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Evolution of the elytral venation and structural adaptations in the oldest Palaeozoic beetles (Insecta: Coleoptera: Tshekardocoleidae)

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The oldest definitive beetle, *Coleopsis archaica* gen. et sp. nov., is described from the earliest Permian (Asselian or early Sakmarian) of Germany (Grügelborn/Saarland). Its elytral venation is typical of the Early Permian Tshekardocoleidae. The elytral venation pattern of the type of *Moravocoleus permianus* Kukalová, 1969 is reconsidered in order to clarify structural peculiarities of the type genus of Moravocoleidae Kukalová-Peck & Beutel, 2011, herein regarded as a junior synonym of Tshekardocoleidae. The new discovery allows reinterpretation of the elytral venation, abdominal laterosternites, and other structures, making it possible to identify a 'subelytral space'. Tshekardocoleoidea and Labradorocoleidae are confirmed as Coleoptera, while Umenocoleidae *sensu nov.* and Umenocoleoidea are restored to Holometabola as a potential sister group of all Coleoptera. The holotype of *Umenocoleus sinuatus* Chen & T'an, 1973 needs to be revised in more detail. '*Moravocoleus*' *perditus* Kukalová, 1969, regarded by Ponomarenko as a member of the genus *Avocoleus*, is excluded from Tshekardocoleidae and preliminarily considered as Archostemata incertae sedis. Oborocoleidae is considered as a taxon of more dubious position (order uncertain for *Oborocoleus* Kukalová, 1969, while *Liberocoleus* Kukalová, 1969 probably belongs to Archostemata (family uncertain)). Protocoleoptera and Paracoleoptera are considered as synonyms of Protelytroptera, while Archecoleoptera is dismissed as a paraphyletic group. *Adiphlebia lacoana* Scudder, 1885, previously proposed as the oldest beetle, is not a member of Coleoptera, as confirmed by Kukalová-Peck & Beutel (2012). The composition of beetle suborders and the origin of the order, which probably took place concurrently with the initial diversification of other holometabolan insects, are briefly discussed.

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Keywords: Early Permian; Coleoptera; forewing venation; phylogeny; taxonomy

Introduction

The timing of origin of many holometabolan orders is still rather disputable. A recent molecular-based dating analysis focusing on arthropods proposed a Late Devonian age for the Holometabola (Rehm *et al.* 2011), although currently the oldest record is an Antliophora from the Bashkirian (early Late Carboniferous) (Nel *et al.* 2007; Labandeira 2011). The oldest beetles are much younger, recorded from the Early Permian, with nine extinct families mostly distinguished according to the morphology of the elytra (e.g. Kukalová 1969; Ponomarenko 1969a; Carpenter 1992; Kirejtshuk & Ponomarenko 2012). The most recent molecular-based datings propose a rather congruent age at 285–266 Ma for beetle subordinal diversifications (Hunt *et al.* 2008; McKenna 2011). Early Permian beetles are mainly represented by isolated elytra or incomplete fossils and, therefore, some families were erected based only on characteristic peculiarities in their venation. Consequently,

some of these fossil taxa indeed have an uncertain position pending further study of more complete specimens. Many of these Permian species and some Mesozoic species (especially in Tshekardocoleidae Rohdendorf, 1944; Labradorocoleidae Ponomarenko, 1969b and Umenocoleidae Chen & T'an, 1973) have sclerotized elytra or tegmina with remains of the primary venation which is dorsally unexpressed in most Recent beetles. The forewings of most Permian beetles look so different from those of advanced beetles that, even if originally described as beetles, some authors later transferred them to cockroaches or to the polyneopteran Protelytroptera. Other species initially described as Protelytroptera were later transferred to the Coleoptera (Kukalová 1969; Ponomarenko 1969a). Recently, Béthoux (2009) revised the Late Carboniferous taxon *Adiphlebia lacoana* Scudder, 1885 and considered it as the most basal and ancient beetle. The Early Permian Tshekardocoleidae are another group considered to be one of the most basal beetle families, with the elytra showing

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a very plesiomorphic venation. Their elytra have some superficial similarities with those of the coriaceous tegmina of some Dictyoptera or Protelytroptera, but until now the differences have not been clearly defined. Therefore, confusion in the attribution of ancient representatives of these orders is still possible because of difficulties in the interpretation of the forewing venation.

Traditionally, the appearance of beetles was considered to have taken place together with the early diversification of the Holometabola (Lameere 1900; Martynov 1938). Rasnitsyn (1980) considered the extinct order Miomoptera or Palaeomanteida as the most 'archaic' group of Holometabola, which could have provided the origin for the Coleoptera, Neuroptera and Antliophora, although the position and monophyly of Miomoptera is still debated (Nel *et al.* 2012). There still is no consensus on the sister-group relationships of the Coleoptera. Crowson (1981) considered that Coleoptera arose from Megaloptera or a megalopteran-like ancestor. The most recent molecular or combined (morphological and molecular) phylogenies have proposed a sister-group relationship of Coleoptera with Antliophora (Beutel *et al.* 2011), Neuropteroidea (McKenna & Farrell 2010; Ren & Ning 2012; Ronquist *et al.* 2012), or in an unresolved position (Talavera & Vila 2011).

Anliophora or the neuropteroid insects have been chosen as putative outgroups in the current study to determine the possible plesiomorphic states of characters. In this paper, a new species considered as the most ancient beetle is described from the Early Permian of Germany. Furthermore, *Moravocoleus permianus* Kukulová, 1969 is reconsidered in order to clarify the structural peculiarities of the type genus of Moravocoleidae, and a concept to discriminate the forewings of beetles from those of other insect groups with coriaceous tegmina is elaborated.

The preparation of the current paper required re-examination of some previously described tshekardocoleids deposited in the collection of the Charles University in Prague. Jakub Prokop provided the study with pictures of these specimens and many ideas for this paper; however, he does not share with the other co-authors some points regarding the interpretation of *Moravocoleus permianus*. The names and composition of the taxa of Coleoptera are mostly followed in accordance with their taxonomic interpretation in the catalogue by Kirejtshuk & Ponomarenko (2012), which contains a more detailed overview on the available data on beetles in the fossil record.

Material and methods

In a paper devoted to the description and discussion of the fossil faunas of two outcrops in the Rotliegend of the Saar-Nahe Basin (Sitters and Grügelborn, Germany), Poschmann & Schindler (2004, p. 304, fig. 7) first published photographs and drawings of a new species described herein and tentatively placed it in the family Tshkardocolei-

dae. Later, Brauckmann (2007, p. 191, fig. 17) refigured this specimen and confirmed its tshekardocoleid identity. Supposed beetle remains from the somewhat older Niedermoschel locality (Jeckenbach Subformation of the Meisenheim Formation) have been mentioned in the literature (Malz & Poschmann 1993; Hörschemeyer 1999), but this fragmentary material, which was not available for study, needs to be re-examined.

The Rotliegend specimen examined and described here consists of a part and counterpart preserved in a laminated siltstone with some organic material still present on the impression. Observations were made using an Olympus SZX9 stereomicroscope and a Tescan Vega LSU scanning electron microscope in the Muséum National d'Histoire Naturelle, Paris (MNHN), and a Leica MZ 7.5 stereomicroscope in the Referat Erdgeschichte at the Generaldirektion Kulturelles Erbe RLP, Mainz (GDKE). Images forming Fig. 4A–C were taken with the specimen immersed in alcohol (isopropanol) using either a Canon DSLR 350D or a Leica DFC 420 digital camera attached to the Leica MZ 7.5. In order to enhance the depth of field, multiple images at differing focal planes were taken and combined into a composite using LAS V2.7 image stacking software (by Leica Microsystems). The composite photographs were processed using Adobe Photoshop 7[©]. Polarized light was used and photographs were taken with various degrees of crossing the polarizing filters (for details of the set-up and a discussion on the use of polarized light see, for example, Bengtson 2000).

Abbreviations used: **Sc**: subcosta; **R**: radius; **RA**: radius anterior; **RP**: radius posterior; **M**: media; **CuA**: cubitus anterior; **CuP**: cubitus posterior; **A1**: more 'costal' (anterior) first anal vein (AA1 + 2 *sensu* Kukulová-Peck 1991); **A2**: second anal vein (AA3 + 4 *sensu* Kukulová-Peck 1991); **A3**: third anal vein (AP *sensu* Kukulová-Peck 1991).

The forewing venation terminology of Ponomarenko (1969a, p. 36, text-fig. 16; see Fig. 3A herein) and Kukulová-Peck (1991, p. 177, text-fig. 6.28; see Fig. 3D herein) was used here as a base. However, some modifications in the interpretation of the median anterior, which is not visible as an independent vein, being either fused with RP (hypothesis of Kukulová-Peck 1991) or completely absent, were proposed. This problem has not been resolved for Holometabola, though it is preferable to name the visible median vein as M rather than MP because there is still no clear evidence of a separation of M into MA and MP and/or a fusion of MA with the radial stem. We also follow Kukulová (1969) concerning the basal fusion of M with CuA rather than Kukulová-Peck (1991, p. 177, fig. 6.28 B), Fedorenko (2009, p. 28, fig. 10) and Kukulová-Peck & Beutel (2012, p. 639, fig. 8A) (see Figs 1–3 herein), all of whom considered that these veins are completely separated in beetles (see discussion below). The exact position and nature of the cubitus posterior (CuP) varied greatly in the different papers of Kukulová-Peck (Kukulová 1969; Kukulová-Peck 1991) and Kukulová-Peck & Beutel (2012).

The vein that Kukalová-Peck (1969) considered as CuP was later considered by the same author as CuA, and by Kukalová-Peck & Beutel (2012) as AA1 + 2. Kukalová-Peck (1991) supposed that CuP was a small intercalary veinlet at the base of the elytra, while Kukalová-Peck & Beutel (2012) considered another intercalary veinlet below CuA as CuP. The problem with both of these interpretations is that in other Permian beetles (i.e. *Eocoleus* or *Avocoleus*) the two veinlets are absent and the areas are filled by a net of small cells. These veinlets in *Moravocoleus permianus* are clearly secondary structures due to the reorganization of the net of cells between the main longitudinal veins. In any case, they can be considered as the true CuP. It is clearly more parsimonious to consider that the hypothesis of Kukalová-Peck (1969; Fig. 3C herein) is the correct hypothesis, there being no argument against it apart from the distal part of CuP being convex, though this is also the case for M(P). This ‘abnormal’ convexity of M and CuP in their distal parts is certainly linked to the sclerotization of the elytra.

A reliable homologization of the anal veins in most cases is scarcely possible and in order to avoid probable confusion the authors do not make strict designation of the anal veins. The ‘adsutural line’ is used for the probable posterior anal vein reaching the elytral apex, which in many Tshekardocoleidae separates one or rarely two rows of cells following the posterior edge of the forewings and the derivative of which in some other groups looks like a line. This structure was named by Lubkin (2007) as ‘A3’ and by Kukalová-Peck & Beutel (2012) as ‘AP3 + 4’.

The holotype of the new species is deposited in the Zentrum für Biodokumentation des Saarlandes (ZfB) under the repository number ZfB 3315. The specimens from Obora were borrowed for re-examination from the collection of the Institute of Geology and Palaeontology at the Charles University in Prague (PrF UK). Other specimens of fossil and Recent beetles, cockroaches and Protelytroptera used for comparison are housed at the Zoological Institute of Russian Academy of Sciences, in St. Petersburg (ZIN) and the MNHN.

Geological setting

The NE–SW-trending late Variscan Saar-Nahe Basin extends over an area of about 120 × 40 km and is thus one of the largest European intramontane basins. It is situated south of the Hunsrück Mountains between the cities of Saarbrücken/Saarland and Mainz/Rhineland-Palatinate. The thickness of the preserved Late Carboniferous to Early Permian basin-fill reaches up to roughly 6.5 km (see Stollhofen & Stanistreet 1994 for an overview). It is notoriously difficult to correlate the European non-marine Rotliegend strata with the international (marine) standard and thus their exact chronostratigraphical position is still unresolved (e.g. Boy & Martens 1991), although some progress has been made in recent years (Menning *et al.* 2005).

The material studied herein comes from an outcrop south of Grögelborn, a village in eastern Saarland, approx-

imately 6 km NNE of the city of St Wendel, Germany. Poschmann & Schindler (2004) interpreted the host sediment at this locality as representing lake stage IV of the so-called Humberg Bed. Stratigraphically, this lake horizon is situated at the top of the Meisenheim Formation (= top of the Odernheim Subformation), which is part of the Glan Subgroup within the Rotliegend Group (= Lower Dyas Group) (see Menning *et al.* 2005, 2006; Boy *et al.* 2012). One important tuff marker horizon, the Pappelberg Tuff, which is slightly older than the Humberg lake sediments, has yielded a $^{206}\text{Pb}/^{238}\text{U}$ age of 297.0 ± 3.2 Ma (Königer *et al.* 2002). Poschmann & Schindler (2004) documented the occurrence of the biostratigraphically important cockroach *Spiloblattina odernheimensis* Schneider, 1982 (*Spiloblattinidae* Handlirsch, 1906) at the Grögelborn locality, which indicates the ‘*Sysciophlebia* n. sp. B–*Spiloblattina odernheimensis* zone’. Schneider & Werneburg (2006, 2012) proposed a Sakmarian age for this horizon (see also Werneburg & Schneider 2006). However, Boy & Schindler (2012) argued for an Asselian age of this layer based on the occurrence of discosauriscid amphibians. As a result, we here consider the top of the Meisenheim Formation (and Humberg Bed) as Asselian or possibly earliest Sakmarian in age. However, for the purpose of this contribution, it should be noted that the Grögelborn locality is undoubtedly older than Obora (Letovice Formation, Bačov and Obora horizons) in southern Moravia, Czech Republic, and belonging to the Sakmarian/Artinskian ‘*Syscioblatta* n. sp. Obora–*Moravamylacris kukalovae* zone’ (*Syscioblatta* Handlirsch 1906: *Spiloblattinidae* and *Moravamylacris kukalovae* Schneider, 1980: *Mylacridae* Scudder, 1868) and fish zone of ‘*Xenacanthus decheni*’ (see Schneider *et al.* 2003; Zajíc 2004; Schneider & Werneburg 2006, 2012; Dostál & Prokop 2009).

Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758

Suborder **Archostemata** Kolbe, 1908

Infraorder **Cupedomorpha** sensu Ponomarenko, 2002

Superfamily **Tshekardocoleoidea** Rohdendorf, 1944

Included taxa. The superfamily currently comprises the families Tshekardocoleidae Rohdendorf, 1944 (most representatives from the Early Permian and one from the Late Permian of Soyana) and Labradorocoleidae Ponomarenko, 1969b (Early Cretaceous) (see below).

Family **Tshekardocoleidae** Rohdendorf, 1944

(= Uralocoleidae Zalesky, 1947; Moravocoleidae Kukalová-Peck & Beutel, 2012, syn. nov.)

Type genus. *Tshekardocoleus* Rohdendorf, 1944.

Diagnosis. Body medium-sized (around 10 mm), elongate oval, moderately convex, with very coarse integument. Head usually not transverse, with well-developed eyes,

free labrum, moderately long maxillary and labial palpi, moderately exposed mandibles, wide mentum and widely separated gular sutures. Antennae apparently 13-segmented, about as long as head and pronotum combined. Pronotum with (sub)explanate sides, widening anteriorly and anterior angles projecting anteriorly. Prosternum with intercoxal process. Procoxal cavities oval and apparently closed posteriorly. Mesoventrite longer than prosternum and slightly shorter or comparable in length to metaventrite. Elytra (forewings) complete, with wide epipleura, acute apices, their venation reticulate with veins much narrower than cells; at least eight main veins, intermediate and sometimes some main veins zigzagged; main veins frequently forked, one to five cells between veins; anal vein following sutural edge of elytra. Hindwings (mostly after Kukulová 1969 and Ponomarenko 1969a, p. 49) somewhat longer than forewings; Sc running at distance from anterior edge of hindwing and rather close to CuA; CuA and CuP subparallel. Metacoxae transverse, medially projecting posteriorly and apparently with femoral plates. Abdomen with five movable ventrites and well expressed laterosternites. Secondary telescopic ovipositor not heavily sclerotized. Legs with comparatively narrow femora and tibiae, and five-segmented tarsi.

Included taxa. *Avocoleus* Ponomarenko, 1969a (Obora, Czech Republic); *Boscoleus* Kukulová, 1969 (Obora); *Coleopsis* gen. nov. (Grügelborn, Germany); *Eocoleus* Kukulová, 1969 (Obora); *Moravocoleus* Kukulová, 1969 (Obora); *Permocoleus* Lubkin & Engel, 2005 (Noble County, Oklahoma, USA); *Prosperocoleus* Kukulová, 1969 (Obora); *Retelytron* Kukulová, 1965 (Obora); *Sylvacoleodes* Ponomarenko, 1969a (Tshekarda, Russia); *Sylvacoleus* Ponomarenko, 1963 (Tshekarda); *Tshekardocoleus* Rohdendorf, 1944 (Tshekarda); *Umoricoleus* Kukulová, 1969 (Obora); *Uralocoleus* Zalessky, 1947 (Krutaya Katushka and Soyana, Russia), and *Votocoleus* Kukulová, 1969 (Obora).

Remarks. The genus *Sylvacoleus* is left in this family pending a further re-examination to solve contradictions in character states mentioned below. Kukulová (1969) excluded *Sylvacoleus* from the Tshekardocoleidae, regarding this family as protelytropteran (now in Polyneoptera) and transferred it to the Coleoptera (Holometabola). Ponomarenko (1969a) and Carpenter (1992) treated this genus as a member of the Tshekardocoleidae in the composition of Coleoptera. Its elytra venation differs strikingly from that of other tshekardocoleids in RA and RP not being clearly defined, CuP not visible, CuA not running parallel to the posterior margin in the distal half of elytron, etc. This genus needs to be revised to find a proper placement for it in Archostemata. *Sylvacoleus* resembles *Permocupes* Martynov, 1933 (Late Permian) in elytral venation and antennal structure (Ponomarenko 1969a, p. 55, figs 29, 37, 65).

Permocoleus was initially proposed without any family attribution but with mention of similarities to *Kaltanicupes ponomarenkoi* Pinto, 1987 (Late Permian) in Permocupedidae Martynov, 1933 (Pinto 1987; Lubkin & Engel 2005; Beckemeyer & Engel 2008). Its attribution to Tshekardocoleidae was proposed by Kirejtshuk & Ponomarenko (2012) because M and CuA are basally fused, and CuA is obliquely curved, nearly reaching the forewing apex and becoming closely parallel to the 'adsutural line', as in this family but unlike any other Permian taxa.

Archicupes jacobsoni Rohdendorf, 1961 (Late Permian), *Kaltanicupes richteri* Rohdendorf, 1961 (Late Permian) (both in Rohdendorf *et al.* 1961), and *Maricoleus valentinae* Shcherbakov, 2009 (Early Permian) (in Shcherbakov *et al.* 2009) are based on isolated elytra and are currently considered as Permocupedidae. They share several characters with Tshekardocoleidae, such as CuA being obliquely curved, nearly reaching the forewing apex and becoming closely parallel to the 'adsutural line', a long common stem of M + CuA, etc. They could be related to this latter family but it is premature to transfer them formally until a phylogenetic revision of the Permian beetles is available.

In the course of the preparation of this paper the holotype of *Moravocoleus perditus* Kukulová, 1969, regarded by Ponomarenko (1969a) as a member of the genus *Avocoleus*, was re-examined (Fig. 7A, B). It was found that this species was drawn and described with some misinterpretations. Because the type specimen was taphonomically deformed it is difficult to correctly trace the positions and outlines of sclerites, and also the forewing venation. In particular, the abdomen is detached and twisted. It has six distinct ventrites (not eight as was drawn by Kukulová, or five as in most Archostemata) and looks very short in comparison with the forewings, which show somewhat abnormal positions apparently for taphonomic reasons. In addition, the forewings are probably partly overlapping, making it difficult to separate the very weak veins of each wing (clear only at their bases). Nevertheless, its head and prothorax are similar to those in many beetles (including some Recent archostematans). Because of these problems, this species can be left in the suborder Archostemata only as *incertae sedis*, taking into consideration that the remains of the archidictyon in the forewings of *Moravocoleus perditus* bear resemblance to Archostemata.

The family Moravocoleidae was recently proposed with a rather short description and diagnosis stating "The new family differs from Tshekardocoleidae by the presence of a small field (protosoulder: Kukulová-Peck & Beutel 2012: 369, fig. 8) at the base of the subcosto-radial field (apomorphy), by bearing a broad intra-anal field basally between AA1 + 2 [CuP in our sense] and AA3 + 4 [first anal vein A1 in our sense] (apomorphy), and by retaining a remnant of CuP (plesiomorphy)" (Kukulová-Peck & Beutel 2012, p. 642) [a small veinlet that we consider here as resulting from the re-organization of the net of cells below CuA, see

discussion above]. As to the ‘intra-anal field’, this feature is rather variable among Cupedomorpha in general and is probably of scant value for discrimination of the families of this infraorder.

Among the taxa that are currently included in the Moravocoleidae, the ‘protoshoulder’ is present in *Moravocoleus permianus*, *Votocoleus submissus* Kukulová, 1969, *Boscoleus blandus* Kukulová, 1969, and possibly *Retelytron conopeum* Kukulová, 1969. This part is not preserved in *Umoricoleus perplex* Kukulová, 1969 and *Prosperocoleus prosperus* Kukulová, 1969. The area between R and Sc that should include the ‘protoshoulder’ is very narrow in the moravocoleid *Eocoleus scaber* Kukulová, 1969, as narrow as in *Avocoleus fractus* (Kukulová 1969). The protoshoulder is not clearly expressed in either species. This last taxon has an area between ‘AA1 + 2’ and ‘AA3 + 4’ (*sensu* Kukulová-Peck & Beutel 2012) as broad as *Eocoleus scaber* and there is thus no reason to exclude it from the same group.

However, some species of other Early Permian families have a ‘protoshoulder’ (e.g. *Sylvacoleus sharovi* Ponomarenko, 1963), with *Uralocoleus ultimus* Ponomarenko, 2000 showing its most prominent expression (see also below in the Discussion). The type specimen of *Tshekardocoleus magnus* Rohdendorf, 1944, which is the type species of the type genus of Tshekardocoleidae, has the area between R and Sc, where the ‘protoshoulder’ should be present, not well preserved, even if it is as broad as in *Eocoleus* and *Avocoleus*. Thus it is not possible to decide whether *Tshekardocoleus* has a ‘protoshoulder’. Also the area between the so-called ‘AA1 + 2’ and ‘AA3 + 4’ is as broad in *Tshekardocoleus* as in *Votocoleus*. Thus these structures are not sufficient to separate the families Tshekardocoleidae and Moravocoleidae.

Ponomarenko (1963) already demonstrated that all characters in the elytral venation which were declared as diagnostic for Moravocoleidae are present in *Tshekardocoleus* and, moreover, the area named by Kukulová-Peck & Beutel (2012) as the ‘protoshoulder’ is also shown in his ground plan for the elytral venation of Tshekardocoleidae (Ponomarenko 1969a, p. 37, fig. 16; see also Fig. 3A herein). Thus, Moravocoleidae is a junior synonym of Tshekardocoleidae.

Genus *Coleopsis* Kirejtshuk, Poschmann & Nel, gen. nov.

Type species. *Coleopsis archaica* sp. nov.

Diagnosis. Body of medium size (7.8 mm); rather elongate, dorsally and ventrally subflattened, with coarsely sculptured integument. Head prognathous, with oval eyes projecting laterally; labrum free and exposed from under frons. Maxillary labial palpi moderately developed, with elongate ultimate palpomeres. Prothorax transverse, its sides subflattened and widening anteriorly; prosternum about as long as pronotum, procoxae suboval and apparently

narrowly separated. Scutellum small and triangular, angular at apex. Mesocoxae apparently suboval, (sub)contiguous. Metepisterna moderately narrow and gradually widening anteriorly. Metaventricle about as long as wide at base and with transverse suture. Metacoxae with their median parts narrowly projecting posteriorly. Abdomen with five ventrites. Elytra wider than prothorax, sides apparently subexplanate, apices conjointly acuminate; shoulders moderately raised; line between Sc and lateral edge (below epipleural ridge); Sc apparently nearly reaching elytral apices; R branching in the distal half of elytra, producing three veins at apices. CuA (+ M) branching into CuA and M at middle of elytra; CuP fusing with first anal vein at elytral base; anal veins approaching suture in anterior half of elytra; cells between veins of elytra rather small and oval, only weak traces of rows along veins. Legs moderately developed, with narrow tibiae.

Derivation of name. The name of this genus is formed from the Greek ‘*coleos*’ (sheath, scabbard) and ‘*opsis*’ (resembling a (specified) thing).

Comparisons. The scutellum of *Coleopsis* gen. nov. is smaller than in other members of the family, at least for those in which it is known, the cells in the distal half of the elytra of the new genus become finer and less regular, and CuA is more strongly curved towards the suture (thus, the elytral cells become somewhat similar to those in *Umenocoleus sinuatus* Chen & T’an 1973 from Umenocoleidae). CuP in *Coleopsis* is arcuately oblique and fused with the first anal vein near the forewing base, forming a distinct triangle very similar to that in *Prosperocoleus*. RP of *Coleopsis* has two well-defined, separate branches emerging from the radial stem (instead of only one as in many members of the family).

The new genus *Coleopsis* differs from:

- *Avocoleus* in elytral apices not extending behind abdominal apex; pronotum widening anteriorly; smaller scutellum; smoother venation and cells, cells markedly smaller and becoming yet smaller and diffuse in distal half of elytra, although in *A. neglegens* (Kukulová 1969) they are also small in area between first anal vein and CuP; CuP arcuately oblique, short and ending on first anal vein well basal to separation of M and CuA, not subparallel to first anal vein; CuA and M branching in middle of elytra rather than in anterior third; RP with two branches instead of only one.
- *Boscoleus* in pronotum widened anteriorly; smaller scutellum; elytral cells much smaller and becoming diffuse in distal half of elytra; CuP ending on the first anal vein, not disappearing at its end; CuA and M branching in middle of elytra rather than in anterior fourth; RP with two branches instead of being poorly defined by one vein.

- *Eocoleus* in smaller scutellum; elytral cells becoming finer and less regular in distal part of elytra, although comparable in size in the area between first anal vein and CuP; CuP oblique and ending on first anal vein, instead of being completely separated from first anal vein; CuA and M branching in middle of elytra (not in anterior third); RP with two branches instead of only one.
- *Moravocoleus* in elytral apices not extended behind abdominal apex; pronotum widened anteriorly; smaller scutellum; smoother venation and cells, cells markedly smaller and becoming yet smaller and diffuse in distal half of elytra, although comparable in size in the area between first anal vein and CuP; CuP not subparallel with first anal vein, both veins not reaching middle of elytra, although in both they are oblique, and CuP ending on first anal vein; CuA and M branching in middle of elytra (rather than in anterior third); RP with two branches instead of only one.
- *Permocoleus* in first anal vein ending at suture before middle of elytra (not closely parallel to suture, from which it is separated by two rows of cells); branching of CuA and M in distal half of elytra (not at basal part or independent); RP with two branches instead of only one.
- *Prosperocoleus* in smaller scutellum; cells markedly smaller (although comparable in size in the area between first anal vein and CuP); CuA and M branching in middle of elytra (rather than in anterior third); RP with two branches instead of only one.
- *Retelytron* in smaller scutellum; cells markedly smaller; CuP arcuately oblique and ending near first anal vein (but not subparallel to first anal vein and reaching sutural edge behind the latter); CuA and M branching in middle of elytra (rather than in anterior third); RP with two branches instead of only one.
- *Sylvacoleodes* in elytral apices not extended behind abdominal apex; cells somewhat smaller and becoming even smaller in distal half of elytra (although diffuse at apices in both); CuP well raised and joined with first anal vein; CuA and M branching in middle of elytra (not independent from elytral base); R with three branches, not unforked or disappearing in distal half of elytra.
- *Sylvacoleus* in pronotum widened anteriorly; elytral apices not extended behind abdominal apex; pro- and mesocoxae (sub) contiguous; cells markedly smaller and becoming even smaller in distal half of elytra (although diffuse at apices in both); CuP well-raised and joined with first anal vein; CuA and M branching in middle of elytra (not independent from elytral base); R clearly branching into three veins (not disappearing in distal half of elytra).
- *Tshekardocoleus* (as redescribed by Ponomarenko 2000) in elytral apices not extended behind abdom-

inal apex; cells slightly smaller and becoming even smaller and diffuse in distal half of elytra; CuP well-raised and joined with first anal vein; CuA and M branching in middle of elytra (but not independent from elytral base).

