

# First 3D reconstruction of a forewing of a fossil Orthoptera: Interpreting the venation pattern in the smallest known cricket with a stridulatory apparatus, †*Picogryllus carentonensis* (Orthoptera, Grylloidea, Oecanthidae)

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## Abstract

Fossil insects are valuable indicators of the evolutionary history of the clades to which they belong. According to their state of preservation, fossil insects are often partially described for key morphological characters, such as forewing venation in crickets (Orthoptera, Grylloidea). In parallel, the use of 3D microtomography is increasingly becoming common for studying some fossils, which allowed here the precise reconstruction and interpretation of the venation pattern in the smallest known cricket with a stridulatory apparatus, †*Picogryllus carentonensis*, found in opaque amber. The 3D reconstructions have revealed the general structure of the venation of the forewing and have enabled the identification of all its veins and cells, validating its similarity with that of extant crickets. Putative homologies are established according to previous studies, and some particularities are observed, such as the presence of two crossveins in the mirror, a rare feature in extant crickets that is discussed in the frame of cricket venation evolution. These findings highlight the importance of 3D microtomography as a powerful tool for examining fossil insects and also provide crucial information for taxonomic identification and evolutionary studies, offering a validated morphological basis for future phylogenetic analyses incorporating fossils.

## Key Words

evolution, Grylloidea, homology, microtomography, morphology

## Introduction

Wings have been a main key driver of the evolution of insects since the Devonian-Early Carboniferous (Grimaldi and Engel 2005), and for over two centuries, the venation patterns of the wings of insects have been harshly debated. Neither the number of main veins present in insect wings (e.g., Comstock and Needham 1898, 1899; Snodgrass 1935; Kukulová-Peck 1991), nor the criteria to identify them is yet universally settled and accepted (see Schubnel et al. 2020). This situation resulted in the simultaneous use of different venation

paradigms, impeding the safe reconstruction of wing evolution in the megadiverse clade of insects. The recent use of 3D microtomography helps to reconsider the question for these falsely-flat structures (Schubnel et al. 2023). Microtomography gives access to the very base of the wing, showing the basivenal structures from which veins emerge. Using the basivenal origins of the veins as criteria for vein homology and identification, and combining them with vein polarity *sensu* Kukulová-Peck (1991), Schubnel et al. (2020) studied the venation of a large sample of Neoptera insects and proposed a general pattern of venation with seven main veins, i.e., the costal

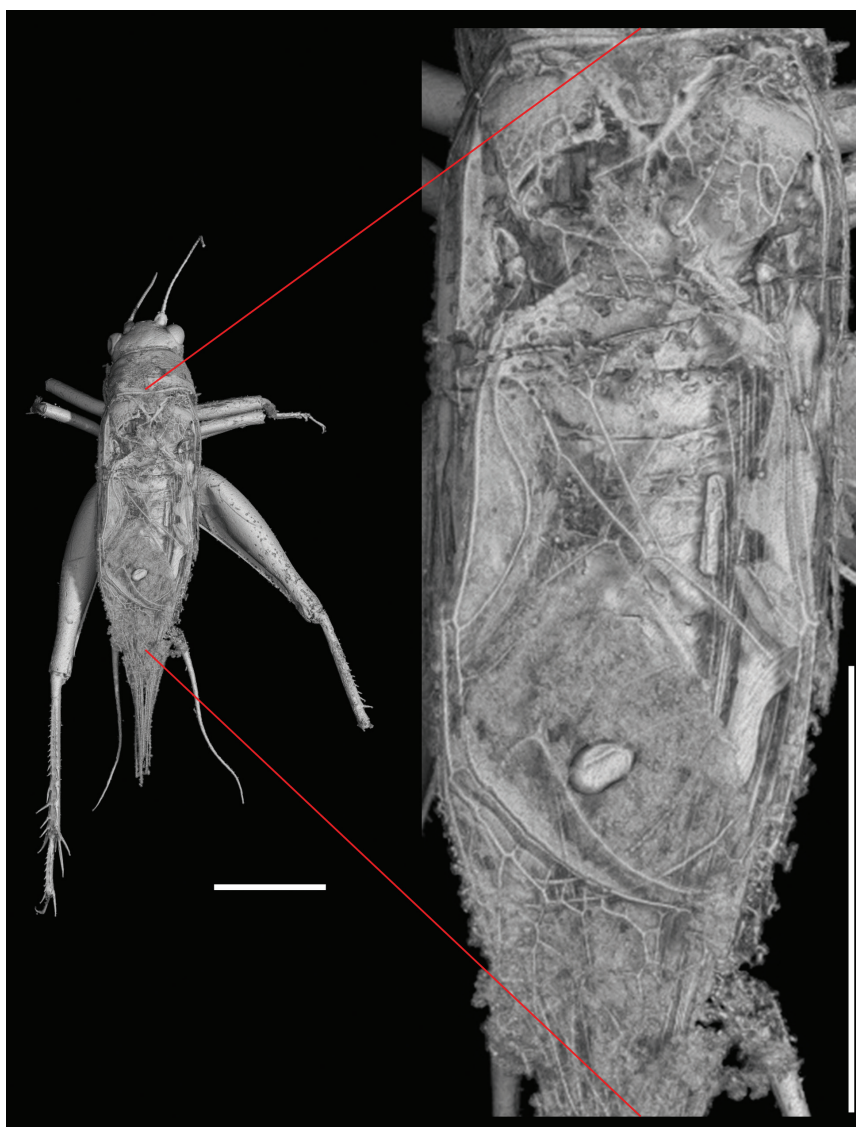
(C), subcostal (Sc), radial (R), median (M), cubital (Cu), postcubital (PCu) and anal (A) veins.

