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Grylloptera – a unique origin of the stridulatory file in katydids, crickets, and their kin (*Archaeorthoptera*)

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> Abstract

Topographic homology conjectures (= THCs) of male forewing venation in extant ensiferan orthopterans (crickets, katydids, and their kin) and their close stem-relatives are re-evaluated, in order to test competing hypotheses on the origin(s) of the file (a row of teeth located on the ventral side of the forewing and used in stridulation). A new set of THCs (= STHC) is proposed, based on morphological data on the species †*zeuneri* Sharov, 1968, *obscura* Walker, 1869, *monstrosa* Uhler, 1864, †*madygenicus* Sharov, 1968: p. 181, *grandidieri* de Saussure, 1877: 287, *bimaculatus* de Geer, 1773, *villosiceps* Chopard, 1951, *frontalis* Walker, 1869, *gryllotalpa* Linnaeus, 1758, *vicinus* Scudder, 1869, and *cantans* Fuesslin, 1775. This STHC is compared to that proposed by Desutter-Grandcolas (2003) and is found to require a smaller amount of transformation to explain the observed morphologies. The favoured STHC implies that the stridulatory file is located along the same vein in all scrutinized taxa (viz. CuPb). Current phylogenetic hypotheses cannot rule out that the file was acquired once only. Furthermore, multiple losses explain the observed distribution more plausibly than multiple acquisitions of a complex structure. A new type of wing venation transformation is evidenced, referred to as tracheal un-capture. It involves a vein abandoning its usual course for another, and leaving a remnant of its previous course, in the form of a cross-vein-like structure ('phantom vein'). The taxon *Grylloptera* is defined under cladotypic nomenclature, and is the lineage in which the character state 'on ventral side, right and/or left forewings with a row of teeth ('file') located along CuPb', as exhibited by *viridissimus* Linnaeus, 1758: p. 430 and *campestris* Linnaeus, 1758: p. 428, has been acquired. Type material is designated.

> Key words

Orthoptera, Ensifera, *Archaeorthoptera*, alignment, parsimony, transformation type, feminization, cladotypic nomenclature.

1. Introduction

Probably, the most conspicuous trait of many orthopteran species is the capacity of males (and some females) to generate sound, mostly aiming at avoiding inter-specific copulation pairing. Among the various and varied apparatuses which evolved in the group, that of ensiferans involves the forewing pair. It is primarily composed of a row of teeth located on the ventral side of the forewing (the file), and of a callous area (the scraper or plectrum) located along the posterior wing margin, expanded dorsally. The file rubbed on the scraper generates vibrations that are transmitted to resonating area(s), such as the 'harp' and the 'mirror' (Michelsen & Nocke 1974; Bennet-Clark 1989; and references therein). Many morphological aspects, such as the surface dedicated to resonating areas, and the number and spacing of teeth on the file, as well as behavioural aspects such as wing velocity during forewings engagement, constrain the resulting song characteristics (e.g. Montealegre-Zetal et al. 2009; Montealegre-Zetal 2009). Although the file occurs in both forewings in stridulating ensiferans, crickets (gryllidaeans & gryllotalpidaeans) usually fold their forewings in the right over left position (but see Masaki et al. 1987), therefore only the right forewing file is used. The situation is reversed in katydids (tettigoniidaeans; in which the left and right forewing stridulating structures show greater asymmetry), and the plesiomorphic condition is represented by ambidextrous insects ('haglidaeans'; Morris & Gwynne 1978; Gu et al. 2012). Notice that many ensiferans, such as king & raspy crickets, and wetas (gryllacrididaeans and their kin), totally lack the corresponding structures, in particular the file.

It has been debated whether structures involved in this mechanism of stridulation, in particular the file, have been acquired convergently (Gwynne 1995; Desutter-Grandcolas 2003) or once only (Zeuner 1939; Ragge 1955; Sharov 1968, 1971). This debate is of prime in-

terest for evolutionary biology, because of the striking similarities of involved elements (OTTE 1992). Notice here that RAGGE (1955) makes no clear statement on the evolutionary origin of the file, but considers the file-bearing vein homologous among ensiferan subgroups. And notice that SHAROV's (1968, 1971) position is not perfectly clear. Contrast "there is no complete homology in the stridulatory apparatus of the fore wings, because the file and the mirror of the Gryllidae and Tettigoniidae consist of different components" to "a primitive stridulatory apparatus appears in the Permian Oedischiidae, which becomes perfected in the families Haglidae and Tettigoniidae" (SHAROV 1971: pp. 51, 146, respectively). The latter statement tends to imply a unique origin of the stridulatory apparatus. At least, SHAROV (1968, 1971) hypothesized a homologous stridulatory apparatus among gryllidaeans and gryllotalpidaeans, a critical point in the debate (see below).

One central issue in this debate is the topographic homologies between forewing veins in different ensiferans, i.e. vein correspondences between species, in an evolutionary context. Recently, original topographic homology conjectures (= THCs) of venation patterns in ensiferans were proposed by DESUTTER-GRANDCOLAS (2003), on which rests a more recent contribution (DESUTTER-GRANDCOLAS et al. 2005). Although based on a large sample (but unspecified at the species level), DESUTTER-GRANDCOLAS's (2003) contribution provides explicit hypotheses on forewing venation homologies only for two gryllidaean species, a gryllotalpidaean, a tettigoniidaean, and various ensiferans lacking a file. DESUTTER-GRANDCOLAS (2003: p. 534) claims that wing venation homologies were reconsidered based on "axillary sclerites and the claval furrow". The resulting conjectures imply that the file is located on different veins in male forewings of gryllidaeans (viz. on vein 'A1') and gryllotalpidaeans (viz. on a 'vein originating from CuP'), hence are not homologous at the primary level. As for tettigoniidaeans, the file is assumed to be located along 'A1' (as in gryllidaeans).

In addition, DESUTTER-GRANDCOLAS (2003) performed a parsimony-based congruence test, based on 85 morphological characters (12 relating to forewing morphology) and involving 12 ingroup terminals (8 at the familial level, 4 at the generic level). The result indicates that ensiferans lacking a file are successive sister-groups of tettigoniidaeans, while gryllidaeans and gryllotalpidaeans form a distinct clade. As a consequence, the most parsimonious character state mapping implies a convergent acquisition of the 'A1 file' in gryllidaeans and tettigoniidaeans (i.e. are not homologous at the secondary level). Notice that despite the fact that gryllidaeans and gryllotalpidaeans are found to be sister-groups, their files could not be found homologous at this step, as the file-bearing veins have been considered non-homologous at the topographic level (thus the presence of files has been assumed non-homologous at the primary level). In summary, a file-like structure would have appeared thrice within ensiferans according to DESUTTER-GRANDCOLAS (2003).

However there are some important issues with DESUTTER-GRANDCOLAS's (2003) hypotheses. Despite considerable conflict, the resulting THCs were not compared with those of previous authors (ZEUNER 1939; RAGGE 1955; SHAROV 1968, 1971; KUKALOVÁ-PECK 1991; GOROCHOV 1995a,b; BÉTHOUX & NEL 2001, 2002). Basic data supporting DESUTTER-GRANDCOLAS's (2003) are minimal: axillary sclerites in their sampled taxa is poorly documented, and homologies in non-ensiferan reference groups are not produced. In addition, the species sample might have been inadequate for developing a well-founded set of THCs (= STHC) across all ensiferans. For instance, despite an extensive fossil record of early ensiferans (SHAROV 1968, 1971; GOROCHOV 1995a,b; PAPIER et al. 2000; BÉTHOUX et al. 2002a), potential key fossil species, such as †*madygenicus* Sharov, 1968: p. 181, were ignored by this author. The present contribution aims at providing a STHC of male forewing venation pattern of ensiferans alternative to that proposed by DESUTTER-GRANDCOLAS (2003).

How THCs can be established, and STHCs compared, is to be clarified here. Using a molecular-based lexicon, a STHC, focusing on a given body part, basically represents an alignment of morphological items across different taxa (ideally species). Establishing morphological THCs is, in contrast to molecular-based approaches, mostly a manual process (although molecular-based approaches involve manual refinements; MORRISON 2009). Morphological alignments are conjectured based on Etienne Geoffroy Saint-Hilaire's 'principe des connections' (RIEPPEL 1988; RIEPPEL & KEARNEY 2002; i.e. REMANE's 1952 topological criterion), and special quality of a given structure (REMANE 1952), assuming an appropriate species sample (i.e. REMANE's 1952 intermediate forms criterion). The rationale in the background is parsimony, i.e. patterns are compared among selected species, and a STHC is established so that the amount of transformation that has to be assumed to explain differences between patterns is minimised (KLASS 2001: p. 230). Measuring the amount of transformation needed for any particular STHC across a specific taxon sample is preferably done – as for phylogenetic analysis – by defining characters and their states and then counting the transformational steps needed to reach each morphological condition in the sample. This is indeed testing various character matrices (based on competing STHCs) for their inherent parsimony. The most parsimonious matrix (containing the lowest number of transformational steps) is then used for phylogenetic analysis. The procedure is basically the same as with molecular data: the most parsimonious alignment of sequences is searched for, and this is then used for phylogenetic analysis. However, the methodology for the analytical step addressing topographic homology in morphology is still little developed, and comprehensive approaches would be quite laborious. A reasonable reduced approach, however, consists in discussing the degree of parsimony of competing STHCs. This is how I will proceed below.

2. Material, methods, and conventions

The cladotypic nomenclatural procedure (Béthoux 2007a,b, 2010b), using Lanham's (1965) species names (elsewhere referred to as uninominal species names; Dayrat et al. 2004), is followed because of its presumed higher optimality (Béthoux 2010b). It might be worth recalling that under the cladotypic procedure taxon names above species level are written in italics and with a majuscule. They will be distinguished from traditional taxon names, which will be vernacularized (e.g. 'orthopterans' are species assigned to the 'order Orthoptera'). Readers can refer to Béthoux (2009b) for the use of 'stem-[taxon]', 'crown-[taxon]', and 'total-[taxon]', widely admitted in the palaeontological literature. According to a request of the editor, for species names used herein (according to cladotypic nomenclature), correspondence with names and classification according to the current traditional nomenclature is given in Appendix 1.

Preparation of extant material follows Béthoux & Wieland (2009). The acronym IWC OB accounts for Insect Wing Collection Olivier Béthoux. Those specimens referred to as IWC OB alone (i.e. without institutional acronym) currently belong to the private collection of the author. As a consequence of negligence, a significant portion of the collection was damaged during a shipment from Australia to France in 2010, after the preparation of the figures of the current contribution. Restoration was performed successfully for most specimens. However the right forewing of the specimen IWC OB 631, illustrated on Pl. 4E, was disrupted. Yet the wing venation can be reconstructed based on the available fragments. Specimens referred to as SNSD and SNSD IWC OB, and ANIC IWC OB, are housed at the Senckenberg Naturhistorische Sammlungen Dresden (Dresden, Germany), and the Australian National Insect Collection (Canberra, Australia), respectively. Specimens referred to as PIN are housed at the Palaeontological Institute of the Russian Academy of Science (Moscow, Russian Federation).

Venation patterns and vein widths were drawn with a SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10x/23 eye pieces, a Plan Apo S 1.0x FWD objective, and a camera lucida. Except for the one reproduced on Fig. 6, photographs were taken using a digital camera Canon EOS 450D and a Canon 50 mm or a Canon MP-E 65 mm macro lens equipped with polarizing filters. Transmitted light was obtained from a VisiLED ACT Basis. Image processing follows Béthoux & Wieland (2009).

Following Béthoux (2008), the serial insect wing venation pattern (Lameere 1922, 1923) is favoured herein, and the associated wing venation nomenclature used, as follows: ScP = posterior Subcosta; R = Radius; RA = anterior Radius; RP = posterior Radius; M = Media; MA = anterior Media; MP = posterior Media; CuA = anterior Cubitus; CuP = posterior Cubitus; AA = anterior Analis; AA1 = first anterior Analis. For CuP branches in *Archaeorthoptera* (including all orthopterans and close stem-relatives; see composition in Béthoux 2007c). I use the nomenclature elaborated by Béthoux & Nel (2001). Corresponding abbreviations are: CuPa = anterior branch of CuP; CuPaα = anterior branch of CuPa; CuPaβ = posterior branch of CuPa; CuPb = posterior branch of CuP. For the sake of discussion, two new labels are introduced: CuPaα1 and CuPaα2 are the anterior and posterior branches of CuPaα, respectively. Veins M, MA, and MP compose a 'system', and MA and MP are 'sectors'. Colour coding for veins follows Desutter-Grandcolas et al. (2005), in order to facilitate comparison between competing STHCs (orange = R, RA, and RP; yellow = M, MA; green = MP; red = CuA; blue = CuP). Adjectives 'convex' and 'concave', when applied to insect wing veins, indicate those veins located on an elevation (such as the upper edge of a roof), or in a depression, respectively (if viewed dorsally). 'Simple' specifies an unbranched condition of a vein or branch. In the text, veins as conjectured by Desutter-Grandcolas (2003) are indicated between inverted commas. It is preliminarily assumed that CuA is simple in crown-orthopterans and their closest fossil relatives.

Following the STHC favoured herein, the name 'handle' refers to an oblique strengthened cross-vein connecting CuPaα or CuPaα2 with CuPaβ near the point of fusion of CuA with CuPaα (Gorochov 1995a,b; Béthoux & Nel 2001; and see Fig. 1A). In various ensiferans numerous oblique strengthened cross-veins occur between CuPaβ and CuPb. One is usually distinctive in that it connects CuPaβ and CuPb at the sharp angle made by the former, and a strong point of inflexion of the latter. This cross-vein will be referred to as the 'column' (according to the nomenclature of harp pieces). The area delimited by CuPaα2 (and CuPaα more proximally, if the handle originates from there; as schematized on Fig. 1E), the handle, and CuPaβ (and possibly another strengthened cross-vein distally) is provisionally referred to as the 'mirror' (indicated in dark purple on the plates). It will be demonstrated that it corresponds to Ragge's (1955) mirror. This definition will be reconsidered in the course of the comparative analysis, owing to a presumed alteration of the course of CuPaα2, viz. *through* the mirror, or the disappearance of the area as delimited by some specific cross-veins. The area enclosed by CuPa / CuPaβ, CuPb, and the column (or the virtual line between the inflexion points of CuPaβ and CuPb where the column is connected, if occurring) is provisionally referred to as the 'harp'. It will be demonstrated that it corresponds to Ragge's (1955) harp, and is indicated in brown on the plates. Another particular area located between CuPaα / CuPaα2, CuPaβ, and the handle, will be considered but left unnamed (indicated in gray on Figs. 1, 4 and Pls. 1–3). Some crickets, such as *grandidieri* de Saussure, 1877: p. 287, have a long cross-vein crossing the mirror transversally; it will be referred to as the 'fissure'.

Special cross-veins (handle, column, fissure) and special areas (mirror, harp) are defined exclusively topologically (if one excludes the special quality that the former are cross-veins and the latter areas), with the entire wing venation as the reference system (i.e. the mirror is in all taxa a homologous area bordered by the same homologized veins). In other words, identification of these elements is not based on particular specific qualities. For instance the mirror area is not defined based on being a large and thin membranous area devoid of cross-veins. If the latter quality is referred to, I use the term speculum. The mirror is thus not necessarily a speculum. The set of teeth located on the ventral forewing side along a single vein and used for sound production is referred to as the 'file'. The file is identified based on this special quality alone.

