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The wing venation of the Triassic stem-Odonata *Triassoneura andersoni* Riek, 1976 (Insecta) brings homologies in the basal complex back to the drawing board

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ABSTRACT
The description of material of the Triassic stem-Odonata *Triassoneura andersoni* Riek, 1976 (Molteno Formation, South Africa), including the single forewing described to date and hitherto unpublished material, including the well-preserved basal half of a hindwing, led to an in-depth reconsideration of the classical proposal that Anisoptera Selys Longchamps, 1854 (dragonflies), Zygoptera Selys Longchamps, 1854 (damselflies) and Anisozygoptera Handlirsch, 1906 share a homologous discoi-

dal cell (forming the triangle/supratriangle area in Anisoptera, and the quadrangle in Zygoptera). Focusing on the basal complex, composed of the discoidal cell and several surrounding elements, we first compared the Triassic species to the extant anisozygopteran *Epiophlebia superstes* (Selys Longchamps, 1889). The rare morphology observed in some hindwings of the latter is best explained by a mosaic of fore- and hindwing features, indicating that the first strengthened cross-vein occurring in the MA-MP area cannot be homologous (or, more adequately, homonomous) among the fore- and the hindwing, and neither is the cell it closes proximally. Considering then the Jurassic stem-anisopteran *Heterophlebia buckmani* (Brodie, 1849), including a rare hindwing morphology similar to that documented in *Epiophlebia superstes*, further reinforces the previous inferences, but also shows that introgression of morphological features from one wing pair to the other is a rampant phenomenon in Odonata Fabricius, 1793. With this perspective, the morphology of the basal complex in Anisoptera, exemplified by the extant *Aeshna cyanea* (Müller, 1764), is best explained by the hypothesis that, at some stage along the stem of the group, the hindwing configuration integrally replaced that of the forewing (i.e., that the latter was 'posteriorized'). Conversely, based on a revision of the Cretaceous stem-zygopteran *Congqingia rhora* Zhang, 1992 and on data on the extant *Chalcolestes viridis* Van der Linden, 1825, the morphology of the basal complex in the total-group of Zygoptera is best explained by the hypothesis that the forewing configuration integrally replaced that of the hindwing (i.e., that the latter was 'anteriorized'). A hypothetical model closely fitting the observed configurations is proposed, involving two modules, resulting from the duplication of a hypothetical primary module, and evolving independently (i.e., being paralogues), controlling the basal complex configuration and retaining the capacity to be activated in either wing pair. The merits of our proposal shall be further tested in light of the morphology of fossil taxa of the 'anisozygopteran' assemblage, it may actually contribute to dismantle, and, in parallel, thanks to the growing body of genomic data on Odonata. This case echoes those of arches in jawed vertebrates and whorls of angiosperm flowers, both involving paralogous structures modelled by paralogous developmental genes.

KEY WORDS
Homonomy,
paralogy,
module,
conamen,
Molteno Formation.

RÉSUMÉ
La nervation alaire de l'odonate souche triasique Triassoneura andersoni *Riek, 1976 (Insecta) amène à reconsidérer les homologies du complexe basal.*
La description de matériel de l'odonate souche triasique *Triassoneura andersoni* Riek, 1976 (Formation Molteno, Afrique du Sud), incluant l'aile antérieure unique décrite à ce jour et du matériel inédit, dont la moitié basale bien préservée d'une aile postérieure, a conduit à une reconsidération approfondie de la proposition classique, selon laquelle les anisoptères (libellules), les zygoptères (demoiselles) et les anisozygoptères partagent une cellule discoïdale homologue (formant la zone triangle/supratriangle chez les anisoptères et le quadrilatère chez les zygoptères). En se concentrant sur le complexe basal, composé de la cellule discoïdale et de plusieurs éléments environnants, nous avons d'abord comparé l'espèce triasique à l'anisozygoptère actuel *Epiophlebia superstes* (Selys Longchamps, 1889). La morphologie rare observée sur certaines ailes postérieures de cette dernière s'explique mieux par une mosaïque de traits des ailes antérieures et postérieures, indiquant que la première nervure transversale renforcée apparaissant dans la zone MA-MP ne peut pas être homologue (ou, plus précisément, homonome) chez les ailes antérieure et postérieure, pas plus que la cellule qu'elle ferme proximalement. Considérer alors l'anisoptère souche jurassique *Heterophlebia buckmani* (Brodie, 1849), incluant une morphologie rare de l'aile postérieure similaire à celle documentée chez *Epiophlebia superstes*, renforce encore les inférences précédentes, mais montre également que l'introgression de caractéristiques morphologiques d'une paire d'ailes à l'autre est un phénomène répandu chez les odonates. Dans cette perspective, la morphologie du complexe basal chez les anisoptères, illustrée par l'espèce actuelle *Aeshna cyanea* (Müller, 1764), s'explique au mieux par l'hypothèse selon laquelle, à un certain stade le long de la souche du groupe, la configuration de l'aile postérieure a intégralement remplacé celle de l'aile antérieure (i.e., que cette dernière a été « postériorisée »). À l'inverse, sur la base d'une révision du zygoptère-souche crétacé *Congqingia rhora* Zhang, 1992 et de données sur l'espèce actuelle *Chalcolestes viridis* Van der Linden, 1825, la morphologie du complexe basal chez le groupe total des zygoptères s'explique au mieux par l'hypothèse selon laquelle la configuration de l'aile antérieure a intégralement remplacé celle de l'aile postérieure (i.e., que cette dernière a été « antériorisée »). Un modèle hypothétique correspondant étroitement aux configurations observées est proposé, impliquant deux modules, résultant de la duplication d'un module primaire hypothétique, et évoluant indépendamment (i.e., étant des paralogues), contrôlant la configuration du complexe basal et conservant la capacité d'être activés dans l'une ou l'autre paire d'ailes. Les mérites de notre proposition doivent être testés plus en détail à la lumière de la morphologie des taxons fossiles de l'assemblage des « anisozygoptères », qu'elle pourrait contribuer à démanteler, et, parallèlement, grâce à l'enrichissement des données génomiques sur les odonates. Ce cas fait écho à ceux des arches chez les vertébrés à mâchoires et des verticilles des fleurs d'angiospermes, tous deux impliquant des structures paralogues modelées par des gènes de développement paralogues.

MOTS CLÉS
Homonomie,
paralogie,
module,
conamen,
Formation Molteno.

INTRODUCTION

Wings of damsel- and dragonflies (Odonata Fabricius, 1793) are fascinating objects, for their variety of configurations seem to obey laws yet challenging to apprehend. Over 320 million years, this organ experienced an intense morphological evolution (Wootton & Kukalová-Peck 2000; Deregnaucourt *et al.* 2023) likely in relation with the outstanding flight performances extant forms display (Dudley 2000; Corbet 2004). Given this strong relation between form and function, it is not unexpected that wing venation had confounding effects on phylogenetic reconstructions, for convergence has been a rampant phenomenon (Nel & Piney 2023a; Yang *et al.* 2023). To worsen the case, extant forms represent a relatively recent subset of all Odonata, with the first crown-group split of Anisoptera Selys Longchamps, 1854 (dragonflies) and Zygoptera Selys Longchamps, 1854 (damselflies) having taken place near the Triassic-Jurassic transition (Kohli *et al.* 2021; Suvorov *et al.* 2022; or slightly later, see Huang *et al.* 2025); and the intense evolution which wings of Odonata underwent tends to obstruct previous conditions, making it difficult to properly assess wing venation homologies in the absence of taxa displaying intermediate configurations (e.g. see Riek & Kukalová-Peck 1984; Deregnaucourt *et al.* 2021b). In this context, a notable issue is the systematics of Triassic and Jurassic fossil taxa commonly referred to as 'anisozygopterans'. How these fossils relate to crown-Zygoptera, crown-Anisoptera and the species-poor family Epiophlebiidae Tillyard, 1914, the only extant member of Anisozygoptera Handlirsch, 1906 (all these taxa forming the crown-Odonata) remains unclear. This situation is, for a good part, due to a dearth of data on the nearest relatives of crown-Odonata, namely the 'triassolestids' (but see Tierney *et al.* 2020), and the fact that the better-known stem-odonatan groups like Archizygoptera Handlirsch, 1906 and Triadophlebiomorpha Pritykina, 1981, likely are highly derived (Nel *et al.* 2012; Béthoux & Anderson 2023). An unfortunate outcome is an uncertainty on fossil taxa which could be used as temporal calibration points for the early splits within crown-Odonata.

The basal complex, located near the wing base and involving, besides main veins, structuring elements derived from cross-venation (i.e., conamina; Yang *et al.* 2023), plays an important role in addressing flight functional demands (Eraghi *et al.* 2023). The fossil record documents the sequence of addition of its structuring elements (Bechly 1996; Fig. 1), the outcome being a structure varying in a modular fashion (Blanke 2018). The configuration of this basal complex has traditionally served as a key feature for identifying the nearest relatives of extant forms (Tillyard 1928; Nel *et al.* 1993; Bechly 1996; Nel & Piney 2023b; among others). Its earliest condition involves the pons, a conamen located between the anterior and posterior Media (MA and MP, respectively), and the cell proximad to it, termed 'discoidal cell' ('dc', cyan area on Fig. 1). The latter is characterized as 'open' in the absence of conamina preceding the pons (Fig. 1A; note that, for some authors, the 'pons' is not a strengthened cross-vein but part of a main vein). It is generally admitted that extant forms and some of their closest extinct relatives share a so-called 'closed discoidal cell', basally delimited by a conamen (termed 'parapons' herein; Fig. 1B, C). This proposal was initially derived from the investigation of Permian damselfly-like forms displaying the open condition, while all extant forms share the closed one (Tillyard 1925a). Put in perspective with the wing morphology of other fossil Odonata known at the time (Tillyard 1925b, 1928), it eventually led to the

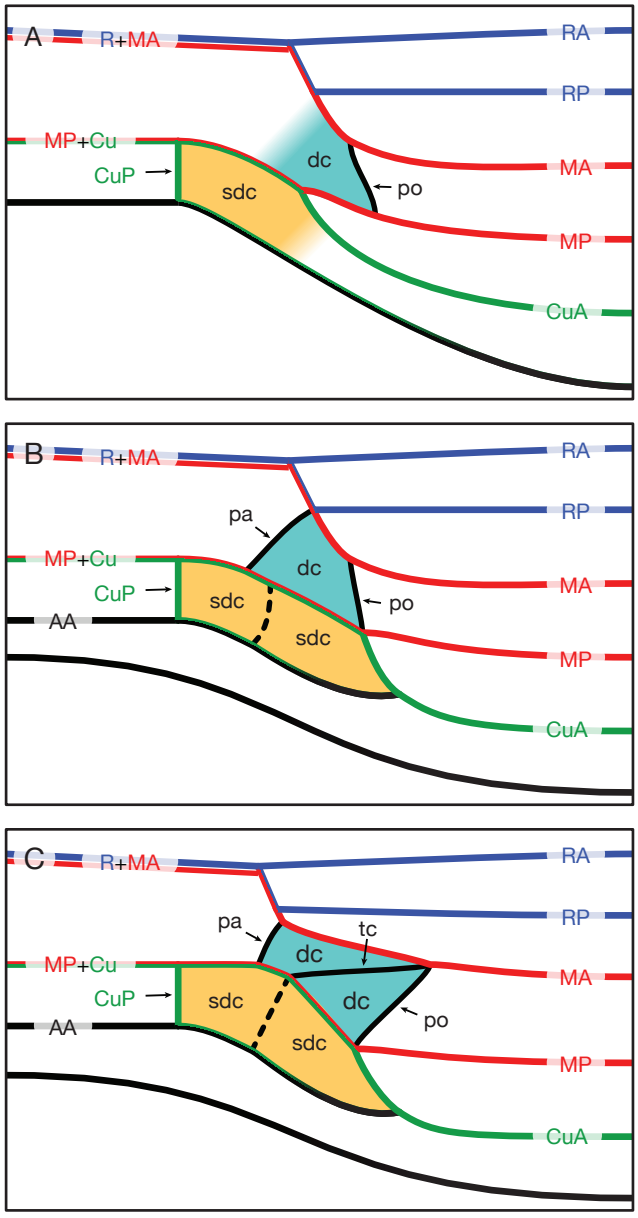


FIG. 1. — Schematic, general evolution of the basal complex under the 1DC proposal: **A**, configuration as in early Stigmoptera Bechly, 1996 (e.g. Archizygoptera Handlirsch, 1906), with the discoidal cell (**dc**) distally closed by the pons (**po**) but open basally, in both wing pairs; **B**, configuration as in *Epiophlebia superstes* (Selys Longchamps, 1889) and crown-Zygoptera, with the discoidal cell (**dc**) closed on both distal and basal sides (by the pons [**po**] and the parapons [**pa**]), in both wing pairs, and the subdiscoidal cell (**sdc**) unsplit, except in the hindwing of the former (**dashed line**); **C**, configuration in crown-Anisoptera, with the discoidal cell (**dc**) split by the triangle conamen (**tc**), and the subdiscoidal cell (**sdc**) usually split in both wing pairs (**dashed line**). Drawings: O. Béthoux.

proposal that Anisoptera, characterized by a discoidal cell that is both closed and split (by the triangle conamen; Fig. 1C), derived from a paraphyletic zygopteran 'grade' (possessing a closed but unsplit discoidal cell; Fig. 1B), itself deriving from a paraphyletic protozygopteran 'grade' (lacking a closed discoidal cell; Fig. 1A) (Fraser 1957; and references therein). The hypothesis of a paraphyletic zygopteran grade is nowadays abandoned, but that of Zygoptera displaying a plesiomorphic condition of the discoidal cell, with respect to Anisoptera, remains. Also, under the current proposal, whether the 'subdiscoidal cell' ('sdc', light orange on Fig. 1) is split or not varies among groups and, in some, between fore- and hindwing.

Herein we newly document the wing venation of the Triassic species *Triassoneura andersoni* Riek, 1976 based on the single forewing described to date and hitherto unpublished material, including a well-preserved basal half of a hindwing. The species can be confidently regarded as more closely related to crown-Odonata than Archizygoptera or Triadophlebiomorpha (or even the meganisopteran assemblage) are. Concurrently, it can be excluded from the less-inclusive Lobodonata Béthoux *in* Tierney A., Deregnaucourt, Anderson, Tierney P., Wappler & Béthoux, 2020, itself including crown-Odonata in addition to some stem-Odonata. Unexpectedly, contrasting the morphology of fore- and hindwing of this species led us to broadly reconsider the homology of elements composing the basal complex.

MATERIAL AND METHODS

Morphological terminology and conventions

We follow the serial insect wing venation groundplan (Lameere 1922, 1923). Essentially based on it, we follow the Odonata wing venation groundplan elaborated by Riek & Kukalová-Peck (1984) and its successive implementations (Nel *et al.* 1993; Bechly 1996; Béthoux 2015; and see Jacquelin *et al.* 2018). Abbreviations adopted for main venation and intercalary veins are summarized in the 'Abbreviations' section (with mention of color-coding, where applicable).

