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ABSTRACT

The fossil species *Prochaeradodis enigmaticus* Piton, 1940, from Menat (France, Paleocene) has been regarded as a crown-Mantodea (praying mantis) and was subsequently used as one of the very few temporal calibration points relevant for the order. Ambiguities in previous descriptions prompted us to re-examine the type material. Based on our new observations and a broad comparative analysis across Dictyoptera, we recognized three independent morphological character states supporting an unequivocal placement of the fossil within Blattodea (cockroaches and termites). These states are: 1) in forewing, the AA area has intercalary veins; 2) in forewing, ScP is short and oblique; and 3) in hind wing, CuA has many posterior branches not reaching the posterior wing margin but the cubital furrow. This new placement discounts the use of this fossil as a Mantodea tree calibration point.

KEY WORDS

Polyneoptera,
Blattaria,
Blattoptera,
Blattida,
dating,
morphology,
palaeoentomology.

RÉSUMÉ

Prières pour une mante fossile non exaucées : *Prochaeradodis enigmaticus* Piton, 1940 est une blatte (Blattodea). L'espèce fossile *Prochaeradodis enigmaticus* Piton, 1940, de Menat (France, Paléocène), a été considérée comme un Mantodea couronne (mante religieuse) et a été, par la suite, utilisé comme l'un des rares points de calibration temporelle pertinents pour l'ordre. Des ambiguïtés dans les précédentes descriptions nous ont amenés à revoir le matériel type. Sur la base de nouvelles observations et d'une analyse comparative couvrant les Dictyoptera, nous avons identifié trois états de caractères soutenant, sans le moindre doute, un placement du fossile au sein des Blattodea (blattes – incluant les termites). Ces états sont : 1) chez les ailes antérieures, aire AA avec des nervures intercalaires ; 2) chez les ailes antérieures, ScP courte et oblique ; et 3) chez les ailes postérieures, CuA avec de nombreuses branches postérieures n'atteignant pas le bord postérieur mais le sillon cubital. Ce nouveau placement compromet l'usage de ce fossile comme point de calibration de l'arbre des Mantodea.

MOTS CLÉS

Polyneoptera,
Blattaria,
Blattoptera,
Blattida,
datation,
morphologie,
paléontologie.

INTRODUCTION

The biologically rich fossil deposits in Menat, France contain a wide array of phyla (Piton 1940; Kedves 1982; Wappler *et al.* 2009; Stroiński & Szwedo 2012). Dating from the period immediately succeeding the K-T impact, many of its insect fossils can be attributed to extant families (Nel & Roy 1996; Nel 2008; Stroiński & Szwedo 2012; Evangelista *et al.* 2017; among others).

The Dictyoptera (a taxon encompassing cockroaches, termites and praying mantises) first found in Menat were described by Piton (1939; 1940). Subsequent publications have added to this fauna (e.g. Nel & Roy 1996) or revised the original taxonomic work (Nel & Roy 1996; Evangelista *et al.* 2017). One species from Menat, *Prochaeradodis enigmaticus* Piton, 1940, gained a particular importance in dating analyses. After it was redescribed by Nel & Roy (1996) it was subsequently considered the oldest fossil representative of the super-family Mantoidea *sensu* Grimaldi (2003).

Upon examination of the original fossil material, we found compelling evidence for a further revision of *P. enigmaticus*. Based on supporting morphological evidence, we place this fossil in Blattodea, and as a putative member of the family Blaberidae.

MATERIAL AND METHODS

Wing morphology terminology and venation homologies

General wing morphology terminology follows Brannoch *et al.* (2017). We follow the serial insect wing venation ground-plan of Lameere (1922, 1923). The corresponding wing venation nomenclature is repeated for convenience, with indication of colour coding:

AA	anterior analis (pink, in forewing only);
Cu	cubitus (green, in hind wing only);
CuA	anterior cubitus;
CuP	posterior cubitus;
M	media;
R	radius (blue, in hind wing only);
RA	anterior radius;
RP	posterior radius;
ScP	posterior subcosta (orange, in forewing only).