The 'tracheal capture' and 'vein translocation' are plausible transformations of the wing venation pattern. A 'tracheal capture' occurs when a main vein follows a pre-existing cross-vein rather than its usual course. A frequent consequence is that this main vein runs fused with its neighbouring main vein (i.e. the one connected with the same cross-vein), and then usually un-fuses and recovers its usual course. This kind of transformation is well documented in plecopterans (BÉTHOUX 2005), for example in hind wings of euholognathans, in which the m-cua cross-vein is captured by the posterior branch of M (BÉTHOUX 2005: figs. 6–7). The 'vein translocation' transformation involves the fusion of a vein with another from the base of the latter. Such transformation has been reported in mantodeans (BÉTHOUX & WIELAND 2009), in the fossil taxon *Tcholmantitanopterida* Béthoux, 2007c (BÉTHOUX 2007c), and in Late Carboniferous cockroaches (GUO et al. in press).

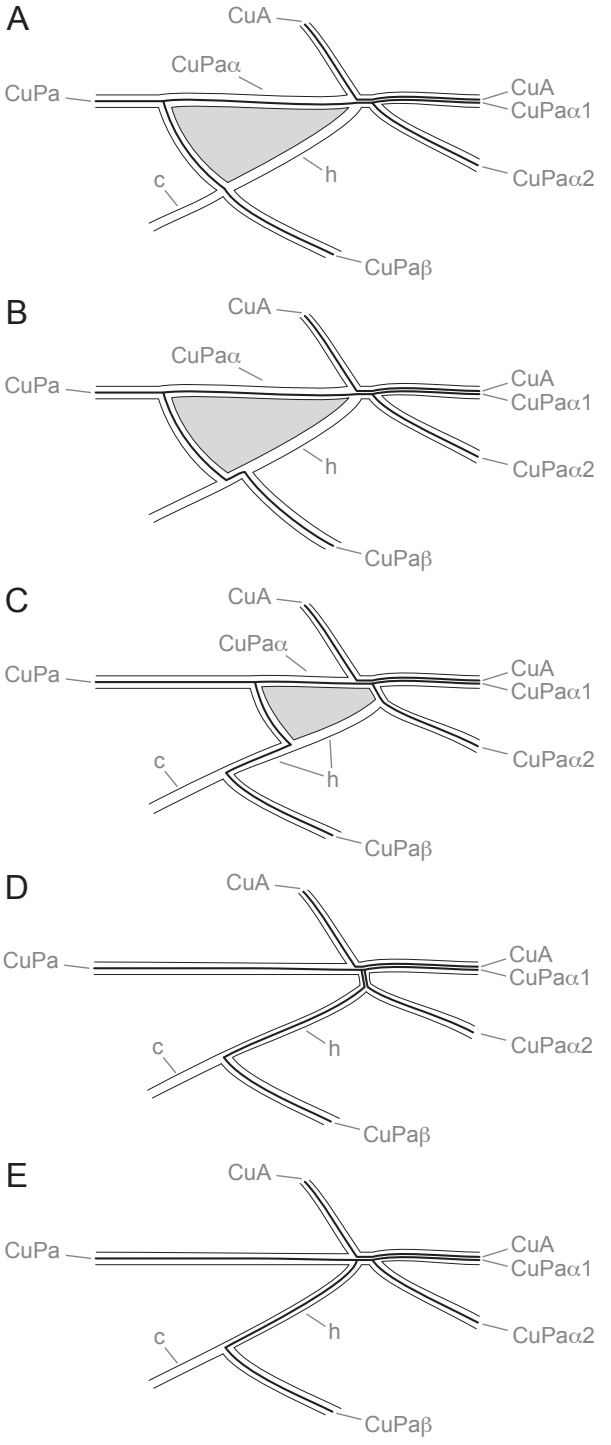

Fig. 1. Schemes representing various conditions of the capture of the handle by CuPaβ. **A**: Condition observed in *obscura* Walker, 1869 and *monstrosa* Uhler, 1864, reference condition, capture absent. **B**: Condition observed in †*zeuneri* Sharov, 1968, partial capture. **C**: Condition observed in *grandidieri* de Saussure, 1877: p. 287, long capture, comparatively distal origin of CuPaβ, handle connected to CuPaα2 after its origin. **D**,**E**: Conditions observed in *bimaculatus* de Geer, 1773, complete capture: **D**: handle connected to CuPaα2 after its origin (as in **C**; and see Pl. 2I); **E**: handle connected to CuPaα2 at its origin (as in **B**; and see Pl. 2H). Abbreviations and indications: CuA = anterior Cubitus; CuPa = anterior branch of CuP; CuPaα = anterior branch of CuPa; CuPaα1 = anterior branch of CuPaα; CuPaα2 = posterior branch of CuPaα; CuPaβ = posterior branch of CuPa; h = handle; c = column; gray area, as indicated on Pls. 1–3; it is understood that CuPa tracheae running within a 'single vein' are represented distinct for the demonstration, but could form a single trachea in actual cases (and see text).

3. Comparative analysis

3.1. Species †*zeuneri* Sharov, 1968

(Pl. 1A,B,G–I)

A useful starting point is the fossil species †*zeuneri* (Madygen, Kyrgyzstan; late Middle to early Late Triassic), since forewing venation THCs (Pl. 1A) can easily be drawn with respect to the venation pattern of stem-orthopterans (SHAROV 1968, 1971; GOROCHOV 1987; CARPENTER 1992; see also BÉTHOUX & NEL 2001: figs. 1–2). Posterior to the anterior wing margin occur successively a concave vein, which is anteriorly pectinate (ScP), a convex stem (R) forked into an anterior branch (RA) and a posterior branch (RP), a composite stem (M + CuA) from which diverges an anterior branch (M;

itself forked into MA and MP, the latter being simple) and a posterior branch (CuA). Posterior to M + CuA occurs a concave vein (CuPa) which forks into an anterior (CuPaα) and a posterior branch (CuPaβ), the latter being simple. The former (CuPaα) fuses with CuA (diverging from M + CuA), the two veins forming a common stem (the red & blue stem on Pl. 1A). From this stem, a first simple posterior branch (CuPaα2) diverges near the point of fusion of CuA with CuPaα, and CuA and CuPaα1 diverge shortly after their fusion. CuPaα1 is posteriorly pectinate, with many branches. Posterior to CuPaβ occurs a simple concave vein (CuPb), followed by a strongly convex and simple vein (AA1). The mirror and harp areas (see conventions) are indicated on Pl. 1B. The file is located on the vein homologized as CuPb (Pl. 1G–I). Unlike stem-orthopterans, but like stridulating ensiferans, the area between CuPa / CuPaβ and CuPb is distinctly broader than surrounding areas, and a handle occurs. The occurrence of this presumably derived character state qualifies †*zeuneri* as a stem-ensiferan (as proposed by Sharov 1968, 1971). Note the oblique course of CuPaβ fused for some distance, through the handle (schematized on Fig. 1B): this is a partial tracheal capture. It is noticeable that CuPaβ is directed towards wing apex during its course through the handle.

3.2. Species *obscura* Walker, 1869

(Pl. 1C–D)

It is straightforward to establish forewing THCs in *obscura* with respect to those established for †*zeuneri* (Pl. 1C). The vein sector ScP is identified based on its concavity and its branching pattern. The vein R is identified based on its location relative to ScP, its strong convexity, and the distal location of its first branching point. The composite stem M + CuA is identified based on its location relative to R and the location of its first branching point, similar to that in †*zeuneri*. The vein M is identified based on its divergence from M + CuA, the basal location of its first branching point, and the bending of the resulting branches, just as in †*zeuneri*. The vein CuA is identified based on its divergence from M + CuA. The branch CuPa is identified based in its location relative to M + CuA, corroborated by the fusion of its anterior branch (CuPaα) with CuA (this supporting the interpretation of CuA as well). In addition this identification is supported by the occurrence of a strengthened cross-vein (viz. the handle) between branches interpreted as CuPaα2 and CuPaβ, and the fact that both CuPaα2 and CuPaβ are simple. The vein CuPb is identified based on its location relative to CuPaβ. This conjecture is also supported by the concavity of this vein, the fact that it is simple, and its location relative to AA1 (itself identified based on its convexity). The mirror and harp areas are indicated on Pl. 1D. The vein homologized as CuPb bears the file, this corroborating the complete THC. Notice the simple MA and MP. Notice the lack of capture of the handle by CuPaβ (corresponding condition schematized on Fig. 1A).

3.3. Species *monstrosa* Uhler, 1864

(Pl. 1E–F)

Forewing THCs in *monstrosa* are also easy to establish. The same reasoning as for *obscura* leads to the hypothesis presented on Pl. 1E and does not need particular clarification. The mirror and harp areas are indicated on Pl. 1F. The vein CuPb, homologized after a sequence of inferences starting from the anterior wing margin, i.e. not taking into account any special quality of this vein, bears the file. The location of the file corroborates the complete STHC for *monstrosa*. Notice the weakness of CuPa, the simple MA and MP, and the mirror forming a speculum.

3.4. Species †*madygenicus* Sharov, 1968: p. 181

(Pl. 2A–B, Fig. 2)

Conjecturing forewing venation primary homologies in the fossil species †*madygenicus* with respect to those established for †*zeuneri*, *obscura*, and *monstrosa* does not require much effort. A proposition is presented on Pl. 2A (presumably male forewing pattern). In addition to arguments used for *obscura*, the simple MA and MP assist the establishment of THCs. The mirror and harp areas are indicated on Pl. 2B. The vein conjectured as CuPb (based on topography) bears the stridulatory file, as preserved on the holotype specimen of *curvatus* Gorochov, 1986 (Fig. 2), which I informally consider as a junior synonym of †*madygenicus* (in case this synonymization will reveal to be incorrect, the two species are at least closely related). Notice the occurrence of a strengthened cross-vein connecting the base of RP with MA, and of a strengthened cross-vein from MA to MP (arrows on Pl. 2B), the connection of the handle with CuPaα2 close to its origin (as opposed to connection with CuPaα, as observed in †*zeuneri*, *obscura*, and *monstrosa*; for this particular trait, as schematized on Fig. 1C), and the oblique origin of CuPb distal to its connection with AA1 (itself indicated by a white cross on Pl. 2A).

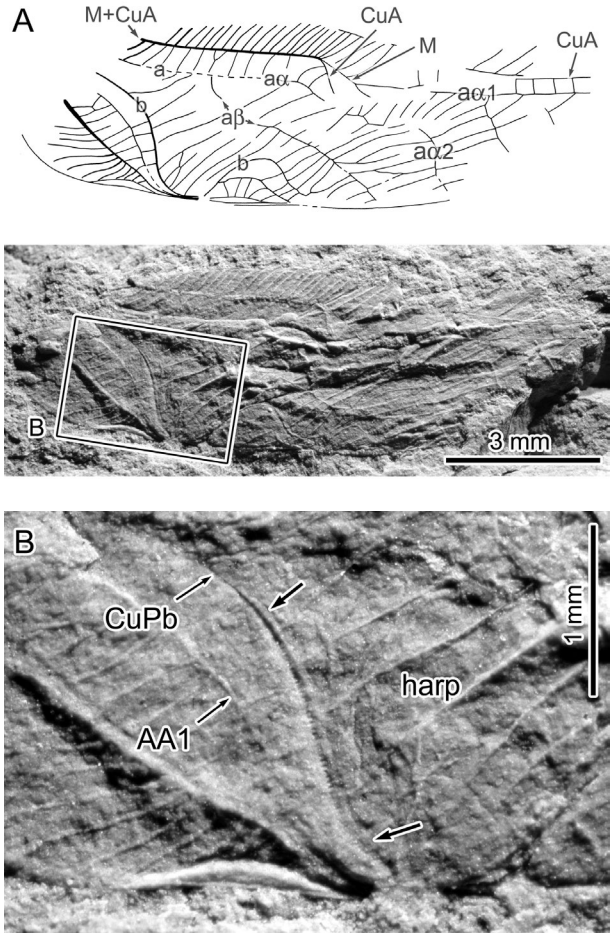

Fig. 2. Species †*madygenicus* Sharov, 1968: p. 181 (PIN 2785/1945, left forewing, positive imprint, reversed; holotype of †*curvatus* Gorochov, 1986, provisionally considered as a synonym of †*madygenicus*; Madygen, Kyrgyzstan, Lower/Middle Triassic; presumably male). **A**: Reconstruction and photograph. **B**: Detail of the file as located on **A** (arrows indicate the approximate beginning and end of the area provided with teeth).

3.5. Species *grandidieri* de Saussure, 1877: p. 287

(Pl. 2C–F)

Of more interest is the male forewing venation of crown-gryllidaeans such as *grandidieri*. From the anterior wing margin, ScP is readily identifiable based on its position, branching pattern, and concavity. In the proximal half of the wing, posterior to ScP, occurs a strong and convex stem, therefore likely to be R. In this area, one can expect to find M + CuA occurring posterior to R. This presumed M + CuA stem (yellow & red stem on Pl. 2C,E) briefly connects to R (white circle on Pl. 2E). Four simple branches diverge from the corresponding stem distal to the 'connection' to R. A vein posteriorly pectinate, with numerous branches, occurs posterior to this set of 'four branches'. This branching pattern suggests that it is CuPaα1 as observed in †*madygenicus*. This identification allows the 'four branches' to be identified: the simple CuA is located immediately anterior to CuPaα1; MP is anterior to CuA; MA is anterior to MP; and RP is anterior to MA. These identifications are corroborated by the location of the presumed RP relative to RA, viz. immediately posterior to it. If the course of these veins is traced backwards, this interpretation implies a fusion of RP with M + CuA at the point of connection with R (white circle on Pl. 2E). The occurrence of strengthened cross-veins connecting the base of RP to MA, and MA to MP, in †*zeuneri* (arrows on Pl. 2B) supports the interpretation drawn for *grandidieri*: MA and MP, and later CuA, could have 'captured' these cross-veins, fusing with RP, and resulting into a composite RP + M + CuA stem. As a consequence, unlike in †*zeuneri*, *obscura*, and *monstrosa*, the first branching points of M (into MA and MP) and of M + CuA (into M and CuA) are located distal to the origin of RP.

The case of CuA adds some complication. Based on its distal part as identified above, CuA does not fuse with CuPaα1. The fusion of CuA (diverging from M + CuA) with a branch of CuPa, defining the *Archaeorthoptera* (BÉTHOUX 2007c) and occurring in †*zeuneri*, *obscura*, *monstrosa*, and †*madygenicus* (schematized on Fig. 3A), must be considered as absent. There is, however, a putative remnant of this fusion. In *obscura* and †*madygenicus* the point of fusion of CuA with CuPaα is superimposed to the point of first branching of CuPaα (Pl. 1C; black cross on Pl. 2A). In *grandidieri* a strong cross-vein occurs opposite to this point (black cross on Pl. 2E; cross-vein indicated by * on Pl. 2F). Therefore, based on its connection with CuPaα at its point of branching, this cross-vein is interpreted as the previous course of CuA as present in †*zeuneri*, *obscura*, *monstrosa*, and †*madygenicus* (Pls. 1, 2A). It will be referred to as 'cua' in the following (and indicated as such on Fig. 3B). Notice that assuming that the divergence of CuA from M + CuA, as observed in †*zeuneri*, *obscura*, *monstrosa* and †*madygenicus*, could simply be displaced distally, does not explain the occurrence of the cross-vein indicated by * on Pl. 2A,E, located in a position identical to that of CuA, before its fusion with CuPaα. Additionally, the point of origin of CuA as a completely distinct vein in *grandidieri* is located nearly opposite to the same point in †*madygenicus* (as schematized on Fig. 3), suggesting that no major displacement occurred.