Orthoptera (grasshoppers, locusts, katydids, crickets, and their allies) presents a venation pattern to which the theoretical pattern of Schubnel et al. (2020) applies very well. Previously, Béthoux and Nel (2001, 2002) proposed a general venation pattern for the superorder Archaeorthoptera (or total group of Orthoptera), identifying several putative apomorphies of the Orthoptera. Schubnel et al. (2020) validated this pattern, modified by the identification of the PCu vein, and confirmed orthopteran putative apomorphies.

Among Orthoptera, Ensifera has experienced high modifications of wing venation in relation to particular uses of the wings, mainly leaf mimicry (Tettigonioidae: Mugleston et al. 2013, 2016; Garrouste et al. 2016), and acoustic communication (Ensifera: Tettigoniidae and Gryllidae: Desutter-Grandcolas et al. 2017). The rearrangement of the veins in these particular functional and / or selective frames may complicate their identification. This is particularly true when considering fossils, as most adults are preserved

as imprints, except for some smaller species preserved in amber (e.g., Gorochov 2010; Desutter-Grandcolas et al. 2021), with very often incomplete wings and difficulties in following vein trajectories (Gorochov 1995). Josse et al. (2023) analysed the pattern of venation of the cricket clade (Ensifera, Gryllidae, Grylloidea and Gryllotalpoidea), well-known for their production of acoustic signals. Sampling both fossil and extant cricket families, and following Schubnel et al. (2020), these authors studied not only the structures responsible for sound production, but the whole forewing venation; they finally proposed hypotheses of vein and cell identities according to precise homology criteria.

The Cretaceous fossil †*Picogryllus carentonensis* Josse and Desutter-Grandcolas, 2023 is the smallest cricket with a full stridulatory apparatus ever described, measuring 3.3 mm in body length. This specimen is exceptionally well-preserved (Fig. 1), enabling a nearly complete description of its body as for an extant species (Desutter-Grandcolas et al. 2023). Its right forewing is damaged, but thanks to the usual superposition of the



**Figure 1.** 3D reconstruction images of †*Picogryllus carentonensis* in dorsal view (from Desutter-Grandcolas et al. 2023). Scale bars: 1 mm.

right (above) and left (below) forewings in crickets, the left forewing is almost fully complete (Fig. 2A, B).

In the present paper, we present the 3D reconstruction of the left forewing venation of †*P. carentonensis*, which is the first 3D reconstruction of the forewing venation in an ancient fossil cricket. We discussed the application of the venation pattern proposed by Béthoux and Nel (2001, 2002) for orthopteran fossils, Schubnel et al. (2020) for neopteran insects, and Josse et al. (2023) for crickets, identifying its putative synapomorphies with the cricket clades and its putative particularities.

## Material and methods

### Studied material

†*Picogryllus carentonensis* was unearthed from a piece of completely opaque amber retrieved in the A1s1-S layer at the Font-de-Benon quarry in Charente-Maritime, France (Desutter-Grandcolas et al. 2023, see figs 1, 2). This amber piece dated back to the Late Albian to Early Cenomanian period, approximately 100 million years ago (Néraudeau et al. 2002; Dejans and Masure 2005; Peyrot et al. 2005; Polette 2019). It has been described in the Podoscirtinae subfamily of the Oecanthidae family (Campos et al. 2022; Desutter-Grandcolas et al. 2023). The amber piece containing †*P. carentonensis* is deposited at the Institut de Géoscience de Rennes, Université de Rennes, France (reference number IGR.ARC-421.1).

### Fossil imaging and 3D reconstructions

The examination of †*Picogryllus carentonensis* involved propagation phase-contrast X-ray synchrotron microtomography (PPC-SRμCT) at the European Synchrotron Radiation Facility (ESFR) beamline ID19 in Grenoble, France. This technique followed the established procedure outlined by Lak et al. (2008). The scanning parameters were set at 30 keV, a propagation distance of 900 mm, and an isotropic voxel size of 20.24 μm. A total of 2 500 projections were captured over a 180° range, with each projection exposed for 0.2 seconds. For the initial analysis of the tomographic data, VG StudioMax (Volume Graphics) was employed, as detailed in the methodology provided by Desutter-Grandcolas et al. (2023). The data used for reconstructions in this study consisted of 2D microtomographic scans in JPEG 2 000 format. These scans were taken in the three spatial planes: X, Y, and Z, resulting in 1 256 scans for X, 1 347 scans for Y, and 1 037 scans for Z.