Besides minor aspects of terminology ('Rs' vs 'RP'), there is broad consensus on the wing venation homologies for cockroaches (except for veins located in the vicinity of the CuP and of the plica prima anterior). As for mantises, issues remain regarding the homologies of the radial and median system in forewing (OB pers. obs.). In this contribution we do not differentiate among the systems and both are collectively labelled 'R&M'. These aspects bear no implications on our conclusions.

MATERIAL PREPARATION AND DATA

The holotype of *Prochaeradodis enigmaticus* is housed in the Palaeontology Unit of the Muséum national d'Histoire naturelle, Paris (specimen no. [MNHN.F.R07003](#)).

Draft drawings of the fossil (Fig. 1) 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). Drawings were finalized using Adobe Illustrator CS6 (Adobe Systems, San Jose, CA, USA) using both draft drawings and photographs.

Photographs were taken using a digital camera Canon EOS 5D Mark III, coupled to a Canon 50 mm macro lens, or to a Canon MP-E 65 mm macro lens (all Canon, Tokyo, Japan), both equipped with polarizing filters. The resulting photographs were optimized using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, USA).

Wings of extant specimens were cut off and mounted in white Euparal medium (Asco Laboratories, Manchester, UK). Slides were then examined and illustrated using the same methods as for the fossil material. The acronym 'IWC OB' refers to the 'Insect Wing Collection O. Béthoux'.

Body length was roughly estimated from the anterior most point of the specimen to the estimated posterior end, assuming the wings either: extend past the end of the body, end at the posterior margin of the body, or the body extends past the wings.

COMPARATIVE ANALYSIS

The specimen's wing characters were assessed and compared to crown-Dictyoptera based on literature. This was primarily done using data from Rehn (1951) formalized in Evangelista

