

# Redescription of the holotype of *Phyloblatta gaudryi* (Agnus, 1903) (Pennsylvanian; Commentry, France), an exceptionally well-preserved stem-dictyopteran

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## ABSTRACT

The holotype of *Phyloblatta gaudryi* (Agnus, 1903), provided from the famous deposit of Commentry (Allier, France), exhibits a pair of forewings and a hind wing in connection, well preserved. Forewings show a network of veinlets in the area between M and CuA, and evidence of a fusion of some branches of M with CuA. It is concluded that the m-cua veinlets belong to M and that a reticulated fusion between M and CuA occurs. This fusion is considered as a homologue of the “dictyopteran forewing arculus”, but as an intermediate polymorphic state between “occurrence of a single discrete arculus” and “no arculus”. The preserved hind wing is devoid of an m-cua arculus, has a multi-branched AA vein on the remigium, and has a vannus of limited extent. The new data on *P. gaudryi* might allow the phylogenetic position of Pennsylvanian stem-dictyopterans with respect to crown-dictyopterans to be better assessed.

## KEY WORDS

Insecta,  
Dictyoptera,  
Pennsylvanian,  
Late Carboniferous,  
wing venation pattern,  
arculus,  
vannus.

## RÉSUMÉ

*Redescription de l'holotype de Phyloblatta gaudryi (Agnus, 1903) (Pennsylvanien ; Commentry, France), un dictyoptère-souche exceptionnellement bien préservé.*

L'holotype de *Phyloblatta gaudryi* (Agnus, 1903), fourni par le fameux site de Commentry (Allier, France), montre une paire d'ailes antérieures et une aile postérieure en connexion, bien préservées. Les ailes antérieures montrent un réseau de veinules dans l'aire entre M et CuA, et la preuve d'une fusion de

## MOTS CLÉS

Insecta,  
 Dictyoptera,  
 Pennsylvanien,  
 Carbonifère tardif,  
 patron de nervation  
 alaire,  
 arculus,  
 vannus.

branches de M avec CuA. Il est conclu que les veinules m-cua appartiennent à M et qu'une fusion reticulée est présente entre M et CuA. Cette fusion est considérée comme un homologue de l'« arculus dictyoptère des ailes antérieures », mais comme un état polymorphique intermédiaire entre « présence d'un arculus unique bien délimité » et « pas d'arcus ». L'aile postérieure préservée ne présente pas d'arcus m-cua, a une veine AA avec de multiples branches sur le rémigium, et a un vannus d'extension limitée. Les nouvelles données sur *P. gaudryi* pourraient permettre de mieux apprécier la position des dictyoptères-souches pennsylvaniens par rapport aux dictyoptères-couronnes.

## INTRODUCTION

Among other aspects, a fossil specimen is worth being described when it shows a new combination of character states or character states not previously documented. Such information can be essential for developing homology hypotheses. Specimens exhibiting several parts of the body that are otherwise only known in isolation are also especially informative. In addition, in the case of winged insects, specimens exhibiting complete wing pairs are important because they allow the range of intra-specific variability to be estimated on the basis of that of intra-individual variation. Such information is particularly relevant for fossil taxa distantly related to extant species.

All these points of particular interest apply to the holotype of *Phyloblatta gaudryi* (Agnus, 1903), which is considered as a stem-dictyopteran (i.e. as a relative of the lineage from which derived cockroaches, termites, and praying mantids), yielded by the famous Pennsylvanian deposit of Commentry (France). Schneider (1983) described intra-specific variability and revised the systematics of the species based on previous literature and published a photograph of the specimen (see also Laurentiaux 1958: pl. XXIV), but a redescription of the holotype is still wanting. Our new observations suggest that the holotype exhibits a new character state for the arculus, a structure occurring in forewings of some stem-dictyopterans, the nature of which is still debated. In addition, the specimen is composed of a well-preserved forewing pair together with a hind wing, preserved as exploded but in connection with the pterothorax.

To date, this is the only known hind wing of this species. This contribution aims to implement the available information on this exceptional specimen and discuss evolutionary implications based on comparison with selected other (stem-)dictyopterans, especially *Miroblatta costalis* Laurentiaux-Vieira & Laurentiaux, 1987.

## MATERIAL AND METHODS

The holotype of *Phyloblatta gaudryi* is housed in the Palaeontology Department of the Muséum national d'Histoire naturelle, Paris (specimen no. MNHN.F.51454). The holotype of *Miroblatta costalis* is housed in the Royal Belgian Institute of Natural Sciences, Brussels (specimen number IRSNB a12103).

By convention, we use the taxon name “Blattoidea” rather than “Blattaria” for the group including cockroaches and termites (following Hennig 1969, 1981). In accordance with editorial policy, the Linnaean nomenclatural procedure is followed, although the cladotypic nomenclature (Béthoux 2007a, b, 2010; applied in Béthoux 2007c, 2008a; Béthoux & Herd 2009) and the recourse to Lanham's species name (Dayrat *et al.* 2004 and references therein) would appear as a viable or potentially superior alternative (Béthoux 2010).