The 3D reconstructions of the forewing of †*P. carentonensis* were made using Avizo Lite 9.5.0 software from Thermo Fisher Scientific. The “Surface view” function within the software facilitated the visualization and study of these reconstructions. Utilizing the insights from these 3D reconstructions, illustrations of the left forewing were produced using Microsoft PowerPoint 2021.

### Venation paradigm

We are using the venation pattern of Josse et al. (2023) for crickets (Orthoptera, Gryllidea) and the paradigm proposed by Béthoux and Nel (2001, 2002) modified by Schubnel et al. (2020). Each of the recognized seven main veins is identified along the whole wing length, from the base (basivenal structures) to the tip. The wing is separated into a lateral and a dorsal field, located respectively along and above the body. We also follow the orientation currently used to describe wing venation, separating anterior vs posterior and proximal (= basal) vs distal margins (Fig. 3).

### Abbreviations

The following abbreviations and colours are listed below, and follow Josse et al. (2023):

#### Main veins and their bifurcations:

**A:** anal (brown);  
**C:** costa (yellow);  
**Cu:** cubitus (orange);  
**M:** media (blue);  
**PCu:** postcubitus (green);  
**R:** radius (pink);  
**Sc:** subcosta (red);  
**“X”A:** anterior branch of “X” vein (light colour);  
**“X”P:** posterior branch of “X” vein (dark colour);  
**“X”A/P; a, b; α, β; 1, 2:** successive dichotomies of main branches of veins in Orthoptera.

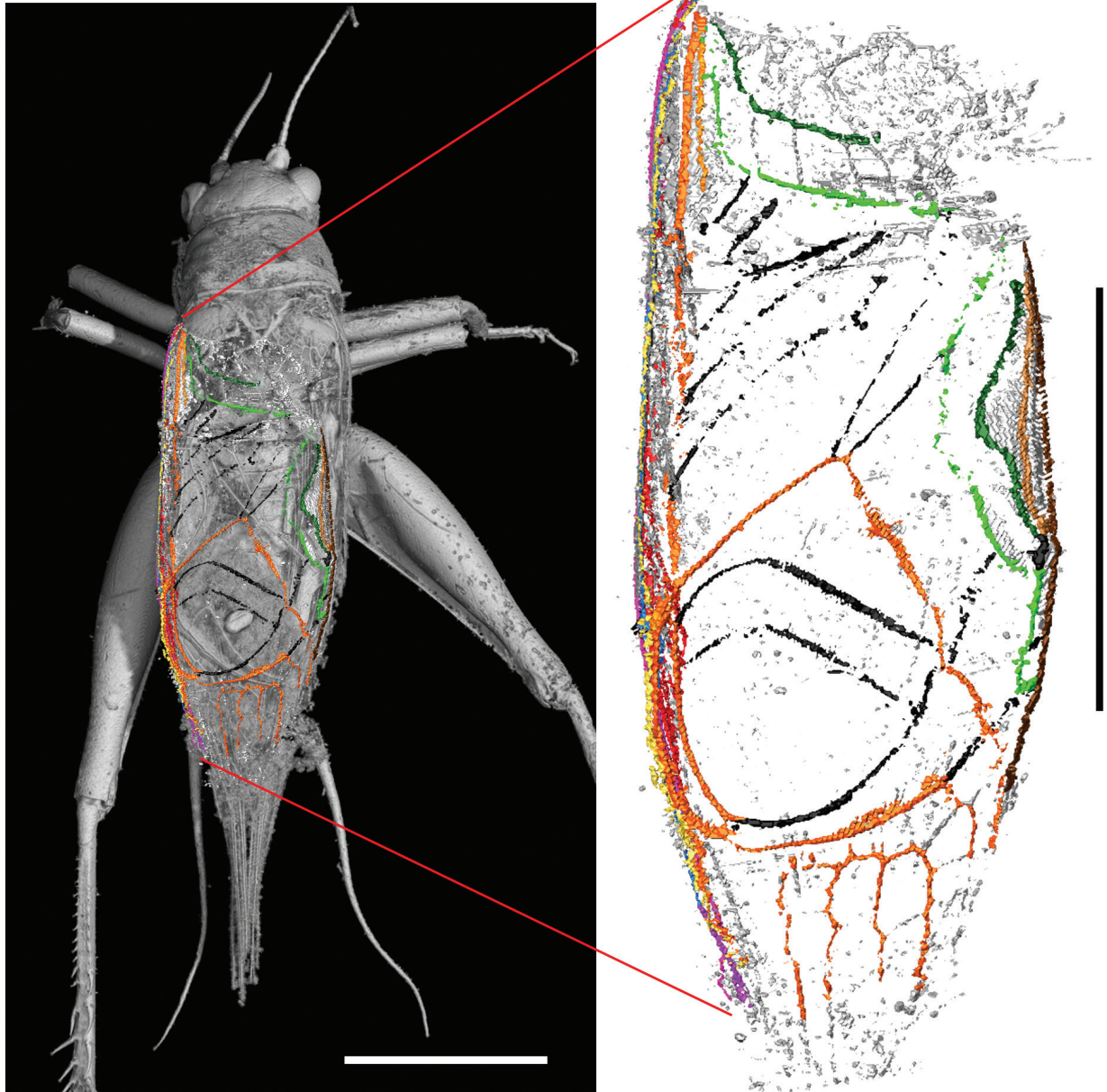
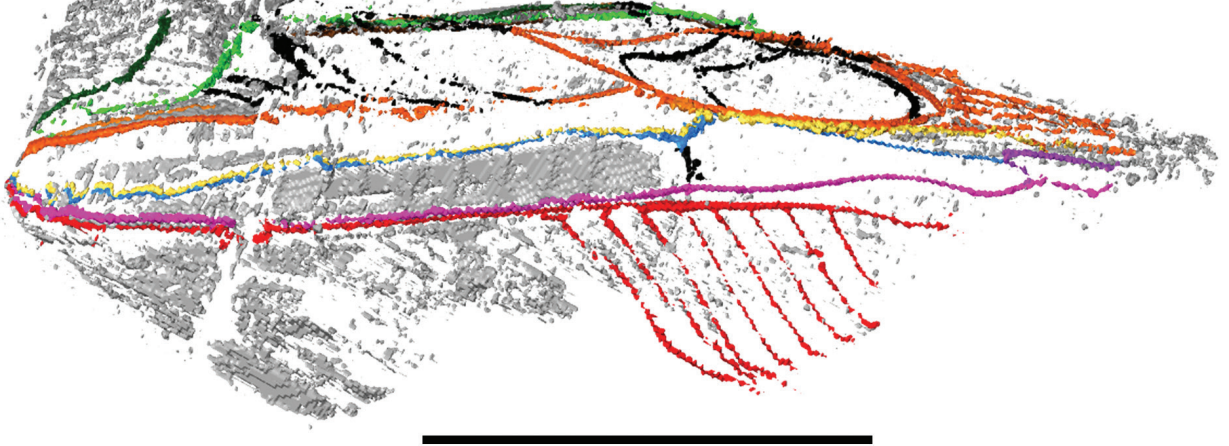
#### Reinforced crossveins (black in figures):