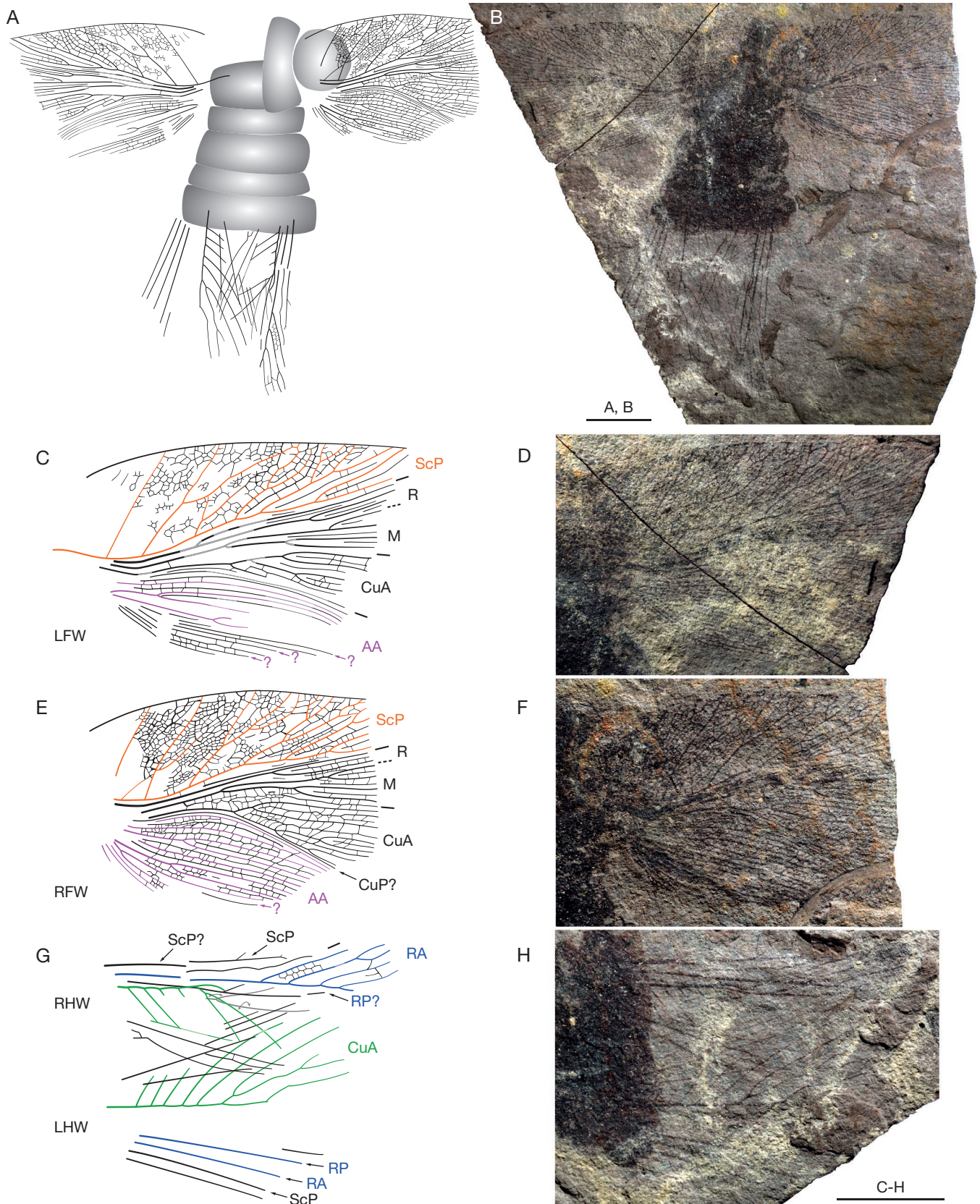


FIG. 1. — *Prochaeradodis enigmaticus* Piton, 1940, specimen [MNHN.F.R07003](#), positive imprint: **A, B**, drawing and photograph (dry-ethanol composite) of general habitus; **C, D**, drawing and photograph (dry-ethanol composite) of left forewing; **E, F**, drawing and photograph (dry-ethanol composite) of right forewing; **G, H**, drawing and photograph (dry-ethanol composite) of hind wings. Scale bars: 5 mm.

et al. (2017), and figures in Rehn (1951) and Brannoch *et al.* (2017). Illustrations and photos from other publications were used as well (e.g. Anisyutkin 2014, 2015; Hopkins 2014). We also provide a new drawing of a Blaberidae (Fig. 2A, B). Note that, in the corresponding species, a branch of R diverges posteriorly from ScP (see Fig. 2A; this trait occurs in many Blattodea; DAE pers. obs.). Polarization of characters was based on fossil families regarded as stem-Blattodea, namely Umenocoleidae, Caloblattinidae, Mesoblattinidae, and Blat-tulidae (see Martinez-Delclos 1993; Vršanský 2007; Barna 2014; Lee 2016; Vršanský & Wang 2017) and on Palaeozoic stem-Dictyoptera for which both fore- and hind wing are known with sufficient details (see Béthoux *et al.* 2011; Guo *et al.* 2013). Note that, as for the character states considered below, the known stem-Mantodea (see Sharov 1962; Grimaldi 2003; among others) do not differ substantially from the crown-Mantodea documented herein (unless mentioned).

SYSTEMATIC PALAEONTOLOGY

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

Genus *Prochaeradodis* Piton, 1940

TYPE SPECIES. — *Prochaeradodis enigmaticus* Piton, 1940 mono-
typic genus.

Prochaeradodis enigmaticus Piton, 1940
(Fig. 1)

TYPE MATERIAL. — Holotype: MNHN.FR07003, a single imprint of a moderately well-preserved individual, composed of: two forewings with, approximately, the distal half missing; a pair of hind wings with their middle parts partly overlapping, with basal-most part hidden and apex missing; some segments of thorax, head (outline?) and abdomen partly visible.

TYPE LOCALITY. — The material was unearthed at the Menat local-
ity (Puy-de-Dôme, France; Piton 1940), regarded as of Paleocene
age (Kedves & Russell 1982).

