

New Lower Cretaceous basal mantodean (Insecta) from the Crato Formation (NE Brazil)

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Abstract: Mantodea are very rare in the fossil record. 28 fossil species are reported since the earliest occurrence of mantodeans in the Upper Jurassic (Tithonian). Here, I describe *Cretophotina santanensis* n. sp. from the Aptian (Lower Cretaceous) Crato Formation of Chapada do Araripe (northeastern Brazil). This species is characterized by long antenna and primitive raptorial forelegs. Morphological characters shared with the living genus *Chaeteessa* would support its assignment to the family Chaeteessidae. The tropical occurrence of the Early Cretaceous genus *Cretophotina* in Gondwana, together with occurrences of the genus *Chaeteessa* from subtropical and temperate zones of Laurasia, implies that members of the family Chaeteessidae achieved nearly cosmopolitan distribution during the Early Cretaceous.

Key words: Fossil insects, Mantodea, Chaeteessidae, *Cretophotina*, *Chaeteessa*, Mesozoic, Aptian.

Introduction

The order Mantodea comprises ~2400 living species (Otte et al. 2013) but its distribution and diversification patterns during the Cretaceous remain poorly known. These predatory insects are mostly relatively large in size and possess raptorial forelegs and cursorial mid and hind legs, and exhibit sexual cannibalism of males during mating (e.g. Beier 1968; Grimaldi 2007). Predatory mantises probably evolved during the Late Jurassic (Vršanský 2002, 2005b) and radiated in the Early Cenozoic (Gratshev & Zherikhin 1993; Grimaldi 2003, 2007). Mantodea can either represent the sister group to Blattaria + Isoptera (and Blattaria is paraphyletic in respect to Isoptera) (Grimaldi 2007) or they independently originated from the cockroach family Libellulidae (Vršanský 2002, 2004, 2010). The family Chaeteessidae belongs to the primitive Mantodea and includes one recent and six fossil genera (Zherikhin 2002, 2005b). The extinct genus *Cretophotina* has four described species (Gratshev & Zherikhin 1993; Vršanský 2002; Grimaldi 2003) and *Chaeteessa* has five recent neotropical species plus one fossil species from the Oligocene to Miocene Dominican amber (Grimaldi 2003; Rondón et al. 2007).

Two mantodeans were reported from the Lower Cretaceous Crato Formation, including *Santanmantis axelrodi* Grimaldi, 2003 and one unnamed mantis (Grimaldi 2003, 2007; Hörnig et al. 2013). The aim of this paper is to describe another new mantodean species from the Lower Cretaceous Crato Formation and to discuss the implications of this finding for Cretaceous distribution patterns and phylogeny of mantodeans.

Material and methods

The specimen described here is deposited in the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS 67583).

The drawings were made on the dry specimen using a camera lucida attached to a Leica MZ125 stereo microscope and digitized by scanning. Photographs were made with a Leica DFC490 digital macro camera. The figures have been edited with the Adobe Photoshop™ CS3 imaging software.