**d1:** diagonal 1 (crossvein between CuPaα and CuPaβ);  
**d2:** diagonal 2 (crossvein between CuPaβ and PCuA);  
**pi:** or pilar (crossvein between, or close to PCuA and the point of contact of CuPaβ with d2);  
**r-m:** crossveins between R and M;  
**s1, s2:** septum 1 and 2 (crossveins between CuPaα2 and CuPaβ);  
**t1, t2:** transverse 1 and 2 (distal crossveins between CuPaβ and PCuA);  
**t3 to t5:** transverse 3 to 5 (distal crossveins between PCu branches and anal branches).

#### Forewing (FW) cells:

**ac:** anal cell;  
**c1, c2, c3:** cell 1, 2, 3;  
**ha:** harp;  
**lc:** lanceolate cell;  
**mi:** mirror;  
**para-mi:** para-mirror;  
**sub-c1, c2:** sub-cell 1, 2, located distally to cells c1, c2;  
**sub-mi:** sub-mirror.



**A****B**

**Figure 2.** 3D reconstructions of venation of left forewing of †*Picogryllus carentonensis*. **A.** Dorsal view; **B.** Latero-dorsal view. Scale bars: 1 mm.

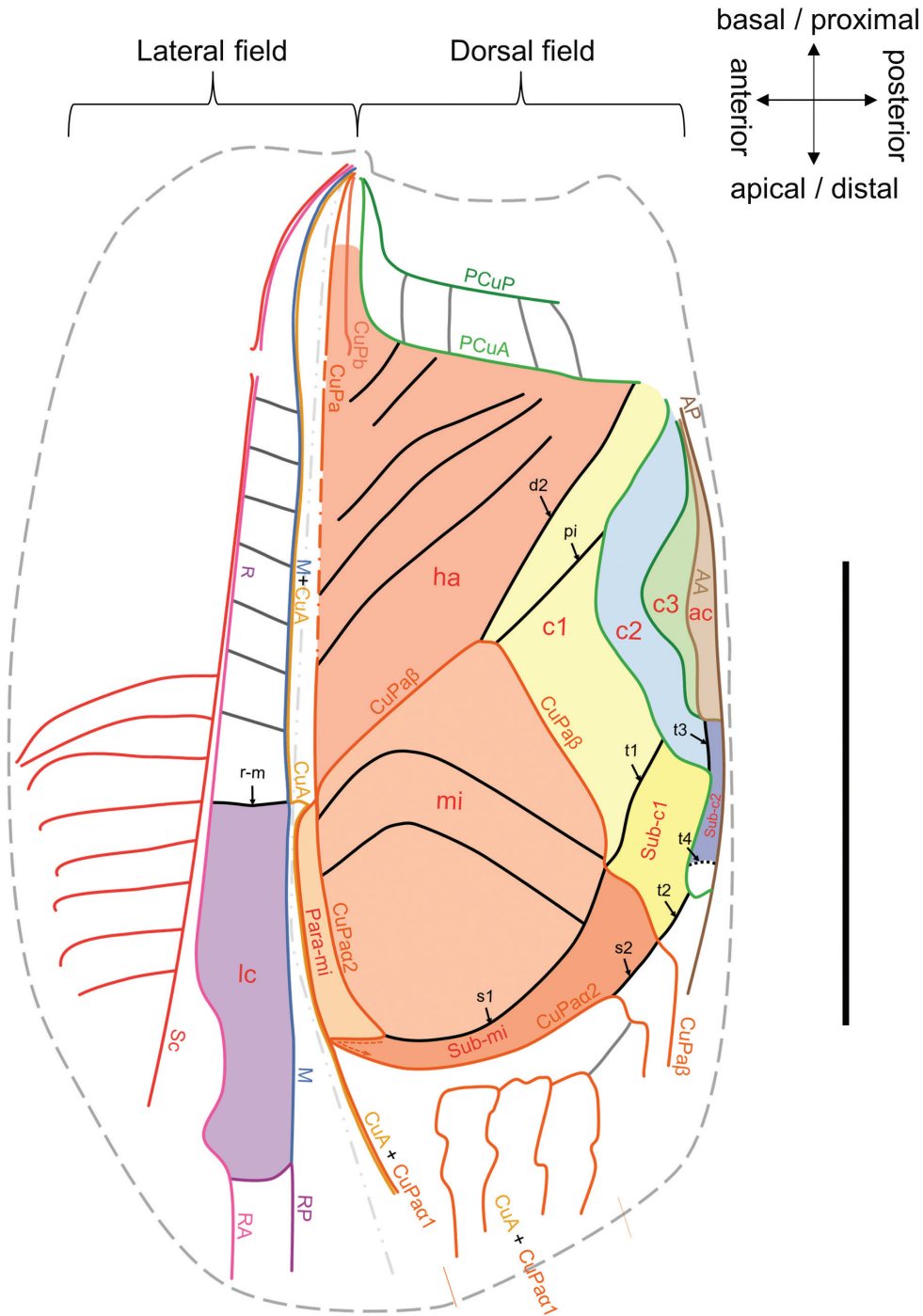
## Results

### 3D reconstructions of the venation of the forewing in †*Picogryllus carentonensis*

The left FW of †*Picogryllus carentonensis* has been protected by the right FW. It is nearly complete, except for the base of anal area and the antero-basal area of the lateral field, which could not be completely reconstructed. Also, the teeth of the stridulatory file, located on the PCuA vein, could not be counted, because of the scan precision and the size of the fossil.

The general structure of the FW of †*P. carentonensis* is similar to that of modern crickets, with a dorsal field and a lateral field clearly separated by a median fold located between CuPa and M+CuA. Distally to this fold, the fan, i.e., a thinner part of the wing membrane, extends between the two fields. The fossil has the lateral fields of the forewings vertical along the insect body, nearly at right angle with the dorsal field, which is flat over the insect dorsum (Figs 1, 2).