Besides main veins, the basal complex involves particular cross-veins, often strengthened. Following Yang *et al.* (2023), we refer to such cross-veins as 'conamina' (singular, 'conamen'); and to the conamen splitting the discoidal cell into two cells as the 'triangle conamen'. Following Deregnaucourt *et al.* (2021a) and Yang *et al.* (2023), we refer to the 'pons' as the conamen located between MA and MP and which, once acquired, was located opposite the second point of maximum curvature of MP; and to the conamen preceding the pons in the MA-MP area (if present) as the 'parapons'.

The identification of further elements composing the basal complex differs under the two proposals considered thereafter. To facilitate discussion, we will refer to the currently accepted one, which assumes that the discoidal cell is homologous in crown-Zygoptera and crown-Anisoptera, as the '1DC' proposal (accounting for 'a single discoidal cell'). The alternative proposal promoted herein supposes the occurrence of four conamina, or four pontes, and will be referred to as the '4P' proposal. Under this proposal, names will prove necessary for 1) the conamen following the pons in the MA-MP area, with the proposed name 'distopons' (i.e., 'distal to the pons'); and 2) the conamen located in the area between MP+CuA and CuP (the latter being either free, or fused with the posterior wing margin or with AA), basal to the MP/CuA split, and ancestrally aligned with the pons, with the proposed name 'infrapons' (i.e., 'under the pons'). Abbreviations adopted for particular cross-veins (including conamina) and associated particular cells are summarized in the 'Abbreviations' section.

Finally, to further ease comparison between the 1DC and 4P proposals, some cells will be color-coded as explained in the 'Abbreviations' section.

On drawings, shaded portions of veins or cross-veins which are sharply delimited denote missing parts which can be reconstructed with confidence. Continuous colour shades denote an open cell, or a vein ending which position cannot be assessed positively.

Abbreviations

Main venation and intercalary veins

AA	anterior Analis;
CuA	anterior Cubitus (green);
CuP	posterior Cubitus (green);
Irp_1-rp_2	intercalary vein between RP1 and RP2 (deep saffron);
Irp_{1+2}-rp_{3+4}	intercalary vein between RP1+2 and RP3+4 (deep saffron);
MA	anterior Media (red);
MP	posterior Media (red);
RA	anterior Radius (blue);
RP	posterior Radius (blue; and all its branches);
RP1+2	anterior branch of RP;
RP1	anterior branch of RP1+2;
RP2	posterior branch of RP1+2;
RP3+4	posterior branch of RP;
ScP	posterior Subcosta.

Particular cross-veins and associated particular cells

ASn	ante-subnodal conamen;
Ax0	first antenodal;
Ax1	second antenodal;
Ax2	third antenodal;
dc	discoidal cell;
dp	distopons;
ip	infrapons;
sdc	subdiscoidal cell;
Sn	Subdnodal cross-vein;
pa	parapons;
po	pons;
tc	triangle conamen.

Color-coded comparison between the 1DC and 4P proposals

1DC proposal:

discoidal cell	cyan;
subdiscoidal cell	light orange.

4P proposal:

pa-po cell	yellow;
po-dp cell	water blue;
CuP-ip cell	pink;
ip-CuA cell	grey.

Institutional collections

GPIT-PV	Palaeontological Collection of the University of Tübingen, Tübingen;
MNHN.F	Palaeontology collection, Muséum national d'Histoire naturelle, Paris;
PRE/F/; BP/2/	Anderson collection, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg.

Comparative analysis

Our comparative analysis follows a traditional approach. To elaborate primary homology conjectures (PHCs; elsewhere referred to as 'THC', accounting for 'topological homology conjecture') we relied on the three main criteria captured by Remane (1956), namely 'similarity in position' [derived from the "principe des connections" from Geoffrey St Hilaire (1830)], 'special or intrinsic similarity' and 'continuity of forms' (de Pinna 1991; Wiley & Lieberman 2011; among others). These criteria are used at the step of 'initial hypotheses of homology' (Wiley 1975, 1981), also called 'primary homology' (de Pinna 1991). It precedes the coding of characters and the search for congruence between them, composing de Pinna's (1991) 'secondary homology' phase.

Considering a given set of patterns, several, competing sets of PHCs (SPHCs) can be elaborated. It is usually admitted that the most likely SPHC shall minimize the amount of transformation necessary to explain differences between the whole set of patterns (Key 1967; Béthoux 2020; among others). Besides incongruence between the criteria cited above, the conjunction test allows challenging a particular SPHC (Patterson 1982).

During our investigation, it became apparent that taxa for which both fore- and hindwing morphology could be documented were essential. Once this was realized, taxa for which first-hand data could be obtained were then favoured. Species which were selected are *Triassoneura andersoni* Riek, 1976 (Figs 2-4), *Epiophlebia superstes* (Selys Longchamps, 1889) (Figs 5; 6), *Heterophlebia buckmani* (Brodie, 1849) (Figs 7; 8), *Aeshna cyanea* (Müller, 1764) (Fig. 9), *Congqingia rhora* Zhang, 1992 (Figs 10; 11) and *Chalcolestes viridis* (Van der Linden, 1825) (Fig. 12). To further facilitate comparison between taxa and between SPHCs, on figures of the basal complex details, a dashed line separates fore- (above the line) and hindwings (under the line). Furthermore, a compilation of details of the basal complex under each of the considered SPHCs is provided as Figure 13. To our knowledge, no known taxon not considered in our comparative analysis challenges our conclusions.

As alluded to above, the comparative analysis of repeated body parts will form a central component of our reasoning. A precise terminology will be needed to characterize their relation. Following Patterson (1982; and references therein, among others), homology is regarded as the relation of any part to another from which 'sameness' is the result of a shared ancestry (the parts then being called 'homologues'). Within this broad concept, the relation between repeated, individualized body parts occurring in a single organism, in mass or serially arranged, and which sameness is the result of a shared developmental mechanism, will be referred to as homonomy (and the parts as 'homonomes'). For example, early winged insects possessed fore- and hindwing which, considered isolated, can hardly be differentiated, and therefore are homonomes. Typically, homonomous parts will evolve in a consistent fashion, i.e., they are not independent, and should be treated as a single part type when comparing different taxa. Following our example, wings of early pterygotes may display a reticulated vs scalariform cross-venation, and it would be inadequate to consider cross-venation for the forewing independently from that of the hindwing. If rightfully treated as a single type, instantiations of homonomes, in different taxa, qualify as orthologues if their variations reflect phylogeny (i.e., the sense commonly given to 'homology'). This corresponds to Hennig's (1966) transformation series.

At the genomic level, the duplication of a gene sequence within a species into several independent copies is called paralogy (Fitch 1970), and the resulting parts paralogues. Later, Nelson (1994) argued that the relation between mammary glands and hairs is best regarded as that of paralogues, in the same way that α and β haemoglobins are (Fitch 1970). As with homonomy, paralogy results in repeated parts within the same species. In contrast, paralogy concerns structures that become independent after duplication. This leads us to the proposal that homonomous parts that subsequently display morphological divergence indicative of a degree of independence may be called paralogues. Following up with our example, in several insect groups the forewing was thickened, while the hindwing, enlarged, gained a folding mechanism allowing its stowing under the forewing in resting position. These part types can be referred to by different names such as 'elytrized wing' vs 'foldable wing', somehow reflecting their homonomous origin. Because these part types are paralogues, one should compare the morphology of each independently from that of the other. If the respective variations (among each paralogue) reflect phylogeny, successive modifications of a given wing type then qualify as orthologues. Yet, referring to both types as paralogues at this hierarchical level acknowledges both their sameness and their independence. In summary, the concept of morphological paralogy conveniently links the transition between undifferentiated and dependant homonomes and well-differentiated, independent orthologues. The reasoning applies to developmental modules, understood as an integrated and relatively autonomous processes within a broader developmental program (Schlosser 2004; and see Eble 2005). Paralogous modules arise from a duplication of a primary one and a subsequent differentiated evolution.

Documentation

General aspects

In all cases detailed below, drawings were finalized using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, United States) using a variety of data as layer(s) of the working document. In some cases, hand-made draft drawings were produced with the aid of a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10×/23 eye pieces, a Plan Apo S 1.0× FWD objective; all Zeiss, Jena, Germany). In such case, 'hand-made drawing' will be mentioned.

Photographs were taken with a variety of combinations of Canon cameras and lenses (all Canon, Tokyo, Japan; all lenses equipped with a linear polarizing filter). In the following, the mention of the used camera body will precede that of the lens. Photograph optimisation (including the generation of composites, and stitching) was performed using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, United States). Unless specified, photographs were taken under dry conditions.

A number of techniques can be employed to improve the information content of photographs of fossil material. In some cases, we resorted to photographs taken under both dry and ethanol conditions and merge them (if so, 'dry-eth composite' is mentioned in figure caption). The light-mirror technique, allowing the polarity of an adpression to appear reverted, was also used in some cases ('light-mirrored'). We also endeavoured to merge photographs of both sides of a fossil specimen ('sides composite'). Finally, more occasionally, the embedding rock was used as reference for white balance ('rwb').

Fossil material

We gathered data on fossil material housed in several institutions whose acronyms (or collection acronyms) are explained in the 'Abbreviations' section.

As for the material of *Triassoneura andersoni* (all PRE/F/ and BP/2/), photographs were taken with an 'EOS 5D Mark III & MP-E 65 mm' set. Final drawings were elaborated based on both hand-made drawings and photographic data. As for the material of *Heterophlebia buckmani* (all MNHN.F), photographs were taken with an 'EOS 5DS R & MP-E 65 mm' set. More specifically, three to four photographs of different areas were taken for each specimen (and, for those with both sides available, for each side) and then stitched to compose an overview. Final drawings were elaborated based solely on photographic data. As for the material of *Congqingia rhora* (GPIT-PV), all photographs were taken with an 'EOS 5DS & MP-E 65 mm' set. Final drawings were elaborated based solely on photographic data.

Extant material

As for *Epiophlebia superstes*, the used material belongs to the professional collection of the first author. Wings were cut off and mounted on slides in Euparal medium. All photographs were taken with an 'EOS 5D Mark III & MP-E 65 mm' set. Final drawings were elaborated based on both hand-made drawings and photographic data (taken with transmitted light), allowing minor corrections to account for distortion due to wing compaction between the cover glass and the slide (affecting the petiole in particular). Photographs of the basal complex (Fig. 6D, E, F) were taken with both transmitted and incident light.

The material of *Aeshna cyanea* used in this study is preserved in ethanol at the Bavarian State Collection of Zoology (ZSM; specimen number GBOL20133). The specimen of *Chalcolestes viridis* used in this study belongs to the professional collection of one of us (ID; collected by L. Villier on 1.IX.2018). For both specimens, wings were cut off and temporarily mounted between a thin white plastic plate and a glass slide. A section of fishing line was placed at the edges of the glass slide, maintaining a space between it and the plastic plate, to prevent damage to the wing corrugation. Photographs were taken with an 'EOS 700D & 50 mm macro lens' set. Final drawings were elaborated based solely on photographic data.

DESCRIPTIVE ANALYSIS

Remark

For consistency, this section complies with the 4P proposal. However, the 1DC proposal will be considered in the Comparative analysis section.

Order ODONATA Fabricius, 1793
Taxon STIGMOPTERA Bechly, 1996
Genus *Triassoneura* Riek, 1976

Type species. — *Triassoneura andersoni* Riek, 1976.

Triassoneura andersoni Riek, 1976
(Figs 2-4)

Triassoneura andersoni Riek, 1976: 597.

Type material. — **Holotype. South Africa** • 1 forewing; Eastern Cape Province, Birds River locality; 31°30'S, 26°50'E; Molteno Formation; Triassic, Carnian; John Anderson leg.; BP/2/21107ab (University of the Witwatersrand, Evolutionary Studies Institute, Anderson coll.; Figs 2A; 3A; 4A, D, G).

Additional material. — **South Africa** • 1 forewing, 1 hindwing, 1 wing (possible hindwing); same data as for the holotype; PRE/F/11872ab, BP/2/4808, PRE/F/10450ab (University of the Witwatersrand, Evolutionary Studies Institute, Anderson coll.; Figs 2B-D; 3B-D; 4B, C, E, F, H, I).

Emended diagnosis. — *Both wing pairs:* Ax2 located slightly basal to the RA/RP+MA split; no cross-vein in the areas delimited by Ax2 and the nodus, and by the anterior wing margin and RA; RA (and to a lesser extent RP1) with a marked inflexion distal to the nodus; Irp_{1+2}-rp_{3+4} originating at mid-length between the RP1+2/RP3+4 and the RP1/RP2 splits; pons present, no conamen preceding it (i.e., discoidal cell open); distal to the pons, occurrence of a conamen (dispons) bridging MA and MP+CuA at the point where the latter splits into MP and CuA; opposite the pons, occurrence of a conamen (infrapons) bridging MP and the posterior wing margin; lobe absent. *Forewing:* petiole weakly pronounced; pons and infrapons oriented obliquely; distance between these structures and the distopons / the MP/CuA split short. *Hindwing:* petiole moderately pronounced, with a marked point of maximum curvature opposite the end of CuP; pons and infrapons almost perpendicular to the wing main axis, distance between these structures and the distopons / the MP/CuA split long (longer than in forewing).

Type locality and stratigraphy. — All specimens considered herein were collected at the 'Birds River' locality (locality codes 'Bir 111' in Anderson & Anderson 1984), South Africa; Molteno Formation; lower Carnian, Upper Triassic (Anderson *et al.* 1998).

