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The beetle-like Palaeozoic and Mesozoic roachoids of the so-called “umenocoleoid” lineage (Dictyoptera: Ponopterixidae fam. nov.)

Les « blattoïdes » paléozoïques et mésozoïques au sein de la lignée dénommée « uménocoléoïde » (Dictyoptera : Ponopterixidae fam. nov.)

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A B S T R A C T

The position of Palaeozoic and Mesozoic roachoids and their relationships to crown-group Dictyoptera is an unresolved problem of insect systematics since Hennig's time. This contribution presents new data based on the wing venation of the Early Cretaceous group Cratovitismioidea (so-called “Umenocoleoidea”) supplemented with the discovery of the first Late Palaeozoic representative. As *Umenocoleus*, type genus of the Umenocoleidae, is considered as a Coleopterida, the roachoids currently included in the Umenocoleidae are transferred to the new family Ponopterixidae, in the new superfamily Cratovitismioidea. *Permoponopterix lodevensis*, a new ponopterixid genus and species, is described as the oldest representative of this superfamily, from the Middle Permian of the South of France. A new species *Ponopterix burkhardi* is described from the Lower Cretaceous of Crato Formation in Brazil. Convergent adaptations of tegmina in Coleopterida, Protelytroptera and Cratovitismioidea are discussed.

Keywords:

Insecta
Umenocoleoidea
Umenocoleidae
Ponopterixidae
Cratovitismioidea superfam. nov.
Middle Permian
Lower Cretaceous
Forewing adaptations

R É S U M É

La position des « blattoïdes » paléozoïques et mésozoïques et leurs liens de parenté au sein des Dictyoptera est un problème non résolu depuis Hennig. La présente contribution propose de nouvelles données basées sur la nervation alaire du groupe du Crétacé inférieur Cratovitismioidea (anciennement nommé « Umenocoleoidea »), complémenté par la découverte de leur premier représentant paléozoïque. Comme *Umenocoleus*, genre type des Umenocoleidae, est considéré comme un Coleopterida, les Dictyoptera actuellement inclus dans les Umenocoleidae sont transférés dans la nouvelle famille Ponopterixidae, dans la nouvelle superfamille Cratovitismioidea. *Permoponopterix lodevensis*, genre et espèce

Mots clés :

Insecta
Umenocoleoidea
Umenocoleidae
Ponopterixidae
Cratovitismioidea superfam. nov.
Permien moyen
Crétacé inférieur
Adaptations de la tegmina

nouveaux de Ponopterixidae, est décrit comme plus ancien représentant de cette super-famille du Permien moyen du Sud de la France. Une nouvelle espèce *Ponopterix burkhardi* est décrite dans le Crétacé inférieur de la formation Crato (Brésil). Les adaptations convergentes des tegmina chez les Coleoptera, Protelytroptera et Cratovitismoidea sont discutées.

1. Introduction

Cockroaches, termites and mantids form the well-supported clade of Dictyoptera (Trautwein et al., 2012). Its history dates back to the Late Palaeozoic with numerous “roachoids” representative of its stem lineage and the Palaeozoic order Paoliida as a sister group (Grimaldi and Engel, 2005; Prokop et al., 2013). One of these “roachoid” lineages is the enigmatic Mesozoic superfamily “Umenocoleoidea” whose members are recorded in amber and lacustrine deposits from the Early Cretaceous of Brazil, Albian–Cenomanian Burmese amber, China, Jordan, Lebanon, Mongolia, Russia, and Late Cretaceous of New Jersey (USA) (Grimaldi and Engel, 2005; Kaddumi, 2005; Ross et al., 2010; Shi et al., 2012). These polyneopteran insects (bearing well developed cerci) have a generally beetle-like appearance with saddle or shield-shaped pronotum, and strongly sclerotized forewings. According to Bechly (2007) they have membranous hindwings with a pattern of venation supposedly similar to the Mesozoic family Blattulidae, but this point needs further investigation. Another significant feature of this group shared with the other extinct “roachoids” is the presence of an external ovipositor, which would prevent its placement among modern cockroaches, but not necessarily in the crown-group Dictyoptera because modern mantises also have short external ovipositors. Blattodea or cockroaches *sensu stricto* (Beccaloni and Eggleton, 2013), are characterized by the presence of ootheca deposited after sclerotization and an internal ovipositor completely hidden in the genital pouch (Grandcolas, 1996). Recently, Kirejtshuk et al. (2013) re-evaluated *Umenocoleus* Chen and T’an, 1973, the type genus of the Umenocoleoidea and Umenocoleidae, and transferred it to the beetle lineage Coleoptera. Thus the genuine “roachoids” previously considered “Umenocoleoidea” are reconsidered here. Additionally, an enigmatic beetle-like sclerotized tegmen recently discovered in the Middle Permian of the South of France (Salagou Formation), plus that of a new, very large beetle-like “roachoid” from the Early Cretaceous Crato Formation in Brazil are described and discussed below.

2. Material and methods

The material was studied using a Nikon SMZ 1500 and an Olympus SZX9 stereomicroscopes. Photographs were taken with an Olympus E3 SLR camera and 3D-images were produced with an Opto-digital Olympus DSX500 microscope. The specimen LdLAP 337 (Museum of Lodève, France) was also examined with a Tescan Vega LSU scanning electron microscope (Environmental SEM)

at the Museum national d’histoire naturelle to observe the characters not clearly visible through the optic stereomicroscope with the Low Vacuum Secondary Electron TESCAN (LVSE mode).

The wing venation nomenclature generally follows Kukulová-Peck (1991).

Wing venation abbreviations used: ScP – subcosta posterior, RA/RP – radius anterior/posterior, M – median vein, CuA/CuP – cubitus anterior/posterior, A1/A2 – first/second anal vein, ads. I. – adsutural line.

3. Systematic palaeontology

Super-order Dictyoptera Clairville, 1798.

Order Blattodea Brunner von Wattenwyl, 1882.

Superfamily Cratovitismoidea Bechly, 2007 stat. nov.

Included families: **Ponopterixidae** fam. nov., Cratovitismoidea Bechly, 2007.

Diagnosis: See below.

Family *Ponopterixidae* Nel, Prokop and Kirejtshuk fam. nov.