**Lateral field** (Fig. 3): Wide; maximum width as large as about 3/4<sup>th</sup> of dorsal field maximum width; length about 4/5<sup>th</sup> of dorsal field length. Three main veins and



**Figure 3.** Interpretive drawing of venation pattern of left forewing of †*Picogryllus carentonensis*, following terminology and colours as in Josse et al. (2023). Fold separating lateral and dorsal field represented by a dashed-dotted line. Scale bar: 1 mm.

their branches visible, i.e., Sc, R and M+CuA, emerging from very close or maybe merged into bullae basivenal. C not visible or absent. Sc long, reaching lateral field apex, pectinate, with branches directed towards anterior edge of wing and occupying most of lateral field, with at least eight visible distinct oblique branches directed anteriorly. R long, bifurcating into RA and RP very distally, at apical end of lateral field. Sc and R parallel and very close on 3/4<sup>th</sup> of lateral field length. M+CuA long, bifurcated in M and CuA at 2/3<sup>rd</sup> of wing length. R and M+CuA are clearly divergent from their bases becoming almost parallel from 2/4<sup>th</sup> of field length, both veins connected by at least seven oblique, weak crossveins plus a reinforced r-m, limiting basally lanceolate cell; r-m rather perpendicular to R and M. Lanceolate cell long and narrow, located in fan between R and M, approximately 4.5 times longer than wide; with a very slight constriction between R and M at its base at level of r-m. RA straight part directed towards distal end of wing, in continuity of R; RP proximally curved, joining M and merging with it, delimitating apical end of lanceolate cell; distally RP separating again from M and with a distal rectilinear vein in continuity of M. M+CuA bifurcating into M and CuA slightly distal to r-m; M straight towards distal edge of wing and posteriorly limiting lanceolate cell to join and merge with RP distally, in fan. MA or MP not visible or absent. CuA very short, crossing median fold and reaching CuPa posteriorly.