The handle can be identified based on its connection with CuPaα2 near the origin of this vein, as in †*madygenicus*. The origin and position of CuPaβ is inferred from the branching pattern of CuPa: it is the first branch to diverge posteriorly from it. In addition, the presumed CuPaβ delimits a speculum, such as in *monstrosa*. Compared to †*zeuneri*, *obscura*, *monstrosa*, and †*madygenicus*, the origin of CuPaβ is likely to be located in a further distal position in *grandidieri* (as schematized on Fig. 1C). This and the partial capture of the handle by CuPaβ (Pl. 2C,E,F; Fig. 1C) likely are coupled conditions. Provided this interpretation, the position of CuPaα2 is self-evident.

A long sclerotized structure occurs posterior to CuPa (arrow without label on Pl. 2C; it is interpreted as CuP

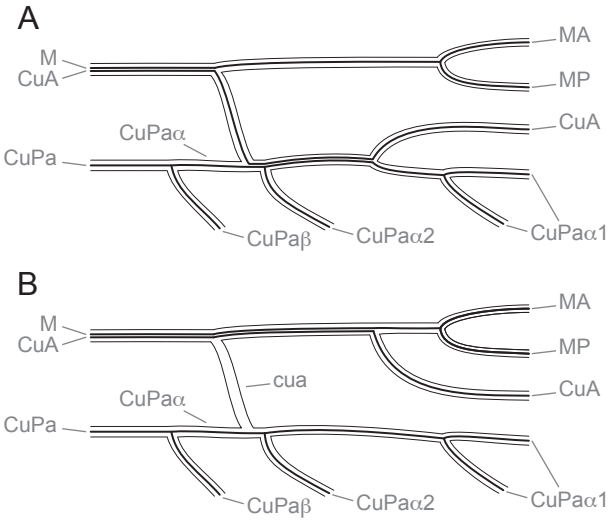

Fig. 3. Schemes representing tracheal un-capture by CuA as conjectured in *grandidieri* Saussure, 1877: p. 287, among others. **A**: reference condition, CuA diverges from M + CuA basally and fuses with CuPaα. **B**: CuA abandons its usual course and diverges from M + CuA distally. Abbreviations and indications as above and: M = Media; MA = anterior Media; MP = posterior Media; cua = cross-vein un-capture by CuA.

by Desutter-Grandcolas 2003). No trachea was observed in this structure, suggesting that it is not a main vein. It will be referred to as the 'callus' in the following. The likely position of CuPb, determined as being posterior to CuPa, is indicated on Pl. 2C. This interpretation is supported by the location of the point of divergence of the presumed CuPb from AA1 (white cross on Pl. 2C), similar to that observed in †*madygenicus* (Pl. 2A), and the similarly sigmoid course of the presumed CuPb distal to this point. This identification of CuPb is also supported by its concavity, and the occurrence of a convex vein (AA1) posterior to it, such as in †*zeuneri* (Pl. 1G,H), *obscura*, *monstrosa*, and †*madygenicus* (Fig. 2B). In addition veins interpreted as CuPaα2, CuPaβ, and CuPb are all simple, as in †*zeuneri*, *obscura*, *monstrosa*, and †*madygenicus*. Ultimately, the whole interpretation is corroborated by the occurrence of a file on the vein identified (independently from this special quality) as CuPb.

Areas determined as harp and mirror are indicated on Pl. 2D. The mirror is a speculum. Notice the weakness of CuA at its origin (Pl. 2F); the occurrence of a fold posterior to CuA (**f** on Pl. 2F); the distal fusion of RP with RA, the strong reduction of the area delimited by CuPa, CuPaβ, and the handle (compare gray areas on Pl. 2B and D, and Fig. 1A and C; resulting from the distal relocation of the first branching of CuPa); the capture of the handle by CuPaβ (with CuPaβ running towards the wing base during its course through the handle, unlike in †*zeuneri*; compare Fig. 1B and C); and the occurrence of a specialized column (**c** on Pl. 2D), and of a strong cross-vein connecting CuPaβ and CuPb distal to the column and opposite the closure of the mirror (**c'** on Pl. 2D).

3.6. Species *bimaculatus* de Geer, 1773

(Pl. 2G–I)

In *bimaculatus* the male forewing venation pattern does not differ significantly from that in *grandidieri*. Therefore it is unnecessary to detail the interpretation provided on Pl. 2G, except for the handle, completely captured by CuPaβ. As a consequence the gray area as delimited on Pl. 2B,D does no longer exist, the CuPaα / CuPaβ fork being nearly superimposed with the CuPaα1 / CuPaα2 fork. Some variation occurs in the vein distally connected with the handle, which is either CuPaα2 near its origin (Pl. 2I; as schematized on Fig. 1D), or CuPaα close to the CuPaα / CuPaβ fork (Pl. 2H; as schematized on Fig. 1E).

3.7. Species *villosiceps* Chopard, 1951

(Pl. 3A–G)

As in the species surveyed above, ScP is readily identifiable in male forewings of *villosiceps* based on its position, which is immediately posterior to the anterior wing margin (supported by the concavity and branching pattern of this vein; Pl. 3A). It is conjectured that posterior to ScP occurs R/RA. In the distal part the vein sectors MA, MP, and CuA can be identified based on the weakness of CuA, the position of MP relative to CuA, and the position of MA relative to MP (Pl. 3A,C–E). These conjectures are supported by the divergence of MA and MP from a common stem (M), and that of M and CuA from a common stem (M + CuA), just as in all species previously investigated (although a fusion of CuA with CuPaα does not occur, as in *grandidieri* and *bimaculatus*). No obvious connection between R / RA and M + CuA was observed in the right forewing of the specimen ANIC IWC OB 2 (Pl. 3A). However the left forewing of the same specimen has a trachea undulating between R / RA and M + CuA near the wing base (Pl. 3F) interpretable as RP, and a supernumerary branch located between R / RA and MA in the distal part (Pl. 3G), which can be interpreted as RP as well. The trachea filling this distal branch diverges from a common stem with MA, suggesting that this stem is composed of RP + MA indeed. These observations suggest that an inconspicuous fusion of RP occurs in the male forewing base in *villosiceps*, probably near the wing base.

The branch CuPa can be identified based on its position relative to M + CuA, and the occurrence of a callus posterior to it. The distal part of CuPaβ is identified based on its connection with the column (Pl. 3B) and its trajectory, similar to that of CuPaβ in *grandidieri* (Pl. 2C) and *bimaculatus* (Pl. 2G). Identification of CuPaα2 is inferred from its position relative to CuPaβ, viz. anterior

to it. At its origin CuPaα2 occurs as a very weakly sclerotized cross-vein-like structure, clearly provided with a trachea though. It must be acknowledged that the section of the handle located between CuPaβ and CuPaα2 is also provided with a trachea (dotted blue line on Pl. 3C), suggesting CuPaα2 originates from a tracheal network reminiscent of the origin of RP* in amorphoscelidaeans (mantodeans; BÉTHOUX & WIELAND 2009: fig. 9). The identification of CuPb is based on its connection with the column (Pl. 3B), its oblique origin from CuPb + AA1 (white cross on Pl. 3A), its concavity, and its position anterior to a convex vein (AA1). This interpretation is corroborated by the location of the file along the vein interpreted as CuPb.

Areas determined as harp and mirror are indicated on Pl. 3B. Note the narrowness of the area between MP and CuA near the origin of MP (Pl. 3A,C), and the basal location of CuPaα1 first fork (white arrows on Pl. 3D,E) in particular in the left forewing.

3.8. Species *frontalis* Walker, 1869

(Pl. 3H–K)

As above, ScP and RA are readily identified in *frontalis*. Posterior to RA, in the basal third of the forewing, likely occurs M + CuA. Three distal branches diverging from M + CuA reach the anterior wing margin. Provided that the most posterior branch is likely CuA, owing to its weakness as in *grandidieri* (Pl. 2F) and *villosiceps* (Pl. 3C–E), the branch anterior to it is likely MP, and the one anterior to MP is likely MA. The vein sectors MA, MP, and CuA, as identified, are simple, like in *obscura*, *monstrosa*, †*madygenicus*, *grandidieri*, *bimaculatus*, and *villosiceps*, corroborating the interpretation. The position of RP is unclear, but provided the result of the comparative analysis in *villosiceps*, it is assumed that RP is fused with M + CuA near the wing base, and that MA actually is RP + MA.

Posterior to (RP +) M + CuA likely occurs CuPa. The occurrence of a callus, identified as a sclerotized structure located posterior to this vein, free of trachea and of limited extent, supports this conjecture. The course of CuPaβ is readily identifiable: as in *grandidieri* (Pl. 2C) and *villosiceps* (Pl. 3A), it is the first branch to diverge posteriorly from CuPa, runs backward (capturing the handle), makes a sharp angle, and then runs towards the wing apex. In turn CuPaα2 is identified based on its position relative to CuPaβ in the distal half of the forewing. As in *villosiceps* its origin involves a tracheal network (dotted lines on Pl. 3J). The origin of the first branch from CuPaα1 is evidenced by a strong trachea, although a tracheal network occurs in this area. The first posterior branch of CuPaα1 is branched, unlike in all species previously investigated. Therefore it is not unlikely that this

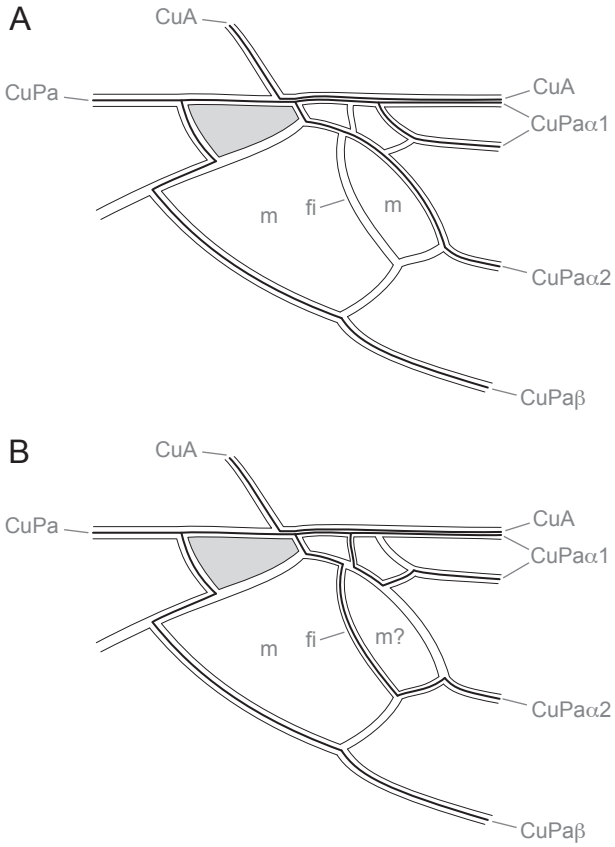

Fig. 4. Schemes representing a plausible capture of the fissure by CuPaα2. **A**: condition observed in *villosiceps* Chopard, 1951. **B**: One of the possible conditions conjectured for *frontalis* Walker, 1869, under which CuPaα2 captures the fissure, CuPaα1 is rerouted, and identification of a portion of the mirror area, as being bordered by CuPaα2, becomes questionable. Abbreviations and indications as for Fig. 1, and: m = mirror area; fi = fissure.

particular vein is actually composed of two branches of CuPaα1, somehow fused.

The course of CuPaα2 requires some discussion. The mirror in all foregoing species, including *villosiceps*, is delimited, by definition, by CuPaα2 (and sometimes CuPaα in addition) and CuPaβ. In some species this area is split in two parts by a cross-vein, the fissure (**fi** on Pl. 3B; see also Pl. 2D and Fig. 4A). There is no such fissure between the veins interpreted as CuPaα2 and CuPaβ in *frontalis*. One option (THC1) is that the fissure was lost, as a consequence of the reduction of the mirror area. If so only the area represented in dark purple on Pl. 3I is to be considered as the mirror. Another possible interpretation (THC2), considering the recurrent occurrence of tracheal captures in related species, is that the fissure has been captured by CuPaα2 (as schematized on Fig. 4B). In turn the previous course of CuPaα2 is captured by the first posterior branch of CuPaα1. Provided the tracheal network from which originate CuPaα2 and the first posterior branch of CuPaα1, and the very basal location of the first fork of CuPaα1 in *villosiceps* (Pl. 3E), this interpretation appears plausible. If so the mirror could be understood as being composed of the cell basal to the 'captured fissure' only, if the definition of the mirror (as being anteriorly

bordered by CuPaα2) is strictly followed (THC2a). Alternatively, the mirror could be newly understood as the area delimited by CuPaβ and the 'sclerotized structure in which CuPaα2 used to run' (in lieu of CuPaα2 itself) as in *villosiceps* (THC2b). The whole area coloured in purple (dark + light) and the identification of the fissure on Pl. 3I (**fi**) follow this interpretation. It is acknowledged that it would require a larger sample to conclude positively on the competing THCs 1 and 2. Uncertainty regarding the mirror identification is accounted for by a lighter coloration of the area anterior to CuPaα2 on Pl. 3I, and by 'm?' on Fig. 4B (indicating its possible exclusion from the mirror, as under THC1 and THC2a).

As in *grandidieri* (Pl. 2C), *bimaculatus* (Pl. 2G), and *villosiceps* (Pl. 3A), the column is connected to CuPaβ at the sharp angle made by this vein. On its other side, the column is connected to CuPb in these species, so is likely the case in *frontalis*. The identification of CuPb as presented on Pl. 3H,J is corroborated by the occurrence of an area filled with sigmoid long cross-veins (i.e. the harp) anterior to it, its concavity, and the occurrence of a strongly convex vein (i.e. AA1) occurring posterior to it. This conjecture on the position of CuPb is supported by the occurrence of the file on this vein.

Areas determined as harp and mirror are indicated on Pl. 3B (and see above). Note the restricted mirror area compared to *villosiceps*, and the lower number of branches of CuPaα1 (6 in *villosiceps*, 4 in *frontalis*).

3.9. Species *gryllotalpa* Linnaeus, 1758

(Pl. 4)

Identification of ScP and RA is evident in *gryllotalpa*. Identification of RP is facilitated by a polymorphic condition. In the distal part of the wing, in the area posterior to RA (indeed RA + RP), one of the 12 examined forewings exhibits a long supernumerary branch distinct from RA ('RP' on Pl. 4F). Six of the 12 examined forewings exhibit a branch originating at the same point that fuses with RA, more or less shortly after its point of origin (Pl. 4D), while other wings show no distinct branch (Pl. 4E). Because RP fuses distally with RA in *grandidieri* (Pl. 2E,F) and *bimaculatus* (Pl. 2G), it is assumed that the vein fusing with RA in *gryllotalpa* is RP as well. This interpretation implies that this point of fusion is relocated basally. It is even fused with the point of contact of M with R [it is a connection of M + CuA and R in *grandidieri* and *bimaculatus*, but RP + M and RA in *gryllotalpa*; see below] in five of the observed forewings (Pl. 4E).

