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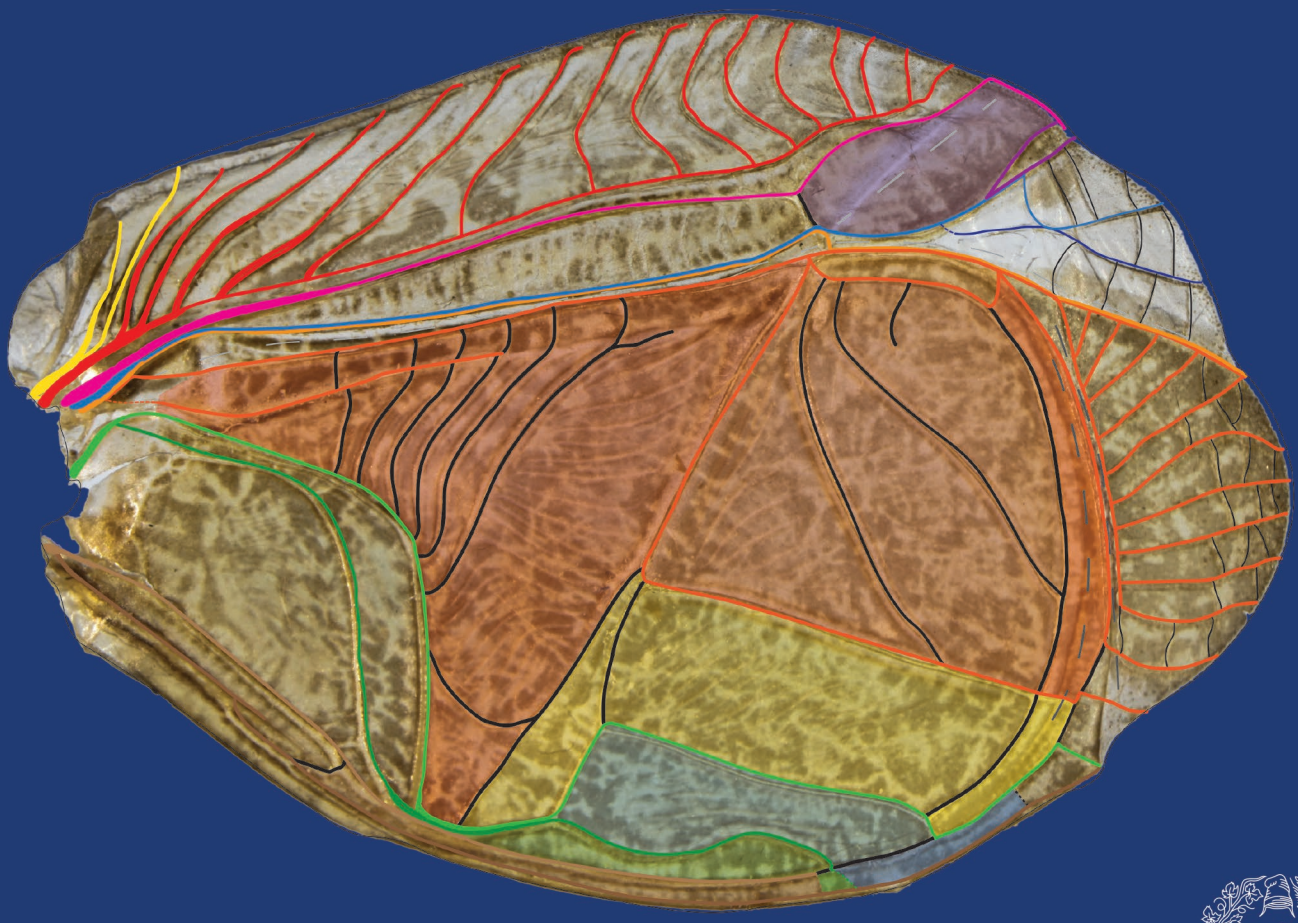

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Venation pattern of *Lerneca fuscipennis* (Saussure, 1874) according to the vein homologies proposed here for Gryllidea.

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# Reconciliation between neontology and paleontology in the Gryllidea (Orthoptera, Ensifera): reinterpreting the venation of the stridulatory apparatus in crickets

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ABSTRACT
The Ensifera are famous for the diversity of their acoustic devices and have been intensively studied for their acoustic behaviour and evolution. They sing mostly by scrapping their forewings against each other. Their apparatus includes a stridulatory file and several broad areas that may play as sound resonators, which homology has been harshly debated. Most previous studies focussed on the functional parts, while the whole forewing venation has been less studied in a comparative context. Here, we extend recent observations with 3D-microtomography to study the venation of the forewing of both modern and fossil Ensifera, focussing more specifically on true crickets (Grylloidea Laicharting, 1781), mole crickets (Gryllotalpidae Leach, 1815) and their fossil allies (†Baissogryllidae Gorochov, 1985, †Protogryllidae Zeuner, 1937). We propose a complete pattern of forewing venation for the Gryllidea Laicharting, 1781, extending the paradigm proposed by Béthoux & Nel (2001, 2002) for fossils. This pattern defines the acoustic and non-acoustic structures using well-defined homologies through the whole Gryllidea. We put in evidence potential apomorphies for Gryllidea, Grylloidea and Gryllotalpidae, but none of the wing traits originally proposed to define the †Baissogryllidae or the †Protogryllidae are found exclusively in these taxa. Our observations support the hypothesis of convergence between crickets and mole crickets for the stridulatory file.

KEY WORDS
Wing morphology, homology, evolution, acoustic communication.

**RÉSUMÉ**
*Réconciliation entre néontologie et paléontologie chez les Gryllidea (Orthoptera, Ensifera) : réinterprétation de la nervation de l'appareil stridulatoire chez les grillons.*
Les Ensifera sont célèbres pour la diversité de leurs appareils stridulatoires et ont fait l'objet d'études intensives sur leur comportement acoustique et leur évolution. Ils chantent principalement en frottant leurs ailes antérieures l'une contre l'autre. Leur appareil comprend une râpe stridulatoire et plusieurs zones élargies qui peuvent jouer le rôle de résonateurs sonores, dont l'homologie a été âprement discutée. La plupart des études précédentes se sont concentrées sur les parties fonctionnelles, mais l'ensemble de la nervation des ailes antérieures a été moins étudié dans un contexte comparatif. Ici, nous étendons les observations récentes en microtomographie 3D pour étudier la nervation de l'aile antérieure des Ensifera modernes et fossiles, en nous concentrant plus spécifiquement sur les grillons vrais (Grylloidea Laicharting, 1781), les courtilières (Gryllotalpidae Leach, 1815) et leurs fossiles apparentés (†Baissogryllidae Gorochov, 1985, †Protogryllidae Zeuner, 1937). Nous proposons un schéma complet de la nervation des ailes antérieures pour les Gryllidea Laicharting, 1781, étendant le paradigme proposé par Béthoux & Nel (2001, 2002) pour les fossiles. Ce schéma définit les structures acoustiques et non-acoustiques en utilisant des homologies bien définies à travers l'ensemble des Gryllidea. Nous avons mis en évidence des apomorphies putatives pour les Gryllidea, les Grylloidea et les Gryllotalpidae, mais aucun des caractères alaires proposés à l'origine pour définir les †Baissogryllidae ou les †Protogryllidae ne sont trouvés exclusivement dans ces deux taxons. Nos observations soutiennent l'hypothèse d'une convergence entre grillons et courtilières pour la râpe stridulatoire.

**MOTS CLÉS**
Morphologie alaire,
homologie,
évolution,
communication acoustique.

## INTRODUCTION

Acoustic communication is widespread in insects. It is involved in different behaviours such as calling for potential mates, competition, or escaping from predators. The insects that mostly rely on acoustics belong to the Hemiptera (cicadas) and the Orthoptera (crickets, katydids, grigs and grasshoppers). However, the diversity of morphological structures for sound emission and reception in Orthoptera are unrivaled (Busnel 1963; Gerhardt & Huber 2002; Robinson & Hall 2002). Within Ensifera (crickets, grigs and katydids), most acoustic species communicate by stridulation with the forewings (elytra), viz. the emission of sounds by friction of differentiated regions of the wings (Dumortier 1963). A row of teeth located on the ventral side of a vein called the 'stridulatory file' on one forewing is rubbed against a reinforced area, called the 'plectrum', on the margin of the other forewing (Bennet-Clark 1989). The vibrations generated at the level of the file are most often modified by wing areas called 'resonators', corresponding to large cells of the wing membrane, like the harp and the mirror in crickets.

Since many years, the question of the origin and evolution of stridulatory apparatuses in Ensifera has been discussed, with / without a phylogenetic reference and with / without hypotheses of homology about the acoustic structures: these methodological failures resulted in a messy situation unfavorable to test evolutionary hypotheses (see Desutter-Grandcolas *et al.* 2017 and references therein). Microtomography studies of forewing venation of Ensifera (Desutter-Grandcolas *et al.* 2017) showed that the file was located on a branch of the posterior cubitus vein (CuPb) in mole crickets (Gryllidea, Gryllotalpidae) and *Cyphoderris* Uhler, 1864 (Tettigoniidea Krauss, 1902, Hagloidea Handlirsch, 1906, Prophalangopsidae Kirby, 1906), whereas it was located on the anterior postcubitus vein (PCuA, interpreted as the first anal vein (A1) in the 2017 study, but see Schubnel *et al.* 2020) in crickets (Gryllidea, Grylloidea) and katydids (Tettigoniidea, Tettigonioidea Krauss, 1902). These results support the hypothesis of convergent evolution for acoustic communication in Ensifera (Ander 1939; Gwynne 1995; Desutter-Grandcolas 2003) and contradict the hypothesis of a single origin of the singing apparatus in Ensifera (Zeuner 1939; Ragge 1955; Sharov 1968; Bailey 1991; Otte 1992; Béthoux 2012; Chivers *et al.* 2017). According to the 'unique origin' hypothesis, the stridulatory apparatus of the Prophalangopsidae is plesiomorphic and the stridulums of katydids, crickets, and mole crickets derive from it. This hypothesis does not consider the other clades of Tettigoniidea, like Rhaphidophoroidea Walker, 1871 (apterous), Stenopelmatoidea Burmeister, 1838 and Schizodactyloidea Blanchard, 1845 (apterous or winged without a stridulum), which would have been therefore devoid of a stridulum ancestrally or would have lost it either ancestrally or convergently. The 'unique origin' hypothesis moreover ignores the monophyly of the Gryllidea (= Grylloidea + Gryllotalpoidea) on one hand, and of the Tettigoniidea (Hagloidea + Stenopelmatoidea + Rhaphidophoridoidea + Tettigonioidea + Schizodactyloidea) on the other hand, although both clades are very well supported by large-scale molecular phylogenies (Song *et al.* 2015, 2020). To test the convergence and the 'unique origin' hypotheses, it would be necessary to confront both of them to well supported hypotheses of primary homology for forewing veins and to a well-supported, large-scale phylogeny of Ensifera. If the latter seems easily attainable today, thanks to the development of mass sequencing (Song *et al.* 2015, 2020), the first condition seems much more out of an immediate reach (Gorochov 1995a, b; Chivers *et al.* 2017; Desutter-Grandcolas *et al.* 2017). It should also be noted that the reduced scope of most studies, limited to the acoustic structures for example,

but not considering the whole wing structures, impedes the full test of comparative structural hypotheses.

In the present paper we test the results previously obtained by microtomography (Desutter-Grandcolas *et al.* 2017; Schubnel *et al.* 2020) and complete them with optical observations to analyse forewing venation in a large sample of Gryllidea. Our aim is to define primary homologies for the whole forewing venation, including acoustic and non-acoustic structures, and propose a new pattern of venation. We then test whether the files of crickets and mole-crickets are homologous. We also propose potential apomorphies of the different clades of Gryllidea, addressing more particularly two highly specialized structures of the forewings of singing crickets, e.g., the 'arculus', a zone of the distal branching of the vein M+CuA that has never been recognized in crickets up to now, and the 'lanceolate cell' defined by Gorochov (1995a, b). Finally, we reconcile the forewing venation homologies in modern crickets with the numerous fossils described as 'crickets' from various forewing remains or imprints. We do not intend to perform genuine phylogenetic analyses using the wing characters that could be defined according to our new pattern of venation: such a phylogenetic approach would necessitate a much larger sample of Gryllidea and should maybe focus on restricted clades in a first step, for example at the family / subfamily level. Both are beyond the scope of the present paper.

Phylogenetic studies of the Gryllidea, and more generally of the Ensifera, suffer from a lack of integration of the fossil record (Nel 2021), notably because of the relative poverty in morphological characters other than those of the wings in fossil descriptions, and because of the lack of clearly identified apomorphies of the cricket clades (Desutter-Grandcolas *et al.* 2021; Campos *et al.* 2022). The oldest fossil record of crickets consists mostly in isolated wings (e.g. Sharov 1968; Gorochov 1995a, b), although some exceptionally complete specimens have been described these last twenty years in amber (Perrichot *et al.* 2002; Xu *et al.* 2020a, b; Jiang *et al.* 2022; Xu *et al.* 2022; Yuan *et al.* 2022; Desutter-Grandcolas *et al.* 2023). Improving our understanding of the forewing venation of crickets *s.l.* will allow to include in the future the fossil record of the Gryllidea into their phylogeny and to draw general evolutionary hypotheses about the clade. This should unlock a new source of apomorphies to better characterize the families and include fossils in future evolutionary analyses based on both morphological and molecular characters (Jouault *et al.* 2021).

## MATERIAL AND METHODS

### Classification

Since the molecular phylogeny of Chintauan-Marquier *et al.* (2016), completed by Campos *et al.* (2022), the upper classification of the Gryllidea is being stabilized. Crickets (*s.l.*) are distributed in two superfamilies, the Gryllotalpoidea and the Grylloidea, made of two and five monophyletic families respectively. The Gryllotalpoidea include the Gryllotalpidae and the Myrmecophilidae Saussure, 1874 (but see Sanno *et al.* 2021 for the relationships of the latter). The Grylloidea include five families, viz. Mogoplistidae Costa, 1855, Trigonidiidae Saussure, 1874, Phalangopsidae Blanchard, 1845, Oecanthidae Blanchard, 1845 (see Campos *et al.* 2022), and Gryllidae Laicharting, 1781, in addition to the Pteroplistinae Chopard, 1936 subfamily.

Two fossil families are also currently included within the Grylloidea, the †Protogryllidae Zeuner, 1937 (late Triassic to Jurassic), and the †Baissogryllidae Gorochov, 1985 (late Jurassic to early Cretaceous) (Cigliano *et al.* 2023). The monophyly and the positions of these two fossil groups in the phylogeny of the Gryllidea have not yet been updated in the recent evolutionary frame (Song *et al.* 2015, 2020; Chintauan-Marquier *et al.* 2016).

### Preparation and observation of specimens

Observations on venation were made from male individuals with a singing apparatus, belonging to the Trigonidiidae, Phalangopsidae, Oecanthidae, Gryllidae, Pteroplistinae and Gryllotalpidae; the Myrmecophilidae are apterous. The Mogoplistidae have very small wings, mostly hidden under an extended pronotum, and thus difficult to observe: they have not been fully studied here and only preliminary results are presented. We also observed forewings of females and forewings of males lacking a complete stridulum. We preliminarily observed several specimens of each species of cricket and mole cricket. The main venation of the cricket species was rather constant, whereas that of the mole crickets showed more individual variation. We therefore checked them more precisely. In total, we examined 39 cricket and mole cricket species (Appendix 1). All observed specimens are deposited in the Orthoptera collections of the Muséum national d'Histoire naturelle (MNHN) in Paris.

In order to facilitate the observation of particular regions of the wing such as the fan, forewings have been separated from the body, softened and placed between two glass slides. In some cases, wings were also examined directly on the specimens, either in natural position folded on the dorsum, or spread laterally to the body. The photographs of the extant specimens were taken with a Nikon D800 mounted on a stereomicroscope or using a Canon 50d with a Canon MPE 65 mm lens mounted on an automated stacking rail. The images are digitally stacked photomicrographic composites made on Helicon Focus 6.7. Drawings were made using a camera lucida mounted on a binocular Nikon SMZ1500. The figures were made with Adobe Illustrator CC 2019.

The venations of the †Protogryllidae and †Baissogryllidae have been analyzed from figures and descriptions from the literature (e.g., Sharov 1968; Gorochov 1984, 1985, 1992, 1995a, b; Gorochov *et al.* 2006), and through photographs of specimens, when possible, thanks to our colleagues (Appendix 3: Figs S5; S6). The photographed specimens (see Appendix 2) are deposited in the collections of the University of Sao Paulo (Brazil, courtesy of Guilherme Ribeiro), the Institute of Paleontology of Moscow (Russia, courtesy of Danil Aristov), and the Institute of Geology and Paleontology of Nanjing (China, courtesy of Chunpeng Xu). The complete list of studied fossils is given in Appendix 2.