REDESCRIPTION

Body (Fig. 1A, B)

Estimated body length 27–35 mm.

Forewings (Fig. 1C–F)

Preserved length about 16.2/13.7 mm (left/right forewing,
respectively); width (broadest part in the preserved wing)
10.1/10.2 mm; area between anterior wing margin and ScP
broad, filled with densely reticulated cross-veins; most basal
part of that area extremely broad, nearly half of wing width; ScP
anteriorly pectinate with secondary forks, with some branches
vanishing in the cross-vein network; R with fewer branches
than M in the preserved part; first fork of CuA opposite or
slightly distal to the first fork of M, with 5–6 branches; CuP
(as inferred from actual remains of it or surrounding veins)

regularly bent, simple; first AA vein simple, with several
additional AA veins, simple or forked; intercalary veins well-
developed, visible between most main veins.

Hind wings (Fig. 1G, H)

Preserved length 11.2/13.8 mm (left/right hind wing, respec-
tively); CuA with numerous posterior pectinate branches, some
being branched (9/6 branches preserved in left/right hind wing,
respectively); most basal branches of CuA short and reach CuP
or vanish shortly before reaching it. Right hind wing: wing
partly damaged (as evidenced by the discontinuous course of
ScP, RA, RP and CuA); ScP with (possibly) anterior veinlets;
occurrence of an intercalary vein between ScP and RA; RA
anteriorly pectinate with at least five branches; intercalary vein
visible between the first two branches of RA; visible branches of
CuA all reaching CuP (or the cubital furrow, not distinguishable).

REMARKS

The exact position of CuP in the forewing is not evident. In
extant cockroaches (e.g. Fig. 2A) it seems to be bordered by
two vein-like structures of unclear identity. Nonetheless, they
are parallel to CuP, hence the course of this vein can be posi-
tively assessed based on these. In the right hind wing of the
fossil specimen we interpreted an isolated, forked vein (dark
grey on Fig. 1G) as a portion of CuA. Given the evidence that
this wing is partly damaged, this is the most likely interpreta-
tion. Moreover, the resulted reconstruction is consistent with
the pattern observed in the other hind wing. Several veins
belonging to hind wings could not be positively identified;
some probably belong to an expanded plicatum.

DISCUSSION

Although the fossil is very incomplete there are sufficient char-
acter states useful for a critical re-evaluation of its placement.
Among Polyneoptera, we agree with Piton (1940) and Nel &
Roy (1996) that *P. enigmaticus* belongs to Dictyoptera, owing
to the posteriorly bent forewing CuP. Note that although it
has sometimes been considered diagnostic of Blattodea (herein
understood as including “Isoptera”) only, this character state is
herein regarded as indicative of affinities with the whole Dic-
tyoptera. Indeed, stem-Mantodea (see Gratshev & Zherikhin
1993; Grimaldi 2003), and, to some extent, *Metallyticus* spp.
(Fig. 2E), display a bent CuP. Within Dictyoptera, we disagree
with Piton (1940) and Nel & Roy (1996) and place this fossil
in Blattodea, as opposed to Mantodea. This proposal rests on
several character states, as follows.

In forewings of *P. enigmaticus* (Fig. 1C–F) and of Blattodea
(Fig. 2A) the area posterior to CuP bears abundant AA branches.
Furthermore, the AA veins initially diverge basally and then
converge apically. In contrast, the anal vein region of Mantodea
(Fig. 2C, E, G, I): 1) have fewer branches; and 2) do not display
the divergence-convergence pattern (but maybe as a consequence
of the straightening of CuP in some). Stem-Dictyoptera have
the same state as in Blattodea. Hence, these states designate
P. enigmaticus as either a Blattodea or a stem-Mantodea.