General description

Fore- and hindwing subequal, total length unknown, estimated at about 56 mm in forewing and 51 mm in hindwing;

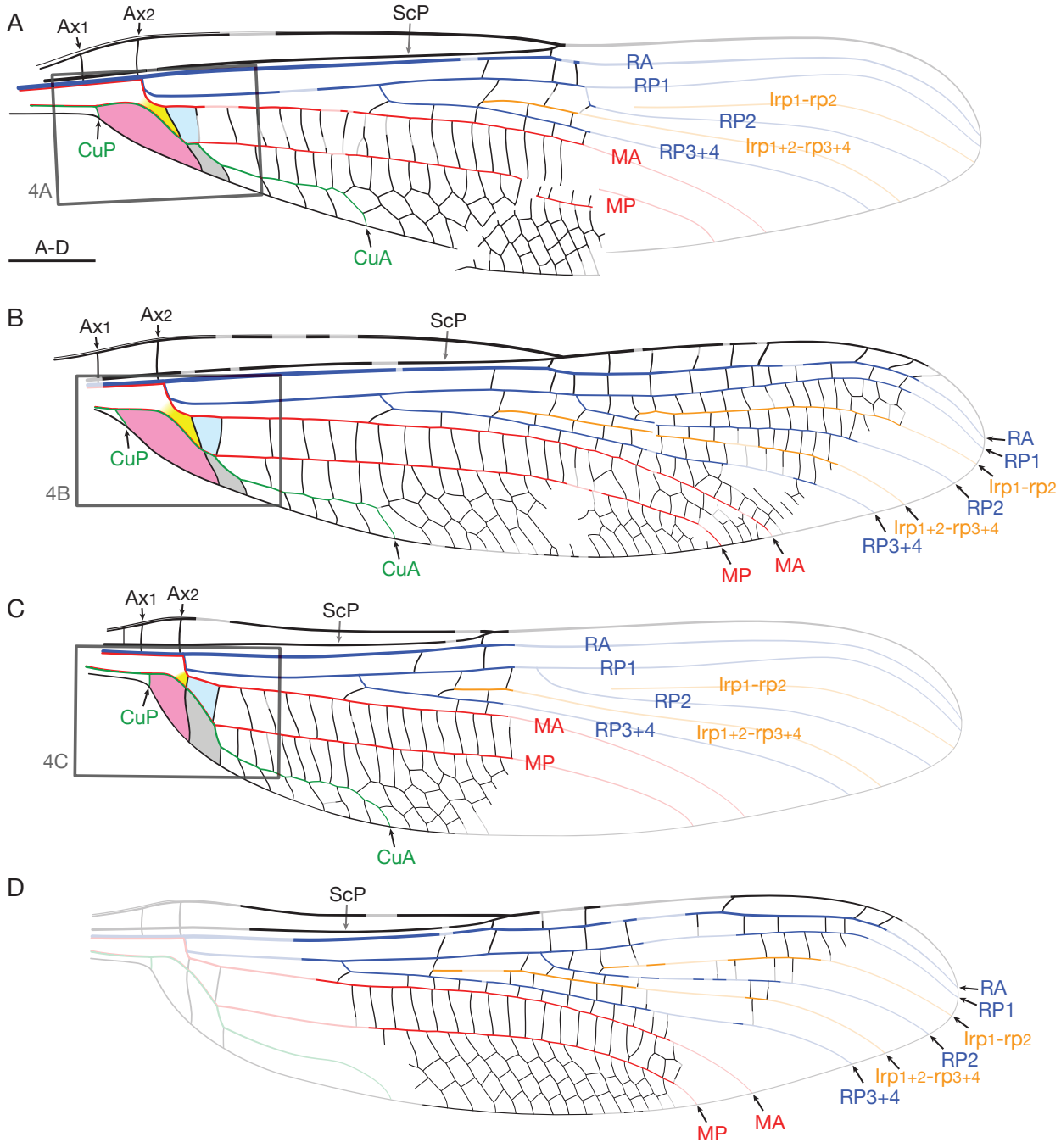


FIG. 2. — Wing venation of *Triassoneura andersoni* Riek, 1976, interpretative drawings (as for the basal complex, under the 4P proposal): **A**, holotype specimen BP/2/21107, left forewing; **B**, specimen PRE/F/11872, right forewing; **C**, specimen BP/2/4808, left hindwing; **D**, specimen PRE/F/10450, left wing, presumably a hindwing. Scale bar: 5 mm. Abbreviations: see Material and methods. Drawings: I. Deregnaucourt, O. Béthoux.

width at level of nodus *c.* 12 mm ; Ax2 located slightly basal to the origin of RP+MA; ScP reaching anterior wing margin near wing mid-length, with a very short nodal cross-vein (Cr) between it and RA; RA (and to a lesser extent RP1) with a marked inflexion distal to the nodus; four post-nodal cross-veins (known in specimen PRE/F/11872 only; Figs 2B; 3B); pterostigma 5.7-7.8 mm long; origin of RP+MA nearly perpendicular to R+MA/R; first cross-vein in the RA-RP area located slightly basal of the nodus (ASn?); RP1+2/RP3+4 split near the first third of wing length; RP1/RP2 split shortly after the end of ScP (i.e., nodus); well-formed main intercalary veins, with Irp_{1+2}-rp_{3+4} originating at mid-length between the RP1+2/RP3+4 and the RP1/RP2 splits, and Irp_1-rp_2 originating close to the RP1/RP2 split; at their origin, both Irp_{1+2}-rp_{3+4} and Irp_1-rp_2 closer to RP3+4 than to RP1+2, and to RP2 than to RP1, respectively; RP3+4 very close to MA for most of its length, diverging distally, resulting in a somewhat broad area between the two veins along the wing margin; pons and distopons present in the area between MA and MP (more distant in hindwing than

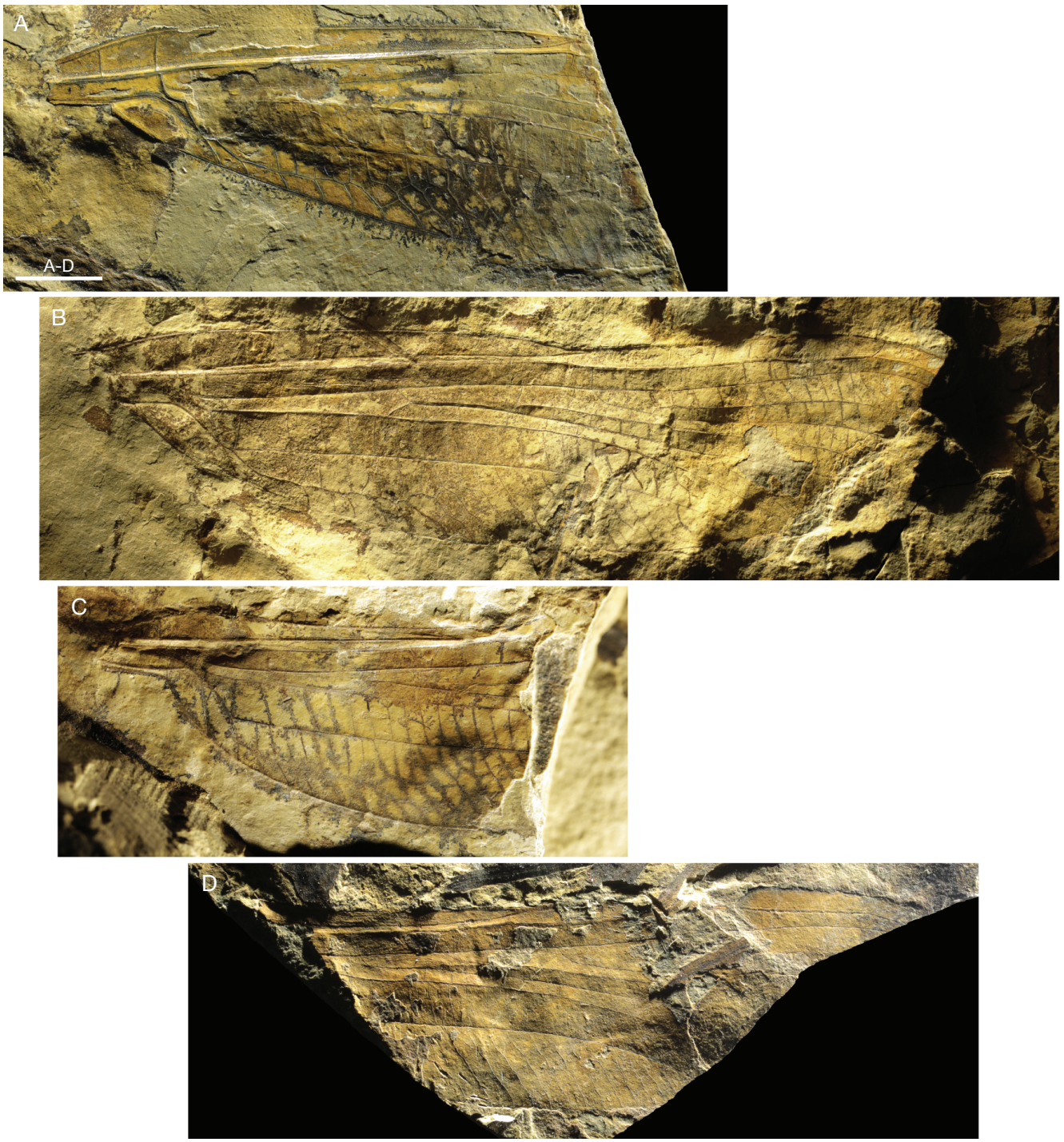


Fig. 3. — Wing venation of *Triassoneura andersoni* Riek, 1976, habitus photographs: **A**, holotype specimen BP/2/21107, left forewing (side as if wing viewed dorsally, flipped horizontally); **B**, specimen PRE/F/11872, right forewing (side as if wing viewed dorsally; dry-eth composite); **C**, specimen BP/2/4808, left hindwing (light-mirrored; dry-eth composite); **D**, specimen PRE/F/10450, left wing, presumably a hindwing (flipped horizontally). Scale bar: 5 mm. Photographs: O. Béthoux.

in forewing), both stronger than regular cross-veins; MA and MP both simple, sub-parallel, separated by a consistently broad area mostly filled with a single row of cells, taller than wide, and with cross-vein network in the distal-most part; MA and MP reaching the posterior wing margin distally, near the third quarter of wing length; at the wing base, MP+Cu close and parallel to the posterior wing margin; CuP diverging from it basal to the nodus, in the form of a very short, strong structure quickly reaching the posterior wing margin; MP+CuA forming a pronounced curve, closely approaching MA and then directed posteriorly; infrapons present, aligned with the pons (distinctly longer in the hindwing than in the forewing); MP/CuA split located opposite the distopons; as a consequence of CuA being very short (without clear end-

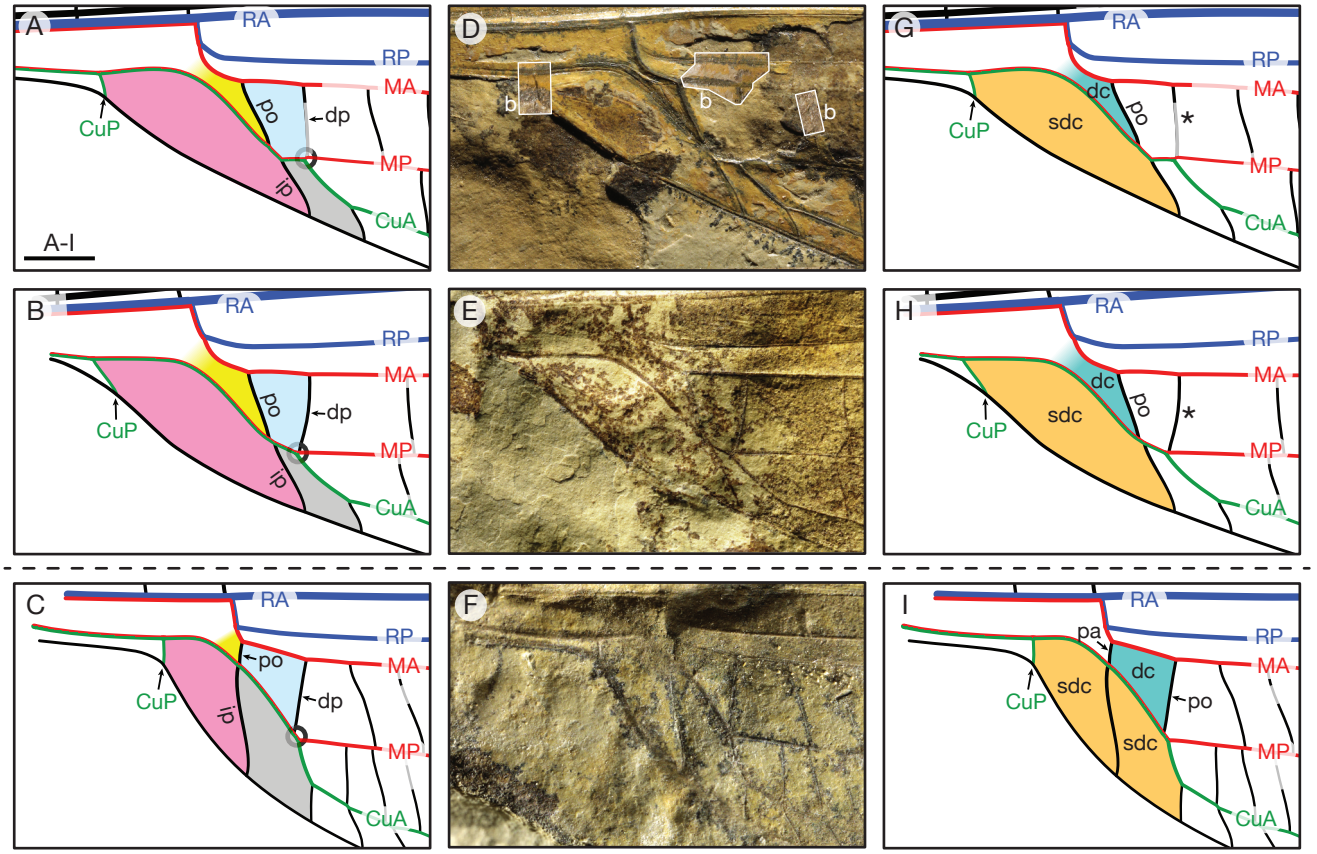


Fig. 4. — Wing venation of *Triassoneura andersoni* Riek, 1976, detail of the basal complex, with interpretation under the 4P proposal (**A**-**C**), photographs (**D**-**F**), and interpretation under the 1DC proposal (**G**-**I**): **A**, **D**, **G**, holotype specimen BP/2/21107 (**D**, '**a**' side with insets from '**b**' side, light-mirrored), location as shown on Figure 2A; **B**, **E**, **H**, specimen PRE/F/11872 (**E**, dry-eth composite), location as shown on Figure 2B; **C**, **F**, **I**, specimen BP/2/4808, location as shown on Figure 2C. Scale bar: 2 mm. Abbreviations: see Material and methods. Photographs: O. Béthoux; drawings: I. Deregnaucourt, O. Béthoux.

ing, but likely reaching the posterior wing margin near the level of the RP1+2/RP3+4 split), area between MP and CuA large, covering about 40% of the posterior wing margin, filled with numerous, slightly oblique, sub-parallel branches, mostly simple; and scalariform cross-veins between them; area between CuA and the posterior wing margin narrow, mostly with a single row of cross-veins; petiole more pronounced in hindwing than in forewing.

Specimen descriptions

Specimen BP/2/21107ab (Figs 2A; 3A; 4A, D, G)
Adpression preserving the basal half of a left forewing in both dorsal (side a) and ventral (side b) aspects; preserved length 33.8 mm, estimated total length about 56 mm, width opposite nodus (restored) 12.3 mm; distal portion of the area between MP and the posterior wing margin disrupted and slightly displaced; basal complex unevenly exposed, visible by combining both sides of the adpression.

Specimen PRE/F/11872 (Figs 2B; 3B; 4B, E, H)
Adpression preserving a sub-complete right forewing (postero-apical area missing) in both dorsal (side a) and ventral (side b) aspects; preserved length 50. 2 mm, estimated total length 56 mm, width opposite nodus 11.5 mm.

Specimen BP/2/4808 (Figs 2C; 3C; 4C, F, I)
Adpression preserving the basal half of a left hindwing in ventral aspect; preserved length 24.8 mm, estimated total length about 51 mm, estimated width opposite nodus 11.8 mm.

Specimen PRE/F/10450 (Figs 2D; 3D)
Adpression preserving a left wing lacking base and a large portion of the postero-apical area in both dorsal (side b) and ventral (side a) aspects; preserved length 38.3 mm, width opposite nodus 11.5 mm; first cross-vein in the RA-RP1+2 area (ASn?) aligned with the origin of Irp_2-rp_{3+4}.

