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New grasshoppers (Orthoptera: Elcanidae, Locustopsidae) from the Lower Cretaceous Crato Formation suggest a biome homogeneity in Central Gondwana

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ABSTRACT

†*Cratoelcana rasnitsyni* sp. nov., new elcanid species, and †*Pseudoacrida sennlaubi* sp. nov., new locustopsid species, are described from the Lower Cretaceous Crato Formation in Brazil, on the basis of two well-preserved compression fossils. The genus †*Cratoelcana* previously comprised its type species †*Cratoelcana zessini* and †*Cratoelcana damianii* whose placement is doubtful and could belong to the Lower Cretaceous genus †*Mimelcana* from UK. The genus †*Pseudoacrida* was previously only known from the Lower Cretaceous of China. The pattern of coloration of the tegmen of †*Cratoelcana rasnitsyni* sp. nov. strongly differs from that of †*Cratoelcana zessini*. The presence of two rounded colored or hyaline spots in the middle of

the tegmen seems to be very frequent among the elcanid species. On the basis of the tegmen venation and pattern of coloration, there are probably no less than five different species of Elcanidae in the Crato Formation; two of them remain to be described. The paleobiogeography of the †Elcanidae and †Locustopsidae are discussed, especially concerning for the Gondwana faunas.

KEYWORDS

Insecta; Orthoptera; new species; paleobiogeography; Cretaceous

Introduction

The Crato Formation is known to be one of the biggest Konservat Lagerstaten of the Lower Cretaceous and more importantly one of the most extraordinary Gondwana fossil sites. Its paleolocation provides important insights on the faunal transfer between the two major blocks of the Gondwana. In fact, during the formation and the fossilisation of the Crato fauna, the deposit was located near the ‘meeting point’ between South America and Africa documenting the fauna of both continents. Additionally, the tremendous quantity of fossil material collected and published makes it one of the most studied insect deposits in the world. However, the paleoenvironment of the Crato Konservat-Lagerstätte (CKL) has long been controversial with numerous inconsistencies depending on the authors (Ribeiro et al. 2021). The recent clarification of this issue argues in favor of a seasonal, semi-arid, shallow lacustrine wetland with a drying gradient around the paleolake and parallels that of the modern alkaline Lake Chad in Africa (Ribeiro et al. 2021). We use this paleoenvironmental reconstruction and the paleoentomofauna of the deposit, especially the orthopteran paleofauna, to propose a migratory scenario between the two Gondwanan blocks and to highlight the biome homogeneity in central Gondwana during the Lower Cretaceous period.

Among the diversified paleoentomofauna of the CKL, the order Orthoptera occupies a central place since it represents more than 15% of the specific diversity of the site with nearly 60 species known to date (Ribeiro et al. 2021: fig. 7). This rich orthopteran diversity suggests that they were already ecologically important during the Mesozoic and played a key role in the paleoecosystem using their biting-chewing mouthparts to feed on leaves or roots. Interestingly, most of the Orthoptera of the CKL belong to fossil families but their phylogenetic placement *inter alia* among the Caelifera may help to refine the timing of divergence of the sub-order or of some extant families. In fact, a recent phylogenetic analyze investigates the evolution of the order using several fossils as calibration points (*e.g.* Song et al. 2020: fig. 1) but the number of these calibrations within the Caelifera is reduced. We are aware of the difficulties of choosing fossils for calibrations and of the scarcity of the fossil record of certain families, but the addition of one or two calibration points within the suborder may help in better understand their radiation.

Caeliferans possess particular sound-producing and auditory organs, they rub their legs against the thickened edges of the forewings to produce songs or stridulate using their mandibles (Grimaldi and Engel 2005) while the sounds are detected by means of auditory organs in the form of tympanal membranes situated on the abdomen. Notwithstanding, numerous fossil families occupy indeterminate positions in the phylogeny of Orthoptera, and this despite recent advances and studies of certain fossils. This problem results in large part from the creation of numerous families without proper apomorphic characters to support them nor discussion to clearly identify their putative sister lineages (Béthoux and Nel, 2002). Among these questionable lineages, the family †Elcanidae is a perfect example, and is considered to represent either a clade (Zessin, 1987; Béthoux and Nel, 2002), a ‘paraphyletic or a sister group to the Caelifera despite having elongate, ensiferan-like antennae (Grimaldi and Engel, 2005: 210). Despite the fact that the family is dominant in the CKL fauna, only two species have been described in the genus †*Cratoelcana* Martins-Neto 1991.

Herein, we describe two new Orthoptera species from the CKL and discuss their paleogeographic implications as well as their placements and the validity of several orthopteran families.

Material and methods

Both fossils derive from the Crato Formation, also called Crato Member of the Santana Formation or Crato Konservat-Lagerstätte (CKL). This deposit is composed of limestone outcropping near Nova Olinda in the northeast Brazilian province of Ceará (7.2° S, 39.4° W: paleocoordinates 12.2° S, 10.8° W) (Barling et al. 2015: fig. 1; Ribeiro et al. 2021: fig. 1). The fossiliferous unit has been dated as Aptian on the basis of its palynology (Pons et al., 1991; Varejão et al. 2021). For a complete and detailed interpretation of the stratigraphy of the CKL please refer to Ribeiro et al. (2021). The fossils described and figure herein are partly compressed three-dimension mineralized replicas. The cuticle was replaced by dark brown iron hydroxide (goethite).

The specimens were prepared by removing limestone matrix from around the body with fine blades and needles; the limestone dust was then removed with slight puffs of compressed air. Figures were composed with Adobe Illustrator CC 2019 and Photoshop CC 2019 software.

We follow the wing venation of Béthoux and Nel (2002) with implementation of Schubnel et al. (2020). We also provisionally follow the phylogenetic hypothesis of Béthoux and Nel (2002) for the position of the †Elcanidae.

Abbreviations: A anal vein; CP costa posterior; CuA cubitus anterior; CuP cubitus posterior; CuPa main anterior branch of CuP; CuPaα most anterior branch of CuP; CuPaβ second branch of CuPa; CuPb main posterior branch of CuP; PCu postcubital vein, MA media anterior; MP media posterior; RA radius anterior; RP radius posterior.

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Systematic Paleontology

Order Orthoptera Olivier, 1789

Superfamily †Elcanoidea Handlirsch, 1906

Family †Elcanidae Handlirsch 1906

Subfamily †Elcaninae Handlirsch, 1906

†*Cratoelcana* Martins-Neto, 1991

Species included

†*Cratoelcana zessini* Martins-Neto, 1991 (type species); †*Cratoelcana damianii* Martins-Neto, 1991 (placement doubtful, see discussion) †*Cratoelcana rasnitsyni* sp. nov.