**Dorsal field:** Dorsal field slightly longer and about 1.5 times wider than lateral field. Three main veins and their branches visible: Cu(P), PCu and A. CuP and PCu bases visible, base of Anal veins not visible. CuP bifurcating in CuPa and CuPb from its base. CuPa long, straight, parallel to M+CuA and longitudinal axis of wing over half dorsal field length, bifurcating in CuPaa and CuPaβ at beginning of dorsal field lower 1/3<sup>rd</sup>; CuPaa immediately dividing into CuPaa1 and CuPaa2; CuPaa1 immediately merging with CuA as CuA+CuPaa1, CuPaa2 continuing distally to CuPa with a trajectory parallel to CuA+CuPaa1. CuPb reduced to a short vein (about 1/6<sup>th</sup> of wing length) parallel to CuPa. PCu bifurcating in PCuA and PCuP from its base, both clearly divergent at their base, then curved at 90° before running parallel to the wing posterior edge. Distal to interrupted zone of PCuA and PCuP, both veins with curved and convex anterior trajectories. Anal node and plectrum not visible. Anal veins not preserved at their bases, but visible more distally with trajectories closely following posterior edge of wing. AA slightly curved and convex anteriorly, AP rather straight. Harp longer than wide (Table 1), right-angled and triangle shaped, maximal length greater than half field length; at least five oblique crossveins connecting CuPa to PCuA. ‘Diagonal’ vein (postero-distal limit of harp) composite, made of a part of CuPaβ, proximally curved, and d2, a reinforced crossvein joining ‘elbow’ of CuPaβ to PCuA at anal node. Mirror medium-sized (Table 1), rather rounded distally, but with straighter edge proximally, because of elbow shape of CuPaβ; crossed by two proximally convex crossveins; distal edge flanked by two long and thin cells, i.e., para-mirror and sub-mirror.

Ant-mirror cell absent (d1 absent). Para-mirror longer than wide (Table 1), slightly widening distally, extending along a large part of mirror anterior edge; distally closed by a zig-zag shaped CuPaa, joining CuA+CuPaa1 at one point, before resuming its trajectory towards posterior edge. Sub-mirror longer than wide, longer than para-mirror, gradually widening posteriorly, along distal edge of mirror in continuity with para-mirror, separated from mirror by a long s1. Distal edge of sub-mirror limited by a part of CuPaa2 and a short s2, which connects it with CuPaβ; s2 shorter than s1. Apical field occupied by CuA+CuPa branches, stem vein of CuA+CuPa stronger and in the continuity of CuPa. Posterior field well preserved, with clear c1, c2, c3, sub-c1, sub-c2 and ac. Sub-c3 difficult to see, very small or absent. Cell c1 long and wide, crossed by pi (Table 1), limited distally by a long t1 (Table 1) aligned in continuity with s1; sub-c1 rather large (Table 1), t2 aligned in continuity of s2; c2 longer than wide, narrower than c1, limited distally by t3; sub-c2 longer and narrower; c3 smaller than c1 and c2; ac long and narrow.

**Table 1.** Measurements of veins and cells of left forewing in †*P. carentonensis*.

Veins	Length (in mm)		
Harp anterior edge	1.27		
Harp posterior edge	0.77		
Harp postero-distal edge	1.11		
s1	0.66		
s2	0.13		
Cells	Maximal length (in mm)	Maximum width (in mm)	Ratio length / width
Mirror	0.89	0.65	1.36
Para-mirror	0.54	0.05	10.8
Sub-mirror	0.66	0.18	3.67
c1	0.89	0.22	4.04
Sub-c1	0.42	0.17	2.47

## Discussion

3D reconstructions are increasingly used to examine the venation in insects and propose putative homologies of their veins (e.g., Schubnel et al. 2023). This method can be applied to both extant and fossil taxa, which may facilitate comparative approaches. For fossil crickets, most venation descriptions were made from the observation of imprints. Several well-preserved specimens have been recently described in amber, for which wing venation could be observed and the functional part of the stridulum fully described when present (e.g., Rust et al. 1999; Xu et al. 2020, 2022; Yuan et al. 2022, see fig. 2). Even during the revision process of this paper, Zheng et al. (2023) described two new fossils of Oecanthidae found in Myanmar amber, Cenomanian, upper Cretaceous, i.e., †*Crassicornus maculatus* Zheng, Yuan & Gu, 2023 and †*Ordicalcaratus inconditus* Zheng, Yuan & Gu, 2023, respectively classified in the Oecanthinae and in the Podoscirtinae, and both twice as large as †*P. carentonensis*. These nicely