The simple branch located posterior to RP / RA + RP in the distal part of the wing is likely MA. If traced backwards, RP and MA diverge from a common stem, briefly connected to RA, like M + CuA in *grandidieri* (white circle on Pl. 2E,F) and *bimaculatus* (Pl. 2G–I). In these species the fusion of RP with M + CuA occurs at this point. In *gryllotalpa*, however, there is a narrow trachea located at the forewing base between R and M (+ CuA) ('RP' on Pl. 4G). It is therefore assumed that RP fuses with M (+ CuA, or not, see below) near the forewing base. In other words, with respect to the condition in *grandidieri* and *bimaculatus*, the fusion of RP with M is relocated near the wing base, but the location of the point of contact of M (+ CuA or + RP) with RA is not altered. These two points are disconnected in *gryllotalpa*, while they are superimposed in *grandidieri* and *bimaculatus*. The fusion of RP with M (+ CuA?) at the wing base is not unlikely, provided THCs developed for *villosiceps* and *frontalis* (Pl. 3A,H, respectively).

Then, in the distal part, the simple branch located posterior to MA is likely MP, and the one posterior to MP is likely CuA. This interpretation is supported by the very weak condition of CuA at its origin, and its location anterior to a fold (**f** on Pl. 4D), as in *grandidieri* (Pl. 2F). In addition the presumed MP and CuA are simple, as previously observed in several species. If traced backwards, MP and CuA diverge from a common stem (short green & red stem on Pl. 4C). The length of this common stem is slightly variable. It is completely absent in one of the investigated forewings (i.e. MP and CuA, as interpreted on Pl. 4C, diverge as soon as they connect). Provided the modification of the course of MP from the condition observed in *villosiceps* (Pl. 3A,C; with MP distinct from CuA throughout) to that observed in *frontalis* (Pl. 3H,J; with MP fused for a long distance with CuA), a short fusion of MP with CuA in *gryllotalpa* is a likely conjecture. A plausible scenario is a translocation of MP onto CuA.

The origin of CuA is not evident. Near the wing base, in the area posterior to M (+ CuA), a weakly sclerotized structure containing a trachea occurs opposite the fusion of RP with M + CuA ('CuA' on Pl. 4G). It is interpreted as CuA diverging from M + CuA and fusing with CuPa. If so, according to the location of the distal part of CuA (see above), this vein sector necessarily runs fused with CuPa for a long distance. Although the fusion of CuA (diverging from M + CuA) with the anterior branch of CuP (viz. CuPa) is the defining apomorphy of *Archaeorthoptera* (Béthoux 2007c), the current case is to be considered as a secondary, convergent acquisition, because (1) the CuA + CuPaα fusion is lost in related and presumably plesiotypic species such as *grandidieri* (see above), and (2) the orthopteran groundplan involves a fusion of CuA with CuPaα, as opposed to CuPa in *gryllotalpa*.

The course of MP basal to its fusion with CuA (viz. basal to the beginning of the green & red stem on Pl. 4C) is conjectured based on the presumed courses of M and CuA. However two alternative options are to be discussed (compare Pl. 4C and H,I). First, provided the weakness of the structure indicated by * on Pl. 4D, it has been conjectured as cua (viz. the previous path of CuA; Pl. 4C) rather than MP (as on Pl. 4H), because cua was

observed to be weak in species such as *bimaculatus* (Pl. 2H,I). Additionally, interpreting * as MP leaves us with a supernumerary cross-vein (? on Pl. 4H), unaccounted for. Second, if the conjecture of a basal fusion of CuA with CuPa is rejected, among other options, CuA could be assumed to recover its previous path (viz. 'cua'; Pl. 4I), with the course of MP conjectured as on Pl. 4C. However, under these conjectures, the structure indicated by '?' on Pl. 4I is left without satisfying interpretation, as is the structure indicated by 'CuA' on Pl. 4G. In summary, the interpretation presented on Pl. 4C maximizes correspondences between R, M, and CuA observed in *grandidieri*, *bimaculatus*, and *gryllotalpa*.

At this stage the course of CuPa branches is easily conjectured (Pl. 4C). Its first fork results into CuPaα and CuPaβ, and CuPaα is forked into CuPaα1 and CuPaα2. The course of CuPaβ, viz. running through the handle (here connected to CuPaα near the CuPaα1 / CuPaα2 fork; as schematized on Fig. 5A), taking a sharp curve at its connection with the column, and then directed towards the wing apex, just as in *grandidieri* (Pl. 2C), supports the identification of this vein. In addition CuPaα2 and CuPaβ are both simple (the former is forked in one forewing out of 12 observed), as in all species previously examined. This interpretation implies that CuPaα1 is, in contrast to all aforementioned species, simple (it is forked in two forewings out of 12). However, such a transformation is plausible, provided the reduction of the number of branches of CuPaα1 in *frontalis* (Pl. 3H; compared to *villosiceps*, Pl. 3A).

Once CuPaβ and the column are identified, the course of CuPb is easily inferred. The position of **c'**, the oblique origin of CuPb from CuPb + AA1, and its concavity support the interpretation provided on Pl. 4C. In addition, the file is located on CuPb, corroborating the whole THC. Notice that the callus occurring posterior to CuPa in *grandidieri* (arrow on Pl. 2C; but also in *bimaculatus*, *villosiceps*, and *frontalis*) is present in *gryllotalpa* (arrow without label on Pl. 4D), and corroborates the identification of CuPb also. Locations of harp and mirror are indicated on Pl. 4B.

3.10. Species *vicinus* Scudder, 1869

(Pl. 5)

The forewing venation of *vicinus* reaches a pinnacle of complication. Comparison with THCs developed for *gryllotalpa* (Pl. 4) eases the identification of RP, M, MA, MP, and CuA (Pl. 5A,C,D): RP likely fuses with M near the wing base; there is no free traversing part of RP (as observed in *gryllotalpa*: 'RP' on Pl. 4G), since the basal parts of M and R are closely located, but the point of divergence of RP from R yet is evident (Pl. 5D). Much farther distally RP diverges from M and fuses with RA; shortly after its divergence from RP, M forks into MA and MP; MA runs towards the apex, while MP runs backwards; CuA fuses with CuPa near the wing base, diverges from CuPa, and fuses with MP; MP and CuA diverge after some distance; cua (* on Pl. 5D) connects RP + M and MP. The fold located posterior to CuA (**f** on Pl. 5D), and the lack of branching of veins identified as MA, MP, and CuA, support this interpretation.

Assuming a simple CuPaα1, as in *gryllotalpa*, the distal parts of CuPaα1, CuPaα2, CuPaβ, and CuPb can be identified based on their relative position (starting from CuPaα1 relative to CuA) and their lack of branching. Tracing CuPaα2 and CuPaβ backwards indicate that they form, in contrast to all previous species, a long common stem. Two different 'transformation series' can explain the formation of this CuPaα2 + CuPaβ stem, with different resulting conjectures on the location of the mirror (series 1, Fig. 5A,B,C; series 2, Fig. 5A,D,E). The first series assumes that the origin of CuPaα2 is displaced basally towards the column, along the handle (already captured by CuPaβ; Fig. 5B); this displacement is continued until CuPaα2 and CuPaβ diverge between the column and **c'** (Fig. 5C). This results in a narrowing of the mirror area (**m** on Fig. 5C). Another, more elaborated transformation series is proposed. In *gryllotalpa* (Pl. 5E; see also Pl. 4B,C) the mirror is distally closed by a strong cross-vein connecting CuPaα2 and CuPaβ. A direct transition from a *grylloptalpa*-like (schematized on Fig. 5A) to a hypothetical intermediate as schematized on Fig. 5D is possible via a simultaneous 'translocation & capture' transformation experienced by CuPaα2 (translocated onto CuPaβ & capturing the cross-vein closing the mirror). In this case the mirror, as defined above (viz. anteriorly bordered by CuPaα2), does no longer exist, unless its definition is reconsidered (as above; uncertainty accounted for by '?' on Fig. 5D,E). The hypothetical intermediate schematized on Fig. 5E, similar to the morphology observed in *vicinus*, results from a relocation of the point of divergence of CuPaα2 and CuPaβ towards **c'** (Fig. 5E). Provided the organization of distal parts of CuPaα1, CuPaα2, and CuPaβ, the pattern conjectured for *gryllotalpa*, the lack of any significantly stronger cross-vein between CuPaα2 and CuPaβ in *vicinus* (such as the one closing the mirror as in *gryllotalpa*; Pl. 4D), and the propensity of tracheal captures and translocations to occur in the group, this is the hypothetical transformation series (and resulting THCs) which is herein favoured. It must be acknowledged that species making suitable intermediates were not identified: indeed each transformation predicts different intermediates (in particular as schematized on Fig. 5B and E).

From this point, identification of CuPb is straightforward, based on its connection to the column, with **c'**, and its oblique origin from CuPb + AA1. This interpretation is supported by the occurrence of a convex vein (AA1) posterior to it. Lastly, the vein independently identified as CuPb bears the file. The location of the harp is indicated on Pl. 5B.

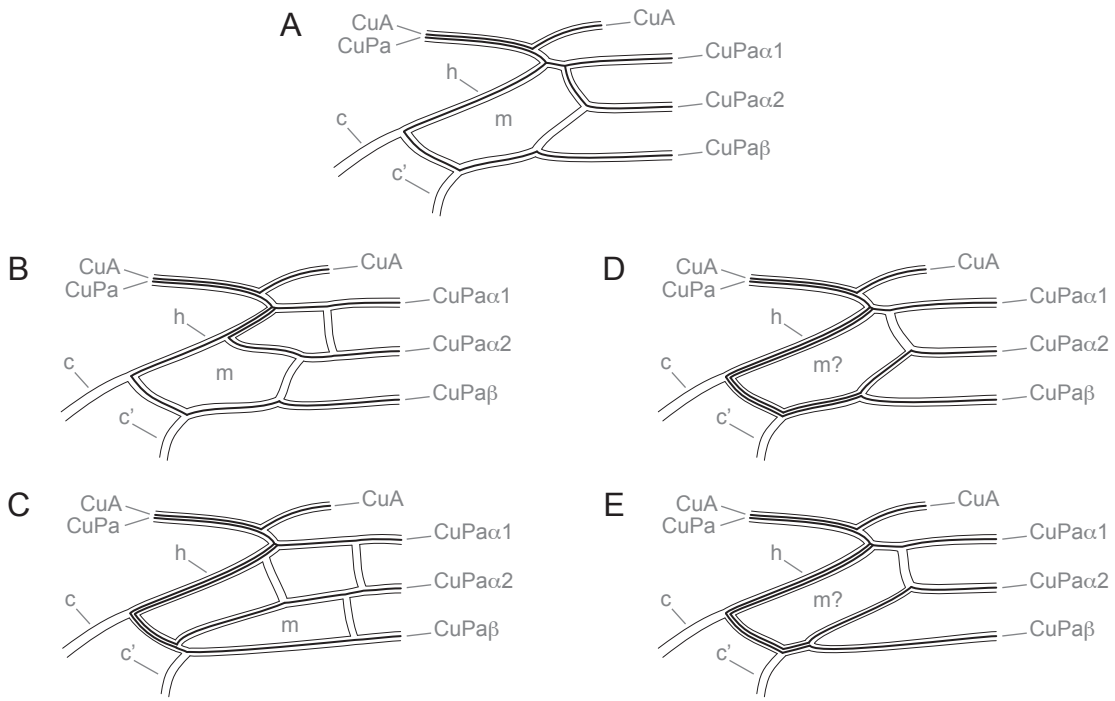

Fig. 5. Schemes representing alterations of the course of CuPaα2 in *vicinus* Scudder, 1869, and location of the mirror area, under competing hypothetical transformation series. **A**: Reference condition, as observed in *gryllotalpa* Linnaeus, 1758. **B**,**C**: Hypothetical transformation series 1. **B**: Hypothetical intermediate, resulting from a relocation of the origin of CuPaα2 along the handle. **C**: *vicinus*-like condition, resulting from the relocation of the point of divergence of CuPaα2 and CuPaβ between c and c'. **D**,**E**: Hypothetical transformation series 2. **D**: Hypothetical intermediate, resulting from a simultaneous 'translocation & capture' experienced by CuPaα2 (translocation onto CuPaβ, and capture of the cross-vein closing the mirror in **A**), identification of the mirror area, as being bordered by CuPaα2, becomes questionable. **E**: Hypothetical intermediate close to a *vicinus*-like condition, resulting from a relocation of the point of divergence of CuPaα2 and CuPaβ, close to c'. Abbreviations and indications as for Figs. 1, 4, and: c' = cross-vein connecting CuPaβ and CuPb distal to the column.

3.11. Species *cantans* Fuesslin, 1775

(Pl. 6)

In this case reference patterns to consider are those represented on Pl. 1, as *cantans* lacks a number of conditions (presumably derived) observed in *grandidieri* and *bimaculatus* (among others), such as the CuA tracheal un-capture, and the fusion of RP with M + CuA (among others). As other tettigoniidaeans, the species *cantans* has a convex vein-like structure occurring in the antero-basal part of the forewing (Pl. 6A). This structure is either secondary, or a genuine ScA, known to occur in various Palaeozoic *Archaeorthoptera* ('C' of Sharov 1968, 1971; Béthoux 2009a). This point is left unresolved for the moment. Posterior to it occurs a concave vein, anteriorly pectinate, which is interpreted as ScP then. The radial system R is easily identified, based on its position relative to ScP, the convexity of (the presumed) R and RA, the location of the point of divergence of RA and RP (compare with †*zeuneri*, Pl. 1A), and the branched condition of RP. Provided the conditions observed above, posterior to R likely occurs M + CuA (Pl. 6A,C). The anterior branch diverging from M + CuA (presumably M) forks distally, while it is forked basally in stem-orthopterans such as †*zeuneri* (Pl. 1A; and Sharov 1968, 1971; among others). The position of MP is therefore unclear. It is represented as diverging from M on Pl. 6. However, unusual morphologies observed in *cantans* suggest that M + CuA might split into MA and MP + CuA: (1) A supernumerary veinlet can occur between the presumed MA and CuA; it is likely to be MP fusing with CuA close to the origin of the latter. (2) A supernumerary anterior branch diverging from the presumed CuA (+ CuPaα1) is likely to be MP diverging from what would then be MP + CuA (+ CuPaα1). This point is not essential for the topic of this contribution and therefore will be left unresolved (informative intermediates seem to be unknown, and investigation of intra-specific variability of key-species would be needed).