†*Cratoelcana rasnitsyni* sp. nov.

(Figs. 1–2)

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Etymology

The species name honors Pr. Alexander Rasnitsyn, eminent palaeoentomologist, for his 85th anniversary. The specific epithet is to be treated as a noun in a genitive case.

Type material

Identifier number 13068 (a well-preserved 3-D fossil in ventral view) currently housed in the private collection of Markus Seenlaub and to be deposited in a Brazilian museum.

Type locality

Araripe Basin, Brazil.

Stratigraphic occurrence

Early Cretaceous, late Aptian or perhaps early Albian, Crato Formation.

Diagnosis

Tegmen large, RP with 11-12 posterior branches; a small dark apical zone, a hyaline transverse band and dark basal part of tegmen with two rounded hyaline spots in middle.

Description

Head preserved in lateral view, 5.6 mm high, prognathous; frons flat; compound eyes large 0.7 mm wide; mandible very strong, 1.7 mm long; antenna quite elongate, 51.0 mm long. Thorax very strong, 4.6 mm long, 5.2 mm high. Profemur strong, 3.9 mm long, 0.9 mm wide, tibia 3.4 mm long, 0.2 mm wide, tarsus not preserved. Only mid tarsus preserved. Hind legs with femur very strong, 12.0 mm long, 1.8 mm wide; tibia 10.4 mm long, 0.9 mm wide, distal half of metatibia dorsally with one proximal small spur (maybe unpaired) and three large spurs (maybe in pairs), apex with at least one ventral spur; tips of spurs apparently sharp, lengths and widths of paired spurs decrease from proximal to distal one (1.51-2.00 mm); tarsus 5.0 mm long, basal tarsomere 2.7 mm long, basitarsomere with at least two ventral spines, apical tarsomere elongate, longer than pre-apical tarsomere but shorter basitarsomere.

Abdomen *ca.* 8.0 mm long, 5.4 mm wide; cercus 2.5 mm long, apparently three-segmented; no ovipositor (male). Tegmen with a small dark apical zone, a hyaline transverse band and dark basal part of wing with two rounded hyaline spots in its middle; tegmen 25.9 mm long, 5.9 mm wide at midlength; CP not discernable but certainly short, not reaching base of CuA; ScP with *ca.* four branches ending in anterior margin; RA preserved *ca.* twenty short oblique branches; more than twenty crossveins between RA and RP; area between RA and RP not widened distally; RP with 11-12 simple longitudinal posterior branches; CuPaα fused with free CuA; presence of two longitudinal veins (MA2 and MP) emerging from M between CuA+CuPaα and base of RP; fusion RP+MA1; no crossveins in area between R and M basal of origin of RP; area between MP and posterior wing margin broad and covered by oblique, regular, long crossveins; CuA+CuPaα reaching posterior margin obliquely; CuP differentiated into CuPa and CuPb about basal sixth of wing; CuPa emerging obliquely from CuP; a distal fusion among CuPaß, CuPb, and PCu.

Suborder Caelifera Ander, 1936

Family †Locustopsidae Handlirsch, 1906

Genus †*Pseudoacrida* Lin, 1982

Species included

†*Pseudoacrida costata* Lin, 1982 (type species) and †*Pseudoacrida sennlaubi* sp. nov.

†*Pseudoacrida sennlaubi* sp. nov.

(Fig. 3)

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Etymology

The species name honors Markus Seenlaub, who allowed us to study the concerned material and will deposit it in a Brazilian museum. The specific epithet is to be treated as a noun in a genitive case.

Type material

Identifier number 16049 (a well-preserved 3-D fossil in ventral view), currently housed in the private collection of Markus Seenlaub and to be deposited in a Brazilian museum.

Type locality

Araripe Basin, Brazil.

Stratigraphic occurrence

Early Cretaceous, late Aptian or perhaps early Albian, Crato Formation.

Diagnosis

Wing venation characters; area between CuA+CuPaα and CuPaβ wide; RP with five branches. Broad darkened zone at wing apex.

Description

Forewing 36.38–37.21 mm long and 5.27–5.29 mm wide (width measured in apical part of wing). Costal area wider basally than apically, with a basal enlargement, tapering toward apex, with numerous c-sca crossveins; ScA and ScP parallel, both nearly straight with numerous sca-scp crossveins; ScA slightly curved, ending in anterior margin near M fork (near wing mid-length); ScP reaching anterior margin at nearly half-length of wing and without conspicuous oblique branches ending in anterior margin (hardly differentiable from crossveins); stem R+M+CuA forking into R and M+CuA well before divergence point of CuPa and CuPb; stem R long and distinctly strong, branched into RA and RP near mid-length of wing; area between ScP and R extremely narrow; an intercalary longitudinal vein in-between RA and anterior wing margin, RA slightly curved towards posterior wing margin, reaching anterior margin close to wing apex; RP with five simple branches encompassing wing apex and reaching posterior wing margin, area between RA and RP slightly broader than area between ScP and R; base of RP and first fork of M nearly opposite; M forking slightly after apex of ScA, M with three branches; CuA short, with a short sub-vertical basal stem, then parallel with CuPa, meeting CuPaα at 3.70 mm after its originating point; CuPa fork far from M fork, and basal to CuA-CuPaα meeting point; CuA+CuPaα long and situate; CuPaβ long and nearly straight; CuPa and CuPb fork located near wing base; space between CuPa and CuPb relatively broad (wider than space between M and CuA); CuPb long, simple, and nearly straight; PCu simple, with a strongly curved basal part, then parallel to CuPb; space between CuPb and PCu extremely narrow; veins CuPaβ, CuPb, PCu, and A1 meeting after wing mid-length in a point separated from posterior wing margin; A2 short entering wing making far from M+CuA fork.

Dark colorations (see drawing and photo for detailed coloration pattern) covering areas between ScP–R and RA–anterior margin, and also along several rows of crossveins between branches of RP and M, and M and Cu; occurrence of several dark spots along PCu; one large spot occupying a wide space from anterior to posterior wing margin at apex.