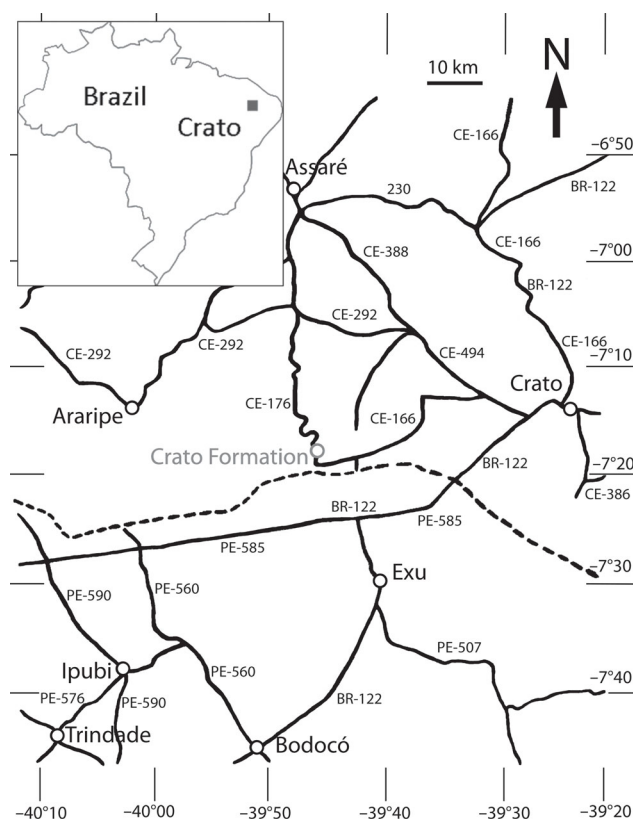


Fig. 1. Location of the Crato Formation (7°19'60" S and 39°50'00" W).

The Crato Formation is exposed in the north-central part of the Chapada do Araripe (Fig. 1), a large plateau in north-eastern Brazil (Martill & Bechly 2007). The limestones from this location contain highly abundant plants, invertebrates and vertebrates (Menon & Martill 2007). All fossils occur in laminated limestones of the Nova Olinda Member of the Crato Formation that correspond to the Aptian stage (~120 Myr) (Martill & Heimhofer 2007). Chapada do Araripe was located at 10° to 15° S during the Early Cretaceous and still within the tropics (Martill 2007). The depositional environment was represented by a lake or lagoon. Hypotheses range between freshwater lake and brackish to hypersaline lagoon with varying depth and extension (Martill & Bechly 2007). Among the fossils, insects dominate both in abundance and taxonomic diversity. More than 300 species, representing over 20 insect orders have been described, among which the terrestrial adult orthopterans, hemipterans, ephemeropterans and odonates (Menon & Martill 2007; Bechly 2007; Heads & Leuzinger 2011).

The nomenclature for fore and hind wings is based on Comstock & Needham (1898), Kukalová-Peck (1991) and Nel & Roy (1996). Abbreviations used: C — Costa, Sc — Subcosta, R — Radius, Rs — Radius sector, M — Media, Cu — Cubitus (A — anterior, P — posterior), A — Anal vein and the nomenclature used for cockroaches, RA + RP + MA would be R + RS.

Systematic paleontology

Order: Mantodea Burmeister, 1838

The traditional classification of mantises by Beier (1968) recognizes eight families: the “basal” mantises with five families (Chaeteessidae, Mantoididae, Metallyticidae, Amorphoscelididae and Eremiaphilidae); and the superfamily Mantoidea with three families (Empusidae, Hymenopodidae and Mantidae), that radiated during the Early Cenozoic (Beier 1968; Grimaldi 2003; Grimaldi & Engel 2005).

The EDNA fossil insect database (active December 15th, 2013) catalogues 28 fossil mantid species. Mantodeans probably originated from the cockroach family Liberiblattinidae during the Middle or Late Jurassic (Vršanský 2002). The phylogenetic analyses indicate that mantises first diversified during the Cretaceous, and explosively diversified (as the Mantoidea) in the Cenozoic (e.g. Grimaldi 2007). Vršanský (2002) described Juramantidae with the earliest mantodean *Juramantis initialis*, which occur also in diverse amber (P. Vršanský, personal communication 2013). To date, the Crato Formation has yielded two species of mantises. One is an unnamed specimen SMNS 66528 (Fig. 2) and the second species represents the primitive *Santanmantis axelrodi* Grimaldi, 2003 (Bechly et al. 2001; Grimaldi 2003, 2007; Grimaldi & Engel 2005); AMNH 1957 from the American Museum of Natural History, New York, USA; SMNS 66519, 66677, 66678, 66679 and 66680 (Fig. 3).

Family: incertae sedis

Species: *Santanmantis axelrodi* Grimaldi, 2003

Fig. 3



Fig. 2. Unnamed mantodean in the Crato Formation. Fore- and hind wings unknown; SMNS 66528.