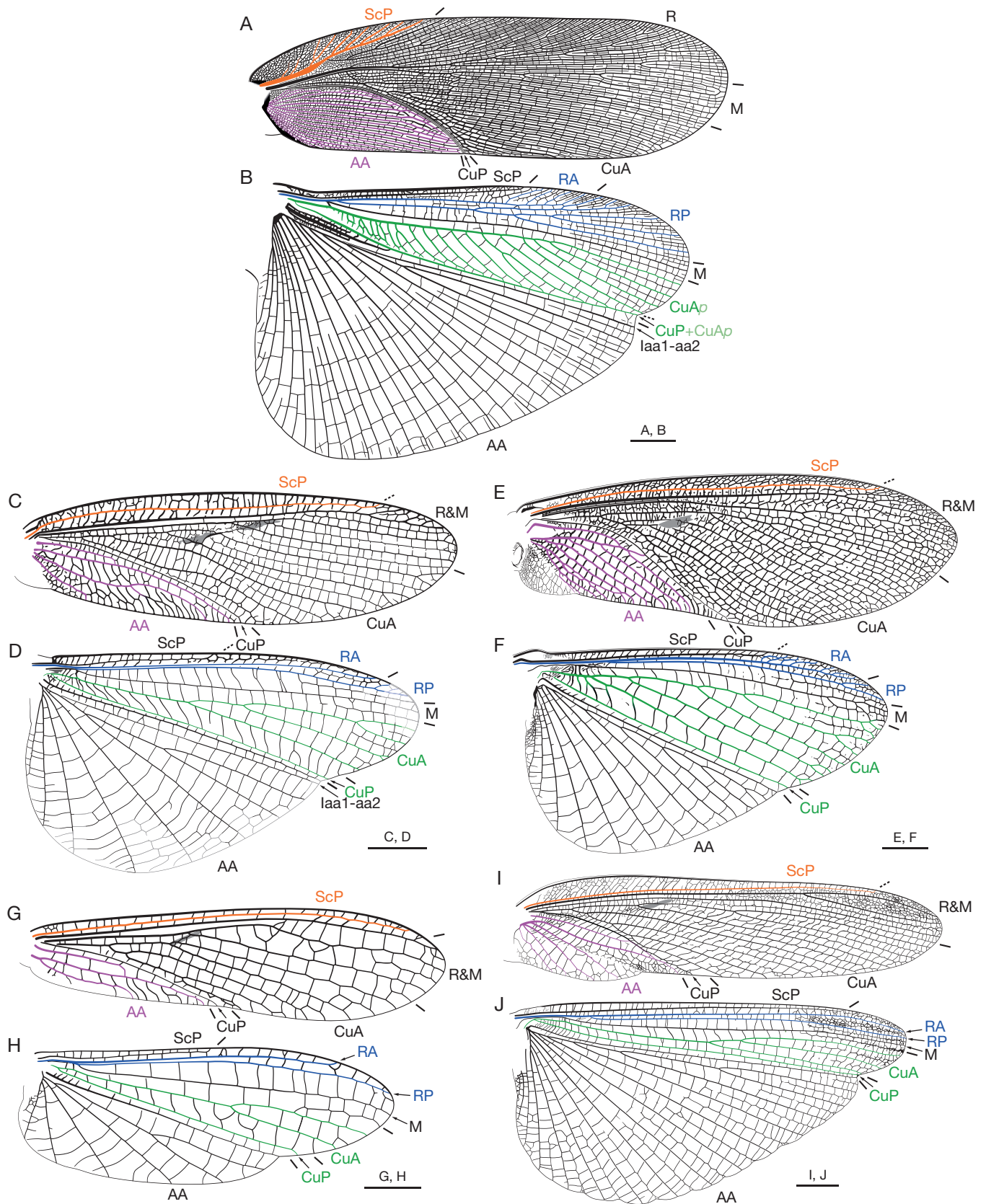


FIG. 2. — Wing venation patterns of selected extant Blattodea and Mantodea: **A, B**, *Molytria* sp. (Blattodea; specimen IWC OB 1219), left fore- (**A**) and hind wing (**B**); **C–J**, representatives of Mantodea (modified from Brannoch *et al.* 2017); **C, D**, *Chaeteessa* sp., fore- (**C**) and hind wing (**D**); **E, F**, *Metallyticus splendidus* Westwood, 1835, fore- (**E**) and hind wing (**F**); **G, H**, *Mantoida maya* Saussure & Zehntner, 1894, fore- (**G**) and hind wing (**H**); **I, J**, *Mantis religiosa* (Linnaeus, 1758), fore- (**I**) and hind wing (**J**). Scale bars: A–F, 2 mm; I, J, 3 mm.