Discussion

Systematic placement of †Cratoelcana rasnitsyni *sp. nov.*

Only Béthoux and Nel (2002: fig. 17) proposed a phylogenetic study to support their placement of the family †Elcanidae as a sister group to Caelifera *sensu stricto*. Among fossil Orthoptera, the †Elcanidae are easily distinguishable from the other fossil family because of their dorsal metatibial spurs, and their long antenna (Figs. 1-2). The most typical character in the wing venation of the alleged clade †Panelcanida Béthoux and Nel, 2002 (= †Elcanidea *sensu* Gorochov (1995a, 1995b) + Caelifera *sensu* Gorochov (1995a, 1995b)), is the fusion of RP with MA and the strict alignment of distal part of RP with MA, present in †*Cratoelcana rasnitsyni* sp. nov. This character is reversed in the Caelifera.

Béthoux and Nel (2002: 57) proposed the following apomorphies supporting the †Elcanidae: 'CP reaching costal margin nearly opposite to origin of CuA from M+CuA or distally' [in †*Cratoelcana rasnitsyni* sp. nov., although not visible, CP was certainly very short], 'absence of crossveins in area between R and M basal of origin of RP' [shared by †*Cratoelcana rasnitsyni* sp. nov.], 'fusion RP+MA1 and not RP +MA' [shared by †*Cratoelcana rasnitsyni* sp. nov.], 'CuPaα fused with CuA at the point of origin of CuA' [shared by †*Cratoelcana rasnitsyni* sp. nov.], 'CuA+CuPaα reaching posterior margin obliquely' [shared by †*Cratoelcana rasnitsyni* sp. nov.], 'CuP differentiated into CuPa and CuPb about the basal sixth of the wing' [although not clearly visible, shared by †*Cratoelcana rasnitsyni* sp. nov.], 'CuPa emerging obliquely from CuP' [shared by †*Cratoelcana rasnitsyni* sp. nov.]. Therefore, †*Cratoelcana rasnitsyni* sp. nov. fits in the †Elcanidae.

Following Gu et al. (2020: 66), '†Elcanidae consists of two subfamilies: †Elcaninae Handlirsch, 1906 and †Archelcaninae Gorochov, Jarzembowski and Coram, 2006 (Gorochov et al., 2006). †Elcaninae would be characterized by presence of 'a distal fusion among CuPaß, CuPb, and 1A [likely PCu]' (a putative apomorphy), while the †Archelcaninae would be characterized by a 'free distal part of CuPaß, CuPb, and 1A' (the contrary state of character and a putative plesiomorphy). †*Cratoelcana rasnitsyni* sp. nov. has a distal fusion of CuPaß, CuPb, and PCu, supporting an attribution to the †Elcaninae. Gu et al. (2020) listed the following genera in the †Elcaninae: †*Probaisselcana* Gorochov, 1989; †*Panorpidium* Westwood, 1854; †*Eubaisselcana* Gorochov, 1986; †*Cratoelcana* Martins-Neto, 1991; and †*Minelcana* Gorochov, Jarzembowski and Coram, 2006.

Following the key to the elcanid genera of Gu et al. (2020), who did not include the genus †*Cratoelcana* in it, †*Cratoelcana rasnitsyni* sp. nov. would fit near the genus †*Mimelcana* because of the following characters: area between RA and RP distally not widened; CuPaβ, CuPb, and PCu distally fused; area between MP and posterior wing margin broad and covered by oblique, regular, long crossveins.

Gorochov et al. (2006: 643) separated †*Mimelcana* from †*Cratoelcana* on the basis of the character: 'Tegmina small (not longer than 14 mm) with relatively few branches of Sc (unlike †*Cratoelcana*)'. †*Cratoelcana rasnitsyni* sp. nov. has clearly longer tegmina and a ScP with more numerous branches than †*Minelcana membranacea* Gorochov et al., 2006, †*Minelcana dubia* (Giebel, 1856), and †*Cratoelcana damianii* Martins-Neto, 1991. Notice that Gorochov et al. (2006) indicated that this last species could 'possibly' belong to the genus †*Minelcana*. †*Cratoelcana damianii* is based on fossils with incomplete venation, after Martins-Neto (1991: figs 36I, 37D, 1992: fig. 3b). But Martins-Neto (1995: fig. 19) proposed the reconstruction of a more complete tegmen, confirming differences with †*Cratoelcana rasnitsyni* sp. nov., and possibly the presence of a broad area between MP and posterior wing margin. Based on these comparisons we assigned our new specimen seems to the genus †*Cratoelcana*.

The type species †*Cratoelcana zessini* Martins-Neto, 1991 is better known although the original figures in Martins-Neto (1991, 1992) are rather poor. Martins-Neto (1995: fig. 22) proposed a new interpretation of the venation on the basis of a more complete tegmen of a specimen that does not belong to the type series. †*Cratoelcana zessini* would have an area between MP and posterior wing margin broad and covered by oblique, regular, long crossveins (considered as 'CuP' by Martins-Neto 1991: fig. 36I), refigured in Martins-Neto (1995: fig. 37); but Martins-Neto (1995: fig. 22)'s reconstruction of another wing shows a very different pattern of the vein MP without any such broad and long area between it and the posterior wing margin. It has also a very long ScP, much longer than that of †*Cratoelcana zessini*. This new specimen certainly belongs to a different elcanid genus. It has also a hyaline tegmen with a darkened zone between anterior wing margin and RA, unlike the type specimen (see below) (Martins-Neto, 1995: fig. 72-73).

Martins-Neto (1991) characterized †*Cratoelcana zessini* by the presence of more than eight branches of RP and tegmen length between 22 and 26 mm, which fit with †*Cratoelcana rasnitsyni* sp. nov. However, the patterns of coloration of the tegmina are different between †*Cratoelcana zessini* and †*Cratoelcana rasnitsyni* sp. nov., *viz.* the former has a series of small dark spots all over the distal half of wing (Martins-Neto 1992: fig. 6) as in some †*Panorpidium* spp. (see Zessin, 1987); while †*Cratoelcana rasnitsyni* sp. nov. has a small dark apical zone, a hyaline transverse band and dark basal part of wing with two rounded hyaline spots in its middle. This last pattern is stable as it is also present in some other specimens attributable to †*Cratoelcana rasnitsyni* sp. nov. (see figures in internet sites https://urlz.fr/fXOs or https://urlz.fr/fXOy).