## State of the art about the interpretation of forewing venation in Orthoptera

As for all insects, orthopteran wings present several types of veins. The main (or primary) veins radiate from the bullae at the wing base and are generally longitudinal. The secondary veins (or crossveins), mostly short and thin, connect the main veins together. Other types of secondary veins may be present, such as the 'intercalaries', i.e., elongate longitudinal veins parallel to the main veins and not directly connected to them (see for example in Odonata, Riek & Kukalová-Peck 1984). Furthermore, wings are generally corrugated, with some veins attached to the wing dorsal membrane (convex veins), while others are attached to the wing ventral membrane (concave veins). Functional constraints can lead to changes in the convexity of the main veins and/or to their fusions, or to reinforcements of secondary transverse veins, making the identification of the veins sometimes less obvious.

Here, we determine the nature of the veins, using their relative position and their polarity. Following Lameere (1922), Kukalová-Peck (1991) and, for Orthoptera, Béthoux & Nel (2001, 2002), we consider that each main vein is divided into a convex anterior vein and a concave posterior vein, a hypothesis largely used in venation studies (Schubnel *et al.* 2020), except by Sharov (1968) and followers who admitted the presence of a convex posterior-most branch of the median vein (the so-called vein M5).

For venation nomenclature, we follow Béthoux & Nel (2001, 2002) modified by Schubnel *et al.* (2020), who demonstrated the presence of a PCu vein in the Neoptera, a hypothesis proposed by Lameere (1922), Snodgrass (1935), Hamilton (1972) or Emeljanov (1977), but neglected by Comstock (1918) or Kukalová-Peck (1991) (see Fig. 1 and the Discussion paragraph). Each main vein has a definite colour (see abbreviations and colours below), with anterior branch (A), generally convex, and a posterior branch (P), generally concave. Within the Orthoptera, each of these branches can subdivide again into two stable branches, which are successively named, from wing base to apex, 'a' and 'b', then 'α' and 'β', then '1' and '2'. For example, the Cu vein divides into two branches CuA and CuP; CuP then divides into CuPa and CuPb; the CuPa divides into CuPaα and CuPaβ; and the CuPaα divides into CuPaα1 and CuPaα2 (in crickets). Crossveins are figured in black, except for some grey veins for which a reasonable hypothesis of primary homology cannot be safely proposed.

Studying the venation of fossil Orthoptera, Béthoux & Nel (2001, 2002) proposed that the superorder Archaeorthoptera Béthoux & Nel, 2002, would be characterized by a fusion at the extreme base of the wing of CuA with M. Orthoptera would also have a branched CuP, which is uncommon in other insects. In Ensifera, CuA would separate distally from M, before merging in CuPa at different levels depending on the groups. We tested and corroborated these hypotheses with our observations (see below).

In the figures and photos, the base of the wing is on the left, and the anterior margin on top.

## Abbreviations

The following abbreviations, symbols and colours are used in the text and figures:

*Main veins and their bifurcations*

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

*Reinforced crossveins (black in figures)*

| | |
|---|---|
| a | crossvein between anal branches proximally to the plectrum; |
| d1 | diagonal 1 (crossvein between CuPaα and CuPaβ); |
| d2 | diagonal 2 (crossvein between CuPaβ and PCuA); |
| pi | pilar (crossvein between 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). |

*Uncertain veins (grey in figures)*

| | |
|---|---|
| cup spl | longitudinal intercalary vein between CuPa and CuPb (may not be homologous between groups); |
| r-m2 | transverse vein between R and M (in mole crickets). |

## Supplementary figures

The figures indicated as supplementary are gathered in the Appendix 3 of the present paper.

## General and functional organisation of a cricket wing

At rest, crickets have their forewings folded longitudinally on the dorsum; they are divided into a dorsal and a lateral field, separated by a longitudinal fold (Fig. 2A) called the median fold, whose distal part is made of a thin, folded membrane, the median fan. The stridulatory apparatus is located on the dorsal field (Fig. 2B): it includes the file, the plectrum, the mirror (mi) and the harp (ha) (Bennet-Clark 1989). An anal node, where several veins are fused together, is situated near the plectrum. Curved veins, called the chords, are situated along the posterior wing margin, distally to this node and posterior to the harp and the mirror.

As in crickets, the forewings of the mole crickets are folded longitudinally on the dorsum and disposed into a dorsal and a lateral field, separated by a median longitudinal fold; this median fold is however less developed than in the Grylloidea (Fig. 2C). At the distal end of the wing, there is an area usually called the 'flexible zone' (Bennet-Clark

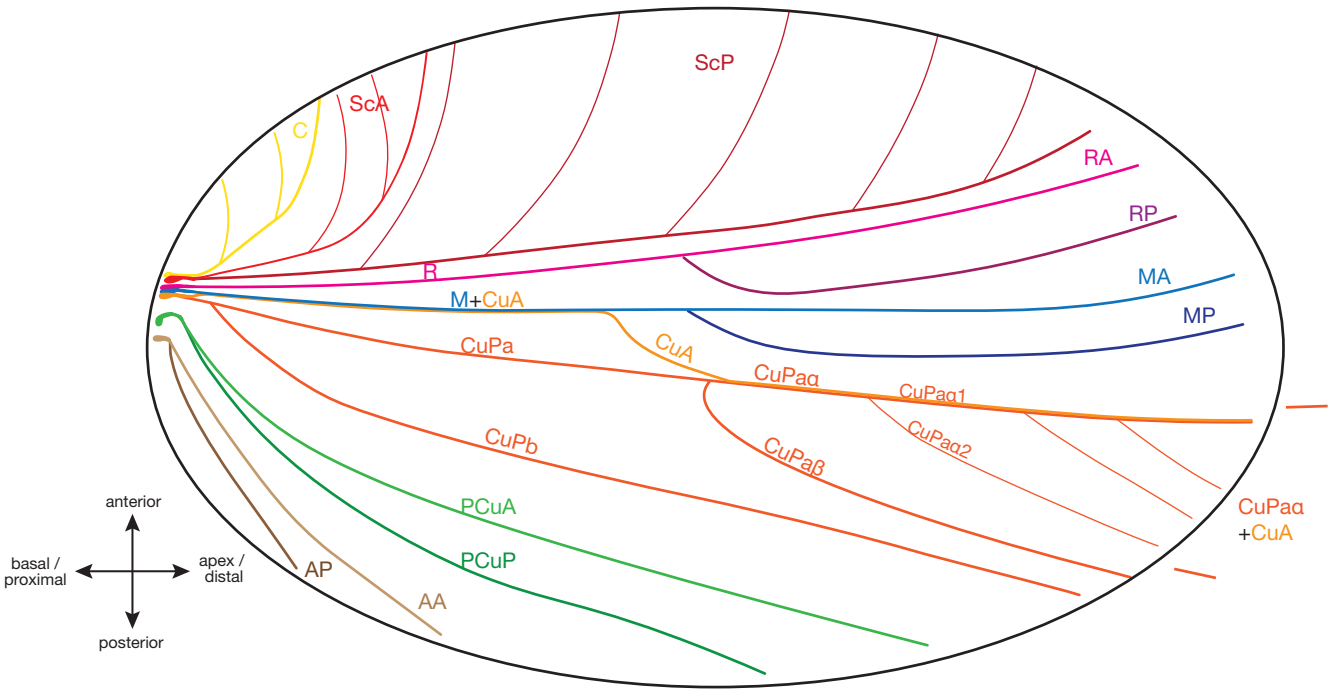


Fig. 1. — Theoretical pattern of venation of a gryllidean forewing (terminology after Béthoux & Nel [2002], modified after Schubnel *et al.* [2020]). Abbreviations and colour code: see text.

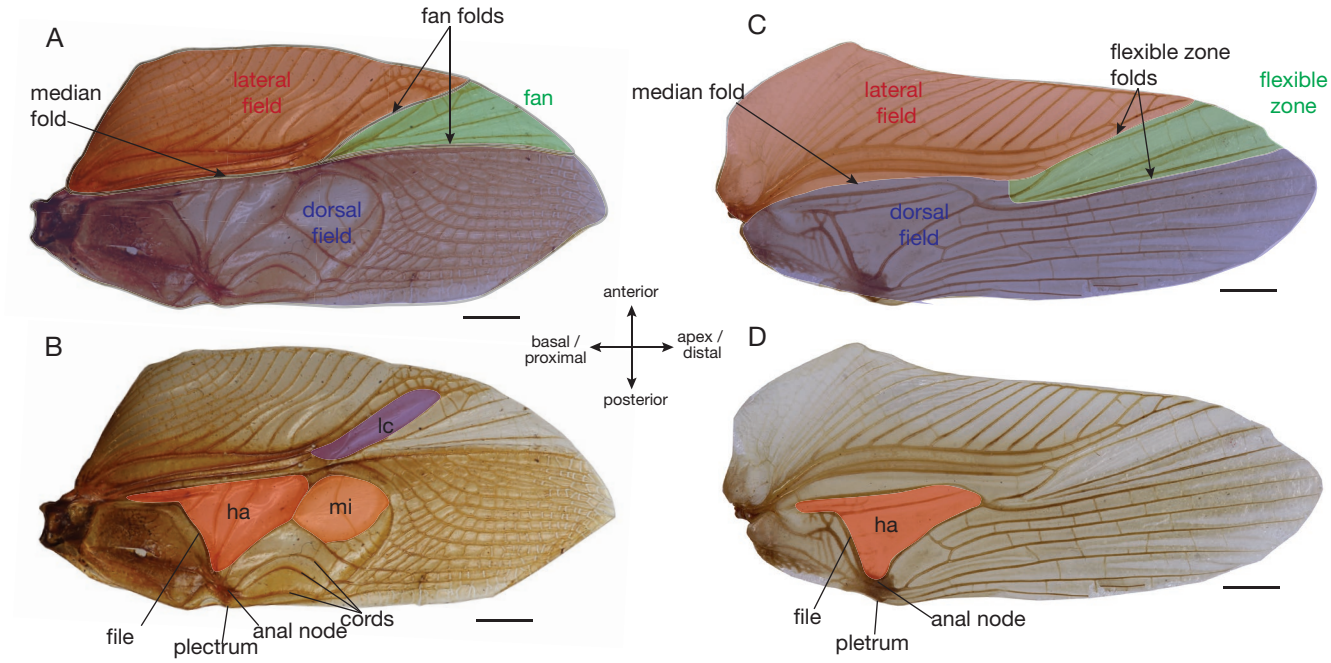


Fig. 2. — Main fields (**A**, **C**) and functional structures (**B**, **D**) of a male grylloid forewing (**A**, **B**: *Brachytrupes membranaceus* (Drury, 1773), MNHN-EO-ENSIF9769) and a male gryllotalpid forewing (**C**, **D**: *Scapteriscus* sp., MNHN-EO-ENSIF3068). Abbreviations: **lc**, lanceolate cell; **ha**, harp; **mi**, mirror. Scale bars: 5 mm.

1989), which could be homologous to the fan of crickets, but which is not folded between the two fields at rest unlike the latter. The functional structures of the stridulatory apparatus are also located on the dorsal field (Fig. 2D). These structures, i.e., a file and a harp, have been named as in crickets because they have very similar aspects and functions and because both groups are very close phylogenetically; their homology is however not so straightforward (see Discussion). Gryllotalpidae have also a plectrum with an anal node, but no mirror.

## RESULTS

### Forewing venation pattern in the modern Grylloidea

*General venation pattern of male Grylloidea*

The overall venation pattern of crickets is shown here on four species, having a stridulatory apparatus considered as 'complete' (file, harp and mirror) and a lanceolate cell: *Natula longipennis* (Serville, 1838) (Trigonidiidae, Trigonidiinae Saussure, 1974: Fig. 3A), *Lerneca fuscipennis* (Saussure, 1874) (Phalangopsidae, Luzarinae Hebard, 1928: Fig. 3B), *Phyllogryllus* sp. (Oecanthidae, Podoscirtinae Saussure, 1878: Fig. 4A), and *Brachytrupes membranaceus* (Drury, 1773) (Gryllidae, Gryllinae Laicharting, 1781: Fig. 4B).

Lateral field. The lateral field is delimited by the anterior edge of the wing and the median fold located between M+CuA and CuPa (Figs 3; 4). At their bases, the veins of this field can be identified, from the most anterior to the most posterior, as C, Sc, R, and M+CuA, originating from often closed or even fused basivenal bullae. Orthoptera are characterized by the presence of a large costal field. In Grylloidea, a C vein is almost always present, even though the number and shape of its bifurcations vary. In some cases, C and Sc bullae are joined, and it can be very hard to distinguish them, and their related branches. The separation between C and Sc is particularly clear in male *Ectotrypa olmeca* Saussure, 1874 (Appendix 3: Fig. S2C) or female *Brachytrupes membranaceus* (Appendix 3: Fig. S4C). In Orthoptera, a rather long ScA and a long pectinate ScP may be both present. In Grylloidea, ScA and ScP are relatively difficult to distinguish. For sake of clarity, we consequently consider the Sc vein *s.l.*, and do not always differentiate C and Sc (then indicated in figures as C+Sc). The shape and bifurcations of C and Sc do not seem related to the presence / absence of a stridulatory apparatus. R is very strong and convex, especially at its base, basally merged with Sc: these two veins are always almost parallel. Basally, the R and M+CuA veins are also very close or even fused in the most basal part of the wing. Distally, the closed lanceolate cell is present (Figs 3; 4). The short vein between M+CuA and R, at the base of the lanceolate cell, is here interpreted as a secondary crossvein called 'r-m'. This vein is sometimes very short (as in *Brachytrupes membranaceus*, Fig. 4A) or even totally absent due to the partial fusion of M+CuA with R (as in *Phyllogryllus* sp., Fig. 4B). This last configuration of the r-m may be an aberration, but it has also been observed in other specimens (for example in *Acheta domesticus* Linnaeus, 1758). More distally, the lanceolate cell is closed by the concave RP: the posterior branch of R emerges very distally compared to the situation in other Orthoptera, but can still be identified in some Grylloidea by its basal concavity (as in *Brachytrupes membranaceu*s, Appendix 3: Fig. S1C). RP is strongly bent proximo-posteriorly, and merges with MA over a short distance, these veins separate again and both have a longitudinal trajectory to the wing apex (Fig. 4). RA is convex and often joins the distal edge of the wing. It can also be strongly reduced or shortened (as in *Lerneca fuscipennis*, Fig. 3B). In many crickets, R is strongly curved just basally to RA/RP fork, thus making the base of RP to have a reverse longitudinal trajectory in the continuity of MA (Figs 3; 4). RP sometimes has the same polarity and ornamentation as the latter vein. The distal part of RP (after its separation with MA), MA and MP often have a rather neutral polarity in modern crickets, which may be related to the thinness of the wing membrane in this folded area. MA and MP can therefore be identified by a slight polarity at their base (MA convex and MP concave) and by their relative positions. Note that RP can be reinforced in the continuity of M so that it resembles an anterior branch of the latter, as in *Phyllogryllus* sp. (Appendix 3: Fig. S2D) for example.

CuA separates from M at the same level or slightly distad the base r-m of the lanceolate cell. It is very short and merges with CuPa$\alpha$ by crossing the median fold (Figs 3; 4). The combination of the transverse vein r-m, of the emerging M and CuA, and of the fusion of CuA with CuPa$\alpha$ results in a composite transverse structure in the mid part of wing. Its function, if any, remains unknown, but it could be a kind of 'arculus' *sensu* Wootton (1992), i.e., a reinforcement of the wing structure in a zone of great functional constraint. Other short veins sometimes cross the median fold between M and CuA+CuPa$\alpha$, but these are not regularly present in all the species and are often much less marked than the CuA (as in *Natula longipennis*, Fig. 3A and *Brachytrupes membranaceus*, Fig. 4A). Therefore, they are here considered as secondary transverse veins.

The median fold marks the boundary between the two fields. Distally, it bifurcates into two distal folds, both making the fan; one of the folds crosses M+CuA (between r-m and the bifurcation of M and CuA) and the lanceolate cell longitudinally, while the other runs along the stem vein of CuA+CuPa$\alpha$.