## ABBREVIATIONS

The wing venation nomenclature follows the serial insect wing venation pattern paradigm (Lameere



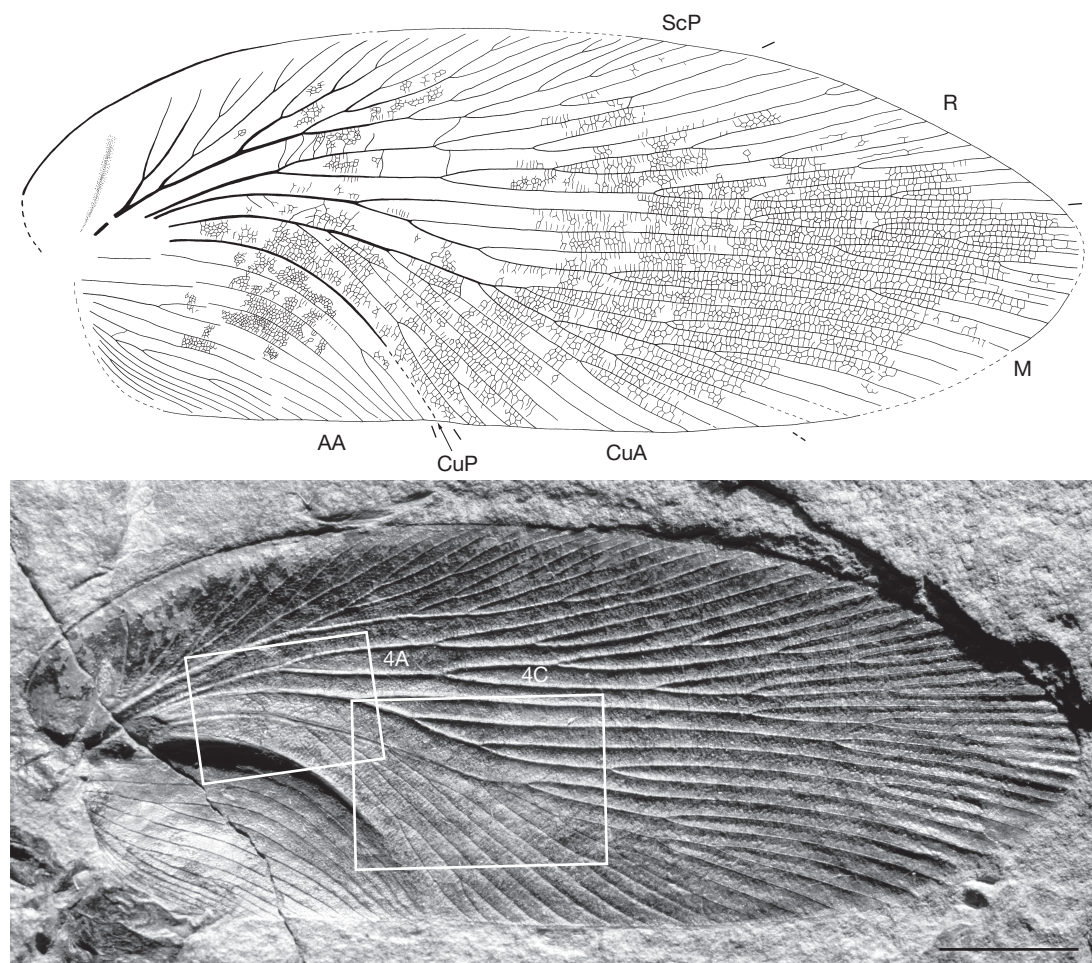


FIG. 1. — *Phyloblatta gaudryi* (Agnus, 1903); holotype specimen (MNHN.FR51454), right forewing; reconstruction and photograph (negative imprint, reversed). See text for abbreviations. Scale bar: 5 mm.

1922, 1923). Wing venation abbreviations relevant for this contribution are repeated for convenience:

AA anterior Analis;  
 AA1 first anterior Analis;  
 AA2 second anterior Analis;  
 CuA anterior Cubitus;  
 CuP posterior Cubitus;  
 M Media;  
 R Radius;  
 RA anterior Radius;

RP posterior Radius;  
 ScP posterior Subcosta.

We follow the convention of Béthoux *et al.* (2009) regarding the radial system in blattodeans.