Interestingly, †*Panorpidium bimaculatum* Gorochov et al., 2006 (Barremian, UK) has a hyaline tegmen with two rounded dark spots in its middle, as in an undescribed elcanid specimen from the Crato Formation figured in the website: https://urlz.fr/fXOA. Therefore, this last fossil is possibly new. Also, the Crato elcanid specimen UVAI-20 (collection of the Museu Dom José e da Universidade Estadual Vale do Acaraú, Sobral-Ce), shows a darkened basal part of tegmen with a hyaline zone crossing its mid part between RA and first branch of RP, quite broader than in †*Cratoelcana rasnitsyni* sp. nov.; but the other specimens UVAI-9, and UVAI-

12 have hyaline tegmina (de Sousa et al. 2016: fig. 6). These fossils possibly correspond to different species. A specimen attributed to †*Cratoelcana damianii* by Martins-Neto (1995: fig. 68) shows nearly completely darkened tegmina with possibly a broad hyaline zone in middle.

Considering the amount of material extracted and figured from the Crato Formation and the relatively good preservation of these fossils, it is quite strange that only two species of †Elcanidae have been described till now. Therefore, we await numerous new species to be described from this deposit. CKL fossils, due to their preservation, may be a key to understand and clarify the phylogenetic placement of the family †Elcanidae within the Caelifera.

Systematic placement of †Pseudoacrida sennlaubi sp. nov.

Sharov (1968) first defined the †Locustopsoidea Handlirsch, 1906 and included in it the families †Locustopsidae Handlirsch, 1906, †Locustavidae Sharov, 1968, and the recent Eumastacidae. Gorochov (1995: 43, fig. 1) considered the †Locustopsoidea (with the families †Locustopsidae and †Locustavidae) as the possible 'ancestors' of the three superfamilies Tetrigoidea, Eumastacodoidea, and Acridoidea, thus a paraphyletic set of taxa. He defined the Locustopsoidea on the basis of the following characters (translation from the Russian): 'The most 'primitive' superfamily †Locustopsoidea includes the Triassic †Locustavidae and the Triassic-Cretaceous †Locustopsidae. They are united by the three-branched MA [M] and the branched MP+CuA [CuA+CuPaα] of the tegmina, as well as the branched MA of the hind wings'. The first character 'M with three branches' seems to be stable among the various taxa in the superfamily, but this character is possibly not so stable at the level of the Caelifera. But if the second character is also present in a majority of taxa currently in the †Locustopsoidea, it is not shared by the genus †*Zessinia* (Martins-Neto 1990: fig. 3; 2003), and our fossil, in which the area between CuA+CuPaα and CuPaβ is divided into an irregular net of small cells.

After Gorochov (1995), the differences in the forewings between the †Locustavidae and the †Locustopsidae would concern the multi-branched CuA+CuPaα in the former vs. two-three-branched in the latter, and the presence of more branches of the anal veins 1A and 2A vs. only one or two in the latter. Gorochov (2005: 273) proposed a different diagnosis for the †Locustavidae: '†Locustavidae differ from †Locustopsidae in the following characters of forewing venation: "C" [ScA] straight or slightly curved, but its distal portion not approximated to the Sc stem in such a manner that costal area near the proximal part of "C" [ScA] is wider than near its distal part [this character is not very clear as it is shared by some †*Locustopsis* spp.]; base of CuA1 [CuPaα] not remote (or only slightly so) from the forewing base, so that CuA2 [CuPaβ] not shorter (sometimes possibly only slightly shorter) than CuA stem up to bifurcation into CuA1 [CuPaα] and CuA2 [CuPaβ] [clearly a symplesiomorphy in the Orthoptera]. Gorochov et al. (2006: 657) reproduced this list of differences between the †Locustavidae and the †Locustopsidae, and proposed to include the recent family Tanaoceridae (all apterous) in the †Locustopsoidea, but they indicated that: 'The differences between †Locustopsidae and recent †Locustopsoidea in the family Tanaoceridae are unclear, as the latter family is apteorus and fossil bodies of †Locustopsidae are insufficiently known'. We wonder what can remain to put these two families together. The Tanaoceridae are currently considered as sister group of the remaining Acridomorpha (Song et al., 2020)

Zessin (1983: 176) proposed the following forewing characters for the †Locustopsidae (extracted, translated and adapted from the German): slender forewings; characteristic splitting of vein M into three long parallel branches in the area near base of RP [same character as in Gorochov 1995)]; CuA+CuPaα branching off anteriorly in an arc-shaped way; CuA+CuPaα with two to four branches [same character as in Gorochov 1995)]; base of RP in proximal half of wing, with several branches [not in the Triassic genus †*Praelocustopsis*]. The anteriorly strongly curved CuA+CuPaα is an interesting character (not kept by Gorochov 1995), not present in the †Locustavidae. But it is more or less pronounced, even in the different species of the genus †*Locustopsis* (see Sharov 1968: fig. 35). Furthermore, some taxa currently in the †Locustavidae have also this character (*e.g.* †*Praelocustopsis* Sharov, 1968), but as this last family is based on dubious and/or plesiomorphic states of characters, these '†Locustavidae' are possibly more related to the †Locustopsidae. †*Praelocustopsis* has also a two-branched CuA+CuPaα. Such an anteriorly curved CuA+CuPaα is infrequent among the modern Caelifera, but present at least in some Charilaidae (Dirsh 1975: fig. 20). Thus it cannot be a synapomorphy of the †Locustopsidae.

As a result, there is no clear synapomorphy in the forewing structures to define the †Locustavidae, †Locustopsidae, and †Locustopsoidea as genuine clades.

The †Locustopsoidea currently comprise the †Bouretidae Martins-Neto, 2001, †Eolocustopsidae Riek, 1976 (included in the †Locustopsidae in the Fossilworks database), †Locustavidae, and †Locustopsidae (after the http://orthoptera.speciesfile.org). The very long CuPa, plus the presence of a simple and strongly curved CuA+CuPaα in †*Pseudoacrida sennlaubi* sp. nov. excludes affinities with the †Locustavidae. The †Eolocustopsidae originally comprised the two genera †*Eolocustopsis* Riek, 1976 and †*Protettavus* Riek, 1976. The later genus was transferred into the †Tettavidae by van Dijk and Geertsema (1999). †*Eolocustopsis* is based on an incomplete forewing in which the number of branches of M and the shape of the vein CuA+CuPaα are unknown (Riek, 1976: fig. 8). Thus, its attribution to the †Locustopsidae is far from being correctly supported. It strongly differs from †*Pseudoacrida sennlaubi* sp. nov. in the basal part of CuA emerging obliquely from M+CuA, among others differences.

†*Bouretia elegans* Martins-Neto, 2001 (Crato Formation) is based on a poorly preserved body with its wings in an extreme bad condition (Martins-Neto 2001: fig. 2, pl. 2). Even its attribution to the †Locustopsoidea is not supported, as noticed by Heads and Martins-Neto (2007: 283).

