

Taxonomic diversity of cockroach assemblages (Blattaria, Insecta) of the Aptian Crato Formation (Cretaceous, NE Brazil)

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Abstract: A comprehensive revision of 981 specimens of fossil cockroaches from the Lower Cretaceous laminated limestones of the Crato Formation of Northeast Brazil shows that they belong to eleven taxa, including *Piniblattella limai*, *P. magna* sp. n., *Perlucipecta santanensis* sp. n., *Raptoblatta waddingtonae*; *Ocelloblattula santanensis* sp. n., *Elisama brevis* (= *E. americana*, syn.n.), *E. hindwingii* sp. n., *Ponopterix axelrodi* (= *P. maxima* syn.n.), *Umenopterix burkhardi* comb. n., and *Cratovitisma oldreadi* (Umenocoleidae=Cratovitismidae syn.n.=Ponopterixidae syn.n.). The family Ectobiidae is numerically most abundant in the assemblage of cockroaches of the Crato Formation (83 % of cockroaches), followed by Blattulidae (13 %) and Umenocoleidae (4 %). 79.2 % of specimens are complete and fully articulated. Members of the family Alienopteridae are probably also present. Representatives of a relatively common Mesozoic superfamily Caloblattinoidea are missing. With the exception of the endemic genera *Cratovitisma* and *Raptoblatta* and the exclusively Gondwanan genus *Ocelloblattula*, all other genera were cosmopolitan. Taxonomic richness of cockroaches of the Crato Formation is thus rather low, and consists of geologically long-ranging and geographically-widespread genera, genera restricted to Gondwana, and short-ranging endemic genera found in the Crato Formation only.

Keywords: Fossil insects, new species, Blattodea, variability, taphonomy, Mesozoic, Early Cretaceous, Gondwana.

Introduction

Cockroaches, mantises and termites represent the traditionally monophyletic Dictyoptera (Hennig 1981; Grimaldi & Engel 2005; Djernaes et al. 2012, 2015; Bai et al. 2016), originating in the Late Carboniferous (Zhang et al. 2012) and being numerically abundant during the Palaeozoic (Schneider 1977; 1978a, b; 1980a, b; 1983; 1984; Schneider & Werneburg 1993). In the Mesozoic, both termites (Isoptera) and mantises (Mantodea) evolved by the pattern (Mantodea+ (“Blattaria”+Isoptera)) (Grimaldi 2007) or independently originated from the cockroach family Liberi-blattinidae (Vršanský 2002; Vršanský & Aristov 2014; Vršanský & Bechly 2015). Cockroaches possessed diverse life habits (Barna 2014) and played an important ecological role as decomposers in the present and past (Zherikhin 1993; Vršanský et al. 2013).

Exceptionally-preserved insects dominate both in abundance and taxonomic diversity in the fossils of the Crato Formation. More than 350 species representing over 20 insect orders have been described, with terrestrial adult orthopterans, hemipterans, ephemeropterans and odonatas (Menon & Martill 2007; Bechly 2007b; Heads & Leuzinger 2011; Barling et al. 2015). Three mantises and six termite species have been described so far (Bechly 2007c; Hörnig et al. 2013; Lee 2014), but about a quarter of the arthropod specimens from the Crato Formation are cockroaches

(Bechly 1998; Menon & Martill 2007; Dittman et al. 2015; n=3,651), with only dozens of species described. The aim of this study is the revision of cockroaches from the Crato Formation, including older descriptions.

Geological setting

The Crato Formation is situated in the north central part of the Chapada do Araripe (Fig. 1), a large plateau in north-eastern Brazil (Martill & Bechly 2007). The formation is an up to 60 m-thick, mixed carbonate-siliclastic sequence dominated in the middle part by laminated micritic limestones, interbedded at the base with claystones, siltstones, and sandstones (Martill & Heimhofer 2007; Barling et al. 2015). The limestones from this location contain gymnosperms and angiosperms, invertebrate fauna with Chilopoda, Arachnida, Crustacea and Insecta, and vertebrate fauna including fish, anurans, turtles, lizards, crocodiles, pterosaurs and birds (Menon & Martill 2007). These fossils occur in the lowermost member of the Crato Formation, namely in the Nova Olinda Member, with an age of ~120 million years, which corresponds to the Aptian stage (Martill 2007; Martill & Heimhofer 2007). Chapada do Araripe was located at 10° to 15° S within the tropics during the Early Cretaceous (Martill 2007). The depositional environment of the Nova Olinda Member was a lake/lagoon water body with water-

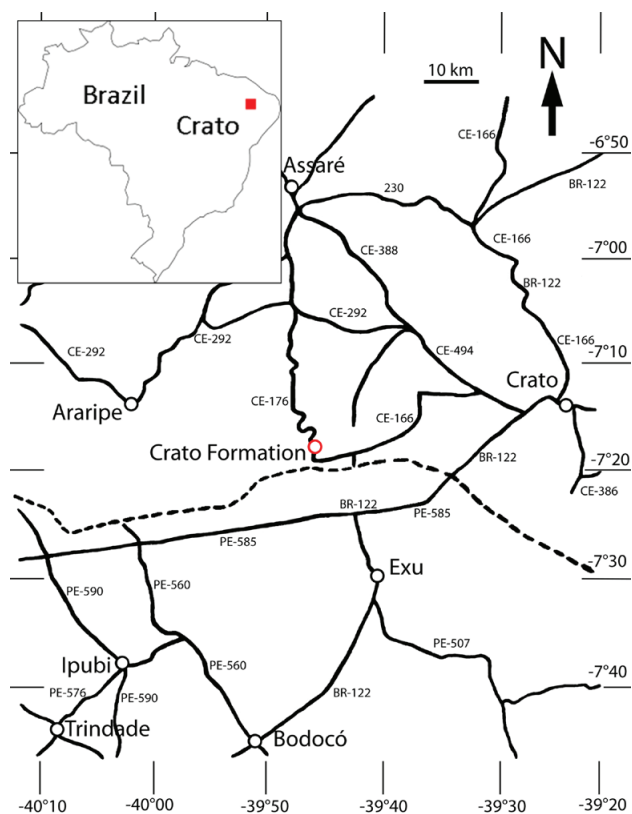


Fig. 1. Location of the Crato Formation (7°19'00" S and 39°40'40" W).

column stratification and bottom-water anoxia allowing exceptional fossilization, with still unclear salinity conditions. Hypotheses range between a freshwater and a brackish lake up to a hypersaline lagoon (Martill & Bechly 2007). Among the fossils of the Crato Formation, insects dominate. According to a large-scale investigation (Bechly 1998; Menon & Martill 2007; Dittman et al. 2015; $n=3651$), about 26 % of arthropod specimens are cockroaches. However, only a dozen cockroach species were reported in the Crato Formation, including some unnamed species and species based on a few specimens (e.g., *Cratovitisma oldreadi* Bechly, 2007; "*Ponopterix*" *burkhardi* Nel, Prokop et Kirejtshuk, 2014; *Raptoblatta waddingtonae* Dittman, Hörnig, Haug et Haug, 2015). Thousands of specimens belong to three dominant species, *Ponopterix axelrodi* Vršanský et Grimaldi, 1999a, *Elisama brevis* (= *E. americana*) Mendes, 2000, and *Piniblattella limai* (Pinto et Purper, 1986; Pinto, 1989) (Vršanský 2004; Bechly 2007a). Using the taphonomic categories of specimen preservation by Martins-Neto & Gallego (2006), about 79.2 % of specimens described here belong to Stage I, 18.8 % belong to Stage II, and 2 % belong to Stage IV. These proportions are in contrast to the results of Martins-Neto (2006), Martins-Neto & Gallego (2006), and Martins-Neto & Tassi (2009) who found that different genera show various preservation states on the basis of large scale field data.

Material and methods

The drawings 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 and 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 Synchroscope Auto-Montage™ software. All figures have been subsequently edited with the Adobe Photoshop™ CS3 imaging software.

Differences between the right and left side of the wings within the same individual were examined. The nomenclature for fore- and hind wings is based on Kukalová-Peck (1991) and Carpenter (1992). Abbreviations used: 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, JP — jugal posterior and the nomenclature used for cockroaches, RA+RP+MA would be R+RS in the system of Comstock & Needham (1898).

The total number of species is interpreted from the two collections, including (1) MSF, Fossils Worldwide, Annesuse Raquet-Schwickert Hebelstrasse 4 D-67734 Sulzbachtal, Germany, with 933 specimens, and (2) SMNS, Staatliches Naturkunde Museum Stuttgart, Germany, with 48 specimens that were used in the systematic analysis.

Results

Systematic palaeontology

Order: Blattaria Latreille, 1810

= Blattodea Brunner von Wattenwil, 1882

Superfamily: Umenocoleoidea Chen et T'an, 1973

Family: Umenocoleidae Chen et T'an, 1973

2007 Cratovitismidae syn.n. — Bechly, 239–249.; synonymization is based on the revision of the *Cratovitisma* below.

2014 Ponopterixidae syn.n.=derived as Ponopterixiidae — Nel, Prokop et Kirejtshuk, 2014 (=Vitisminae Vršanský et Ansoerge, 2001 eventual jun. syn., in which case derived as Vitismidae Vršanský et Ansoerge, 2001 according to ICZN principle of coordination for family-group names); synonymization is based on the description of *Umenopterix* (see below) and its affinities to *Umenocoleus*.

Monophyletic beetle-like lineage with families Umenocoleidae and Alienopteridae Bai et al., 2016, stemming from Vitisminae. The representatives of this family are known since the earliest Cretaceous of Siberia (Vršanský 2003a).