In forewings of *P. enigmaticus* and Blattodea the AA area has intercalary veins (Figs 1C-F; 2A). This state is absent in all described Mantodea (Fig. 2C, E, G, I). Being absent in stem-Dictyoptera we consider its presence derived within the context of Dictyoptera; hence this state indicates that *P. enigmaticus* is a Blattodea. Note that the feature is distributed widely within Blattodea (DAE and OB, pers. obs.) but poor documentation of intercalaries in literature disallows further characterization.

Nel & Roy (1996) referred to the very wide ‘costal area’ (herein ‘area between anterior wing margin -awm- and ScP’) as indicative of affinities of *P. enigmaticus* with Choeradodinae (within Mantodea). However, a wide awm-ScP area is far from unique to a subset of Mantodea: it is indeed common among leaf-mimicking insects. Moreover, this area is wide only in its basal half in *P. enigmaticus* (Fig. 1C, E) as in Blattodea (Fig. 2A). Although the apical-most section of ScP is not preserved in the fossil, it is highly probable that this vein reached the awm very basally. In contrast, ScP is very long and parallel to the longitudinal axis of the forewing of Mantodea (Fig. 2C, E, G, I). Stem-Dictyoptera display an intermediate condition, suggesting the short and oblique ScP of Blattodea, and the long and straight ScP of Mantodea are both apomorphic conditions. Hence *P. enigmaticus* is likely a Blattodea.

In the hind wings of *P. enigmaticus* RA: 1) has numerous branches; and 2) its first fork is located basally (Fig. 1G). Nearly all Blattodea have a similar, multiply branched, hindwing RA whose branches originate before the termination of ScP. In the vast majority of Mantodea, RA is simple in the hind wing (Fig. 2H, J). *Metallyticus* spp. (Fig. 2F) are the only notable exceptions: RA has several anterior branches, but they occur very distally. Additionally, note that some Mantodea, in particular leaf-mimics, can display anterior, weak veinlets diverging from RA, which can hardly be considered genuine branches. Stem-Dictyoptera display the same state as *P. enigmaticus* and Blattodea, hence the fossil is either a Blattodea or a stem-Mantodea.

In the hind wings of *P. enigmaticus* CuA has many posterior branches not reaching the posterior wing margin (pwm) but the cubital furrow (cf) (Fig. 1G). The number of such basal branches varies among Blattodea. Morphologies comparable to that observed in *P. enigmaticus* (namely, very numerous basal branches) occur in some Blattellinae (family Ectobiidae – probably a paraphyletic assemblage; see, among others, Klass & Meier 2006, Djernæs *et al.* 2012, Legendre *et al.* 2015) and Blaberidae (see, e.g., Fig. 2B). In the vast majority of Mantodea, CuA branches all reach the pwm (Fig. 2D, H, J). The only putative exceptions are *Metallyticus* spp., in which a few structures, located between the main stem of CuA and cf, could be interpreted as CuA veinlets (colored as a green-to-black gradient in Fig. 2F). Stem-Dictyoptera display the same state as Mantodea, hence *P. enigmaticus* is a Blattodea, and likely a relative of Blattellinae or Blaberidae.

Due to the relatively poor preservation, the shape of the pronotum is not evident. However, if it is as described by Nel & Roy (1996; i.e., with broad side lobes) this is consistent with a placement of *P. enigmaticus* in Blattodea or as

stem-Mantodea, given that stem-Dictyoptera and nearly all Blattodea possess this state. Note that it must then be assumed that crown-Mantodea secondarily lost the state –except for leaf-mimic ones, which probably re-gained it.