The monotypic genus *Santanmantis* Grimaldi, 2003 includes *S. axelrodi*. According to Grimaldi (2003, 2007) and Grimaldi & Engel (2005), it is a relatively small mantis, body 9.5–10.5 mm long. Habitus similar to the living basal mantises, with notably short abdomen and body, pronotum nearly square. Antenna about the same length as the body. Fore and hind wings extended well beyond the apex of the abdomen. Forewings partially sclerotized, pseudovein (a very well developed claval suture) is larger than in any other living or extinct mantis. The primitive raptorial forelegs were folded under the thorax, and the mid and hind legs were long, gracile and with retained cursorial function.

Family: Chaeteessidae Handlirsch, 1920 *sensu* Gratshev & Zherikhin, 1993

Type species: *C. filata* Burmeister, 1838 (Fig. 4)

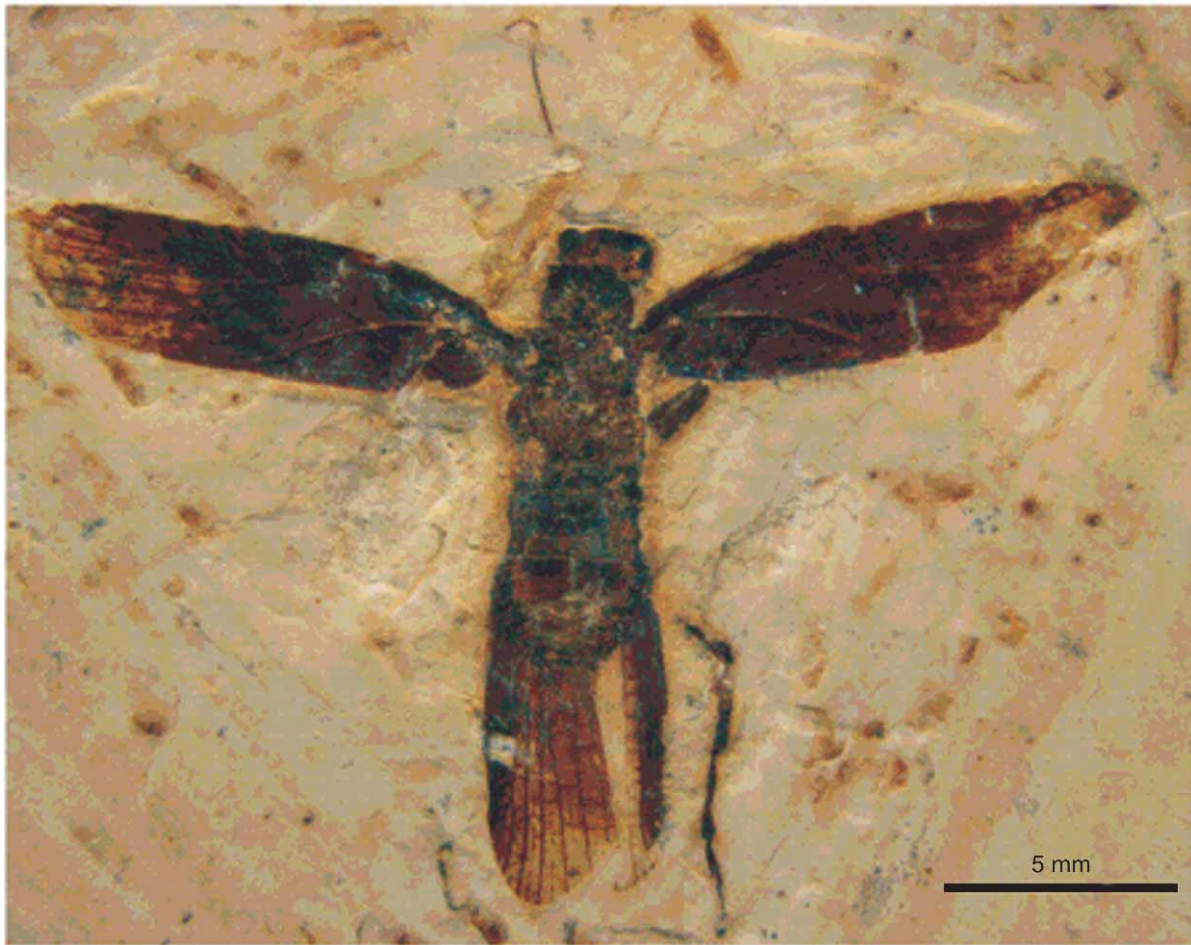


Fig. 3. *Santanmantis axelrodi* Grimaldi, 2003; SMNS 66677.

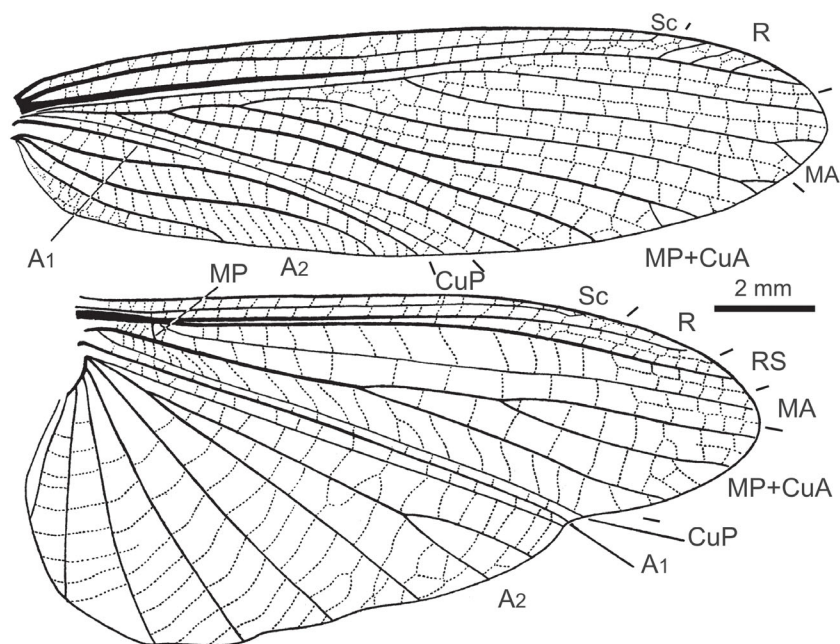


Fig. 4. Fore- and hind wings of *Chaeteessa filata* Burmeister, 1838 (after Smart 1956, with changed designations of the veins from Sharov 1962).

The family seems to be paraphyletic (Gratshev & Zherikhin 1993; Grimaldi 1997).

Diagnosis: (modified after 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 colour 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); *Vitimphotina* Gratshev & Zherikhin, 1993 (Lower Cretaceous, Siberia); *Baissomantis* Gratshev & Zherikhin, 1993 (Lower Cretaceous, Siberia); *Kazakhphotina* Gratshev & Zherikhin, 1993 (Upper Cretaceous, Turonian); *Megaphotina* Gratshev & Zherikhin, 1993 (Oligocene, Russia) a species within uncertain genus for nymph in Upper Cretaceous amber from Siberia *Chaeteessites minutissimus* Gratshev & Zherikhin, 1993 and probably one amber specimen from Japan (Upper Cretaceous, Northeast Japan; deposited in Kuji Amber Museum, Japan; brief reported by National Geographic News, April 25, 2008).

Remarks: Diagnostic characters *Chaeteessa filata*, *Cretophotina tristriata*, and *C. santanensis* n. sp. are shared with the present specimen, supporting the categorization of the genus *Cretophotina* which is close to *Chaeteessa* within Chaeteessidae.