If we compare †*Pseudoacrida sennlaubi* sp. nov. to the other locustavid genera, †*Pseudoacrida sennlaubi* sp. nov. differs from †*Schwinzia* Zessin, 1983 (early Jurassic of Germany) in the longer ScA reaching the level of the base of RP, and the absence of branches of CuA+CuPaα (Zessin 1983: fig. 5). †*Plesioschwinzia* Zessin, 1988 (early Jurassic of Germany), †*Liadolocusta* Handlirsch 1906 (early Jurassic, Germany, revised with a poor figure by Bode 1953: pl. 5, fig. 74), †*Parapleurites* Brauer, Redtenbacher and Ganglbauer, 1889 (Jurassic, Russian Federation), †*Cratozeunerella* Martins-Neto 1998, and †*Cratolocustopsis* Martins-Neto, 2003 (Crato Formation) have a short ScA, a broad area between C and RA in distal part of wing, and a short CuA separating from M well distal to a longer CuPaα, unlike †*Pseudoacrida sennlaubi* sp. nov. (Zeuner 1942; Bode 1953; Sharov 1968: fig. 35E; Zessin 1983: figs 40-41, 1988: fig. 6; Martins-Neto 1998: fig. 2; Martins-Neto 2003: fig. 6). Also, their CuA+CuPaα are not making a strong anterior curve. The attribution of these taxa to the †Locustavidae would need a re-examination.

†*Phaneropterites* Handlirsch, 1906 (type species *P. germari* Münster, 1828, late Jurassic, Germany), is putatively put in the genus †*Locustopsis* by Zessin (1983: fig. 31). Together with †*Conocephalella* Strand, 1928 (replacement name for *Conocephalites* Handlirsch, 1906, late Jurassic, Germany), they are poorly known taxa hardly comparable to any other †Locustopsidae (Deichmüller 1886: pl. 2, fig. 12; Zeuner 1942: pl. 1, fig. 13).

The two species of the genus †*Locustrix* Martins-Neto, 2003 (†*L. gallegoi* Martins-Neto, 2003 and †*L. audax* Martins-Neto, 2003, Crato Formation) have short ScA, not reaching the level of the base of RP. The forewing of †*Locustrix audax* is very incompletely known with nearly no information on all the medio-cubital-anal areas (Martins-Neto 2003: fig. 2D). †*Locustrix gallegoi* has a better preserved forewing, with vein M two-branched and a small area between CuA+CuPaα and CuPaβ (Martins-Neto 2003: fig. 2E).

Gorochov et al. (2006) included the early Jurassic genus †*Orichalcum* Whalley, 1985 (UK) in the †Locustopsinae. This genus was originally in the †Triassomanteidae Tillyard, 1922. It shares with the later family the presence of specialized vein between M and RP (an anterior branch of M ending into RP?) that is absent in the †Locustopsidae. It strongly differs from †*Pseudoacrida sennlaubi* sp. nov. in the broad area between RA and C in its distal part, and a very short basal free part of CuA (Whalley 1985: fig. 21).

†*Araripelocusta* Martins-Neto, 1995 (Crato Formation) and †*Britannacrida* Gorochov et al., 2006 (early Cretaceous, UK) have a very short CuA, transverse between M+CuA and CuA+CuPaα, and a simple M (Martins-Neto 1995: figs 4-5; Gorochov et al. 2006: fig. 36). †*Zeunerella* Sharov, 1968 (Cretaceous), †*Locustopsis* Handlirsch, 1906 (Jurassic - early Cretaceous), †*Mesolocustopsis* Hong and Wang, 1990 (early Cretaceous, China and UK), and †*Zessinia* Martins-Neto, 1990 (early Cretaceous, UK and Crato Formation) have also a very short CuA but a branched M (Zeuner 1942; Zessin 1983; Martins-Neto 1990: figs 1-3, 2003; Hong and Wang 1990; Gorochov et al. 2006: figs 31-33).

†*Zessinia vikingi* Martins-Neto, 2003 is an enigmatic species, based on fossils with incompletely known forewings in which the basal part of CuA is not preserved. Thus its attribution the genus †*Zessinia* is not accurate (Martins-Neto 2003: fig. 4). But, after Martins-Neto, 2003: 221), its forewing ranges from 29 to 32 mm long and 6 mm wide, vs. 39.2 mm long and 5.3 mm wide for †*Pseudoacrida sennlaubi* sp. nov. (much elongate and narrow wing); and its base of RP is distal to fork of M, vs. opposite in †*Pseudoacrida sennlaubi* sp. nov.

†*Pseudoacrida costata* Lin, 1982 (early Cretaceous of China) strongly resembles †*Pseudoacrida sennlaubi* sp. nov. in the general pattern of the veins ScA, ScP, R and M, and veinlets and crossveins in costal area; base of RP opposite first fork of M; the basal part of CuA emerging at right angle from M+CuA and being very long before its fusion with CuPaα; and simple CuA+CuPaα; The main differences are the area between CuA+CuPaα quite narrower in

†*Pseudoacrida costata* than in †*Pseudoacrida sennlaubi* sp. nov., and the presence of only four branches of RP in †*P. costata* vs. five in †*Pseudoacrida sennlaubi* sp. nov. (Lin 1982: pl. 30, fig. 7). The patterns of coloration are also quite similar except for the broad darkened zone at wing apex in †*Pseudoacrida sennlaubi* sp. nov. These differences do not justify a genus separation between the two taxa.

Paleobiogeographic implications in central Gondwana

The Gondwana landmass breakup involved profound tectonic and geologic events and resulted, *inter alia*, in the separation of South America from Africa and subsequent major speciation events. Daly et al. (1989) indicated that the rifting in the South Atlantic occurred progressively from south to north along reactivated older tectonic lineaments dating from the late Triassic–early Jurassic. The separation of South America + Parana and South Africa (Seton et al., 2012), corresponding to the paleolatitude of the Crato Formation, occurred during the end of the Early Cretaceous. According to temporal estimate of the ‘Central’ segment of the South Atlantic margin opening, based on a widespread Aptian salt basin formation, the separation in the Benue Trough was at least 118 Ma (Nürnberg and Müller 1991). However, Torsvik et al. (2009) refined the opening history in this section, suggesting that seafloor spreading only reached north of the Walvis Ridge – Rio Grande Rise at *ca.* 112 Ma. Thereby, direct faunistic transfers between the two landmasses of South America and Africa were still possible during the late Early Cretaceous.