Dorsal field. At the base of the dorsal field, from the most anterior to the most posterior veins, there are six veins: CuPa, CuPb, PCuA, PCuP, and two anal veins (AA and AP) (Figs 3; 4). CuPa is very thin, concave and continuous toward the wing distal margin. Following Desutter-Grandcolas *et al.* (2017), we consider that Grylloidea have a shortened CuPb. Indeed, between CuPa and PCuA, we can easily notice a very short vein radiating from the Cu basivenal bulla. CuPb is usually easily observed in Phalangopsidae, Oecanthidae and some Gryllidae, as a most often faint vein, that can reach at most half wing length in some specimens (see for example *Lerneca fuscipennis*, Fig. 3B). However, in observed Trigonidiidae, CuPb is extremely thin and tangy to the file (PCuA) (Figs 3A; Appendix 3: S1A). An intercalary vein can also be present between CuPa and CuPb, which we named here 'cup spl' (supplementary cubital posterior) although its homology with that of other families is questionable (see Discussion). This vein differs from CuPb in that it is not connected to any main vein base, which is our strongest argument for primary venation homology between the main veins. PCu can be identified thanks to its strong and curved base, and divides from its base into two branches, PCuA and PCuP. PCuA bears the stridulatory teeth ventrally; it is rather strong, convex basally then concave (reversed polarity in connection with the stridulation process); PCuP is slightly concave. PCuA and PCuP are relatively parallel at their base; they join more posteriorly

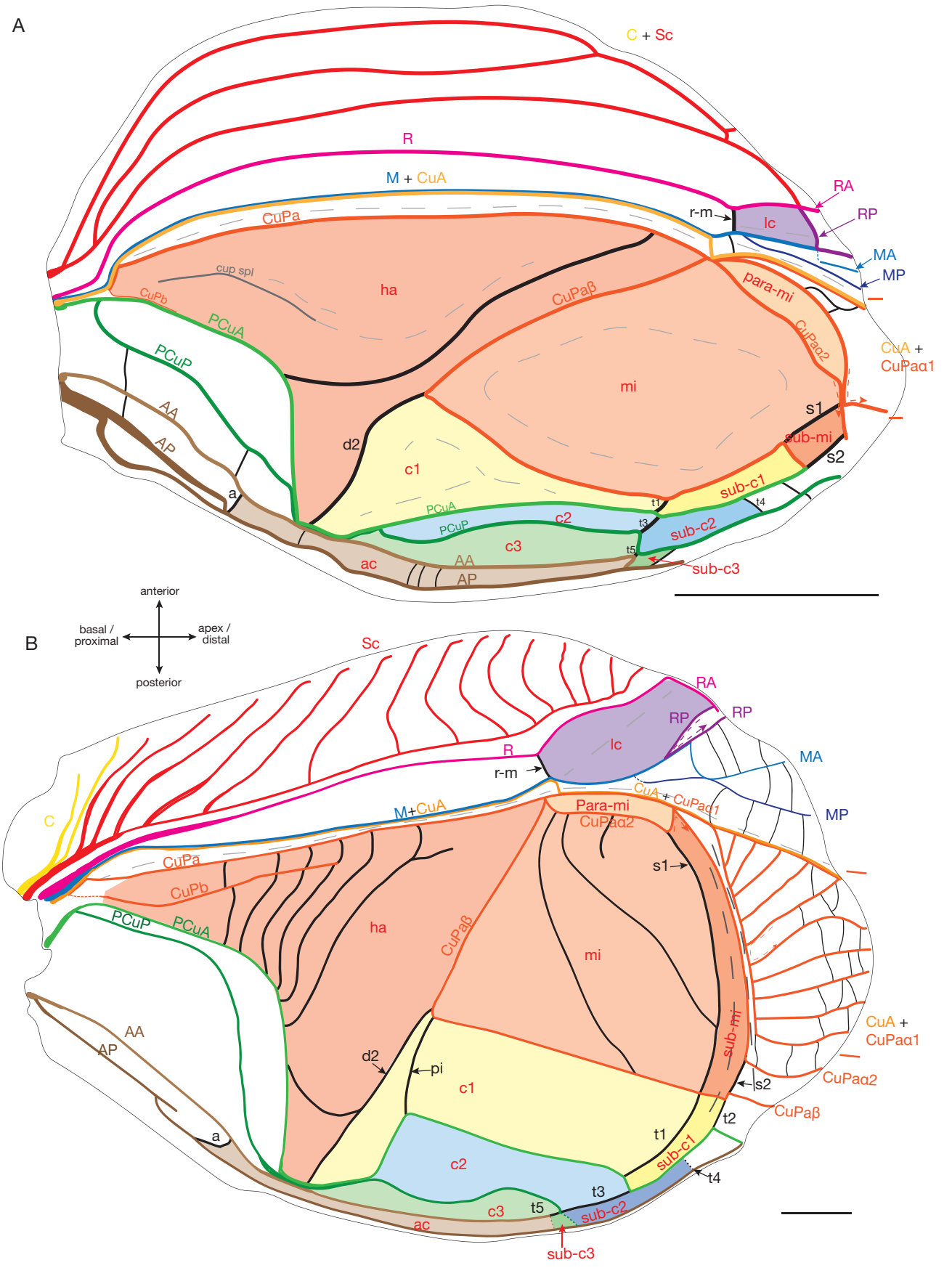


Fig. 3. — Hypothesis of primary homology of venation of male Grylloidea: **A**, *Natula longipennis* (Serville, 1838) (MNHN-EO-ENSIF9933, Trigonidiidae); **B**, *Lerneca fuscipennis* (Saussure, 1874) (MNHN-EO-ENSIF9780, Phalangopsidae). Abbreviations and colour code: see text. Scale bars:1 mm.

in the anal node, near the plectrum. The common base of AA (slightly convex) and AP (slightly concave) is more posterior to that of the PCu (Figs 3; 4). The configuration of the anal veins is quite variable among the species, and presents a strong intraspecific, or even intraindividual, variation. AA is generally well-differentiated whereas the AP vein can be reduced to a network of several veins. AA usually joins the two branches of the PCu in the anal node, whereas the very thin AP often runs along the posterior edge of the wing. In the specimens we studied, a reinforced crossvein 'a' joins AA and AP proximally to the plectrum, closing an anal cell (ac) basally (Figs 3; 4).

Distally to the file, the Grylloidea have a large triangular cell called the harp, bounded proximally by the PCuA (the file), anteriorly by CuPa and distally by the beginning of the CuPaβ and a reinforced crossvein (named here the diagonal 2 (d2)), aligned with the first part of CuPaβ, and joining the plectrum (Figs 3; 4); d2 corresponds to half of the traditional 'diagonal' of the cricket wing (e.g., Vicente *et al.* 2015), or to the 'column' *sensu* Béthoux (2012). The harp is often crossed by a variable number of transverse or oblique crossveins, except in the Trigonidiidae, where it is crossed by a unique longitudinal crossvein. The CuPaβ configuration could result from a capture of its base by the crossvein diagonal 1 (d1) in modern Grylloidea (see sections on fossil families and Discussion).

The antero-distal area of the dorsal field is occupied by CuPa and its branches. Some particular cells are observed in the different species. A large rounded cell is present between the CuPaβ and CuPaα2: it corresponds to the mirror *sensu stricto* (mi, Figs 3; 4) and is bounded by two crossveins, the diagonal crossvein d1 anteriorly and a crossvein that we called septum 1 (s1) distally. The contour of the mirror is often uniformly reinforced, complicating the differentiation between main and secondary veins; they are here identified according to their relative positions. Anteriorly to d1, a very little cell may separate CuPaβ and CuPaα2 in some species: this cell is named here the ante-mirror (ant-mi, in *Brachytrupes membranaceus* and *Phyllogryllus* sp., Fig. 4). In *Lerneca fuscipennis* (Fig. 3B), ant-mi and d1 are totally absent and the bases of CuPaβ and CuPaα2 are fused. Posteriorly to the mirror but still between CuPaβ and CuPaα2, there is another cell, named sub-mirror (sub-mi, Figs 3; 4), limited by s1 and by septum 2 (s2). The sub-mirror is more or less elongate, long in *Lerneca fuscipennis* and *Phyllogryllus* sp. (Figs 3B; 4B), shorter and wider in *Brachytrupes membranaceus* (Fig. 4A).

The short CuA vein fuses with CuPaα1 (anterior branch of CuPaα) after its bifurcation with CuPaα2. While CuPa is relatively thin and concave on the first half of the wing, it becomes much thicker after its fusion with CuA and becomes rather convex. CuA+CuPaα1 is distally branched with a strong 'stem-vein' in the continuity with CuPa (and the base of CuPaα) and a series of weaker branches directed postero-distally. In *Lerneca fuscipennis* and *Phyllogryllus* sp. CuPaα2 merges very partially (just as a contact point) with CuA+CuPaα1 and closes a well-delimited cell between CuA+CuPaα1 and CuPaα2, located anterior to the mirror and named here the para-mirror ('para-mi', Figs 3B; 4B). Para-mi is present in the species with a long sub-mi.

The distal part of dorsal field is very variable between species, individuals, and even between the two forewings of the same individual, notably because of a non-stable number of branches of CuA+CuPaα1, making their identification little informative, except for the first ones. In some species, the branches of CuA+CuPaα1 are partially fused (often in their middle), giving a pectinate aspect of distally oriented veins, with some closed cells between bases of the branches and their fused part (as in *Lerneca fuscipennis*, Fig. 3B).

On the posterior area of the wing, distad the anal node and the plectrum, PCuA, PCuP and AA separate again. The distal parts of PCuA (generally named first chord, as the most anterior chord) and PCuP (generally named second chord) have curved trajectories. AA may also be curved and forms a third chord, i.e., the most posterior chord. Some stable cells can here be identified. A large cell c1 is located between CuPaβ (posterior edge of the mirror) and PCuA. It is bounded basally by d2 and distally by the crossvein t1. The configuration of c1 crossveins is variable, but one reinforced crossvein, here named the 'pilar' (pi), is often present in the middle of c1, often very close to the bend of CuPaβ and its contact point with d2. The pilar exists in *Lerneca fuscipennis* and *Phyllogryllus* sp. (Figs 3B; 4B). Distally to c1, another cell, herein named sub-c1, is distally bounded by t2. This cell is located posteriorly to the sub-mi. Posteriorly to c1, a large cell c2 is situated between the first and second chords, and distally bounded by the crossvein t3. Distally to c2, between PCuA and PCuP (and sometimes also AP, as in *Phyllogryllus* sp. or *Lerneca fuscipennis* (in which there seem to be more vein fusions than in *Brachytrupes membranaceus*)), a sub-c2 cell is bounded distally by t4. A cell c3 is located between PCuP and AA, bounded distally by t5. Distad this last vein, a sub-c3 cell is present between PCuP and AA, just before these two veins go into AP. A last cell (anal cell, ac) is located between AA and AP and is bounded basally by a supposed reinforced crossvein a (Figs 3; 4). More distally, AA and PCuP merge with AP (which runs along the posterior margin of the wing). PCuA can continue its trajectory to the distal edge (as in *Brachytrupes membranaceus*, Fig. 4A) or join the end of AP (as in *Lerneca fuscipennis* or *Phyllogryllus* sp., Figs 3B; 4B).

*Grylloidea: special venation patterns*

We do not aim to exhaustively list all the venation patterns of crickets, which are extremely diversified, but we present some cases for which the general venation pattern needs to be adapted.

In all families of Grylloidea, many species have 'shortened' forewings. In these species, the base of the wing has often nearly the same configuration as in the species with long forewings. But their more distal structures (fan, lanceolate cell, and sometimes cells of the mirror) are variously reduced, as in *Landreva* sp. (Gryllidae, Landrevinae Saussure, 1878; Fig. 5A), or even absent as in *Nemobius sylvestris* (Bosc, 1792) (Trigonidiidae, Nemobiinae Saussure, 1877; Fig. 5B).

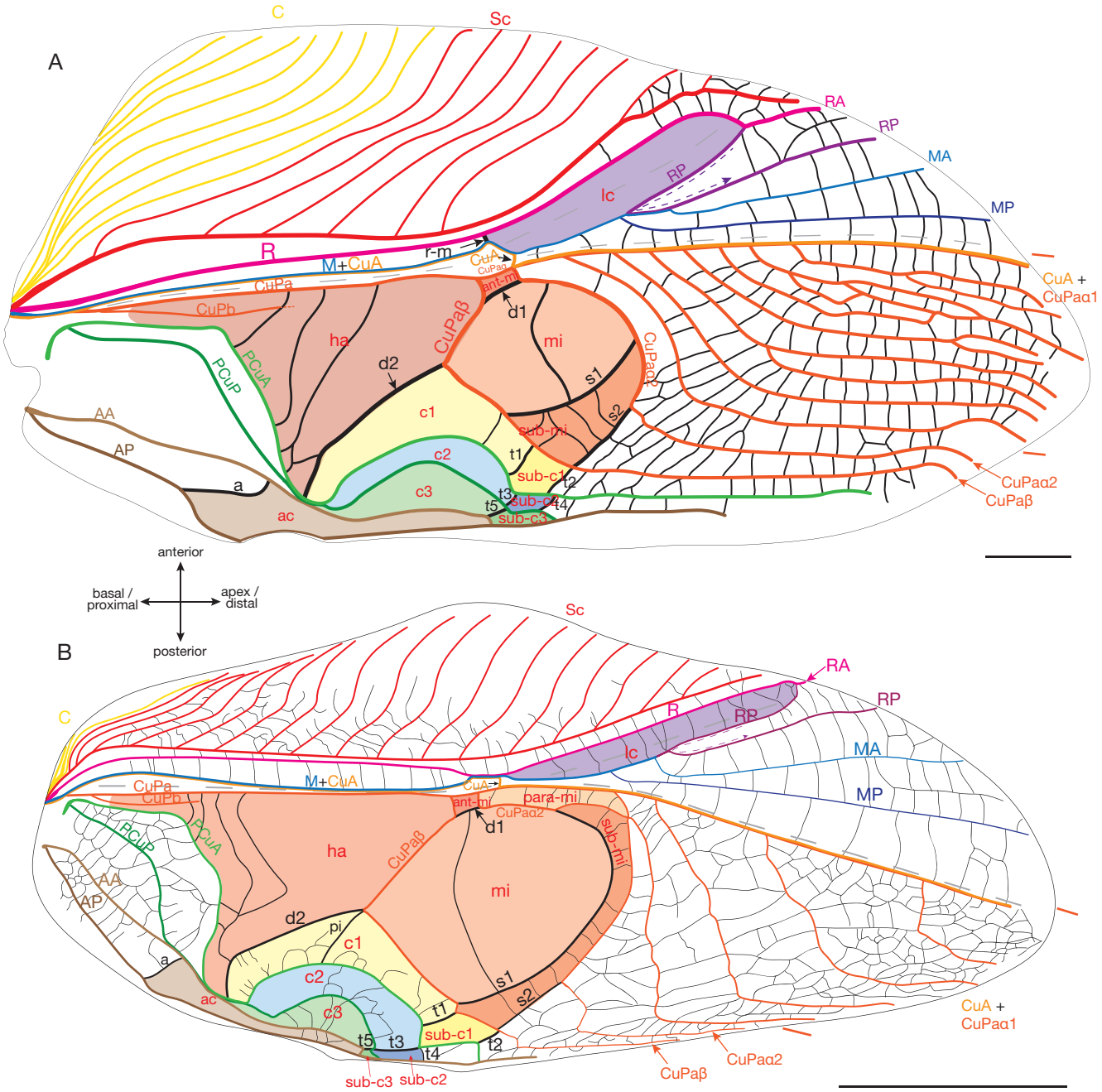


FIG. 4. — Hypothesis of primary homology of venation of male Grylloidea: **A**, *Brachytrupes membranaceus* (Drury, 1773) (MNHN-EO-ENSIF9769, Gryllidae); **B**, *Phyllogryllus* sp. (MNHN-EO-ENSIF9768, Oecanthidae). Abbreviations and colour code: see text. **Grey dash lines** represent folds. Scale bars: 5 mm.

In many species, males do not have a complete singing apparatus (Fig. 5C, D). The apparatus can be reduced to the file, the rest of the venation being very similar to that of the female (Oecanthidae, Tafaliscinae Desutter-Grandcolas, 1988, e.g., *Tafalisca lineatipes* Bruner, 1916; Fig. 5C). Or venation can be identical in males and females (Oecanthidae, Podoscirtinae, *Aphonomorphus* sp.; Fig. 5D). Males with a strongly reduced apparatus, as well as the females (Appendix 3: Fig. S3), do not have a lanceolate cell on the lateral field: the identities of the veins located in the lateral field and in the fan thus remain uncertain, because the relative convexity of the veins is hardly visible on the dorsal edge of their wings, while the median fold is strongly marked. However, following the hypothesized venation of the stridulatory apparatus, and thanks to the low relative convexity of veins, RA seems to follow a straight path to the distal edge of the wing, while RP merges with M. The fusion of RP with M would thus occur before its bifurcation into MA and MP, contrary to males with complete stridulatory apparatus. In the males devoid of a stridulum, the fan is also clearly longer and starts much more basally than in the singing males. If the fan is assumed to be homologous between males and females, the two veins inside these long fans must

be MA and MP. RP would then be in the continuity with M, while the latter usually separates from RP and extends into the fan where it branches into MA and MP: RP thus strongly resembles an anterior branch of M (Fig. 5C, D). Indeed, the vein identified here as RP is slightly concave in females (in ventral view). The strongly marked median fold between the lateral and dorsal fields leads to a strongly reduced CuA, which is hard to see. CuA merges with CuPa, i.e., the most anterior vein of the dorsal field. The latter is concave at its base and becomes convex distally close to M+CuA, suggesting a fusion of CuA with CuPaα as in singing males. Males without an apparatus have no CuPb at all. The veins posterior to the CuPa are PCu, notably curved at base and always with two branches PCuA and PCuP, and A, divided into AA and AP.