Emended description (after Vršanský (2003a)): Small (mostly under 20 mm), beetle-like cockroaches with head

which can be derived and globular (eventually orthognathous); antenna with wide segments and very long setae in transversal rows; pronotum with paranota tending to reduce; with legs eventually short and strong. The most characteristic are heavily sclerotized forewings with reduced venation and with the presence of cup-like cells. Hind wing venation generally of early polyphagoid form (that is 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 hairs; females with short external ovipositor. Species are most probably diurnal with similar flight activity of both males and females because of the same body size, with sexual dimorphism not much pronounced.

Genus: *Cratovitisma* Bechly, 2007
Cratovitisma oldreadi Bechly, 2007 (Fig. 2)

Diagnosis (improved after Bechly 2007a): Body length of 6.9 mm, forewing length 5.3 mm. As in *Vitisma*, the forewings are broader than in *Ponopterox* (max. 2 mm wide), strongly sclerotized. The vein CuP seems to be strongly curved and delimits a typical cockroach anal field in the forewings. The hind wing venation is similar to that of *Vitisma*, thus more dense and round than in *Ponopterox*, and with pterostigma. The transverse head seems to place this new genus and species closer to standard Umenocoleidae than

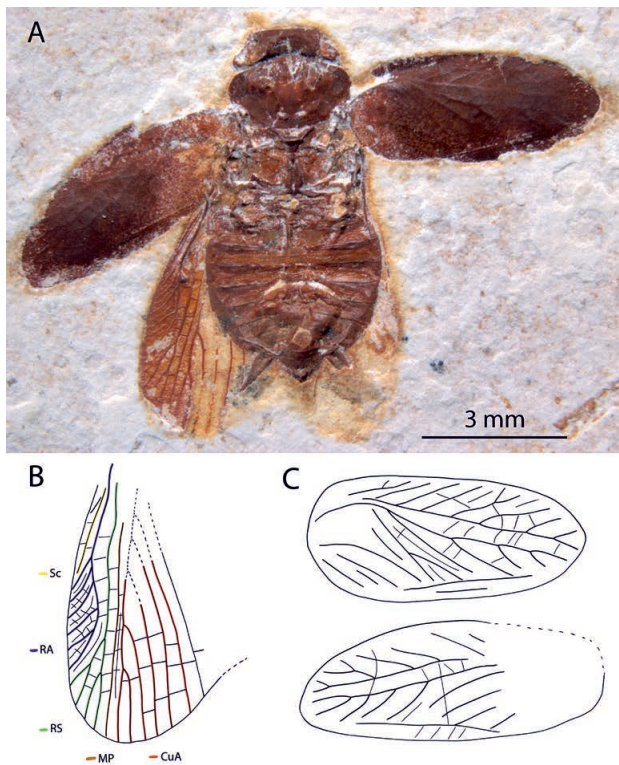


Fig. 2. *Cratovitisma oldreadi* Bechly, 2007, holotype; SMNS 66000-127. **A** — Habitus. **B** — Hind wing. **C** — Right and left forewings.

Vitisma (which is also now proved to belong to Umenocoleidae based on the amber record).

Emended description: The head is transverse as in Umenocoleidae (different from *Vitisma* type) and the antennae are also similar to Umenocoleidae, thus shorter than the body. The pronotum is flat and disk-like as in *Jantaropterox* Vršanský et Grimaldi in Vršanský (2003a), *Vitisma* and true cockroaches, very different from *Ponopterox* and *Umenocoleus*. Forewing, Sc bifurcated, Radius with eight branched, M with five to six branched, CuA similar with Genus *Ponopterox* to have a single terminal fork, CuP strongly curved and delimits a typical cockroach's 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 *Ponopterox 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 Umenocoleidae species in the Crato Formation, also clearly shorter than that in *Elisama brevis* (= *E. americana*) (Blattulidae).

Genus: *Ponopterox* Vršanský et Grimaldi in Vršanský (1999a)

Ponopterox axelrodi Vršanský et Grimaldi in Vršanský (1999a); 2003a (Fig. 3)

1999 *Ponopterox axelrodi*. — Vršanský et Grimaldi, 167–176.

2007 *Ponopterox maxima*. — Bechly, 239–249 syn. n.; synonymization is based on the revision below.

Emended description: Body 5.0 to 8.0 mm long. Head spherical, 1.8 to 3.0 mm wide. Antenna about the same length with body, 7.1 to 8.3 mm long, the first three segments elongate, the others very short. Forewing 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. Hind wing pterostigma present, 5.2 to 6.3 mm long, is almost the same length as the forewing. 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. Legs cursorial, heavily mounted with spurs. All tarsi 5-segmented. Female with external ovipositor at least 0.67 to 0.9 mm long, is approximately 10 %–12.12 % of body length. Male with distinct styli and with phallomere of a primitive type. Cerci placed closer to each other than in the female. Cercus 0.7 to 1.5 mm long, with 11–13 segments.

Description of other specimens: SMNS 66326 (Fig. 3D) — Male. Hind wing well preserved. SMNS 66329 — Female. Ventral view. Compound eyes well preserved. Abdominal segments clearly. SMNS 66334 (Fig. 3K) — Probably male. Hind wing only partly visible. SMNS 66335 — Female. Ventral view. Abdomen swelled. SMNS 66336 (Fig. 3L) — Male. Forewing venation visible, varies between right and left sides. Hind wing RA with four-branched and RS with two stem-branches. SMNS 66338 (Fig. 3N) — Female.

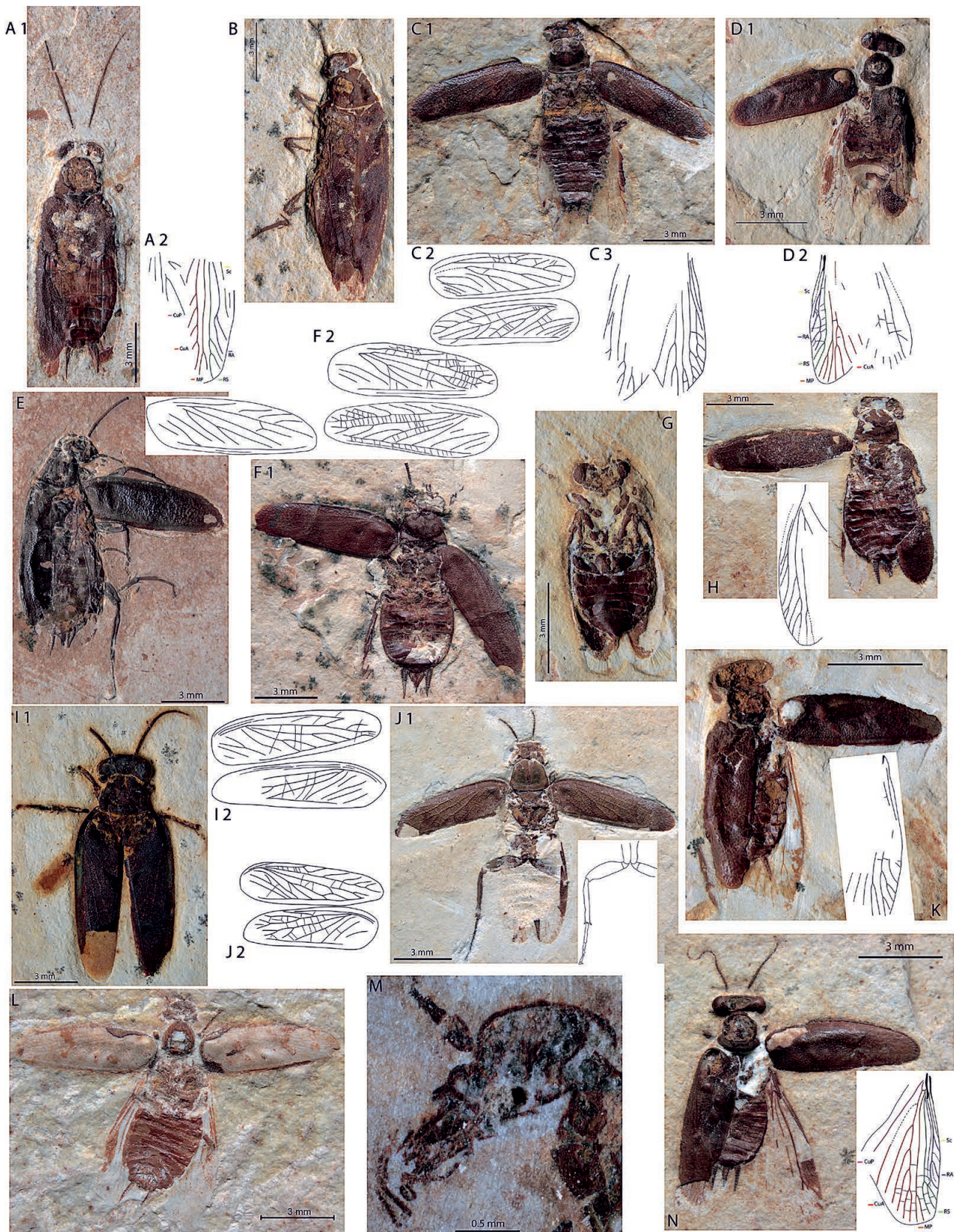


Fig. 3. *Ponopterix axelrodi* Vršanský et Grimaldi, 1999 (= *Ponopterix maxima* Bechly, 2007). **A** — SMNS 66323. **B** — 66324. **C** — 66325. **D** — 66326. **E** — 66327. **F** — 66328. **G** — 66329. **H** — 66331. **I** — 66332. **J** — 66337. **K** — 66334. **L** — 66336. **M** — 67574. **N** — 66338.

Hind wing preserved completely. Cerci and ovipositor clearly visible.