- *Umoricoleus* in cells markedly smaller and becoming yet smaller and diffuse in distal half of elytra (although nearly comparable in size between first anal vein and CuP); CuP and first anal vein not reaching middle of elytra (rather than CuP slightly curved and disappearing at the level of anterior third of first anal vein); CuA and M branching in middle of elytra (rather than in anterior 2/5th); R clearly branching into three veins (not unbranched).
- *Uralocoleus* (after key by Ponomarenko 1969a and description of an additional species by Ponomarenko 2000) in the CuP comparably raised and joined with the first anal vein; CuA and M branching in the middle of elytra (not independent from elytral base); R clearly branching into three veins (rather than into two veins).
- *Votocoleus* in apparently smoother venation and cells, cells markedly smaller and less regular in distal part of elytra; CuP arcuately oblique and ending on first anal vein (not reaching sutural edge behind middle of elytron); CuA and M branching in middle of elytra (not in the anterior third); R clearly branching into three veins (not into two veins).

Coleopsis archaica Kirejtshuk, Poschmann & Nel, sp. nov.
(Figs 1, 4)

Derivation of name. The epithet of the new species means it is an ancient, archaic beetle (Latin ‘*archaicus*’).

Material. Holotype: ZfB 3315 (original collector’s number 720-Pa, b), part and counterpart, sex unknown; the part represents the impression of the whole beetle dorsum with the outlines of ventral sclerites expressed as clear lines (metepisternum, metakatepisternal suture and abdominal ventrites) weakly traced as depressions (coxae, femora and tibiae), but with antennae, tarsi, right protibia, left mesotibia and posterior legs not observable; the counterpart represents the impression of the dorsum with the missing anterior part of the head and most appendages; the epipleura, right metafemur and metatibia are also visible.

Horizon and locality. Rotliegend, top of Meisenheim Formation, corresponding to an Asselian or earliest Sakmarian age; Grügelborn/Saarland, Germany.

Description. Body length (with elytra) 7.8 mm, width 2.8 mm, elytra length 6.3 mm; apparently slightly to moderately convex dorsally and subflattened ventrally. Integument of dorsal sclerites with rather coarse sculpture including coarse and dense oval punctures, interspaces between them apparently coarsely microreticulate; elytra

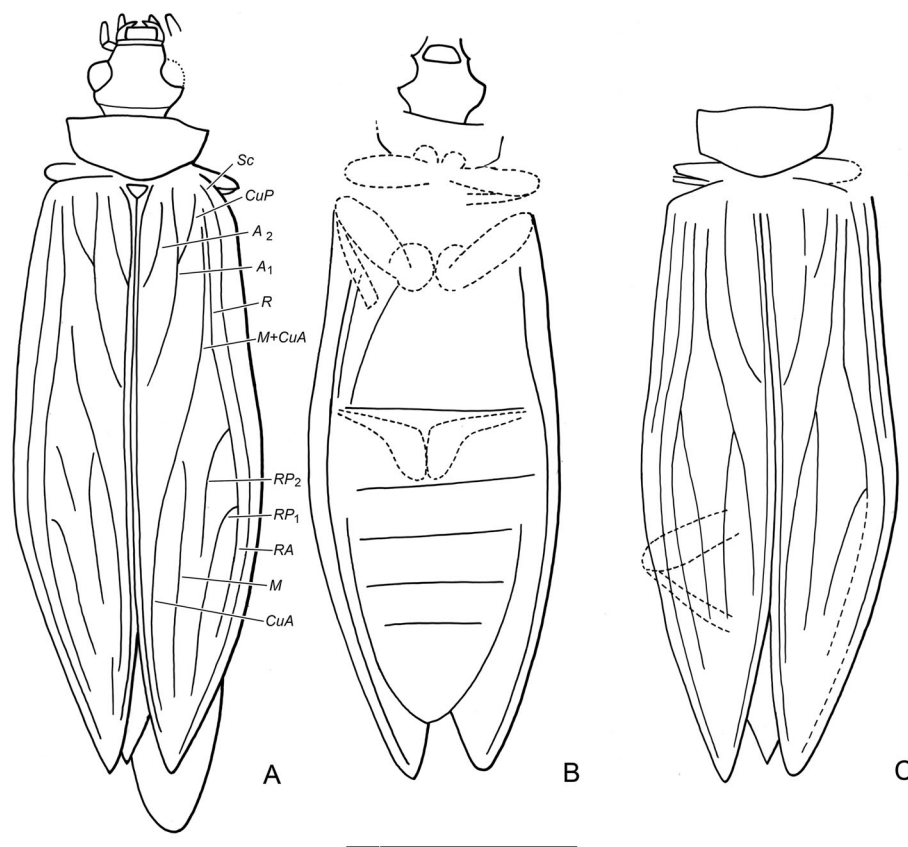


Figure 1. Reconstruction of *Coleopsis archaica* gen. et sp. nov. (Tshekardocoleidae), holotype, ZfB 3315. **A**, part, body, dorsal; **B**, part, ventral; **C**, counterpart, body, dorsal with outline of right femur and tibia by broken line. Body length (with elytra) 7.8 mm. Scale bar = 2.2 mm. Abbreviations of veins: A₁: first anal; A₂: second anal; CuA: cubitus anterior; CuP: cubitus posterior; M: median; M + CuA: fused median and cubitus anterior; R: radial; RA: radial anterior; RP₁: first radial posterior; RP₂: second radial posterior; Sc: subcostal.

with suboval cells showing a weak tendency to be arranged in rows corresponding to the main veins.

Head slightly wider than long, with moderately large oval eyes; anterior edge of frons apparently with bordered anterior edge. Mandibles rather small, slightly exposed beyond labrum, with gently curved outer edge. Labrum rather wide and long, about 2.5 times as wide as long. Mentum transverse (about twice as wide as long) and narrowing apically. Maxillary palpi moderately long, with ultimate palpomere about 2.5 times as long as wide, slightly narrowing anteriorly. Prothorax rather short; pronotum about 2.5 times as wide as long, apparently slightly and gently convex, its sides seemingly widely (sub)-explanate and somewhat wider anteriorly; prosternum before procoxae about as long as procoxae, procoxae suboval and apparently narrowly separated. Mesoventrite apparently about as long as prosternum. Mesocoxae apparently suboval, (sub)-contiguous and much larger than procoxae. Metepisterna about four times as long as wide and broadly attached to mesocoxae. Metaventrite about as long as wide at base and with transverse suture. Metacoxae slightly oblique and their mesal parts strongly

projecting posteriorly. Abdomen with ventrites 1–3 subequal in length, ventrite 4 shorter, hypopygidium (ventrite 5) more than twice as long as each of ventrites 1–3 and with rounded apex; pygidium rather sharply acuminate at apex, which extends far behind apex of hypopygidium.

Elytra much wider than prothorax, with very broadly curved sides, together about 2.3 times as long as wide, apparently moderately convex. Between Sc and lateral edge there is a line (more clearly visible on counterpart) that could correspond to an intercalary vein or epipleuron. The presence or absence of a protoshoulder between Sc and radius cannot be decided due to preservation, but if present, this area would be very narrow close to wing base. R branched with base of RP₁ at elytral middle, RP₂ at distal 2/5th and RA vanishing distally (maybe ending at the forewing apex). CuA (+ M) branching into CuA and M at elytral middle. CuP fusing with first anal vein anterior to the end of second anal vein. First anal vein about twice as long as second. ‘Adsutural’ line along whole elytral sutural edge (posterior margin). Cells arranged in longitudinal rows interspaced by intercalary veins. Area between CuA

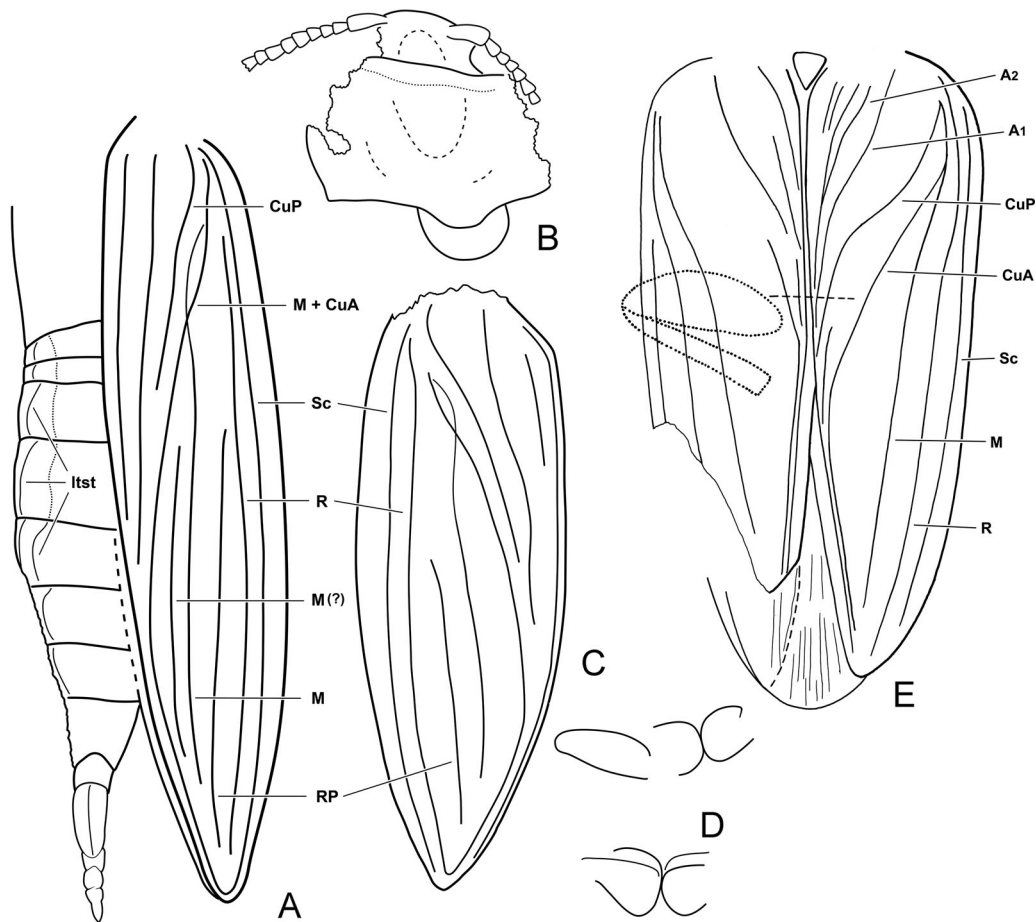


Figure 2. A–D, *Moravocoleus permianus* Kukulová, 1969 (Tshekardocoleidae), holotype, PrF UK: 1/1968; body length 7.9 mm. **A**, reconstruction of the abdomen and right elytron showing the laterosternites (ltst); **B**, head with antennae, pronotum and scutellum; **C**, left elytron; **D**, mesocoxae with right mesofemur and metacoxae of the counterpart. **E**, *Umenocoleus sinuatus* Chen & T'an, 1973, reconstruction of the elytra and hind leg of the holotype from the photograph in Chen & T'an (1973) (Umenocoleidae, order uncertain); scutellum, elytra and hindwing apices in dorsal aspect with outline of left femur, tibia and metakatepisternal suture shown by broken line; body length 17.0 mm. Abbreviations of veins: A₁: first anal; A₂: second anal; CuA: cubitus anterior; CuP: cubitus posterior; M: median; M + CuA: fused median and cubitus anterior; R: radial; RP: radial posterior; Sc: subcostal.

and first anal vein with three rows of cells. Triangles formed by CuP and first anal vein with four rows of cells. Distal halves of elytra with increasingly indistinct and denser rows of progressively finer cells. Membrane apex of right hind wing with rounded outline exposed behind elytron.

Femora comparable in shape and proportions, gently curved along anterior and posterior edges, 2.5–3.0 times as long as wide, metafemora somewhat longer than pro- and mesofemora. Tibiae comparable in shape and proportions, apparently thickening apically, about one-third as thick as femora.

Genus *Moravocoleus* Kukulová, 1969

Type species. *Moravocoleus permianus* Kukulová, 1969.

Remarks. Initially Ponomarenko (1969a) proposed the genus *Avocoleus* for three species (*Moravocoleus fractus*,

M. neglegens and *M. perditus*) with three rows of cells between RA and RP, but the current study of the latter shows that it cannot be assigned to any tshekardocoleid genus (see above). As a result, *Moravocoleus* is now represented by only four specimens (deposited in PrF UK) of its type species.

The drawings published by Kukulová (Kukulová 1969, p. 143, text-fig. 1; Kukulová-Peck & Beutel, 2012, p. 639, text-fig. 8) differ from each other and from what the present authors are able to reconstruct after study of the holotype and three paratypes (Fig. 2A–D).