### Forewing venation pattern in fossil †Protogryllidae and †Baissogryllidae

As currently defined, the †Protogryllidae and †Baissogryllidae show a similar and relatively stable venation patterns (Pérez de la Fuente *et al.* 2012; Wang *et al.* 2019). The general organisation of their forewings is almost similar to that of modern crickets, with a lateral field and a dorsal field, a median fold, and a fan between R and CuA (possibly corresponding to a flexible zone, as in mole crickets).

Lateral field. In these fossils, the location of the putative C is often not preserved. The most anterior visible vein is Sc, which has the same pectinate branching as in modern Grylloidea (Fig. 6). Posteriorly, R is present and strongly convex. Then, the M is fused basally with CuA. A lanceolate cell (Fig. 6) is present between R and M: it is basally closed by a short transverse vein (r-m) located at the level of the divergence of M with CuA, and distally closed by a curved RP that partially merges with MA (as in modern Grylloidea, see above). Contrary to the latter, some †Protogryllidae have several secondary transverse veins in the lanceolate cell, as for example †*Angarogryllus angaricus* (Sharov, 1968) (Fig. 6A). In others, like †*Falsispeculum karatavicum* (Sharov, 1968) (Fig. 6B), veins between R and M+CuA at the base of the lanceolate cell are very similar and none is stronger than the others, complicating the identification of r-m among the crossveins. This crossvein r-m can either have an oblique direction towards wing base (obliquely inverted) between R and M (Fig. 6A, B, D), or be rather transverse (Fig. 6E, C). Some †Baissogryllidae (e.g., †*Anglogryllus lyristes* Gorochov, Jarzembowski & Coram, 2006, Fig. 6E) have a short r-m making a 'constriction' of the base of the lanceolate cell (Fig. 6E), a situation similar to that of the modern Grylloidea (Figs 3; 4; 5A).

R divides distally into a convex anterior branch RA and a rather concave posterior branch RP, well visible in †*Angarogryllus angaricus* (Appendix 3: Fig. S5A). RP is strongly curved basally and partially fuses with MA. The latter, also well visible in †*Angarogryllus angaricus*, is clearly convex. The fan is often very poorly preserved in fossils, especially for the MP branch. However, applying a conservative approach, we consider that M divides into two branches MA and MP (notably slightly visible in the unidentified †Baissogryllidae no. CCNH-293, Fig. 6D). These two branches are relatively thin and present in the fan (a situation similar in the modern Grylloidea).

Dorsal field. The clearly convex CuA diverges from M and joins CuPa crossing the median fold (well visible in †*Angarogryllus angaricus*, Appendix 3: Fig. S5A). In the †Protogryllidae and some †Baissogryllidae, the CuA is longer and oblique (Fig. 6A, B, C), whereas in other †Baissogryllidae, it is transverse between the two fields (Fig. 6D,E). CuA merges with CuPaα, after its bifurcation with CuPaβ and before the bifurcation between CuPaα1 and CuPaα2. Between CuPaα and CuPaβ, there is a strong crossvein, which corresponds to d1 (Fig. 6). Another strong crossvein d2, in alignment with d1, is present between CuPaβ and the anal node at the level of the plectrum. The harp is thus located between CuPa, CuPaβ, d2 and PCuA. In observed †Protogryllidae and †Baissogryllidae (see Appendix 3: Figs S5; S6), we noticed a reduced vein in the harp that could correspond to the CuPb, because of its base connected to that of CuPa. These fossils have two branches of PCu, PCuA and PCuP, with their characteristic strong and curved base (Fig. 6). While it has been suggested that the †Baissogryllidae and †Protogryllidae may have a file as in modern crickets (i.e., on the highly curved PCu), no stridulatory teeth are visible on photographs or illustrations of fossil specimens that we have studied. Some teeth are however visible on the PCuA in some undescribed baissogryllids from the lower Jurassic of Luxembourg (H. J. and A. N., pers. obs.), supporting this hypothesis, but it cannot be generalized to all baissogryllid and protogryllid fossils. Two anal veins, AA and AP, are located posteriorly. In the †Baissogryllidae that we observed (Fig. 6C, D, E) but not in the †Protogryllidae (Fig. 6A, B), the area between the CuPaα2 and CuPaβ is widened: by its position, this area could correspond to the mirror cell *s. str.* (mi) of modern crickets, but it is distally opened and not closed by s1 as it is in modern crickets.

### Forewing venation pattern in Gryllotalpidae

According to our hypothesis, the venation of the lateral field of mole crickets is almost the same as in the crickets *s. str.* and fossil families. Indeed, even if their bases are very close, we can identify the C, Sc, R and M+CuA (Fig. 7).

Lateral field. In the proximal half of the wing, Sc, R and M+CuA veins are almost parallel to each other. The C is fused basally with the Sc, and is composed of several slender branches directed anteriorly. Sc has the same branching shape as in Grylloidea, and we also do not distinguish between ScA and ScP in mole crickets. R, posterior to Sc, is strong and convex. M+CuA is the most posterior vein of the lateral field. Four distal branches are usually present in the lateral field and in the so-called 'flexible zone' (Fig. 7): The two most anterior veins are identified as RA and RP, while the other two may be MA and MP. RA and RP are both strong, but the RP appears to be slightly concave compared to the very convex RA. MA is clearly stronger than MP and convex, while MP is concave. Just at the base of the flexible zone, a small cell is visible. According to our hypothesis, this small cell could be homologous to the lanceolate cell of Grylloidea and fossil taxa (Fig. 8). This interpretation necessitates numerous vein reorganisation (i.e., change of vein polarity and thickness), but it is well-supported

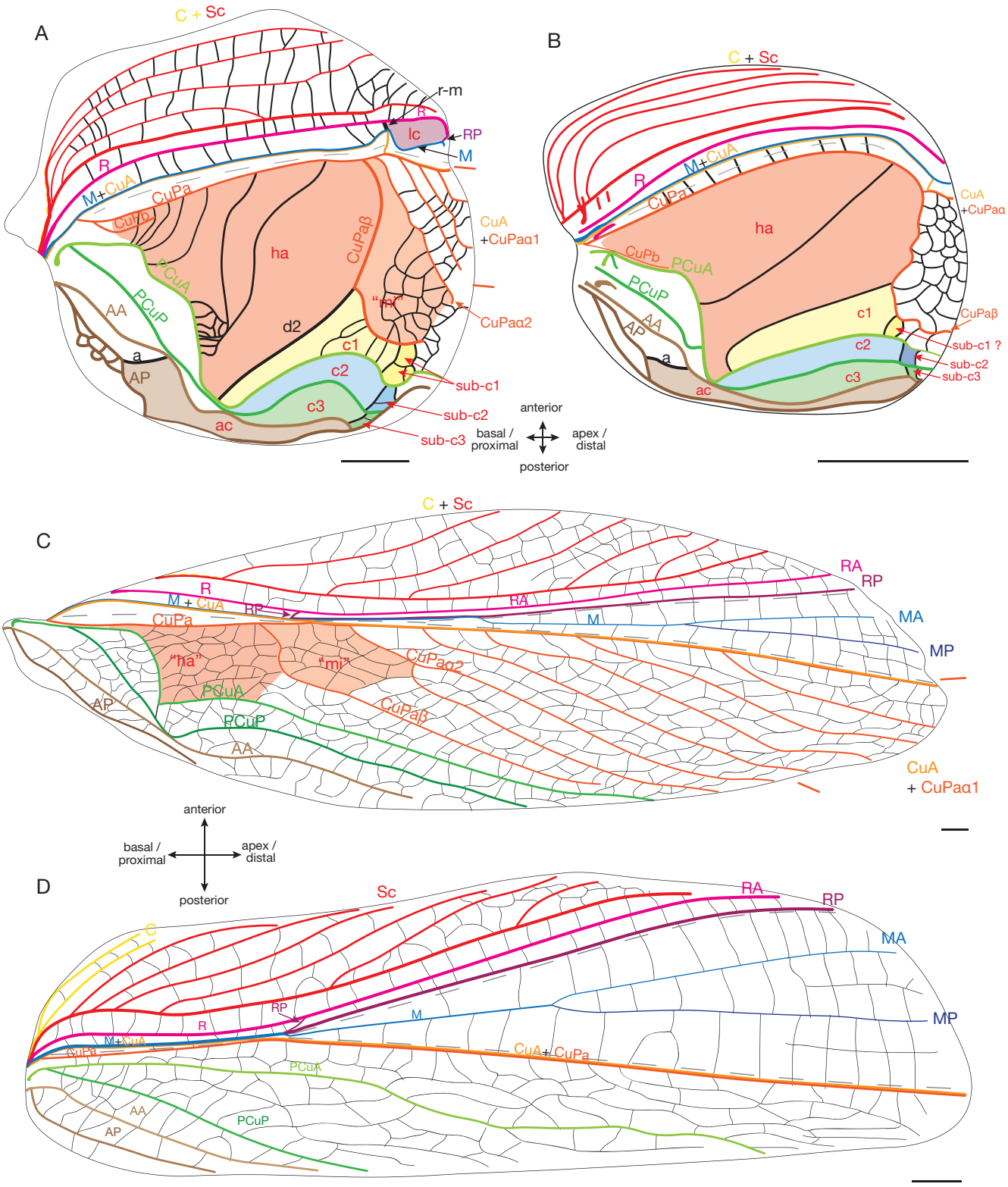


FIG. 5. — Hypothesis of primary venation homology in male Grylloidea with particular forewing venation: **A**, **B**, species with 'shortened' wings; **B**, **C**, species with 'reduced' stridulatory apparatus. **A**, *Landreva* sp. (MNHN-EO-ENSIF9775, Gryllidae); **B**, *Nemobius sylvestris* (Bosc, 1792) (MNHN-EO-ENSIF9786, Trigonidiidae); **C**, *Tafalisca lineatipes* Bruner, 1916 (MNHN-EO-ENSIF9760, Oecanthidae); **D**, *Aphonomorphus* sp. (MNHN-EO-ENSIF9764, Oecanthidae). Abbreviations: **'ha'**, distally opened harp; **'mi'** distally opened mirror; others and colour code: see text. **Grey dash lines** represent folds. Scale bars: 1 mm.

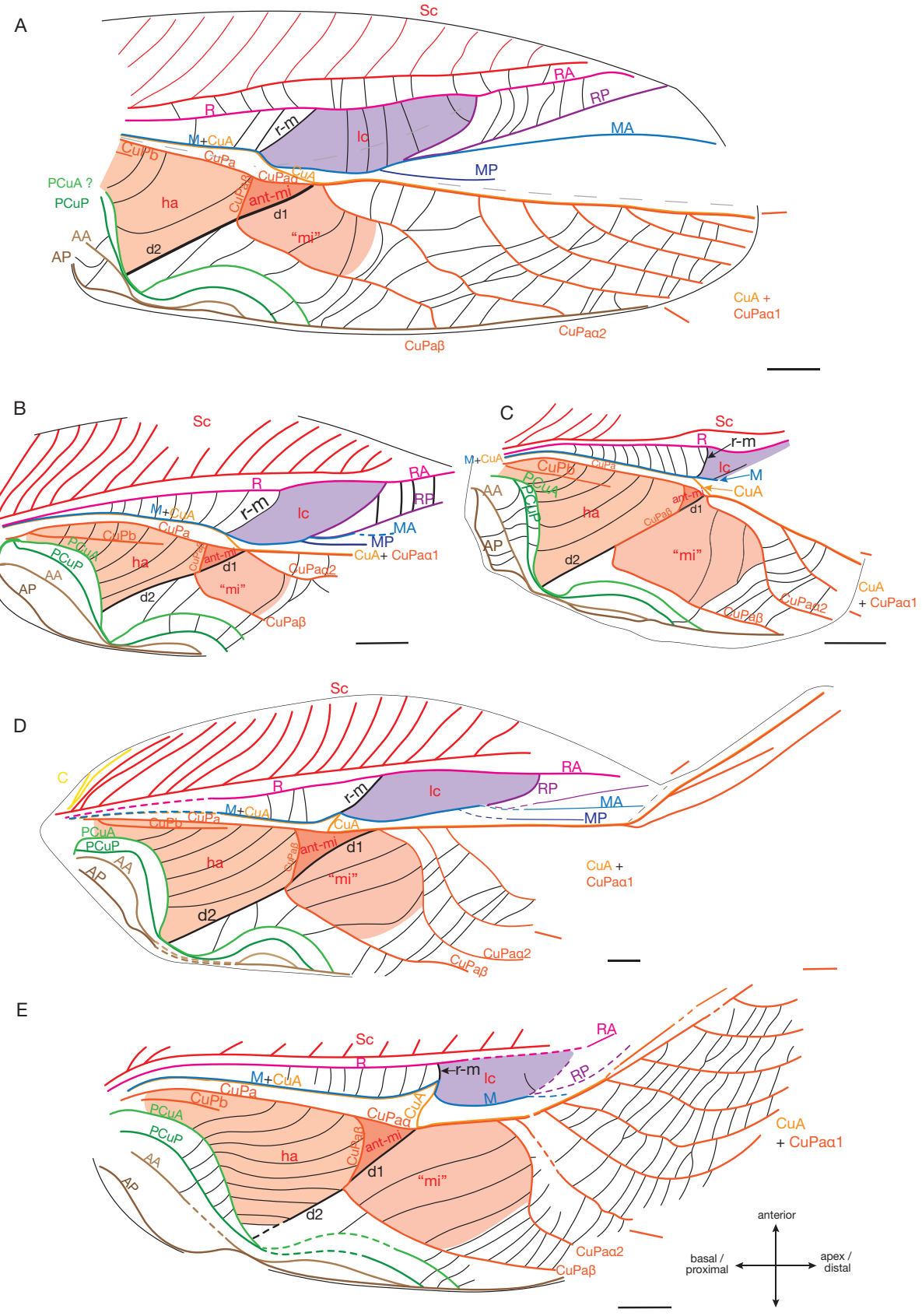


Fig. 6. — Hypothesis of primary venation homology of male forewing of †Protogryllidae (**A**, **B**) and †Baissogryllidae (**C**-**E**): **A**, †*Angarogryllus angaricus* (Sharov 1968), PIN 1873-16; **B**, †*Falsipseculum karatavicum* (Sharov 1968), PIN 3791/1345; **C**, †*Neosharategia paradoxa* Gorochov, 1992, PIN 4270-210a; **D**, †Baissogryllidae sp., CCNH-293; **E**, †*Anglogryllus lyristes* Gorochov *et al.*, 2006, MNEMG 2003.46. Abbreviations: **"ha"**, distally opened harp; **"mi"**, distally opened mirror, others and colour code, see text. **Grey dash lines** represent folds. Scale bars: 1 mm.