Remarks: *Ponopterix axelrodi* differs from *Ponopterix maxima* Bechly, 2007 by the smaller 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 (although this variability is not significant because it can also be found in the same species). However, on the basis of the similarity of fore- and hind wings and on the basis of a gradual transition in body size between *P. axelrodi* and *P. maxima*, (Table 1), I conclude that these two species belong to a single species.

Emended description of specimens categorized to *Ponopterix maxima* Bechly, 2007: Body 7.5 to 12.5 mm long. Antenna at least 6 mm long and about half of body length. Head broader than in *P. axelrodi*, especially between the compound eyes; pronotum comparatively larger and broader and saddle-shaped. Forewing 6.4 to 10.5 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, generally 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, 2nd, 3rd and 5th segments about the same length and the 4th segment extremely short. Female with external ovipositor at least 0.8–1.3 mm long, about 7.84 %–12.26 % of body length. Cercus in roach form, 12 to 16 segments.

Description of other specimens: SMNS 66323 (Fig. 3A) — Male. Length of the antenna is about ½ of the body length. Large compound eyes. Hind wing only partly visible. SMNS 66324 (Fig. 3B) — Lateral side. Femur of three legs well preserved. SMNS 66325 (Fig. 3C) — Male. Venation of both forewings clearly preserved. Hind wing with pterostigma and large part of venation identifiable. SMNS 66327 (Fig. 3E) — Female. Legs well preserved, tarsus with five segments, first segment elongated, 2nd, 3rd and 5th segment about the same length, 4th segment extremely short. Abdomen swelled. SMNS 66328 (Fig. 3F) — Female. The venations of both forewings clearly visible. Ovipositor and cercus well preserved. SMNS 66330 — Female, ventral side. Legs well preserved especially in femur and coxa part. SMNS 66331 (Fig. 3H) — Female. Forewing heavily sclerotized, venation reduced. Hind wing partly preserved. SMNS 66332 (Fig. 3I) — holotype. Compound eyes well preserved. The venations of forewings clearly visible. SMNS 66333 — Female. Head broader than the other specimens. Fore and hind wings only partly preserved. SMNS 66337 (Fig. 3J) — Male. Venation of forewings clearly visible. Hind leg well preserved, including coxa part. 66562 — Female. Forewing clearly. Abdomen swelled. Cercus and ovipositor well preserved. SMNS 67574

(Fig. 3M) — Probably male, lateral side. Mouthpart well preserved, maxillary palps and labia palps visible.

Genus: *Umenopterix* gen. n.

Type species: *Ponopterix burkhardi* Nel, Prokop et Kirejtshuk, 2014

Diagnosis: The pronotum fully developed, standard, transversal with fully developed paranotalia. CuP strongly sigmoidally curved.

Description: as for species (see Nel et al. 2014).

Derivation of name: Named after family Umenocoleidae and Genus: *Ponopterix*.

Remarks: The genus apparently represents an early offshoot of the family, descending from taxa close to the type genus *Umenocoleus*, which also has unique sigmoid curvature of the clavus (including *U. nervosus*, see Zhang 1997). This character was the sole argument against the categorization of *Umenocoleus* within cockroaches, but the present genus fully valid categorization (of the whole family) within Blattaria. The above inference is also supported by the “standard” morphology of round, transversal pronotum, with fully developed paranotalia — a character lost in all “Petropterix” lineages, but retained in the second lineage represented by *Vitisma* and to some extent by *Jantaropterix*. Therefore, the present species must be placed in a new genus, whilst any relation with *Ponopterix* is unlikely, but these characters unequivocally support the assignment of this species (and also *Umenocoleus* as the type of the Umenocoleidae) within cockroaches.

**Superfamily: Corydioidea Saussure, 1864
(Brues & Malander, 1932)**

(=Polyphagoidea Walker, 1868) (Princis, 1960)

Family: Blattulidae Vishniakova, 1982

=Araripeblattidae Mendes, 2000 syn.n. (synonymization based on the paragraph below)

Type genus: *Elisama* Giebel, 1856.

Remarks: The family originated in the Late Triassic. It represents a dominant cockroach family at many sites ranging from the Early Jurassic to the Early Cretaceous for more than 100-million years (Wang et al. 2007a,b).

Genus: *Elisama* Giebel, 1856

= *Ctenoblattina* Scudder, 1886 (Vršanský 2005a–c)

= *Araripeblattula* Mendes, 2000 syn.n.

Type species. *Blattidium molossus* Westwood, 1854

***Elisama brevis* Mendes, 2000 comb.n.** (Fig. 4)

2000 *Araripeblattula brevis* — Mendes, 23–35.

2000 *Blattopteris beckeri* — Mendes=*Araripeblattula beckeri* Martins-Neto et al., 2010

2010 *Araripeblattula cesae* — Martins-Neto et al., 2010

2002 *Elisama americana* — Vršanský, 1–16.

Table 1: Body length Frequency distribution 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 and shows no sexual dimorphism.

Body size range (mm)	6.0–6.5	6.5–7.0	7.0–7.5	7.5–8.0	8.0–8.5	8.5–9.0	9.0–9.5	9.5–10.0	10.0–10.5	10.5–11.0	11.0–11.5
Specimen No.	1	2	1	1	2	2	0	1	2	3	2

Emended discussion (after Martins-Neto et al. 2010): the family Araripeblattidae differs from Blattulidae Vischniakova, 1982, the closest family, by contact points of first RA branch with the anterior wing border (RA1-ending), MA2-origin, and contact of CuP with the posterior wing border (CuP-ending) are arranged in one line slightly transverse to the wing long axis. In Blattulidae, the point of MA2-origin is situated slightly backward of the line RA1-ending and CuP-ending (see also Martins-Neto et al. 2005). However, this main difference does not apply to this study. Apart from the lines from RA1-ending, MA2-origin and CuP-ending of *Araripeblatta brevis* variant, both intra-specific (even between right and left forewings in the same specimen) and interspecific (Fig. 5A–K), there are no significant differences 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. 5L–O). *Araripeblatta* is here considered a junior synonym of *Elisama* and belongs to family Blattulidae. Indeed this RA1-MA2-CuP lines are clearly different but between Blattulidae and *Piniblattella limai* (= *Mesoblattina limai*) (Ectobiidae) (Fig. 5P–S).

Differential description: *Elisama brevis* differs from *Piniblattella limai* by smaller body size. It is similar to genus *Ocelloblattula* Anisytukin et Gorochov, 2008 (Blattulidae) and other primary Upper Jurassic family Caloblattinidae Vršanský et Ansoerge, 2001 by head with three ocelli residing in the forehead between the compound eyes (Anisytukin & Gorochov 2008; Vršanský 2008a). The ovipositor of *E. brevis* (about 10.13–16.67 % of body length) is tendentious convexer than that in Umenocoleoidea both species in the Crato Formation (by *P. axelrodi*: 10–12.12 % and by *P. maxima*: 7.84–12.26 %), and still clearly longer than that in *Cratovistima* sp. (SMNS 66000-127 by 7.89 %).

Emended diagnosis and description: Small-sized roaches. Antenna about the same length as body. Body length between 7.9–9.5 mm. Head wide and clearly longer than the fore margin of pronotum. Pronotum is about 1.5 times wide as the head, approximately of round shape, except in the posterior part where it is sharp gradually. Forewing 8.0–10.2 mm long and 2.4–3 mm wide. Sometimes slightly sclerotized. It is possible that coloured band pattern reduced accompanies with the degree of sclerotization. Wing fore margin arcuate basally, almost straight further. Costa area as wide as subcosta area. Sc very short, not reaching the apical third of a wing. RA+RS with total of 13–16 branches, instead of ten. M with three–four branches. CuA with four–six branches, rarely seven (SMNS 67572 right side, Fig. 4J), CuP extremely curved and Anal veins reach the hind margin. Hind wing

about the same length as the forewing and 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, Fig. 4F), CuP should be alone and probably reaching the end of the wing. Fore and hind wings show very low morphological differences (Tables 2, 3). Legs presented long and strong spines. Tarsus normally has all five segments. Abdomen in female is tendentious more 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 unsegmented styles.

Description of other specimens: SMNS 66000-125 (Fig. 4A) — Male. Eye big, place by the side of the head and area in-between is large. Pronotum is about 1.5 times as wide as head, nearly rounded, except in the hind part sharp gradually. SMNS 67563 (Fig. 4C) — Female. Forewings sclerotized. Hind leg has long and strong spines. Ovipositor present. SMNS 67564 (Fig. 4G) — Female. Large compound eyes well preserved. Fore and hind legs tibia with several long, thin spines. Terminalia with unsegmented styli. SMNS 67565 (Fig. 4I) — Female. Pronotum sclerotized, nearly rounded and about 1.5 times long as head width. Forewing sclerotized. Abdomen rounded. Ovipositor short, well preserved. SMNS 67566 (Fig. 4F) — Female, with the complete and unfold fore and hind wings. SMNS 67567 (Fig. 4H) — Female. Hind wing in the anterior margin, that is RA area, sclerotized, or that is pterostigma. Abdomen rounded. Ovipositor sharp. SMNS 67568 (Fig. 4E) — Female. Antenna about the same length as the body. Mid and hind legs tibia with several long, strong spines. SMNS 67569 (Fig. 4D) — Female. Pronotum is about 1.5 times as wide as the head, nearly rounded, except in the hind point sharp. Mid leg femur with several short spines. SMNS 67570 (Fig. 4K) — Female. Abdomen swelled. Ovipositor and cerci well preserved. SMNS 67571 (Fig. 4B) — Female. Abdomen rounded. Cerci with numerous sensilla. SMNS 67572 (Fig. 4J) — Female, with the complete and unfold fore and hind wings. Full length mid leg is preserved, tarsus with five segments with pretarsus, the lengths are probably 0.9, 0.6, 0.2, 0.2 and 0.3 mm, five segments with total of 1.8 mm long.

