9)		X(5.5)	X(5)		3.8(3)()	4.8(5.5)(3.5totally)	7(5)		>2	0.8
66314	10	13		13(4)	12.5	3.5(4.8)	3.5(4.5)		3.5 (3.8) (1.2)0.7)0.3)0.3)0.5)	3 (5) (1.2)0.9)0.7)0.3)0.8)	6.5(4.8)		3	
66315		13		10.3(3.5)		3.2(4.6)	3.5(4.5)				6.5(4.8)			
66319	9.5	14	3.1(2.5)	13(3.8)	13	4(5)	3(4.8)			4.5 (5.3) (0.8)0.6)0.3)0.3)0.5)	7(6)		3	
66322		11.7		13(3.8)		3.5(4.8)	2.8(4.5)			5 (5.2) (1.3)0.8)0.3)0.3)0.6)	5.5(5.3)		2.7	
67573				12(4.2)	12									
unknown species B										6 (6.6)				
66000-116	6	17.8		16 (4.8)	16	4.7 (6.2)	4.5 (6)		5	(2.5)0.8)0.7)0.2)0.9)	8.2 (7)		3.5	
66310	41	25		21		5.8 (8.9)	6 (8.2)		X (6) (5.1totally)	X (10.9) (>6totally)	14 (10.6)		5.2	

Appendix I Body size of Blattaria

Body size: mm					hind	_	Meso/						~ .	
long(wide)	Antenna	Body length	Head	Forewing	Wing	Pronotum	Metathorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci	Styli
unknown species B														
66313	32	22.3			19.5	5.1	5.5 (7.8)	5 (5.5) ()	5.6 (5.5) (2.8)0.7)0.5)0.4)1)	6.5 (6.5) (3)0.8)0.4)0.4)1.2)	12 (8)		4.8	
66317	17	21.7		19 (5.8)		5.5 (7.8)	6 (7.2)		5.5 (5) ()	6.5 (6.5) (2.2)0.8)0.3)0.8)	11 (8.8)		4	<u> </u>
66318	31	25		19.5 (6.2)		5.2 (7.8)	5.5 (7)			7 (9) ()	15 (9.5)		5.5	
66320		23		19.8		5.3 (7.4)	6.2			7? (8.5) (2.7)1.1)0.7)0.3)1.2)				<u> </u>
														<u> </u>
unknown genus/species C														<u> </u>
66308	11	9.5	X (1.8)	7.5		2.2 (3.5)	2	x (x) (0.8)0.3)0.2)0.2)0.4)		2.6 (2.8) (x)	4.9 (4)		1.7	
66309	9	8.8	X (1.7)	8.2		2 (3)	2.5 (3.6)			3? (3.6) (1.3)0.3)0.2)0.2)0.3)	4.5		1.7	
66311	7.5	11.9				2.8 (4.1)	2.8 (4.5)	x (1.4) (0.5)0.3)0.3)0.2)0.6)		4 (3.5) (1.8)0.3)0.2)0.3)0.3)			1.5	0.3
66321	9	9.7	1.9 (1.8)			2.5 (3.7)	2.5 (4?)	1.7 (2) (x)	2 (2.2) (0.9)0.3)0.3)0.2)0.3)	3 (3.2) (1.5)0.5)0.3)0.2)0.4)	5 (4.3)		1.7	

Appendix II Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
Mantodea												
Chaeteessa												
67583	31	2 (4)		23 (6)		5 (3)	8.5 (8?) (5?)					
Orthoptera												
Gryllidae												
Araripegryllus megacephalus												
Martins-Neto, 1991c		2-3.5 (3.5-5) *	14-18.5 *						7-11 (6-9.5) (-) *		8.5-11 *	
66488	>24	3 (5)	15		>17	6.5 (6)	3.5 (-) (-)		10.5 (8.5) (2)1)	8.5 (5)	>8	>13.5
66505	>20	3 (5)	18		23	7 (5.5)	4 (4)	4	13 (8.5) (2.5)1.5)1)	11 (7.5)	>9	>6
66508		3 (5)	15.5		22	7 (4.5)	3.5 (3)	4 (3.5) (-)	11 (9) (2)	8.5 (5.5)	>9	>10
Araripegryllus femininus												
Martins-Neto, 1991c		1-2 (2-3) *	9-13.5 *	10-13 (3.5-6.5) *					5-10 (3.8-6.5) (2-3.5) *		5.9-9 *	6-12 *
66686	>4	1.5 (3)	9.5		14.5	4.5 (3.5)			7.5 (5.5) (-)	5 (3.3)	>4.5	>7
Araripegryllus spinosus												
Martins-Neto, 1991c		0.8-1.5 (2-3) *	9-12.5 *	6-14 (3-6) *					5-12 (3.5-9) (2-3.2) *		4-5.5 *	4-6 *
66483	>1.5				12		2 (1.8)	2.5 (2) (1)0.3)0.2)0.5)	6 (4.8) (1.5)0.8)1)	5.5 (3)		>5
67579		0.7(1.8)	10.2	7 (3.8)	12	4.7 (3.5)			6 (4.5) (1.8)0.8)	5.5 (3)	4.3	>5.3