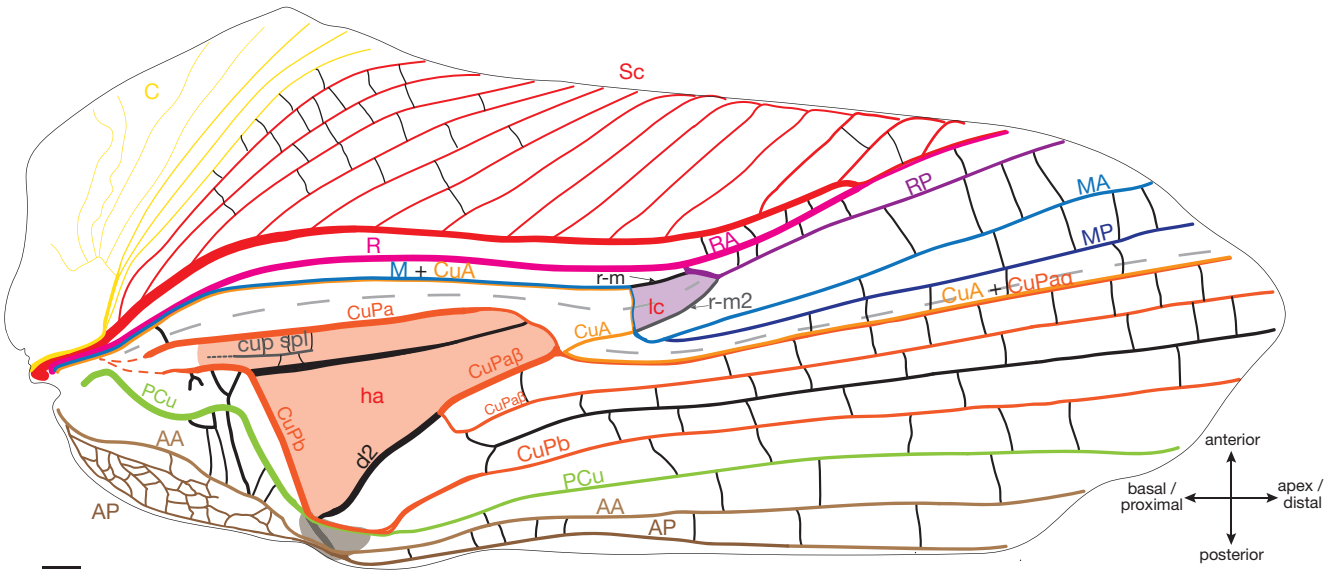


FIG. 7. — Hypothesis of primary venation homology of forewing of male *Scapteriscus* sp. MNHN-EO-ENSIF3069 (Gryllotalpidae). Abbreviations and colour code: see text. **Grey dash lines** represent folds. Scale bar: 1 mm.

by similarities between this cell and the lanceolate cell of fossil crickets (as in †*Angarogryllus angaricus*, Fig.8A), as shown by: the presence of a curved crossvein r-m between R and M; the presence of a fold crossing part of M+CuA after its point of contact with r-m and then crossing this cell; the relative positions of the veins that define the lanceolate cell of crickets; and the relative convexities of the four distal veins of this area (RA/RP and MA/MP). According to this scheme, r-m would have been reinforced in the continuity of the M+CuA in some species as *Scapteriscus* sp. (Fig. 8C), while the weak transverse vein that borders basally the lanceolate cell would be the 'real' M+CuA. But this pattern is not present in all Gryllotalpidae: for example, in *Gryllotalpa* sp. (Fig. 8B), r-m is slightly oblique (as in some †Protogryllidae) and weaker than the main veins (except the part of M+CuA that forms the base of the lanceolate cell, which is as weak as in *Scapteriscus* sp.). In fact, the polarity and orientation of the veins delimiting this cell are variable according to the species, making the identification of the vein bordering distally the lanceolate cell very complicated: it will be called here 'r-m2' because of its relative position (Fig. 8), but we are aware of three possible interpretations for these veins. A first hypothesis would consider this very strong and convex 'r-m2' as another anterior branch of MA, but this would imply a change in convexity distally, when this branch merges with RP (because RP+MA would be concave). Another hypothesis is that 'r-m2' is the result of the capture of the base of RP (before its fusion with MA, see in †*Angarogryllus angaricus,* Fig. 8A) by the very distal part of RP (after its separation with MA, Fig. 8A), a scheme that could apply to some Grylloidea (like *Phyllogryllus* sp., see Fig. 4B). Finally, r-m2 could just be a reinforced crossvein between R and M. Clearly, the origin of the 'r-m2' vein cannot be determined with certainty according to our observations.

As in crickets, mole crickets have a median fold between M+CuA and CuPa (Fig. 8). This fold is clearly less marked than in the Grylloidea. We can also notice that two distal folds border the flexible zone: one crossing the lanceolate cell and the other running along CuA+CuPaα.

Dorsal field. From the most anterior to the most posterior, the following veins are present: CuPa, CuPb, a simple PCu, AA and AP (Fig. 8). CuPa begins with a more or less straight trajectory oriented toward the distal margin; it then curves slightly posteriorly before dividing into an anterior CuPaα and a posterior CuPaβ. CuPaα merges with the CuA at its base. In the observed specimens, CuA+CuPaα is simple. CuPaβ is oblique and bent proximally on its first part, then curves sharply to orient distally and begins a trajectory parallel to the CuA+CuPaα (Fig. 8). An oblique and strongly reinforced secondary vein d2 is in continuity with the base of CuPaβ and connects it to the anal node (Fig. 8). CuPb is very blurred at its base, although it originates from the same basivenal bulla as CuPa (see Desutter-Grandcolas *et al.* 2017). CuPb is strongly curved at right angle and bears teeth on its ventrally side (= stridulatory file). A strong longitudinal vein identified as a secondary vein connects CuPa with CuPb in the harp. On several mole cricket specimens that we observed (as in *Scapteriscus* sp, Fig. 7; Appendix 3: Fig. S7C), we noticed the presence of a short vein that we identify tentatively as a 'cup spl' (see Discussion). A large cell is present between d2 and CuPb, posterior to the harp; it is not homologous to the harp, nor to the mirror of the Grylloidea, because it is not delimited by the same veins. We propose to name it the subharp cell. The PCu has a characteristic curved and rounded base. CuPb and PCu merge at the plectrum level, before separating distally to the plectrum and running rather parallel to the longitudinal axis of the wing (Fig. 8). The AA vein is often well-differentiated from the base, while AP sometimes forms a network of small undifferentiated veins at its base. The anal veins fuse at the level of the plectrum before dividing again distally and running parallel to the longitudinal axis of the wing.

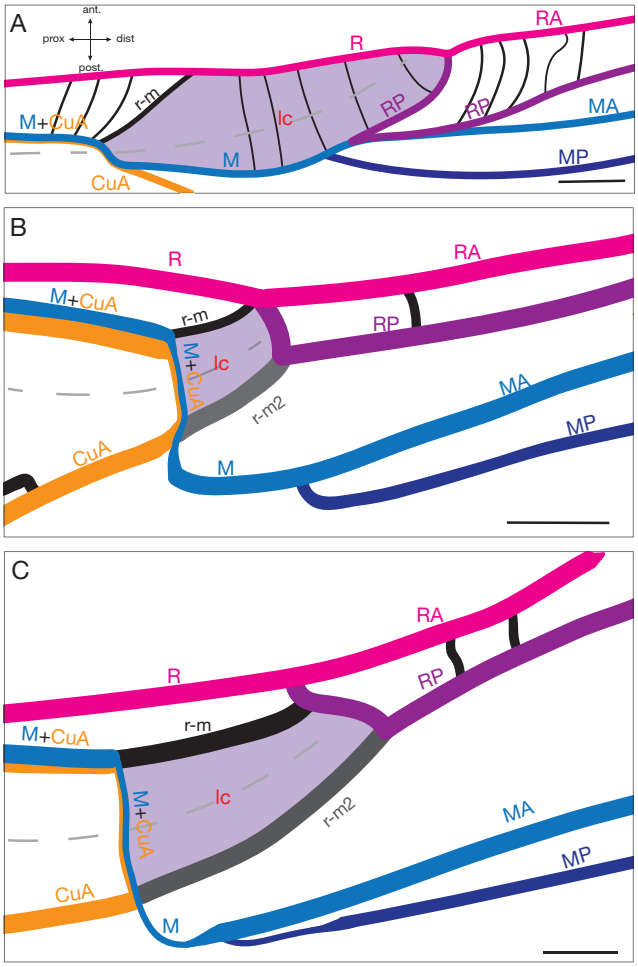


Fig. 8. — Hypotheses of primary venation homology of forewing of **A**, †*Angarogryllus angaricus* (Sharov 1968) (PIN 1873-16, †Protogryllidae, cf fig. 6A); **B**, *Gryllotalpa* sp. (MNHN-EO-ENSIF3938, Gryllotalpidae); **C**, *Scapteriscus* sp. (MNHN-EO-ENSIF3068, Gryllotalpidae). Abbreviations and colour code: see text. Scale bars: 1 mm.

In the distal half of the dorsal field, between the CuA+CuPa$\alpha$ and the posterior margin, vein configuration is highly variable among the species, or even between the two wings of the same species, or the two wings of the same individual (as in *Gryllotalpa* sp., Appendix 3: Fig. S7A, B). Additional veins, which we consider as intercalary secondary veins, may even be inserted between the main veins (Fig. 8). However, if vein fusions or branching may vary in this area, all these veins are generally parallel to each other and run parallel to the longitudinal axis of the wing.

## DISCUSSION

### The venation pattern of Archeorthoptera fits Gryllidea

Several hypotheses of venation homologies have been proposed for Orthoptera, even during the last 50 years (Zeuner 1939; Ragge 1955; Sharov 1968; Kukalová-Peck 1991; Gorochov 1995a, b; Béthoux & Nel 2001, 2002; Desutter-Grandcolas 2003; Béthoux 2012 ). The model of Béthoux & Nel (2001, 2002) primarily designed for fossil Orthoptera, applies however very well to Gryllidea, provided it is modified to include a postcubital vein, after recent microtomographic studies (Schubnel *et al.* 2020). We will discuss here more specifically three homology issues related to the identity of the MP vein, the identities of the veins delimiting the lanceolate cell and/or occurring in the fan zone (together with the definition of an arculus in crickets), and the identity of the stridulatory file through the Gryllidea.

*MP Vs 'CuA'*

Two interpretations of the global venation of orthopteran forewings still oppose today: the interpretation of Béthoux & Nel (2001, 2002) (see also Béthoux 2007), and the interpretation proposed by Sharov (1968) and followed by Gorochov (1995a, 1995b, 2005) (see also Rasnitsyn 2007). The main divergence between the 'Béthoux-Nel' and the 'Sharov-Gorochov' hypotheses relates to a short vein connecting M to the Cubital vein. For sake of clarity, the names of the veins will be given with quotation marks in the 'Sharov-Gorochov' paradigm, and without quotation mark in the 'Béthoux-Nel' paradigm. According to 'Sharov-Gorochov', the short vein is the 'MP'. Indeed, this vein separates from the median vein and could correspond to its posterior branch. This 'MP' would then merge with 'CuA' (itself emerging from a common stem with CuP), giving a branched vein called 'MP+CuA'. In 'Béthoux-Nel', this small vein is identified as the CuA: this interpretation implies a fusion at the extreme base of the wing of CuA with M, a character considered as a synapomorphy of the Archaeorthoptera (Béthoux & Nel 2001, 2002). This hypothesis is based on several observations. Firstly, the short vein ('MP' *vs.* CuA) is clearly convex in Archaeorthoptera (Béthoux & Nel 2001, 2002), which means that it corresponds to the anterior branch of a main vein. In present-day crickets, the vein 'MP' *vs.* CuA is located in a fold and its convexity cannot be observed easily, but it appears to be convex in some fossil crickets (see †*Angarogryllus angaricus*, Appendix 3: Fig. S5A). Secondly, the CuPa *vs* 'CuA' vein is clearly concave at its base in modern crickets, and would rather correspond to a posterior branch. Finally, 3D reconstructions of wing bases show that an anterior branch of Cu emerges from its basivenal bulla and joins the vein M, in agreement with the hypothesis of a basal capture of CuA by M (Desutter-Grandcolas *et al.* 2017). We will consequently adopt the 'Béthoux-Nel' paradigm in the following discussion.

*Lanceolate cell, fan (or flexible zone) venation and arculus*

The venation of the distal zone of the lateral field is quite difficult to interpret, hence the strong divergence between hypotheses of different authors. The vein bordering basally the lanceolate cell and interpreted here as a crossvein r-m, is very strong, so that this vein has been interpreted as a primary vein in many previous studies (Desutter-Grandcolas 2003; Béthoux 2012). The 'Sharov-Gorochov' hypothesis does not detail the trajectories of the main veins as much as more recent studies, so it is difficult to know how these authors interpret the vein at the base of the lanceolate cell. However, their interpretation of the distal parts of RA and RP (called 'RS') generally fit our interpretations.

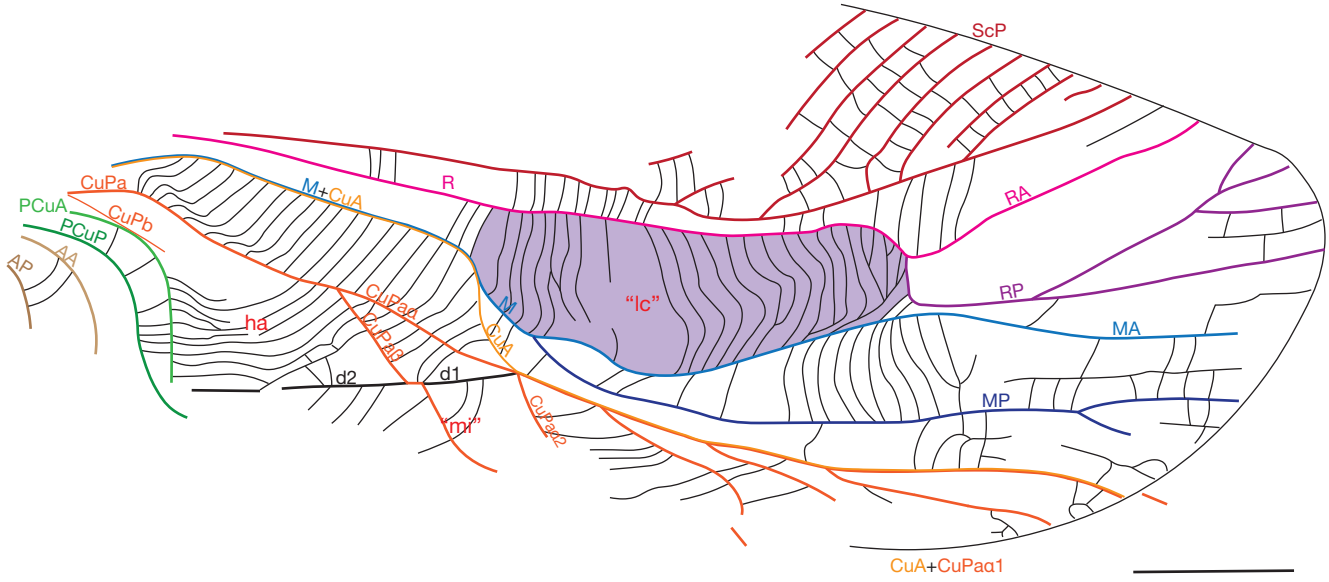


FIG. 9. — Hypotheses of primary venation homology of forewing of †*Liassophyllum caii* Gu & Ren, 2012 (CNU-ORT-NN2009008, †Tuphelidae). Modified from Gu *et al.* (2012). Abbreviations and colour code: see text. Scale bar: 5 mm.

In Béthoux (2012), the vein that we interpret as the end of RP (distad its bifurcation with M) is identified as the very base of RP, and the lanceolate cell is consequently closed by RA and RP that would meet distally (at the point that we interpret as the bifurcation of RA and RP). According to this author, RP would be partially fused with M+CuA, then with M after the re-emergence of CuA, and the veins located in the fan would therefore be (RP+)MA, MP, and CuA. Béthoux (2012) considered the posterior-most vein of the fan as the apical part of CuA, which would no longer be fused with CuPa in Gryllidea (contrary to all other Orthoptera). As a CuA is still very clearly visible between M and CuPa, and as CuA+CuPaα1 is clearly convex (whereas CuPa is concave before its fusion with CuA) in Grylloidea, Gryllotalpidae, †Protogryllidae and †Baissogryllidae, we consider here that the fusion CuA+CuPaα1 is maintained up to the apex of the wing (*contra* Béthoux 2012). For the lanceolate cell, our observations of the venation patterns in diverse fossil and modern Grylloidea lead us to propose another hypothesis. In modern Grylloidea, the vein r-m at the base of the lanceolate cell is often stronger than the other transverse veins between R and M+CuA, whereas in some fossils such as †*Falsipseculum karatavicum* (Figs 6B; Appendix 3: Fig. S5B), r-m is similar to the other crossveins. Thus, by comparing the venation of modern species of Grylloidea with the fossil families †Protogryllidae and †Baissogryllidae, we notice that the vein located at proximal side of the lanceolate cell appears as a reinforced secondary vein (our r-m), which would mean that the bifurcation of R into RA and RP is situated more distally. Other elements support this hypothesis of a rather distal RA and RP fork: First, the angle formed between R and the base of RP remains the same in Grylloidea (Figs 3; 4), compared to †Baissogryllidae and †Protogryllidae (Fig. 6). Second, the reversed longitudinal trajectory observed in RP could be related to the distal curvature of R before the RA/RP bifurcation in modern Grylloidea; the straighter base of the RP in †Protogryllidae or †Baissogryllidae (Fig. 6) would then be the potential plesiomorphic state of R. This hypothesis is in agreement with the convexity hypothesis of Kukalová-Peck (1991).

The Middle Jurassic †*Liassophyllum caii* Gu & Ren, 2012 (Fig. 9), originally assigned to the †Haglidae †Cyrtophyllitinae Zeuner, 1935 and then to the †Tuphelidae Gorochov, 1988 (Hagloidea), has stridulatory teeth (i.e., a file) on PCuA, as in Tettigonioidea and Grylloidea (Gu *et al.* 2012, 2021; Desutter-Grandcolas *et al.* 2017), and a reduced CuPb very near to the PCuA, as in Grylloidea. Its M vein is branched into two well-defined branches, MA and MP, whereas M is simple in Tettigonioidea (Gorochov 1995a, b; Garrouste *et al.* 2016). Also, a strong oblique 'diagonal' vein is present on its dorsal field, and this vein is composed of two veins that could be homologous to our d1 and d2. Therefore, †*Liassophyllum caii* could be closer to Gryllidea than to Tettigoniidea (see below Taxonomic and phylogenetic implications). The wing of †*L. caii* is widened between the R and M+CuA, being very similar to the lanceolate cell of the †Protogryllidae, †Baissogryllidae and modern Grylloidea, especially with a basal part at the same level as CuA. Its RP is very distal, curved proximally, and is very close to MA, but not fused with it. No strong, well-differentiated 'r-m' vein is visible at the proximal side of the putative lanceolate cell. This venation and a potential position of †*Liassophyllum caii* in the stem group of Gryllidea are thus in favor of our hypothesis of a secondary and reinforced crossvein r-m at the base of the lanceolate cell in Gryllidea. The lanceolate cell would be more distal in modern Grylloidea than in †*Liassophyllum caii*.