In summary, there is compelling evidence that *P. enigmaticus* is not a Mantodea but a Blattodea, *contra* Nel & Roy (1996). To some extent, the position of the species within the latter group can be further investigated. In the forewing of *P. enigmaticus* ScP has no apparent posterior branch (herein regarded as the basal-most branch of R translocated onto ScP; see Material & Methods and Fig. 2A). Such branch is present in all Blattodea except Blattidae and Blaberidae. The absence of translocation is likely the plesiomorphic state, as it occurs in stem-Dictyoptera. This state indicates that *P. enigmaticus* is likely a crown-Blattidae or crown-Blaberidae, or a stem relative of any other family. As mentioned above, CuA has many branches reaching cf in *P. enigmaticus*. This state is unique to Blattellinae and Blaberidae. All the characters displayed by this taxon are congruent with a placement in Blaberidae. However, lack of data prevent a formal placement of this taxon as a crown- or stem-representative of this clade (or its sister group).

The wide awm-ScP area and the dense cross-vein reticulation may be reminiscent of leaf mimicry. In following Piton (1940), Nel & Roy (1996) compared *P. enigmaticus* with *Choeradodis* and other genera of leaf-mimicking Mantodea. Among cockroaches, this kind of mimicry mostly occurs in Blaberidae, primarily in Epilamprinae, many of whom have the appearance of dead leaves (DAE, pers. obs.; Anisutkin 2014, 2015). Nel & Roy (1996) concluded that these characters are not useful for systematic placement among Mantodea because they may be convergently derived, and we hold the same is true within the context of Blattodea.

The new placement we propose has implications for dating analyses. Grimaldi (2003) cited *P. enigmaticus* as the oldest fossil member of the Mantodea super-family Mantoidea. It has been subsequently used as a fossil for time calibration of the Mantodea tree in multiple phylogenetic analyses (e.g. Legendre *et al.* 2015; Wang *et al.* 2017). The new placement obviously means that it is an inappropriate calibration point for Mantodea. Legendre *et al.* (2015) also listed *Arvenineura insignis* Piton, 1940, from the same locality as *P. enigmaticus*, as stem-Chaeteessidae. The characters listed by these authors are: 1) the shape of the stigma (see footnote to table 1); and 2) the posterior branch of CuA being simple. As for (1), although the particular state displayed by *A. insignis* was not specified by Legendre *et al.* (2015), the species shares with Chaeteessidae a comparatively long stigma. This state is a putative plesiomorphy, as it occurs in *Cretophotina tristriata* Gratshev & Zerikhin, 1993 (see Grimaldi 2003: fig. 5b, c), regarded as a stem-Mantodea (Grimaldi 2003). As for (2), the state is also a putative plesiomorphy, as it also occurs in *C. tristriata* but also in *Santanmantis axelrodi*, both regarded as a stem-Mantodea (Grimaldi 2003). Moreover, it is not present in the holotype of *A. insignis* Pinto, 1940 (Nel & Roy 1996: fig. 1). In summary, the placement of *A. insignis* as crown-Mantodea

is not evident. Given the above, to our knowledge, there are no formally described and well-assigned fossil crown-Mantodea (but see Ehrmann 1999; Zherikhin 2002: fig. 384, and Ross in press) suitable for date calibration.

As a putative Blaberidae from the Menat deposit, *P. enigmaticus* holds equal ranking with “*Gyna*” *obesa* Piton, 1940 as the oldest member of this family (Evangelista *et al.* 2017). The poor preservation of both fossils unfortunately precludes us from establishing a formal higher-ranking classification to nest these taxa, which may not be closely related.

CONCLUSIONS

The fossil insect species *P. enigmaticus*, known from a single imprint fossil from Menat, is a representative of Blattodea (possibly a Blaberidae) and not a Mantodea. There are three independent morphological characters supporting this placement unambiguously. The new placement makes it an invalid fossil for calibration of the Mantodea tree, as it has been used in the past. If a Blaberidae, it ranks as the oldest known representative alongside “*Gyna*” *obesa* Piton, 1940.

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