Diagnosis. Body of medium size (somewhat less than 10 mm); rather elongate, dorsally and ventrally subflattened, with coarsely sculptured integument. Head prognathous, with oval eyes projecting laterally. Prothorax transverse, its sides subflattened and widening anteriorly; prosternum about as long as pronotum, procoxae suboval

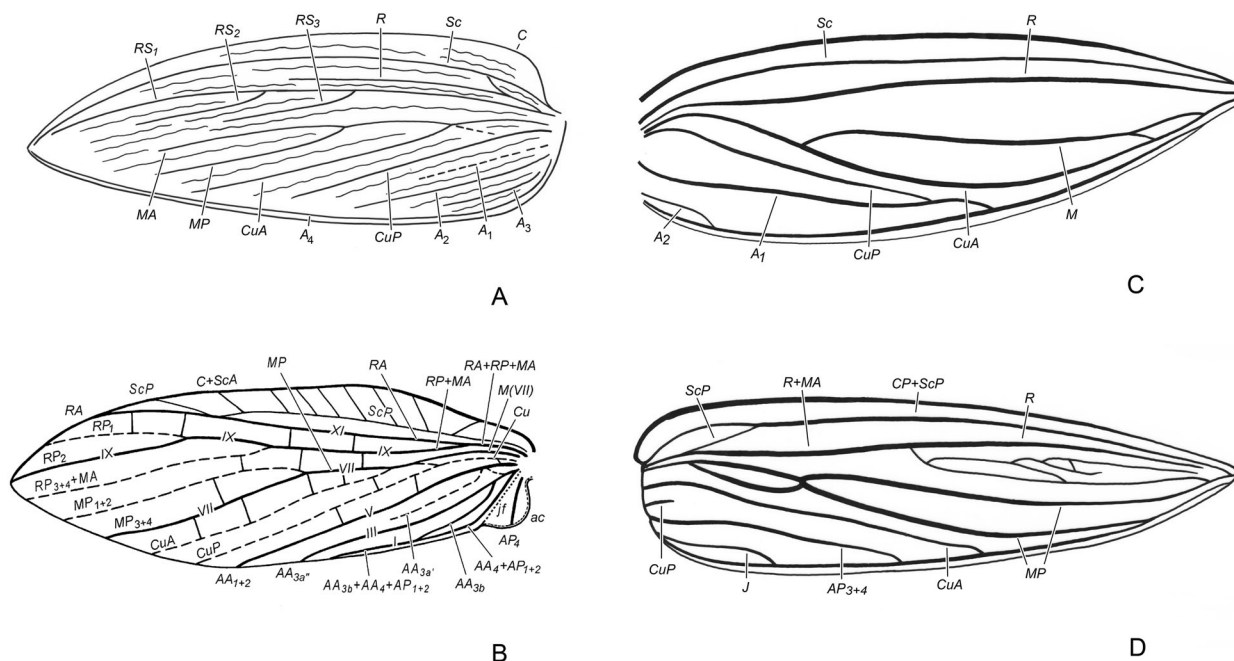


Figure 3. Different proposals of ground plans for beetle elytral venation. **A**, hypothetical ground plan of Tshekardocoleidae after Ponomarenko (1969a, p. 37, fig. 16); **B**, hypothetical ground plan of Coleoptera after Fedorenko (2009, p. 28, fig. 10); **C**, reconstruction of *Moravocoleus permianus* (Tshekardocoleidae) after Kukulová (1969, p. 144, fig. 2); **D**, reconstruction of *Votocoleus submissus* Kukulová, 1969 (Tshekardocoleidae) after Kukulová-Peck (1991, p. 177, fig. 6.28 B) with changes. Abbreviations of veins: A₁: first anal; A₂: second anal; A₃: third anal; AA₁₊₂: anal anterior 1 + 2; AA₃: anal anterior 3; AA₄: anal anterior 4; AP₁₊₂: anal posterior 1 + 2; AP₄: anal posterior 4; C + ScA: costa + subcosta anterior; Cu: cubitus; CuA: cubitus anterior; CuP: cubitus posterior; Jf: jugal fold; M: median; MA: median anterior; MP: median posterior; R: radius; RA: radius anterior; RP₁: first radius posterior; RP₂: second radius posterior; RP₃₊₄: radius posterior 3 + 4; RS₁: radial sector 1; RS₂: radial sector 2; RS₃: radial sector 3; Sc: subcostal; ScP: subcosta posterior.

and apparently narrowly separated. Scutellum very wide and broadly arcuate at base. Mesocoxae apparently suboval, (sub)-contiguous. Metacoxae with their median parts widely projecting posteriorly. Abdomen apparently with seven looking like eight tergites and laterosternites. Elytra wider than prothorax, sides subexplanate, apices conjointly acuminate; shoulders strongly raised; Sc apparently nearly reaching elytral apices; a small protoshoulder in basal part of area between Sc and R, more elevated than the rest of this area and limited distally by a small convex ‘vein’ between R and Sc (not concave as indicated by Kukulová-Peck & Beutel 2012). R branching in the middle of elytra, producing two veins at apices; CuA (+ M) branching into CuA and M at the anterior third; CuP more or less vanishing distally in area between CuA and first anal vein; anal veins approaching suture nearly rectilinear; one curved intercalary vein between anterior parts of M and CuP, ending in the point where M branches into MA and MP; cells on elytra moderately large and subquadrate, sometimes transverse; four rows of cells between RP and MA. Legs moderately developed and with narrow tibiae.

Moravocoleus permianus Kukulová, 1969
(Figs 2A–D, 3C, 5)

Material. Holotype: PrF UK 1/1968, part and counterpart, female; the part represents the impression of the whole dorsum with visible head, antennae, pronotum, scutellum, elytra, most of left hindwing, part of pterothorax and most part of abdomen with exposed ovipositor (but legs are not traceable); the counterpart represents the impression of a mixture of the dorsum with underside of pterothorax, elytra, and abdomen with remains of ovipositor. Paratypes: PrF UK 3/1968, impression of about distal 7/9 of right elytron with removed sutural part due to the break of the host matrix; PrF UK 6/1968, impression of the entire right elytron with removed apex due to the break of the host matrix; PrF UK 11/1968, unclear impression of the entire right elytron which could be conspecific with other mentioned specimens of the type series, although it is shorter and wider than the elytra of others.

Horizon and locality. Early Permian, Sakmarian/Artinskian, Letovice Formation; Obora, Boskovice Basin, Czech Republic.

Supplement to description of the holotype (female). Body length (with elytra) 7.9 mm. Head wide (apparently much wider than long), with moderately large oval eyes; median part of vertex elevated and consisting of three

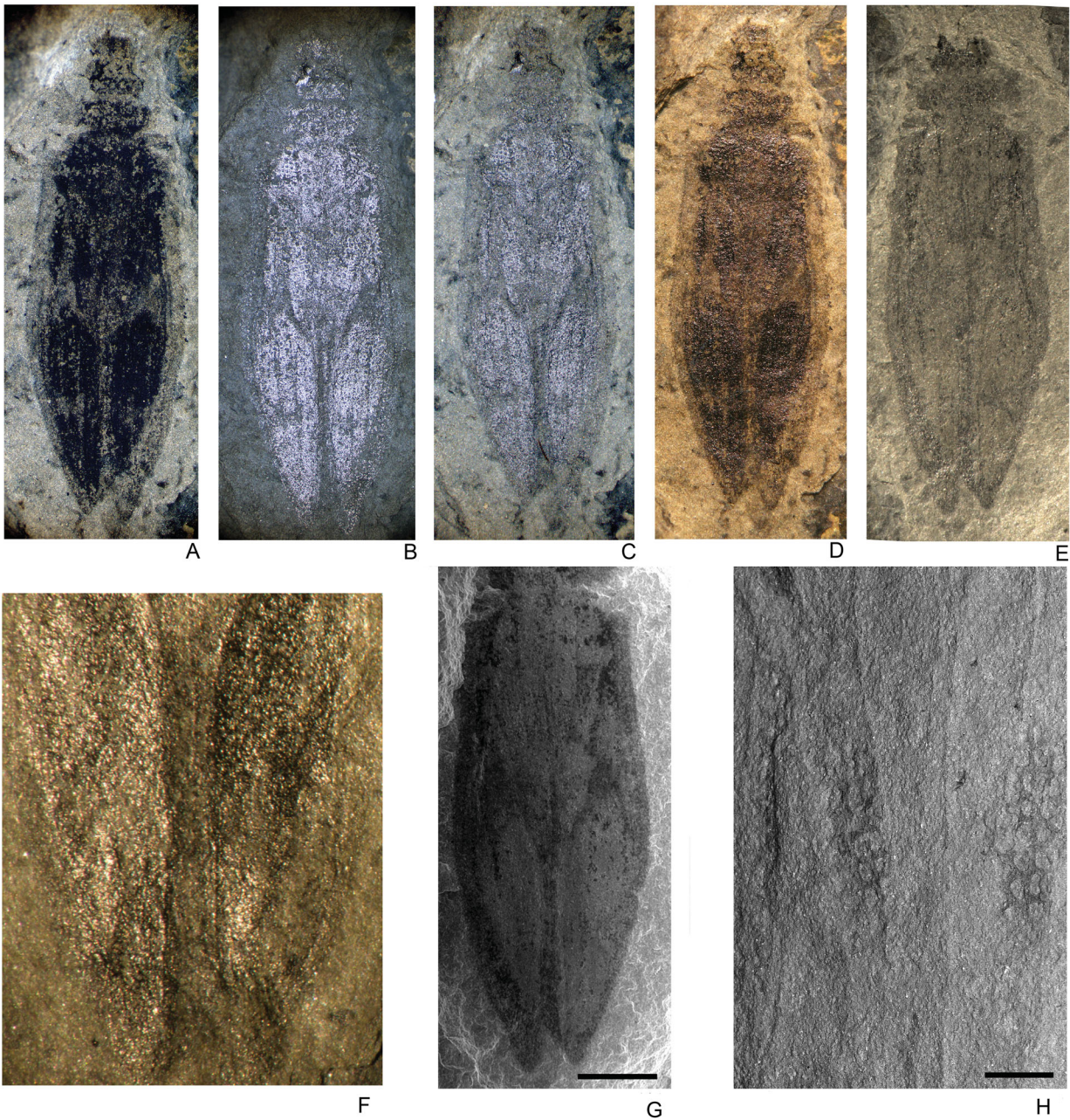


Figure 4. *Coleopsis archaica* gen. et sp. nov. (Tshekardocoleidae), holotype, ZfB 3315. **A–C**, part, body immersed in alcohol (isopropanol); **A**, with polarizing filters completely crossed (with linear polarized light completely extinct); **B**, without crossing polarizing filters; **C**, with polarizing filters approximately halfway crossed. **D–F**, in normal lighting; **D**, part, body; **E**, counterpart, body; **F**, part, elytral apices. **G–H**, counterpart, scanning electron microscope (SEM) micrographs; **G**, body, scale bar 1 mm; **H**, elytral base, scale bar 250 μm. Body length (with elytra) 7.8 mm.

conjoined swellings. Prothorax short; pronotum probably about twice as wide as long, slightly and gently convex, its sides seemingly widely (sub)-explanate and wider anteriorly; median part subtriangularly elevated with widest part at anterior edge. Scutellum about one third as wide as prothoracic base. Mesocoxae apparently suboval,

(sub)-contiguous. Metacoxae transverse and their mesal parts widely projecting posteriorly. Femora moderately wide and moderately long. Abdomen, probably with seven looking like eight apparently membraneous tergites and exposed laterosternites, the looking like anteriormost two of which are shortest and represent the sclerites of the first

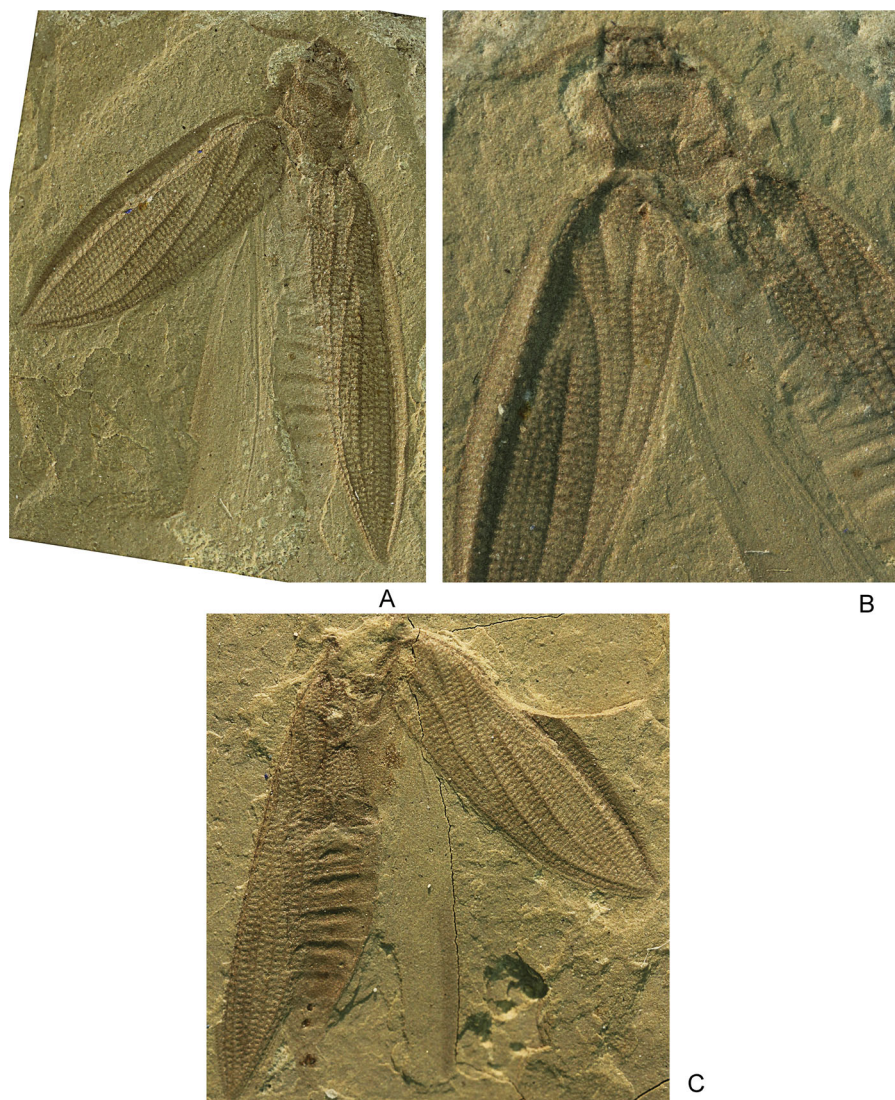


Figure 5. Holotype of *Moravocoleus permianus* Kukalová, 1969 (Tshekardocoleidae), PrF UK: 1/1968. **A**, part, body; **B**, part, anterior part of body; **C**, counterpart, posterior part of body. Body length 7.9 mm.

abdominal segment; pygidium with arcuately excised apex. Exposed ovipositor apparently not heavily sclerotized.