Type genus. *Ponopterix* Vršanský and Grimaldi in Vršanský (1999a).

Other genera. *Blattapterix* Vršanský, 2003, *Petropterix* Vršanský, 2003, *Elytropterix* Vršanský, 2003, *Jantaropterix* Vršanský, 2003 and *Permoponopterix* gen. nov.

Diagnosis. See below.

Genus ***Permoponopterix*** Nel, Prokop and Kirejtshuk gen. nov.

Type species. *Permoponopterix lodevensis* sp. nov.

Etymology. Named after the Permian Period and the genus *Ponopterix*.

Diagnosis. Forewing (tegmen) characters only; tegmen narrow elongate; RP, M and CuA simple; no distinct bulge on surface of tegmen; tegmen strongly convex; a pronounced adsutural line; a pronounced shoulder at base of M, CuA and CuP.

Permoponopterix lodevensis Nel, Prokop and Kirejtshuk sp. nov. (Figs. 1A–C and 2A–D).

Etymology. Named after the Lodève area.

Material. Holotype specimen LdLAP 337 A-B (imprint and counterimprint of a tegmen), additional specimen LdLAP 169 B; Lapeyrie collection, stored at the Musée Fleury in Lodève, France.

Type locality. Specimen LdLAP 337 is from outcrop F34 of “Les Vignasses”, specimen.

LdLAP 169 is from outcrop “Les Canals III” (Garric, 2000), near Lodève, Hérault, France.

Type stratum. Salagou Formation, Mérifons member, Middle Permian, Guadalupian (Schneider et al., 2006).

Diagnosis: As for the genus.

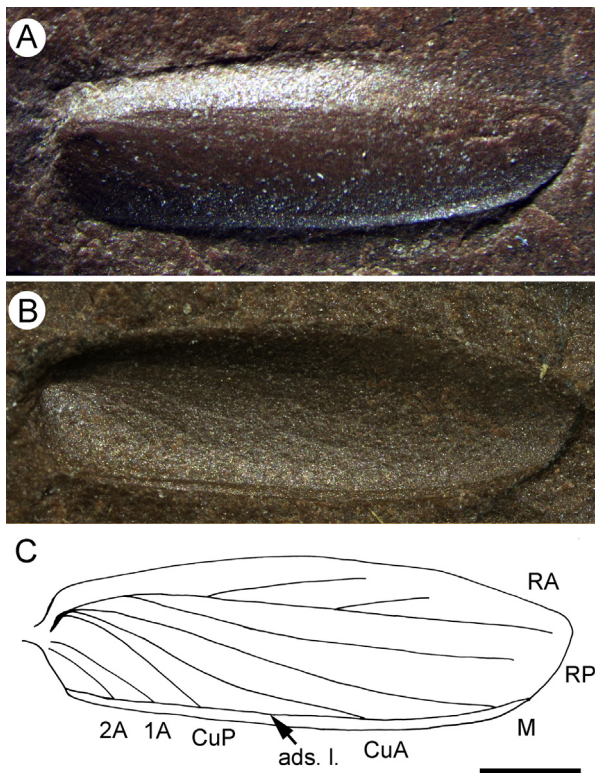


Fig. 1. (Colour online.) *Permoponopterix lodevensis* sp. nov. holotype specimen No. LdLAP 337 (Musée of Lodève, France–Lapeyrie collection): **A–B**, photographs of imprint and counterimprint of tegmen; **C**, line drawing of wing venation (scale bars represent 1 mm).

Fig. 1. (Couleur en ligne.) Spécimen holotype de *Permoponopterix lodevensis* sp. nov. n° LdLAP 337 (musée de Lodève, France – Collection Lapeyrie): **A–B**, photographies d’empreintes et contre-empreintes de tegmen; **C**, dessin au trait de la nervation alaire (les barres d’échelle représentent 1 mm).

Description: The description is based only on the type specimen LdLAP 337 because the additional specimen LdLAP 169 is poorly preserved and does not add information.

Tegmen complete with only costo-apical part partly deteriorated and covered with sediment, 5.3 mm long, 1.7 mm wide, tegmen strongly convex; more precisely transverse section of tegmen in its middle, flat in its anterior part, strongly convex at level of veins M and CuA and less convex along posterior margin (see Fig. 2A–D); tegmen surface covered with small punctuations (cells?) mainly in its distal part; the tegmen was probably originally sclerotized because of its strong convexity and traces of cellulation; a pronounced shoulder at base of Radius; vein ScP not visible, maybe absent; a broad and flat ascending area between anterior wing margin and Radius, 0.5 mm wide; R forked into RA and RP 1.0 mm from wing base; RA convex, with two visible faint anterior branches and main stem straight, ending near wing apex; RP less convex (less distinct) simple and slightly curved, ending near wing apex; M, CuA and CuP fused with R at wing base, all separated from radial stem 0.3 mm from wing base; a strong shoulder at this point; M and CuA simple and slightly anteriorly curved; M ending on posterior adsutural line 4.6 mm from

