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At the dawn of the great rise: †*Ponomarenkia belmonthensis* (Insecta: Coleoptera), a remarkable new Late Permian beetle from the Southern Hemisphere

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The first complete beetle body fossil from the Australian early Late Permian fossil site Belmont is described here, †*Ponomarenkia belmonthensis* sp. nov., attributed to a new extinct family †Ponomarenkiidae. Shortly before a dramatic biodiversity crisis at the end of the Palaeozoic, it documents profound transitions in the evolution of Coleoptera, today by far the most species-rich group of insects and the largest order of organisms. †*Ponomarenkia* displays transitional states of several important characters, excluding it from the ancestral earliest stem-group coleopterans (e.g. †Tshecardocoleidae), but also from the four ‘modern’ extant suborders. In contrast to †Tshecardocoleidae, †Permocupedidae and †Rhomboleidae, it lacks the ancestral very broad and apically truncated prosternal process and a broad prothoracic postcoxal bridge, features suggesting a position in Coleoptera *sensu stricto*, i.e. the crown group of beetles. However, it does not share apomorphic features with extant Archostemata (e.g. narrowed neck region), Polyphaga (e.g. internalized propleura), Adephaga (e.g. elongated metacoxae with strongly developed metacoxal plates) or Myxophaga (broadly separated mesocoxae). †*Ponomarenkia* likely belongs in the stem group of one of the extant suborders or in the stem group of a clade comprising more than one of them.

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Keywords: Coleoptera; new taxon; Middle–Late Permian; phylogeny; early evolution

Introduction

The Permian was a critical period in evolutionary history on Earth, with the largest crisis in this history unfolding towards the end of the Palaeozoic era. The study of fossil beetles has proved that they are good tools for investigating environmental and evolutionary changes in the latest Palaeozoic and the earliest Mesozoic (Ponomarenko 2004, 2016). Morphologically, species recorded from Brazil, South Africa, European Russia and Australia differ only slightly, and consequently some of them were even included in the same genus. Such a strong similarity of Gondwanan and Angaraland beetles is rather puzzling, taking into consideration very distinct differences between the floras of the two continents (Naugolnykh & Ponomarenko 2010).

Most Permian beetles found to date are only represented as isolated elytra, which provide very limited information. Only a few completely preserved Permian beetles suitable for comparative morphological study have been

discovered. All of these came from temperate latitudes and the tropical belt, but fossils from southern Gondwana have remained unknown.

The entomofauna of the Tatarian insect beds within the Newcastle Coal Measures at Belmont (north of Sydney) has been known since the end of the nineteenth century (Knight 1950) and has yielded several thousands of insect imprints of at least 11 orders (Riek 1968), with beetles making up almost 20% of all findings (Beattie 2007). Despite a high amount of accumulated fossil material, very few beetles have been described from Belmont, and all of them were only represented by isolated elytra (Tillyard 1924).

A peculiarity of the Belmont locality is an eruption event that produced a volcanic ash dump. This caused a ‘snapshot’ kill, making it possible to interpret percentages of insect fossils in ecological modelling. The insect biocoenosis in the Belmont coal swamps and channel systems was dominated by representatives of four insect orders: †Protelytroptera (stem-group dermapterans), Hemiptera

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(Auchenorrhyncha), Mecoptera and Coleoptera. The most abundant group of this beetle assemblage is the †Permosynidae, recently partly transferred to the family †Rhombocoleidae by Ponomarenko (2003). Other groups are †Permocupedidae, †Rhombocoleidae, †Taldycupedidae, †Asiocolidae, †Permosynidae and †Schizocoleidae. This confirmed the presence of all Upper Permian beetle families in Gondwana (Yan *et al.* 2013). Permosynid beetles inhabited ponds including the water surface as a specific habitat, while archostematan species probably inhabited rotting tree trunks (Beattie 2007).

In the present study we describe and analyse for the first time complete beetle body fossils from the Gondwanan Belmont locality of the Late Permian pre-crisis time. During this period, ancestors of the superdiverse modern groups Adephaga and Polyphaga started to emerge, eventually leading to a remarkable diversity explosion in the Triassic and the later Mesozoic.