Remarks

We submit that the set of the four specimens considered above are fore- and hindwing(s) of the same species. First, differences in size and general shape are very minor and compatible with variations observed in extant species (Bridges 1994; d'Aguilar & Dommanget 1998), which may be linked to multiple factors, such as seasonal variations and/or the importance of territoriality (Serrano-Meneses *et al.* 2008; Wong-Muñoz *et al.* 2011). Then, two distinct configurations of the basal complex can be distinguished (Fig. 4). The first one is exemplified in the specimens BP/2/21107 and PRE/F/11872 (Fig. 4A, B, D, E, G, H); and the second in the specimen BP/2/4808

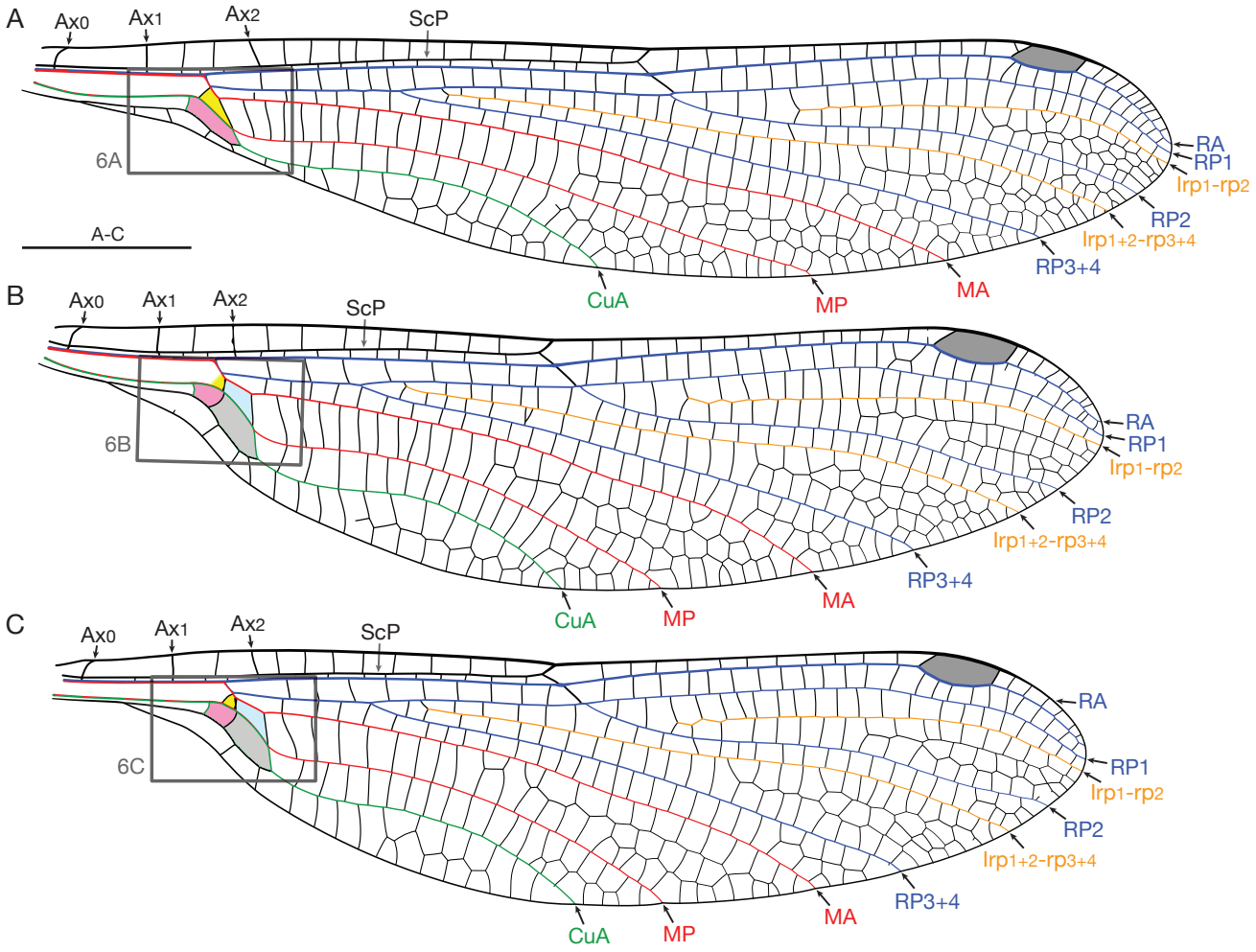


FIG. 5. — Wing venation of *Epiophlebia superstes* (Selys Longchamps, 1889), all female, drawings (as for the basal complex, under the 4P proposal): **A**, exemplar of forewing venation; **B**, **C**, exemplars of hindwing venation, with most common form (same side of the same individual as in **A**) (**B**) and rarer variant (**C**). Scale bar: 5 mm. Abbreviations: see Material and methods. Drawings: O. Béthoux.

(Fig. 4C, F, I). In the former, the pons and the infrapons are very oblique. As a consequence, the CuP-ip cell (in pink on Fig. 4) and the ip-CuA cell (in grey on Fig. 4) differ in size, the former being much larger. In the second configuration, the pons and the infrapons are almost perpendicular to the wing main axis, and the CuP-ip and the ip-CuA cells occupy a similar area. Another consequence of the orientation of the pons/infrapons line is that the pons and distopons are most distant in the second configuration. Such differences can be explained by a moderate differentiation of the fore- vs the hindwing. Indeed, in the Triassic stem-odonate *Italophelbia gervasutii* Whalley, 1986, differences in the configuration of the fore- and hindwing basal complexes are much more pronounced (see Bechly 1997). As for the specimen PRE/F/10450 (Figs 2D; 3D), the preserved parts do not allow the wing pair it belongs to to be assessed with certainty. Nevertheless, judging from its size, it is plausibly a hindwing. Regardless, it is doubtless that it belongs to *Triassoneura andersoni*.

Resolving the inner systematics of Triassolestidae and closely related taxa, including early Lobodonata, is not the primary aim of this study. The available data for these groups are too limited to support a robust analysis at this stage. Moreover, our data suggest that both wing pairs may be needed to improve the current situation. Notably, it is plausible that species currently assigned to the genus *Progonophlebia* Tillyard, 1925b may actually represent hindwings of Mesophlebiidae species otherwise known from forewings. Nevertheless, our new data support the view that the closest relative of *Triassoneura andersoni* may be *Triassolestodes epiophlebioides* Tillyard, 1918, known from a very incomplete forewing from the Triassic of Australia (see Nel *et al.* 2002).

COMPARATIVE ANALYSIS

As a preliminary clarification, the following discussion focuses exclusively on conamina composing the basal complex and on cells they delimit or border. The course of main veins is regarded settled, or at least as irrelevant to the present argument. Several species will be considered successively, according to consensual phylogenetic scheme, itself based on characters independent from the basal complex. Support for these rela-

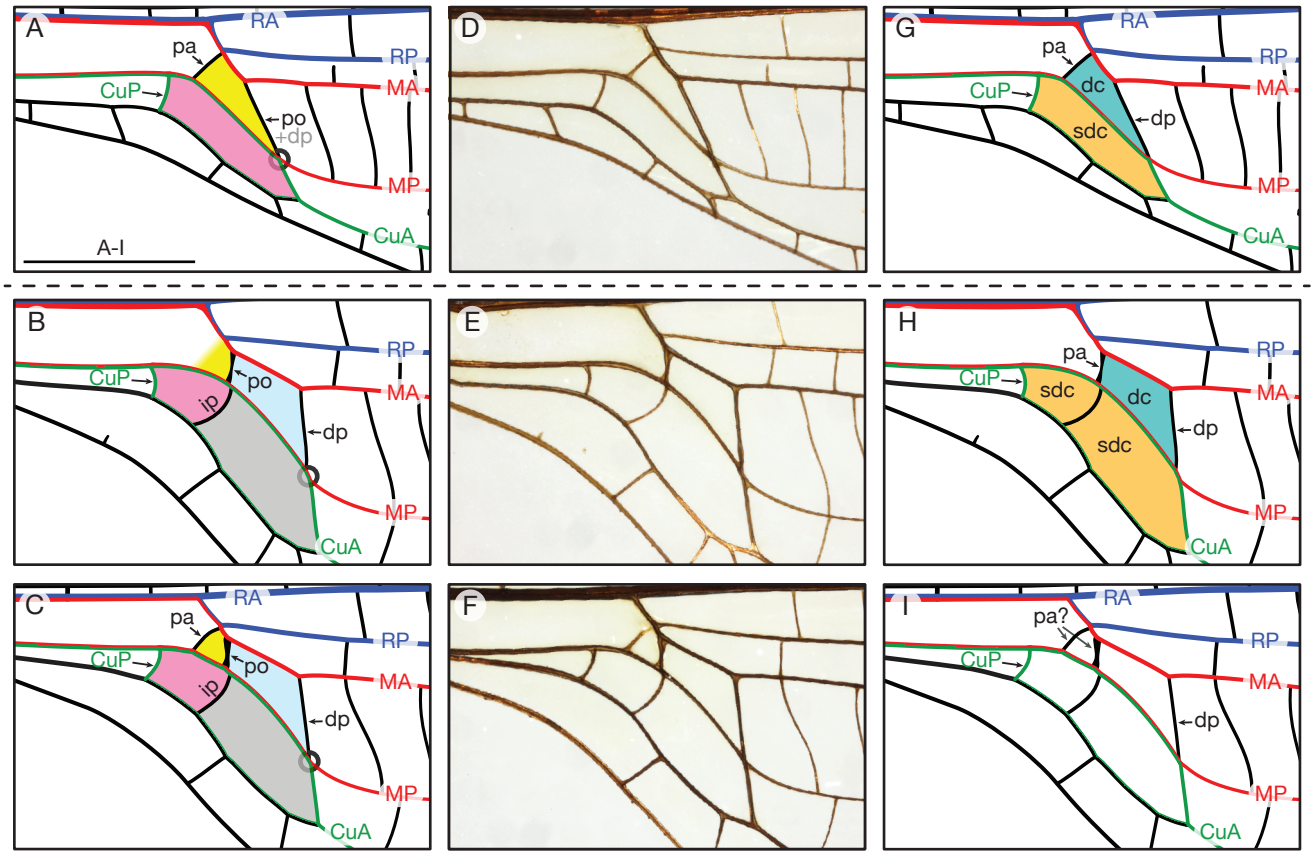


Fig. 6. — Wing venation of *Epiophlebia superstes* (Selys Longchamps, 1889), all female, detail of the basal complex, with interpretation under the 4P proposal (**A**-**C**), photographs (**D**-**F**), and interpretation under the 1DC proposal (**G**-**I**; tentative in **I**): **A**, **D**, **G**, exemplar of forewing venation, location as shown on Figure 5A; **B**, **E**, **H**, exemplar of the most common form of hindwing (same side of the same individual as in **A**), location as shown on Figure 5B; **C**, **F**, **I**, exemplar of variant form of hindwing, location as shown on Figure 5C. Scale bar: 2 mm. Abbreviations: see Material and methods. Photographs and drawings: O. Béthoux.

tionships will be introduced in the course of the reasoning. In the case of *Triassoneura andersoni*, the orientation of the RP+MA stem at its point of origin, nearly perpendicular to R+MA, indicates a closer relationship to crown-Odonata than to Archizygoptera or even Triadophlebiomorpha. In more distant relatives of crown-Odonata, this stem is very oblique, whereas in crown-Odonata it is consistently perpendicular to R+MA. Furthermore, regardless of the favoured SPHC, *Triassoneura andersoni* exhibits conamina that are absent in Archizygoptera but present in crown-Odonata (the distopons under the 4P proposal; and the parapons in the hindwing under the 1DC proposal). Conversely, it lacks a lobe (i.e., a developed area between AA/CuP+AA and the posterior wing margin; see Tierney *et al.* 2020). This absence places it outside crown-Odonata and more distantly related to it than any of the species considered subsequently.

The phylogenetic position of *Triassoneura andersoni* being established, a PHC alternative to that used in its redescription must first be considered (Fig. 4G-I). As will become clear, this alternative provides the necessary starting point for the 1DC proposal. Under the 1DC interpretation, the forewing of *Triassoneura andersoni* has an open discoidal cell and an unsplit sub-discoidal cell (Fig. 4G, H). In the hindwing (Fig. 4I), the observed configuration is best explained by a closed discoidal cell (i.e., the parapons is present) and by a split sub-discoidal cell. This PHC implies a stronger differentiation between fore- and hindwing than does the 4P proposal (Fig. 4A-C). Indeed, under the latter, both wing pairs share a common conamen, the distopons, which connects MA and MP+CuA at the point where the latter splits into MP and CuA (dark circle on Fig. 4A-C). In contrast, under the 1DC proposal, the corresponding structure is an unnamed conamen in the forewing (* on Fig. 4G,H) but the pons in the hindwing (Fig. 4I). Moreover, under the 4P proposal, wings of both pairs share the exact same set of conamina (namely, pons, distopons and infrapons), the only difference lying in their relative positions (with po and ip closer to the RP/MA split in the hindwing).

The next species to consider is *Epiophlebia superstes* (Figs 5; 6). Its wing morphology has long attracted attention (Fraser 1938; Asahina 1954; Nel *et al.* 1993; among others). Although it possesses a petiole (Fig. 5), a feature reminiscent of Zygoptera, the species belongs to a species-poor lineage more closely related to Anisoptera than to Zygoptera (Kim *et al.* 2014; Bybee *et al.* 2021; Kohli *et al.* 2021; Suvorov *et al.* 2022; among others). Huang *et al.* (2025) instead recovered it as sister to a clade comprising of Zygoptera and Anisoptera, but this alternative placement does not affect the present discussion.