Appendix II Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
Araripegryllus nanus												<u> </u>
Martins-Neto, 1991c		1 (2) *	9-12 *	6-8.5 (3.5-4.5) *					6.5 (4) (2.8) *			<u> </u>
66484		3 (2.5)	11		10	4.5			7 (5)	6.5		>2
Araripegryllus serrilhatus												
Martins-Neto, 1991c		2 (3) *	11.5-14 *						6-7 (3-3.5) (-) *			8.5-9
66485	25	1.7(2.5)	12		16	5.5 (4)	2.5	3.5 (2.5) (1)0.7)0.3)0.6)	8 (5.8) (2.5)0.4)0.8)	6.5(4.5)	8	13
unknown (probably Gryllidae)												
66510	33	2(1)	6.5		8	2.5	2	2.8	5 (4) (1.8)0.4)0.7)	4 (2.6)	4	6
Baissogryllidae												
Cearagryllus perforatorius												
Martins-Neto, 1991c			24-30.5 *	25-35 (9) *					16-16.5 (15-15.5) (-) *		14.5-32.5 *	
67578		6 (5)	30 ?	29	33	12 (8)	9 (>3) (-)	9 (6) (3.5)1)-)-)	19 (17) (3)1.5)	20 (9)	31	
Cearagryllus microcephalus												
Martins-Neto, 1991c			22 *								32-38 *	
67577		5 (2.5)	25.5	32 (11)	35	7.5 (9)			18 (19)	18 (9)	36	6.5
Cearagryllus robustus												
67580			21	25	28	8 (3.5-6)				13 (7)		5
												<del> </del>

Appendix II Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
												<u> </u>
Cearagryllus gorochovi												
67581		3.5(3.5)		>24 (>7)		7 (5)						1
												-
Caririgryllus brachypterus												-
66687		1 (1.6)	6		8	3 (2.2)	2 (-) (-)	2 (-) (-)	4.2 (-) (-)	3 (2)	3.8	3.8
Gryllotalpidae												
Cratotetraspinus fossorius												
66490		2	13		12	6 (4)	4 (2) (1)0.5)0.7)	5 (2.8) (1.4)0.3)0.7)	8.5 (5) (2)0.2)1)	7 (4)		>3
66496		1.5	16			7 (4)			8 (5.5) (2)	9 (4)		
67590		1.5	16		18	8 (4.5)			9.5 (5.5) (2)0.2)1.2)	8 (4.5)		5
Locustopseidea												
Zessinia vikingi												
66499+66692				34.5 (5)								
Cratozeunerella												
unknown species												
67586				34 (4.5)	24				? 12 (>8) (-)			
Cratozeunerella godoii												
67588			20 ?	24 (4)	25	7 ?			11.5 (>6) (-)	13 (3.6)		
												<del>                                     </del>
												丄

Appendix II Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
Araripelocustidae												
Araripelocusta longinota												
66509		2.5 (5)	14	26 (4.5)	26?	6 (6.5)			11 (9)-)-)	8 ?		+
unknown species												<del>                                     </del>
67587		2 (4)	17	21 (3)	19	6 (5)				11 (4)		
67589		3 (4)		22 (4)	20	9 (7)						
Tridactylidae												
Cratodactylus ferreirai												
Martins-Neto, 1990b			5-9.5 <mark>α</mark>			2.5-4.5 (-) α			3-6 (-) (-) α	2.5-5 α		
66489			13	7 (2)		5 (4)			7 (-) (-)	8		
66495			9.3			4.5 (3)		2 (2) (0.3)0.5)	5 (-) (-)	4.8	1.5	1.8
Cratodactylus kellneri												
Martins-Neto, 1990b			5-8 α			1.5-2 <mark>α</mark>			3.5-6 (-) (-) α	3.5-6 <mark>α</mark>		
66494	>1.2	0.8 (0.7) ?	6			2.8 (2)	0.5 (0.6) (0.35)0.09)	1.2 (-) (-)	4.5 (-) (-)	3.2 (1.8)	2	
66688	2	0.8 (1.5)	6			1.5 (2)		2 (1.6) (0.3)0.4)	4 (-) (-)	4.1	2.3	0.6
66689			6			2 (1.8)			4.5 (-) (-)	4	2	
unknown species												
66493	0.9	0.8 (0.8)	4		4	1.3 (1.5)	0.6 (0.6) (0.15)0.35)	1 (0.5) (0.25)0.1)	3.8 (-) (-)	2.5	1.4	
66504	2.3	0.8 (0.5)	4			1.3	1.2 (1) (-)	1.5 (1) (-)	2 (1.8) (0.7)	2.5		