Material and methods

The Belmont insect bed is located within the Upper Newcastle Coal Measures of New South Wales. It consists of a thin chert seam within the Belmont Conglomerate Member within the upper part of the Coudace Bay Formation. It varies in thickness from approximately 20 cm to a reported 800 cm. At all sampled sites, over an area of outcrop of approximately 20 km², the bed varies in thickness between 20 and 32 cm, with a most common thickness of approximately 30 cm. The Croudace Bay Formation consists of sandstones, conglomerates, coal and minor volcanic chert and shales (Disessel & Moelle 1988). The geometry and lithology of the Belmont Conglomerate is indicative of a major, upper flow-regime river channel or channel system, grading into a lower flow regime with a fining of facies further downstream (Brown *et al.* 1968).

The pre-eruptive environment during the Tatarian in the Belmont area consisted of the upper delta tract of a gravel channel system flowing through and within a regional coal swamp. A series of overbank ephemeral pools existed, which probably periodically filled and then dried out over a number of years, building up layers of silty mud and sand of varying thickness. Prior to the volcanic event, which resulted in the formation of the insect seam, a Conchostraca (clam shrimps, Branchiopoda) bloom had developed as the pools became shallow and started to dry out. A community of water beetles co-habited with conchostracans. Fish trapped in these pools died, possibly due to anoxia, and were in a state of advanced decomposition. Swamp banks beside the ponds were lined with †*Phyllothea*, †*Glossopteris*, †*Gangamopteris*, less common †*Noeggerathiopsis*, and rare †*Sphenopteris* and †*Annularia* plants. A community of swamp insects existed based upon primary production by the swamp plants. A

single volcanoclastic event occurred, depositing a blanket layer of tuff over the swamps and filling the shallow ephemeral pools (Beattie 2007).

The fossil specimens were examined dry using Leica M165C and Zeiss Stemi 2000 microscopes. The photographs were taken with Leica DFC 425 and Keyence VHX – J20 digital cameras. Line drawings were prepared based on photographs using image-editing software: CorelDRAW X4 and Adobe Photoshop CS. Drawing conventions are: solid line, distinct margin; dashed line, indistinct margin and structures overlapping each other; dashed and dotted line, fold; dark grey, posteriorly open procoxal cavities. On the reconstruction (Fig. 4), red (grey) dotted lines are reconstructed parts, and solid black lines are characters restored after type material.

The following measurements were recorded (depending on the state of preservation): total body length (excluding length of everted abdominal sternites and genitalia); maximum body width; length and width of elytra, head, pronotum, abdomen; for legs, only the length was specified.

All fossils are deposited in the Australian Museum, Sydney.

In the following, Archostemata (*sensu stricto*) is used for the suborder in the sense of Beutel (1997) and Beutel *et al.* (2008), with the majority of extinct Permian families regarded as stem-group Coleoptera. Archostemata *sensu lato* refers to the concept of Ponomarenko (1969) with Archostemata also including Permian stem-group beetles (e.g. †Tshecardocoleidae, †Permocupedidae).

Systematic palaeontology

Class **Insecta** Linnaeus, 1758

Order **Coleoptera** Linnaeus, 1758

†**Ponomarenkiidae** fam. nov.

Type genus. †*Ponomarenkia* gen. nov.

Diagnosis. Head with subocular ridges. Prothorax with very short and narrow intercoxal process and exposed pleura. Mesoventrite lacking anteromedian pit but with transverse ridge delimiting katepisternum; mesocoxal cavities mainly closed by broad mesepimeron. Metaventrite with transverse ridge and discimen but without exposed metatrochantin. Elytra striated, elongated, apparently not closely adjusted to lateral sides of abdomen. Abdomen with five exposed sternites distinctly differing in length; terminal ventrite (sternite VII) distally narrowing and apically pointed.

Occurrence. Upper Permian, Tatarian insect beds, Newcastle Coal Measures, Belmont, north of Sydney, Australia.