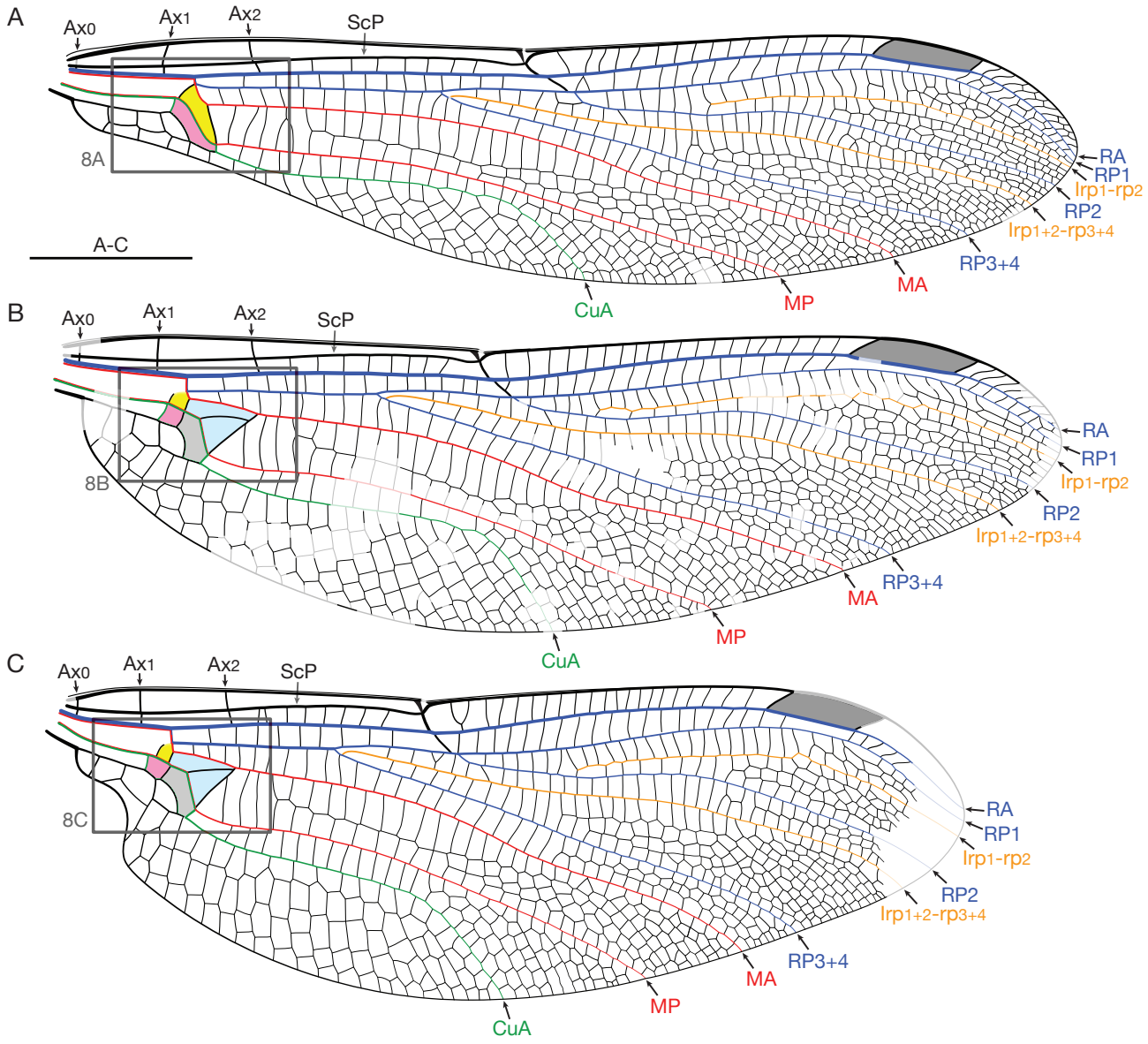


Fig. 7. — Wing venation of *Heterophlebia buckmani* (Brodie, 1849), interpretative drawings (as for the basal complex, under the 4P proposal): **A**, specimen MNHN.F.A57606, right forewing, presumably male; **B**, specimen MNHN.F.A57603, left hindwing, female; **C**, specimen MNHN.F.A57600, left hindwing, male. Scale bar: 5 mm. Abbreviations: see Material and methods. Drawings: N. Yang, O. Béthoux.

Regardless of the favoured SPHC, the basal complex differs markedly between fore- (Fig. 6A, D, G) and hindwing (Fig. 6B, E, H) in this species; and the hindwing occasionally exhibits an atypical configuration (Fig. 6C, F, I). Under the 4P proposal (Fig. 6A-C), the hindwing basal complex (Fig. 6B) closely resembles that of *Triassoneura andersoni* (Fig. 4C). The same set of conamina can be identified, including the distopons connecting MP+CuA at the point where this stem splits into MP and CuA (dark circle on Fig. 6B). The main difference concerns the orientation and length of the infrapons and, concurrently, the shape of the ip-CuA cell. It must be emphasized that the pons is particularly robust, with a dorsal reinforcement (Fig. 6E), and connects MA not at the point where it diverges from RP+MA but slight distal to it.

The forewing basal complex (Fig. 6A) is more challenging to interpret in comparison with that of *Triassoneura andersoni* (Fig. 4A). A prominent oblique structure connected to MA some distance from its origin is best interpreted as the pons, given its position, orientation, and strength. The more basal conamen in the same area can then be identified as the parapons. It links two particular points, namely 1) the divergence of RP-MA; and 2) the point of maximum curvature of MP+CuA. These points lie very close together in the forewing of *Triassoneura andersoni* (Fig. 4A), and appear to have been subject to mechanical stress, as suggested by creases visible in the specimen BP/2/21107 (Fig. 4D). It is therefore plausible that selection favoured the acquisition of a reinforcing conamen in this position. The key, remaining question concerns

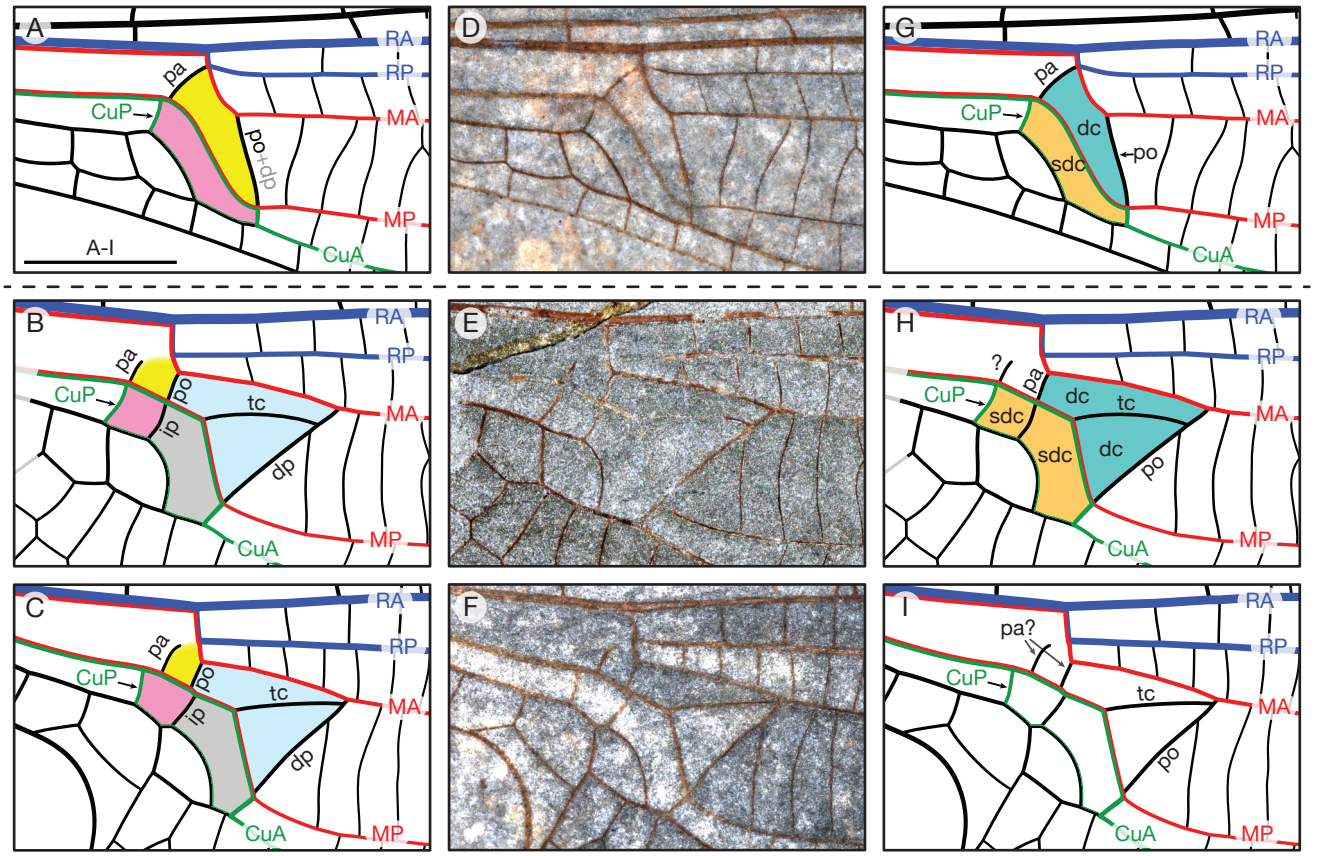


Fig. 8. — Wing venation of *Heterophlebia buckmani* (Brodie, 1849), detail of the basal complex, with interpretation under the 4P proposal (**A**-**C**), photographs (**D**-**F**; all under ethanol, rwb, and crossed polarized light), and interpretation under the 1DC proposal (**G**-**I**; tentative in **I**): **A**, **D**, **G**, specimen MNHN.F.A57606, right forewing, presumably male (**D**, sides composite), location as shown on Figure 7A; **B**, **E**, **H**, specimen MNHN.F.A57603, left hindwing, location as shown on Figure 7B; **C**, **F**, **I**, specimen MNHN.F.A57600, left hindwing (**F**, sides composite), location as shown on Figure 7C. Scale bar: 2 mm. Abbreviations: see Material and methods. Photographs: O. Béthoux; drawings: N. Yang, O. Béthoux.

the fate of the distopons and of the ip-CuA cell. Since the identified pons is connected to MP+CuA at the point where this stem splits into MP and CuA (dark circle on Fig. 6B), a position occupied by the distopons in both wing pairs of *Triassoneura andersoni*, we submit that a basal shift of the MP+CuA splitting point led the distopons to either vanish or fuse with the pons. As a consequence of the same shift, CuA may have approached the infrapons, which may have ultimately vanished or fused with CuA, resulting in the collapse of the ip-CuA cell. Under this PHC, the fore- and hindwing of *Epiophlebia superstes* differ substantially from one another.

At the first glance, the 1DC proposal offers a more straightforward solution. The mere addition of the parapons to the forewing of *Triassoneura andersoni* (Fig. 4G) results in a configuration consistent with that of *Epiophlebia superstes* (Fig. 6G); while the hindwing basal complexes of both species are very similar. That homonomous parapontes are present in both fore- and hindwing (Fig. 6G, H) is a key point of this proposal. However, the rare configuration some hindwings display (Fig. 6C, F, I), involving two conamina basal to the pons, contradicts this conjecture. Such variation, in a critical area of the wing, is rare among extant Odonata and, as a result, has already been considered by previous authors (see below). The conamen nearest to the pons shares the particular strength and position of the putative hindwing parapons (Fig. 6E, H); while the other shares the position of the putative forewing parapons (Fig. 6D, G). It follows that structures identified as homonomous parapontes in the fore- and the hindwing co-occur in such hindwing and therefore fail the conjunction test. This case is particular in that the two structures supposedly homologous (here, homonomous) are not present in separate organisms, as in the classical 'arm vs wing angel case', but in separate, serially homonomous structures. Fraser (1938, 1957) addressed this case by considering the rare hindwing configuration as the premise of the anisopteran condition, with the conamen closer to the pons identified as the triangle conamen. However, this interpretation does not hold, for, as we reiterate, the two co-occurring 'parapontes' clearly share traits particular to the 'forewing parapons' for the more basal, and to the 'hindwing parapons' for the more distal (and see the following case). In contrast, under the 4P proposal the co-occurring conamina are not considered homonomous (Fig. 6C): they are the forewing parapons (Fig. 6A) and the hindwing pons (Fig. 6B). It is then conceivable that they could co-occur, but it entails that the rare hindwing experienced a slight 'anteriorization'.

The next species to consider is the Early Jurassic *Heterophlebia buckmani* (Figs 7; 8), whose wing morphology is well documented (Tillyard 1925b; Nel *et al.* 1993; Jouault

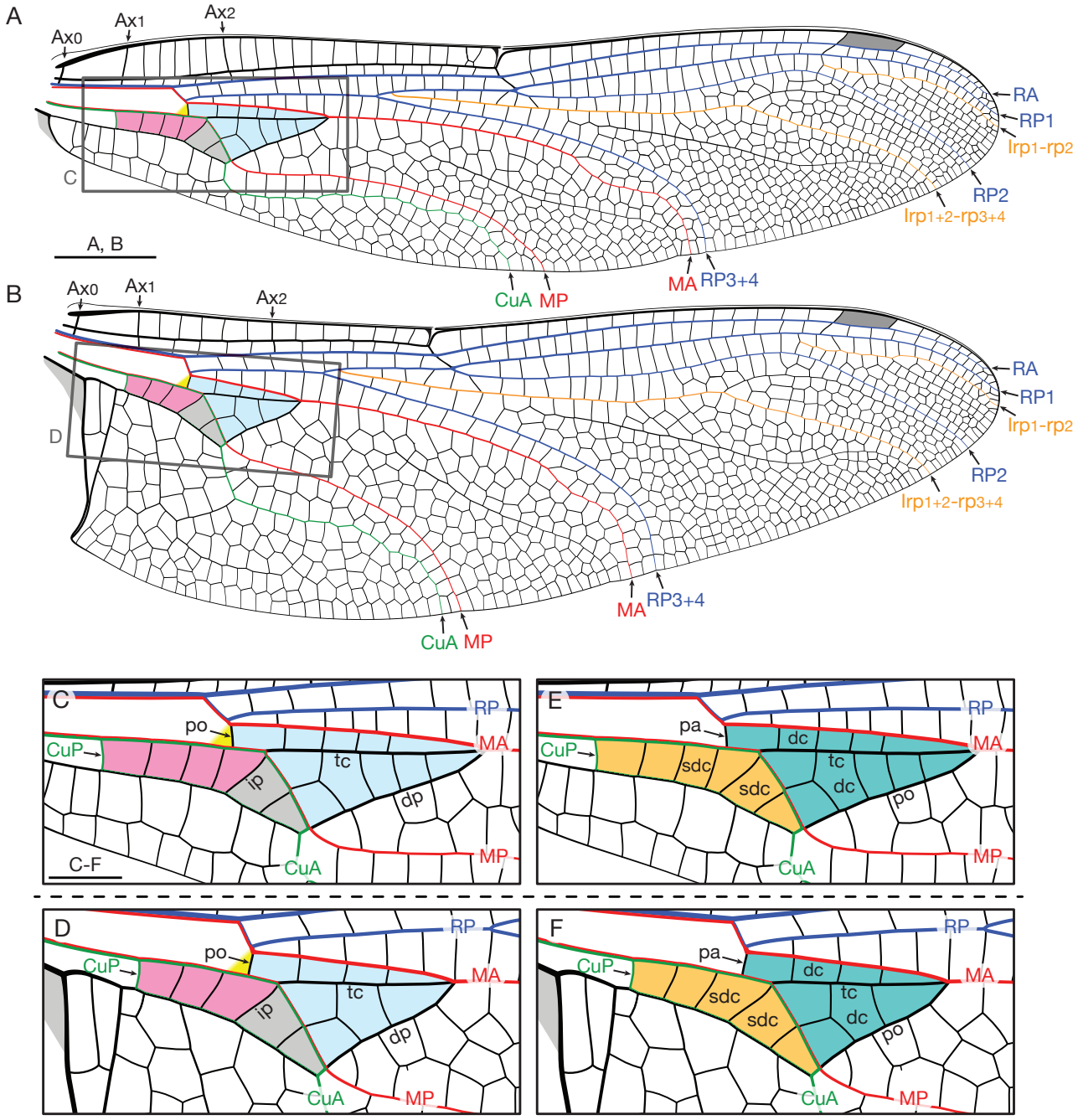


Fig. 9. — Wing venation of *Aeshna cyanea* (Müller, 1764), male: **A**, **B**, interpretative drawings (as for the basal complex, under the 4P proposal) of exemplar forewing (**A**) and hindwing (**B**); **C**-**F**, detail of the basal complex, with interpretation under the 4P proposal (**C**, **D**) and under the 1DC proposal (**E**, **F**) for forewing (**C**, **E**; location as shown on **A**) and hindwing (**D**, **F**; location as shown on **B**). Scale bars: A, B, 5 mm; C-F, 2 mm. Abbreviations: see Material and methods. Drawings: O. Béthoux.

et al. 2022). The hindwing specimens selected here are relevant to the present discussion, though not necessarily representative of the species' most common morphology. Regardless of the favoured SPHC, the forewing basal complex does not differ substantially from that of *Epiophlebia superstes* (under the 4P proposal, compare Figs 6A and 8A; under the 1DC proposal, compare Figs 6G and 8G). The principal difference lies in the presence of the triangle conamen in the hindwing, in both female (Figs 7B; 8B, E, H) and male (Figs 7C; 8C, F, I). It splits the po-dp cell under the 4P proposal (Fig. 8B, C) and the discoidal cell under the 1DC proposal (Fig. 8H; cell not color-coded on Fig. 8I). Its presence has long been taken as evidence that *Heterophlebia buckmani* is a stem-Anisoptera (Tillyard 1925b; Nel *et al.* 1993; Bechly 1996).