Genus: *Cretophotina* Gratshev & Zherikhin, 1993

Type Species: *C. tristriata* Gratshev & Zherikhin, 1993

According to the previous studies (Gratshev & Zherikhin 1993; Vršanský 2002; Grimaldi 2003), the genus was known exclusively on the basis of wings from the Cretaceous of Asia. Characteristics as follows: costal field distinctly wider than field between ScP and RA; RP+MA apically with five to eight terminal branches; MP with two to three branches; CuA with six to ten terminal branches; CuP branch separated from main stem and distinctly curved. Pseudovein is present.

Composition: *C. tristriata* Gratshev & Zherikhin, 1993 (Lower Cretaceous, Siberia); *C. mongolica* Gratshev & Zherikhin, 1993 (Lower Cretaceous, Mongolia); *C. serotina* Gratshev & Zherikhin, 1993 (Upper Cretaceous, Kazakhstan) and *C. selengensis* Vršanský, 2002 (Lower Cretaceous, Mongolia).

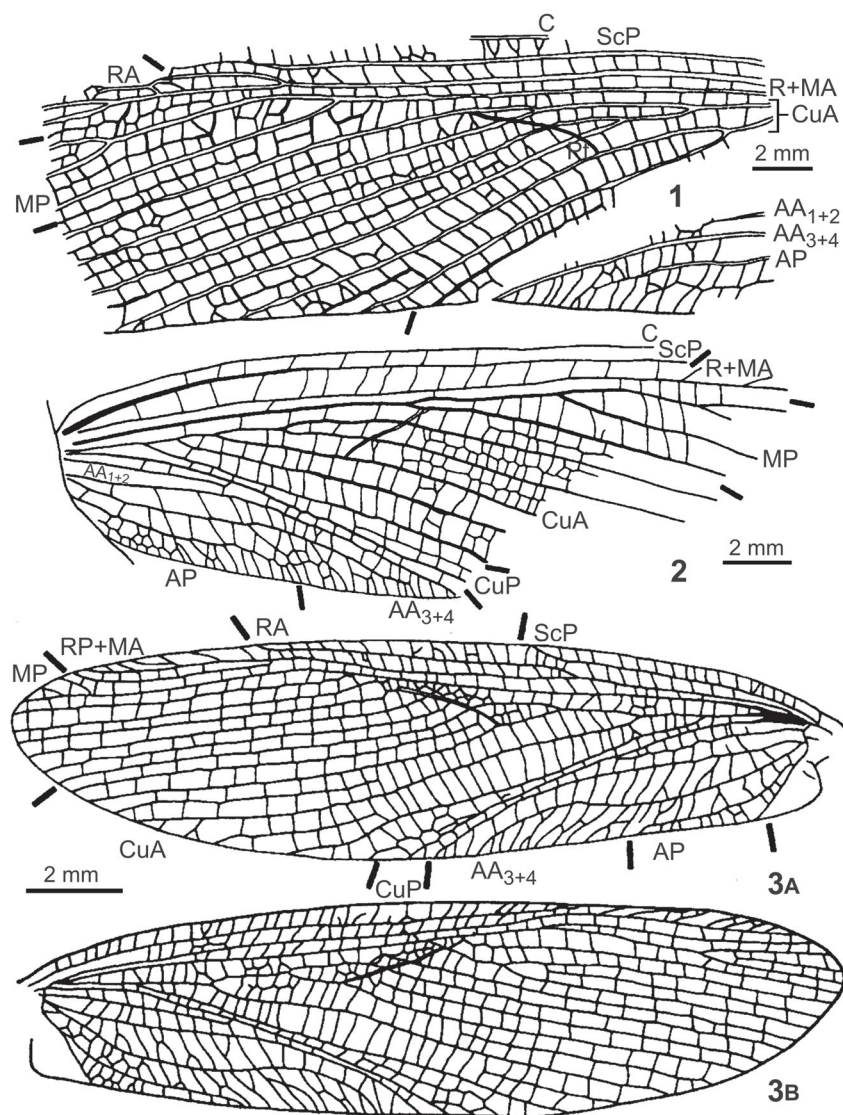


Fig. 5. 1-2 — Wings of *Arvernineura insignis* Piton, 1940, France, Paleocene. **3** — *Chaeteessa valida* Perty, 1833, Living species, female: A — left forewing, B — right forewing (after Nel & Roy 1996).