Description. Head prognathous with mouthparts parallel to horizontal cephalic axis, but functional complex formed with prothorax distinctly sloping downwards, forming an

angle of approximately 15° with horizontal axis of main part of postcephalic body. Ventral side reinforced by subocular ridges. Frons with prominent acute anterior angles.

Prothorax with exposed pleura and narrow and short intercoxal process. Procoxae and exposed protrochantins transverse. Mesoventrite with procoxal rests and longitudinal and transverse sutures; anteromedian mesoventral pit lacking. Striated elytron almost 5 times longer than its own width, reaching abdominal apex posteriorly, together distinctly wider than abdominal ventrites. Metaventrte with distinct internal longitudinal ridge (discrimen) and transverse metakatepisternal suture. External metatrochantins absent. Metacoxae broad, laterally reaching beyond lateral margin of metaventrte, with posterior emargination fitting with metafemur but lacking coxal plates developed as duplicatures.

Abdomen with five ventrites. Apical sternite VII with drawn-out acute apex.

Genera included. Monotypic.

†*Ponomarenkia* gen. nov.

Type species. *Ponomarenkia belmonthensis* sp. nov.

Diagnosis. As for the family.

Description. Small, elongate-oval beetles. Head large, transverse, posterior part concealed by pronotum. Mandibles almost half as long as head, distinctly curved apically, with clearly defined molar areas. Antennae 11 segmented, moniliform. Compound eyes medium sized, laterally inserted, not protruding. Gular plate large, half as wide as head, with narrowed posterior margin and wide and deeply impressed sutures. Subocular lines present.

Prosternum with distinct anterolateral sockets for distal part of antenna. Prosternal intercoxal process apically rounded, not reaching posterior procoxal margin. Mesoscutellar shield exposed. Procoxal rests narrow, transverse, continuing onto anterior edges of mesanepisterna. Mesocoxae narrowly separated by elongate-triangular, acute anteromedian process of metaventrte. Only very narrow part of metanepisterna participating in mesocoxal closure. Pro- and mesotrochantins well-developed and -exposed, transverse, the former several times as wide as long. Elytra with with distinct oblique shoulder region and nine striae with punctures; nearly parallel sided over a long distance, very slightly narrowed at metathoracic region; posteriorly together forming rounded apex. Metaventrte sub-parallel; discrimen reaching anterior third; anteromedian process overlapping with mesokatepisternum. Metacoxae medially adjacent; with posterior emargination fitting with metafemur.

Abdomen wedge-shaped in ventral view, with rather weakly sclerotized ventrites. Ventrte 3 (sternite V) distinctly shorter than others.

Derivation of name. After the palaeontologist A. G. Ponomarenko, in recognition of his comprehensive and profound contribution to the knowledge of fossil Coleoptera.

Species included. Monotypic.

Occurrence. Upper Permian, Tatarian insect beds, Newcastle Coal Measures, Belmont, north of Sydney, Australia.

†*Ponomarenkia belmonthensis* sp. nov.
(Figs 1–4)

Diagnosis. As for the family.

Derivation of name. After type locality Belmont (NSW).

Material. Holotype 40278 and paratype 41618. Deposited in the Australian Museum, Sydney.

Occurrence. Upper Permian (Tatarian), Tatarian insect beds, Newcastle Coal Measures, Belmont, north of Sydney, Australia.

Description. Mandibles with thickened outer margins and blunt apices lacking additional teeth; molar areas oval, occupying more than one-third of mandibular length. Fifth antennomere 1.5 times as long as 6–7 and 1–4, which are of equal size; antennomere 8 about 1.5 times as long as 9 and 10; antennomeres 9–10 of equal size; apical antennomere oval, as long as previous two combined. Subocular line half as long as eye.

Prosternum beaded along anterior and posterior margins, as long as or slightly longer than procoxae (excluding length of intercoxal process). Procoxae strongly transverse, twice as wide as long, separated by intercoxal process up to the mid-length. Protrochantins 4 times as wide as long. Propleuron narrow, almost as long as head, as wide as one-third of procoxal width. Mesoscutellar shield with rounded posterolateral angles and nearly straight posterior edge. Procoxal rests half as long as procoxae. Anterior margins of mesanepisterna excised as part of procoxal rest, fitting with posterior procoxal surface. Metaventrte beaded anteriorly and laterally; very slightly narrowing anteriorly; posterior angles protruding posterolaterally.