Discussion

Elytral venation of Coleoptera

Elytral venation is clearly expressed in *Coleopsis* gen. nov. and other Tshekardocoleidae. Furthermore, some highly specialized characters present in this insect are also visible in some other fossil species that have elytra more similar to those of modern beetles than to those of the Tshekardocoleidae. The following interpretation of the venation is here proposed.

Vein subcosta (Sc). In *Coleopsis* and the other Tshekardocoleidae, Sc is simple, moderately concave, and reaches the

forewing (elytral) apex. In other Permian and more recent beetles, it is generally not clearly visible, either fused with R as in the Recent *Prolixocupes latreillei* (Solier 1849) (see Ponomarenko 1969a, p. 117, fig. 63), or with the costal margin, or even vanishes in the area between the C and R (as in other Recent members of the subfamily Cupedinae). Lastly in some Tshekardocoleidae (e.g. *Votocoleus submissus*), there is a basal elongate and narrow lens-like ‘proto-shoulder’ between Sc and another (secondary) vein in the subcostal area as a secondary specialization. This structure is also well expressed in some other fossil beetles (*Sylvacoleus* and *Labradorocoleus*) or faintly visible in *Boscoleus* (Fig. 6B, C), but not in *Coleopsis* gen. nov.

Radial veins (R, RA, RP). In *Coleopsis* and the other Tshekardocoleidae, R is very long with RA being simple and reaching the forewing apex. Three conditions for RP

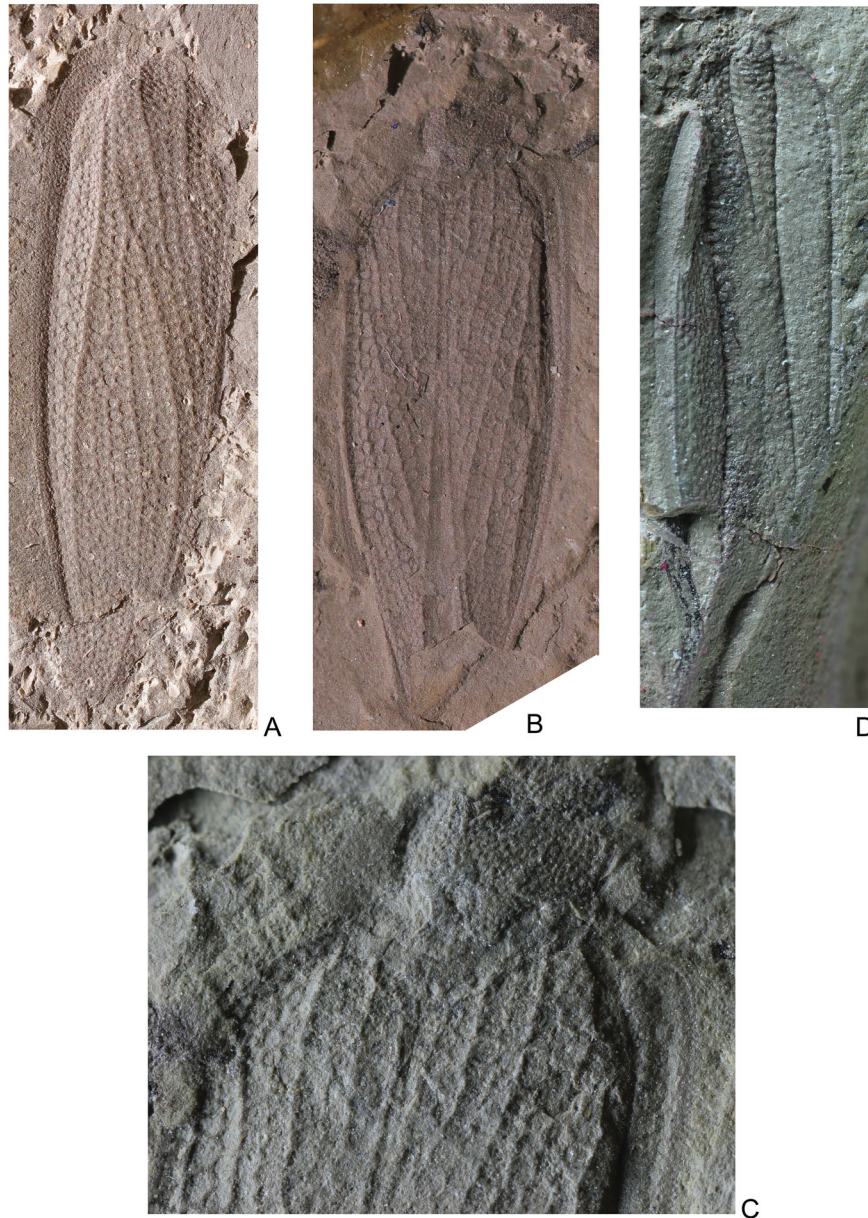


Figure 6. Early Permian Archostemata. **A**, elytron of *Votocoleus submissus* Kukulová, 1969 (Tshekardocoleidae), holotype, PrF UK: 2/1968, length 11 mm. **B, C**, *Boscoleus blandus* Kukulová, 1969 (Tshekardocoleidae), holotype, PrF UK: 5/1968, length 12.3 mm; **B**, body; **C**, pronotum, scutellum and elytral base. **D**, elytron of *Liberocoleus intactus* Kukulová, 1969 (family incertae sedis), holotype, PrF UK: 15/1968, length 7.4 mm.

were observed: (1) either no independent RP; (2) RP with a single branch; or (3) RP with simple branches emerging successively from the radial stem. In other more advanced Permian beetles, R is unbranched or only has rudiments of the division into RA and RP close to the forewing apex. Such a configuration of the radial veins occurs also in some Neuroptera (*viz.* Osmylidae Leach, 1815 and Berothidae Handlirsch, 1906). This represents a convergent transformation.

Median vein (M). In all Antliophora and Neuropteroidea, potential beetle sister groups, CuA is fused with M relatively far from the forewing base so that the independent basal parts of M and CuA are long and clearly visible. In *Coleopsis* and the other Tshekardocoleidae, M is fused with the convex CuA very close to the base of the elytron, then the two veins separate, the median vein being clearly less convex than the radial stem and CuA. This condition of M is also present in the holometabolan ground plan according to

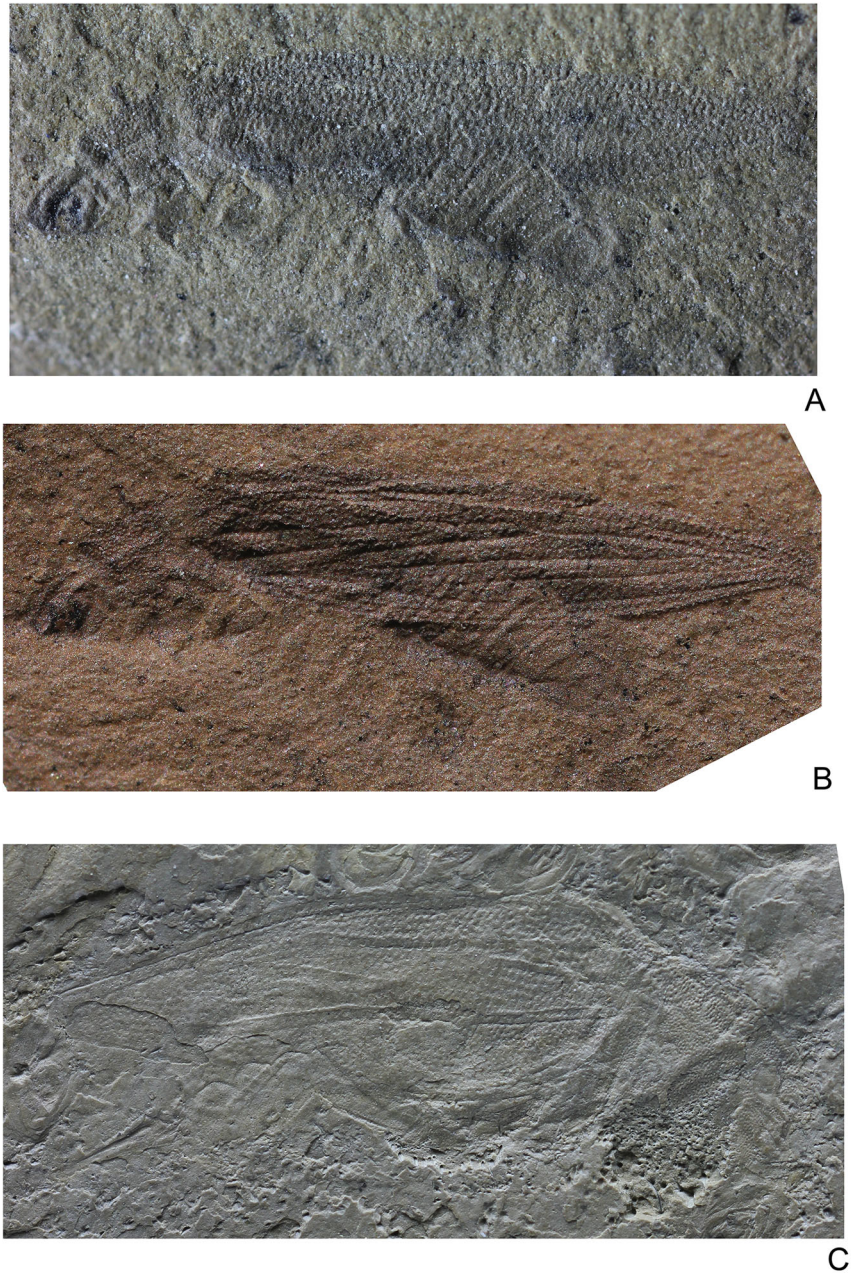


Figure 7. Early Permian insects. **A, B**, body of *Moravocoleus perditus* Kukulová, 1969 (Coleoptera, incertae sedis), holotype, PrF UK: 14/1968, length 5.1 mm; **A**, part; **B**, counterpart. **C**, body of *Oborocoleus rohdendorfi* Kukulová, 1969 (order uncertain), holotype, PrF UK: 7/1968, length 11.2 mm.

Kukulová-Peck (1991). Note that Kukulová-Peck's (1991, p. 177, fig. 6.28 B) interpretation of a complete separation between CuA and M in the Tsherkardocoleidae is unlikely because, in this case, M would have a fork with a concave anterior branch while its posterior branch would be clearly more convex. Such a pattern of venation is highly unusual in insects, especially following Kukulová-Peck's (1991) ground plan of insect venation. The favoured interpretation,

which follows Kukulová (1969), is more consistent with the typical pattern of all pterygote insects in which the anterior branches of all main veins are more convex than the posterior ones. It is thought that in Tsherkardocoleidae, the relatively concave M is basally fused with the convex CuA and re-emerges distally as a vein more concave than CuA. This basal fusion of M + CuA is still visible in some Recent beetles (Richter 1935, p. 53, fig. 15) and seems

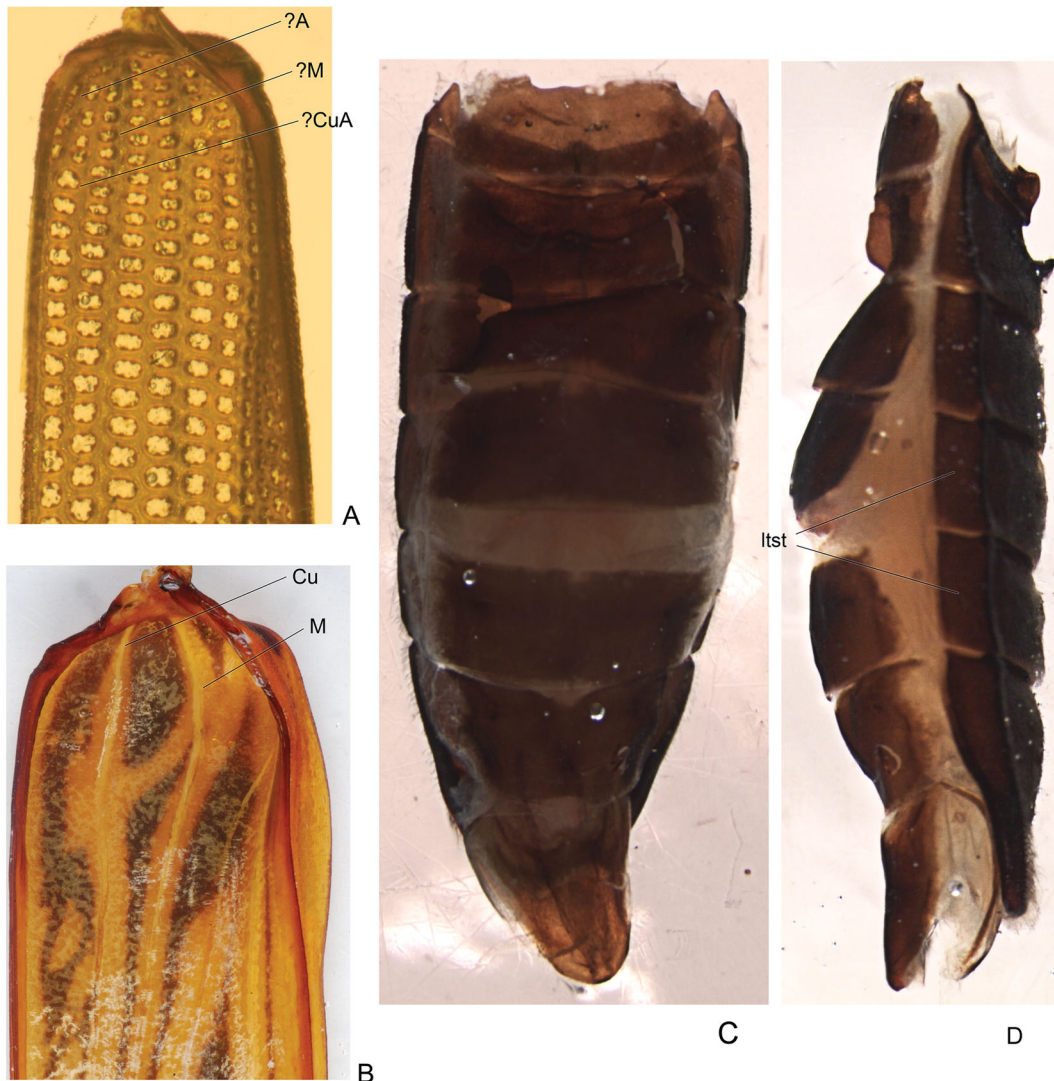


Figure 8. Recent Coleoptera. **A**, lower (inner) surface of base of right elytron of *Cupes concolor* Westwood, 1835 (Cupedidae, Archostemata), MNHN, “N.J.”, “Coll. M.Pic”. **B**, same features in *Macrodonia cervicornis* (Linnaeus, 1758) (Cerambycidae, Polyphaga), MNHN, French Guiana. **C, D**, abdomen of *Priacma serrata* (Leconte, 1861) (Cupedidae, Archostemata), ZIN “Montana, Hathead Co, Glacier Nat. Park, West Glacier, USA, 17 May 1993, Ivie”; **C**, dorsally; **D**, laterally. Abbreviations: ltst: laterosternites; A: anal; Cu: cubitus; CuA: cubitus anterior; M: median.

to be associated with a similar pattern of venation and tracheation (Fig. 8A, B; Richter 1935, p. 41, figs 7, 9, 43). The vein M + CuA is well distant from the radial stem.