Elisama hindwingnii sp. n. (Fig. 6A)

Holotype: SMNS 67573.

Derivatio nominis: Name partially referring to well preserved hind wings.

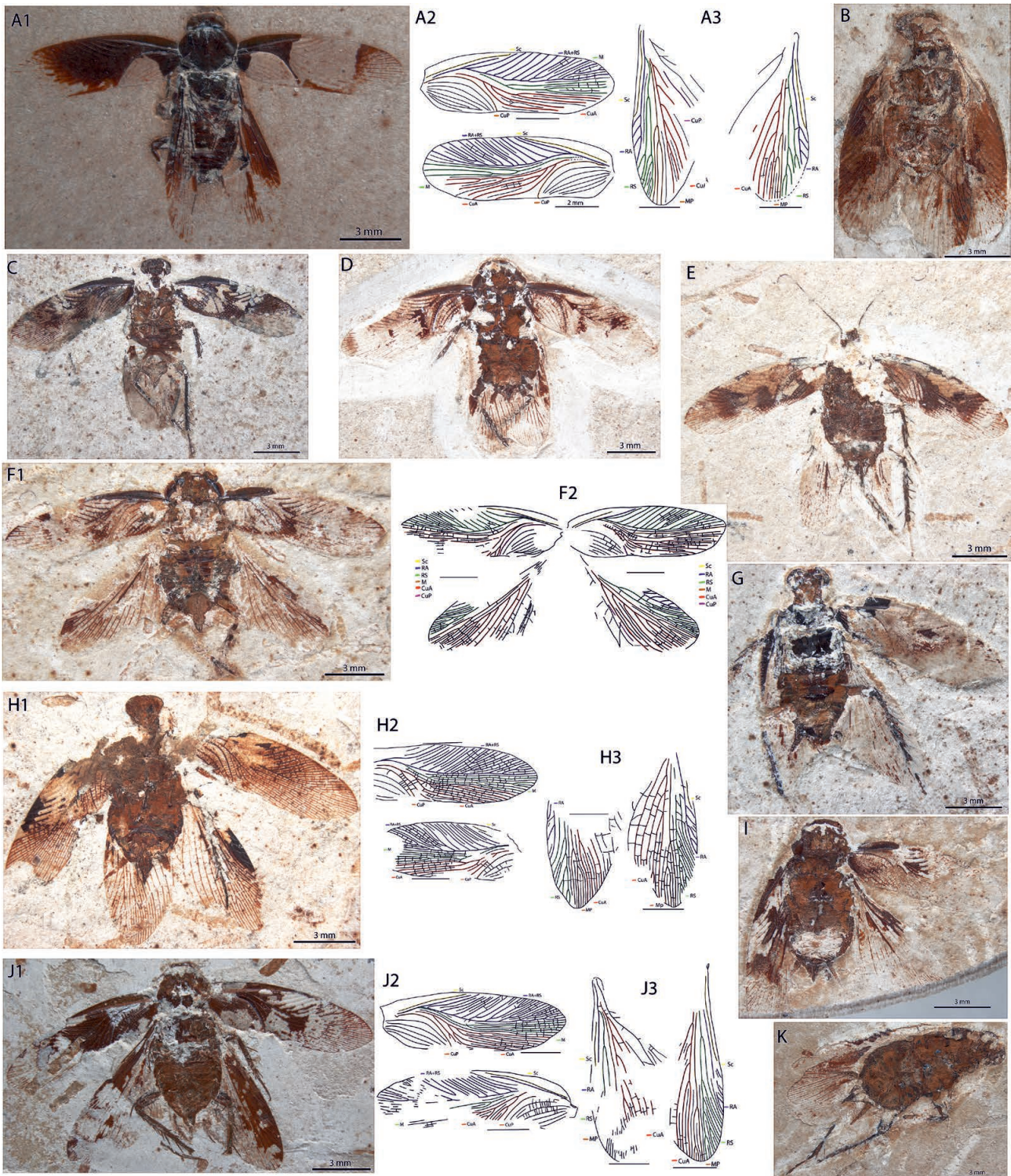


Fig. 4. *Elisama brevis* Mendes, 2000. **A** — SMNS 66000-125. **B** — 67571. **C** — 67563. **D** — 67569. **E** — 67568. **F** — 67566. **G** — 67564. **H** — 67567. **I** — 67565. **J** — 67572. **K** — 67570.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, North-East Brazil.

Differential diagnosis: Forewing at least 12 mm long. Hind wing, except with probably slightly larger size

otherwise very similar to *E. 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 *E. tsaganica* Vršanský, 1999b 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

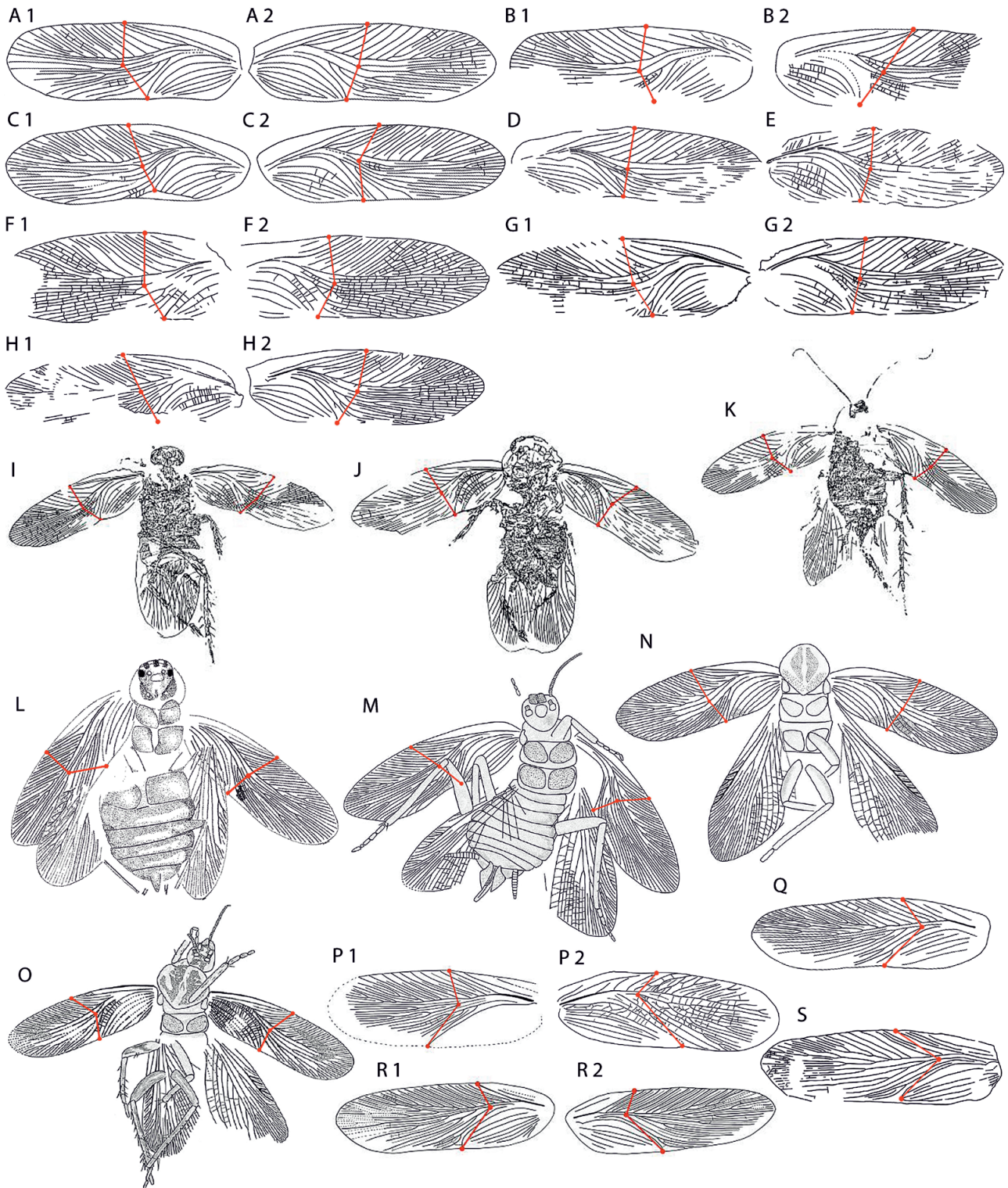


Fig. 5. The line RA1-ending, MA2-origin and CuP-ending. **A–K** — *Elisama brevis*. **L** — *Elisama parallela*. **M** — *E. extenuate*. **N** — *E. cuboides*. **O** — *Habroblattula drepanoides*. **L–O**: After Vršanský 2003b; Wang et al. 2007a, b. redrawn here; **P–S**: *Piniblattella limai* (Pinto et Purper, 1986). Not to the same scale.

seven, MP two to four, CuA four to seven, CuP simple and A1 two to four branches). Later two morphological differences between *E. parallela* and *E. tsaganica* are not diagnostic, and can present sexual dimorphism (Vršanský 2003b).

Description: Forewing 12 mm long and much close to *E. parallela* both in size and form. Forewing detail unknown and is not less than 12 mm long and 4.2 mm wide. Hind wing Sc alone, reaching less than $\frac{1}{2}$ length of the anterior margin,

Table 2: Forewing venation variability of *Elisama brevis* Mendes, 2000.