## SYSTEMATIC PALAEONTOLOGY

Super-order DICTYOPTERA Latreille, 1829  
 Order BLATTODEA  
 Brunner von Wattenwyl, 1882

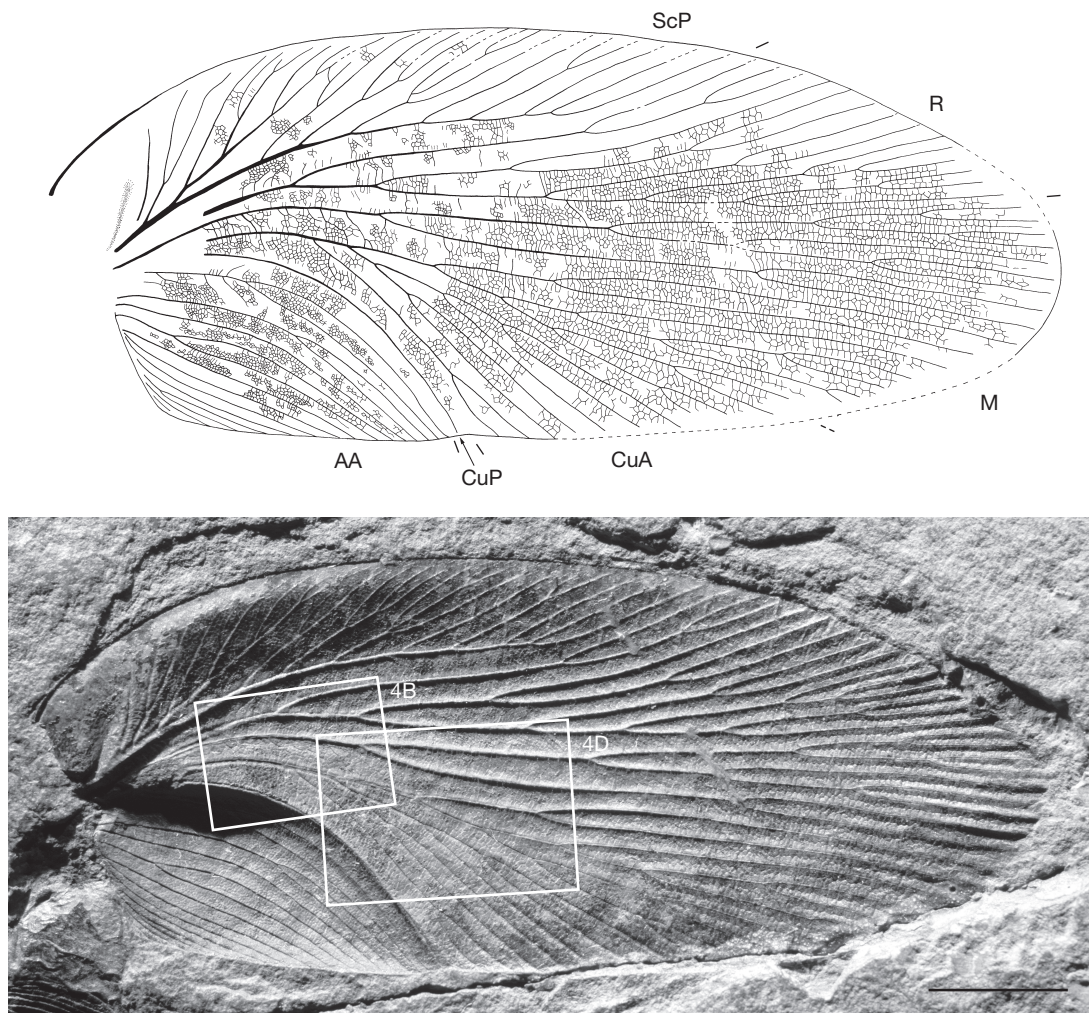


FIG. 2. — *Phyloblatta gaudryi* (Agnus, 1903); holotype specimen MNHN.F.R51454, left forewing; reconstruction and photograph (negative imprint). See text for abbreviations. Scale bar: 5 mm.

## Genus *Phyloblatta* Handlirsch, 1906

### *Phyloblatta gaudryi* (Agnus, 1903)

DESCRIPTION. — Negative imprint, right and left forewings, and left hind wing of a single individual, connected to remains of the pterothorax (wing venation described as if viewed from a positive imprint; numerical data: right/left side); **forewings**: length 35.8/34.0 mm, width 14.3/14.8 mm; ScP reaching anterior wing margin at between 60 and 75% of the wing length; ScP concave, with numerous anterior branches; R concave, branched

about 7.5/6.8 mm distal to wing base, with no regular branching pattern; R with 13/14 branches; M (excluding its branches associated with CuA) branched distal to R, concave, anteriorly pectinate in right forewing, irregularly branched in left forewing; M with 11/9 branches free of CuA; convex transverse to oblique, and somewhat irregular veinlets interconnecting M and CuA proximal to the branching of both, with a stronger basal veinlet and one/several weaker veinlets; CuA convex; branches of M diverging from CuA + M *partim* concave; M *partim* + CuA with 17/18 branches; CuP simple, strongly curved, strongly concave, reaching the posterior wing margin near 40% of wing length; anal area with 16/14