This hypothesis therefore implies that the lanceolate cell could be homologous between †*Liassophyllum caii*, †Protogryllidae, †Baissogryllidae and modern Grylloidea. Indeed, there is a

very strong similarity in cell shape, orientation and number of main veins around the cell in all these taxa. The polarity of the veins could be modified in some modern species. The hypothesis of RP at the base of the cell of Grylloidea would therefore be less parsimonious.

We show that mole crickets also possess a lanceolate cell. This cell, identified by Gorochov (1995a, b) in †Protogryllidae, †Baissogryllidae and Grylloidea, had never been identified in the Gryllotalpidae before. Venation is much more difficult to interpret in mole crickets, especially because of the strong variability of the forewing venation, sometimes with differences between the two wings of the same individual (Appendix 3: Fig. S7A, B). Moreover, the fossil record of Gryllotalpidae is rather poor and mainly consists of apterous juvenile specimens (not considering very badly preserved imprints from the Brazilian early cretaceous Crato formation: see Martins-Neto 1991). The study of their venation is thus limited to extant species. A true lanceolate cell, although significantly smaller, is however clearly delimited by the same veins in Gryllotalpidae (Figs 8; Appendix 3: Figs S7; S8) and in other observed Gryllidea, and can consequently be considered homologous. Apart from the shape and location of the cells, Gryllotalpidae and Grylloidea are similar by: the proximal edge of the cell formed by a reinforced and curved crossveins (r-m) and a short part of CuA, just before the bifurcation of M and CuA; the fold crossing longitudinally M+CuA and the lanceolate cell; and the four distal veins RA, RP, MA and MP, whose relative convexities are easy to observe. Distal to the lanceolate cell, RP is often somewhat curved proximally at its base, although the interpretation of the r-m2 is problematic. Unlike grylloid females, a lanceolate cell is also present in the female mole crickets, which may be related to sound production (Hoffart *et al.* 2002 and references within) (Appendix 3: Fig. S8A, B).

Whatever the variations observed in and around the lanceolate cell, it is clear that the venation pattern of crickets presents a reinforced structure, which we interpret here as an arculus. Different types of 'arculus' *sensu* Wootton (1992) exist among the Pterygota. In the basal-most Archaeorthoptera, the arculus is constituted by the bases of M, CuA, and the distal end of CuPaα (Nel *et al.* 2012: fig. 1C). In the Gryllidea, the arculus is located much more distally and reinforced by r-m.

*Origin of the file*

The origin of the stridulatory apparatus in the Ensifera is still a source of debate, especially for the file (Béthoux 2012; Chivers *et al.* 2017; Desutter-Grandcolas *et al.* 2017). X-ray microtomography analyses of the base of forewings showed that the file vein does not always originate from the same basivenal bulla depending on the group (Desutter-Grandcolas *et al.* 2017): in the Tettigonioidea and Grylloidea, the file is on a vein that comes from the basivenal bulla of PCu, while the file vein originates from the basivenal bulla of Cu in the Gryllotalpidae and Prophalangopsidae. Our observations of the basal venation of Gryllidea corroborate this hypothesis, identifying the file as part of the PCuA in the Grylloidea and †Baissogryllidae p.p., and as part of the CuPb in the Gryllotalpidae. According to this hypothesis, the Grylloidea also have a reduced CuPb. This latter, which originates from the basivenal bulla of Cu, should not be confused with the intercalary vein (without bulla) that we named cup spl, present in several groups (e.g. Trigonidiidae, Gryllotalpidae, etc.). Such an intercalary vein is also present in the †Permostridulidae Béthoux *et al.* 2003 (Archaeorthoptera †Caloneurodea Martynov, 1938), in which it bears small teeth and makes a file (Béthoux *et al.* 2003). In the crickets, this intercalary vein could correspond to a reinforcement of this area which is under the constrain of the strong curvature of the file vein (CuPb or PCuA). It does not exist in observed Phalangopsidae, Oecanthidae, and Gryllidae, where this function could be fulfilled by the CuPb, and which forewings often present intense corrugation. Indeed, the CuPb corresponds to the file in the Gryllotalpidae, or is very thin and close to the PCuA in the Trigonidiidae (and in Mogoplistidae, L. F., A. N. and L. D. pers. obs.). The different cup spl observed are therefore not necessarily homologous, even though it can be hypothesized that they perform a similar function.

The hypothesis of a convergent occurrence of the stridulatory file in crickets and mole crickets may seem difficult to conceive in the general context of homologies on the more distal structures of the forewings (lanceolate cell, diagonal, harp, branching of CuP, etc.) and because of the sistership relation of Grylloidea and Gryllotalpoidae in modern molecular phylogenies. It is clear that the files of these two groups do not come from the same basivenal bulla and are thus not homologous, but how can we explain this pattern of evolution? Could this convergence be the result of a 'transfer' of the stridulatory teeth to different veins under functional constraints? Could it be related to the underground habits of the Gryllotalpidae? This question could be answered by further studies of different fossil groups (†Protogryllidae, †Baissogryllidae, but also 'Hagloidea', which are clearly non monophyletic, and hopefully adult fossil Gryllotalpidae) to include them in future molecular and morphological phylogenies with a more complete study of the venation. Transcriptomic studies could also help to understand the evolution of the file in the Gryllidea.

## New venation pattern in the forewings of fossil and extant Gryllidea

*Redefinition of the singing apparatus and other forewing structures (Table 1)*

In Gryllidea, the file is located on the most anterior part of a strongly curved vein (almost at right angle) at the base of the forewings; it is very concave and bears teeth ventrally. According to our forewing pattern of venation, the file is located on the PCuA in Grylloidea and on the CuPb in the Gryllotalpidae. In some observed †Baissogryllidae, a file is located on the PCuA. The other observed †Baissogryllidae and the †Protogryllidae have a strongly curved PCuA that could similarly bear a file, but no direct observation of teeth has yet attested it.

The harp is a large triangular cell that occupies the main part of the basal half of the dorsal field. It is bordered by the file (PCuA in Grylloidea, and possibly in †Baissogryllidae

TABLE 1. — Comparison of venation characters in modern Grylloidea, Gryllotalpidae, †Protogryllidae, †Baissogryllidae, †*Liassophyllum caii* Gu & Ren, 2012 and Tettigonioidea, according to the forewing pattern presented in the present paper. Abbreviations: see text.

| | **Gryllidea** | | | | ***Incertae sedis*** | **Tettigoniidea** | |
|---|---|---|---|---|---|---|---|
| | **Grylloidea** | **Gryllotalpidae** | **Protogryllidae** | **Baissogryllidae** | ***†Liassophylum caii*** | **Prophalangopsidae (*Cyphoderris*)** | **Tettigonioidea** |
| File | Present: part of PCuA | Present: part of CuPb | Putatively present: a part of PCuA | Observed in one taxon: part of PCuA | Present: part of PCuA | Present: part of CuPb | Present: part of a branch of PCu |
| Harp | Present: between PCuA (file), CuPa, CuPaβ and d2 ; crossed by a more or less short CuPb and by one (in Trigonidiidae) or several crossveins | Present: between CuPb (file), CuPa, CuPaβ and d2; crossed by one reinforced longitudinal crossvein | Present: between PCuA (putative file), CuPa, CuPaβ and d2; crossed by a more or less short CuPb and several crossveins | Present: between PCuA (putative file), CuPa, CuPaβ and d2; crossed by a more or less short CuPb and several crossveins | Present: between PCuA (file), CuPa, CuPaβ and d2; crossed by a more or less short CuPb and several crossveins | Present between CuPb (file), CuPa, CuPaβ and d2; crossed by several crossveins | Absent? (venation of this area needs to be reinterpreted) |
| Mirror | Mirror *s. s.* present: widened, closed by s1 | Absent | Mirror *s.l.* present: not widened, distally open | Mirror *s.l.* present: widened cell, distally open | Mirror *s.l.* present: not widened, open distally | Mirror *s.l.* present: cell widened, distally open | Non homologous resonator |
| Lanceolate cell | Present: small, medium or very elongated; distally located | Present: very small, closed distally by a r-m2 (homology of this vein problematic) | Present: large, elongated and central | Present: large, elongated and central | Absent, but wide cell in the same place | Absent | Absent |
| Diagonal vein | Present: d1 and d2 present, well differentiated and reinforced; d1 partially or totally captured with CuPaβ | Present: d2 present, well differentiated and reinforced ; d1 totally captured by CuPaβ | Present: d1 and d2 present, well differentiated and reinforced; d1 partially captured by CuPaβ | Present: d1 and d2 present, well differentiated and reinforced; d1 partially captured by CuPaβ | Present : d1 and d2 present, well differentiated and reinforced; d1 partially captured by CuPaβ | Absent: only d1 present, well differentiated and reinforced; d2 absent or not differentiated | Absent or strongly differentiated? |
| Chords | Present: PCuA, PCuP (+/- AA) curved posteriorly to mirror cell; interchord cells (c1, c2, c3, subc1, subc2, subc3) present, almost devoid of crossveins (except pi in c1) | PCu, AA and AP straight. Chords s. str. absent. No interchord cells | Present: PCuA, PCuP (+/- AA) curved posteriorly to mirror cell; some undifferentiated crossvein in interchord cells (c1, c2, c3, Subc1, subc2, subc3) | Present: PCuA, PCuP (+/- AA) curved posteriorly to mirror cell; some undifferentiated crossvein in interchord cells (c1, c2, c3, Subc1, subc2, subc3) | Non visible | Absent? curved veins (CuPb, PCu) visible but very thin distal to anal node; connected by many crossveins | Absent |

and †Protogryllidae; CuPb in Gryllotalpidae) proximally, the CuPa anteriorly, the base of CuPaβ distally and d2 posteriorly. It can be crossed by a strong longitudinal crossvein or several weak ones. It is also often crossed by a reduced vein (CuPb) parallel to CuPa, in Grylloidea, †Baissogryllidae and †Protogryllidae.

The mirror is a round cell on the dorsal field. It is bordered proximally by CuPaβ, antero-distally by d1 and CuPaα2. The mirror *s. str.* is postero-distally closed by s1 and present only in modern Grylloidea. The mirror *s.l.* of †Baissogryllidae and †Protogryllidae is located between CuPaβ, d1, and CuPaα2, but not closed distally by s1; moreover it is widened in †Baissogryllidae (as in modern Grylloidea), but not in †Protogryllidae. In Grylloidea and some †Protogryllidae and †Baissogryllidae, the mirror is surrounded by some other smaller cells, i.e., ant-mi (between CuPaβ, CuPaα, CuPaα2 and d1), para-mi (between CuA+CuPaα1 and CuPaα2 and distally closed by a point where both merge) and sub-mi (between CuPaβ, CuPaα2, s1 and s2).

The lanceolate cell is located distally in the lateral field, just at the anterior limit; it is crossed longitudinally by the anterior fold of the flexible zone (called 'fan' in Grylloidea). It is an elongated cell located between R anteriorly and M posteriorly. Basally, it is limited by the reinforced crossvein r-m, and by a short part of M+CuA (just basad the separation of M and CuA). Distally, R divides into RA and RP, and the lanceolate cell is closed by a RP (proximally bent and joining MA). In Gryllotalpidae, this cell is very small, and the vein closing distally to the lanceolate cell is called here r-m2 because of the difficult interpretation of this vein. Additional observations will be necessary to confirm the homology of r-m2 with the RP of Grylloidea.

The 'diagonal' vein traditionally defined as the vein separating the harp from the chords and mirror, is actually composed of two reinforced crossveins d1 and d2, the first one being partially or completely captured (or replaced) by the base of CuPaβ. In modern Grylloidea, †Baissogryllidae and †Protogryllidae, d1 is partially or totally captured by the base of CuPaβ while it is always totally captured (and replaced) in Gryllotalpidae.

The chords correspond to portions of PCuA, PCuP, and AA curved distally to the anal node: they join distally, near the posterior edge of the wing, and delimit several cells (named c1, sub-c1, c2, sub-c2, c3 and sub-c3, on figures) that are most often devoid of crossveins, except c1 that can be crossed by some weak veins and/or a strong pilar vein. This area of the wing is variable among the taxa and its venation is to be interpreted with precaution in comparative studies.

*Taxonomic and phylogenetic implications*

The redefinition of the forewing venation in Gryllidea offers new diagnostic morphological characters (Table 1). Potential apomorphies can be proposed for the different groups, which will have to be tested on a larger sample of taxa and through genuine phylogenetic analyses. Today, few cricket clades have been studied for their phylogenies using morphological characters in addition to molecular data, i.e., Eneopterinae (Gryllidae: Robillard & Desutter-Grandcolas 2004; Vicente *et al.* 2017) and Oecanthidae (Campos *et al.* 2022). Both clades validate the pattern of venation we propose for complete forewing venation; they also present original reduced acoustic devices, not studied here, but that will have to be reanalyzed in the next future to reconsider the potential apomorphies proposed by the authors for each clade in the new venation frame: this task is beyond the scope of the present paper, even though several taxa have already been checked in the present study (see Appendix 1). The morphological and molecular phylogeny of the Nemobiinae (Trigonidiidae) is presently reconstructed, with the same purpose (Faberon *et al.* in prep.).

The infra-order Gryllidea is characterized by the presence of the composite and strong vein called the 'diagonal', not visible in modern species of Prophalangopsidae (Hagloidea) and Tettigonioidea. This vein is made of the two cross veins d1 and d2, which could be homologous respectively to the handle (h) and the column (c) defined in some fossils currently classified as 'Hagloidea' by Sharov (1968) or Gorochov (1995a, b) (Béthoux & Nel 2001, 2002; Béthoux 2012). In some of these fossils, d1 and d2 are thinner and less differentiated (especially d2) than in modern Grylloidea, Gryllotalpidae, †Baissogryllidae and †Protogryllidae. In others, they are aligned and very strong, as in †*Liassophylum caii* (Fig. 7), making a true 'diagonal' similar to that of modern and fossil Gryllidea. The Gryllidea are also characterized by the shape of CuPaβ. Gorochov (1995b) proposed that the strong basal curvature of CuPaβ could be an apomorphy of his 'Grylloidea' (almost corresponding to the Gryllidea *sensu* Cigliano *et al.* 2023). This character results from the capture of d1 by the base of CuPaβ, which could be an apomorphy of the Gryllidea. Gryllidea are finally characterized by the presence of a fold between M+CuA and CuPa (separating the dorsal and lateral fields), a flexible zone (= median fan in the Grylloidea) located distad this fold, and a lanceolate cell *s. str*. The characteristic widening of the cell between R and M observed in many 'Hagloidea' could probably be homologous to the lanceolate cell, but it is not closed basally by a reinforced r-m and distally by a reversed and bent RP.

The Grylloidea are characterized by the presence of a reinforced cross vein s1 which closes distally the mirror cell *s. str.*: this character could be a synapomorphy of the crown group. A mirror *s.l.*, i.e., a cell not closed distally by a reinforced s1, is present in the †Baissogryllidae, †Protogryllidae or Prophalangopsidae (Hagloidea); it is not widened in the †Protogryllidae. Grylloidea have two particular cells around the mirror, i.e., para-mi and sub-mi, in addition to the cell ant-mi which is present in †Baissogryllidae, †Protogryllidae and Prophalangopsidae ('Hagloidea'). The so-called 'mirror' of the Tettigonioidea is not surrounded by the same veins and cannot be homologous to the mirror of crickets: it should consequently be named differently to avoid any confusion, and we propose the generic term resonator. Indeed, the venation of the Tettigonioidea and their allies should be reinterpreted from the very base of the forewing, in order to compare more precisely the venation patterns of the different groups of Ensifera. The Grylloidea have a bifurcated PCu with an anterior branch bearing the stridulatory teeth on ventral side. They also have a variable, but always reduced, CuPb and they possess chords and their characteristic cells, posteriorly to the mirror. In some fossils currently classified in 'Hagloidea', similar 'chords' are present, but contrary to the crickets, those are connected by many crossveins, which could reveal plesiomorphic. Lastly, the Grylloidea have a very distal lanceolate cell, variable in size, with a RA/RP fork located very close to the apical edge of the wing; all other Ensifera have a more central RA/RP fork on the wing, whether they have a lanceolate cell or not.