Appendix II Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
Bouretidae												
Bouretia elegans												
66487		8 (5)	28		46.5	8? (8)	10 (6) (2)-)-)	10 (5.5) (4.5)-)-)	28 (27) (3)2.5)-)	20 (10.5)		
67585		6.5 (3)		41	41?	10 (6)		10 (4.3) (2.3)-)-)	>21 (-) (-)	X (7)		
Elcanidae												
Cratoelcana zessini				22-31.2 (5.2-7.2)								
Martins-Neto, 1992				B (3.2-7.2)								
66492		8 (3.8)	30	41 (6)		13 (9)	7 (5)	6 (5.5) (-)	16 (17)	17 (8)		
66500	42	4 (1.5)	13	27 (5.8)		4.5 (5)	4 (4.5) (1.7)0.5)1.3)	Tarsus (1.5)0.5)1)	11 (11) (3.5) -	8.5 (5.5)	12	
66566	66	6 (2)	14	28 (6.2)		6 (6)	5.3 (5) (1.7)0.2)1.5)	5 (5) (1.5)0.5)1)	12 (11.5) (3)1.5)	8 (6)	>3	
67584				23 (5)	19 (8)				Femur 12			<u> </u>
Cratoelcana damianii												
Martins-Neto, 1992				9.5-14 (2-3.9) ß								
66491	36		9	15 (2.8)		4?(4)	4 (3.5) (1.5)0.3)1)	6 (4) (1.5)-)-)-)	11 (8) (2)1)	5(4)	12	2.3
66498	21	3.5(1.2)	6	13.5(3)		2.5(2.5)			6 (5) (2.7)1)	3.5(2.5)	>5	
66690	18	3(1.5)	6.5	13(3)		2.5(2.8)	X (1.7) (0.7)0.2)0.8)		6? (5) (1.7)1)	4(2.5)	5	<u> </u>
66503 (not sure)	15	1	4	7 (1.3)		1.5 (1.5)	1.2 (1.3) (0.4)0.2)0.6)		3.5 (3) (1.2)0.8)	2.5(1.3)		

Appendix II
Body size of Mantodea and Orthoptera, data: \* After Martins-Neto 1991c; α After Martins-Neto 1990b; β After Martins-Neto 1992.

Body Size: mm (long/wide)	Antenna	Head	Body length	Forewing	hind Wing	Thorax	Foreleg; fem (tib) (tar)	mid Leg; fem (tib) (tar)	hind Leg; fem (tib) (tar)	Abdomen	Ovipositor	Cerci
Hagloidea												
66481		3 (3)?	24	31 (5.5)	30	7 (6)	6 (8.5) (0.7)0.8)0.8)0.7)2.5)	6 (-) (-)	11 (9) (1.3)1)1.2)1)3)	17 (8.5)	3	
66482	19	2.5(6)	17.5	24 (3)	24	5.5 (5)	4 (5) (0.5)0.7)0.7)0.5)1.2)	Tarsus (0.7)0.7)0.5)0.5)1.3)	8 (6) (0.8)0.5)1)0.5)1.8)	12 (5.5)	2	
67582			18.5	29	29	5.5(5.5)		5 (5) (0.7)1)0.7)0.5)2)	11.5 (8.5) (1)1)1)0.5)2.5)	13 (8)		
extra (no number)	66	5(4)		33 (10)	30 (9)	10(9)	8 (6) (1.8)1.2)0.5)1.5)	8 (-) (-)	15 (11.5) (3)1.5)1.8)2)			
												-
problematic												+
Locustopseidae												
66497			16?	22 (4.7)		7(8)	5 (4.5) (1)0.5)1.5)		12.5 (10.5) (4 totally)			
67575+67576			>20	25?	25?	9 (7)				11 (3.8)		
unknown												
66479	18	7 (5)	20		36	5 (6)	8 (7) (3)1)1.5)	10 (-) (3.5)1)-)	20? (19.2) (4.7)1.5)1)	15 (8)	35	
66480	38	4 (7)	32		35	10 (9)	9 (8) (-)	10 (8) (2)-)-)	15 (12) (3.5)1.8)2.5)	22 (11)		3?
66502			>6.2	10 (3?)	11	>2 (2)			5.7 totally	4.2 (1.8)	>2	