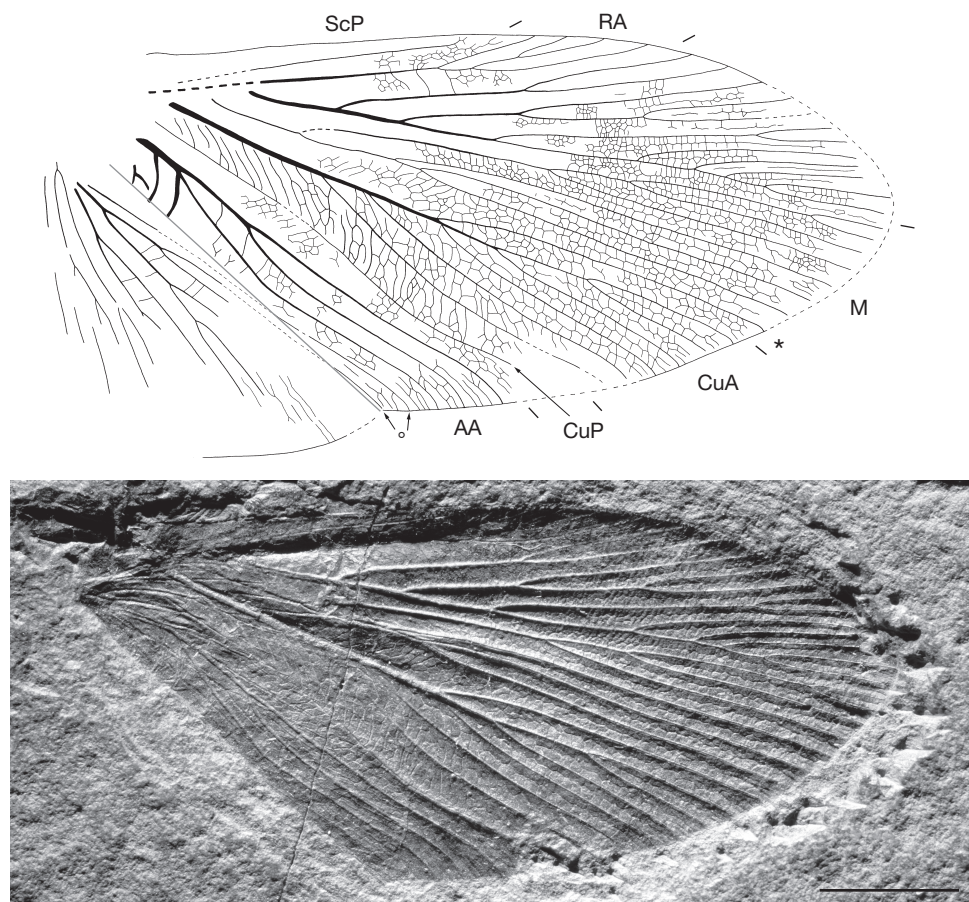


FIG. 3. — *Phyloblatta gaudryi* (Agnus, 1903); holotype specimen MNHN.F.R51454, left hind wing; reconstruction (continuous grey line indicates the remigium-vannus fold. \*, indicates a branch of M diverging from CuA; °, indicates branches that cross the remigium-vannus fold) and photograph (negative imprint). See text for abbreviations. Scale bar: 5 mm.

AA branches, all reaching the posterior wing margin; **hind wing**: length 29.4 mm, width of remigium 13.3 mm; vannus folded over remigium (whether the vannus is provided with longitudinal folds, or not, cannot be observed); ScP concave, reaching the anterior wing margin at mid-length; R convex, branched 5.7 mm distal to wing base; RA convex, branched distally, with four branches; RP concave, branched 3.9 mm distal to its origin, anteriorly pectinate, with 11 branches; M concave, weak at its origin, with three branches free of CuA; a simple branch of M diverges anteriorly from M *partim* + CuA; CuA located in a depression but concave, posteriorly pectinate, with six branches; CuP concave, sigmoid, weak, simple; AA(1?) (located on the remigium) with three branches reaching the posterior wing margin; basal to its main fork, AA(1?) emits two

strong struts posteriorly; fold separating the remigium from the vannus crossing two veins (Fig. 3[°]), and reaching the posterior wing margin at 38% of wing length; vannus moderately large, filled with numerous branches (belonging either to AA1 or AA2, see below).

#### REMARKS

The specimen most likely experienced moderate plastic deformation during fossilisation, as indicated by the forewings aspect ratio, differing in the right and left forewings. The difference observed in the fossil individual exceeds that observed between right and left forewings of *Periplaneta americana* (Linnaeus, 1758) (Schneider 1977: fig. 2).

## VARIABILITY

As detailed by Schneider (1977: 81, pl. 2), the forewing venation of *Phyloblatta gaudryi* is particularly variable with respect to other Palaeozoic stem-Dictyoptera. In particular the number of terminal branches and branching pattern of each vein (sector) varies considerably (e.g., the number of terminal branches of the anterior branch of R ranges from 1 to 9 (Schneider 1977: pl. 2, figs 12, 11, respectively).