The main characteristics of the venation pattern of Gryllotalpidae is that the distal veins are very rectilinear, parallel between them and with the longitudinal axis of the wing. This character is not present in any other Ensifera. In the Grylloidea, some females or males without a stridulatory apparatus may show the distal veins of the dorsal field parallel to each other, but they show a clear angle with the longitudinal axis of the wing and are not parallel to it (Appendix 3: Fig. S7D). The Gryllotalpidae have also a smaller lanceolate cell than other acoustic Gryllidea, and the basal part of their CuA has a pronounced postero-basal direction. In all other specimens observed in the other groups, the CuA is always either transverse or has a less pronounced postero-basal direction.

The †Protogryllidae and †Baissogryllidae are currently classified in the Grylloidea (Cigliano *et al.* 2023), but this may result from confusion between the successive classifications used for crickets, and recurrent variations in taxonomic levels. The relationships of these two families with the extant Grylloidea, and even within the Gryllidea, have in fact never been tested by phylogenetic analyses: our hypothesis of character states will have to be included in a large-scale morphological

phylogeny of both extant and fossil cricket taxa. Yet previous results on Orthoptera or Ensifera phylogeny can already be used to reconsider the present state of knowledge about fossil groups, at least as far as plesiomorphic states are concerned. The †Protogryllidae and †Baissogryllidae share several potential synapomophies with the Gryllidea, that could be used to include them in this infra-order, i.e., forewings organized in two fields separated by a fold and a flexible zone (or fan); a strong diagonal vein formed by d1 and d2; a CuPaβ curved at its base and bent as a result of the partial capture of d1; and a lanceolate cell *sensu stricto*. The veins of the distal half of the dorsal field of †Protogryllidae and †Baissogryllidae are not parallel to the longitudinal axis of the wing, thus not allowing to bring them closer to the Gryllotalpidae. Their lanceolate cell is often more developed and rather central in location, contrary to modern Grylloidea (Gorochov 1985, 1995b; Gorochov *et al.* 2006). But the †Baissogryllidae and †Protogryllidae have a bifurcated PCu, as in modern Grylloidea, even though a true file (curved PCuA with ventral teeth) has been observed only in some †Baissogryllidae for now. Species in these two families have a CuPa branching very similar to that in the Grylloidea. Finally, the †Baissogryllidae have a wide cell between CuPaβ and CuPaα2, like modern Grylloidea, an enlargement that is also present in some modern Prophalangopsidae.

No putative apomorphy could be identified to support the †Baissogryllidae and †Protogryllidae as monophyletic entities. They are currently separated by their respective periods of occurrence, with the †Protogryllidae dating from the Triassic to the Upper Jurassic, and the †Baissogryllidae from the Jurassic to Lower Cretaceous (Gorochov *et al.* 2006). A species from the Lower Jurassic of China, †*Sinagryllus xinjiangensis* Wang *et al.*, 2019 has recently been described as a †Baissogryllidae (Wang *et al.* 2019; Xu *et al.* 2019), which is supported by the presence of a widened mirror *s.l.* (Appendix 3: Fig. S6D). But such a wide area is also present in Grylloidea and in Prophalangopsidae (Hagloidea), and could reveal a homoplasy in a phylogenetic frame. The lack of the reinforced s1 could be a plesiomorphy within Ensifera. The †Baissogryllidae are often characterized (and separated from the Grylloidea) by the configuration of the transverse veins of the mirror *s.l.*, that Gorochov (1995b) described as 'rather parallel to the base of CuA2' (which corresponds to d1 captured by CuPaβ). The veins located between CuPaβ and CuPaα2 are however oriented in the same way in Hagloidea and †Protogryllidae, whether they have a widened cell (mirror *s.l.*) or not. The orientation of these veins could therefore be a plesiomorphy within Ensifera. In many †Baissogryllidae, as in the type genus of the family *Baissogryllus* Sharov, 1968, the r-m is elongated and directed proximally before its fusion with M+CuA, but this character seems to be shared with some †Protogryllidae as †*Angarogryllus angaricus* (Fig. 6A) and could be plesiomorphic or homoplastic. In addition, some †Baissogryllidae have a rather transverse and short r-m, as †*Anglogryllus lyristes* (Fig. 6E), which makes a 'constriction' at the base of the lanceolate cell as observed in Grylloidea. All these characters will have to be reconsidered in true phylogenetic analyses, in order to test potential apomorphies and hypothesize on a safe ground the monophyly of the †Baissogryllidae. Note however that some †Baissogryllidae show an important distal extension of the forewing dorsal field distally (Fig. 6D), which has never been mentioned and interpreted previously: if confirmed, this character could constitute an apomorphy of a restricted fossil group, related to †*Baissogryllus* (A.N., pers. obs.).

In the same way, Gorochov (1995b) states that Sc and CuPa veins are strongly divergent in the †Protogryllidae, but this character is present in many Hagloidea and Tettigonioidea: it could be a potential symplesiomorphy of the Ensifera. Currently the †Protogryllidae are mainly 'characterized' by the absence of a widening between CuPaβ and CuPaα2, i.e., by the putatively plesiomorphic absence of a mirror (even *s.l.*) (Gorochov 1995b). This character is however observed in many other Ensifera, such as the Gryllotalpidae, some Hagloidea and Tettigonioidea. †Protogryllidae are also distinguished from the extant male Grylloidea with a reduced, mirrorless stridulum, by the presence of a large and centered lanceolate cell on the lateral field and the presence of a strong diagonal vein. They consequently cannot be considered as Grylloidea with a reduced stridulum.

## CONCLUSION

Wings have been a major innovation in the evolution of insects (Prokop *et al.* 2023) and their use for communication is ancient (Schubnel *et al.* 2021). Few insect orders have however use their wings to communicate as much as the Orthoptera, and especially the Ensifera. The diversity of the structures, behaviours and acoustic signals known in this clade is huge and acoustics have clearly been a dominant and constant player in their diversification. Knowing the evolutionary history of this group and retracing the successive modifications that occurred since the early diversification of Ensifera is a fascinating issue. One of the main problems encountered since hundreds of years and not yet solved is the reconciliation of fossil and modern venation patterns. We tackle this problem for the Gryllidea, a major group within Ensifera, and even within this scope we met problems to interpret venation of modern species (especially Gryllotalpidae) and to compare them with ensiferan fossils. The obvious non-monophyly and poor characterisation of many fossil groups would oblige to consider each fossil separately in comparative studies. Our observations provide a solid base to compare species venation and test putative homologies. We also describe wing venation with well-defined characters that could be incorporated in a phylogenetic data matrix, more efficiently than usual functional characters (as for example 'presence vs absence of a stridulatory file', 'presence vs absence of a "mirror"', etc.). We have not solved all the problems, but our results update the current state of art of forewing venation in the Gryllidea and settle the grounds for the use of wing venation in phylogenetic studies of the clade. The comparison with Tettigoniidea is now still more necessary to understand the historical modification of acoustic communication in Ensifera.

## Author contributions

**Hugo Josse.** Observations; interpretations of modern and fossil specimens (equal); visualisation; original draft (equal); review and editing (equal).

**Léo Faberon.** Observations, interpretations (equal) and visualisation of Trigonidiidae crickets; review and editing (equal).

**Thomas Schubnel.** Observations; interpretations of modern and fossil insects (equal); visualisation; original draft (equal); review and editing (equal).

**André Nel.** Administration of the project (equal); interpretations of modern and fossil specimens (equal); original draft (equal); review and editing (equal).

**Laure Desutter-Grandcolas.** Administration of the project (equal); interpretations of modern specimens (equal); original draft (equal); review and editing (equal).

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## Conflict of interest

The authors declare that they have no conflict of interest.

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APPENDIX 1. — List of specimens observed in the MNHN Orthoptera collections. Supplementary figures gathered in Appendix 3.

| Family, subfamily | Tribe | Genus | Species | | Identified | Sex | Inventory number | Origin | Figures |
|---|---|---|---|---|---|---|---|---|---|
| OECANTHIDAE | | | | | | | | | |
| Oecanthinae | Oecanthini | *Oecanthus* | *rufescens* | Serville, 1838 | L. Desutter | ♂ | MNHN-EO-ENSIF9765 | New Caledonia | |
| Tafaliscinae | Tafaliscini | *Tafalisca* | *lineatipes* | Bruner, 1916 | L. Denadai de Campos | ♂ | MNHN-EO-ENSIF9760 | Jamaica | 5C; S3C |
| | Paroecanthini | *Paroecanthus* | *simplex* | Gorochov, 2011 | L. Denadai de Campos | ♂ | MNHN-EO-ENSIF9782 | Mexique | |
| | | *Angustitrella* | *vicina* | (Chopard, 1912) | L. Denadai de Campos | ♂ | MNHN-EO-ENSIF9783 | French Guiana | |
| | | *Ectotrypa* | *olmeca* | Saussure, 1874 | L. Denadai de Campos | ♂ | MNHN-EO-ENSIF12163 | Mexico | S2C |
| Podoscirtinae | Podoscirtini | *Archenopterus* | *bouensis* | Otte, 1987 | L. Desutter | ♂ | MNHN-EO-ENSIF3935 | New Caledonia | |
| | Aphonomorphini | *Aphonomorphus* | sp. | | | ♂ | MNHN-EO-ENSIF9764 | French Guiana | 5D; S3D |
| | Phyllogryllini | *Phyllogryllus* | sp. | | | ♂ | MNHN-EO-ENSIF9768 | Guadeloupe | 4B; S2B |
| PHALANGOPSIDAE | | | | | | | | | |
| Luzarinae | Luzarini | *Luzara* | *obscura* | Desutter-Grandcolas, 1992 | L. Desutter | ♂ | MNHN-EO-ENSIF5876 | French Guiana | |
| | | *Lerneca* | *fuscipennis* | (Saussure, 1874) | L. Desutter | ♂/♀ | MNHN-EO-ENSIF9780, MNHN-EO-ENSIF9781 | French Guiana | ♂: 3B; S1D / ♀: S4A |
| Phalangopsinae | Phalangopsini | *Endecous* | *Itatibensis* | Rehn, 1918 | L. Desutter | ♂ | MNHN-EO-ENSIF9761 | Brazil | |
| | Homoeogryllini | *Homoeogryllus* | *xanthographus* | Guérin-Ménevile, 1844 | L. Desutter | ♂ | MNHN-EO-ENSIF9779 | Farm strain | |
| | | | *orientalis* | Desutter, 1985 | L. Desutter | ♂ | MNHN-EO-ENSIF3069 | Mozambique | |
| | | | *affinis lyristes* | Gorochov, 1988 | L. Desutter | ♀ | MNHN-EO-ENSIF9784 | Rwanda | Fig. S4B |
| Paragryllinae | Aclodini | *Paraclodes* | *guyanensis* | Desutter-Grandcolas, 1992 | L. Desutter | ♂ | MNHN-EO-ENSIF9762 | French Guiana | |
| | Paragryllini | *Aclogryllus* | sp.. | | L. Desutter | ♂ | MNHN-EO-ENSIF9785 | Equateur | |
| Phaloriinae | | *Phaloria* | sp. | | L. Desutter | ♂ | MNHN-EO-ENSIF3078 | Philippines | |
| GRYLLIDAE | | | | | | | | | |
| Eneopterinae | Eneopterini | *Eneoptera* | *guyanensis* | Chopard, 1931 | L. Desutter | ♂ | MNHN-EO-ENSIF9766 | French Guiana | |
| | Lebinthini | *Ligypterus* | *fuscus* | Chopard, 1920 | L. Desutter | ♂ | MNHN-EO-ENSIF9767 | French Guiana | |
| | Lebinthini | *Agnotecous* | sp. | | T. Robillard | ♂ | MNHN-EO-ENSIF9937 | New Caledonia | |
| | Nisitrini | *Nisitrus* | *vittatus* | (Haan, 1844) | T. Robillard | ♂ | MNHN-EO-ENSIF9938 | Laboratory strain | |
| Pentacentrinae | Pentacentrini | *Pentacentrodes* | sp. | | L. Desutter | ♂ | MNHN-EO-ENSIF9776 | Madagascar | |
| Gryllinae | Gryllini | *Brachytrupes membranaceus* | | (Drury, 1773) | L. Desutter | ♂/♀ | MNHN-EO-ENSIF9769/ MNHN-EO-ENSIF12162 | Republic of Congo/ Guinea | ♂: 2A, B; 4A; S2A / ♀: S4C |
| | | *Acheta domesticus* | | (Linnaeus, 1758) | | ♂ | MNHN-EO-ENSIF9777 | Farm strain | |
| Landrevinae | Landrevini | *Landreva* | sp. | | L. Desutter | ♂ | MNHN-EO-ENSIF9775 | India | 5A; S3A |
| TRIGONIDIIDAE | | | | | | | | | |
| Trigonidiinae | Trigonidiini | *Anaxipha* | sp. | | L. Desutter | ♂ | MNHN-EO-ENSIF9770 | French Guiana | |
| | | *Natula* | *longipennis* | (Serville, 1838) | | ♂ | MNHN-EO-ENSIF9933 | Indonesia | 3A, B; S1A, B, C |
| Nemobiinae | Nemobiini | *Nemobius* | *sylvestris* | (Bosc, 1792) | L. Desutter | ♂ | MNHN-EO-ENSIF9786 | France | 5B; S3B |

Appendix 1. — Continuation.

| Family, subfamily | Tribe | Genus | Species | | Identified | Sex | Inventory number | Origin | Figures |
|---|---|---|---|---|---|---|---|---|---|
| MOGOPLISTIDAE | | | | | | | | | |
| Mogoplistinae | | *Ornebius howensis* | | Chopard, 1951 | L. Chopard | ♂ | MNHN-EO-ENSIF10119 | Lord Howe Island | – |
| Incertae sedis | | | | | | | | | |
| Pteroplistinae | Pteroplistini | | sp. | | L. Desutter | ♂ | MNHN-EO-ENSIF9763 | Borneo | – |
| GRYLLOTALPIDAE | | | | | | | | | |
| Gryllotalpinae | Gryllotalpini | *Gryllotalpa africana microphtalma* | | Chopard, 1936 | L. Chopard | ♂ | MNHN-EO-ENSIF9771 | Senegal | S7F |
| | | | sp. | | | ♂ | MNHN-EO-ENSIF9772 | Italy | S7E |
| | | | sp. | | | ♀ | MNHN-EO-ENSIF9773 | Vietnam | S8F |
| | | | sp. | | | ♂ | MNHN-EO-ENSIF9774 | Java | S8D |
| | | | sp. | | | ♂ | MNHN-EO-ENSIF3938 | Crete | 8B; S7A, B |
| | | | *elegans* | Chopard, 1934 | R. Roy | ♀ | NA | no origin | S8A, B |
| | | *Scapteriscus* | sp. | L. Desutter | | ♂ | MNHN-EO-ENSIF3068 | Colombia | 2C, D; 7; 8C; S6C |

Appendix 2. — List of fossils observed from photographs or illustrations from the literature.

| Family, genus | Species | Authors | Inventory number | Epoch | Deposit | Figures |
|---|---|---|---|---|---|---|
| PROTOGRYLLIDAE | | | | | | |
| *Angarogryllus* | *angaricus* | (Sharov, 1968) | PIN 1873-16 | lower jurassic | Ust-baley (Russia) | 6A; 8A; S5A |
| *Falsispeculum* | *karatavicum* | (Sharov, 1968) | PIN 3791/1345 | lower jurassic | Mikhailovka (Russia) | 6B; S5B |
| BAISSOGRYLLIDAE | | | | | | |
| *Anglogryllus* | *lyristes* | Gorochov *et al.*, 2006 | MNEMG 2003.46 | lower cretaceous | Auclaye (UK) | 6E; S6C |
| *Baissogryllidae* | sp. | | CCNH-293 | lower cretaceous | Crato (Brazil) | 6D; S6B |
| *Neosharategia* | *paradoxa* | Gorochov, 1992 | PIN 4270-210a | lower jurassic | Shar-Teg (Mongolia) | 6C; S6A |
| *Sinagryllus* | *xinjiangensis* | Wang *et al.* 2019 | NIGP171454 | lower jurassic | Sangonghe formation, Xinjiang (China) | S6D |

APPENDIX 3. — Photos of studied material called as supplementary figures in the present paper.

FIG. S1. — Forewings of male Grylloidea with hypothesis of venation: **A**, **B**, *Natula longipennis* (Serville, 1838) (MNHN-EO-ENSIF9933, Trigonidiidae); **C**, *Anaxipha* sp. (MNHN-EO-ENSIF9770, Trigonidiidae); **D**, *Lerneca fuscipennis* (Saussure, 1874) (MNHN-EO-ENSIF9780, Phalangopsidae). Abbreviations: see text. Scale bars: 1 mm.

FIG. S2. — Forewings of male Grylloidea with hypothesis of venation: **A**, *Brachytrupes membranaceus* (Drury, 1773) (MNHN-EO-ENSIF9769, Gryllidae); **B**, *Phyllogryllus* sp. (MNHN-EO-ENSIF9768, Oecanthidae); **C**, lateral field of *Ectotrypa olmeca* Saussure, 1874 (MNHN-EO-ENSIF12163, Oecanthidae). Abbreviations: see text. Scale bars: 1 mm.