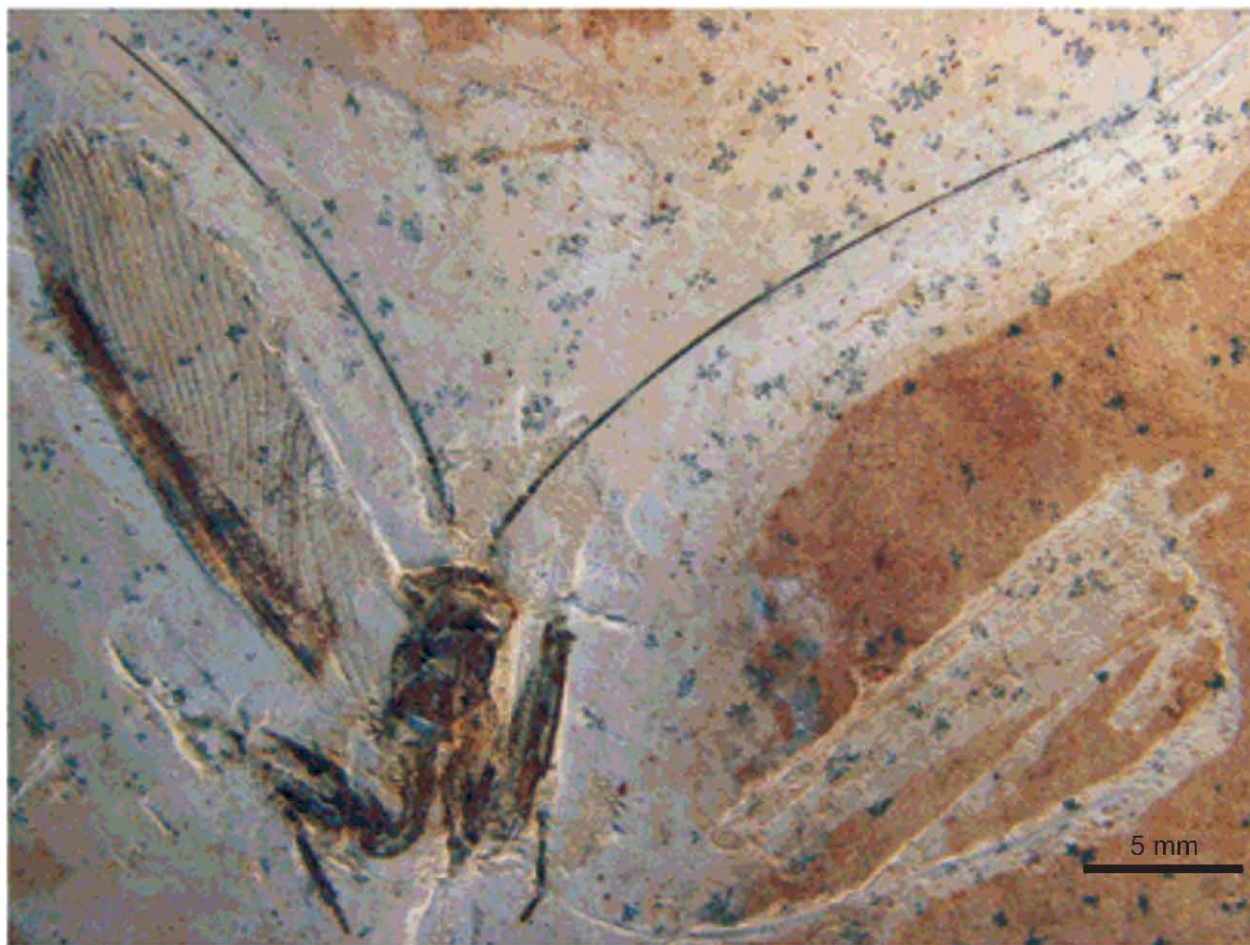


Fig. 6. *Cretophotina santanensis* n. sp., holotype; SMNS 67583.