## DISCUSSION

## STEM-DICTYOPTERAN FOREWING ARCULUS AND NATURE OF ANTERIOR “CUA-BRANCHES”

An oblique sclerotized structure located in the area posterior to the stem of M occurs in forewings of many “lower neopterans”, such as Archaeorthoptera, plecopterans, some (stem-)dictyopterans (e.g., †Archimylacridae Handlirsch, 1906, such as *Miroblatta costalis* in Figure 5; and †Blattinopsidae Bolton, 1925), and paoliidans, an enigmatic group of Late Carboniferous insects exhibiting neoptery (see Prokop & Nel 2007). Rasnitsyn (2007) proposed that this structure is homologous in all these taxa, and is a posterior convex stem of the Media named M<sub>5</sub>. According to Rasnitsyn & Quicke (2002) this structure is plesiomorphic within pterygotans.

However, in Archaeorthoptera, new evidence suggests that the corresponding convex “oblique structure” is actually CuA diverging from M + CuA and joining a branch of CuP (Béthoux 2005b, 2008b; Béthoux & Nel 2002). In plecopterans the respective structure is free of trachea (Béthoux 2005a) indicating that it is a cross-vein, hence is not homologous to the “archaeorthopteran arculus”. Given that similar arculus-like structures can be non-homologous, the nature of the paoliidan arculus must be considered as uncertain. In the stem-dictyopterans concerned, the forewing arculus is most likely a posterior branch of M (as in Rasnitsyn’s hypothesis), or a strengthened cross-vein (Béthoux 2008b). Indeed the fact that, in this group, CuA emits posterior convex branches basal to its connection with the convex arculus (Béthoux 2008b: fig. 4; Fig. 5) contradicts one aspect in Rasnitsyn’s (2007) hypothesis, namely

that CuA turns convex only once connected to the convex M<sub>5</sub>-arculus.

Both forewings of the holotype of *Phyloblatta gaudryi* exhibit a network of convex veinlets occurring in the area posterior to the main stem of M, with one veinlet being moderately stronger than the others (Figs 1; 2; 4A, B). There is an important variation in conditions in the right and left forewings. In the former (Figs 1; 4A) a main arculus occurs, with a single weak veinlet anterior to it. In addition, disorganized veinlets stronger than regular cross-veins occur more distally. In the left forewing (Figs 2; 4B) a series of 4 veinlets occur distal to the main one. Variation observed in the holotype of *P. gaudryi* demonstrates that the species is polymorphic in this character. We interpret this condition with several traversing (M to CuA) veinlets as a multipartite arculus, and distinguish this from a discrete arculus with a single (usually stronger) such vein.

Schneider (1983), based on information published in Meunier (1916-1921), indicated that a discrete arculus is present only in 8 of 12 forewings of *P. gaudryi*. Our new observations suggest that veinlets of a multipartite arculus could be inconspicuous if not observed under appropriate light settings. Therefore the condition “arculus absent”, assumed for 4 forewings by Schneider (1983), could be “multipartite arculus present” indeed. It is not excluded that veinlets of a multipartite arculus also occurred in the 8 forewings showing a single main arculus vein. Anyhow, interpretations by Schneider (1983) support the view that *P. gaudryi* exhibits several “arculus” conditions. The state exhibited by the holotype specimen can be considered as the occurrence of a “multipartite arculus”, or of a main arculus with several additional reticulations, a case never documented earlier in stem-dictyopterans.

At this stage, the multipartite arculus could be a) a set of strong cross-veins; or b) a set of veinlets from M. A point to consider is that several concave veins diverge anteriorly from the convex CuA. They could be 1) branches of CuA whose elevation has been altered as a consequence of a strengthening, as is apparently the case for the whole radial system (such alteration has been observed in grylloblattidan insects: Béthoux & Nel 2010); or 2) branches of M.