A very weak vein occurs posterior to M + CuA. Based on this position, and on the similar 'special quality' exhibited by CuPa in *monstrosa* (Pl. 1E), this vein is likely to be CuPa. It reaches the posterior branch of M + CuA (i.e. CuA or MP + CuA) without obvious branching, unlike in †*zeuneri*, *obscura*, *monstrosa*, and †*madygenicus* (Pl. 1A,C,E, Pl. 2A, respectively). After fusion with CuA, it is assumed that CuPaβ and CuPaα2 form a common stem, and that both captured the handle (as conjectured above for *vicinus*, Pl. 5; likely a convergence). According to this interpretation the CuPaβ + CuPaα2 stem would be directed backwards for some distance, and then the two components diverge. As a consequence of the complete

capture of the handle by CuPaβ, the area indicated in gray on Pls. 1–3 is absent. This interpretation is supported by two structural details: (1) the occurrence of a strong cross-vein (**c** on Pl. 6C) at the point of inflexion of the presumed CuPaβ, connecting the latter to CuPb: it is the column as identified earlier; and (2) the area between the presumed CuPaα2 and CuPaβ, which then is the mirror, is a speculum, as observed in *grandidieri*, among others. At this step identification of CuPb is evident, as being located posterior to CuPa and connected to CuPaβ by the column. The vein interpreted as CuPb bears the file.

4. Discussion

According to the STHC developed above, stem-ensiferans, *obscura*, *monstrosa*, stem-gryllidaeans, gryllidaeans, gryllotalpidaeans, and tettigoniidaeans all have a stridulatory file located along CuPb. This is basically the conclusion of RAGGE (1955) and SHAROV (1968, 1971), under their respective STHC. DESUTTER-GRANDCOLAS's (2003) STHC will be discussed below, and contrasted to the one favoured herein, according to their respective amounts of transformations required to explain the observed patterns. Various scenarios on the evolution of the file will be considered then. A new transformation type of insect wing venation patterns will then be outlined based on the current cases, and nomenclatural implications considered under the cladotypic procedure.

4.1. STHCs and amounts of needed transformations

DESUTTER-GRANDCOLAS (2003) mostly relied on axillary sclerite morphology for establishing forewing venation THCs in male ensiferans. However the supporting illustrations are inconclusive, and data on groups used as reference, viz. acrididaeans and phasmidans, were not provided. The initial criterion for the strength of a phylogenetic hypothesis, allowing analysis to be transparent and reproducible, viz. appropriate illustration or description (KLASS 2001), is therefore not fulfilled. Provided these deficiencies it is impossible to discuss inferences drawn from sclerite morphology by DESUTTER-GRANDCOLAS (2003). Only the resulting interpretations can be considered.

As mentioned above, discrepancies between wing venation THCs resulting from DESUTTER-GRANDCOLAS's (2003) investigation, and those previously proposed (ZEUNER 1939; RAGGE 1955; SHAROV 1968, 1971; KUKALOVÁ-PECK 1991; GOROCHOV 1995a,b; BÉTHOUX & NEL 2001, 2002; among others) are significant. Regarding total-ensiferans, DESUTTER-GRANDCOLAS (2003; followed by DESUTTER-GRANDCOLAS et al. 2005) interprets as 'R' and 'M' veins that have been widely recognized as ScP, and RA & RP, respectively, by virtually all previous authors (ZEUNER 1939; RAGGE 1955; SHAROV 1968, 1971; HENNIG 1981; KUKALOVÁ-PECK 1991; CARPENTER 1992; GOROCHOV 1995a,b; BÉTHOUX & NEL 2001, 2002; with minor discrepancies on vein nomenclature, such as 'Rs' instead of 'RP'). DESUTTER-GRANDCOLAS's (2003) interpretation implies a loss of the whole RP ('R' does not have a posterior branch) and a reduction of ScP, two vein sectors that are well developed in all stem-orthopterans (documented in literature published prior to acceptance of DESUTTER-GRANDCOLAS 2003: ZEUNER 1962; CARPENTER 1966; SHAROV 1968, 1971; GOROCHOV 1986, 1987; BÉTHOUX et al. 2002a,b; among others), but also in most pterygotans (CARPENTER 1992; BELAYEVA et al. 2002). In addition, it would imply that R, as consensually identified in all pterygotans (LAMEERE 1922, 1923; SÉGUY 1959; WOOTTON 1979; KUKALOVÁ-PECK 1991; BELAYEVA et al. 2002; GRIMALDI & ENGEL 2005), is concave instead of being convex. The author provides no justification for these THCs and corresponding transformations.

It could be argued that this issue has no effect on THCs elaborated within ensiferans: correct topographic homologies can be unravelled whichever groundplan interpretation is followed for orthopterans (one could have equally followed RAGGE's 1955 or SHAROV's 1968 interpretations). However, DESUTTER-GRANDCOLAS's (2003) conjectures are problematic when non-orthopteran reference groups are taken into consideration, as done in the corresponding contribution. How the author interpreted the forewing venation of acrididaeans and phasmidans is unclear. This point is crucial because the clade composed of gryllidaeans and gryllotalpidaeans, whose representatives are assumed to exhibit non-homologous files, is sister-group to the rest of ensiferans according to DESUTTER-GRANDCOLAS's (2003) phylogenetic hypothesis. As a consequence, how topographic homology conjectures have been established with respect to reference groups for these two critical taxa is all but clear, although essential.

Regardless of these issues, the STHC by DESUTTER-GRANDCOLAS (2003; see also DESUTTER-GRANDCOLAS et al. 2005) and the one developed herein in section 3 are contrasted on Pl. 7 A,C and B,D, respectively, showing the gryllidaean *grandidieri* and the gryllotalpidaean *vicinus*, and in the following. The herein favoured STHC implies:

(1) a CuA simple in both gryllidaeans and gryllotalpidaeans (**1** on Pl. 7B,D, respectively); according to DESUTTER-GRANDCOLAS's (2003) STHC, CuA (red vein) is abundantly branched in gryllidaeans (Pl. 7A) and reduced (limited to wing base) in gryllotalpidaeans (Pl. 7C) (no intermediate condition reported);

(2) matching branching patterns of CuPaα2, CuPaβ, and CuPb (viz. all are simple) in gryllidaeans and gryllotalpidaeans (**2** on Pl. 7B,D); according to Desutter-Grandcolas's (2003) STHC, CuP (blue vein) is reduced in gryllidaeans (Pl. 7A) and branched in grylloptalpidaeans (Pl. 7C; with a single stem reaching the posterior wing margin) (no intermediate condition reported);

(3) matching cross-veins specialized as column in both gryllidaeans and gryllotalpidaeans (**3** on Pl. 7B,D); according to Desutter-Grandcolas's (2003) STHC, the corresponding structure is interpreted as a CuA branch in gryllidaeans (Pl. 7A) and a cross-vein in gryllotalpidaeans (Pl. 7C);

(4) a convex condition of AA1 in both gryllidaeans and gryllotalpidaeans (**4** on Pl. 7B,D); according to Desutter-Grandcolas's (2003) STHC, the presumed AA1 is concave in gryllidaeans, and convex in gryllotalpidaeans;

(5) an oblique origin of (a simple) CuPb from CuPb + AA1 in both gryllidaeans and gryllotalpidaeans (**5** on Pl. 7B,D); according to Desutter-Grandcolas's (2003) STHC, this branching point corresponds to the origin of AA1 in gryllidaeans (Pl. 7A), and of several AA branches (or a branched AA1) in gryllotalpidaeans (Pl. 7C);

(6) a corresponding location of the file in both gryllidaeans and gryllotalpidaeans (**6** on Pl. 7B,D); according to Desutter-Grandcolas's (2003) STHC, the file is located along AA1 in gryllidaeans (Pl. 7A), and along the posterior branch of CuP in gryllotalpidaeans (Pl. 7C).

The herein favoured STHC implies a lower number of branches of CuPaα1 and a connection of MP with CuA in gryllotalpidaeans (absent in gryllidaeans), but similar morphological conditions have been assumed in *villosiceps* and *frontalis* (Pl. 3). This STHC also implies a fusion of CuPaα2 with CuPaβ, and a fusion of CuPaα1, CuPaα2, and CuPaβ in gryllotalpidaeans, but various transformation series can plausibly support this conjecture (Fig. 5).

In conclusion the amount of transformation needed to explain the observed morphologies according to the STHC herein favoured is significantly lower than that of Desutter-Grandcolas's (2003), and implies transformations documented by intermediate conditions (partly from cases based on related species). The concern that Gwynne's (1995) phylogenetic hypothesis is "methodologically flawed", "especially for hypotheses of primary homology (Desutter-Grandcolas 2003: pp. 525, 528, respectively) equally applies to Desutter-Grandcolas's (2003) STHC.

A result of the comparative analysis conducted herein is that stridulatory files are located along the same vein in all extant ensiferan species possessing it and documented so far, and in all fossil ensiferans in which the structure is preserved and documented. The stridulatory apparatus in this group is then homologous at the topographic and primary levels, a proposition already supported by Zeuner (1939), Ragge (1955), and partly by Sharov (1968, 1971).

4.2. Which kind and how many transformations of the stridulatory file?

According to phylogenies proposed by Desutter-Grandcolas (2003) and Jost & Shaw (2006) gryllidaeans and gryllotalpidaeans are sister-groups. Given, in addition, the identical location of the file in both groups (on CuPb), as proposed above, assuming homology of the file in the two taxa (at the secondary level) is clearly more parsimonious than non-homology. As for tettigoniidaeans (if understood as including katydids, *monstrosa*, and closely related species; Desutter-Grandcolas 2003), the file is also present on CuPb. However, because of the topology of the phylogenetic tree favoured by Desutter-Grandcolas (2003), in which several groups lacking a file are nested as successive sister-groups of tettigoniidaeans, parsimony dictates that the file was acquired separately in tettigoniidaeans (this scenario costs 2 steps). Desutter-Grandcolas (2003) advocates a convergence, but if a stem-ensiferan such as †*zeuneri* is taken into account, it must be assumed that a file was also acquired independently in this species (3 steps). Alternatively, it could have been acquired at the base of the tree, lost in the sister-group of gryllidaeans + gryllotalpidaeans, and re-appeared in tettigoniidaeans (3 steps). A scenario involving a re-appearance is not unlikely (see Whiting et al. 2003; but see Trueman et al. 2004), but a unique gain followed by multiple losses is either not (Desutter-Grandcolas 1997).

An alternative phylogenetic hypothesis of ensiferans was provided by Jost & Shaw (2006). If †*zeuneri* is added at the base of the tree, a unique origin and multiple losses is as parsimonious as a hypothesis of multiple acquisitions (or acquisition and loss at the base of the tree). According to Legendre et al. (2010), Jost & Shaw's (2006) dataset does not strongly support basal nodes of the phylogeny drawn by the authors. If so we are left with THCs only (i.e. homology at the secondary level is not testable at the moment). And, as demonstrated above, the stridulatory file is identically located in all surveyed ensiferans, i.e. its homology has to be assumed at the primary level. Therefore the hypothesis that the file was only acquired once is currently the most parsimonious hypothesis.

It is worth noticing that in gryllidaeans the loss of stridulatory structures can be prompted by the mutation of a single locus (Tinghitella 2008), and this may even have a positive fitness value (Zuk et al. 2006). Considering, in addition, the complexity of stridulatory structures, their loss or gain are unlikely to be equally probable

(OTTE 1992; JOST & SHAW 2006). A unique origin of this complex structure, followed by multiple losses (possibly resulting from feminization events), is therefore a likely explanation for the distribution of the file among ensiferans. Notice that partial feminization has also been evidenced based on an unusual specimen in mantodeans (BÉTHOUX 2010a).

Finally, the lack of support for the various hypotheses on ensiferan relationships (LEGENDRE et al. 2010) leaves an additional option open: the file could have been acquired once in a clade including all ensiferan taxa that have a file, i.e. gryllidaeans, gryllotalpidaeans, tettigoniidaeans, and their stem-relatives (proposed composition of *Grylloptera* as defined in 4.4; with possible 'inner' losses resulting from feminization), and excluding gryllacrididaeans and their kin, which have no file at all, not even vestigial.

4.3. A new transformation type: tracheal un-capture

Vein fusion and un-fusion, vein translocation, and tracheal capture have been reported as plausible transformations of the insect wing venation pattern (BÉTHOUX 2009b). Indeed the evolution of male forewing venation pattern in ensiferans provides several instances of them. An additional transformation was documented in the course of the comparative analysis, which can be referred to as 'tracheal un-capture'. It involves a vein abandoning its usual course for another, and leaving a remnant of its previous course in the form of a cross-vein-like structure, free of trachea (a sort of 'phantom' vein). The THC for *grandidieri* male forewing venation implies such a transformation for CuA (remnant indicated by * on Pl. 2F, and referred to as 'cua' in the text; see also Pl. 2H; compare with Pl. 1,2A; and see Fig. 3). Basically, this transformation type is the matching of the tracheal capture, as is un-fusion with respect to fusion. The documentation of this transformation type concurs with the view that the cross-vein vs. main vein distinction might be artificial to some extent (BÉTHOUX & SCHNEIDER 2010). The new transformation type will have to be considered in the establishment of THCs in other insect groups.

4.4. Nomenclatural implications

It is the main property of cladotypic nomenclature to associate a hypothesis of full homology (topological, primary, and secondary) of a given structure or condition, occurring in two species (at least), to a taxon name. Therefore the hypothesis that all ensiferans exhibiting a file located along CuPb acquired it from a common ancestor can be translated into a nomenclatural act. Should the secondary homology hypothesis be discarded by forthcoming investigations, consequences would be limited: the proposed name would simply refer to a polyphyletic assemblage, while it will still reflect a clear cut historical hypothesis. The composition given below is by no means definitive, nor defining. Indeed, under cladotypic nomenclature the composition of a taxon is merely an outcome of its character-state-based definition, and of a phylogenetic hypothesis. For example, should gryllacrididaeans and their kin be demonstrated to have derived from a *Grylloptera* and then lost the file, they would de facto belong to the *Grylloptera*, without need for nomenclatural emendation.

Taxon *Archaeorthoptera nom.* Béthoux & Nel, 2002, *dis.-typ.* Béthoux, 2007c

Taxon *Grylloptera nom.* Haeckel, 1896, *dis.-typ. n.*

Definition. Species that evolved from the (segments of the) metapopulation lineage in which the character state 'on ventral side, right and/or left forewings with a row of teeth ('file') located along CuPb', as exhibited by *viridissimus* Linnaeus, 1758: p. 430 and *campestris* Linnaeus, 1758: p. 428, has been acquired (venation designations as herein).

Cladotypes. (1) ♂ of *viridissimus* Linnaeus, 1758: 430, '*viridissimus* Linnaeus, 1758: 430 | *Tettigonia viridissima* | det. by O. Béthoux, 2011', '44°56′01–06″N, 5°46′12–15″E | Power Plan area, Le Villaret, | Isère, France | 11.viii.11, coll. by O. Béthoux', 'Cladotype *Grylloptera* | *nom*. Haeckel, 1896, | *dis.-typ*. Béthoux, 2012' (coloured in red); and (2) ♂ of *campestris* Linnaeus, 1758: 428, '*campestris* Linnaeus, 1758: 428 | *Gryllus campestris* | det. by O. Béthoux, 2011', '44°57′24–26″N, 5°44′41–42″E | Béthoux's orchard, La Motte | d'Aveillans, Isère, France | 1.v.11, coll. by O. Béthoux', 'Cladotype *Grylloptera* | *nom*. Haeckel, 1896, | *dis.-typ*. Béthoux, 2012' (coloured in red). Both cladotypes pinned, with forewings outstretched, housed at the SNSD (see Fig. 6).