First abdominal ventrite (sternite III) strongly narrowed medially, in midline distinctly shorter than second one; third ventrite one-third as long as preceding one; fourth ventrite twice as long as third; apical ventrite (sternite VII) as long as penultimate one.

Measurements. Body length: 4.5 mm, width 1.8 mm; head length 0.7 mm, width 0.7 mm; pronotal length 0.7 mm, width 1.1 mm; elytron length 3.6 mm, width 1.0 mm; abdominal length 1.9 mm, width 1.5 mm; mesofemoral length 0.5 mm; metafemoral length 0.4 mm.

Remarks. Gular sutures thick, suggesting well-developed internal ridge.

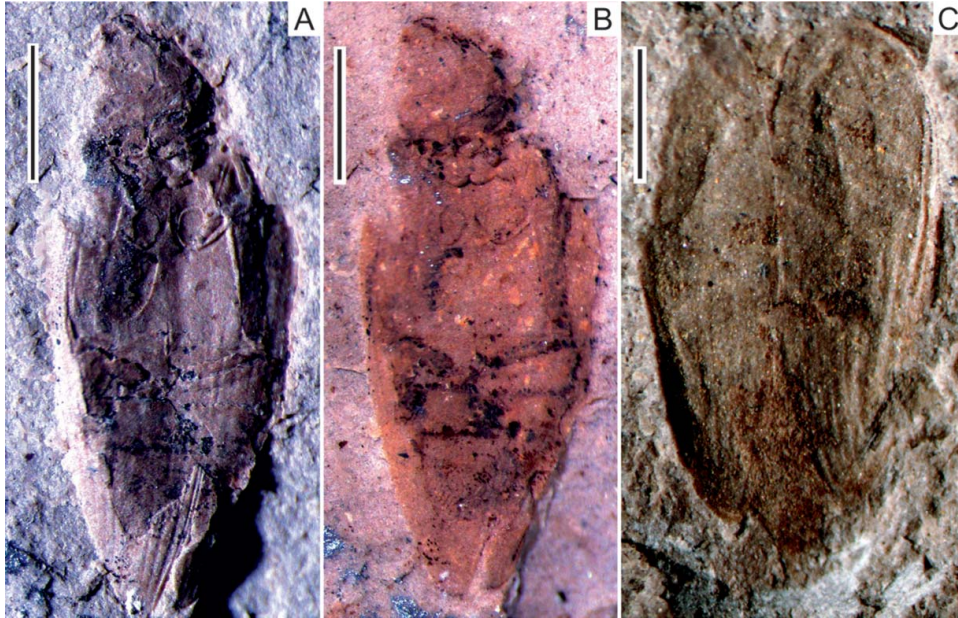


Figure 1. Habitus photos of †*Ponomarenkia belmonthensis* sp. nov. **A, B**, holotype 40278; **C**, paratype 41618. Scale bars = 1 mm.

Discussion

The unusually robust exoskeleton of beetles distinctly increases the chance of preservation. Coleopteran remains are also easily transported by water without major damage. Therefore, beetles are occasionally more abundant in certain localities than the living species themselves were in their natural environment. The oldest well-preserved imprints were found in 300 Ma localities.

The most important character complex (Fig. 5) that developed in the earliest evolutionary stage of Coleoptera (earliest Permian, possibly latest Carboniferous) was a strongly sclerotized body without exposed membranes: an ‘armour strategy’ providing mechanical protection against predators and enabling beetles to penetrate narrow spaces. The prothorax with a broad prosternal process and a broad postcoxal bridge was apparently part of this, but these features were lost during the Late Permian, favouring an increased movability of the head-prothorax complex.