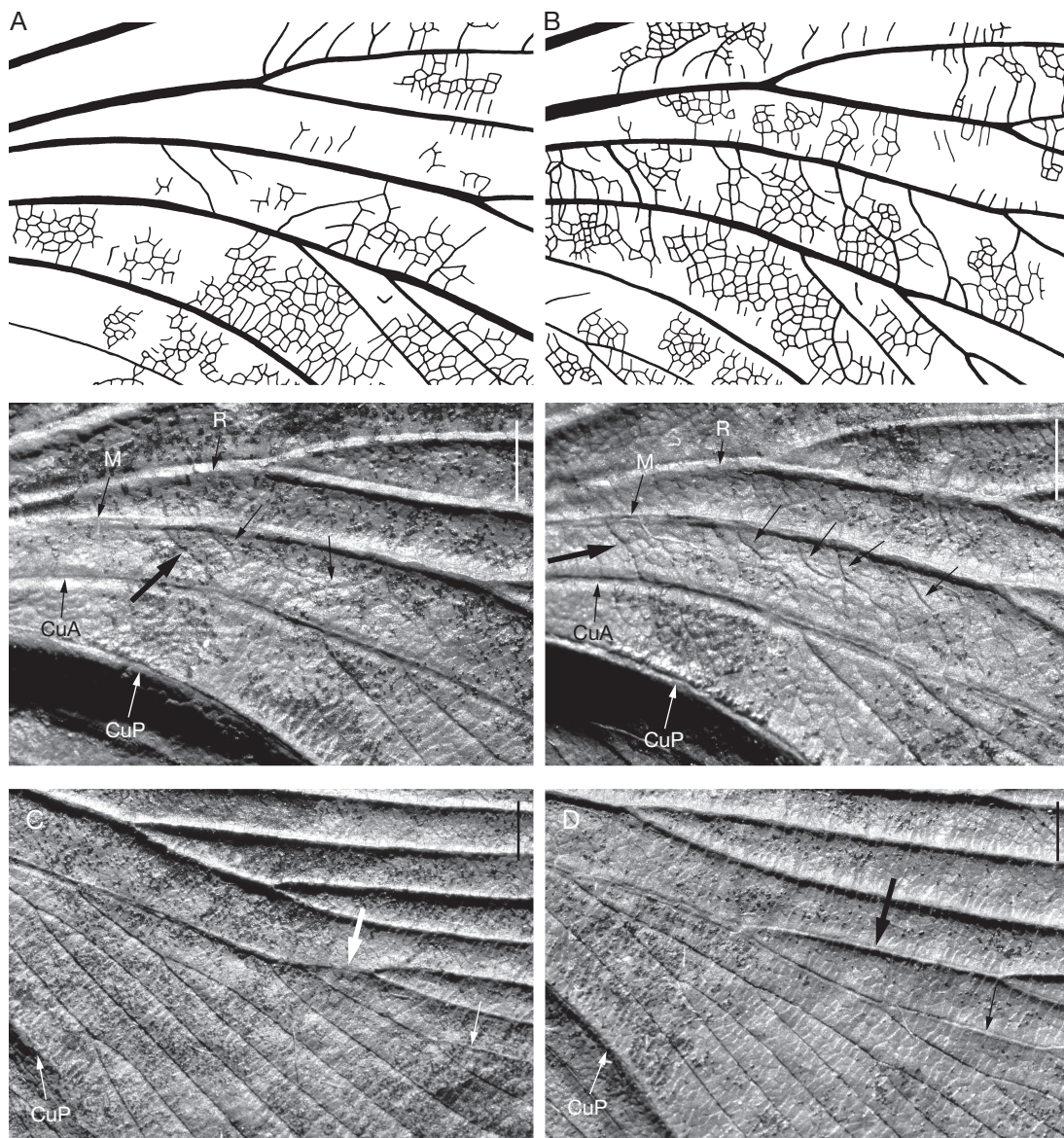


FIG. 4. — Details of the forewing venation of *Phyloblatta gaudryi* (Agnus, 1903); holotype specimen MNHN.FR51454: **A, B**, detail of the area between M and CuA, forewing base; arrows without labels indicate veinlets; their thickness indicates strength of indicated veinlet; **A**, right forewing, reconstruction and photograph, location as indicated by “4A” in Figure 1 (negative imprint, reversed); **B**, left forewing, reconstruction and photograph, location as indicated by “4B” in Figure 2 (negative imprint); **C, D**, detail of the divergence of M branches from M partim + CuA, forewings; arrows without labels indicate branches of M diverging from M partim + CuA; their thickness indicates strength of indicated vein; **C**, right forewing, location as indicated by “4C” in Figure 1 (negative imprint, reversed). **D**, left forewing, location as indicated by “4D” in Figure 2 (negative imprint). See text for abbreviations. Scale bars: 1 mm.

In hind wings of extant praying mantids (OB pers. obs.), extant cockroaches (Rehn 1951), and Permian cockroaches (Tillyard 1937a, b; Schneider

1984), CuA is posteriorly pectinate. In *P. gaudryi* forewings, if branches interpreted as belonging to M are omitted (under hypothesis 2), CuA is pos-

teriorly pectinate also. Therefore we interpret the supernumerary “concave anterior branches of CuA” as belonging to M. This evidence for a fusion of some branches of M with CuA (2) suggests that the “veinlets” belong to M (b).

It must be noticed that the “veinlets” are convex, while true branches of M would be expected to be concave. However cross-veins are convex in forewings of *P. gaudryi*. Therefore it is plausible that M veinlets are rerouted as weak tracheae through the cross-vein network. If so, elevation of cross-veins would not be affected. This interpretation is supported by observations made on forewings of mantises, in which a “veinlet” can take the form of a trachea running in the membrane, with no particular elevation (Béthoux & Wieland 2009: fig. 8). Finally we suggest that, in *P. gaudryi*, a reticulated fusion involves a series of posterior M veinlets with CuA, rerouted through cross-veins, as schematized in Figure 6.

Interestingly a similar type of fusion, involving a different set of veins, was documented in amorphoscelidaeans (mantodeans) by Béthoux & Wieland (2009: figs 8, 9). In some species a vein fusion, its lack, and a network of weak tracheae (occasionally totally disconnected from the venation) co-occur. In mantodeans, along the presumed morphocline, states preceding and following this polymorphic state are less variable.