Paracladotypes. Nine specimens of *viridissimus* Linnaeus, 1758: p. 430 (all with same labels as cladotype except for type label, reading 'Paracladotype *Grylloptera* | *nom*. Haeckel, 1896, | *dis.-typ*. Béthoux, 2012', coloured in green), five males pinned (three of them with both forewings outstretched, two with left forewing outstretched), and two males and two females preserved in ethanol; and ten specimens of *campestris* Linnaeus, 1758: p. 428 (all with same labels as cladotype except for type label, reading 'Paracladotype *Grylloptera* | *nom*. Haeckel, 1896, | *dis.-typ*. Béthoux, 2012', coloured in green), four males pinned (one of them with both forewings outstretched, three with right wing outstretched), and four males and two females preserved in ethanol; all collected and determined by the author, and housed at the SNSD.

Discussion. The antonym of the defining character state is 'on ventral side, forewings without a row of teeth

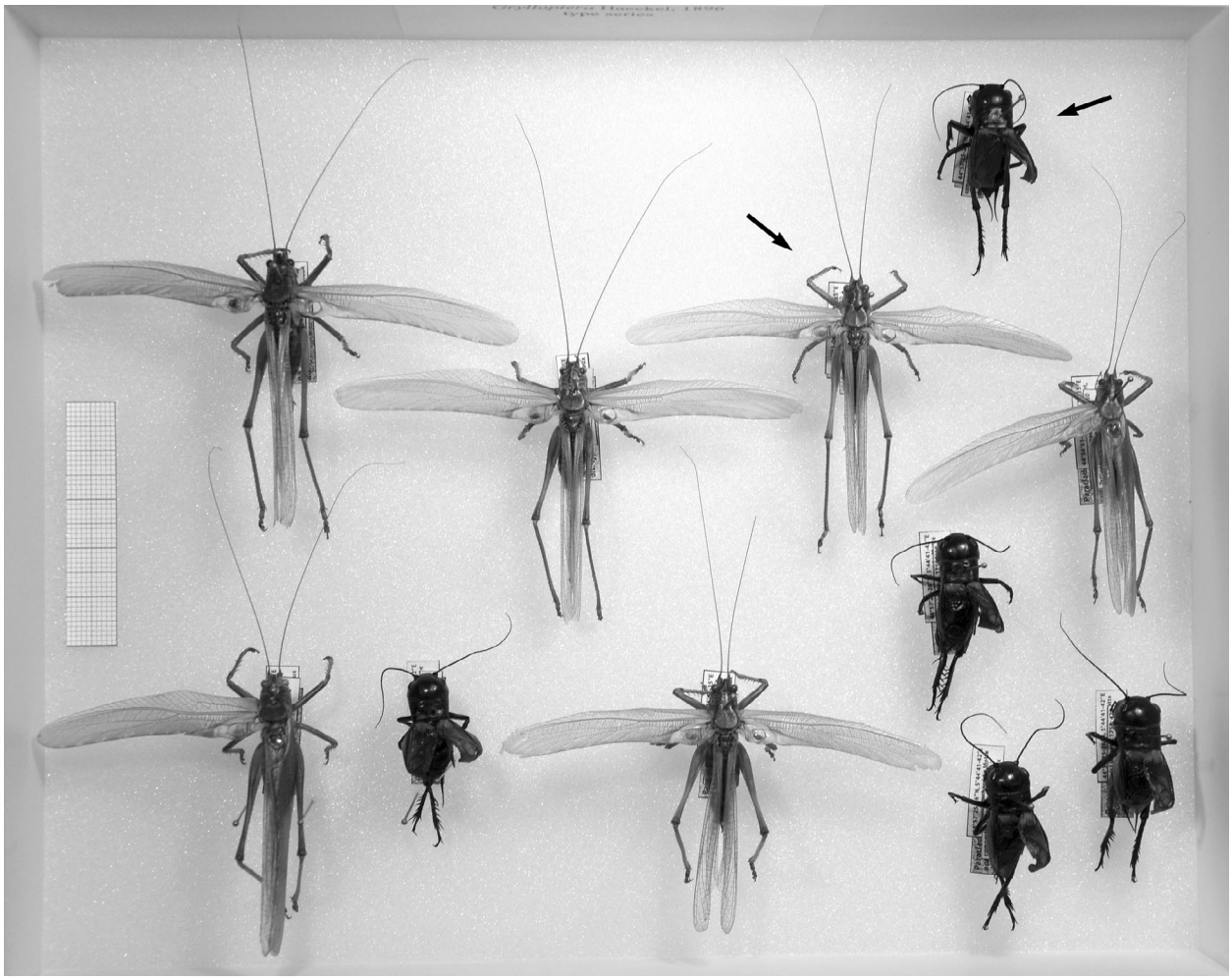

Fig. 6. Type series of *Grylloptera nom*. Haeckel, 1896, *dis.-typ. n*. Arrows indicate cladotypes (other specimens are the paracladotypes of the pinned series).

('file') located along CuPb'. All putative extant sister-groups of *Grylloptera* lack a file, and it has never been observed in Late Carboniferous *Archaeorthoptera* considered as stem-saltatorians. Therefore the proposed defining character state is considered as derived.

According to available phylogenetic and palaeontological data the file was originally acquired only in the male sex, and its occurrence in some females of *Grylloptera* is secondary. Should this prove to be incorrect, the fact that both selected cladotypes are males does not imply that the defining character state should read 'in males, on ventral side, forewings with a row of teeth forming a file, located along CuP'. The option is left open instead. The functional file is located on the right forewing in *campestris*, and on the left forewing in *viridissimus*, but in each case the overlapped wing also possesses a file. The plesiomorphic condition is represented by an ambidextrous insect (Morris & Gwynne 1978; Gu et al. 2012), and the proposed definition aims at encompassing all known cases, and evolutionary scenarios.

The name choice for this taxon is to be discussed. According to Haeckel (1896) the taxon 'Grylloptera' encompasses cockroaches, praying mantises, and stick-insects in addition to *Archaeorthoptera*, and therefore differs from the composition proposed herein, limited to a subset of *Archaeorthoptera* (note that Linnaeus's 1758 genus name '*Gryllus*', initially encompassing several of the currently defined orders, experienced a similar reduction of the number of its referents). However, the rare recent usages of the name 'Grylloptera' (e.g. Ingrisch 1990) refer to a subset of *Archaeorthoptera* similar to 'Ensifera'. Indeed both names have been considered as synonyms (Eades et al. 2011). However, the name 'Ensifera' explicitly refers to the sword-shaped ovipositor of katydids and crickets, and is therefore pre-occupied (although type material was never designated), i.e. is not suitable for the current purpose. The name '*Gryllus*' is widely used as a genus name under the traditional nomenclatural procedure, and therefore was avoided. Finally, provided that adaptation of the name 'Grylloptera' prevents the erection of a new name, that its modern usage is cryptic, and that its referents are not deeply modified, this option was favoured.

It is also necessary to discuss the consideration of the defining character state for taxonomic and nomenclatural purposes by previous authors. In addition to a few ad-

ditional ones, literature search was limited to contributions by ZEUNER (1939), RAGGE (1955), SHAROV (1968, 1971), and GOROCHOV & RASNITSYN (2002). Only a single entry, found in the latter, requires discussion. GOROCHOV & RASNITSYN (2002) provide a classification of orthopterans (their fig. 430) in which the node 9 is supported by the character state 'male elytral stridulatory apparatus with sinuate CuP forming stridulatory vein'. This formulation and that proposed for the defining character state of *Grylloptera* differ in two essential aspects. First GOROCHOV & RASNITSYN's (2002) formulation encompasses hypothetical orthopterans able to use CuP as a 'stridulatory vein' in the absence of file, although the file itself is the focus of the proposed formulation. Second, GOROCHOV & RASNITSYN's (2002) formulation refers to a behavioural trait (viz. stridulation), while the proposed one is restricted to a morphological one. Although the morphology arguably is associated with behaviour, many ways of stridulating have been developed in various orthopteran lineages. It is not unlikely that some cousins of *Grylloptera*, devoid of a file, are/were able to stridulate by using several veins, including CuPb. These are excluded by the proposed definition, while their position is not evident according to GOROCHOV & RASNITSYN's (2002) formulation. Therefore I suggest that the proposed character formulation is to be considered as new.

The choice of the cladotypic species was prompted by their abundance, even in nearby locations, and easy identification. Note that both *campestris* and *viridissimus* were initially assigned to the genus '*Gryllus*' (LINNAEUS 1758; and to a genus-group taxon – of unspecified rank in the original publication – for the latter, namely *Tettigonia*), the name *Grylloptera* was derived from. Cladotypes and male paracladotypes had a functional file, as they were located (and collected) based on their song performance.

Composition. All saltatorian *Archaeorthoptera* excluding caeliferans, and gryllacrididaeans and their kin. It will be argued elsewhere that the latter group likely never acquired the file.

5. Conclusion

This contribution demonstrates the importance of proper consideration given to both fossil and recent material for inferring insect wing venation THCs, whenever possible (BÉTHOUX 2009b). This approach proved to be relevant for *Grylloptera*, composed of species which experienced 250 MY of intense modification in male forewing venation, and characterized by morphologies which are the result of an accumulation of modifications, making identification of particular elements impossible without considering intermediates. The wing venation of *gryllotalpa* and *vicinus* (in particular the course of CuA) are examples of such saturated morphologies (a concept matching site saturation with DNA-based investigations). As a consequence of the use of forewings for producing sounds in males, the expansion of vibrating areas reduced the space allocated to the main venation pattern, and cross-veins acquired a dominant role in specific areas. This disparity might have been prompted by the necessity to develop song distinctiveness, allowing conspecific individuals to identify each other, and inter-specific pairing to be avoided, with a high potential to trigger morphological radiation. This hypothesis could be tested based on THCs proposed in this contribution and the evolutionary history of the group, as documented in the fossil record.

More generally, this contribution emphasizes the primacy of THCs in phylogenetic investigations (see also KLASS 2001). In this step, for both morphological and molecular datasets, competing alignments (i.e. character matrices) can be compared by a measurement of their overall correspondence (or consistency, or parsimony), possibly computerized. But as long as fully automated procedures are not yet available, the initial step is to be manual in morphology. Beyond difficulties to develop appropriate algorithms in this case, the manual approach has the substantial advantage of allowing transformation types previously unreported to be predicted (such as feminization, tracheal un-capture), what a machine might have trouble to perform yet.

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Appendix 1

Names and classification of species referred to in the main text according to the current traditional nomenclature (Eades et al. 2011), and approximate correspondence with current cladotypic nomenclature. [Provided on request of the editor]

	Archaeorthoptera
Orthoptera [1]	
Ensifera [2]	
	Grylloptera
Hagloidea Handlirsch, 1906 [3]	
†Haglidae Handlirsch, 1906 [3]	
†*Archihagla* Sharov, 1968	
†*Archihagla zeuneri* Sharov, 1968	†*zeuneri* Sharov, 1968
Prophalangopsidae Kirby, 1906 [4]	
Prophalangopsis Walker, 1871 [5]	
Prophalangopsis obscura (Walker, 1869)	*obscura* Walker, 1869
Cyphoderris Uhler, 1864 [5]	
Cyphoderris monstrosa Uhler, 1864	*monstrosa* Uhler, 1864
†Gryllavidae Gorochov, 1986 [6]	
Gryllavus Sharov, 1968	
†*Gryllavus madygenicus* Sharov, 1968	†*madygenicus* Sharov, 1968, 181
†*Paragryllavus* Gorochov, 1986	
†*Paragryllavus curvatus* Gorochov, 1986	*curvatus* Gorochov, 1986
Grylloidea von Laicharting, 1781	
Gryllidae von Laicharting, 1781 [7]	
Brachytrupes Serville, 1838	
Brachytrupes grandidieri (de Saussure, 1877)	*grandidieri* de Saussure, 1877
Gryllus Linnaeus, 1758	
Gryllus bimaculatus de Geer, 1773	*bimaculatus* de Geer, 1773
Gryllus campestris Linnaeus, 1758	*campestris* Linnaeus, 1758
Riatina Otte & Alexander, 1983	
Riatina villosiceps (Chopard, 1951)	*villosiceps* Chopard, 1951
Riatina frontalis (Walker, 1869)	*frontalis* Walker, 1869
Gryllotalpidae Leach, 1815 [7]	
Gryllotalpa Latreille, 1802 [8]	
Gryllotalpa gryllotalpa (Linnaeus, 1758)	*gryllotalpa* Linnaeus, 1758
Scapteriscus Scudder, 1868 [8]	
Scapteriscus vicinus Scudder, 1869	*vicinus* Scudder, 1869
Tettigonioidea Krauss, 1902	
Tettigoniidae Krauss, 1902	
Tettigonia Linnaeus, 1758	
Tettigonia cantans (Fuesslin, 1775)	*cantans* Fuesslin, 1775
Tettigonia viridissima (Linnaeus, 1758)	*viridissimus* Linnaeus, 1758

[1] Understood as crown-group; if understood as total-group (i.e. including all species more closely related to extant Orthoptera than to any other extant group of insects), it includes *Archaeorthoptera*.

[2] Understood as composition-based name in its current usage, viz. Orthoptera excluding Caelifera; however the name itself refers to the sword-shaped ovipositor, occurring in Carboniferous *Archaeorthoptera* (pers. obs.), so 'Ensifera' understood as 'possessing a sword-shaped ovipositor' includes all extant Orthoptera, and *Archaeorthoptera*.

[3] A paraphyletic assemblage; if considered as including the common ancestor of its included species, and all descendants of this common ancestor, its composition roughly equates that of *Grylloptera*.