SMNS	Forewing		(Right/Left)					Total
	SC	RA+RP	M	CuA	CuP	A		
66000-125	1/1	13/12	3/3	4/6	1/1	7/6	29/29	
67564	1	15	4	6	1	6	33	
67565	1	14	3	4	1	6	29	
67566	1/1	13/14	3/3	5/6	1/1	7/8	30/33	
67567	1/1	14/14	4/3	6/5	1/1	5/5	31/29	
67572	1	16	3	6	1	6	33	

Table 3: Hind wing venation variability of *Elisama brevis* Mendes, 2000.

SMNS	Hind wing		(Right/Left)				Total
	SC	RA	RS	MP	CuA		
66000-125	1/1	4/4	6/6	3/3	6/6	20/20	
67564	1	5	7	3	6	22	
67565	1/1	4/4	6/6	3/3	6/6	20/20	
67566	1/1	6/5	6/6	3/3	6/7	22/22	
67567	1/1	5/4	7/7	3/3	6/6	22/21	
67571	1	5	6	3	6	21	
67572	1	4	7	3	6	21	

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 the wing characters and its large size, this specimen is a representative of the genus *Elisama*, but does not belong to *E. brevis*, very similar is also the hind wing of genus *Kridla* Vršanský, 2005.

Remarks: *E. hindwingnii* sp. n. is similar to *E. parallela* both in size and form. Generally the hind wing is larger than in other species of the genus.

Differential description: It 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). It differs from *Elisama fragmentaria* Vršanský, 2005 by larger size of hind wing (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 2005b,c). It differs from *Elisama brevis* Mendes, 2000 by larger size of hind wing (in *E. brevis* 8.5–10 mm long) and wing venations (in *E. brevis* Sc alone, RA four to five, RS six to seven, MP three and CuA six branches). It differs from *Habroblattula drepanoides* Wang, Liang et Ren, 2007 from Liaoning, China by hind wing of 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).

Character of preservation: Only one pair complete and nearly unfolded hind wing preserved.

Genus: *Ocelloblattula* Anisyutkin et Gorochov, 2008

Type species: *Ocelloblattula. ponomarenkoi* Anisyutkin et Gorochov, 2008.

Stratigraphic range: Hauterivian–Aptian.

Geographic range: Gondwana.

Ocelloblattula santanensis sp. n.

Holotype: SMNS 66558

Derivatio nominis: Named after the city of Santana do Cariri near the type locality.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, North-East Brazil.

Diagnosis: This species is very similar to *Elisama brevis* both in size and form, it differs from the forewing preserved with a distinctly band colour pattern (Figs. 6, 7), these discontinuous markings suggest membership of the genus *Ocelloblattula* Anisyutkin et Gorochov, 2008 (family Blattulidae). Head with very large and globular compound eyes, probably three ocelli (SMNS 66558, Fig. 6C) reside in the forehead between the compound eyes.

Description: Small size roaches. Antenna about the same length as body. Body length between 7.9–8.2 mm. Head wide and clearly longer than the fore margin of pronotum. Pronotum is about 1.5 times wide as the head, approximately of round shape, except in the posterior part where it is sharp gradually. Forewing is morphologically very similar to *Elisama brevis* (Table 4), 8.0–8.9 mm long and 2.4–2.7 mm wide and shows rust red colour. Foreleg tibia is about the same length as tarsus.

Superfamily: Blattoidea Latreille, 1810

Family: Ectobiidae Brunner von Wattenwyl, 1865
(=Blattellidae Karny, 1908)

Genus: *Piniblattella* Vršanský, 1997

Type species: *Mesoblattina vitimica* Vishniakova, 1964

Composition: *Piniblattella sharingolensis*, Vršanský, 2005; *P. minuta* Vršanský, 1997.

Stratigraphic range: (probably Berriasian) Hauterivian–Albian.

Geographic range: Cosmopolitan.

***Piniblattella limai* (Pinto et Purper, 1986) (Fig. 8)**
1986 *Mesoblattina limai*. — Pinto et Purper, 6–10.

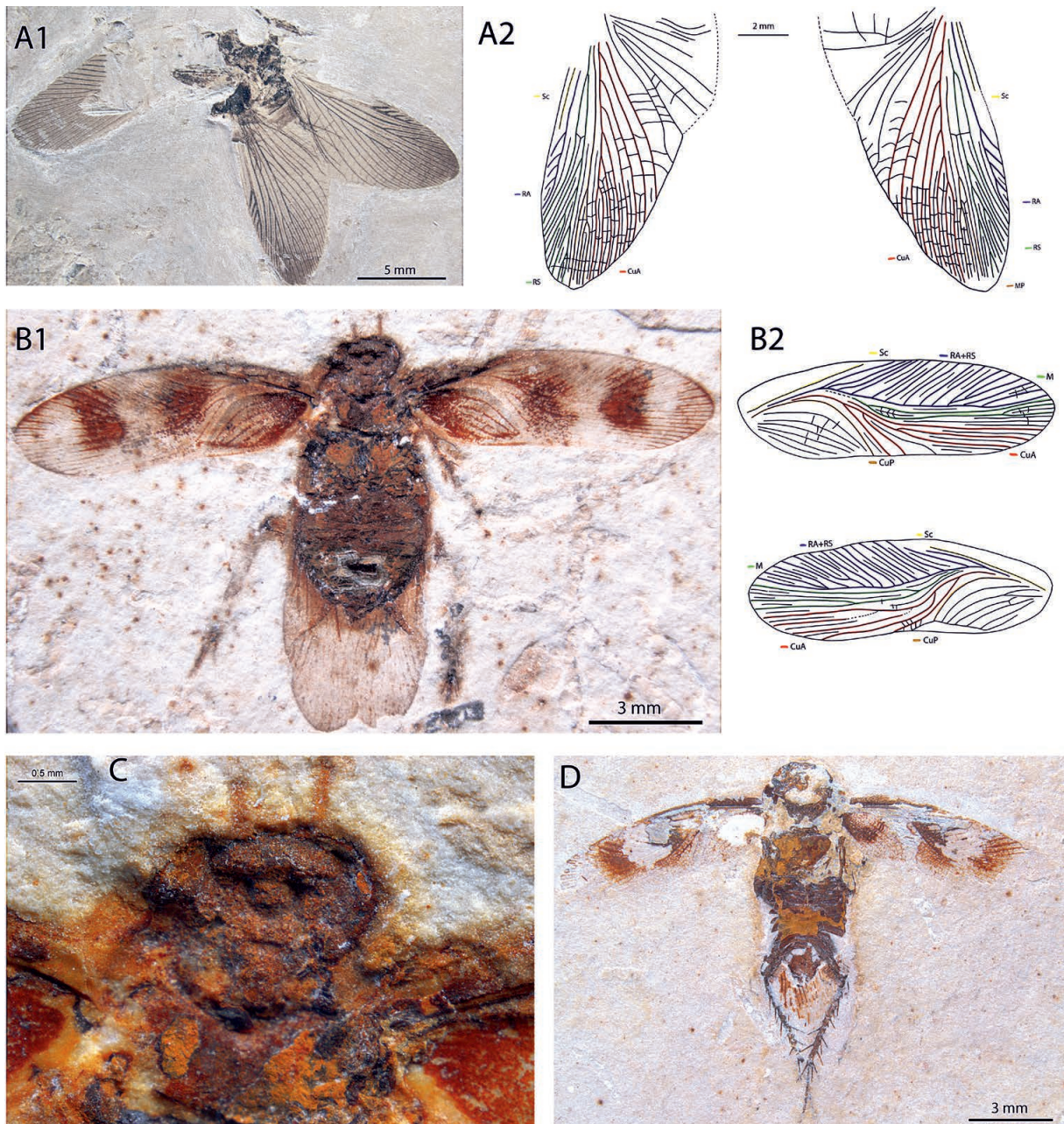


Fig. 6. **A** — *Elisama hindwingii* sp. n.; SMNS 67573. 1. Fore- & hind wings. 2. Hind wings. **B–D:** *Ocelloblattula santanensis* sp. n. **B** — SMNS 66558. **C** — Forehead having probably three ocelli. **D** — 66316.

Diagnosis (improved after Pinto & Purper (1986), Bechly (2007a)): Body length 11–14 mm; antenna about as long as body; pronotum subcircular, very broad (about 2–2.33 times of head width) with very broad lateral lobes; forewing venation typically ectobiid with costa area short, Sc bifurcated, R 8–11 branches (some of them bifurcated), MA 4–6 branches (some of them bifurcated), CuA generally bifurcated, several anal veins simple and ending on CuP, intercalary veins and crossveins present (not as few as mentioned in the original description). It differs from *Piniblattella magna* sp. n., by significantly smaller size, forewing CuA with fewer branches (in *P. magna* sp. n. three to five) and

A-veins not fused. It differs from *P. vitimica* by generally smaller size (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 fewer branches than *P. vitimica* (2–5 dichotomizing branches and 12–22 veinlets) and CuA with only two main branches (*P. vitimica* one to seven veinlets). Compared to the other species of genus *Piniblattella* differs by less veins-venations.

It differs from *P. sharingolensis* Vršanský, 2005 by forewing without intercalaries. Hind wing unknown.