FIG. S3. — Forewings of male Grylloidea with particular forewing venation (**A**, **B**) with 'shortened wings', (**C**, **D**) with 'reduced' stridulatory apparatus: **A**, *Landreva* sp. (MNHN-EO-ENSIF9775, Gryllidae); **B**, *Nemobius sylvestris* (Bosc, 1792) (MNHN-EO-ENSIF9786, Trigonidiidae); **C**, *Tafalisca lineatipes* Bruner, 1916 (MNHN-EO-ENSIF9760, Oecanthidae), **D**, *Aphonomorphus* sp. (MNHN-EO-ENSIF9764, Oecanthidae). Abbreviations: **"ha"**, distally opened harp; **"mi"**, distally opened mirror; others, see text. Scale bars: 1 mm.

FIG. S4. — Forewings of female Grylloidea with hypothesis of venation: **A**, *Lerneca fuscipennis* (Saussure, 1874) (MNHN-EO-ENSIF9781, Phalangopsidae); **B**, *Homoeogryllus* affinis *lyristes* Gorochov, 1988 (MNHN-EO-ENSIF9784, Phalangopsidae); **C**, lateral field of *Brachytrupes membranaceus* (Drury, 1773) (MNHN-EO-ENSIF12162, Gryllidae). Abbreviations: see text. Scale bars: 1 mm.

FIG. S5. — Forewings of †Protogryllidae with hypothesis of venation: **A**, †*Angarogryllus angaricus* (Sharov, 1968), PIN1873-16; **B**, †*Falsispeculum karatavicum* (Sharov, 1968), PIN 3791/1345. Credit: Danil Aristov. Abbreviations: see text. Scale bars: 1 mm.

FIG. S6. — Forewings of †Baissogryllidae with hypothesis of venation: **A**, †*Neosharategia paradoxa* Gorochov, 1992, PIN4270-210a; **B**, †Baissogryllidae sp., CCNH-293; **C**, †*Anglogryllus lyristes* Gorochov *et al.*, 2006, MNEMG 2003.46; **D**, †*Sinagryllus xinjiangensis* Wang *et al.*, 2019, NIGP171454. Credits: A, Danil Aristov; B, Guilherme Ribeiro; C, image from Gorochov *et al.* (2006); D, Xu Chunpeng. Abbreviations: see text. Scale bars: 1 mm.

FIG. S7. — Forewings of male Gryllotalpidae with hypothesis of venation: **A**, **B**, *Gryllotalpa* sp. MNHN-EO-ENSIF3938, left elytron, image returned with mirror effect (**A**), right elytron (**B**); **C**, *Scapteriscus* sp. MNHN-EO-ENSIF3069, right elytron; **D**, **E**, **F**, venation of lanceolate cell and flexible zone in three differents specimens of *Gryllotalpa* sp. (D, MNHN-EO-ENSIF9774, **E**, MNHN-EO-ENSIF9772, **F**, MNHN-EO-ENSIF9771). Abbreviations: see text. Scale bars: 1 mm.

FIG. S8. — Forewings of female Gryllotalpidae with hypothesis of venation: **A**, **B**, *Gryllotalpa elegans* Chopard, 1934, full elytron (**A**), putative lanceolate cell and flexible zone (**B**); **C**, *Gryllotalpa* sp, MNHN-EO-ENSIF9773. Abbreviations: see text. Scale bars: 1 mm.


Fig. S1. — Forewings of male Grylloidea with hypothesis of venation: **A**, **B**, *Natula longipennis* (Serville, 1838) (MNHN-EO-ENSIF9933, Trigonidiidae); **C**, *Anaxipha* sp. (MNHN-EO-ENSIF9770, Trigonidiidae); **D**, *Lerneca fuscipennis* (Saussure, 1874) (MNHN-EO-ENSIF9780, Phalangopsidae). Abbreviations: see text. Scale bars: 1 mm.

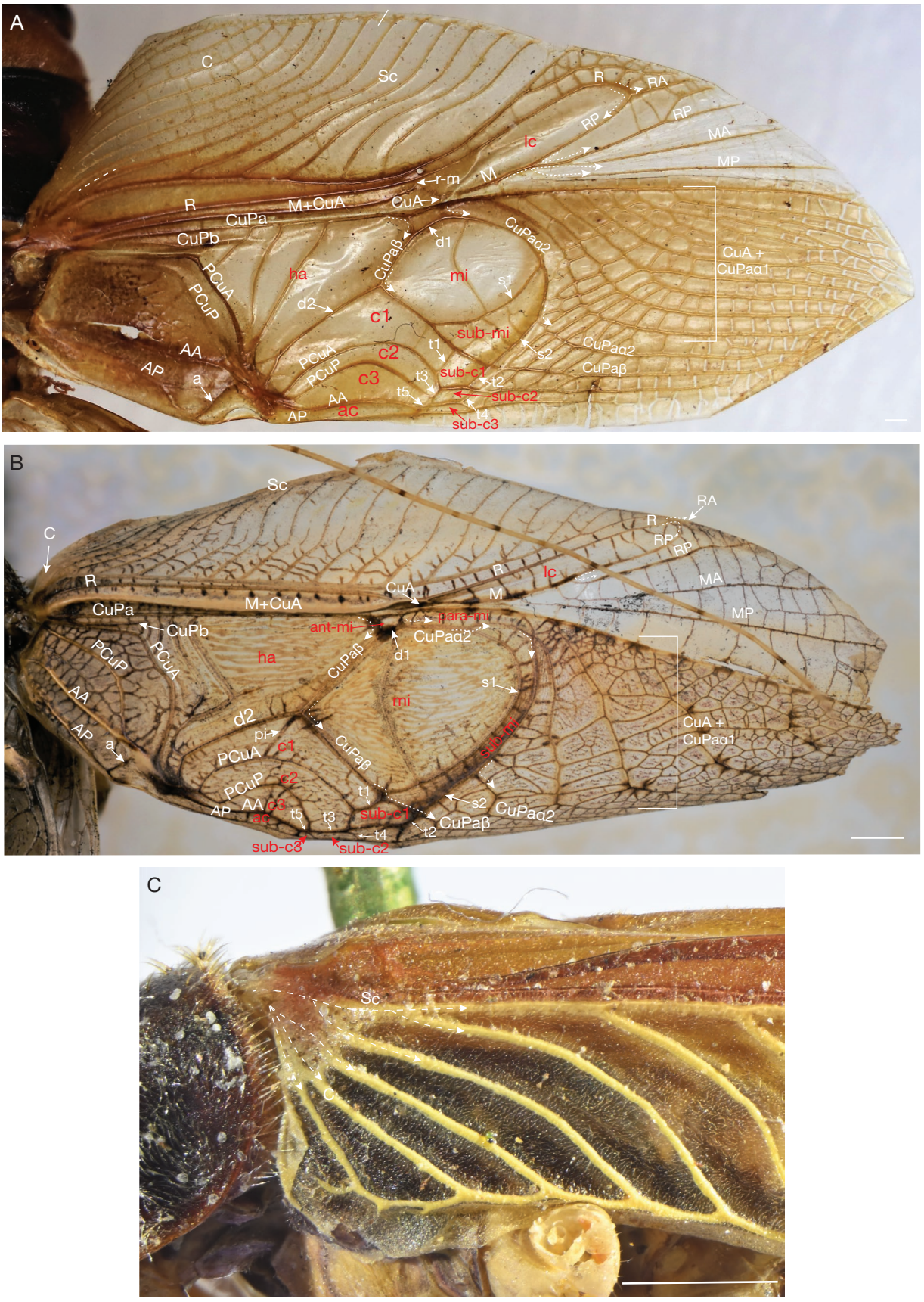


FIG. S2. — Forewings of male Grylloidea with hypothesis of venation: **A**, *Brachytrupes membranaceus* (Drury, 1773) (MNHN-EO-ENSIF9769, Gryllidae); **B**, *Phyllogryllus* sp. (MNHN-EO-ENSIF9768, Oecanthidae); **C**, lateral field of *Ectotrypa olmeca* Saussure, 1874 (MNHN-EO-ENSIF12163, Oecanthidae). Abbreviations: see text. Scale bars: 1 mm.


FIG. S3. — Forewings of male Grylloidea with particular forewing venation (**A**, **B**) with 'shortened wings', (**C**, **D**) with 'reduced' stridulatory apparatus: **A**, *Landreva* sp. (MNHN-EO-ENSIF9775, Gryllidae); **B**, *Nemobius sylvestris* (Bosc, 1792) (MNHN-EO-ENSIF9786, Trigonidiidae); **C**, *Tafalisca lineatipes* Bruner, 1916 (MNHN-EO-ENSIF9760, Oecanthidae), **D**, *Aphonomorphus* sp. (MNHN-EO-ENSIF9764, Oecanthidae). Abbreviations: **"ha"**, distally opened harp; **"mi"**, distally opened mirror; others, see text. Scale bars: 1 mm.


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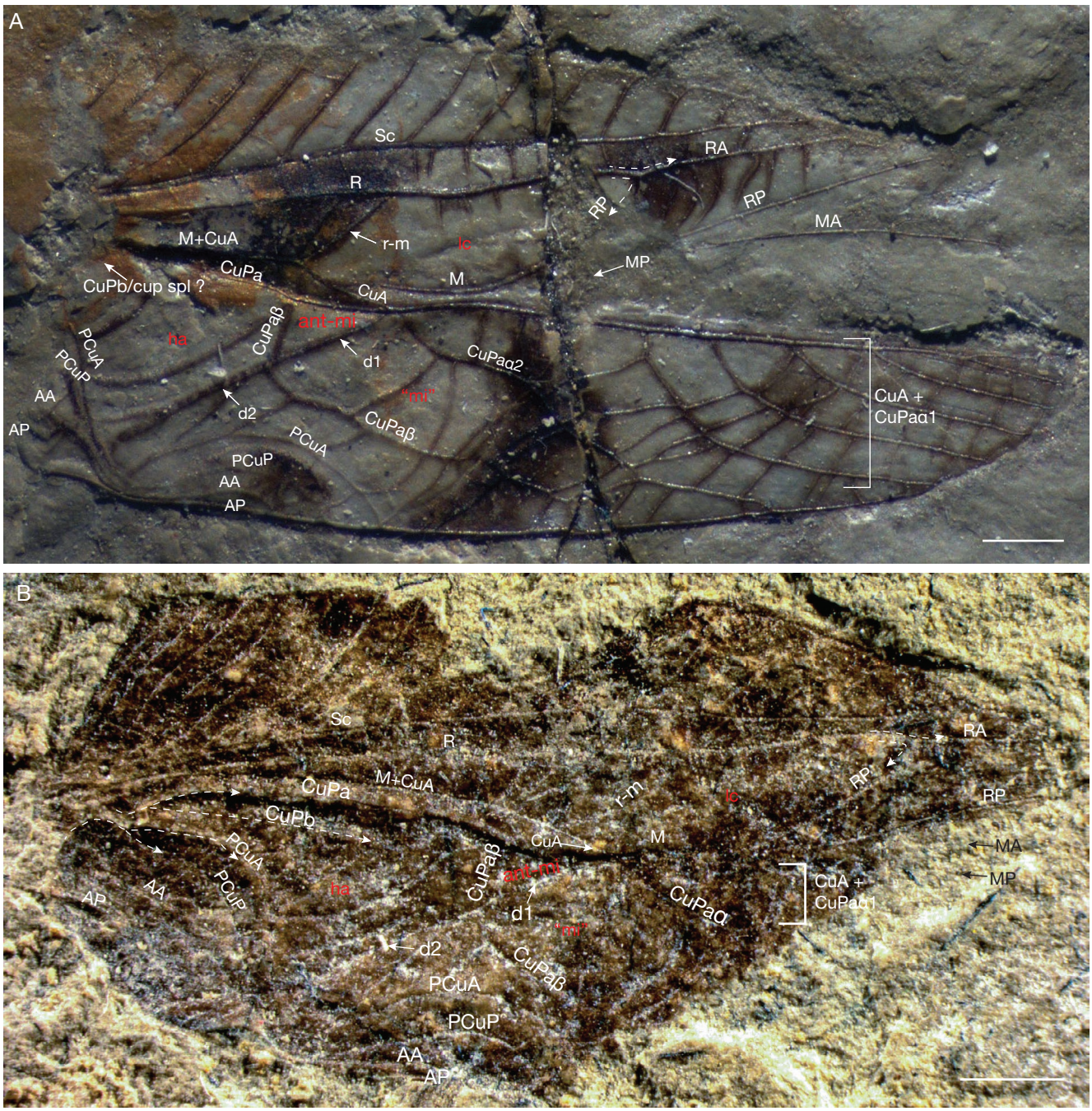


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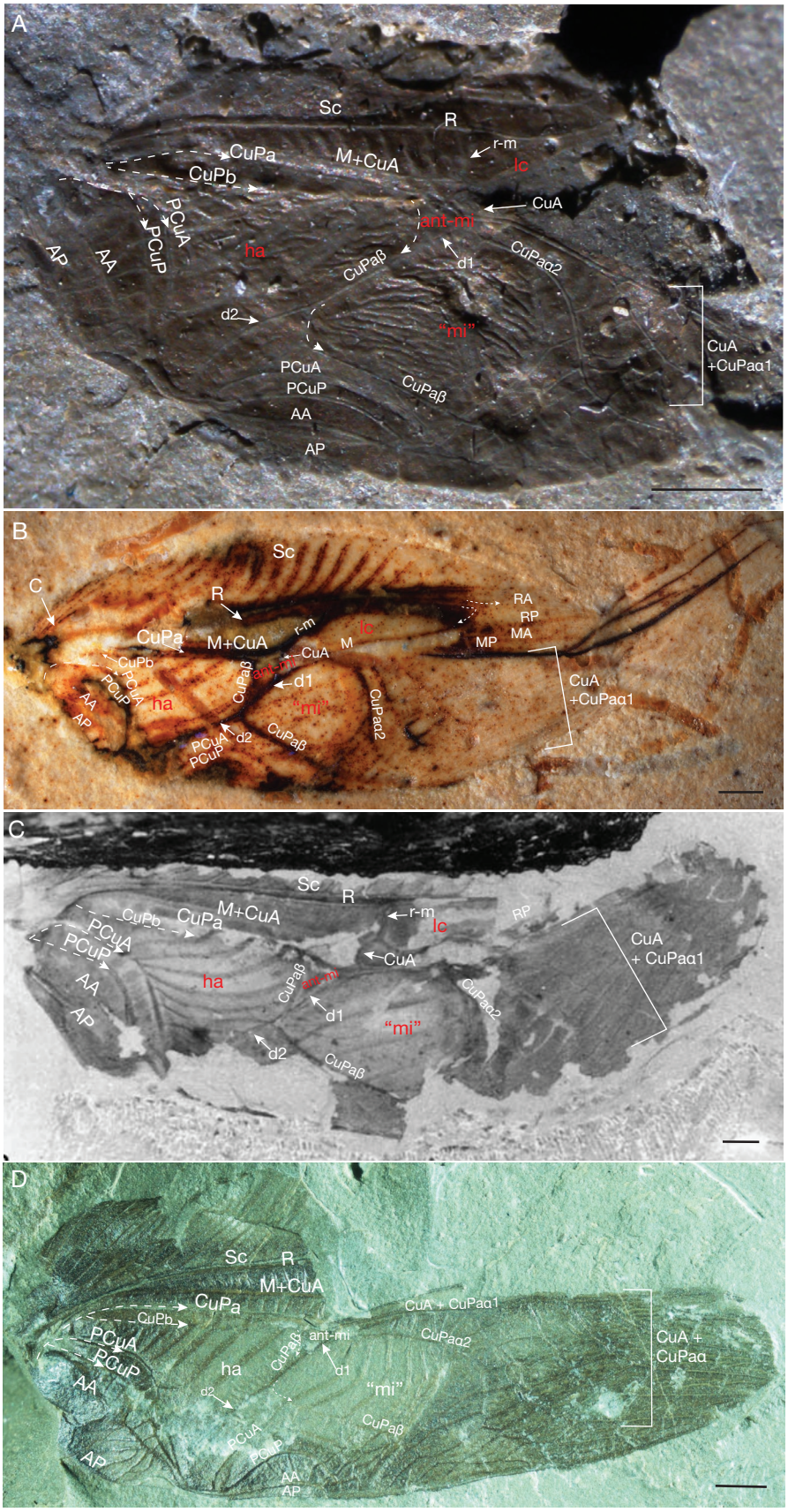


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FIG. S8. — Forewings of female Gryllotalpidae with hypothesis of venation: **A**, **B**, *Gryllotalpa elegans* Chopard, 1934, full elytron (**A**), putative lanceolate cell and flexible zone (**B**); **C**, *Gryllotalpa* sp, MNHN-EO-ENSIF9773. Abbreviations: see text. Scale bars: 1 mm.