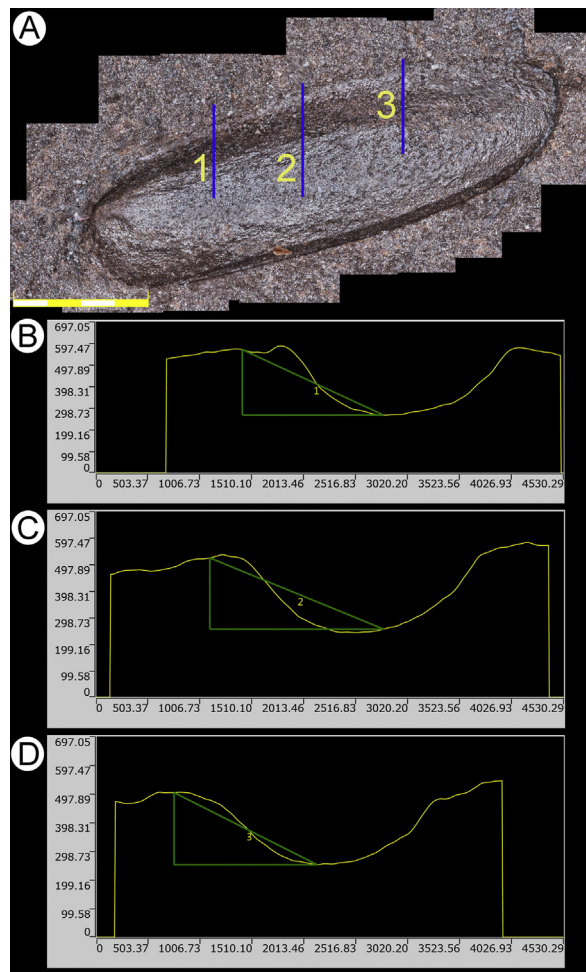


Fig. 2. (Colour online.) *Permoponopterix lodevensis* sp. nov. holotype specimen No. LdLAP 337 (Musée of Lodève, France – Lapeyrie collection): **A**, photograph of tegmen with indication of three relief cross-sections; **B–D**, diagrams showing the tegmen relief on the cross-sections (respectively B for section 1, C for section 2, and D for section 3) by use of an Opto-digital Olympus DSX500 microscope (scale bar represents 2 mm).

Fig. 2. (Couleur en ligne.) Spécimen holotype *Permoponopterix lodevensis* sp. nov. n° LdLAP 337 (musée de Lodève, France – Collection Lapeyrie): **A**, photographie de tegmen, avec indication de trois coupes transversales en relief; **B–D**, diagrammes montrant le relief du tegmen sur les coupes (respectivement B pour la coupe 1, C pour la coupe 2 et D pour la coupe 3), obtenues au microscope opto-digital Olympus DSX500 (la barre d’échelle représente 2 mm).

wing base; M less convex than CuA; CuA ending on posterior adsutural line 3.5 mm from wing base; simple concave CuP reaching adsutural line 1.8 mm from wing base; adsutural line strongly marked, concave and closely parallel to posterior forewing margin, 0.1 mm apart; three anal veins present, distally fused to constitute an adsutural line closely parallel to posterior wing margin; no crossveins.

Discussion. According to an original combination of morphological characters this strange fossil could be related to several different groups. First, it shares some similarities with Coleoptera, with the following characters: tegmina very convex and probably strongly sclerotized; all veins (except RA) simple and rather weakly marked

on tegmina; a posterior adsutural line. But it cannot be attributed to this clade because of the following characters: RA with anterior branches; M, CuA, and CuP basally fused with radial stem. The Coleopterida and their sister group Skleropectera (*Stephanastus* Kirejtshuk and Nel, 2013, Late Carboniferous) have a M+CuA completely separated from radial stem and a simple RA (Kirejtshuk et al., 2013; Nel et al., 2013). *Permoponopterix* gen. nov. has a tegmen venation completely different from that of a Glosselytroidea, mainly lacking a broad precostal area and markedly less developed median veins (see Béthoux et al., 2007). Another group candidate for a placement of this fossil is the Proteleptoptera (Tillyard, 1931, currently thought to be related to the Dermaptera (Gorochov and Anisyutkin, 1998; Haas and Kukulová-Peck, 2001; Hennig, 1981), mainly on the basis of the hindwing venation.

The type family, genus and species of the Proteleptoptera are the Protelytridae, and *Protelytron permianum* (Tillyard, 1931) (see Fig. 3A, B). *Permoponopterix* shares with *Protelytron* a series of characters, viz. RP, M, CuA, CuP, and anal veins simple; presence of an adsutural line; presence of a broad rather flat area between Radius and anterior wing margin. Although the tegmina of the modern Dermaptera retain very few veins, difficult to interpret, few Mesozoic fossils show a more developed tegmen venation. *Sinopalaeodermata neimonggolensis* Zhang, 2002 known from the Middle/Upper Jurassic of Daohugou in China has all the veins simple, and an anal vein parallel to the posterior wing margin, but the vein branching at the wing base is not clearly preserved (see Zhang, 2002: text-fig. 2, Plate 1). The protodyplatid *Microdiplatys perfectus* Vishniakova, 1985 known from the Middle Jurassic of Siberia is an isolated tegmen showing all the main structures also present in the Protelyptoptera (Vishniakova, 1985: 147, fig. 1).

Permoponopterix differs from *Protelytron* (and the other Proteleptoptera) and *Microdiplatys* in the three veins M, CuA and CuP fused with radial stem near wing base (instead of having a long stem Cu from which CuA and CuP emerge, see Carpenter, 1992), RA with anterior branches, ScP indistinct (or absent), instead of being strongly marked in its basal part, adsutural line concave instead of being convex in the Proteleptoptera (our observations in several Proteleptoptera), and no costal expansion at the wing base. Note that *Austrelytron* Kukulová, 1966 was supposed to have a CuA basally separated from CuP and fused with median vein, after Kukulová (1966), unlike *Protelytron*. In reality, *Austrelytron* has a venation of the same type as *Protelytron* with a long common stem Cu from which CuP and CuA separate rather close to the posterior wing margin, similar to e.g. *Protelypteron furcatum* Carpenter, 1939 (see Figs. 3C and 4).

The last candidate group is the Mesozoic dictyopteran lineage of so-called "Umenocoleoidea" from the Crato Formation in Brazil (*sensu* Bechly, 2007). Vršanský (2003a) proposed to include in this group several taxa from the Mesozoic of Asia. The enigmatic taxon *Umenocoleus* Chen and T'an, 1973 (type genus of the Umenocoleidae) differs from the true dictyopteran taxa that have been mixed with it in the following points: CuA fused with M, the stem of Cu+M is well separated from radius in basal part of wing, RA