Description: Pronotum subcircular, hind margin relatively straight, about twice the width of the head, fore

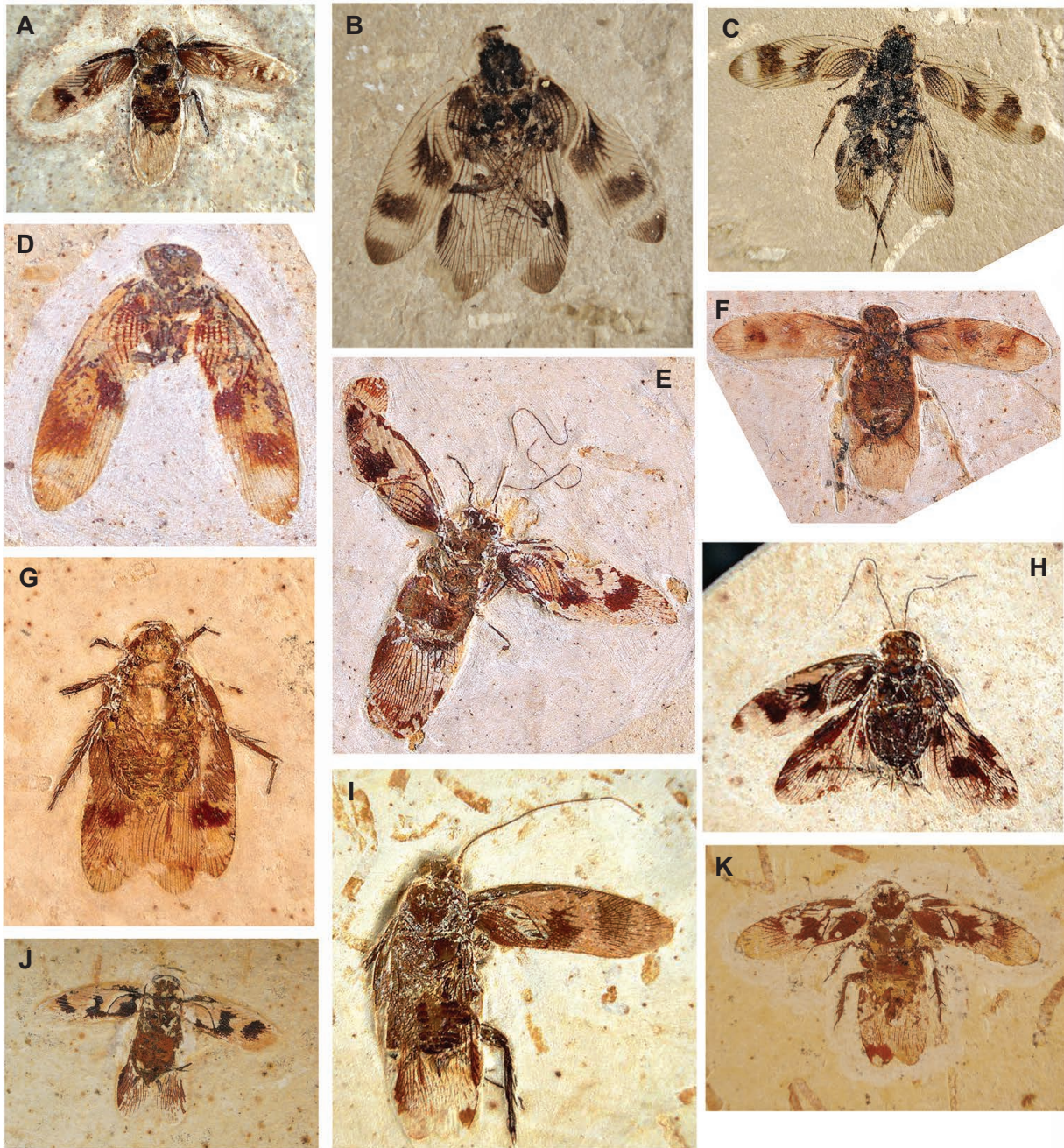


Fig. 7. *Ocelloblattula santanensis* sp. n. Uncatalogued specimens from diverse private collections.

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: 10.3–13.0 mm long and 3.5–4.2 mm wide, Sc typically blattellid with bifurcated, RA+Rs with a total of 15–23 branches, M with six–nine branches in total (except SMNS 66315 left side with five, Fig. 8C), CuA with two branches (except SMNS 66315 left side with four). Forewings show very low morphological differences (Table 5). Hind wing: about 12–13 mm long, detail still unknown. Cerci in typical

roaches form and about 14 segments. Terminalia with unsegmented styli.

Description of other specimens: SMNS 66312 (Fig. 8A): 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 the width of the head. Thorax with coxa in roaches form. Terminalia near cerci with one pair styli, unsegmented. SMNS 66314 (Fig. 8B): Antenna shorter than body length. Mid- and hind leg tarsus long and well preserved. SMNS 66315 (Fig. 8C): The venation between left and right forewings clearly different, especially in M and CuA. In the right side, CuA with

Table 4: Forewing venation variability of *Ocelloblattula santanensis* sp. n.

<i>O. santanensis</i>	Forewing						Total
	SC	RA+RP	M	CuA	CuP	A	
SMNS							
66316	1/1	14/14	3/3	4/4	1/1	7/8	30/31
66558	1/1	15/15	3/3	5/5	1/1	6/6	31/31
Fig.7A	1/1	15/13	3/3	5/5	1/1	6/7	31/30
Fig.7B	1/1	13/14	4/4	5/4	1/1	8/7	32/31
Fig.7C	1/1	13/15	3/4	5/4	1/1	8/7	31/32
Fig.7D	1/1	14/14	3/3	4/3	1/1	6/6	29/28
Fig.7E	1/1	16/-	3/-	4/4	1/1	7/7	32/-
Fig.7F	1/1	15/13	4/4	4/4	1/1	6/6	31/29
Fig.7G	1/-	15/-	-	-	-	-	-
Fig.7H	1/1	15/13	4/5	5/5	1/1	7/7	33/32
Fig.7I	1/-	13/-	4/-	5/-	1/-	7/-	31/-
Fig.7J	-/1	-/13	-/5	-/4	-/1	-/6	-/30
Fig.7K	1/1	16/15	3/3	4/5	1/1	7/7	32/32

two- and M with a total of nine branches, that is more in “normal” form. On 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 possible, that the left side is still in nymph phase, but the sclerotization in both sides is quite equal. SMNS 66319 (Fig. 8E): Pronotum about double width of head. Its fore margin is almost the same length as the head. SMNS 66322 (Fig. 8D): Hind leg tibia with several spines. Terminalia with one pair well preserved cerci, 14 segments.

***Piniblattella magna* sp. n.** (Fig. 9)

2007 Unnamed new genus and species A. — Bechly, 248–249.

Holotype: SMNS 66000-116.

Paratypes: SMNS 66310; 66313; 66317; 66318; 66320.

Derivatio nominis: Named after the large size.

Stratum typicum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locus typicus: Chapada do Araripe, vicinity of Nova Olinda, southern Céara, North-East Brazil.

Differential diagnosis (improved after Bechly 2007a): The species is categorized within *Piniblattella*, which differs from *Mesoblattina* by forewing with less M branches and A with less numerous reticulations. Pronotum shield-like, forewing with M strongly branched and CuA with just two major branches. Large size roaches. Body length 17.8–25.0 mm; antennae distinctly longer than body (31 mm in a specimen with 25 mm body length); pronotum very large with 2.15–2.33 times of head width and with very broad lateral lobes; pronotum broadest in the middle of the posterior half; forewing generally less than body in length, venation typically blattellid. It differs from *P. limai* by its distinctly larger size and in having forewing CuA three–five branches (in *P. limai* the CuA is with two branches), and the A-veins fused often especially in the base part. It differs from

P. vitimica by generally larger size and forewing M with fewer branches (by *P. vitimica* with 2 to 5 dichotomizing branches and 12 to 22 veinlets). Larger compared with other *Piniblattella* spp.

Description: Antenna shorter than double the body length (2×17.8 –27.0 mm). The top of head slightly protrudes from the fore margin of pronotum. Pronotum broad, approximately oval shape, posterior half much wider and hind margin relatively straight. Forewing: 16–21 mm long and 4.8–6.2 mm wide, Sc with two major branches, each one sometimes has several (two–four) terminal branches, RA+RS with 18–20 branches, 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. Forewings show very few morphological differences (Table 6). Hind wing is about the same length as forewing and is 16–19.5 mm long. Hind leg tarsus is about $\frac{3}{4}$ of the length of the tibia and with five or four (SMNS 66000-116, 66317; see Fig. 9A–B) 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 with 17–20 segments.

Description of other specimens: SMNS 66000-116 (Fig. 9A): Body size (17.8 mm) relatively smaller than in the other specimens of this species. Pronotum broad and well preserved. The male external genitalia presented with hook-like structure. Unusual hind leg tarsus, left side with five but right side with four segments. The right side tarsus (totally 4.7 mm) is shorter than the left side tarsus (totally 5.1 mm). On the basis of the length of each segment, the “third” segment should be lost by right side. This “four segments tarsus-” (Vršanský 2002 reported it from a Cretaceous mantodean *Jantarimantis zherikhini*), which reflects incomplete regeneration (Bohn 2003), is not rare, in specimen SMNS 66317 both sides of hind leg tarsus with only four segments. SMNS 66310 (Fig. 9C): Body size relatively large. Antenna (41 mm long) is about shorter than double of body length (25 mm). Cerci well preserved, about 20 segments. SMNS 66313 (Fig. 9F): Mid and hind leg tarsus with five segments. SMNS 66317 (Fig. 9B): Hind leg tarsus with four segments. SMNS 66318 (Fig. 9E): Forewing Sc with several branches. Abdomen swelled. SMNS 66320 (Fig. 9D): Forewing Sc with two major branches, the Sc2 has further terminal branches. Hind wing is only partly preserved.

Family: Mesoblattinidae Handlirsh, 1906

Genus: *Perlucipecta* Wei et Ren, 2013

***Perlucipecta santanensis* sp. n.** (Fig. 10)

2007 Unnamed genus and species B. — Bechly, 249.

Holotype: SMNS 66308.

Paratypes: SMNS 66309; 66311; 66321.

Derivatio nominis: Named after the city of Santana do Cariri near the type locality.