Cretophotina santanensis n. sp.
Figs. 6–8

Holotype: SMNS 67583.

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: Assigned to *Cretophotina* on the basis of thorax that lacks elongation, with primitive raptorial forelegs with retained cursorial function, without *Chaeteessa*-similar spines. *C. santanensis* differs from other members of the family Chaeteessidae in having antenna of moderate width, elongated $\sim 1\frac{1}{2}$ time as long as forewing. Pseudovein moderate. Forewing very similar to the *Chaeteessa valida* Perty, 1833 (see Nel & Roy 1996) (Fig. 5), but differs in RP+MA and CuA more branched. M (MP) extremely reduced.

Fig. 7. *C. santanensis* n. sp., holotype; SMNS 67583; Head and thorax part.

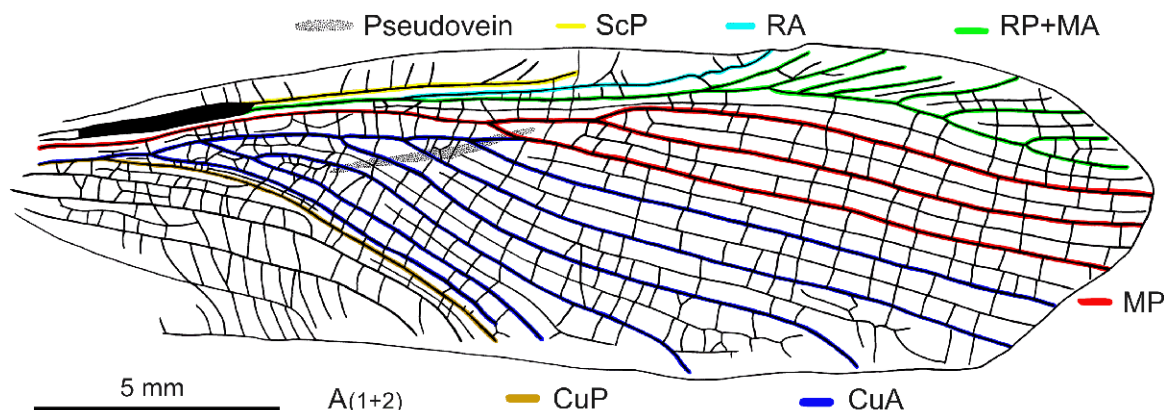


Fig. 8. *C. santanensis* n. sp., holotype; SMNS 67583; Forewing.

Description: Antenna filiform, 31 mm long and with more than 110 segments. Head 2 mm long and 4 mm wide is moderately wider than the thorax (5 mm long and 3 mm wide) from dorsal view and with big compound eyes located laterally. Pronotum slightly longer than wide, ending in the anterior margin of thorax and seems a little bit shorter than living Chaeteessidae. Raptorial foreleg without preserved spines, coxa robust, 8 mm long, femur 8.5 mm tibia 8 mm and tarsus segmented, about 5 mm long. Forewing elongated and nearly ellipse, 23 mm long and 6 mm wide. Pseudovein slightly longer than other *Cretophotina* and *Chaeteessa*. Sc about $\frac{1}{2}$ of whole wing length, subcostal area much narrower than costal area. RA long and origin in about anterior $\frac{1}{3}$ level of wing. RP+MA (fused) with eight branches. MP extremely reduced and with three branches. CuA with six branches. It is possible, that the first branch of CuA fused with MP3 (discussed below). CuP is adjacent and parallel with CuA6. Anal with at least three (possible four) branches.

