This contribution is published to honor Prof. Vladimir Chikatunov, a scientist, a colleague and a friend, on the occasion of his 80th birthday.

The first finding of an asiocoleid beetle (Coleoptera: Asiocoleidae) in the Upper Permian Belmont Insect Beds, Australia, with descriptions of a new genus and species

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ABSTRACT

A new genus and species of Archostematan beetles, *Gondvanocoleus chikatunovi* n. gen. & sp., is described from an isolated elytron from the Upper Permian Belmont locality in Australia. *Gondvanocoleus* n. gen. differs from other members of the family Asiocoleidae in having only one row of cells in the middle part of the elytral field 3 and in having unorganized cells not forming rows near the elytral apex. Further relationships of the new genus with other asiocoleids are discussed. The fossil record of the Asiocoleidae is briefly overviewed.

KEYWORDS: Coleoptera, Archostemata, Asiocoleidae, beetles, new genus, new species, Permian, Lopingian, Australia, Gondwana, fossil record.

РЕЗЮМЕ

Новый род и вид жуков-архостемат, *Gondvanocoleus chikatunovi* n. gen. & sp., описаны по изолированному надкрылью из верхнепермского местонахождения Бельмонт в Австралии. *Gondvanocoleus* n. gen. отличается от остальных родов семейства Asiocoleidae присутствием только одного ряда ячей в средней части предшовного поля и не организованных в ряды ячей в апикальной части надкрылья. Обсуждены связи нового рода с другими азиоколеидами. Дан краткий обзор палеонтологической летописи Asiocoleidae.

КЛЮЧЕВЫЕ СЛОВА: Coleoptera, Archostemata, Asiocoleidae, жуки, новый род, новый вид, Пермская система, Татарский отдел, Австралия, Гондвана, палеонтологическая летопись.

INTRODUCTION

Interest in the study of fossil beetles and their place in the phylogeny of Coleoptera has significantly increased in recent years (Ponomarenko 2013; Ponomarenko *et al.* 2014; McKenna *et al.* 2015, 2019). Along with traditional methods of paleontological description and analysis summarized in Rasnitsyn (2002) and Grimaldi & Engel (2005), data from cladistics and genomics have also been used resolve subordinal

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and high-level phylogenetic relationships in beetles, and fossils serve as calibrating markers (Hunt *et al.* 2007; McKenna *et al.* 2015, 2019; Zhang *et al.* 2018).

Despite significant results in the beetle phylogeny, achieved with modern methods, it appears that the evolutionary history of Coleoptera includes many extinct terminal branches, which are often unfit for the computer-based models due to insufficient number of characters. However, it is impossible to construct a comprehensive Coleoptera phylogeny without the study of extinct groups such as Asiocoleidae.

The cuticle is usually more rigid in Coleoptera than in many other insects. so that the beetle remains can be transported by running water and deposited in coarse grained sediments. As a result, beetles can be found more often as compression fossils compared to other insects. Usually isolated elytra, abdominal ventrites and pronota are found. Unfortunately, the correct systematic placement of most of such imprints can seldom be established. However, with the growing number of descriptions based on completely preserved fossils, chances of identifying isolated sclerites, especially elytra, are also increasing (Ponomarenko 2008a, 2016). Studying such taxa sheds light on diversification and evolution of different types of elytra through time (Fig. 1), with lattice venation pattern becoming rarer as smooth elytra of Schizocoleidae and Permosynidae got more abundant near the Permian-Triassic boundary (Ponomarenko 2013, 2016). At the very end of the Permian, beetles most likely belonging to the Adephaga and Polyphaga suborders appeared. During the Early Triassic ecological crisis, the beetle diversity decreased and very few, apparently aquatic, forms persisted. In the Middle Triassic, the coleopteran diversity restored again. Comparing elytra from a locality of unknown temporal provenance with a reference diagram (Fig. 1) may give a justified insight into the locality's age.