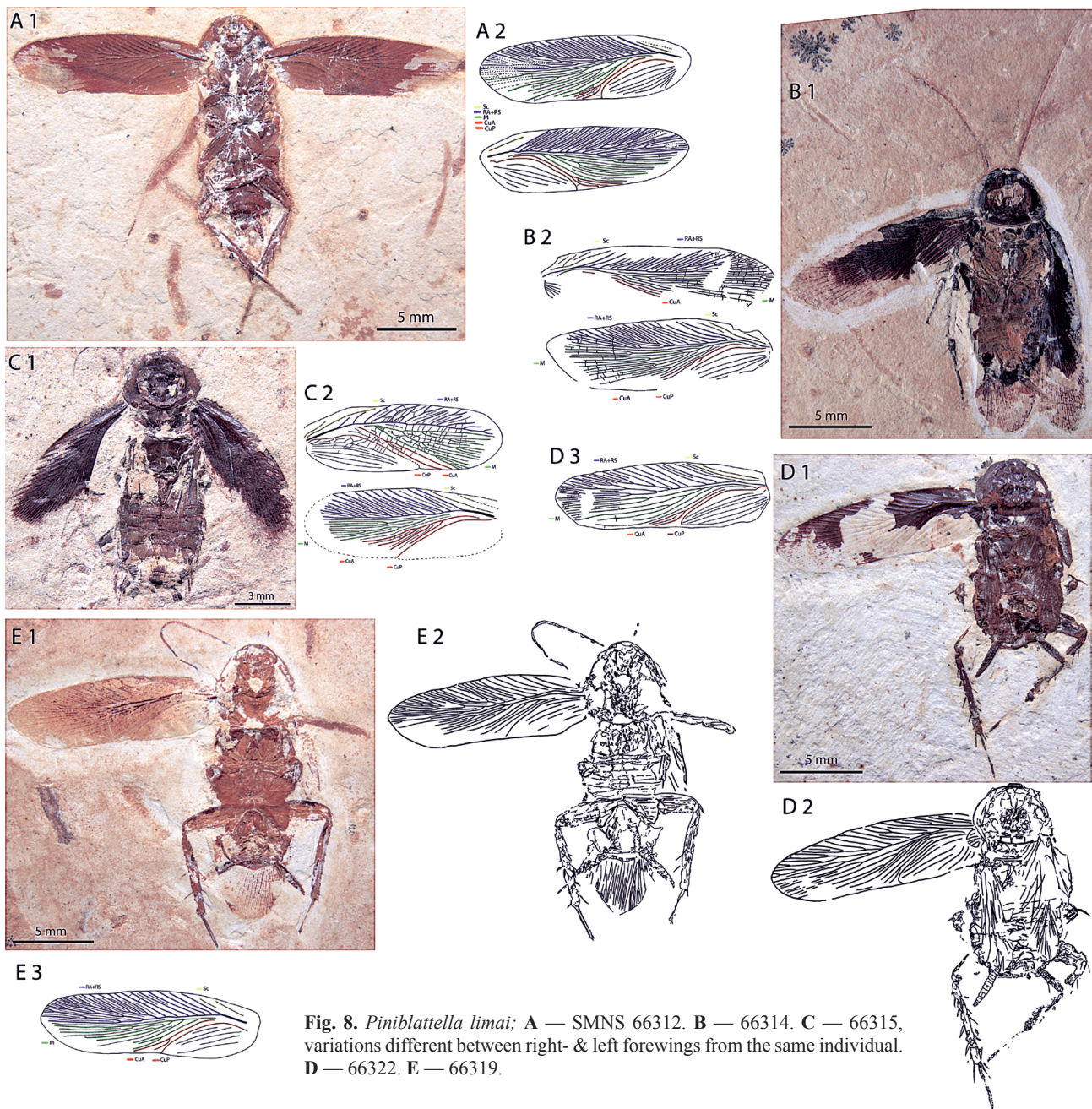


Fig. 8. *Piniblattella limai*; **A** — SMNS 66312. **B** — 66314. **C** — 66315, variations different between right- & left forewings from the same individual. **D** — 66322. **E** — 66319.

Stratum: Lower Cretaceous, Upper Aptian, Nova Olinda Member of Crato Formation.

Locality: Chapada do Araripe, vicinity of Nova Olinda, southern Ceará, North-East Brazil.

Diagnosis: Small-sized roaches. Body about 8.7–11.9 mm length; shape of body longish oval; antennae about as long as body; pronotum much broader than head (width 3.0–3.7 mm, thus 1.8–2 times head width), posteriorly broader than anteriorly, but with narrower lateral lobes than blattellid species mentioned above; forewing thin, venation with a broad costal margin.

Description: First time reported by Bechly (2007a). Antenna a little longer than body length. Body about

8.7–11.9 mm long. The top of head slightly protrudes from the fore margin of pronotum. The hind margin of pronotum is relative straight. Forewing, costal 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. Fore-, mid-, and hind legs show similar patterns, 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 fourth segment shorter, the fifth segment elongated again and with claws and pretarsus. Cerci in roaches form, 13–14 segments. Treminalia with unsegmented styli.

Table 5: Forewing venation variability of *Piniblattella limai*.

SMNS	<i>Piniblattella limai</i> (Right/Left)						Total
	SC	RA+RP	M	CuA	CuP	A	
66312	2/2	21/22	9/6	2/2	1/1	7/6	42/39
66314	2/2	19/18	6/8	2/2	1/1	6/6	36/37
66315	2/2	16/14	9/5	2/4	1/1	5/5	35/31
66319	2	23	7	2	1	5	40
66322	2	18	7	2	1	6	36

Table 6: Forewing venation variability of *Piniblattella magna* sp. n.

SMNS	<i>Piniblattella magna</i> (Right/Left)						Total
	SC	RA+RP	M	CuA	CuP	A	
66000-116	2/2	19/20	7/13	2/2	1/1	8/6	39/44
66317	2/2	19/19	8/11	4/3	1/1	8/9	42/45
66318	3/4	19/19	8/9	3/5	1/1	10/10	44/48

Description of other specimens: SMNS 66308 (Fig. 10A): Antenna slightly longer than the body length. Fore- and hind wings overlap and only partly identifiable, those are: 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. SMNS 66309 (Fig. 10B): Forewing probably thinner, only the base part slightly sclerotized. Hind leg well preserved. SMNS 66311 (Fig. 10C): Hind leg well preserved. Terminalia with unsegmented styli. SMNS 66321 (Fig. 10D): Ventral side. Head with a pair of large compound eyes. Mouth parts, including labrum, maxillary- and labial palps partly visible. In thorax, the coxal and the trochanters were well preserved.

**Genus: *Raptoblatta* Dittmann, Hörnig,
Haug et Haug, 2015**

Remarks: Predator regarded as a relative of praying mantodeans, with venation with characteristic reticulations visible on the apical parts of both left and right forewings as well as hind wings. This taxon is difficult to discriminate from the dominant Laurasian as well as Gondwanan *Archimesoblatta*, and is very closely related to Gondwanan *Gondwablatta*, with identical forelegs (spines were not preserved), but with a different pronotum. Pronotum of *Raptoblatta* is apparently misinterpreted and has a standard, vaulted, small and transversal shape. Nevertheless, it is different from *Gondwablatta*. The carnivorous mode of life might explain the lack of other predatory lineages of cockroaches in numerous localities with occurrence of *Archimesoblatta*. Nevertheless, categorization within Mesoblattinidae excludes the mantodean relation.

***Raptoblatta waddingtonae* Dittmann, Hörnig,
Haug et Haug, 2015**

Material: Monotypic, holotype only. Axelrod Institute, University of Guelph, Canada: AI 514

Diagnosis: Medium-sized, roach-like, winged insect with wide abdominal segments and cockroach-type cerci; most prominent structure is the foreleg with the row of femoral and tibial spines; the median side of the distal region of the femur is concave - this region is equipped with small spines; and has nearly the same length as the tibia.

Discussion

The ecologically-dominant family of the order Blattaria in the Crato Formation is represented by the family Ectobiidae, with about 83 % of the cockroach specimens. This result is similar to that of Vršanský (2004) who also reported that this family accounts for 60 % of the cockroaches in the Crato Formation based on the American Museum of Natural History (AMNH, New York) collection. Blattulidae represent about 13 % of the cockroaches. This study shows a surprisingly low abundance of the family Umenocoleidae (only 4 %) compared to the AMNH collection, which shows that the Umenocoleidae are represented by up to 15 % of all roaches (Vršanský 2004). Although the Cretaceous cockroach assemblages differ from the Jurassic cockroach assemblages (this transition was characterized by the temporal change in the dominance of particular families), Blattulidae remain dominant during the Cretaceous, together with the Ectobiidae (Vršanský 2002). Blattulidae are also dominant in the Yixian formation (Late Jurassic/Early Cretaceous) of northern China (Wang et al. 2007b). The Crato dictyopterans (see also Lee 2014) show similarities with those at the Cretaceous localities of Mongolia (e.g., Vršanský 2003b, 2008b) and Chernovskie Kopi in Russia (Barna 2014), namely Chaeteessidae, Ectobiidae, Blattulidae and Umenocoleidae. The Upper Jurassic assemblage from Shar-Teg (Mongolia) shows a more even cockroach assemblage with Blattulidae (38 %), Mesoblattinidae (25 %), Liberiblattinidae (13 %) and Caloblattinidae (25%) (Vršanský 2005b,c; Barna 2014). The cockroach assemblage of the Lower Cretaceous in Montsec (Spain) is dominated by blattulids and mesoblattinids (Vršanský and Ansoerge 2001). The lack of the family Fuziidae (Vršanský et al. 2009) in the Crato Formation supports an endemic status of the family in Inner Mongolia (China, Daohugou).