At this stage, the rare occurrence in the hindwing of an incomplete conamen basal to the pons (4P proposal) or parapons (1DC proposal) deserves attention (Fig. 8B, C, E,

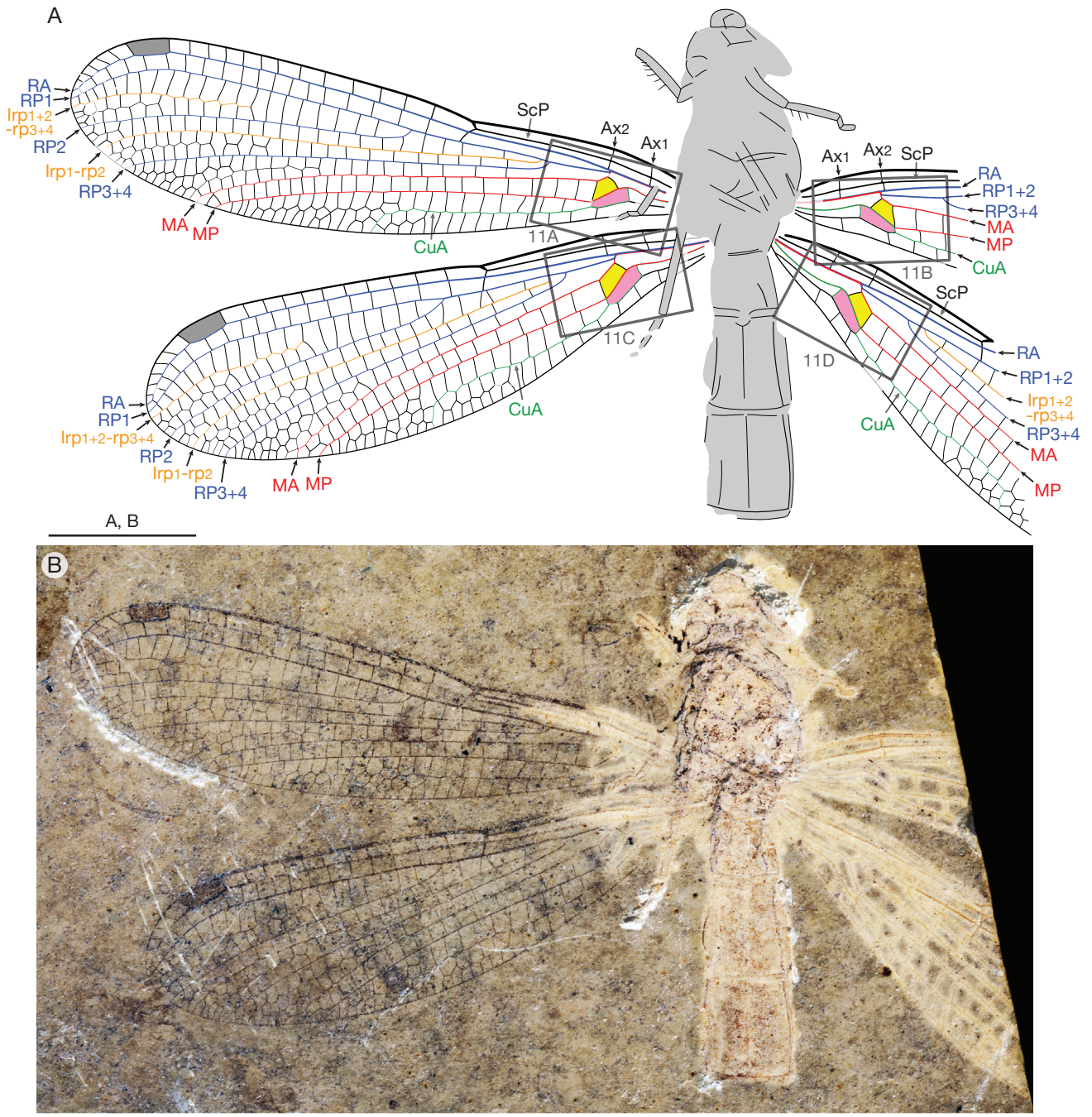


FIG. 10. — Habitus of *Congqingia rhora* Zhang, 1992, holotype specimen GPIT-PV-78012 (side as if viewed dorsally): **A**, interpretative drawing; **B**, photograph (composite of low angle of incidence light photograph and of zenithal light and cross-polarized light photograph). Scale bar: 5 mm. Abbreviations: see Material and methods. Photograph and drawing: O. Béthoux.

F, H, I). This configuration as already been reported previously (Nel *et al.* 1993). Under the 4P hypothesis (Fig. 8B,C) this structure is interpreted as a vestigial forewing parapons. By contrast, the 1DC proposal offers no satisfactory explanation: the structure must either be regarded as a vestige of uncertain nature (? on Fig. 8H) or imply that the parapontes of fore- and hindwing are not homonomous (Fig. 8I). It must be recalled that Fraser (1938, 1957) interpreted the rare hindwing configuration of *Epiophlebia superstes* as the early stage in the origin of the triangle conamen, involving three conamina in total (two closing the discoidal cell and one splitting it). However, in addition to counterarguments mentioned above, the unequivocal triangle conamen occurring in *Heterophlebia buckmani* in addition to these three conamina makes such an interpretation untenable. Finally, it must be emphasized that hindwings of both *Epiophlebia superstes* and of *Heterophlebia buckmani* display an essentially identical rare configuration. This indicates that it is not a mere, accidental 'anomaly' but a phenotype likely arising from a recurring underlying process.

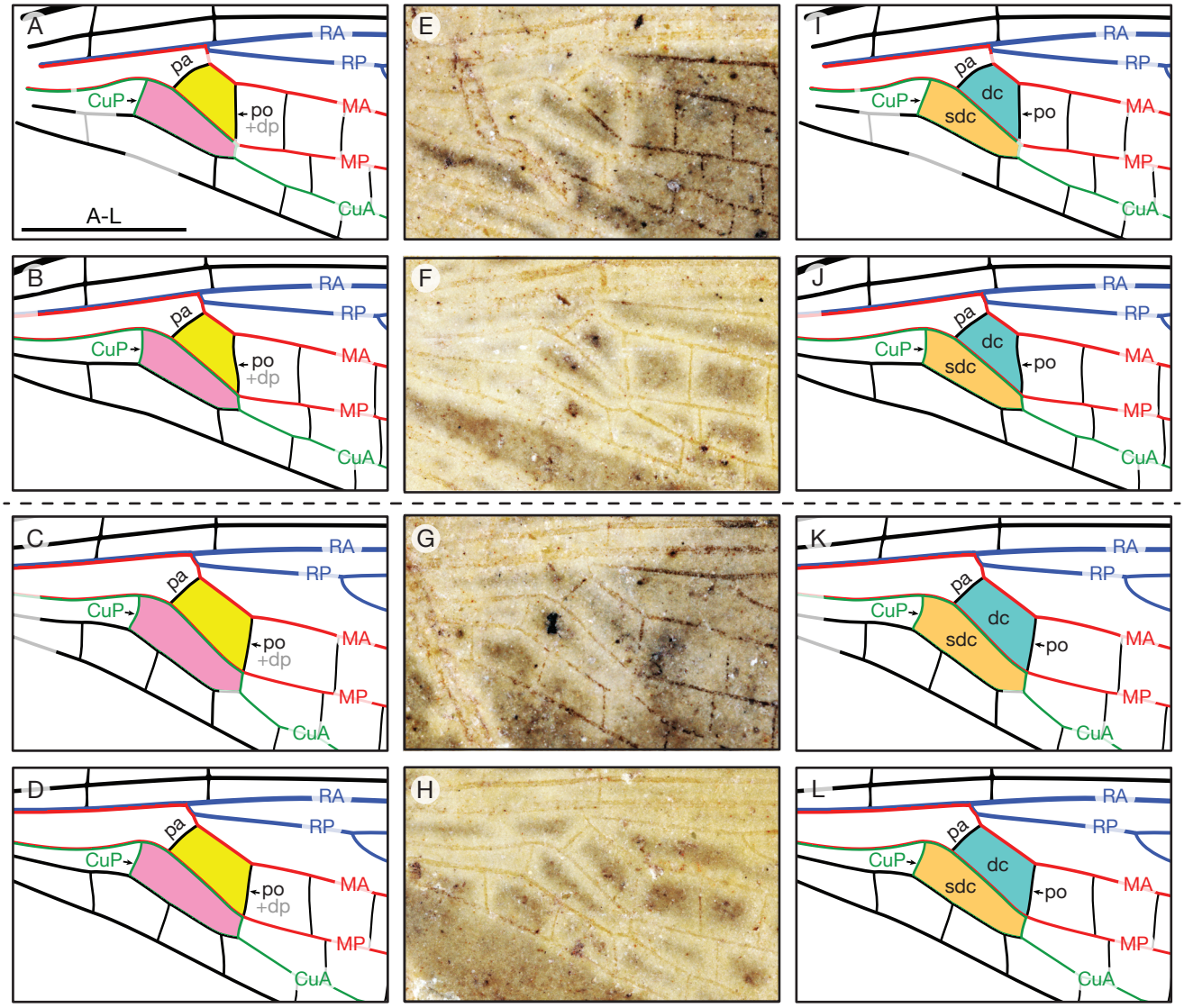


FIG. 11. — Wing venation of *Congqingia rhora* Zhang, 1992, detail of the basal complex in the holotype specimen GPIT-PV-78012, with interpretation under the 4P proposal (**A**-**D**), photographs (**E**-**H**; all with zenithal light and crossed-polarized light), and interpretation under the 1DC proposal (**I**-**L**), locations as shown on Figure 10A: **A**, **E**, **I**, left forewing (photograph flipped horizontally); **B**, **F**, **J**, right forewing; **C**, **G**, **K**, left hindwing (photograph flipped horizontally); **D**, **H**, **L**, right hindwing. Scale bar: 2 mm. Abbreviations: see Material and methods. Photographs and drawings: O. Béthoux.

Crown-Anisoptera can be represented by *Aeshna cyanea* (Fig. 9). Under either proposal, one must assume that the triangle conamen, present only in the hindwing of *Heterophlebia buckmani* (Figs 7; 8), was subsequently acquired in the forewing. Tillyard (1928: 171), based on his 1925b account, had already noted a "strong tendency for the development of the hindwing to outrun that of the fore" in *Heterophlebia buckmani* and its other fossil relatives. The apparent introgression also concerns the particular orientation of the distopons/pons (4P/1DC proposals), and the splitting of the sub-discoidal cell / the presence of the infrapons (4P/1DC proposals). No intermediate conditions are known. The simplest interpretation is that the forewing configuration was entirely replaced by that of the hindwing. This process may be provisionally called 'posteriorization'.

With these cases in mind, the condition in Zygoptera can be examined. The Lower Cretaceous species *Congqingia rhora* (Figs 10; 11) is particularly informative. As emphasized in the original description, it combines an 'anisozygopteran' body shape with a Zygoptera-like wing venation, and has been regarded as a stem-Zygoptera (Archibald *et al.* 2021). In this species, fore- and hindwing are nearly identical (Fig. 10), differing only slightly in the proportions of elements composing the basal complex (Fig. 11). Among patterns surveyed previously, both wing pairs closely resemble the forewing of *Epiophlebia superstes* (Fig. 6A, D, G). While this can be expected for the forewing of *Congqingia rhora*, it is less so in the hindwing. Explaining this pattern through a series of independent transformations is possible under both the 4P and 1DC proposals but is somewhat cumber-