Vein cubitus anterior (CuA). In *Coleopsis* and other Tshokardocoleidae, CuA is convex and simple, obliquely curved, nearly reaching the forewing apex and becoming closely parallel to the ‘adsutural line’. In more advanced Permian beetles (e.g. *Cytocupes* Rohdendorf, 1961 in Rohdendorf *et al.*, 1961 in Permocupedidae, *Tychiticupes* Rohdendorf, 1961 in Taldycupedidae Rohdendorf, 1961), it is generally more straight and ends near the forewing apex, and is still more or less obliquely curved (e.g. *Schizo-*

taldycupes Rohdendorf, 1961 in Rhombocoleidae Rohdendorf, 1961, *Tricoleodes* Ponomarenko, 1969a in Tricoleidae Ponomarenko, 1969a).

Note. In the holometabolous ground plan, the forewing CuA and CuP separate from a common basal stem, clearly visible in Neuropteroidea, Amphiesmenoptera and Antliophora. This stem is extremely short (or absent) and the free part of CuA is greatly reduced (or even not visible) in the Hymenoptera. The situation in modern beetles is not very clear. Tshokardocoleidae give only a partial answer to the problem because of the poor preservation of the extreme base of the elytra in the fossils. Nevertheless, the

two veins CuA and CuP are independent and very close to the base of the elytron. Thus their common stem, if present, is very short.

Vein cubitus posterior (CuP). *Coleopsis* has a CuP that is concave, short, oblique, and ends at the first anal vein, as in the tshekardocoleids *Prosperocoleus* and *Moravocoleus*, and somewhat similar to that in *Avocoleus neglegens* but not *A. fractus* (in the latter the first anal vein is subparallel to CuP, which disappears in the network of cells between CuA and the first anal vein before the end of the first anal vein). A configuration identical to that of *Coleopsis* gen. nov. can be observed in some Permocupedidae, e.g. *Kaltanicupes major* Ponomarenko, 1963 has a CuP joining with the first anal vein in the anterior two-fifths of the latter; many species of *Permocupes* have a less raised CuP distally fused with the first anal vein (Ponomarenko 1963). A condition for CuP similar to that of *Coleopsis* is also present in the Permian *Asiocoleus novojilovi* Rohdendorf, 1961 (Asiocoleidae Rohdendorf, 1961) and *Schizotaldycupes ananjevi* Rohdendorf, 1961 (Rhombocoleidae), as well as in some other Permian beetles. CuP seems to be completely fused in the more advanced Coleoptera (see Richter 1935, p. 53, fig. 15). CuP ending in A1 is rather rare among the insects but seems to be characteristic of (Permian) beetles because of the absence of a claval fold in the elytra. In more advanced beetles, CuP is not longer visible as an independent vein, probably fused with A1 at the forewing base.

Anal veins. In *Coleopsis*, the two (or three) anal veins are moderately curved and reach the posterior forewing margin at an oblique angle, as in other Tshekardocoleidae. In more advanced Permian beetles, the first (plus maybe the second) anal vein(s) parallels the elytral sutural edge and CuA, M and other main longitudinal veins, and ends in the distal third of the elytra, e.g. *Eocupes* Rohdendorf, 1961 in Rohdendorf *et al.*, 1961, *Cytocupes* (both in Permocupedidae), *Tychiticupes* (in Taldycupedidae Rohdendorf, 1961 in Rohdendorf *et al.*, 1961), *Schizotaldycupes* Rohdendorf, 1961 in Rohdendorf *et al.*, 1961 (in Rhombocoleidae). Nevertheless, Tshekardocoleidae share with these more advanced beetles the presence of an 'adsutural line' on each elytron. This could be formed from the fusion of the anal veins and participate in the mechanism (shelves and slots) interlocking the elytra along the suture. Kukulová-Peck & Beutel (2012) homologized this line with the anal posterior (AP) 3 + 4.

In conclusion, Tshekardocoleidae and the more advanced beetles share several elytra characters that support the hypothesis of the inclusion of the former in Coleoptera: (1) a shortened CuP that is generally distally fused with the first anal vein in several Tshekardocoleidae and other definite Permian beetles (Permocupedidae, Asiocoleidae and Rhombocoleidae); in some tshekardocoleids (*Avocoleus neglegens*, *Umoricoleus*, *Eocoleus* and *Retelytron*), CuP does not clearly end on the first anal vein but either vanishes

in the area between CuA and the first anal vein or ends in the 'adsutural line'; (2) the anal veins (plus CuP) distally fused into an 'adsutural line'; (3) veins CuA and M fuse at the forewing base and are distally separated; (4) M + CuA is completely separated from the radial stem; and (5) veins Sc, RA and RP(s) are not forked and go to the forewing apex. Thus the new data confirm Ponomarenko's (1969a) and Carpenter's (1992) hypotheses of an attribution of Tshekardocoleidae to Coleoptera rather than to Protelytroptera (see discussion below).

Veins M and CuA of antliophorans and neuropteroids are basally separated, becoming fused in the basal third of the forewing and separating again more distally. The main difference in beetles, including Tshekardocoleidae, is that their M and CuA are fused at or near the elytral base. The long fusion of M with CuA in Tshekardocoleidae is probably plesiomorphic as it is identical to that in the antliophorans and neuropteroids. In other beetles, including modern ones, M and CuA have a common stem but separate immediately. This basal common stem can be traced by the tracheation in some Recent representatives of the families Cucujidae Latreille, 1802, Cerambycidae Latreille, 1802 and others (Richter 1935).

Ground plan pattern of beetle elytral venation

The ground plan pattern of venation in beetle elytra can be summarized as follows: Sc simple, reaching the forewing apex, R independent; RA convex and simple; RP less convex and with one or two simple branches emerging separately from the radial stem; M less convex than R and CuA, simple, and basally fused with CuA but distally separating from it; M + CuA completely separated from the radial stem; CuA simple, obliquely curved and nearly reaching the forewing apex, closely parallel to the first anal vein in the distal third of the forewing; CuA and CuP separating at the forewing base or very close to it; CuP a relatively short and rather concave simple vein, more or less vanishing in the area between CuA and first anal vein or distally fused with the first anal vein or with the 'adsutural line'; the first anal vein convex and more or less parallel to the posterior forewing margin; second anal vein of comparable convexity, shorter but also more or less parallel to the posterior margin; a third anal vein present, also closely parallel to the posterior forewing margin in its distal part and fused with the second and first anal veins to constitute an 'adsutural line'.

A fusion of CuA with M is also present in Paraneoptera and Archaeorthoptera, but in the two latter clades M + CuA is also fused with the radial stem or strongly approximates it, which is not the case in Coleoptera (Béthoux & Nel 2002; Nel *et al.* 2012).

Position of the Umenocoleidae

Umenocoleidae Chen & T'an, 1973 were originally considered as beetles, but were later transferred to the Prote-

lytroptera (Chen & T'an 1973; Carpenter 1992), and even to the Blattodea as the type family of a new superfamily Umenocoleoidea (Vršanský 2003a) to comprise the Umenocoleidae and possibly the Recent blattodean families Anaplectidae Walker, 1868 and Oulopterygidae Rehn, 1951 (a junior synonym of Polyphagidae Walker, 1868). The holotype of the type genus and species, *Umenocoleus sinuatus* Chen & T'an 1973 (Early Cretaceous of Yumen, Gansu Province, China), is supposed to be deposited in the collection of the Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences; however, this specimen cannot be currently located and instead is expected to be in the collection of the Shanghai Entomology Institute (Wang Bo pers. comm.). Accordingly comments upon this species are based on published figures. In addition to *U. sinuatus*, Vršanský (2003a, b, 2004) included several Mesozoic taxa from Siberia, Mongolia, China and North and South America in Umenocoleidae. Later Grimaldi & Engel (2005) considered Umenocoleoidea as the stem group to dictyopteran insects. Bechly (2007) revised the assigned material from the Crato Formation, Brazil, and excluded the Recent families Anaplectidae and Oulopterygidae from Umenocoleoidea, while adding the fossil Cratovitismidae Bechly, 2007 and Vitismidae Vršanský & Ansoerge 2001 (originally considered as a polyphagid subfamily).

Carpenter (1992, pp. 149–150) transferred *Umenocoleus* to Protelytroptera because of the “filiform and segmented nature of the antennae and the peculiar venational pattern”. Based on the published data, the holotype specimen of *Umenocoleus sinuatus* has antennae with numerous short segments, unlike modern beetles, which generally have 11 segments (some can have less and others more), but this character should be checked again. If its antennae are indeed so multi-segmented, this could even be a plesiomorphy for beetles and *Umenocoleus* since the antliophoran and neuropteroid insects also have numerous short antennal segments. The antennae in Tsherkardocoleidae and Permocupedidae have 13 antennomeres, in contrast to most beetles, while some members of Recent groups possess antennae with much more than 11 antennomeres (up to 40 antennomeres in some members of the polyphagan Rhipiceridae Latreille, 1834). Figures of the holotype of *Umenocoleus sinuatus* (Chen & T'an 1973; Carpenter 1992) show partly exposed and certainly unfolded hind wings with some traces reminiscent of dense venation or corrugation, between slightly ‘open’ and partly damaged apices of the forewings. These exposed parts of the hindwings seem not to extend beyond the apices of the forewings, and the former differ from those in members of true Coleoptera. Lastly, figures of this specimen in the aforementioned publications show a convex triangle between the bases of the forewings that resembles a scutellum in most beetles. This feature is characteristic of Polyneoptera, but sclerotization and remains of sculpture on the median triangle between the bases of the forewings in cockroaches

could sometimes simulate a beetle scutellum. Thus, this triangle seems to have a transverse separation from the disc of the pronotum that is not very clear and could represent a continuation of the pronotal sclerite with a transverse groove between it and the pronotal disc.

In general the tegminal venation of *Umenocoleus sinuatus* (Fig. 2E) is quite similar to that of Tsherkardocoleidae and exactly corresponds to the ground plan pattern of venation in beetle elytra as defined above: it has a simple Sc reaching the forewing apex; a simple R (as RP is absent in *Umenocoleus*, which could be a derived condition convergency with modern beetles, see below); less convex simple M basally fused with convex simple CuA; M + CuA separated from the radial stem; CuA obliquely curved and nearly reaching the forewing apex, closely parallel to the first anal vein in the distal third of the forewing; CuP and CuA separated at the forewing base; CuP reaching the first anal vein; and three anal veins closely parallel to the posterior forewing margin. Also *Umenocoleus* has fairly numerous small cells between the main veins, as in Tsherkardocoleidae.

In contrast, other taxa currently included in Umenocoleoidea have a quite different forewing venation, with Sc not reaching the forewing apex, an anteriorly branched RA (when visible), a long CuP clearly separating the anal area from the remainder of the tegmina and not distally fused with the first anal vein, the anal veins not distally fused in an ‘adsutural line’ and closely parallel to the posterior wing margin, and CuA not becoming closely parallel to the distal half of the posterior wing margin. Of course, what is visible in the antenna, pronotum and head structure of *U. sinuatus* is comparable to character states for these structures in Dictyoptera from the Crato Formation that are currently included in Umenocoleoidea, but these states are not diagnostic of any order.

Therefore, it is here proposed to restrict Umenocoleidae, and consequently Umenocoleoidea, to *Umenocoleus sinuatus* and also Lower Cretaceous *U. nervosus* Zhang 1997 from Zhixin (Jilin Province, China: Zhang 1997), excluding from this family group all the other taxa currently included, i.e. Vitismidae, Cratovitismidae, and the following genera: *Blattapterix* Vršanský, 2003a, *Petropterix* Vršanský, 2003a (a taxon already named in Vršanský *et al.* 2001), *Elytropterix* Vršanský, 2003a, *Jantaropterix* Vršanský, 2003a, and *Ponopterix* Vršanský & Grimaldi in Vršanský 1999. All of these taxa remain in the Dictyoptera, but the monophyly of this group should be confirmed through further studies. In particular it is not clear why the Vitismidae should be related to these other taxa based on a tegminal venation apparently different from that of the fossils from the Crato Formation.

The main features in the forewing venation differing between *Umenocoleus* and Tsherkardocoleidae (and other beetles) are as follows: the anal veins and CuP are closely parallel to each other and to the posterior wing margin, not

exactly fused into an ‘adsutural line’ but showing double subparallel lines in the distal parts, which extend a distance along the inner elytral edge; and the comparatively longer CuP ends on the first anal vein near the middle of the forewing, leaving a very broad area between CuP and the first anal vein with particularly fine and dense, diffuse cells. These characters could correspond to plesiomorphies compared to the ‘adsutural line’ in true beetles. In addition, this peculiar character of the inner tegminal edges of *Umenocoleus* makes it difficult to suppose that the interlocking connection between its forewings was similar in function to that in true Coleoptera.