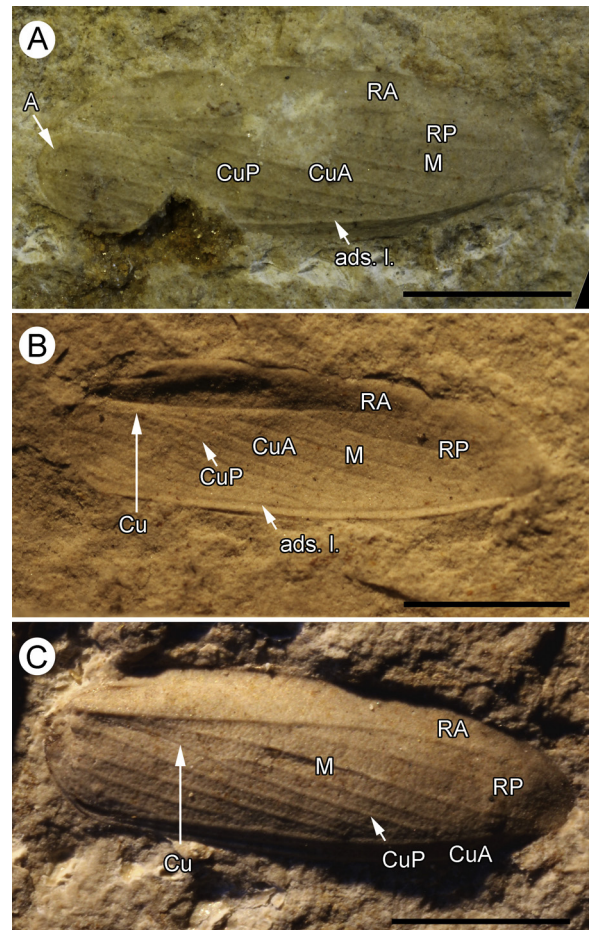


Fig. 3. (Colour online.) Photographs of *Protelytron* spp.: **A**, *Protelytron permianum* (Tillyard, 1931) No. MCZ 3889a (Museum of Comparative Zoology, Cambridge, USA); **B**, *Protelytron angustum* Carpenter, 1933, Holotype No. MCZ 3371 (Museum of Comparative Zoology, Cambridge, USA); **C**, *Protelytron furcatum* Carpenter, 1939, Paratype MCZ 3885 (Museum of Comparative Zoology, Cambridge, USA; scale bars represent 2 mm).

Fig. 3. (Couleur en ligne.) Photographies de *Protelytron* spp. : **A**, *Protelytron permianum* (Tillyard, 1931) n° MCZ 3889a (Museum of Comparative Zoology, Cambridge, MA, États-Unis); **B**, *Protelytron angustum* Carpenter, 1933, Holotype n° MCZ 3371 (Museum of Comparative Zoology, Cambridge, MA, États-Unis); **C**, *Protelytron furcatum* Carpenter, 1939, Paratype MCZ 3885 (Museum of Comparative Zoology, Cambridge, États-Unis ; les barres d'échelle représentent 2 mm).

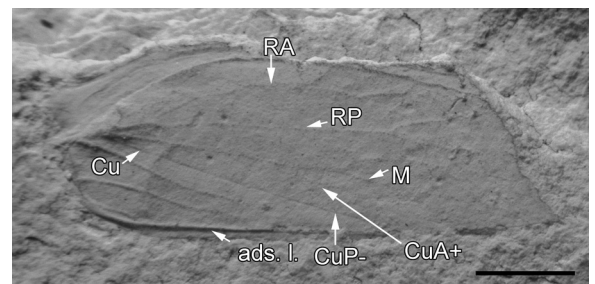


Fig. 4. Photograph of *Austrelytron tillyardi* Kukulová, 1966 No. In45525 (The Natural History Museum, London, UK; scale bars represent 2 mm).

Fig. 4. Photographie d'*Austrelytron tillyardi* Kukulová, 1966 n° In45525 (The Natural History Museum, Londres, Royaume-Uni ; les barres d'échelle représentent 2 mm).

is simple. These characters are typical of the Coleoptera lineage (Kirejtshuk et al., 2013).

Thus, the Dictyoptera that are currently put in the “Umenocoleidae” and “Umenocoleoidea” have to be removed from these taxa and put separately under other family and superfamily names. Currently, the “Umenocoleoidea” sensu Bechly (2007) comprise the three families Vitismidae Vršanský, 2001, Cratovitismidae Bechly, 2007 and the “Umenocoleidae” sensu Bechly (2007), while Vršanský (2003a) added the two modern families Anaplectidae and Oulopterygidae in this group. Note that Lee and Shi-Wei (2011) separated the Cratovitismidae from the “Umenocoleoidea” and maintained the Anaplectidae and Oulopterygidae in this superfamily, a hypothesis that Bechly (2007) rejected and nonetheless that would have to be considered also with respect to morphological characters put forward in classifications based on modern species (e.g. Grandcolas, 1996; Grandcolas and Pellens, 2012; Princis, 1960). However, Anaplectidae and Oulopterygidae have key synapomorphies of modern cockroaches, i.e. presence of ootheca deposited after sclerotization and internal ovipositor, which exclude them from the “Umenocoleoidea”.

We propose to create the family Ponopterixidae fam. nov. for the species that were included in the so-called “Umenocoleidae” (with the exclusion of *Umenocoleus*), i.e. five Mesozoic genera with 10 species: *Blattapterix* Vršanský, 2003, *Petropterix* Vršanský, 2003, *Elytropterix* Vršanský, 2003, *Jantaropterix* Vršanský, 2003 and *Ponopterix* Vršanský and Grimaldi in Vršanský (1999a). We propose to choose the genus *Ponopterix* as type genus of this new dictyopteran family, with the following new amended family diagnosis: head transverse; pronotum saddle-like and much narrower than head (except in *Jantaropterix*); sclerotized forewing only with rather reduced wing venation; legs spiny and tarsi very long (nearly as long as tibia) and apparently five-segmented (first segment the longest, second segment the second longest) as in cockroaches; cerci with about 13 segments; females with a short but external, i.e. projected from genital pouch, ovipositor. Consequently, the positions of these dictyopteran taxa that were previously included in the superfamily “Umenocoleoidea” have to be reconsidered.