Indeed, based on previous literature, Schneider (1983) mentioned that a single strong arculus is not always present in *P. gaudryi* (and see above). Therefore we hypothesize that *P. gaudryi* is a similar “polymorphic intermediate” regarding the arculus, i.e. it exhibits different conditions and a unique, unfixed, condition. It must be noted that the forewing venation of *P. gaudryi*, with respect to contemporaneous stem-dictyopterans, is unusually variable: only the number of branches from R, and the sum of the branches from M and CuA, are comparatively stable (Schneider 1983).

With reference to the serial insect wing venation pattern, a fusion of a posterior branch of M with CuA is a derived character state. It would indicate that a number of Pennsylvanian stem-dictyopterans (or stem-blattodeans) form a monophyletic group. Alternatively (though less parsimoniously), how-

ever, the fusion could be secondarily absent in the lineage from which crown-dictyopterans (or crown-blattodeans) derived. Secondary absence might be favoured by the fact that an arculus is common in more ancient stem-dictyopterans, and occurs sporadically in more recent groups (Schneider pers. obs.). But this hypothesis remains to be tested by proper character state polarization via outgroup comparison, conditions in plecopterans and paoliidans being of greatest interest.

#### HIND WING MORPHOLOGY AND VENATION

The forewing pair of the holotype of *P. gaudryi* is associated with a well-preserved hind wing. Association of fore- and hind wings of Pennsylvanian stem-dictyopterans (or stem-blattodeans) is rare. This hind wing exhibits a number of remarkable traits. Unlike crown-dictyopterans (see Rehn 1951; Ragge 1955) but like all other Late Palaeozoic dictyopterans (Tillyard 1937b; Schneider 1984; OB pers. obs.), it is devoid of an m-cua “arculus” (which is a strengthened cross-vein in dictyopteran hind wings, according to Béthoux [2008b]).

A unique trait is the divergence of a posterior branch of M (Fig. 3[\*]) from CuA without evidence of fusion near the wing base. If this unique apparent anterior branch of CuA is omitted, this vein sector is posteriorly pectinate, such as in hind wings of extant praying mantids (OB pers. obs.), extant cockroaches (Rehn 1951), and Permian cockroaches (Tillyard 1937a, b; Schneider 1984). Therefore the oblique anterior branch of “CuA” is interpreted as a branch of M. A translocation (i.e. the posterior branch of M is rerouted along CuA from the wing base) might be advocated here. Such alterations of the wing venation pattern are documented in †Tcholmanvissiidae Zalesky, 1934 (Béthoux 2007c) and praying mantids (Béthoux & Wieland 2009). This condition might have been uncommon in *P. gaudryi*.

The vannus is delimited from the remigium by a fold that crosses veins originating on the vannus (Fig. 3[°]). Veins originating anterior to this fold most probably belong to AA. They are not differentiated into a simple anterior branch (AA1) and a branched posterior branch (AA2) such as in stoneflies (Béthoux 2005a) and extant cockroaches (Smart’s