Palaeogeographical distribution of genera reveals interesting patterns. Only *Ocelloblattula* is limited to Gondwana, while *Perlucipecta*, *Piniblattella*, *Elisama* and possibly *Petropterix* ("*P.*" *maxima*) were also present in Laurasia. *Cratovitisma*, *Ponopterix*, *Raptoblatta* (possibly *Archimesoblatta*) and the new genus *Umenopterix* are endemic. It follows that the primitive taxa are shared with Laurasia, while the more advanced cockroaches are either indigenous or restricted to Laurasia (while progressive Raphidiommidae as well as rather primitive Caloblattinidae were missing). On the other hand, phylogenetically-advanced Laurasian taxa such as *Praeblattella* (although recorded in the New Jersey amber), *Tarakanula*, *Elytropterix* and *Petropterix* do not occur in the Crato Formation.

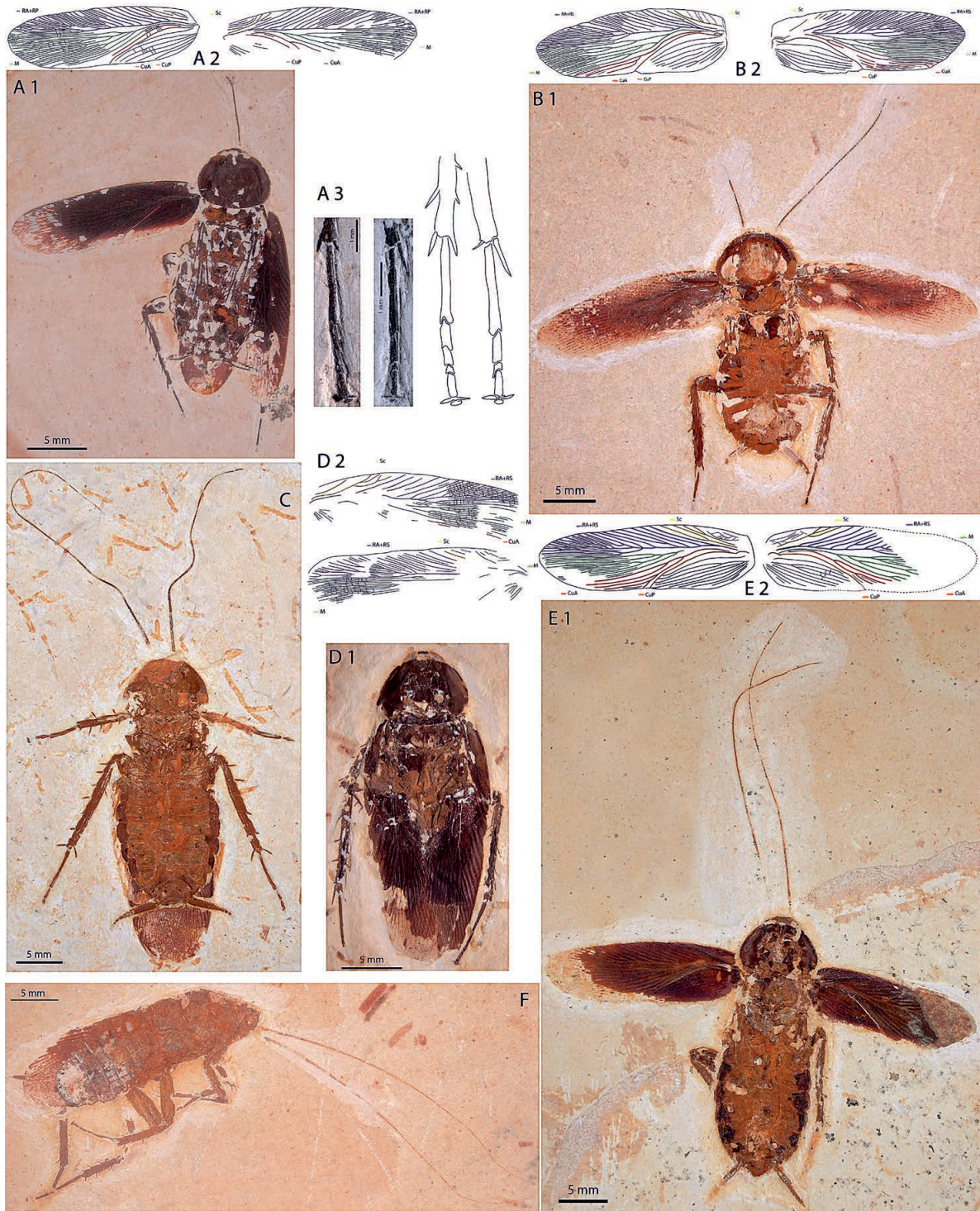


Fig. 9. *Piniblattella magna* sp. n. **A** — holotype habitus; SMNS 66000-116, right & left hind legs tarsus with four—five segments. **B** — SMNS 66317. **C** — 66310. **D** — 66320. **E** — 66318. **F** — 66313.

Phylogenetic context is congruent with the Aptian datings of the locality. While it is impossible to delimit the phylogenetic status for *Elisama* spp., and *Piniblattella* spp. because they do not possess phylogenetically important characters, *Perlucipecta* can be regarded as somewhat more advanced than its Yixian congener *Ponopterox* and *Ocelloblattulla* are

assumed to be extremely advanced taxa in spite of some primitive characters, the latter genus furthermore also occurs in earlier Lebanon amber (without Plesiomorphies). On the other hand, *Cratovitisma* and *Umenopterix* are extremely primitive compared to all (including the stratigraphically basalmost ones) Cretaceous localities because they possess

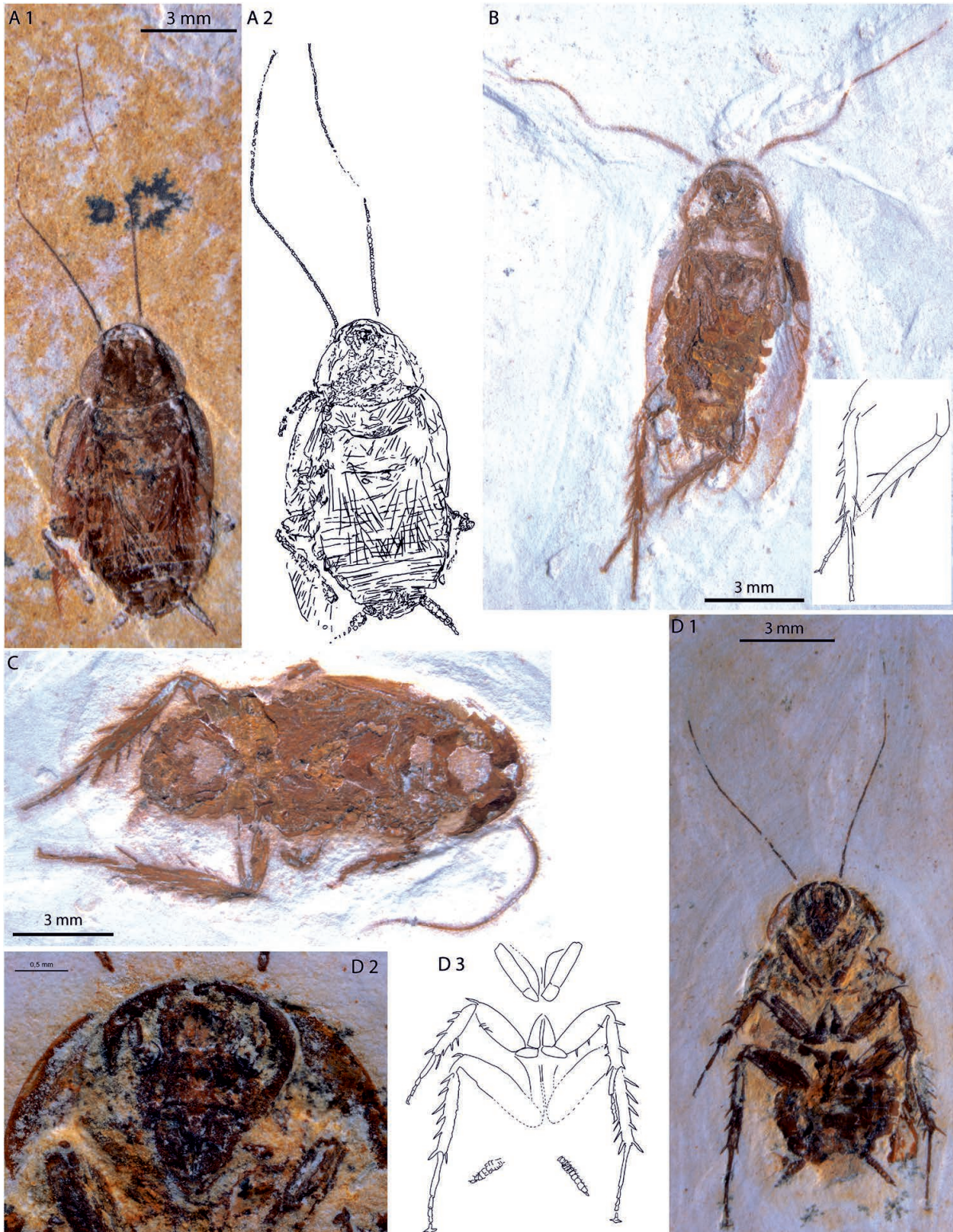


Fig. 10. *Perlucepecta santanensis*. sp. n. **A** — holotype habitus: SMNS 66308. **B** — 66309. **C** — 66311. **D** — paratype habitus: 66321.

characters such as standard pronotum with fully developed paranotalia.

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