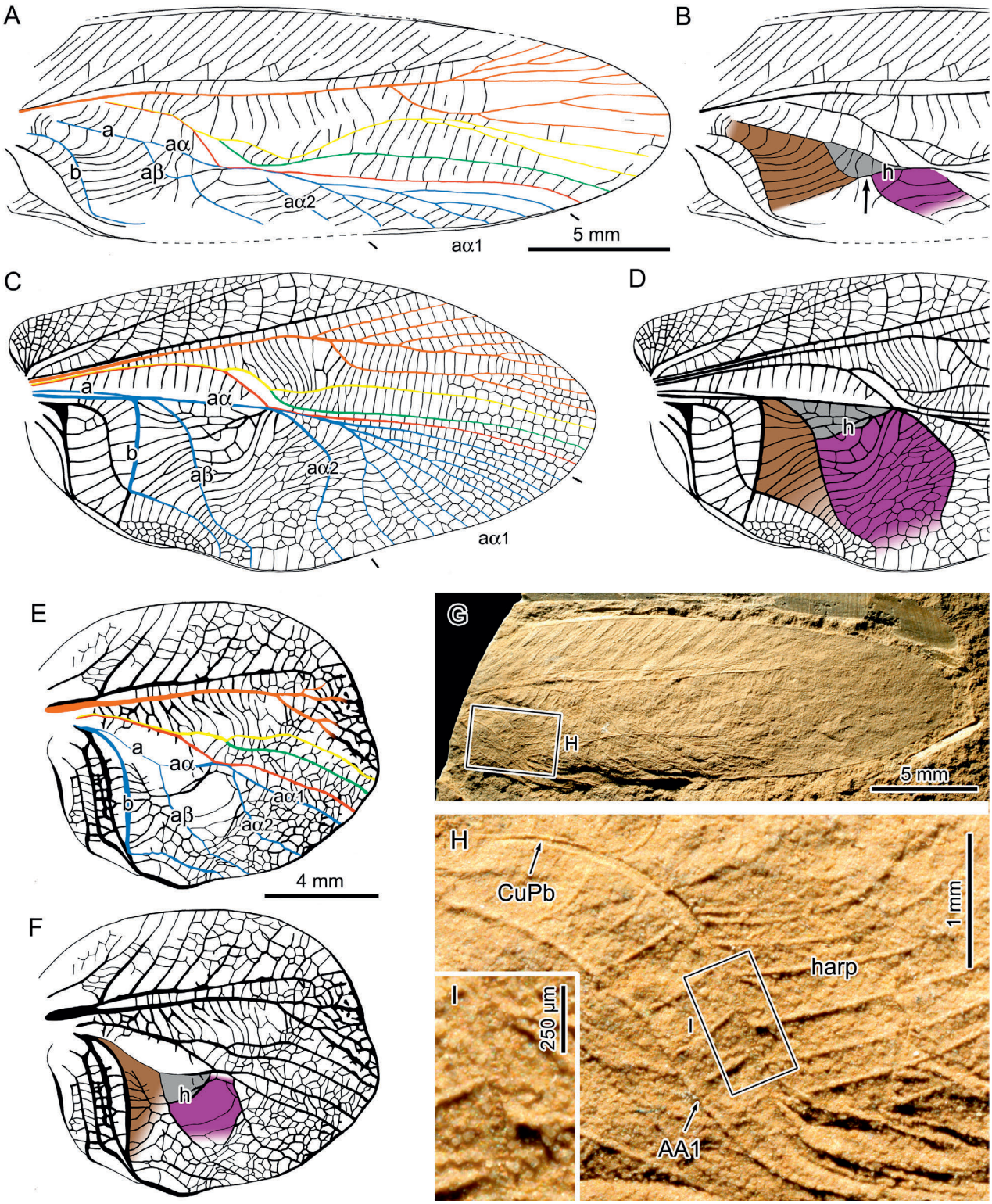
[4] Considered paraphyletic by Desutter-Grandcolas (2003).

[5] Considered a close-relative or member of Tettigonioidea by Desutter-Grandcolas (2003).

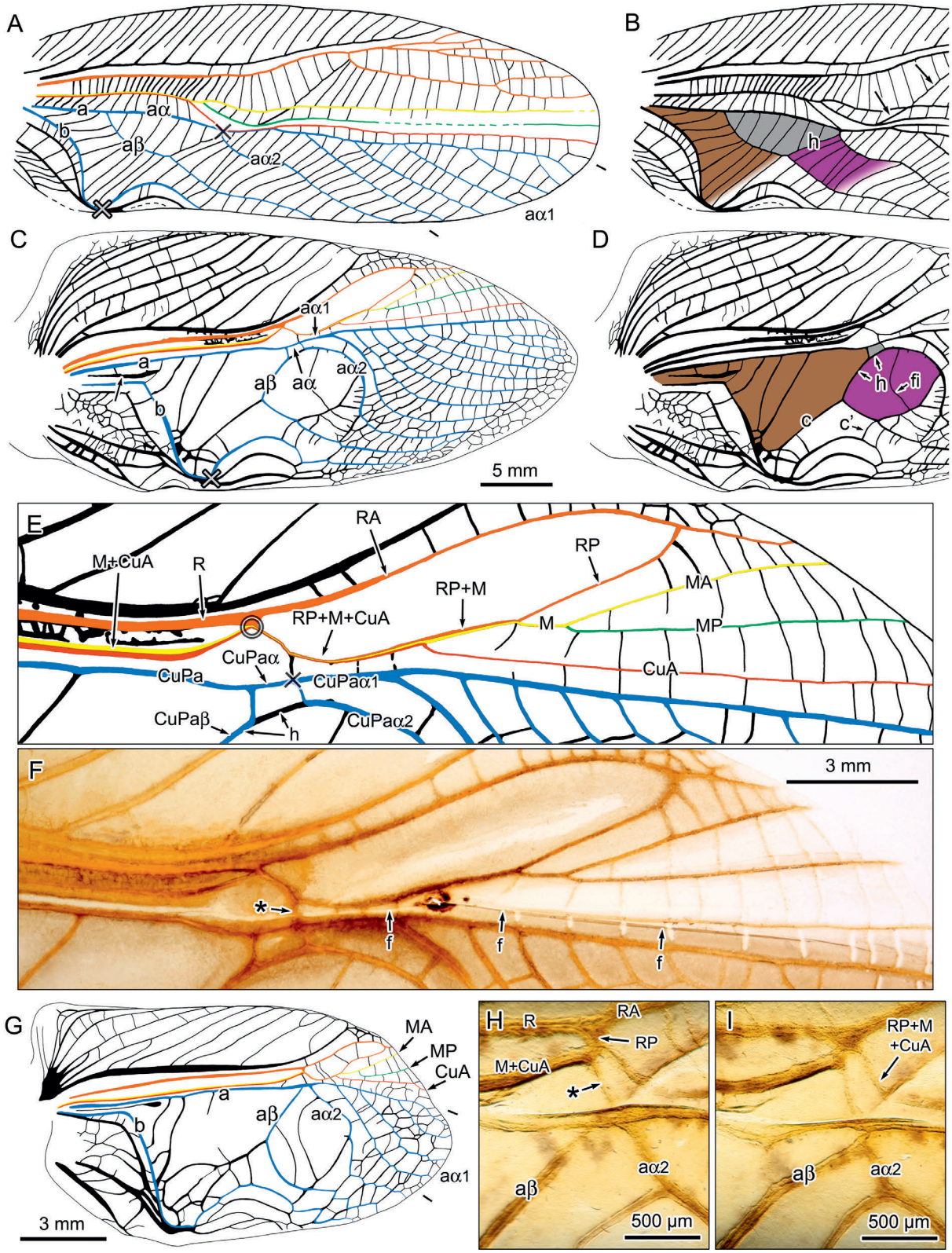
[6] A paraphyletic assemblage; if considered as including the common ancestor of its included species, and all descendants of this common ancestor, its composition roughly equates that of Grylloidea.

[7] If 'Gryllotalpidae' is considered a family, Gryllidae is most likely paraphyletic.

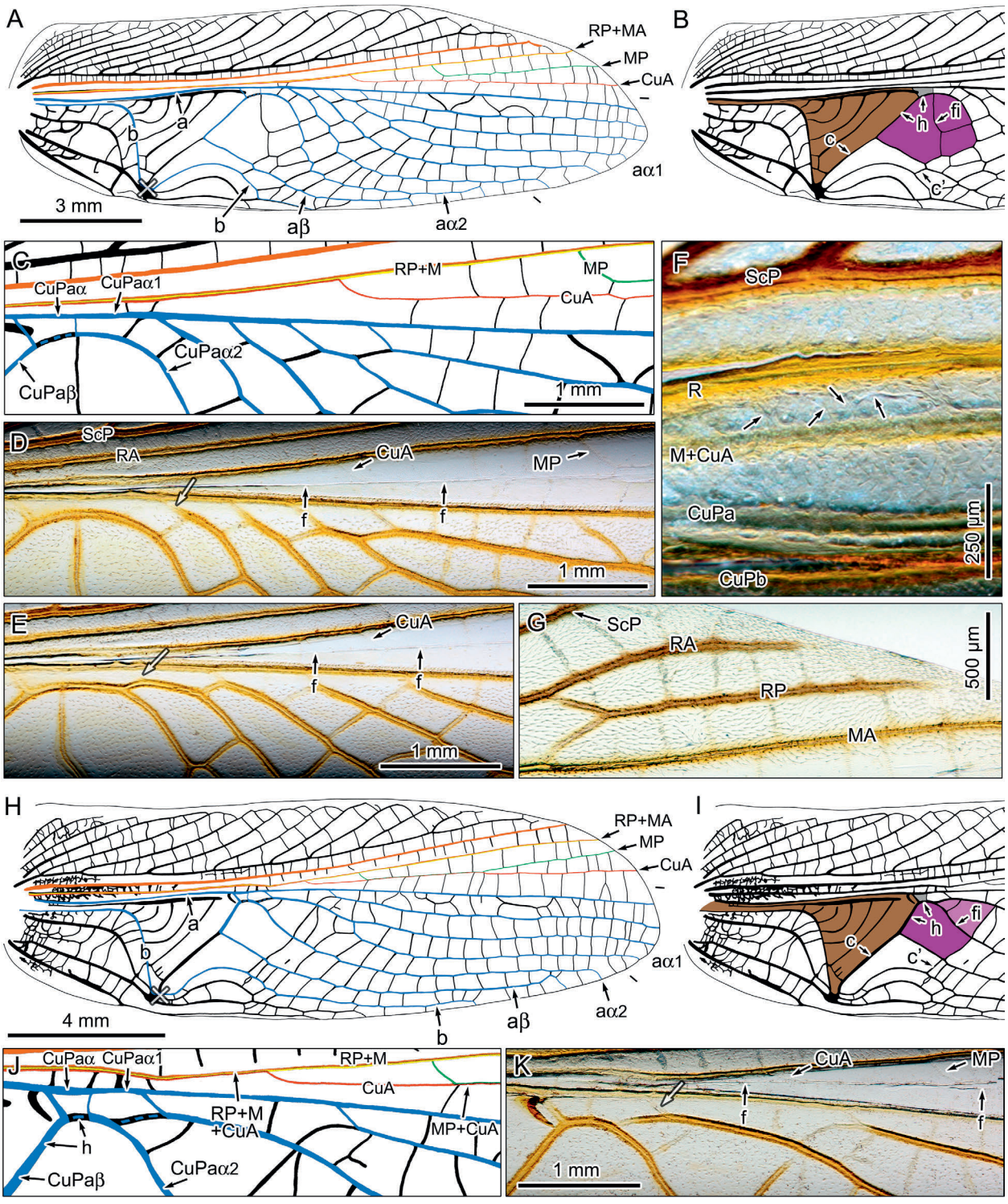
[8] If '*Scapteriscus*' is considered a genus, *Gryllotalpa* is most likely paraphyletic.



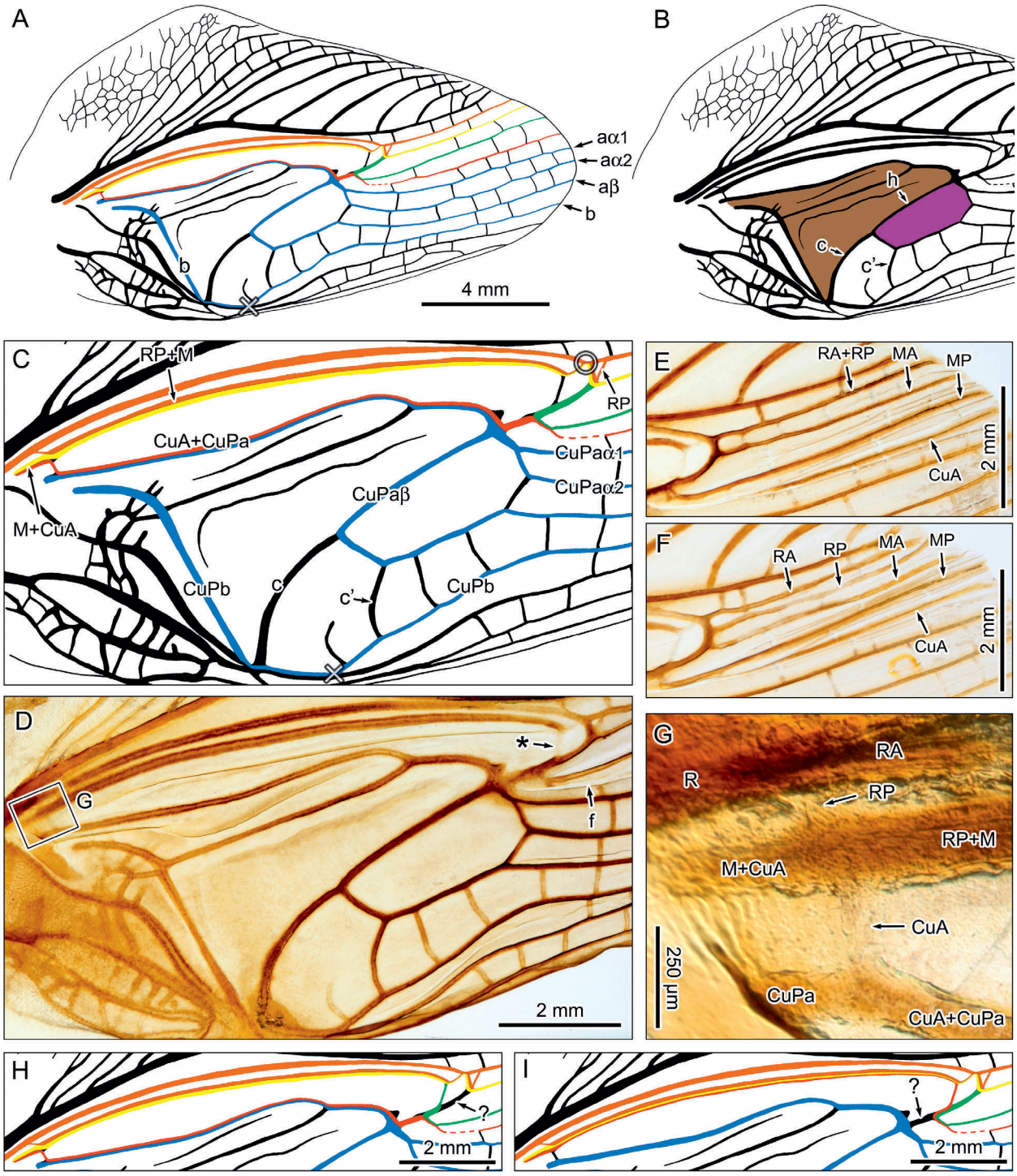
Pl. 1. A–F: Conjectures of male forewing venation topographic homologies (**A**,**C**,**E**) and location of mirror (dark purple), harp (brown), and CuPaα/CuPaβ/handle (gray) areas (**B**,**D**,**F**) in various *Grylloptera* species. **A**,**B**: Species †*zeuneri* Sharov, 1968 (drawing of the holotype PIN 2240/4019, right forewing; Madygen, Kyrgyzstan, Lower/Middle Triassic). **C**,**D**: Species *obscura* Walker, 1869 (holotype, right forewing; drawing modified from Sharov 1968 according to photographs). **E**,**F**: Species *monstrosa* Uhler, 1864 (based on IWC OB 531, left forewing). **G–I**: Photographs of †*zeuneri* Sharov, 1968 (holotype PIN 2240/4019, right forewing, positive imprint; Madygen, Kyrgyzstan, Lower/Middle Triassic). **G**: Habitus. **H**: Detail of the file as located on **G**. **I**: Detail of the file as located on **G**. Veins colour coding, abbreviations, and indications: orange, R, RA, and RP; yellow, M and MA; green, MP; red, CuA; blue, CuP; AA1 = first anterior Analis; a = CuPa; aα = CuPaα; aβ = CuPaβ; b = CuPb; h = handle; and see text.