The extinct beetle family Asiocoleidae is known mainly from isolated elytra. It was described by Rohdendorf (1961) as a monotypic taxon for peculiar elytra from the Middle Permian of the Kuznetsk Basin, southwestern Siberia. The lattice venation, presence of well-visible veins with fields of cells between them supported inclusion of the Asiocoleidae into Archostemata (Rohdendorf 1961; Ponomarenko 1969). The family has been also identified as a problematic group of early "pancoleoptera" (alongside with Taldycupedidae), which has basically given asiocoleids the *incertae sedis* status (Beutel 2005).

The Asiocoleidae remained monotypic for a few decades until abundant material from the European Russia reduced the hiatus between the Asiocoleidae, most basal Early Permian Tshekardocoleidae and Tricoleidae, which resulted in merging of Asiocoleidae and Tricoleidae into one family, with the latter becoming a junior subjective synonym (Ponomarenko 2011). Thus, there are 11 genera of asiocoleids to date. Asiocoleids are rather small beetles; one of the few full body findings—the Late Jurassic *Loculitricoleus tenuatus* Tan & Ren, 2009—is 9.3 mm long, another one—the Middle Permian *Asiocoleopsis hongi* Ponomarenko, Yan & Huang, 2014—is about 3 mm long (although its head and pronotum are almost indistinguishable), and an average asiocoleid elytron is 6–7 mm long.

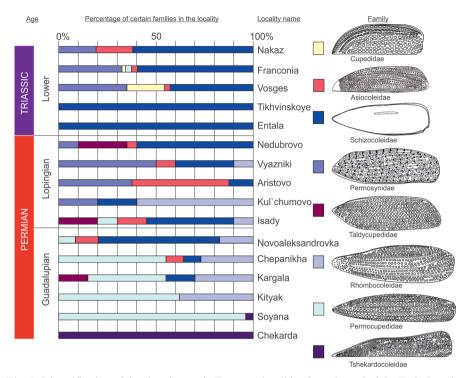


Fig. 1: Diversification of the elytral types in European localities from the end of the Early Permian up to the Middle Triassic.

Most asiocoleids are known from Asia, including those from localities on the South China plate, which situated south of the equator during the Permian. The Asiocoleidae are known from the Middle Permian Kaltan locality, Kemerovo Region, Russia (Ponomarenko 1969), the Middle Permian (Capitanian) Yinping locality in China (Ponomarenko *et al.* 2014). There is also an elytron known form the Severodvinian Novoaleksandrovka locality in the Orenburg Region, Russia (Ponomarenko 2013). The main bulk of asiocoleid species come from the Late Permian localities (Isady, Vyazniki, Aristovo, Nedubrovo; Fig. 1). Among all Late Permian localities with asiocoleids, Vyazniki is the closest to Belmont in terms of its age (Ponomarenko 2016). Few asiocoleids are known from the end of Late Triassic (Olenekian) Khej-Yaga locality (Ponomarenko 2008*b*). The family persists until the Late Jurassic, its latest representatives being known from the Callovian–Oxfordian Lagerstätte Daohugou in China (Tan & Ren 2009) and the Tithonian of Shar-Teg, Mongolia (Ponomarenko & Yan 2014).

The Upper Permian Belmont locality in New South Wales, Australia, represents a still-water freshwater basin extending along a river chain with swampy shores. Belmont is one of the richest sources of the Late Permian beetles, with more than 50 specimens found there; however, there is only a single record of the Asiocoleidae (Beattie 2007). Insects are reported from sediments of volcanic origin alongside flora, conchostracans and fishes. In still-water deposits the Permosynidae beetles are found together with rare beetle larvae. The Belmont locality is peculiar due to harbouring the most ancient representative of the coleopteran crown group, *Ponomarenkium belmonthense* Yan, Lawrence, Beattie, & Beutel, 2017 of its own family Ponomarenkiidae (Yan *et al.* 2017, 2018).

The swampy lake deposits contain mainly isolated wing fragments of Hemiptera, Mecoptera, Protelytroptera, Grylloblattida sensu lato, Psocoptera, Neuroptera and Coleoptera (Permocupedidae, Asiocoleidae, Taldycupedidae, Permosynidae, Rhombocoleidae and Schizocoleidae (Yan *et al.* 2013)), as well as a few wings of Trichoptera, Protorthoptera and Plecoptera. Most complete fossils belong to Psocoptera (Psocidae), Hemiptera Sternorrhyncha (Psyllidae) and Coleoptera (Beattie 2007). Most Coleoptera elytra from Belmont belong to the Permosynidae, bearing striae, which are usually uncommon for Archostemata.