Reconstruct the paleobiogeographic history of taxa is rarely easy because of the scarce fossil record but the geological history of major tectonic blocs or continents is of great help to better refine the proposed hypotheses.

Like many extinct families, the †Locustopsidae and the †Elcanidae had wide distributions during the Cretaceous. The †Locustopsidae differ from many other fossil insect families in having African (Gondwana) representatives. In fact, †*Locustopsis africanus* Ansorge, 1991 described from the Lower Cretaceous of Egypt is direct evidence of the presence of the family in the North-Est Gondwana (Ansorge 1991). This deposit is older than the CKL, but the Gondwana was united as a single entity at this time. Later, during the Albian, the CKL was a part of a broad intra-continental savanna, relatively dry with seasonal precipitation, extending at the same latitude in central Africa (Fig. 4) (Sewall et al. 2007; Chaboureau et al. 2012). This peculiar palaeobiogeography and the record of two different representatives of the family on both Gondwana blocks, associated with uniform palaeoclimatic conditions may explain the radiation of the family between South America and Africa and thereby and the record of †*Pseudoacrida sennlaubi* sp. nov. in the Crato Formation. Its presence in South America before the complete separation of this landmass from Africa suggests that the family †Locustopsidae was present in the Central Gondwana region (in the Eastern part of South America) during the early Cretaceous (Fig. 4). Thereby, the †Locustopsidae present around the Crato paleolake may have radiated from or towards the African mainland in a homogenous biome, colonizing new areas under similar palaeoclimatic conditions (Fig. 4). Unlike taxa that fly badly, the Orthoptera, especially those with locust-like tegmina, fly very well and are able to disperse over a great distance, even in the past (Ataabadi et al. 2019). This ability has surely contributed to the wide distribution of both †Locustopsidae and †Elcanidae. Additionally, these insects were not constrained in central Africa by a large arid desert zone (Sewall et al. 2007) and putatively able to reach the outskirts of this zone in forest with abundant food or around paleolake with fresh vegetation.

The †Elcanidae does not have African Cretaceous representative but several species are known from the West Burma Block (WBB) (Gu et al. 2020). This block possesses a particular paleobiogeographic history resulting in putative faunal input from Gondwana (*e.g.* Jouault and Nel 2020; Poinar 2018), late input from Laurasia (Jouault 2021), and was isolated long enough for an endemic fauna to develop there (*e.g.* Jouault et al. 2021). In fact, the WBB has experimented with a tumultuous geological history with a long migration from Gondwana. The WWB was located near the Australian block in East Gondwana during the Early Jurassic (Seton et al. 2012; van Hinsbergen et al. 2012) and break-up from the Gondwana + Australian block between the Late Jurassic and the Early Cretaceous (Heine et al. 2004; Heine and Müller 2005). Westerweel et al. (2019) refined these estimates and agreed with previous works, suggesting that the separation dated back *ca.* 125 Ma and assumed that the Terrane became an isolated island in the Meso-Tethys only after *ca.* 120 Ma. The main Burmese amber deposit i.e. Noije Bum was therefore completely isolated from the Gondwana or the Laurasia during the resin formation and production during *ca.* 20 Ma (Heine et al. 2004; Seton et al. 2012; Licht et al. 2020). Therefore, the †Elcanidae trapped in Burmese amber may originate from Laurasia or Gondwana depending on the faunal transfer. Interestingly, representatives of the †Elcaninae subfamilies are known from the CKL and from the WBB (Kočárek 2020). We may assume that the Gondwana elcanine fauna has colonized the WBB throughout South Africa prior to the separation of the block from the South-east Gondwana, but additional evidence and investigation in Southern Africa, maybe in the Orapa deposit, will be needed to confirm this hypothesis.

Conclusion

The descriptions of †*Cratoelcana rasnitsyni* sp. nov. and †*Pseudoacrida sennlaubi* sp. nov. highlight the underestimated orthopteran diversity in the Crato Formation. Regarding the numerous fossils of the order (Orthoptera), the distinctive coloration patterns or diagnostic wing venation recorded on specimens documented in the literature, it is urgent to review all the orthopteran fauna of Crato Formation and provide an exhaustive inventory of its diversity. The key position of the Crato Formation deposits, close to the separating point of South-America and Africa before the Gondwana break-up, allows to document the faunas of the central part of the Gondwana during the Lower Cretaceous. Therefore, documenting the insect fossils of this unique deposit allows to infer potential scenarios of migrations or diversifications between South-America and Africa which help in understanding the evolutionary history of many clades.

Among the fossils described herein, †*Pseudoacrida sennlaubi* sp. nov. is of great interest because it is new case of a very broad distributions of an insect genus during the early Cretaceous, ranging from China to South America. Similar situations are known in the Neuropteran family Mesochrysopidae with several genera present in China, Spain and the Crato Formation (Nel et al. 2005; fossilworks database). These taxa are certainly more ancient, probably of a Jurassic origin. The description of †*Cratoelcana rasnitsyni* sp. nov. also points the limits of the placement of †*Cratoelcana zessini* in the genus †*Cratoelcana* and indicates that a new genus will surely have to be described to accommodate this fossil species.