Vršanský and Ansoerge (2001) created the Vitisminae in the Polyphagidae Saussure, 1864 (junior synonym of the Corydiidae Saussure, 1864, see Beccaloni and Eggleton, 2013), for the Mesozoic genus *Vitisma* Vršanský, 1999 (Vršanský, 1999b). Later Vršanský (2003b, 2005) transferred this subfamily in the Holocompsidae Rehn, 1951. Bechly (2007) erected the family Vitismidae and put it together with the Cratovitismidae Bechly, 2007 and the other Dictyoptera attributed to the “Umenocoleidae” in the superfamily “Umenocoleoidea”. The difficulty is that he proposed no clear synapomorphy to support this hypothesis. The most obvious character of the “Umenocoleoidea” sensu Bechly (2007), viz. Dictyoptera with beetle-like appearance, with sclerotized tegmina, although present in *Vitisma*, is not really sufficient to characterize a precise group of Blattodea, because very different roaches of different families have sclerotized tegmina, i.e. *Therea* Billberg,

1820 from Corydiidae (Grandcolas, 1993), *Prosoplecta* Saussure, 1864, *Calhyphornna* Saussure and Zehntner, 1893 from Ectobiidae (Anisyutkin, 2013; Grandcolas, pers. obs.; Roth, 1994), *Diploptera* Saussure, 1864, *Derocalymma* Burmeister, 1838 and *Paraplecta* Shelford, 1907 from Blaberidae (Rehn, 1951; Grandcolas, pers. obs.). *Vitisma* has an anteriorly pectinate radius in its tegmina with a series of eight simple parallel anterior branches of R reaching the costal margin and intercalaries veinlets between them, which is not the case for the Ponopterixidae (or the Cratovitismidae). Other characters are as follows: “hindwing with prominent pterostigma”, similar pterostigmata are present in modern *Oulopteryx* Hebard, 1921 for instance; “hindwing venation similar to Blattulidae” Vishniakova, 1982, a Mesozoic family. It is difficult to specify the apomorphic characters that diagnose the blattulid pattern of hindwing venation. Therefore we consider that the attribution of the Vitisminae to the “Umenocoleoidea” is unsupported and we provisionally return the Vitisminae to the Holocompsidae.

Bechly also created the family Cratovitismidae for the Crato taxon *Cratovitisma oldreadi* Bechly, 2007. He indicated that “Vršanský (personal communication) thinks that this new taxon could rather represent a transition between †Liberiblattinidae and †Umenocoleidae. He doubts that it is related to †Vitisminae, which belong to Holocompsidae and have a reduced ovipositor and a very different forewing venation.” The tegmina venation and ovipositor of *Cratovitisma* are nearly identical to those of the Ponopterixidae, although it does not have a saddle-like pronotum.

Consequently, we propose to group together the two families Cratovitismidae and Ponopterixidae in the new superfamily Cratovitismioidea, based on an emended diagnosis, modified from that proposed by Bechly (2007): small roachoid habitus but with beetle-like appearance; large compound eyes; antennae filiform but shorter than body; tegmina sclerotized strongly convex in section; tegmina with a very particular basal fusion of M, CuA and CuP with the stem of radius in tegmina (synapomorphy); tegmina with at least a (more or less pronounced) shoulder at or near the bases of M, CuA and CuP; presence of a concave posterior adsutural line on tegmina (synapomorphy); tegmina with small punctuations (cells); hindwings membranous and with distinct pterostigma; roach-like cerci; female with a small but distinct external ovipositor. The superfamily Umenocoleoidea and the family Umenocoleidae are then reduced to the sole generic taxon *Umenocoleus* with two members (*U. sinuatus* Chen and T’an, 1973 and *U. nervosus* Zhang, 1997).

The modern *Oulopteryx* with tegminous fore wings have also a fusion of M (and CuA in part) with radial stem, but their CuP is not fused with radial stem and they have no adsutural line (Fig. 5A, B). They have tegmina covered with small cells, which renders this character less significant than what Vršanský (2003a) or Bechly (2007) supposed. They also strongly differ from the Cratovitismioidea in their highly specialized hindwing venation (Grandcolas, 1996; Grandcolas and Pellens, 2012).

The two synapomorphies of the Cratovitismioidea are clearly visible in the following taxa: *Blattapterix*, *Ponopterix* [note that Vršanský (2003a: 11) erroneously indicated that *Ponopterix* has the median vein not basally fused with

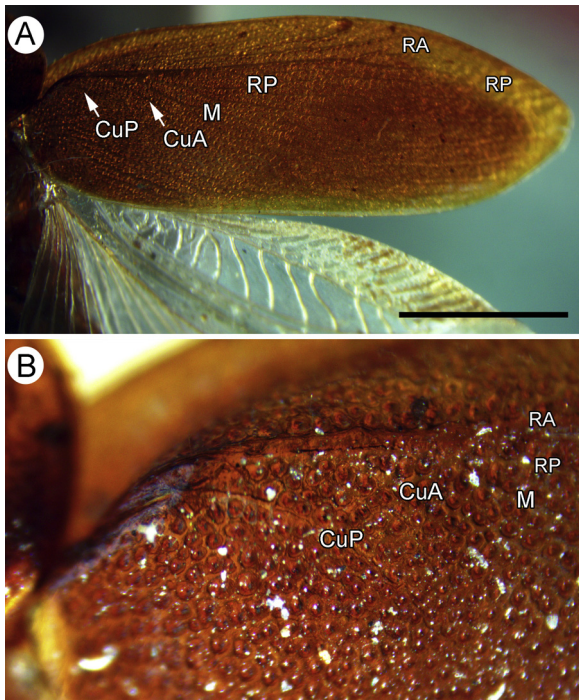


Fig. 5. (Colour online.) *Oulopteryx dascilloides* Hebard, 1921, holotype, Paricabo, French Guiana, E. Le Moutl leg., Muséum national d'histoire naturelle, Paris: **A**, photograph of tegmen (length 6.5 mm); **B**, photograph of tegmen base (scale bar represents 2 mm).

Fig. 5. (Couleur en ligne.) Holotype d'*Oulopteryx dascilloides* Hebard, 1921, Paricabo, Guyane française, leg. E. Le Moutl, Muséum national d'histoire naturelle, Paris: **A**, photographie de tegmen (longueur 6,5 mm), **B**, photographie de la base du tegmen (la barre d'échelle représente 2 mm).

radius in tegmina; see Figs. 6A, B and 7A–C], *Petropterix*, *Elytropterix*, and *Cratovitisma* [clearly visible in Bechly (2007: fig. 11.23a) and in Lee and Shi-Wei (2011): (figs 10–11)]. These characters seem to be absent in *Jantaropterix* [at least Vršanský (1999a: 11) indicated that M is not basally fused with R in this genus, and he did not figure any posterior adsutural line]. This taxon also differs from the other *Ponopterixidae* in the shape of the pronotum, not saddle-like. The exact relationships of this last genus would need further investigations. Vitismidae, Anaplectidae and *Oulopterygidae* have not the two synapomorphies of the *Cratovitismoidea* and no external ovipositor, which renders highly improbable their attribution to this clade.