In conclusion, it is proposed that *Umenocoleus sinuatus* could be restored to Holometabola, probably in a very basal position, and perhaps as a sister group to all other beetles, including Tsherkardocoleidae; the clade (Tsherkardocoleidae + more derived beetles) is supported by the presence of a well-defined ‘adsutural line’ and short CuP. The left posterior leg and metakatepisternal suture of this *Umenocoleus* are reminiscent of those in other beetles, although similar legs occur in Blattodea and Protelytroptera. The apparently movable head with large eyes and thorax of *Umenocoleus* are similar to those of Polyphaga rather than other beetles. Clarifying the relationships of *Umenocoleus* will require a re-examination of the type specimens.

Umenocoleus is a Cretaceous taxon, which could appear at odds with the hypothesis of a very basal position as a sister group of all other Coleoptera. It would then correspond to the last representatives of a ‘ghost’ lineage dating from the Late Carboniferous.

Relationships of Tsherkardocoleidae and Umenocoleidae with Protelytroptera

Kukalová (1969) considered Tsherkardocoleidae to be a member of the order Protelytroptera Tillyard, 1931 (= Protocoleoptera Tillyard, 1924; Paracoleoptera Laurentiaux, 1953; Protelytrida Rohdendorf, 1977), as did Carpenter (1992) for the Umenocoleidae. Protelytroptera is currently considered as the stem group of the modern Dermaptera (Gorochov & Anisyutkin 1998; Grimaldi & Engel 2005), which is also interpreted either as a subgroup Protelytrina of the Forficulida (Shcherbakov 2002) or Dermapterida after Martynov (1925) and Boudreaux (1979). All of these hypotheses are (more or less) supported by the hindwing venation, known for some Protelytroptera only (e.g. *Protelytron* Tillyard, 1931). The protelytropteran tegmina venation differs from that in Tsherkardocoleidae and Umenocoleidae, particularly in CuP being completely separated from the first anal vein, CuP and the anal veins not distally fused into an ‘adsutural line’, CuA not distally running parallel to the posterior forewing margin, and M separated from CuA (at least in the type genus, *Prote-*

lytron, but also in numerous other genera, even if in some genera such as *Planelytron* Kukalová, 1965 these veins are supposed to be fused). These important differences confirm that Tsherkardocoleidae and Umenocoleidae belong to Holometabola and are not related to Protelytroptera.

Positions of Labradorocoleidae and Oborocoleidae

The Early Cretaceous *Labradorocoleus carpenteri* (Labradorocoleidae Ponomarenko, 1969b) is based on a single elytron and was originally described as a beetle related to Tsherkardocoleidae (Ponomarenko 1969b). However, it was later suggested to be a cockroach (Ponomarenko 2000), probably taking into consideration that the anal vein of *Labradorocoleus* closest to the posterior edge follows it for some distance and becomes more widely separated than in Tsherkardocoleidae. However, *Labradorocoleus* shares with Tsherkardocoleidae and other Permian beetles several characters, such as an obliquely depressed anterior-outer corner of the elytron (visible in the tsherkardocoleids *Votocoleus submissus*, *Sylvacoleus richteri* Ponomarenko, 1963 and *Sylvacoleodes admirandus* Ponomarenko, 1969a; Ponomarenko 1963, 1969a; Kukalová 1969) (Fig. 6A). Note that although it could appear similar to a separation of the anterior outer corner occurring in the forewing of some cockroaches, the structures do not have the same organization and therefore are not considered homologous (the separation is formed by an oblique Sc in the cockroaches; Fig. 9). The organization of R with two simple branches of RP emerging successively from the radial stem is also a trait shared by *Labradorocoleus carpenteri* and some Tsherkardocoleidae (and other Permian beetles). Even if M in the elytron of *L. carpenteri* is convex as other longitudinal veins in its distal part, it is clearly less convex at its base where it is joined with CuA, just as in Tsherkardocoleidae. Its distal free CuA is subparallel to M and to the posterior forewing margin; CuP is not traceable: either it is extremely short at the forewing base or it is completely fused with the first anal vein. Also, the anal veins in the elytron of *L. carpenteri* are very long and extend to near the forewing apex (a character present in some Permian beetle genera, viz. *Schizotaldycupes* and *Tricoleodes*; see above for the ground plan pattern of beetle elytral venation). Therefore, it is reasonable to assign Labradorocoleidae to Coleoptera. Nevertheless an attribution of this family to Tsherkardocoleoidea is premature, because the venation of *Labradorocoleus* is more similar to that of beetles more characteristic of the Mesozoic, especially in the straight CuA and the extremely short or completely reduced CuP.

One important problem remains with *Labradorocoleus*, i.e. the presence and position of the radial stem and of RA.



A



B



C



D

Figure 9. Recent species of Blattodea. **A, B**, tegmina of *Phoraspis* sp. (Blaberidae), ZIN ‘Santa-Leopoldina’; length of tegmina 8.6 mm; **A**, dorsally; **B**, ventrally. **C, D**, tegmina of *Prosoplecta* sp. (Blattellidae), ZIN ‘Vietnam, Prov. Gia Lai, 50–60 N Kannack, Con Cha Rang, h 1000–1200, 17.IV.1995, A.V. Gorokhov’; body length 9.3 mm; **C**, dorsally; **D**, ventrally.

The two branches of RP emerge successively from what looks like a very concave vein, interpreted as Sc by Ponomarenko (1969b) and Carpenter (1992, p. 284, fig. 175), but there is neither convex RA nor radial stem, which is quite unlikely for an insect. Furthermore, there is what looks like a ‘protoshoulder’ zone just above this concave vein,

limited anteriorly by a rather weak but still distinct vein. Either this concave vein is really concave and represents Sc, in which case the venation of *Labradorocoleus* is quite unique among beetles and even insects, or the concavity of this vein is the result of a deformation and/or a break of the elytron along this line due to the probable high convexity of the elytron itself. In this case, the concave line follows the original (convex) R and RA, the structure looking like a ‘protoshoulder’ is really homologous to the ‘protoshoulder’ of *Moravocoleus* and of *Votocoleus*, and Sc is rather weak, ending on the anterior margin before mid length of the elytron. The second option is more parsimonious in terms of homology of structures among beetles. If confirmed, it would also support the hypothesis that the presence of a ‘protoshoulder’ is not a strict apomorphy of Moravocoleidae.

Both genera of Oborocoleidae Kukalová, 1969 (namely *Oborocoleus* Kukalová, 1969 and *Liberocoleus* Kukalová, 1969) have a general character of sculpture of the integument (thorax and elytra with fine venation, and also with small and somewhat irregular cells) somewhat similar to that in *Coleopsis* gen. nov. The original interpretation of the forewing venation of *Oborocoleus rohdendorfi* by Kukalová (1969) seems to be misleading because her drawing is actually an interpretation of a mixture of both elytra (two elytra superimposed in part) as a unique elytron (Fig. 7C). There is some deformation of the elytra as well so that the veins are quite difficult to follow. Perhaps what was interpreted in the original description as ‘A3’ is the costal margin; what was originally interpreted as ‘Sc’ probably does not belong to the elytron but to the body itself; what the author interpreted as the ‘A2’ is in fact the costal margin of another elytron; there seems to be a break along the vein she named ‘A1’; although the vein named as ‘Sc’ is concave (normal situation) and ‘A2’ is convex, which is quite unusual, but it would be normal if it is in fact ‘Sc’ of the second elytron visible from below. At the same time in the holotype of *Oborocoleus rohdendorfi* there seem to be five ventrites as in other archaic Coleoptera, and the abdominal apex appears to possess a flattened ultimate segment consisting of a long ventrite 5 and long tergite 7. Finally, the hypognathous head and rather strange legs of this species cannot be compared with beetles. Therefore, this genus and correspondingly the family Oborocoleidae can be scarcely regarded as belonging to any recognized order. In any case the absence of CuA and M, considered by Kukalová (1969) to be one of the main characters of the Oborocoleidae, is not demonstrated at all.

Liberocoleus intactus Kukalová, 1969 (sole species of *Liberocoleus*) is represented by two partly superimposed incomplete coleopteran-like elytra that seem to be more similar to those of Tshokardocoleidae and Permocupedidae than to any other archostematan family (Fig. 6D). Following Kukalová’s (1969) interpretation, the veins she named ‘Sc’ and ‘R’ show the same convexity, which is unlikely as these veins are normally of an inverted convexity in insects,

particularly in these Permian beetles. In addition, her 'Sc' runs very close to the forewing margin. It is likely that 'Sc' in the original description is in fact the second anal vein, while the 'R' in the description is the first anal vein, this vein being simple. Also, the 'CuP' in the description is a vein vanishing in the area between CuA and the first anal vein in the basal fourth of the elytron, as in many Permian beetles; CuA is very incompletely preserved, with the base covered by the second elytron; M, R and Sc are not visible. At the moment, it is advisable to keep *Liberocoleus* as 'familia incertae sedis' until a more detailed study can be completed.

Position of *Adiphlebia lacoana*

Béthoux (2009) treated the Late Carboniferous taxon *Adiphlebia lacoana* Scudder, 1885 (Mazon Creek, Carbon-dale Formation; Middle Pennsylvanian; type species of Adiphlebiidae Handlirsch, 1906) as a beetle that is the sister group of all other Coleoptera. This species was originally proposed as a 'Neuropteroid Palaeodictyopteran'. Kukalová-Peck & Beutel (2012) revised *A. lacoana* and considered it to be a member of Holometabola, possibly related to the neuropteroid insects. However, the presence of numerous veins emerging from CuA in the area between the main stem of CuA and M is a character of Dictyoptera and Paoliida (see the revision of Paoliida by Prokop *et al.* 2012). An intercalary vein between Sc and RA is present in some Recent Blattodea, viz. the blattid genus *Pelmatosilpha guianae* Hebard, 1926 (in Blattidae Handlirsch, 1925) (Grandcolas, pers. comm.), and straight and subparallel main veins can be found also in other clades (viz. extinct Glosselytrodea). Thus, the present authors suppose that this enigmatic fossil is better considered as a member of a poly-neopterous lineage, still undetermined, with possible relationships to Dictyoptera and Paoliida.

Functional morphology of Permian and modern beetle elytra

Fedorenko (2009, p. 30) proposed a ground plan for the coleopterous elytron morphology. Regarding the epipleuron, he wrote: "According to this ground plan, there were the following veinal trunks at the base of the elytron: C + ScA and RA rimmed the elytral side margin (morphologically, the costal one) and the edge between the epipleuron and the disc, respectively, while Sc passed along the epipleuron". In general the radial stems of insect wings are convex, while subcostal ones are concave. R and Sc of *Coleopsis* gen. nov. are located along the elytral lateral edge and Sc apparently coincides with an explanate lateral stripe. A more or less similar vein pattern can be observed in other Tsherkardocoleidae and many Permian beetles. On the other hand, rather important information on a prob-

able origin of the epipleuron comes from the structures of Recent species, and in particular their embryology, which was summarized by Comstock & Needham (1898), Jeannel (1926, p. 322, fig. 95) and later Richter (1935). In the pupae of an even rather advanced coleopterous family like Cerambycidae (Polyphaga, Cucujiformia) six tracheae (C, Sc, R, M, Cu, A) are present. Each trachea emerges independently from the transverse tracheal trunk at the base of the elytra, except for M and Cu, which form a common stem. Thus the epipleura in Tsherkardocoleidae were formed by the structural elements initially located anteriorly from Sc. The beetle epipleuron is a rather essential part of the mechanism of locking the elytra with the thoracic and abdominal segments.

Ponomarenko (1969a) considered that most Archostemata sensu lato had a widely expanded epipleuron. However, the Permian fossils frequently do not demonstrate this feature very clearly, although many representatives of Palaeozoic beetles with exposed outlines of sclerites on their undersides make such an assumption possible. Nevertheless, imprints of many Tsherkardocoleidae, as well as many other Palaeozoic beetles, show the clear lateral sloping and widely explanate sides of the elytra. Thus, their elytral sides seem to envelop tightly the abdominal sides. It can be scarcely supposed that the elytra were explanated along the sides, leaving the insect body unprotected, as the more complex shoulders are a characteristic feature of beetles (in contrast to cockroaches). The lines between Sc and the lateral edge in the anterior half of the elytra of *Coleopsis* gen. nov. could be interpreted as traces of the lower carina of the epipleura. If so, and if the 'adsutural' lines in the new genus and other Tsherkardocoleidae could form the sutural locking mechanism, it can be supposed that the elytra of the oldest known beetle family already possessed adaptations for a defensive function, like Recent groups of the order. These include the protection of the hindwings, pterothoracic and membraneous abdominal sclerites, as well as the formation of a subelytral space for better thermoregulation and preventing desiccation. This set of adaptations could enable the Permian beetles to breathe whilst being inside a very wet substrate or even under water. Such a predisposition in structural adaptations facilitated the further progressive mastery of freshwater environments. The elytra of both mid-Permian and later beetles frequently also bear a transversely oblique 'schiza' (Ponomarenko 1969a) or 'locking flange' (Crowson 1981) and sublateral lamina in addition to the usual patches along the lateral sides of elytra. All these structural adaptations seem to be more characteristic of aquatic beetles as an additional means to keep the elytra and abdomen immobile with respect to each other, although the carinate 'schiza' occurs also in groups including only or mostly terrestrial representatives (e.g. Coccinellidae Latreille, 1807; Mordellidae Latreille, 1802; Curculionidae Latreille, 1802; Fedorenko 2009). The function of 'schiza' is still not clear because the

explanation of the direct fixation of elytra and abdomen by this structural element has a difficulty because its location is coincidental with the lateral side of the folded hindwing.

The epipleura of the Mesozoic and Cenozoic Cupedinae are rather narrow, with the lateral carina usually interpreted as homologous to Sc (Fig. 8A). The venation of the Palaeozoic beetles makes it possible to suppose that the epipleural ridge was formed by another structure (maybe ScA) in other taxa currently included in Archostemata (Tshekardocoleidae, Permocupedidae, etc.). In Cupedidae, Sc was later fused with this structure. The extrapolation of Sc of Cupedidae as the lateral carinae in all other Archostemata was a reason for misinterpretation of the origin of the elytral lateral carina (e.g. Fedorenko 2009).