preserved fossils are described by optic means, thanks to their preservation in clear amber, and increase the number of fossils that are now available to study the Oecanthidae cricket clade. However, optic observations present limitations in terms of resolution and anatomical details, which make homology assessments tricky. Scanning Electronic Microscope has occasionally allowed better observations of wing structures, as demonstrated by the study of the stridulatory vein in a fossil katydid (Gu et al. 2012), the study of the ultrastructure of the wing of an Odonata (Appel et al. 2015), and the study of the wing venation in a Hemiptera (Franielczyk-Pietryra et al. 2023). 3D microtomography is a real progress in the venation study, as shown by the number of papers that use it (e.g., Desutter-Grandcolas et al. 2017; Garwood and Sutton 2010; Walker et al. 2014; Jacquelin et al. 2018; Schubnel et al. 2020, 2023). In the present paper, microtomography allowed the reconstruction of the left forewing of †*P. carentonensis*, although located under the right forewing, and revealed the very details of its venation, despite the precision of the scans not being optimal due to the small size of the specimen. Here, the limitations of microtomography for a specimen of such a small size prevents the reconstruction of the stridulatory file, which in turn could have been used to hypothesize the frequency of the calling song of †*P. carentonensis*. Employing nanotomography for a more detailed scan may be a solution here. However, it is important to note that despite the potential for accessing finer details, the results may not necessarily be better. It would certainly increase the resolution of the reconstructed specimen and that of the interpreted area, but given the apparent damage in these regions, it would probably not help to reconstruct the missing structures. It is anyhow the first time that an almost complete 3D venation pattern is reconstructed in a fossil Orthoptera.

### FW venation in †*Picogryllus carentonensis*

Applying Josse et al. (2023) wing venation patterns for crickets to the reconstruction of the venation of †*Picogryllus carentonensis*, the veins Sc, R, M, Cu, PCu, and A can readily be identified. The base of the Sc is not preserved, which impedes recovering the Costal vein and separates the anterior and posterior branches of Sc. But Sc is pectinate, as observed for ScP in many modern crickets (Josse et al. 2023). †*Picogryllus carentonensis* presents characters identified as synapomorphies of the Orthoptera by Béthoux and Nel (2001, 2002), i.e., the fusion M+CuA and the fusion CuA+CuPa $\alpha$ 1. Also, its two PCu veins (PCuA, PCuP) have the usual shape of these veins, with a strongly curved proximal part (Schubnel et al. 2020).

As in all acoustic crickets, †*P. carentonensis* has a lanceolate cell delimited proximally by r-m and distally by the zigzag-shaped RP; M and CuA separate at the level of the anterior margin of the lanceolate cell; and the two PCu veins run near the posterior margin of the wing, making the so-called chord veins of crickets (Josse et al. 2023). The harp and the c1 cell are separated by

the crossvein d2 (commonly called the diagonal in cricket wing), and the mirror is delimited by CuPa $\alpha$ 2 (anterior margin), CuPa $\beta$  (proximal margins) and the crossvein s1. Finally, an arculus is present, made of the crossvein r-m and the vein CuA after its separation from M (Fig. 3).

As in many Grylloidea, CuP has a posterior branch; when present, CuPb goes usually no further than the most distal harp veins (as in Phalangopsidae crickets for example: see Josse et al. 2023, fig. 3B); in †*P. carentonensis*, CuPb is short, not reaching the most proximal harp veins, as frequently observed in crickets of the supertribe Podoscirtidi (Campos et al. 2022). The mirror is bordered by only two long and narrow cells, i.e., para-mi and sub-mi, and not by the cell sub-c1, which is adjacent to the mirror by one corner. The cell c1 includes the strong crossvein pi, and the mirror is crossed by two parallel, strong crossveins. Finally, the crossvein d1 and the cell ant-mi, sometimes present near the anterior margin of the mirror, are lacking.

Forewing venation in crickets has not been analysed on a firm basis of primary homology setting, although several venation patterns have been hypothesized in the last twenty years (Rasnitsyn and Quicke 2002; Robillard and Desutter-Grandcolas 2004; Béthoux 2008). Josse et al. (2023) proposed a general pattern of FW venation for crickets with acoustic apparatus, which they also apply to male crickets with incomplete apparatus, crickets lacking acoustic structures, and females.

The reconstruction of the FW venation of †*P. carentonensis* generates a pattern that is fully compatible with the proposal of Josse et al. (2023). The homologies proposed by Josse et al. (2023), validated by our own data, will have now to be incorporated in phylogenetic studies of large cricket clades, to test hypotheses of forewing evolution, especially for the shape and limit of the mirror and nearby cells (para-mi, ant-mi, sub-mi), that may delimit vibrating areas. The interpretations of FW venation of †*Crassicorpus maculatus* and †*Ordicalcaratus inconditus* are congruent with our own reconstructions and interpretations of †*P. carentonensis*; the cells around the mirror, not identified individually by Zheng et al. (2023) because of cross-publishing of their work and that of Josse et al. (2023), seem actually present in both fossils, but their identification, and the identification of the veins delimiting and crossing the mirror will have to be checked with more details.