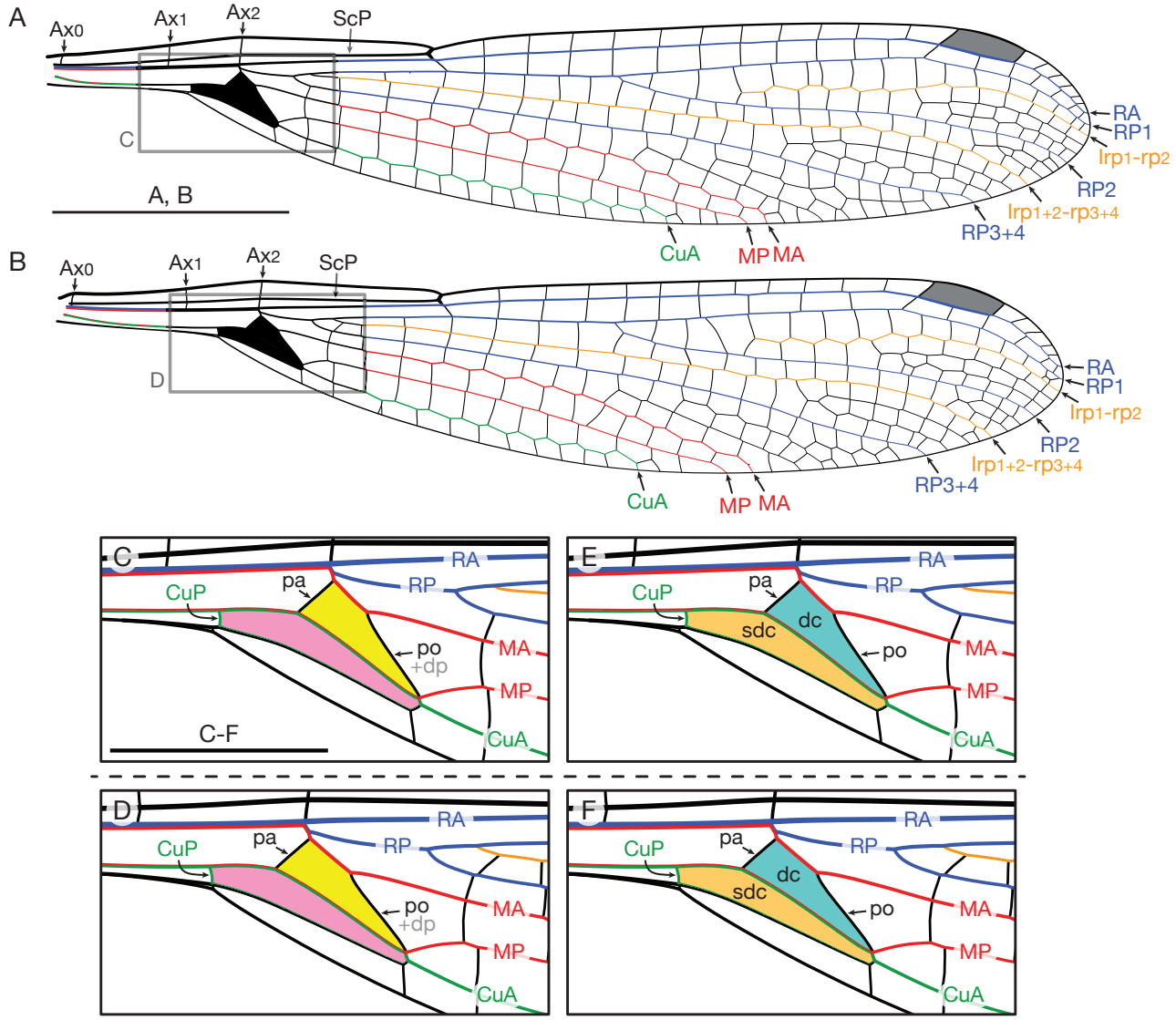


Fig. 12. — Wing venation of *Chalcolestes viridis* (Van der Linden, 1825), female: **A**, **B**, interpretative drawings (as for the basal complex, under the 4P proposal) of exemplar forewing (**A**) and hindwing (**B**); **C**-**F**, detail of the basal complex, with interpretation under the 4P proposal (**C**, **D**) and under the 1DC proposal (**E**, **F**) for forewing (**C**, **E**; location as shown on **A**) and hindwing (**D**, **F**; location as shown on **B**). Scale bars: A, B, 5 mm; C-F, 2 mm. Abbreviations: see Material and methods. Drawings: O. Béthoux.

some. Basically, in a way or another, the configuration of the basal complex must have become correlated with that of the forewing. Under the 1DC model, for example, the conamen splitting the sub-discoidal cell must have been lost, and the shape of the discoidal cell must have been altered. A simpler interpretation is that the hindwing underwent an 'anteriorization'. If we assume so for both proposals, then *Conggingia rhora* does not decisively favour either the 4P or the 1DC proposal.

Finally, for a broader perspective, the wing venation of the crown-Zygoptera *Chalcolestes viridis* is considered (Fig. 12). Under either proposal, the basal complex (Fig. 12C-F) does not differ substantially from that of *Conggingia rhora* (Fig. 11); or, more adequately, the degree of difference is comparable under both proposals.

DISCUSSION

Morphological interpretations under the 4P and 1DC proposals are summarized and contrasted on Figure 13. This compilation shows to which extent they differ, in particular regarding extant Anisoptera and Zygoptera. Also, as noted above for *Triassoneura andersoni*, assuming, 1) in the forewing, an open discoidal; and 2) in the hind wing, a closed discoidal cell and a split sub-discoidal cell, is consistent with the 1DC hypothesis. On the basis of Figure 13 and the preceding analysis, the respective merits of the two proposals can be assessed.

An advantage of the 4P proposal is that it requires fewer differences between the fore- and hindwing of *Triassoneura andersoni*. This point becomes particularly relevant if one considers the possibility that Odonata might have become

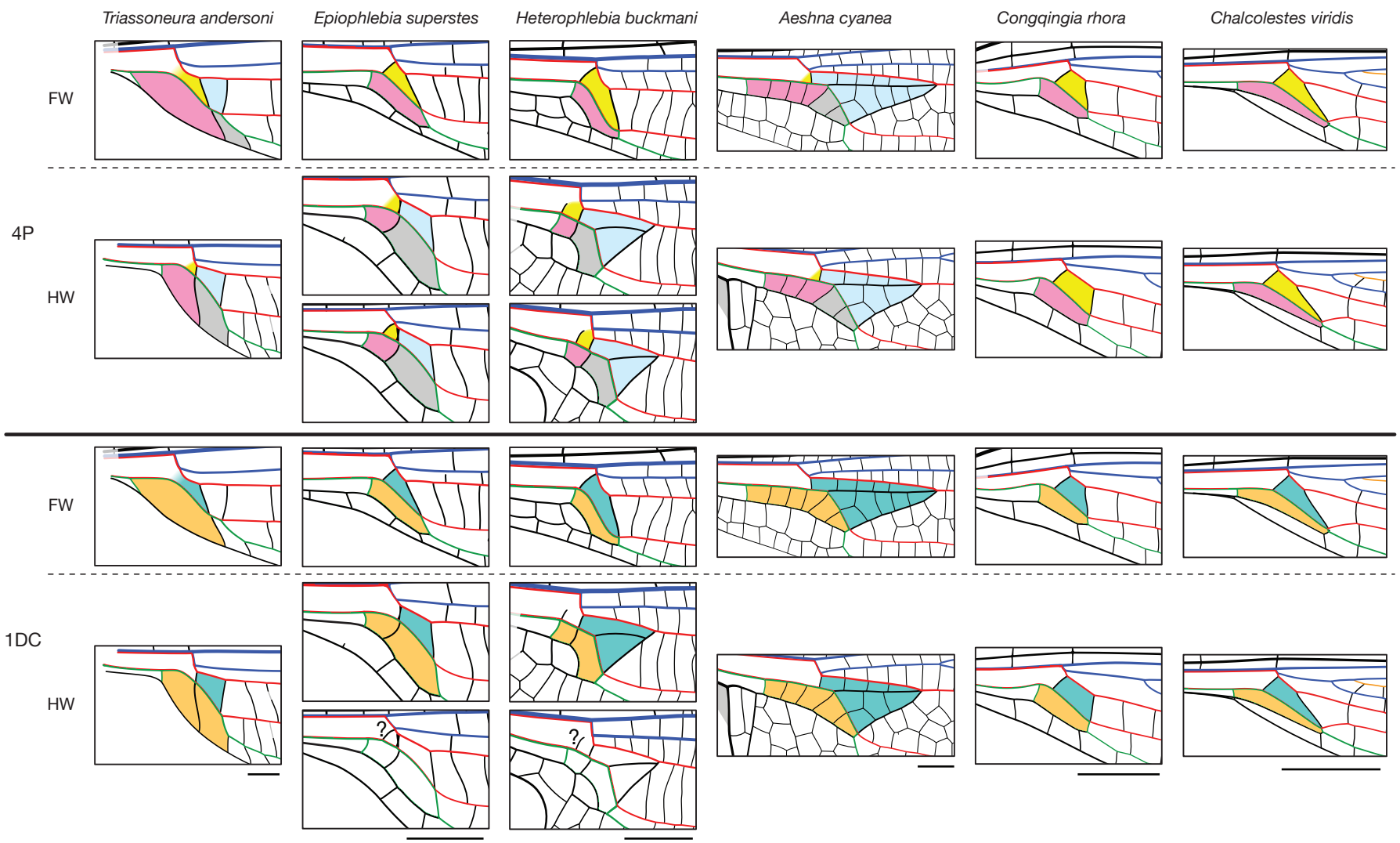


Fig. 13. — Compilation of details of the basal complex (*Triassoneura andersoni* Riek, 1976, *Epiophlebia superstes* (Selys Longchamps, 1889), *Heterophlebia buckmani* (Brodie, 1849), *Aeshna cyanea* (Müller, 1764), *Congqingia rhora* Zhang, 1992; *Chalcolestes viridis* Van der Linden, 1825) under the 4P and 1DC proposal (*Triassoneura andersoni* Riek, 1976, specimen BP/2/21107 omitted; *Congqingia rhora* Zhang, 1992, left wings omitted). Scale bars (applicable to a column): 2 mm. Drawings: as indicated previously.

extinct at that stage. Under such scenario, the morphology of younger taxa becomes irrelevant. In other words, that the 4P proposal may need to advocate modifications possibly unparsimonious to explain the morphology of younger taxa can be seen as a subordinate step. This new perspective has general implications for the elaboration of sets of PHCs. Rather than attempting to encompass a large set of morphological patterns and elaborate individual PHCs that, collectively, minimize the amount of transformation necessary to explain them (Key 1967; Béthoux 2012, 2020), their respective temporal occurrence may be relied on to select a point to start from, and to then engage in a stepwise process. Much like the choice of an outgroup under a formal cladistic analysis, the choice of this starting point, here *Triassoneura andersoni*, can strongly influence the outcome. Here, it was the previously unknown morphology of the hindwing basal complex in this species that prompted the development of an alternative set of PHCs. Notably, other fossil discoveries that significantly reshaped wing venation PHCs in Odonata, such as the Carboniferous Geroptera (Riek & Kukalová-Peck 1984; and see Béthoux *et al.* 2021) and the Triassic *Moltenagrion koningskroonensis* Deregnaucourt *et al.* 2021b (see original description), were also positioned near the base of a sequence leading to younger taxa. Together, these cases suggest that SPHCs may be effectively developed by considering the temporal succession as documented in the fossil record, while provisionally setting aside the youngest taxa during the initial phases of comparative analysis. The new criterion of 'consistency with temporal occurrence' may conflict with other criteria classically identified to elaborate SPHCs, namely similarity in position, special or intrinsic similarity, and continuity of forms, just as these criteria may conflict with each other. Objective ways to disentangle such cases are yet to be developed.

Returning to our more specific case, the 1DC proposal further failed to account for the rare occurrence of supernumerary conamina in hindwings of both *Epiophlebia superstes* and *Heterophlebia buckmani*. The 4P proposal accommodates this condition by assuming a slight anteriorization of the hindwing; in other words, that the forewing morphology somehow 'introgressed' into that of the hindwing. The 4P proposal further predicts, in Anisoptera, the basal complex of both wing pairs is derived from that of a hindwing essentially similar to that of *Epiophlebia superstes*; whereas in Zygoptera the basal complex of both wing pairs is derived from that of a forewing essentially similar to that of *Epiophlebia superstes.* In each lineage, therefore, the basal complex of one wing pair is inferred to have overtaken that of the other. Before proceeding further, it must be emphasized that the 1DC proposal also needs to advocate an 'influence' of the hindwing over the forewing to explain the morphology of the forewing basal complex in *Aeschna cyanea*.

It will now be submitted that the rampant occurrence of more or less drastic morphological introgression among wing pairs is adequately explained by a model positing two paralogous modules controlling the configuration of the basal complex, hereafter 'α' and 'β', initially activated in the fore- and hindwing, respectively, but retaining the capacity to be activated in either wing pair. Developmental modularity is pervasive across organisms, and insect wing morphology is no exception. For example, the inhibition of the Hox gene *Ultrabithorax* converts the metathoracic wing (hindwing) into a forewing in neopteran insects (Tomoyasu *et al.* 2005; Pavlopoulos & Akam 2011; Medved *et al.* 2015; among others). At the macroscopic level, the dissociation between wing identity and segmental position indicates modular organization. A more specific case is the loss of the complex male stridulatory apparatus in the forewing of the field cricket *Teleogryllus oceanicus* (Le Guillou, 1841). At least in one feminized male phenotype, this transformation is controlled by a single master switch (Tinghitella 2008; and see Bailey *et al.* 2024). Similarly, male feminization affecting sexually dimorphic wing colour patterns provides further evidence of modular control (Béthoux 2010). It must nevertheless be acknowledged that these cases are best explained by the interaction of a default program with a modifier, producing consistent unidirectional transitions from one state to another. By contrast, the present case requires a model permitting bidirectional transformations (both posteriorization and anteriorization). This requirement motivates the hypothesis of two paralogous modules, rather than a single module subject to optional modification.

To clarify the argument, two hierarchised aspects will be considered separately. They are the divergence and evolution of modules (Fig. 14A) and their activation in each wing pair (Fig. 14B). These components can be combined eventually (Fig. 14C). Module evolution can be conceptualized as a hierarchy where an ancestral module splits into paralogues that subsequently diverge while persisting in the same taxa (Fig. 14A). A premise to our model is the acquisition of a primary module specific to the basal complex. Such acquisition plausibly coincided with that of the pons, the first conamen to be part of the basal complex and present in Triadophlebiomorpha, Archizygoptera and all taxa considered here. In Triadophlebiomorpha and Archizygoptera, fore- and hindwings show no evident differences in basal complex morphology (Pritykina 1981; Nel *et al.* 2009, 2012; Li *et al.* 2013; Felker 2023; Béthoux & Anderson 2023). By contrast, *Triassoneura andersoni*, *Epiophlebia superstes* and *Heterophlebia buckmani* exhibit varying degrees of differentiation between wing pairs. This pattern suggests that module duplication most likely occurred in a hypothetical common ancestor of the latter taxa, although an earlier duplication with initially inconspicuous phenotypic effects cannot be excluded.

According to our model, divergence between modules remained moderate in *Triassoneura andersoni*. It mostly involves the position of po and dp, located more basally in module β (as observed in the hindwing) than in module α (as observed in the forewing). Because of a lack of data on close relatives of this species, it cannot be determined whether one of these modules displays a plesiomorphic condition (i.e., present in the hypothetical primary module) or whether both are derived. Yet, po is very oblique in Triadophlebiomorpha and Archizygoptera (with some exceptions), a condition shared with module α, which may therefore approximate the ancestral state. This uncertainty is represented in Figure 14A by mapping both character states along the stems of the respective modules.