Permoponopterix shares with the *Cratovitismoidea* the following characters; RA not anteriorly pectinate with few anterior branches; M, CuA and CuP basally fused with the radial stem, a pronounced adsutural line, a pronounced shoulder at the base of M, CuA and CuP (see Fig. 1A–C). The lack of information on the pronotum shape in *Permoponopterix* forbids us to determine if this structure was saddle-like as in the *Ponopterixidae* or not as in *Cratovitismoidea*. Nevertheless, the elongate shape of the tegmina of *Permoponopterix* would support an attribution close to the *Ponopterixidae* rather than to the *Cratovitismoidea*, which have more rounded tegmina. *Permoponopterix* is Permian while the other *Ponopterixidae* are Cretaceous, suggesting that they could belong to

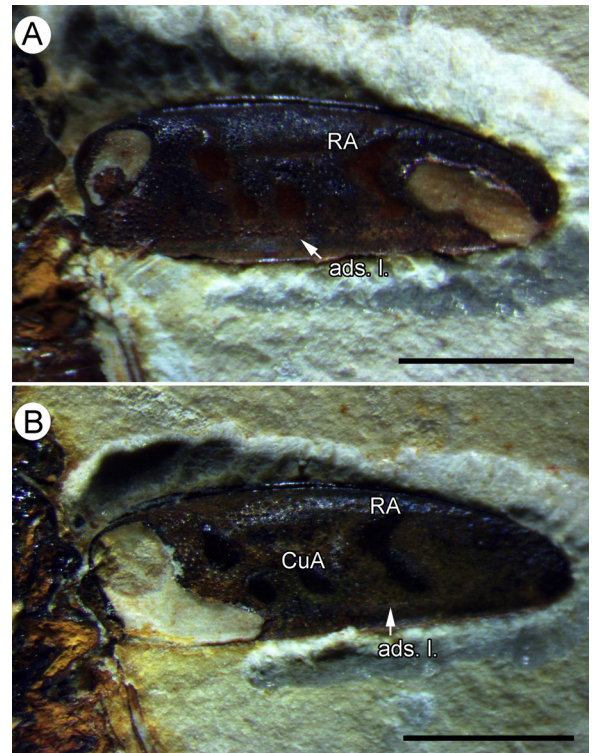


Fig. 6. (Colour online.) *Ponopterix axelrodi* Vršanský and Grimaldi (in Vršanský, 1999a), specimen no. 3, Coll. Borschukewitz, stored in the Entomology collections, Muséum national d'histoire naturelle, Paris: **A**, detail of right tegmen; **B**, detail of left tegmen, bulges visible as black areas devoid of punctuations (scale bars represent 2 mm).

Fig. 6. (Couleur en ligne.) *Ponopterix axelrodi* Vrsansky and Grimaldi (in Vršanský, 1999a), spécimen n° 3, Coll. Borschukewitz entreposée dans les collections d'entomologie, Muséum national d'histoire naturelle, Paris: **A**, détail du tegmen droit; **B**, détail du tegmen gauche; renflements visibles sous forme de zones noires dépourvues de ponctuations (les barres d'échelle représentent 2 mm).

different families but we prefer not to create a different family for this taxon because of the lack of information on its body structures.

Genus *Ponopterix* Vršanský and Grimaldi (in Vršanský, 1999a).

Type species. *Ponopterix axelrodi* Vršanský and Grimaldi (in Vršanský, 1999a). Other species. *Ponopterix maxima* Bechly, 2007, *Ponopterix burkhardi* sp. nov.

Ponopterix burkhardi Nel, Prokop and Kirejtshuk sp. nov. (Figs. 8A–D).

Etymology. Named after Mr Burkhard Pohl, who communicated the type specimen for this study.

Material. Holotype specimen WDC-CCFB-8 (B045), Wyoming Dinosaur Center-Crato, Wyoming, USA.

Type locality. Southern Ceará, Araripe Basin, North-East Brazil.

Type stratum. Early Cretaceous (Aptian, ca. 115 Ma), Crato Formation.

Diagnosis. Tegmina ca. 22 mm long, bulges on tegmina distributed as follows: a large one in anal area, two between CuP and CuA, one on CuA and one on posterior branch

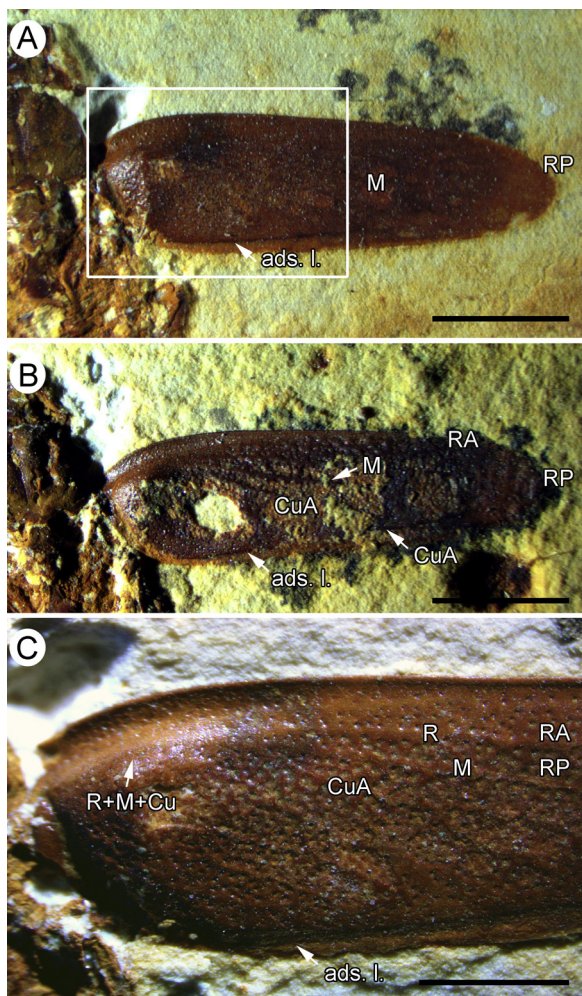


Fig. 7. (Colour online.) *Ponopterix maxima* Bechly, 2007, specimen No. 19, Coll. Borschukewitz, stored in the Entomology collections, Muséum national d'histoire naturelle, Paris: **A**, detail of right tegmen; **B**, detail of left tegmen; **C**, enlarged area of right tegmen delimited by a white rectangle (scale bars represent: A, B, 2 mm, C: 1 mm).