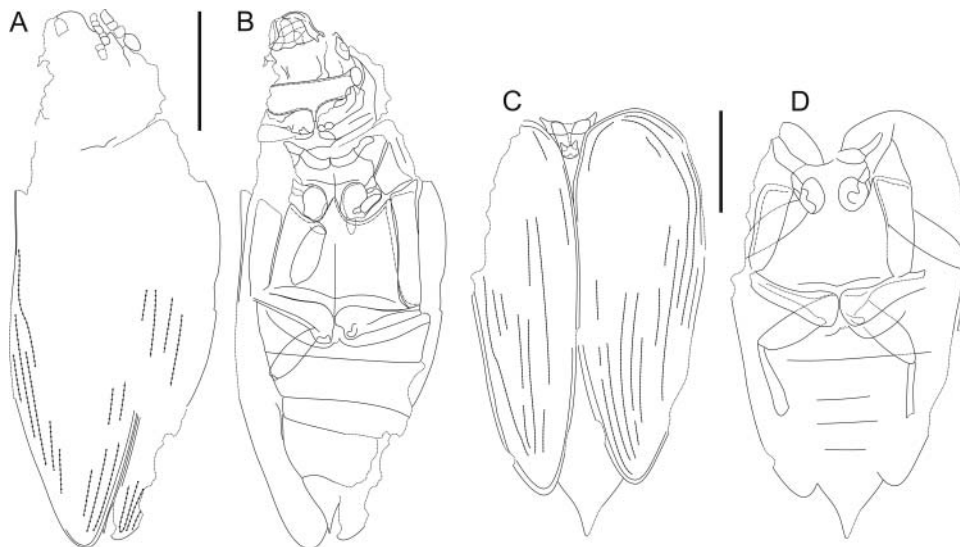


Figure 2. Line drawings of †*Ponomarenkia belmonthensis* sp. nov. **A, B**, holotype; **C, D**, paratype. Scale bars = 1 mm.

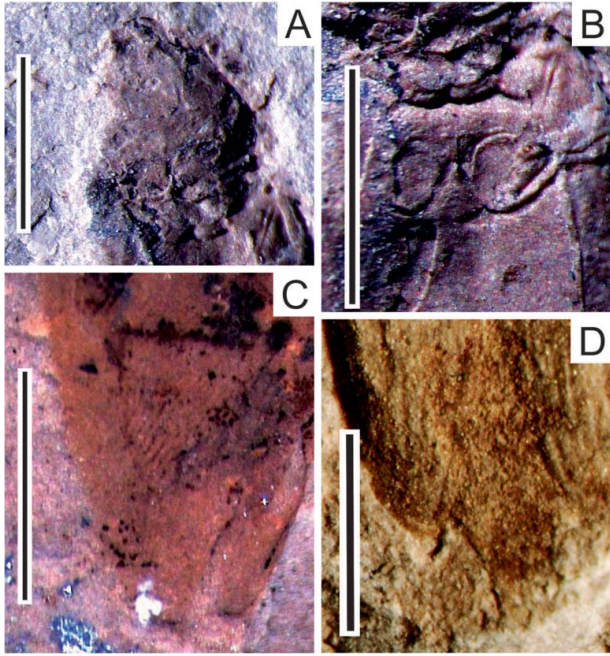


Figure 3. Morphological details of †*Ponomarenkia belmonthen-sis* sp. nov. **A–C**, holotype 40278; **D**, paratype 41618. **A**, details of head and pronotum; **B**, mesoventrite; **C**, **D**, abdominal apex. Scale bars = 1 mm.