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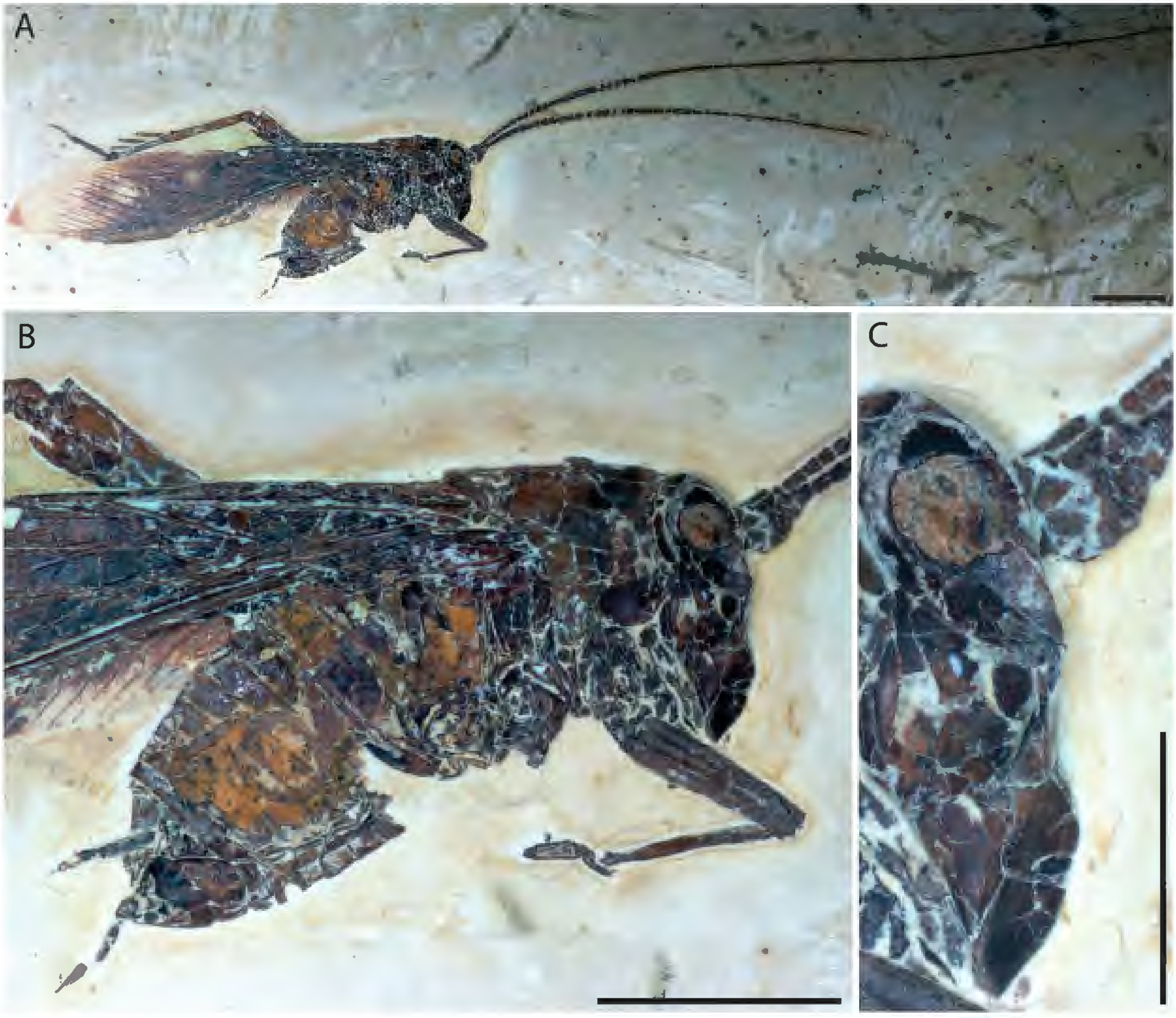
Figure caption:

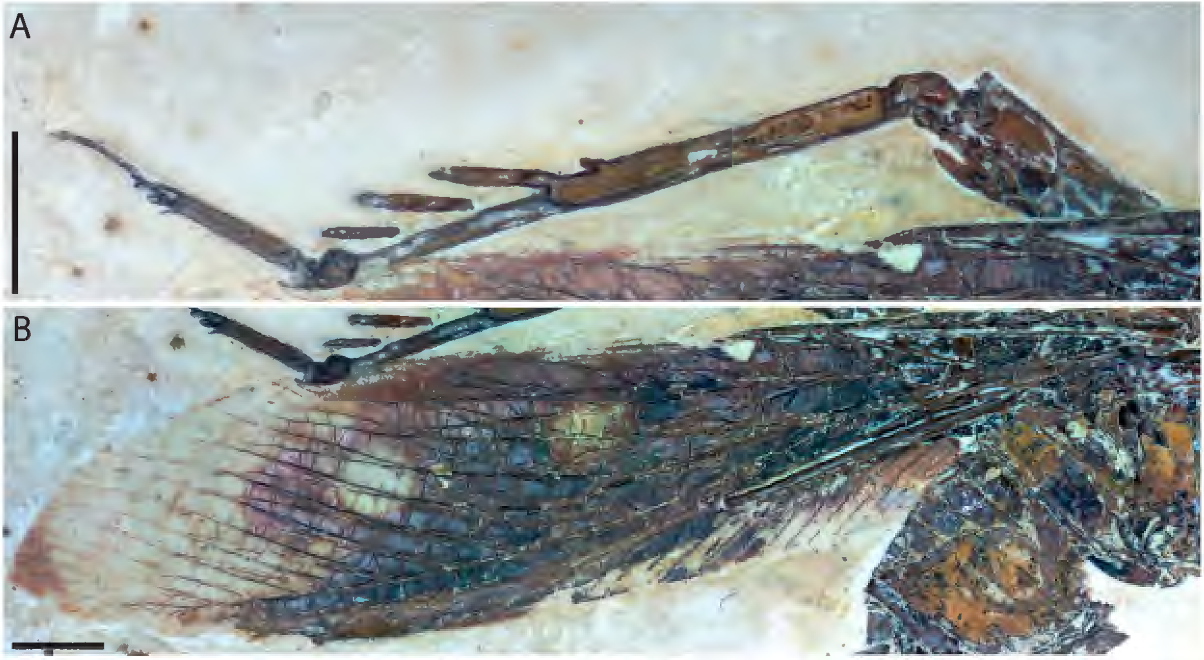
Figure 1. *Cratoelcana rasnitsyni* sp. nov., holotype 13068. (A) habitus in lateral view; (B) detailed view of body; C) detailed view of head. Scale bars: 5 mm (A, B); 2.5 mm (C).