Fig. 7. (Couleur en ligne.) *Ponopterix maxima* Bechly, 2007, spécimen n° 19, Coll. Borschukewitz, entreposé dans les collections d'entomologie, Muséum national d'histoire naturelle, Paris : **A**, détail du tegmen droit ; **B**, détail du tegmen gauche ; **C**, zone agrandie du tegmen droit délimitée par un rectangle blanc (les barres d'échelle représentent 2 mm pour A et B et 1 mm pour C).

of M near posterior wing margin; ScP with clear anterior pectination.

Description. Head and abdomen missing; thorax incompletely preserved, with pronotum saddle-like (a hyperbolic paraboloid structure with a strongly convex median part and anterior and posterior margins laterally raised), 5.5 mm long, 5.3 mm wide; enlarged mesepisterna visible behind pronotum; tegmina complete with only apex partly deteriorated and covered with sediments, 22.3 mm long, 6.6 mm wide, tegmina strongly sclerotized and strongly convex, with several bulges in basal half: a large one in anal area, two between CuP and CuA, one on CuA and one on posterior branch of M near posterior wing margin; tegmina surface covered with small punctuations

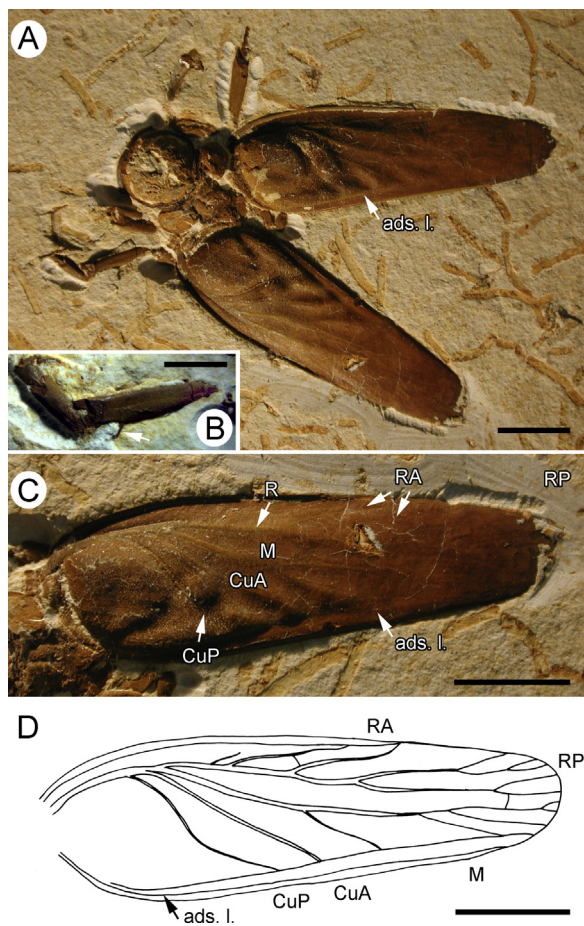


Fig. 8. (Colour online.) *Ponopterix burkharti* sp. nov., Holotype specimen No. WDC-CCFB-8, Wyoming Dinosaur Center-Crato, USA: **A**, photograph of habitus; **B**, photograph of mesothoracic tibia having a strong subapical outer spines; **C**, detail of left tegmen; **D**, line drawing of left tegmen venation (scale bars represent: A, C, D 5 mm, B 2 mm).

Fig. 8. (Couleur en ligne.) Spécimen holotype de *Ponopterix burkharti* sp. nov. n° WDC-CCFB-8, Centre-Crato du Dinosaur, Wyoming, États-Unis : **A**, photographie de l'habitus ; **B**, photographie du tibia mésothoracique possédant une épine externe subapicale robuste ; **C**, détail du tegmen gauche ; **D**, dessin au trait de la nervation du tegmen gauche (les barres d'échelle représentent 5 mm pour A, C, D et 2 mm pour D).

(cells?) mainly in its basal part; a pronounced shoulder between costal margin and Radius; costal margin thick; a concave vein ScP visible, anteriorly pectinate, 7.3 mm long; a broad and flat ascending area between costal wing margin and Radius, 1.3 mm wide; R forked into RA and RP 11.3 mm from wing base; RA convex, with three visible faint anterior branches and main stem straight, going to wing apex; RP less convex (less distinct) simple and slightly curved, ending near wing apex; M, CuA and CuP fused with R at wing base, CuP separated from radial stem 3.6 mm from wing base, CuA 4.2 mm, M 5.0 mm; a strong shoulder in this area; M with four distal branches; CuA simple and slightly anteriorly curved; distal branches of M ending on posterior adsutural line 18.7 mm from wing base; M less convex than CuA; CuA ending on posterior adsutural line 11.3 mm from wing base; simple concave CuP reaching adsutural line 8.8 mm from wing base; adsutural line strongly marked,