Discussion

Although mantodeans originated in the Tithonian (Vršanský 2002), they were still rare during the earliest Cretaceous. For example, they were not found at Yixian (Liang et al. 2010) and at Chernovskii Kopi (Barna 2014). The superfamily Mantoidea radiated during the Early Cenozoic, leading to a high diversity of extant species (e.g. Grimaldi & Engel 2005). The living genus *Chaeteessa* with five extant and one extinct species is restricted to the Southern America (Grimaldi 2003; Rondón et al. 2007). In addition to the morphologically similar and phylogenetically related genus *Cretophotina* from the tropical Crato Formation, *Cretophotina* occurred in Laurasia in warm subtropical and warm temperate zones of Siberia, Mongolia and Kazakhstan (Zherikhin et al. 1999; Vršanský 2002; Grimaldi 2003). The geographical distribution of the family Chaeteessidae in the Early Cretaceous thus seems to be widely cosmopolitan.

Cretophotina santanensis has a long antenna, longer than $1\frac{1}{2}$ of whole wing length. This character is a unique symplesiomorphy with cockroaches. The new species shows a typical mantid forewing and Chaeteessidae body, with thorax

short and not as slim as modern mantises (see Figs. 6–7). The genus *Chaeteessa* has a unique arrangement of thick, dark foreleg spines, virtually forming a basket and primitively lacks a feature found in all other living mantises (Grimaldi & Engel 2005). The forelegs of *C. santanensis* are primitive raptorial, which means that they lack spines and retain their cursorial function, so that they resemble the most basal Janthimantidae and Juramantidae. Specimen SMNS 67583 forewing shows no colouration so that it is similar to Asian *Cretophotina* with very little colouration. In analogy to cockroaches, the partially colourless wings could mean comparatively open habitat (Vršanský et al. 2009).

Colouration was extensive in the genus *Santanmantis*. In *C. santanensis* the forewing has the first branch of CuA fused with MP3, which is designated as a deformation. This new species is thus also similar to most basal mantodeans with deformations, including the earliest mantodean *Juramantis initialis* (Vršanský 2005b). *C. santanensis* forewing is similar to the forewing of *Chaeteessa valida* Perty, 1833 (Fig. 5.3), and differs by RP+MA and CuA being more branched and by the origin of CuP being much closer to CuA6 (in *C. valida* and *C. filata* the origin of CuP is much deeper). *C. santanensis* differs from *C. tristriata* by the forewing ScP being much shorter (shorter than $\frac{1}{2}$ of wing length, while in *C. tristriata* ScP longer than $\frac{2}{3}$ of whole wing length), by RP+MA with more branches (up to eight branches, while in *C. tristriata* RP+MA with five branches) and CuP much straight. *C. santanensis* forewing differs from *Chaeteessa filata* Burmeister, 1838 and *Lithophotina floccosa* Cockerell, 1908 by having the long RA. The forewing of this specimen is larger than *C. valida* (about 17.3 mm long), *C. filata* (about 17 mm long) while length of the *Cretophotina selenginesis* Vršanský, 2002 (about 20 mm long), is 23 mm long.

It is difficult to interpret the phylogenetic relationships of *C. santanensis* (nevertheless, no plesiomorphic characters are observed). Ten short fossil mantodean specimens were found so far in the Crato formation, corresponding to an extremely small proportional abundance of this order among several dozens of thousand of fossil insect reported from the Crato Formation (Bechly 2010). This rarity contrasts with the dominance of predatory cockroaches Raphidiomimidae in the Jurassic (Vishniakova 1973; Liang et al. 2009, 2012)

and Mutoviidae in the Upper Permian of Isady in north-western Russia (Vršanský & Aristov 2012). These mantodeans and also predatory Eadiidae (Vršanský 2009) are missing in the Crato Formation.

Conclusions

Cretophotina santanensis n. sp. is described in America for the first time and has a close relationship to living *Chaeteessa* in tropical Southern America. The new species shows a basal mantodeans type with some symplesiomorphy to cockroaches.

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