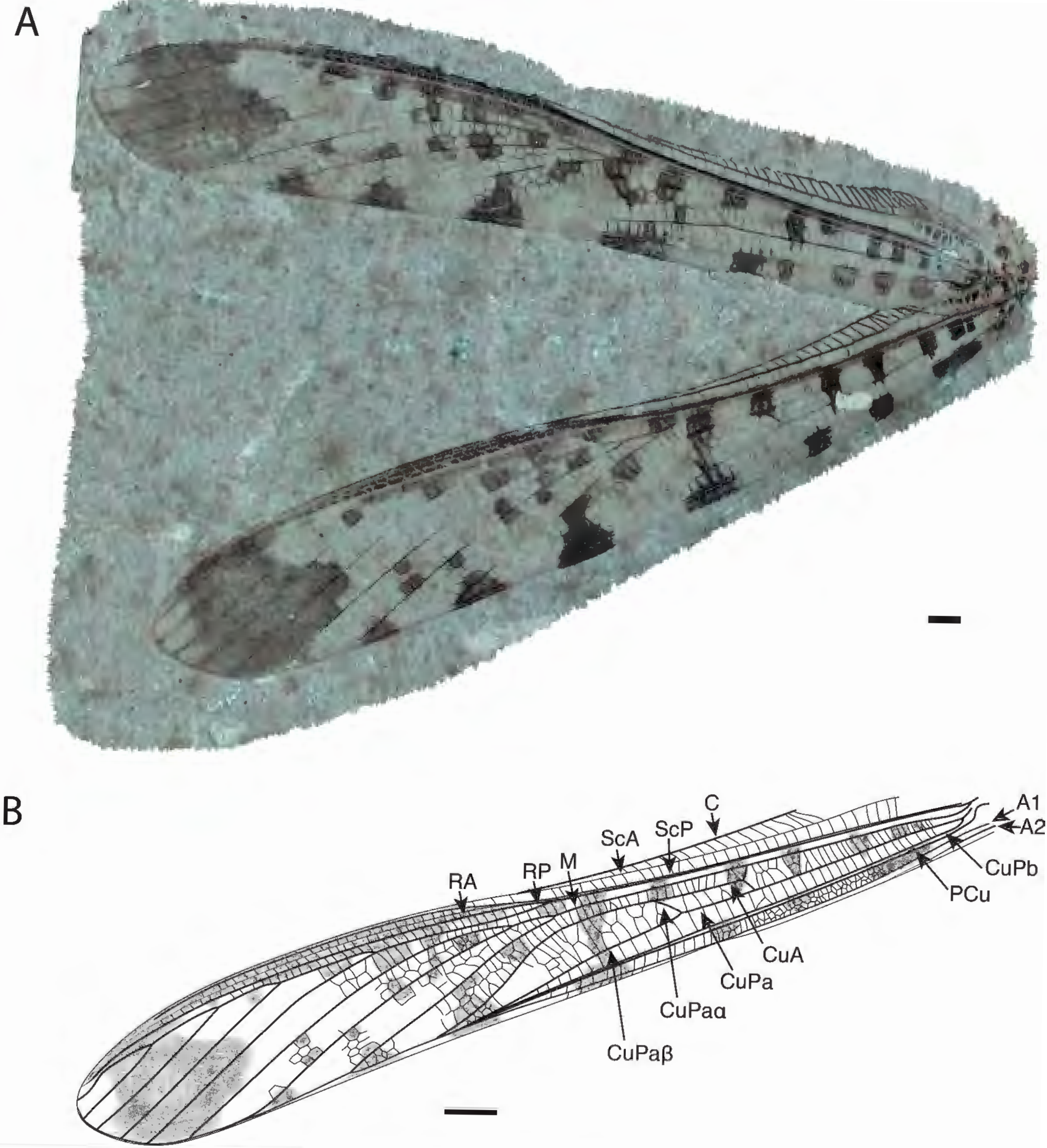
Figure 2. *Cratoelcana rasnitsyni* sp. nov., holotype 13068. (A) detailed view of hind tibia; (B) detailed view of wings. Scale bars = 2.5 mm (A); 2 mm (B).

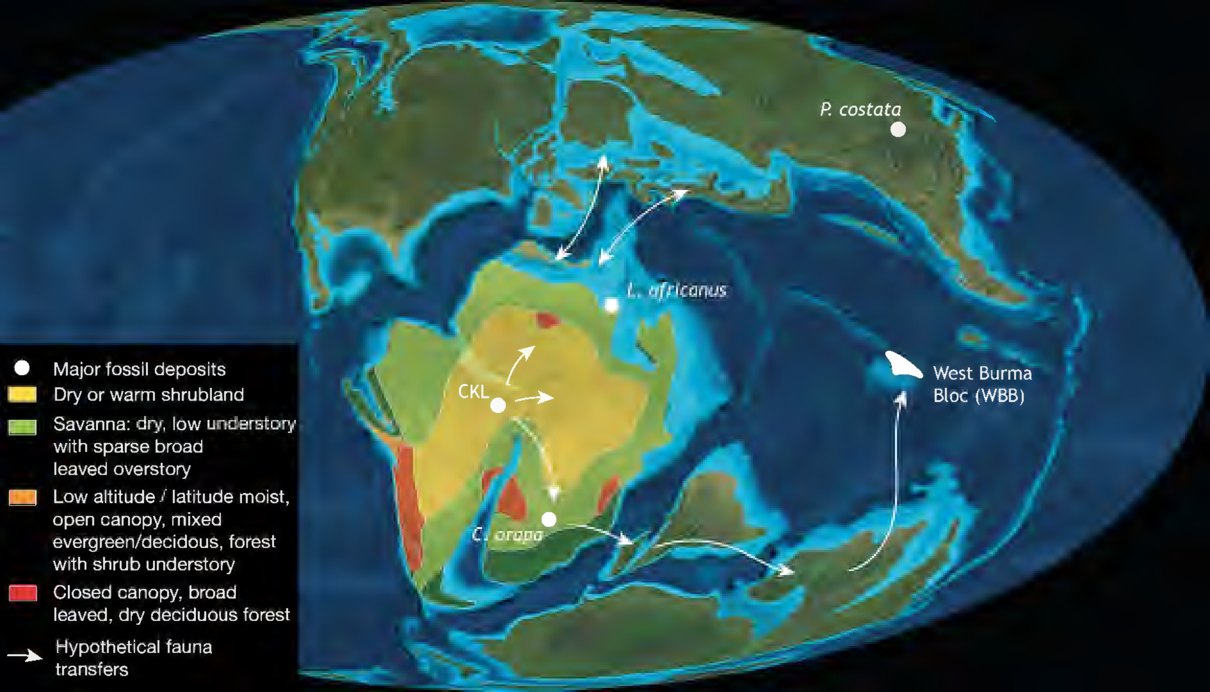
Figure 3. *Pseudoacrida sennlaubi* sp. nov., holotype 16049. (A) detailed view of hind tibia; (B) interpretative line drawing of wing venation with names of veins labelled. Scale bars = 1 mm (A); 2 mm (B).

Figure 4. Paleomaps of Albian period (modified from Scotese, 2014) with over imposed climatic conditions from Sewall et al. (2007).


A
B
C


A
B


A
B
C
ScA
ScP
A1
A2
RP
M
RA
CuPb
PCu
CuA
CuPa
CuPaα
CuPaβ


P. costata
L. africanus
West Burma Bloc (WBB)
CKL
C. orapa
● Major fossil deposits
Dry or warm shrubland
Savanna: dry, low understory with sparse broad leaved overstory
Low altitude / latitude moist, open canopy, mixed evergreen/decidous, forest with shrub understory
Closed canopy, broad leaved, dry deciduous forest
→ Hypothetical fauna transfers