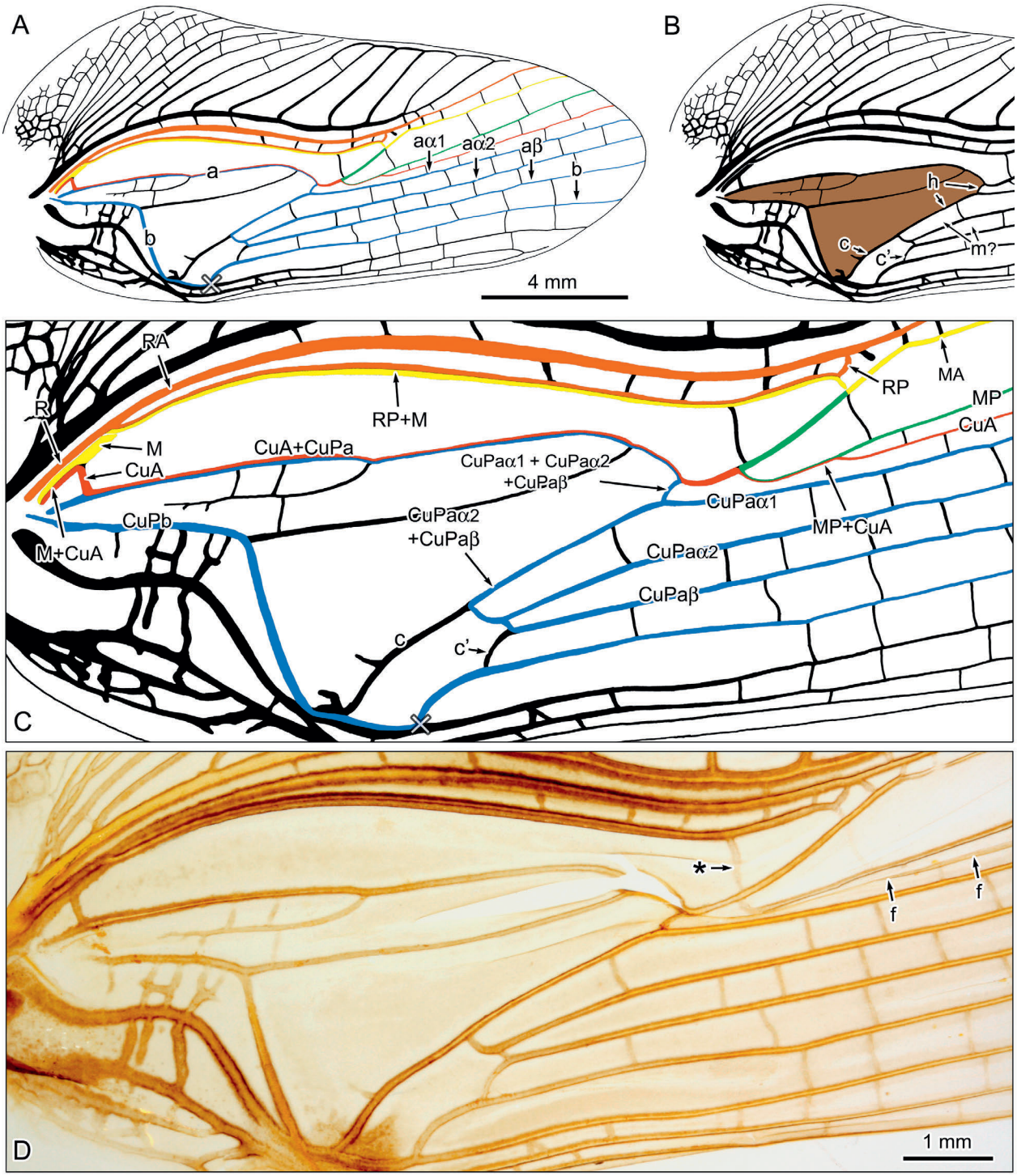
Pl. 2. Conjectures of male forewing venation topographic homologies (**A**,**C**,**E**,**G**), location of mirror (dark purple), harp (brown), and CuPaα/CuPaβ/handle (gray) areas (**B**,**D**), and photographs of details (**F**,**H**,**I**) in various *Grylloptera* species. **A**,**B**: Species †*madygenicus* Sharov, 1968: p. 181 (modified from Sharov 1968). **C**–**F**: Species *grandidieri* de Saussure, 1877: p. 287 (IWC OB 502, right forewing; on **C**, the arrow without label indicates a sclerotization located between CuPa and CuPb). **E**,**F**: Detail of antero-distal part. **G**–**I**: Species *bimaculatus* de Geer, 1773 (IWC OB 601). **G**,**H**: Left forewing. **I**: Right forewing. **H**,**I**: Detail of fusion of RP with M + CuA, and of the branching pattern of CuPa. Veins colour coding, abbreviations, and indications: orange, R, RA, and RP; yellow, M and MA; green, MP; red, CuA; blue, CuP; AA1 = first anterior Analis; a = CuPa; aα = CuPaα; aβ = CuPaβ; b = CuPb; h = handle: c = column; c' = cross-vein connecting CuPaβ and CuPb distal to the column and opposite the closure of the mirror; f = fold; fi = fissure; * indicates the remnant of the course of CuA; black cross, white cross, and white circle indicate the point of fusion of CuA with CuPaα1, the fork of CuPaα (resulting into CuPaα1 and CuPaα2), and the point of divergence of connection of M + CuA with R (and fusion of RP with M + CuA); and see text.



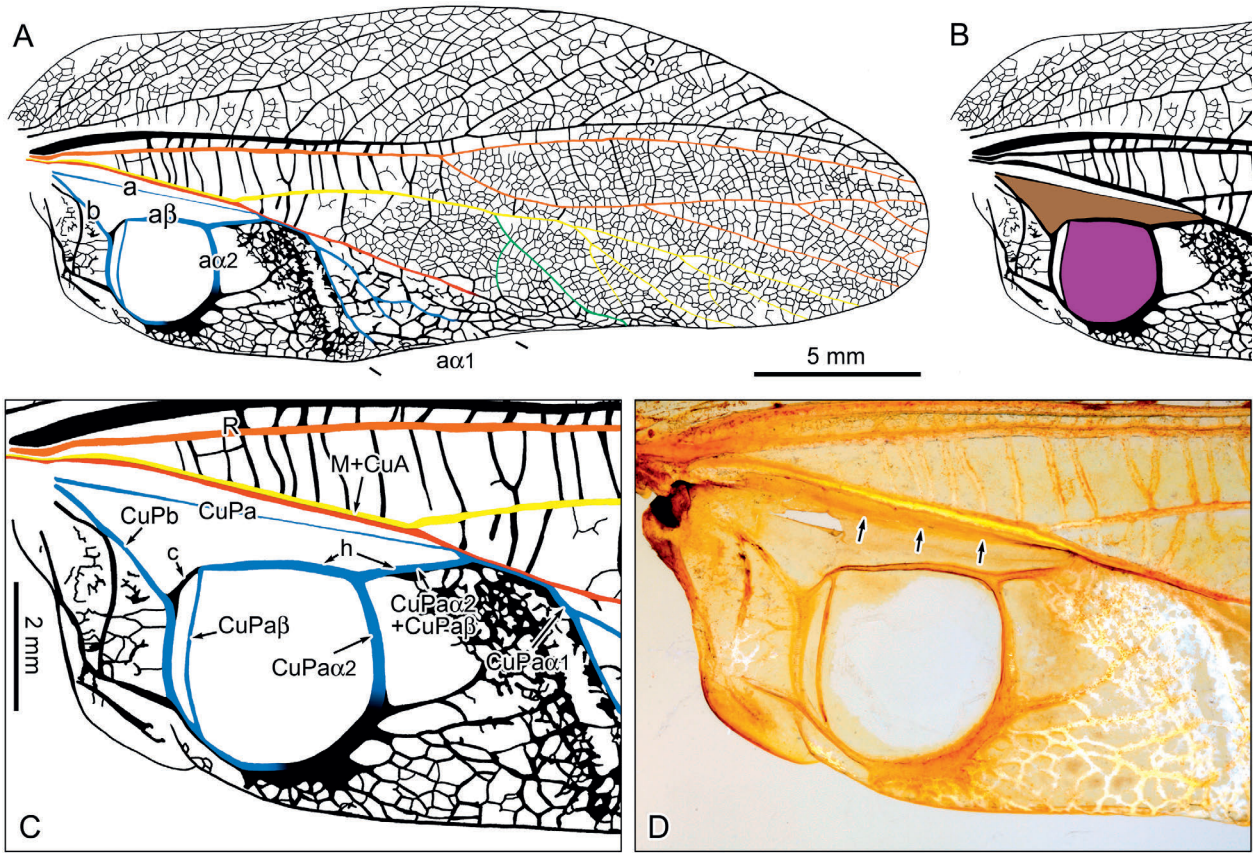
Pl. 3. Conjectures of male forewing venation topographic homologies (**A**,**C**,**H**,**J**), location of mirror, harp, and CuPaα/CuPaβ/handle areas (**B**,**I**), and photographs of details (**D**–**G**,**K**) in various *Grylloptera* species. **A**–**G**: Species *villosiceps* Chopard, 1951 (ANIC IWC OB 2). **A**–**D**: Right forewing. **E**–**G**: Left forewing. **C**–**E**: Detail of central area. **F**: Detail, basal half, central area (arrows indicate a trachea undulating between R / RA and M + CuA). **G**: Detail, antero-distal area. **H**–**K**: Species *frontalis* Walker, 1869 (ANIC IWC OB 1, left forewing). **I**–**K**: Detail of central area. Colour coding, abbreviations, and indications as above, and: light purple accounts for uncertainty in extension of mirror; white arrows indicate the origin of the first posterior branch of CuPaα1.



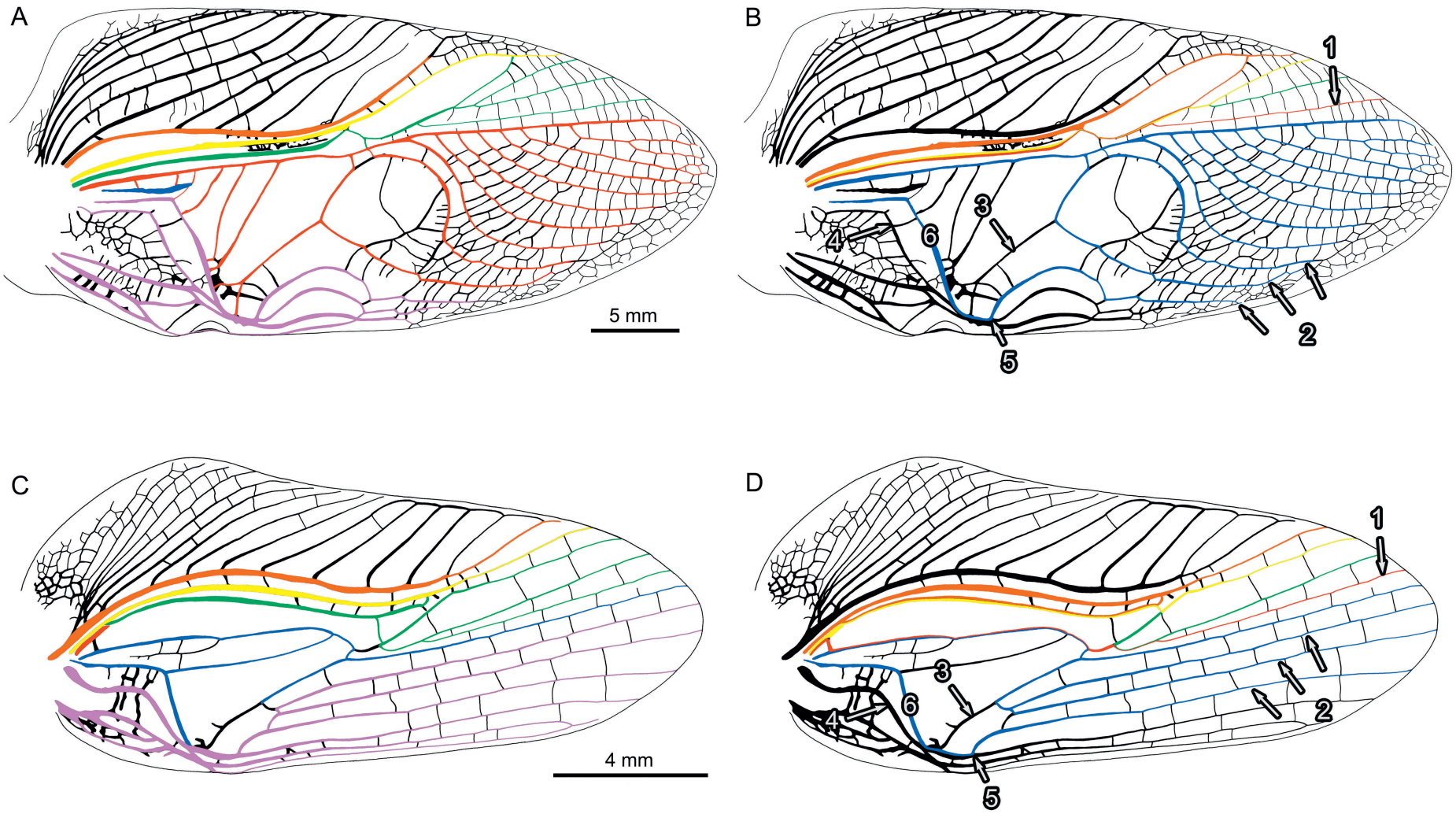
Pl. 4. Conjectures of male forewing venation topographic homologies (**A**,**C**), location of mirror and harp areas (**B**), photographs of details (**D**–**G**), and alternative conjectures (**H**,**I**) in *gryllotalpa* Linnaeus, 1758. **A**–**D**, **G**–**I**: IWC OB 634, left forewing. **C**,**D**: Detail of postero-basal area. **G**: Detail of basal area, as located on **D**. **E**,**F**: IWC OB 631, detail of antero-distal area. Colour coding, abbreviations, and indications as in previous plates.



Pl. 5. Conjectures of male forewing venation topographic homologies (**A**,**C**), location of mirror area (**B**), and photograph of details (**D**) in *vicinus* Scudder, 1869 (specimen IWC OB 509, left forewing). **C**,**D**: Detail of the postero-basal area. Colour coding, abbreviations, and indications as above, and: m? indicates the possible locations of the mirror according to two competing THCs.



Pl. 6. Conjectures of male forewing venation topographic homologies (**A**,**C**), location of mirror and harp areas (**B**), and photograph of details (**D**), in *cantans* Fuesslin, 1775 (specimen SNSD IWC OB 30, right forewing).



Pl. 7. Comparison of male forewing venation pattern in *grandidieri* (**A**,**B**) and *vicinus* (**C**,**D**), according to conjectures elaborated by Desutter-Grandcolas (2003) (**A**,**C**; see also Desutter-Grandcolas et al. 2005; tentative interpretation), and to those elaborated herein (**B**,**D**). Colour coding, abbreviations, and indications as above and: mauve, AA veins (not considered in **B**,**D**); 1 = simple CuA; 2 = CuPaα1, CuPaβ, and CuPb simple; 3 = cross-vein specialized as column; 4 = convex AA1; 5 = oblique origin of CuPb from CuPb + AA1; 6 = file located on CuPb. Colour coding, abbreviations, and indications as in previous plates.