MATERIALS AND METHODS

The studied material comes from the Pincombe's Outcrop, Belmont–Warners Bay area near Newcastle, New South Wales (northern Sydney Basin, Australia), where the mid-Lopingian insect-bearing deposits of the Croudace Bay Formation are exposed over an area of approximately 10–20 km². The deposits consist of sandstones, conglomerates, shales, coal seams and tuffs. The holotype of the new species is kept at the Australian Museum, Sydney.

The material was examined dry and under alcohol, using Nikon SMZ1000 stereomicroscope and a Zeiss Discovery V20 microscope. The photographs were prepared using an attached digital camera DXM1200 (on Nikon) and an AxioCam HRc (on Zeiss Discovery). Line drawings were prepared on photographs using CorelDRAW X8 and Adobe Photoshop CC software.

When dealing with compression fossils of isolated elytra, it is important to bear in mind that these are projections on the embedding rock. Thus, the three-dimensional structure of the elytron is prone to deformations due to the tectonic stretching of the rock in one or several directions, tilting in a sediment, or all of these combined. When the elytron is attached to a beetle, its sutural margin is straight, but it is curved in isolated or spread elytra (Fig. 2). Seeing elytral imprints of unnatural shape is not uncommon in compression fossils.

Veins were labelled as typical wing veins in the original description of *Asiocoleus*, and this continues in recent discourse (Kirejtshuk *et al.* 2014), but we have doubts in simple transferring of wing venation labelling onto highly-modified elytra, thus we label veins with numbers in the present study.

Elytra on Fig. 1 are modelled after the following taxa: *Sylvacoleus sharovi* Ponomarenko, 1969, Tshekardocoleidae (Ponomarenko 1969: 55, fig. 29); *Cytocupes angustus* Rohdendorf, 1961, Permocupedidae (Rohdendorf 1961: 406, fig. 329); *Schizotaldycupes ananajevi* Rohdendorf, 1961, Rhombocoleidae (Rohdendorf 1961: 415, fig. 342); *Taldycupes khalfini* Rohdendorf, 1961, Taldycupedidae (Rohdendorf, 1961: 423, figs 352, 353); *Permosyne dentata* Ponomarenko, 2003, Permosynidae (Ponomarenko 2003: 172, fig. 1 with minor changes); Schizocoleidae indet. (Ponomarenko 2004: 186, fig. 1f); *Notocupes nigrimonticola* Ponomarenko, 1969, Cupedidae (Ponomarenko 1969: 88, fig. 50).

TAXONOMY

Order Coleoptera Linnaeus, 1758 Suborder Archostemata Kolbe, 1908 Family Asiocoleidae Rohdendorf, 1961

The elytron of the described specimen belongs to the Asiocoleidae due to the presence of the main veins (Fig. 2d) and a net of intercalary veinlets between them, forming polygonal cells. It differs from other Archostemata *sensu lato* in the cells structure that is not organized in 2–3 parallel rows, but forms an irregular pattern.

Genus Gondvanocoleus Ponomarenko, n. gen.

LSID: urn:lsid:zoobank.org:act:440700C4-C127-4195-926D-EBBCF7B29C82.

Type species: Gondavanocoleus chikatunovi n. sp.

Diagnosis: Elytron convex (judging from unnaturally shaped margins), with three main veins and four fields. Vein 2 reaching $\frac{3}{4}$ elytral length, other veins end before it with vein 1 being shortest. Elytral fields with 1–6 rows of cells at midlength, with up to 3 rows at base of second field and 5 rows at base of marginal field (field 4). Cells are quadrangular or pentagonal, noticeably wider than veins, with well visible tubercles in cell margins.

Comparison: The new genus differs from other members of Asiocoleidae in having a single row of cells in the middle part of field 3 and in peculiar, uniformly arranged cells near the elytral apex.