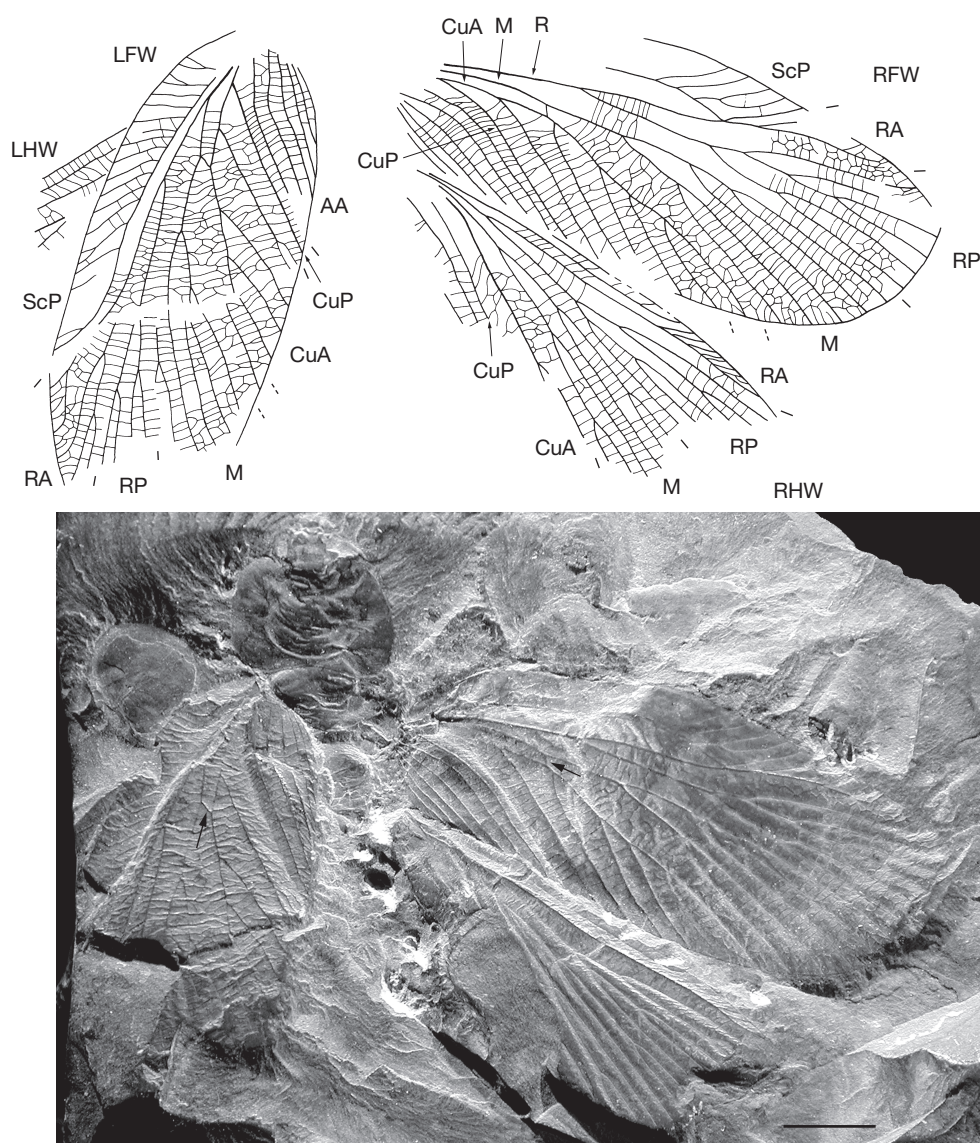


FIG. 5. — *Miroblatta costalis* Laurentiaux-Vieira & Laurentiaux, 1987; holotype specimen IRSNB a12103, reconstruction of the wing venation and photograph (positive imprint; arrows indicate forewing arculi). See text for abbreviations. Scale bar: 5 mm.

[1952] “1V” and “2V”; among other authors). It is unclear whether the “AA1” of extant dictyopterans is homologous to the whole set of branches anterior to the fold, or to the anterior-most branch of this set of branches. Concurrently, the nature of the branches posterior to the fold is difficult to assess (either AA2 or AP). Apices of branches crossing

the remigium-vannus fold exhibit the same relief as genuine AA branches, and might belong to this sector then.

#### CROSS-VENATION AND VEINLETS

Cross-venation is well-preserved in the forewing pair and hind wing of the holotype of *P. gaudryi*.

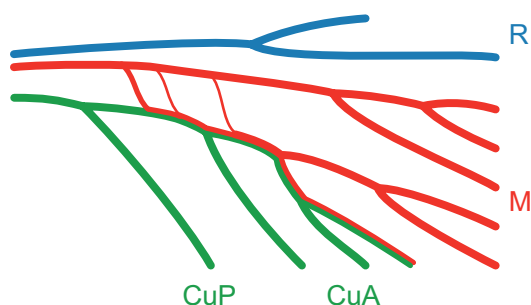


FIG. 6. — Interpretation of the forewing medio-cubital area in *Phylloblatta gaudryi* (Agnus, 1903). See text for abbreviations.

Its organization is not uniform along the wings. In forewings the area posterior to CuP is provided with very small cells. Individual cells tend to occupy a larger surface along the wing margin. Cross-vein walls organized as secondary convex intercalary veins occur at the wing apex only, between branches of RP and M in forewings, and between branches of RP, M, and CuA in the hind wing. In the middle of forewings the cross-vein network is denser than at the apex or along the posterior wing margin. The dense cross-venation of forewings probably resulted in a strengthening of this organ, in relation to its plausible use as a protective device. Convexity of forewing cross-venation is comparatively well-preserved, suggesting that they were sclerotized to some extent.

In forewings a number of veinlets appear as intermediates between the cross-venation and the main vein network. Besides the arculus, such veinlets were observed between ScP and the anterior branch of R, between branches of R, between the posterior branch of R and the anterior branch of M, and in the anal area (Figs 1, 2). Rather than advocating environmental pressure (see Vršanský 2005) we suggest that the occurrence of such veinlets could be the mere result of relatively low developmental constraints acting on wing venation.

## CONCLUSION

Based on new observations on the holotype of *Phylloblatta gaudryi* we suggest that the “dictyopteran forewing arculus” is composed of a (set of) posterior

branch(es) of M. The species *P. gaudryi* exhibits a variable and unfixed condition, in which fusion is evidenced by a reticulation of veinlets. The hind wing of *P. gaudryi* is devoid of an m-cua arculus, and exhibits no evidence of AA1 and AA2 differentiation. The new data on *P. gaudryi* might allow the position of Pennsylvanian stem-dictyopterans with respect to crown-dictyopterans to be better assessed.

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