### Particularities in †*Picogryllus carentonensis*?

Although it exhibits a remarkable similarity in wing venation to extant Oecanthidae, †*Picogryllus carentonensis* also displays unique characteristics in its FWs, as the presence of two crossveins in the mirror. Few crickets present two crossveins, or more, in the mirror. The number of crossveins in the cell homologous to the true mirror of crickets varies among the fossils currently classified as †Baissogryllidae, or as †Protogryllidae. This postero-distally cell is open, even enlarged in †Baissogryllidae (Josse et al. 2023, fig. 6), but, it is not closed by a reinforced s1

as in true crickets. Extant phalangopsid crickets, such as *Paragrillus* Guérin-Méneville, 1844, *Rumea* Desutter, 1988, *Paragrillodes* Karny, 1909 and their relatives, have up to six concentric crossveins in their mirror, while winged Phaloriinae have usually two transverse ones, as the Luzarinae *Lerneca fuscipennis* (Saussure, 1874) (Josse et al. 2023, fig. 3B). All these crickets emit loud calls; they also have long, wide, flexible forewings, except *Paragrillodes*, whose forewings do not cover more than half of the abdomen and are somewhat corneous. Some taxa of the Oecanthidi supertribe have been reported with two crossveins in the mirror (Campos et al. 2022), but applying the pattern defined by Josse et al. (2023) to taxa of the genus *Oecanthus* Serville, 1831, shows that the mirror of Oecanthidi has in fact only one crossvein, and that the most proximal cell of the mirror is actually a highly modified c1 cell. In many contemporary crickets, the mirror is involved in sound propagation (Dambach and Gras 1995; Mhatre et al. 2012). The presence of crossveins in the mirror could then be related to wing vibration, as the large, flexible forewings may actually need to be reinforced to resist to vibration. The presence of an arculus revealed by Josse et al. (2023) in singing crickets and mole crickets, but lacking in mute crickets and females, goes in the same direction. Both †*Crassicorpus maculatus* and †*Ordicalcaratus inconditus* present only one vein across the mirror (see Zheng et al. 2023, figs 3B and 4D), but the presence of an arculus will have to be checked on the fossils.

Could this reinforcement hypothesis also apply to †*P. carentonensis*? †*P. carentonensis* is actually the smallest cricket ever found with a stridulatory apparatus, in both the extant and fossil species, measuring only 3.3 mm in body length, and the smallest complete apparatus ever documented. In extant crickets, the smallest species are usually apterous, i.e., ant-loving crickets Myrmecophilidae or some Nemobiinae (Trigonidiidae) crickets, and the smallest singing crickets are much larger than †*P. carentonensis* (Bennet-Clark 1999). As the frequency of the calling song increases with the decrease of cricket size (Bennet-Clark 1999), the crossveins of †*P. carentonensis* may have allowed the call of this species to remain in relatively low frequencies. Detailed studies of wing vibration are now necessary to test the role of these veins as reinforcement structures, whatever the size of the forewings.

Can phylogeny bring information about the evolution of these veins? The †Baissogryllidae, †Protogryllidae, and Phalangopsidae are not closely related to the Oecanthidae (Chintauan-Marquier et al. 2016; Campos et al. 2022), and †*Picogrillus* is nested within the Oecanthidae phylogeny (Ferreira 2023). When comparing the crossveins present in the mirror region of †*P. carentonensis* to those observed in *Lerneca fuscipennis* for example (Phalangopsidae, Luzarinae, see Josse et al. 2023, fig. 3B), it is clear that in both specimens, the crossveins exhibit identical connections: each crossvein is linked to CuPaa2, with one also connected to CuPaβ, and the other connected to s1 crossveins. In the same way, the veins in the mirror

of some †Baissogryllidae and some †Protogryllidae could be homologous to the veins of †*P. carentonensis*, although oriented longitudinally (and not transversally). Nevertheless, the venations of †baissogryllid and †protogryllid differ from that of †*P. carentonensis* by the presence of d1 and of an ant-mirror cell (Josse et al. 2023, fig. 6). These crossveins may support a hypothesis of primary homology, but most probably are homoplastic in the frame of cricket phylogeny.

## Conclusion

The application of 3D microtomography is a real progress in the examination of wing venation in fossil insects. The venation pattern observed in †*Picogrillus carentonensis* is congruent with the pattern proposed by Josse et al. (2023) for crickets, and the synapomorphies of Orthoptera identified by Béthoux and Nel (2001, 2002) for Archaeorthoptera. The reconstruction also highlights unique features of the forewing, like the presence of two crossveins in the mirror, a characteristic not commonly observed in extant crickets, which could be linked to functional properties of the forewing. These findings will support further investigations into the evolution of acoustic structures in crickets. The exquisite preservation of the venation pattern of the fossil †*Picogrillus carentonensis* also holds significant importance for evolutionary biology. It will prove invaluable when constructing a morphological matrix for tip dating (solely reliant on morphological data), total-evidence (incorporating both molecular and morphological data for extant taxa, alongside morphological data for extinct taxa), or total-evidence dating studies (additionally considering ages) (e.g., Ronquist et al. 2012; Jouault et al. 2021, 2022). Fossils lack molecular data, but precise morphological information are most valuable for accurate fossil placements, which contribute to the renewal of morphological phylogenetic studies (e.g., Kealy and Beck 2017; Beck et al. 2023; Coiro et al. 2023).

## Data availability

Untreated CT-scans are available upon request to the corresponding author, and for scientific work at: <https://doi.org/10.5281/zenodo.8270385>.

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