Remark: This elytron was provisionally attributed to the genus *Tetracoleus* Ponomarenko, 2009 (Ponomarenko 2013).

Gondvanocoleus chikatunovi n. sp.

(Fig. 2)

LSID: urn:lsid:zoobank.org:act:C95ADCAC-E84B-4AD0-B866-23E491A8BD11.

Etymology: The species is named in honour of Prof. V.I. Chikatunov, a coleopterist from the Steinhardt Museum of Natural History, Tel Aviv, Israel.

Description: Elytron 11.5 mm long, 2.7 mm wide, i.e. $4.3 \times as$ long as broad, widest at its base, then narrowing to asymmetrical apex. Outer margin with rather narrow epipleuron, covered in up to 5 rows of small tubercles, with about 50 cells in each row. First vein (from sutural margin) barely reaches elytron's midlength, bending outwards near apex; next vein longest, reaches apical fourth; third vein slightly longer than first one. There are up to six rows of cells in subcostal (first) field; next

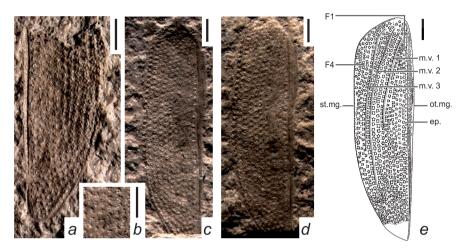


Fig. 2: Gondvanocoleus chikatunovi n. gen. & sp., holotype: (a) – print; (b) – details of cell organization; (c, d) – counterprint; (e) – interpretative line drawing. Abbreviations: F1, 4 – elytral fields 1, 4; m.v. 1, 3 – main veins 1, 3; st.mg. – sutural margin; ot.mg. – outer margin; ep – epipleuron. All scale bars = 1 mm.

field have three rows reaching apical fifth; third field have three rows near base, then two, and further apically one; sutural (fourth) field with 5 rows at elytral base and three rows in distal half.

Holotype: no. 41401, right elytron; Permian, Lopingian, Newcastle Coal Measures, Booraloo Subgroup, Croudace Bay Formation; Australia, New South Wales, Belmont locality.

DISCUSSION

The present study is focused on bringing more attention to collections of Belmont coleopterans. If Belmont beetles are all identified and formally described whenever possible, ratios of the elytral types could be calculated as it has been done for other localities (Fig. 1). Every beetle fossil from around the Permian–Triassic boundary is important for understanding evolution of the elytral structure. Belmont palaeoenvironments are reconstructed as a snapshot event due to a volcanic eruption and subsequent ash burial. The coleopteran familial composition in the Belmont taphocoenosis is characteristic for the Permian–Triassic transition, with a high proportion of Permosynidae with striated elytra, which is more common among Adephaga and Polyphaga, instead of lattice-structured elytra of most Permian beetles.

The peculiarity of *Gondvanocoleus* lies in having cells on the flattened outer margin fully replaced by rows of tubercles. This makes the genus similar to asio-coleids previously attributed to Tricoleidae, viz. *Tricoleus, Tricoleodes* and *Sogd-elytron*, but *Gondvanocoleus* noticeably differs in lacking of a 'tail-like' projecting elytron apex. The absence of a shortened vein (called A₂ in Ponomarenko (1969) and Kirejtshuk *et al.* (2014)) near the sutural margin of *Gondvanocoleus* also separates it from most of Asiocoleidae genera, although this could result from a damaged elytral

base. However, the oldest asiocoleid *Asiocolepsis hongi* also has only three distinct veins with the middle one branching, a condition absent in *Gondvanocoleus*. It is also worth mentioning that except *Asiocolepsis*, all asiocoleids, including Jurassic members, have elytral cells of more or less same size.

It is hard to establish an evolutionary trend in the Asiocoleidae elytral morphology, thus we refrain from labelling *Gondvanocoleus* characters as apomorphic or plesiomorphic, but in having unbranching veins and a simple elytron apex, *Gondvanocoleus* is morphologically mostly similar to the Jurassic *Loculitricoleus* Ponomarenko, 2014.

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