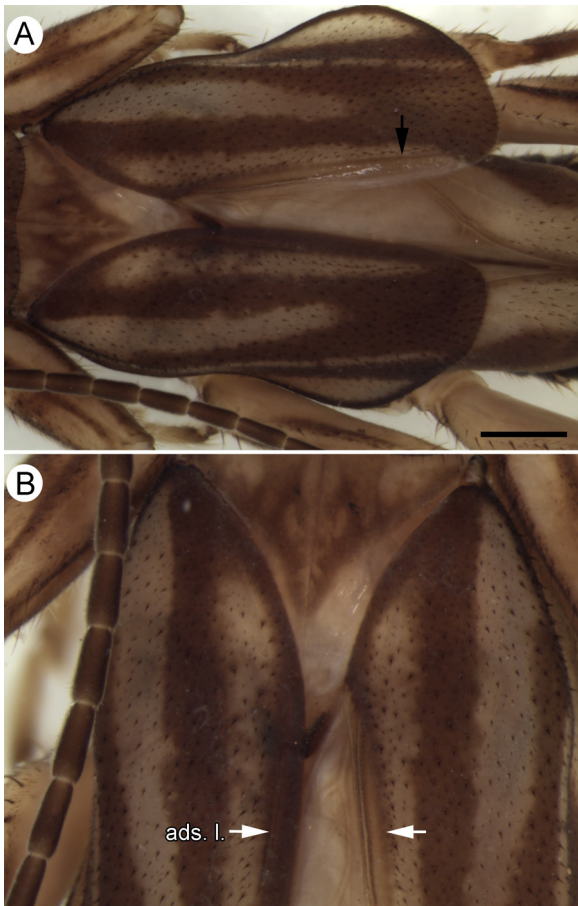


Fig. 9. (Colour online.) *Cranopygia appendiculata* Hincks, 1955, Cambodia, southern part of Elefan mountains, Phnom-Bokor National park, 700–1000 m, 18–22 October 2003, A. Gorochov & M. Berezin coll., Zoological Institute of RAS, St.-Petersburg; **A**, photograph of tegmina; **B**, photograph of basal parts of tegmina (scale bar represents 10 mm).
Fig. 9. (Couleur en ligne.) *Cranopygia appendiculata* Hinks, 1955: **A**, photographie de tegmina; **B**, photographie de parties basales de tegmina (la barre d'échelle représente 10 mm).

concave and closely parallel to posterior forewing margin, 0.8 mm apart; anal area with faint anal veins very indistinct, distally fused and ending in an adsutural line closely parallel to posterior wing margin; no crossveins. Legs very fragmentary; prothoracic with stout femora and slender tibiae, mesothoracic legs with slender tibiae with at least one strong subapical outer spine (see Fig. 8A, B); tarsi poorly preserved.

Discussion. This fossil clearly belongs to the Ponopterixidae and is closely related to the two species from the Crato Formation, i.e. *Ponopterix axelrodi* Vršanský and Grimaldi (in Vršanský, 1999a) and *Ponopterix maxima* Bechly, 2007. *Ponopterix burkhardi* sp. nov. strongly differs from both of them in its distinctly larger size (tegmina 22.3 mm long instead of 4.9–7.5 mm for *P. axelrodi* and 7.5–12.5 mm for *P. maxima*), the distribution of the bulges on the tegmina (bulges nearly absent in *P. maxima* except in the anal area; while *P. axelrodi* has one large bulge in anal area, two along CuP, one transverse on CuA and M in middle

of tegmina, one small on CuA near posterior margin, and a transverse one, bean-shaped, near apex of M (see Figs. 6A, B and 7A, B); and the presence of a more distinct ScP with anterior pectination, while in *P. maxima* and *P. axelrodi*, this vein appears as a concave line close to radial stem).

4. Conclusions

Permoponopterix is the first Palaeozoic and the oldest record of the Cratovitismioidea (so-called “Umenocoleoidea”). This clade was considered to belong to the dictyopteran stem by Grimaldi and Engel (2005), on the basis of the distinct external ovipositor. This position is congruent with their presence in the Permian and their Cretaceous representatives could then be somehow relict.

Similar situations of Mesozoic records of Late Palaeozoic clades can be found in very different Hexapoda, viz. Triassic Monura (Bechly and Stockar, 2011); Early Cretaceous Crato Coxopteroptera (Staniczek et al., 2011); or even Hypoperlida in the middle of the Cretaceous (pers. obs.).

The Coleoptera, Protelytroptera, Dermaptera, and these Dictyoptera: Cratovitismioidea have convergently developed several specialized structures on their tegmina, viz. the presence of a (more or less) distinct flat costal area between anterior tegmina margin and radius (also present in many modern coleopteriform cockroaches, see Shelford, 1912), the presence of an adsutural line (see Figs. 1–2, 5–9), a reduction of the number of branches of the main veins, and a shoulder at the level of the bases of the median and/or cubital veins. These structures are absent in modern Blattodea. A faint vein along the posterior tegmina margin is also present in the modern Dermaptera.

The “adsutural line” is perhaps an important structural element participating in the interlocking of forewings. It could have different origin in the polyneopteran groups, Coleoptera and *Umenocoleus*. In beetles and *Umenocoleus*, it seems to be the result of the successive fusions of the anal veins or anal and cubital veins into a single convex vein parallel to the posterior margin of the tegmina (clearly visible in the case of *Umenocoleus*) and forming in Coleoptera a perfect mechanism for interlocking (Breed and Ball, 1908; Kirejtshuk et al., 2013). In the Protelytroptera and the Dermaptera, it is also a convex structure that seems to have a similar origin (or distinct rib looking like vein), while in *Permoponopterix* and *Ponopterix*, the adsutural line is concave, suggesting that it is of different origin, maybe a false vein, a fold due to the flat posterior margin. It is especially clear in *Ponopterix axelrodi* in which the flat posterior margin is devoid of punctuation, unlike the rest of the tegmina (see Fig. 6).

These differences in the convexity of the “adsutural line” in *Umenocoleus* and in the Cratovitismioidea support the hypothesis that these insects are not related.

The Permian beetles (but not more recent Coleoptera), the Cratovitismioidea and numerous modern Blattodea with sclerotized forewings also share the presence of small and more or less oval cells in tegmina. These cells could be similar in both their origin (transformations of secondary veins and/or primary cells) and function (strengthening of forewing rigidity).

The presence of bulges on the tegmina surface (especially developed in *Ponopterix axelrodi* in which they are smoother than the rest of the surface of the tegmina) could reflect disruptive patterning, breaking up the outline of the insect, linked to mimetism on the surface of tree trunks. Similar structures can be found in the modern Grylloidea Podoscirtidae Cearacesaini, and some beetles (Cerambycidae, Curculionidae), suggesting analogous niches for the Ponopterixidae, especially from the Crato Formation. On the other hand, the presence of remarkable mimetic similarity between modern brightly coloured cockroaches (genus *Prosoplecta*) and some groups of beetles with an open lifestyle on the surface of the substrate (Shelford, 1912), seems to result from a combination of similar interactions with environment and predispositions due to similar “ancestral” interstitial habitats.

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