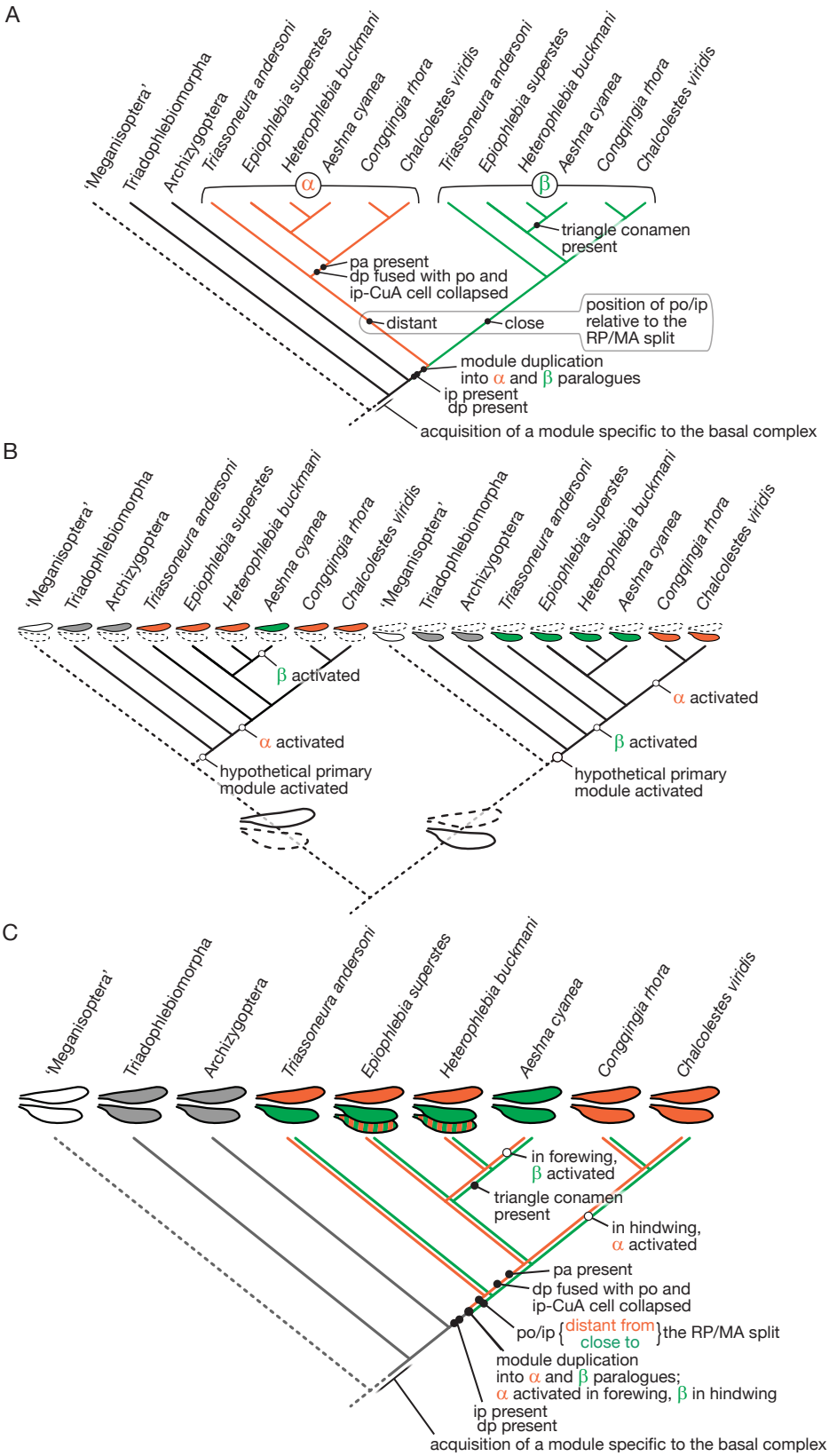


FIG. 14. — Acquisition of character states under the 4P proposal assuming a model involving two paralogous developmental modules (α, β) controlling the configuration of the basal complex, equally activatable in fore- or hindwing (wing color-coding indicative of the basal complex condition only, as opposed to the entire wing; dashed branches, module presumed absent): **A**, postulates on module divergence and morphological evolution (the root represents the absence of module specific to the basal complex); **B**, postulates on module activation in fore- and hindwing (the root represents a wing undifferentiated into a fore- or a hindwing); **C**, combination of postulates on modules evolution and activation (wing hatched in **orange** and **green**, occasional co-activation of α and β). Abbreviations: see Material and methods. Illustration: O. Béthoux, V. Rineau.

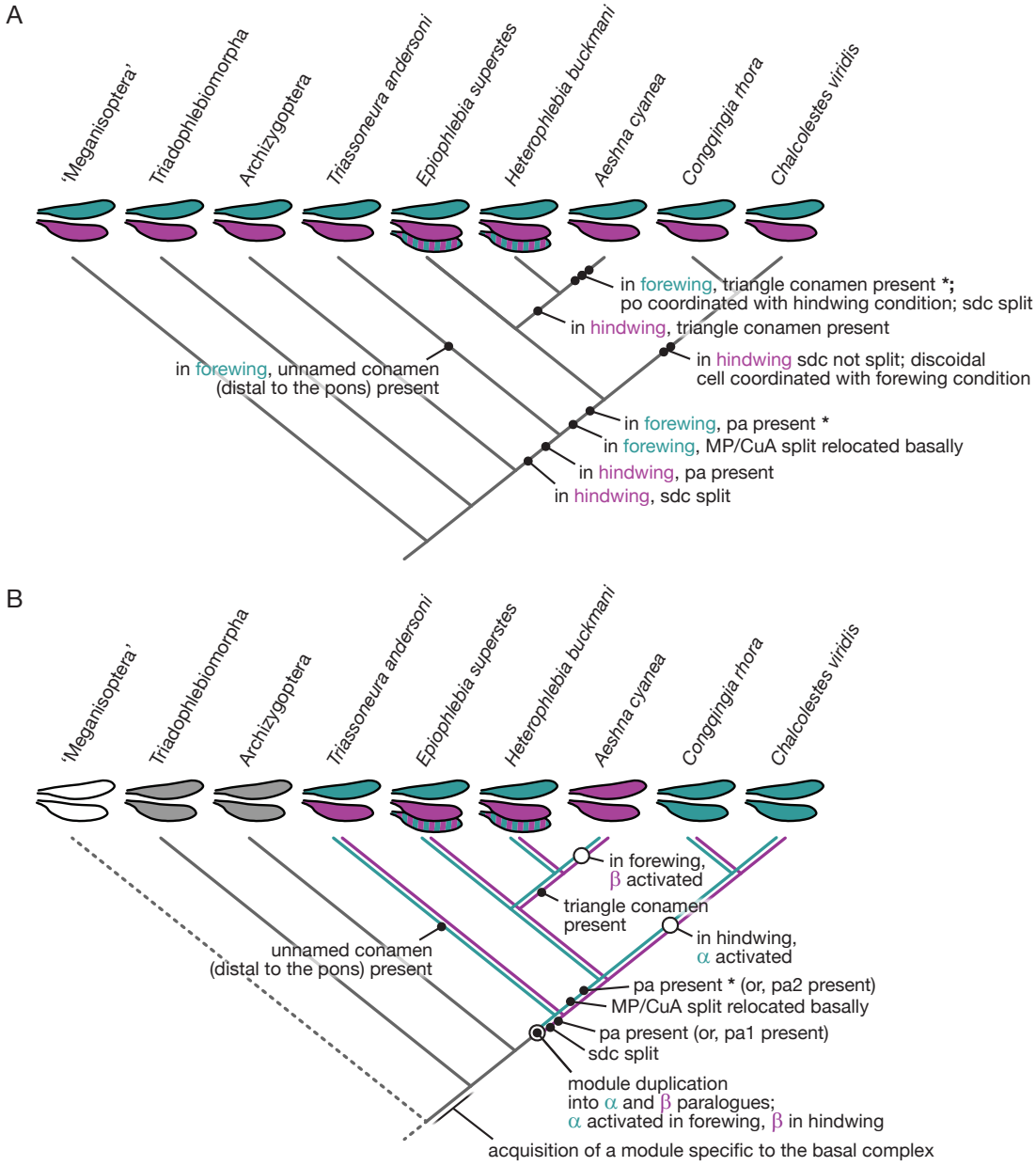


FIG. 15. — Acquisition of character states under the 1DC proposal (wing color-coding indicative of the basal complex condition only, as opposed to the entire wing): **A**, traditional scenario, involving independent transformations (i.e. anteriorization or posteriorization not involving modular organization; * indicates a character state acquired in forewing but previously acquired in hindwing); **B**, hybrid scenario assuming a modular organization similar to that considered for the 4P proposal (* indicates a character state acquired in module α but previously acquired in the module β; **pa1** and **pa2** account for pa structures not homologous between fore- and hindwing; **dashed branch**, module presumed absent). Abbreviations: see Material and methods. Illustration: O. Béthoux, V. Rineau.

Prominent morphological changes noticed when comparing the forewings of *Triassoneura andersoni* and *Epiophlebia superstes* are 1) the gain of pa; and 2) the concurrent loss of dp (presumably fused with po) and of the ip-CuA cell. It is postulated that these changes belong to module α. Another important change is the gain of the triangle conamen, in the hindwing, noticed at the *Epiophlebia superstes* – *Heterophlebia buckmani* transition, and present in *Aeshna cyanea*. The corresponding character state is presumptively assigned to module β.

Module activation can likewise be conceptualized hierarchically, with fore- and hindwing evolving separately within the same taxa (Fig. 14B). As mentioned above, the model assumes that, ancestrally, module α was activated in the forewing and module β in the hindwing. The marked 'posterization' inferred for the forewing of *Aeshna cynaea* commands to postulate that the module β is activated instead of module α; while the marked 'anteriorization' inferred for the hindwings of *Congqingia rhora* and *Chalcolestes viridis* brings the postulate that the module α is activated, instead of module β.

When combined (Fig. 14C) these postulates closely match the 'anteriorization' and 'posteriorization' events identified above. The model allows for the possibility that, during early

stages of module differentiation, occasional co-activation of α and β within a single wing pair may have occurred, producing limited morphological intermingling. It can therefore account for the rare hindwing configuration observed in *Epiophlebia superstes* (Fig. 5C) and *Heterophlebia buckmani* (Fig. 8B, C), in which a vestigial to complete parapons, a feature diagnostic of module α, appears in an otherwise β-controlled hindwing (cases indicated by orange-hatched green hindwing on Fig. 14C). Both species are comparatively well sampled and exhibit heteropterous module activation, making them well-suited for identifying co-activation. Such event may in fact be more frequent than documented herein. Notably, activation of module β in an otherwise α-controlled wing may remain morphologically inconspicuous, because typical traits of module α (notably the the po-dp and ip-CuA cells) were lost early in the evolution of that module.

Whether α and β can be regarded as genuine modules can be addressed by considering several qualifying criteria. Under the proposed scenario, elements constituting each module display strong internal integration: except perhaps in *Triassoneura andersoni*, instantiations of α are more similar to one another than to any instantiation of β, and vice versa. Integration is therefore greater within than between modules, satisfying the minimal definition of morphological module (Eble 2005). In addition to integration, relative autonomy is a key criterion of developmental modularity (Schlosser 2004). Geometric morphometrics by Blanke (2018) demonstrated that the basal complex in Anisoptera, interpreted here as an instantiation of β, vary in a relative independence with respect to the remaining wing structures. Finally, the successful activation of α and β outside their primary locations (β in the anisopteran forewing; α in the zygopteran hindwing) supports their status as genuine morphological modules and suggests that they correspond to underlying developmental modules.

The 4P proposal (Fig. 14C) and the 1DC proposal (Fig. 15) can be directly compared in terms of character state acquisition. For the 1DC hypothesis, both a traditional version (Fig. 15A) and modular one (Fig. 15B) must be considered. The 4P and traditional 1DC proposals produce nearly identical distributions of character state acquisitions, especially within the crown-group, but the character states themselves differ in nature. Under the traditional 1DC proposal (Fig. 15A), multiple character state acquisitions are distributed along the stem leading to *Aeshna cyanea* (affecting the forewing) and along the stem leading to *Congqingia rhora* and *Chalcolestes viridis* (affecting the hindwing). Interpreting these changes within a modular framework, such that each set of transformations is treated as a single module shift (Fig. 14C), yields a more parsimonious evolutionary scenario.

A modular reinterpretation of the 1DC proposal (Fig. 15B) strengthens the similarity in character state distributions between the 4P and 1DC hypotheses (Figs 14C; 15B). A further, possible modification of the 1DC proposal involves proposing that pa was acquired independently in the forewing and hindwing, i.e., through parallel evolution (hence 'pa1' and 'pa2' on Fig. 15). Therefore, these structures would not be strictly homologous, which accommodates their potential co-occurrence. However, this substantially revised 1DC model still requires differences between the fore- and hindwing of *Triassoneura andersoni* more marked than under the 4P proposal. At its most fundamental step, this is because the acquisitions of ip and dp are assumed to have occurred before module duplication.

Overall, these comparisons suggests that the phylogenetic backbone of crown-Odonata is unlikely to be significantly altered by the new proposal, as, as we reiterate, assumed character state acquisitions differ in number and nature but are located along the same branches (with one exception). Therefore, the 4P and 1DC proposals are unlikely to deliver different topologies based on this species sample. It must also be emphasized that the 4P proposal would have a very minor impact, if any, on the phylogeny of extant forms, for Anisoptera and Zygoptera do not share an expressed module and, as a result, would be coded independently from each other for the basal complex. Nonetheless, it can be emphasized that it is congruent (to the same extent as the 1DC proposal) with the prevailing hypothesis on the relationships between species herein considered, which underpinned the sequence of our comparative analysis.

CONCLUSION

Overly simplified, the 4P proposal predicts that the hindwing basal complex of *Triassoneura andersoni* (Fig. 4C) prefigures the condition found in both wing pairs of Anisoptera (parapons absent, and infrapons present; Fig. 9); while, with the addition of the parapons and the coordinated loss of both distopons and infrapons (as assumed for the forewing of *Epiophlebia superstes*; Fig. 6A), the forewing basal complex of *Triassoneura andersoni* (Fig. 4A,B) prefigures that of both wing pairs of Zygoptera (parapons present, and distopons and infrapons absent; Fig. 12). The 4P proposal also implies that the triangle/supratriangle in Anisoptera and the quadrangle in Zygoptera, considered homologous under the 1DC proposal, are not. More broadly, the model assigns a central role to paralogous modules that would have evolved independently yet remain activatable in either wing pair. This framework better accounts for particular cases hitherto inadequately addressed. Hybrid proposals remain less satisfactory than to the 4P hypothesis.

Although our novel proposal entails a reconsideration of the homology of the discoidal cell in extant forms, it is unlikely to substantially impact their inner phylogeny, as Anisoptera and Zygoptera would be coded independently from each other for the basal complex. However, applying it to the assemblage of 'anisozygopteran' fossils is a promising venue. Concurrently, the growing body of morphometric data (Blanke 2018) and genomic data (Newton *et al.* 2023) may allow testing our core hypotheses, despite the paucity of 'heteropterous' extant species.

The present case recalls well-documented examples of paralogous morphological structures patterned by paralogous

developmental genes. These include the differentiation of mandibular, hyoid and gill elements of jawed vertebrate arches (Gillis *et al.* 2013; and see Quint *et al.* 2000), and of the organ types within the concentric whorls of the angiosperm flower (Bowman & Moyroud 2024). Taken together, these examples suggest that pre-existing serial homonomy provides a favourable substrate for the emergence of paralogy. What distinguishes the present case is the key role played by fossil material in revealing the pattern, for the morphology of extant taxa is too derived (with the partial exception of the relictual *Epiophlebia superstes*). Also, the apparent independence between modules identity and site of activation makes the case particularly relevant. It calls for a clearer conceptual separation in comparative morphology between the nature of potential paralogues and their positional expression.

Author contribution statement

Conceptualization, OB, ID, VR; Data curation, OB, ID, JMA; Formal Analysis, OB, ID, YN, VR; Funding acquisition, OB, JMA; Investigation, OB, ID, YN, VR; Methodology, OB, ID, VR; Project administration, Supervision, Validation, OB; Writing – original draft, OB, ID; Writing – review and editing, OB, ID, YN, JMA, VR.

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