Different groups of cockroaches demonstrate strong similarities between their tegmina and beetle elytra (Shelford 1912), such as the simulation of epipleura due to the thickening of Sc in the anterior part of the forewing or sometimes the thickened R extends far along the outer edge of the forewings (Fig. 9), although in both cases a clear interlocking mechanism between forewings and abdomen is not present. Furthermore, the posterior edges of forewings in cockroaches lying on the abdomen do not form any interlocking mechanism, as the edge of one forewing somewhat covers the edge of the other one without any fixation.

Another important feature confined to beetles is the interlocking mechanism formed by the elevated mesoscutellum (or 'scutellum') and longitudinal grooves (fissures) and ledges ('males': Fiori 1972) thereby providing a coaptation of the elytra along their posterior edges. This element of the interlocking mechanism seems to be connected in origin with the anal veins traceable in advanced beetles, as the remains of one anal vein or one trachea going along the suture as has already been shown by Handlirsch (1906–1908), although this trace is not always expressed in advanced beetles (Comstock & Needham 1898, p. 563, fig. 50). In Tshekardocoleidae and Permocupedidae, the successive anal veins go into the 'adsutural' line along the whole elytral suture to complete it. In many Early Permian beetles this anal vein extends between the cells from both its sides, while the 'adsutural line' of *Coleopsis* gen. nov. follows the suture without any intervening cells. Thus this character of the new genus seems to be in a more advanced condition than in the later tshekardocoleids from Obora, Tshekarda, etc.

The membrane apices of the hindwings in *Coleopsis* gen. nov. are clearly extended beyond the elytral apices and they seemed to be able to fold, as in *Moravocoleus permianus* (Kukalová 1969, p. 143, text-fig. 1, pl. 2). The fossil record does not support the opinion of Haas & Beutel (2001), who considered that transverse folding as having evolved only in the mid-Permian with the formation of a closed subelytral space. Fedorenko (2009) proposed a hypothetical schema for the evolution of the transverse folding of Tshekardocoleidae, which admits that the initial elytra

extended far beyond the abdominal apex. However, the Early Permian tshekardocoleid species with known hindwings (*Moravocoleus permianus* and *Coleopsis archaica* sp. nov.) provide evidence that they had already very long hindwings which should have had transverse folds to protect the soft membrane of the forewing apices, although *Umenocoleus* seems to have a comparable length of forewings and hindwings. At the same time the elytra of some Early Permian beetles were somewhat extended beyond the abdominal apex (Ponomarenko 1969a, p. 54, figs 29, 30), but these cases could be explained by secondary structural transformations or postmortem deformation during fossilization as in the short abdomen of '*Moravocoleus perditus*' (see above).

Thus, summarizing our observations on *Coleopsis* gen. nov., it is possible to say that the level of structural organization of the elytra and their coordination with other organs were essentially comparable in all Tshekardocoleidae and that this level was already very close to that seen in other beetles. Additional evidence comes from *Moravocoleus* in the paper by Kukalová (1969, pl. 2) where the laterosternites (dorsal part of the abdominal ventrites) are more or less clearly visible. These structures are characteristic of Coleoptera and seem to be a basal feature for the whole order, although they show rather great variability within the order (even within groups of one family; Hansen 1997; Kirejtshuk 1998). In the pterygote ground plan, the laterosternites represent the pleural derivative (Snodgrass 1931); however, holometabolans usually have them completely fused with the sternal plates. In Coleoptera, the laterosternites are also mostly visible from above (beneath the elytra) and sometimes also the distinct parasternites are separated as stripes between the main part of the laterosternites and the membrane with the spiracle or very rarely laterosternites secondarily became completely isolated (Kasap & Crowson 1975; Crowson 1981; Hansen 1997; Deuve 2001). Finally, the sclerites located between the spiracles and tergites are usually named laterotergites (Crowson 1981). The abdominal spiracles are located on pleural or tergal derivatives, but never on sternal ones. Beutel & Leschen (2005) also regarded these structures as plesiomorphic for beetles. These structural adaptations play an essential role in the interaction of the coleopterous elytra and the abdomen (Kasap & Crowson 1975), resulting in creation of the subelytral space. Their presence in *Moravocoleus* gives further evidence of functional fitting of the abdomen and elytra in Tshekardocoleidae. In Recent Archostemata, the laterosternites are isolated by a lateral ridge in members of Cupedidae which have them as vertically situated and heavily sclerotized stripes (Fig. 8C, D; also Ponomarenko 1969a, p. 35, fig. 15), while in Micromalthidae Barber, 1913 and Recent Jurodidae Ponomarenko, 1985 they look like lateral stripes of the plane of ventrites bending dorsally without isolation (more so in Jurodidae and less in Micromalthidae) (the lateral parts of the ventrites

in Crowsoniellidae Iablokoff-Khnzorian, 1983 were not studied). It is important to mention that the vertical position of the laterosternites in Cupedidae is congruous with the inner surface of the elytral sides in the cupedids (Fig. 8A). However, most extinct archostematan groups, including the oldest members of Tshekardocoleidae, seem to have the structure of the abdomen and elytral sides comparable with that in many Recent groups of Adephega and Polyphaga.

The problem of classifying basal beetle lineages

As many characters of Tshekardocoleidae show a rather advanced structural composition and mosaic transitions of different organs (including in the elytra) in other groups of Coleoptera, the former separation of the suborders Protocoleoptera, Archecoleoptera Crowson, 1981 and Myxophaga from the suborder Archostemata (e.g. Tillyard 1924; Crowson 1955, 1975; Kirejtshuk 1991; Lawrence *et al.* 2011; Ślipiński *et al.* 2011; Kukalová-Peck & Beutel 2012) is not advisable. In particular, it would be better not to use the name Protocoleoptera, which was proposed only for the family Protocoleidae (Tillyard 1924) and is now placed in the order Protelytroptera (Forbes 1928; Carpenter 1992). The same applies to Paracoleoptera, which was proposed for the family Permophilidae Tillyard, 1924, and also belongs to Protelytroptera (Kukalová 1966; Carpenter 1992). Archecoleoptera was introduced by Crowson (1981) for Early Permian beetle groups except Tshekardocoleidae. However, the relationships between these groups remain very obscure and the usage of this term in a taxonomic sense is scarcely warranted because it is probably a paraphyletic taxon and includes the Late Permian taxa united based upon a certain structural similarity which could appear as a convergence from the Early Permian tshekardocoleid ancestor. The most recent discussion of 'Protocoleoptera' concluded: "Protocoleopteran apomorphies (absent in modern Coleoptera) include: small field basally between ScP and RA present; elytral shoulder placed basally on AA1 + 2 (instead of basally on MP & CuA)" (Kukalová-Peck & Beutel 2012, p. 642). However, as shown above, current knowledge on the distribution of the mentioned 'apomorphies' does not allow their use for systematics and evolutionary interpretations.

Myxophaga was proposed by Crowson (1955) for a few Recent families. Subsequently, Forbes (1957), who treated these families as near to 'Hydradepaga' uniting aquatic groups of Adephega, pointed out some serious contradictions in the interpretation which are based mainly on hindwing venation and folding. Ponomarenko (1973, 2002) insisted on the impossibility of separating Myxophaga from Archostemata *sensu lato* including extinct groups, except some differences in larvae of Recent representatives, and regarded these Recent families as a superfamily Microsporoidea in the infraorder Schizophoromor-

pha (Ponomarenko 2002). However, in recent publications Myxophaga are frequently treated *sensu* Crowson (1955) (Kirejtshuk & Ponomarenko 2012), with four families represented in the Recent fauna or also with some extinct families from Archostemata (Bouchard *et al.* 2011). In the latter case, the 'suborder Myxophaga' seems to lose any significance in the context of phylogeny-based systematics.

It is still not clear how to interpret the presence of 13-segmented antennae in Tshekardocoleidae and Permocupedidae, as well as the multisegmented antennae of *Umenocoleus sensu stricto*. Likewise, interpretation of the more or less sclerotized acuminate structure behind the abdomen of some Tshekardocoleidae is unclear (reminiscent of an ovipositor?). The abdominal apex of *Moravocoleus* as figured by Kukalová (1969, pl. 2) scarcely looks as heavily sclerotized as what was shown in Kukalová's drawing (p. 143, fig. 1). Therefore, the further hypothesis of the presence of the primary ovipositor in members of this family is very uncertain. Moreover, a pair of sclerites exposed behind the ultimate ventrite looks somewhat similar to the paraproct of beetles, which is located at the base of the projecting secondary telescopic ovipositor.

Nevertheless, further studies of Palaeozoic beetles could provide crucial evidence of the primary diversification of the order and separation of the basal groups. Fedorenko & Ponomarenko (2012) described some late mid-Permian isolated beetle hindwings that could belong to Asiocoleidae and/or Taldycupedidae, as these wings correspond in size with species of these families collected at the same outcrop. The authors showed that two of the examined hindwings are similar to those known in the suborder Polyphaga rather than in Archostemata or Adephega and Myxophaga, although they considered that one of them could belong to a 'cupedomorphan' beetle (?Taldycupedidae) and another to a 'schizophoroid' (?Asiocoleidae). Another important conclusion of these authors is that because there is no trace of either the primary base of CuP nor the base of the first anal vein (AA1 + 2) in the 'schizophoroid' hindwing examined by them, they regard the common ancestry of the species based on these hindwings and the main lineage to Adephega-Myxophaga as earlier than the mid-Permian. Thus, the division of the suborder Archostemata seems to be very premature, in which its conception will only become possible through additional revisions of extinct groups and substantiation of some relationship concepts in Palaeozoic beetles.

Origin of the Coleoptera

The finding of *Coleopsis* gen. nov. makes it possible to consider the ancestors of the beetles among the Carboniferous radiations of the holometabolan groups hypothetically proposed by Labandeira (2011) on the basis of *Srokalarva*: Kukalová-Peck, 1997 (a probable antliophoran proposed by Labandeira (2011) on the basis of *Srokalarva* Kukalová-Peck 1991 (a probable antliophoran)), *Pteridotorichnos*

Labandeira & Phillips, 2002 (probable traces of the activity of a taxon belonging to the stem group of Hymenoptera), and *Westphalomerope* Nel *et al.* 2007 (Protomerotopina, Mecopteroidea).

The global climate of the late Palaeozoic underwent dramatic changes, including in atmospheric composition, transition from a greenhouse mode (thermo-era) to an icehouse mode (cryo-era) (beginning in the Late Carboniferous), which were characteristic of a 'monsoonal' or 'seasonal' circulation (Chumakov 2004; Eastwood 2008) and which governed major changes in the global biota. The general view of terrestrial ecosystems in the Early Permian of Euramerica (Laurussia) can be characterized by aggradations of lowlands in many areas with more seasonally dry conditions in comparison with the Carboniferous wetlands. The plant fossil record documents the predominance of xerophytic seed plant assemblages in the latest Carboniferous and Early Permian of lowland deposit environments. Thus, the record of wetland floras became augmented by new plants living in seasonally dry climatic conditions referred to as 'summer wet' (Rothwell & Mapes 1988; Ziegler 1990). Ponomarenko (1969a) considered that the origin of beetles could have taken place at around the time of the first diversifications of holometabolous insects with larvae inhabiting internal substrates. He thought that the larvae of archaic beetles could have been soft and erucoid, like many Recent xylomycetophagous beetles living inside substrates. In Tshekarda some holometabolous larvae were found that demonstrate erucoid appearance with segmented legs (Ponomarenko 1969a) but are also sometimes strongly desembryonized (i.e. emergence at an earlier stage of the standard embryonic development at an earlier level of structural differentiation) and legless (Ponomarenko 1983). Crowson (1975, 1981) developed this concept further, supposing that subcortical life was the initial state for the Tshekardocoleidae and was the principal one for many groups of Coleoptera in the Palaeozoic and later. Kirejtshuk (1991) concluded that xylomycetophagy was the initial diet at least for the most archaic coleopteran larvae. Finally, it could be supposed that the first beetles had a rather long period of larval development and a comparatively short life for the imagines. All of these circumstances created few chances for the first beetles to be fossilized. It is probable that the first beetles inhabiting internal substrates were in rather strong competition with cockroaches and protelytropterans. The possible ability of larvae to develop in a more coherent material could have provided them with some chance of escape from very strong competition during the early stages of their ontogenesis and also some opportunity for development inside submerged parts of plants. On the other hand, such an initial mode of larval life in combination with imaginal structural adaptations of early beetles can explain a further transition of some groups of beetles into mid-Permian semiaquatic and aquatic habitats of Laurussia.

In fact, beetles are extremely rare in the earliest Permian rocks, their rarity not due to sampling bias. In the Saar-Nahe Basin this is reflected in the Niedermoschel insect taphocoenosis (Hörnschemeyer 1999). Here as well as at Grügelborn, the sediment has been altered by a magmatic intrusion and the insect remains are readily observable as shiny, silvery structures on the bluish-grey siltstone. About 1000 insect remains have been recorded (some are indeterminate thoracic or other fragments), but we estimate that there are less than 0.5% supposed beetle remains. Their rarity might be due to and/or exaggerated by taphonomic factors related to the possible lifestyles of these Early Permian beetles as being more or less cryptic animals living in wood. Later in the mid-Permian, the beetles still remained rather rare in many terrestrial palaeoenvironments and seem to be absent in some of them, e.g. the Guadalupian of Lodève where this order has never been recorded among thousands of insect remains. A taphonomic bias or depositional factors cannot be advocated for this taphocoenosis because some of the insect remains found are much more delicate than beetle elytra. The 'red bed' Permian of Lodève is also characterized by a scarcity of plant macrofossils (wood, leaves, etc.). This suggests that beetles could have lived in close association with trunks and wood also during the mid-Permian. During the Late Permian and the Early Triassic, basal diversifications of many holometabolous insect groups such as Neuroptera, Coleoptera and Trichoptera took place. As a result beetles are quite diverse and frequent in the Middle Triassic of the Grès des Vosges (Papier *et al.* 2005), and also in younger deposits, unlike in the Permian. All of the Late Triassic to more Recent insect taphocoenoses typically have modern profiles with a dominance of beetles in terms of species diversity, unlike those from the Permian.

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