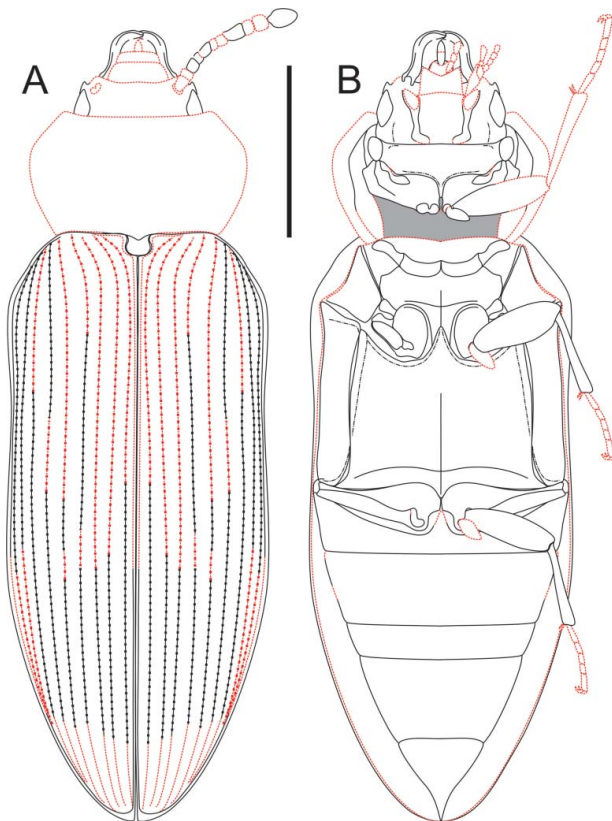


Figure 4. Habitual reconstruction of †*Ponomarenkia belmonthen-sis* sp. nov. in **A**, dorsal; and **B**, ventral views. Scale bar = 1 mm.

Later in the Mesozoic the ‘ancestral’ condition re-evolved in some subordinate taxa, for instance Rhysodini and Cicindelinae (Adephaga, Carabidae). Even though the broad prosternal process and closed procoxal cavities are missing in the related Neuropterida and Strepsiptera, which do not show any tendency of reinforcing their exoskeleton, it is very likely ancestral for beetles as indicated by the branching pattern in the stem lineage (Beutel 1997; Beutel *et al.* 2008). The strong sclerotization enabled early beetles to penetrate under bark (e.g. of early conifer trees), like adults of extant Archostemata (*sensu stricto*). Ancestral characters of extant archostematans (Cupedidae and Ommatidae) such as a tuberculate cuticular surface and a wedge-shaped head are likely be related to a preference for subcortical habitats.

Coleoptera were represented by a single family †Tshekardocoleidae in the Early Permian, and their diversity was low during the entire period. In this period beetles were most likely consumers of decomposing wood. Aquatic, semiaquatic (riparian, hygropetric) and terrestrial detritus consumers and predators appeared apparently during the terminal Permian. †Tshekardocoleidae was placed as the sister group of all the remaining extant and extinct beetles (Beutel 1997). During most of the Middle Permian, the beetle fossils also belonged to the stem lineage of Coleoptera (Fig. 5; Beutel 1997; Beutel *et al.* 2008), forming early branches of the traditional Archostemata (archostematan grade) as defined by Ponomarenko (1969). In contrast, beetle fossils of the terminal Middle Permian display characters of the two advanced ‘modern’ suborders. Adephaga are represented by Trachypachidae and possibly a second family (A. Ponomarenko, pers. comm. to E. Yan). The presence of Polyphaga is suggested by abundant striated elytra, some of which very likely belonged to representatives of this suborder.

The most ancient locality with fossil beetles probably belonging to Adephaga or Polyphaga (or a possible common stem lineage) is Yinping in the south of China. The age of this locality is estimated as Upper Capitanian (late Middle Permian). In Yinping, a seemingly ancestral beetle belonging to Polyphaga or their closest ancestors (stem lineage) was found, and also a fossil belonging to the enigmatic family †Triaplidae, arguably a key aquatic taxon of Adephaga. These beetles are completely unknown in contemporaneous European Russian and Siberian localities. They appear only in the Upper Vyatkian and Eryakovian deposits, which are usually believed to be of the same age as the Changxingian. This distribution pattern suggests that ‘higher’ beetles (excluding the Coleoptera stem lineage) emerged in the Southern Hemisphere, as assumed for different groups of tetrapod vertebrates of this period (Ponomarenko *et al.* 2014).

In the terminal Permian, beetles with wood-associated larvae disappear from the fossil record, with possible descendants re-appearing in the Middle Triassic.

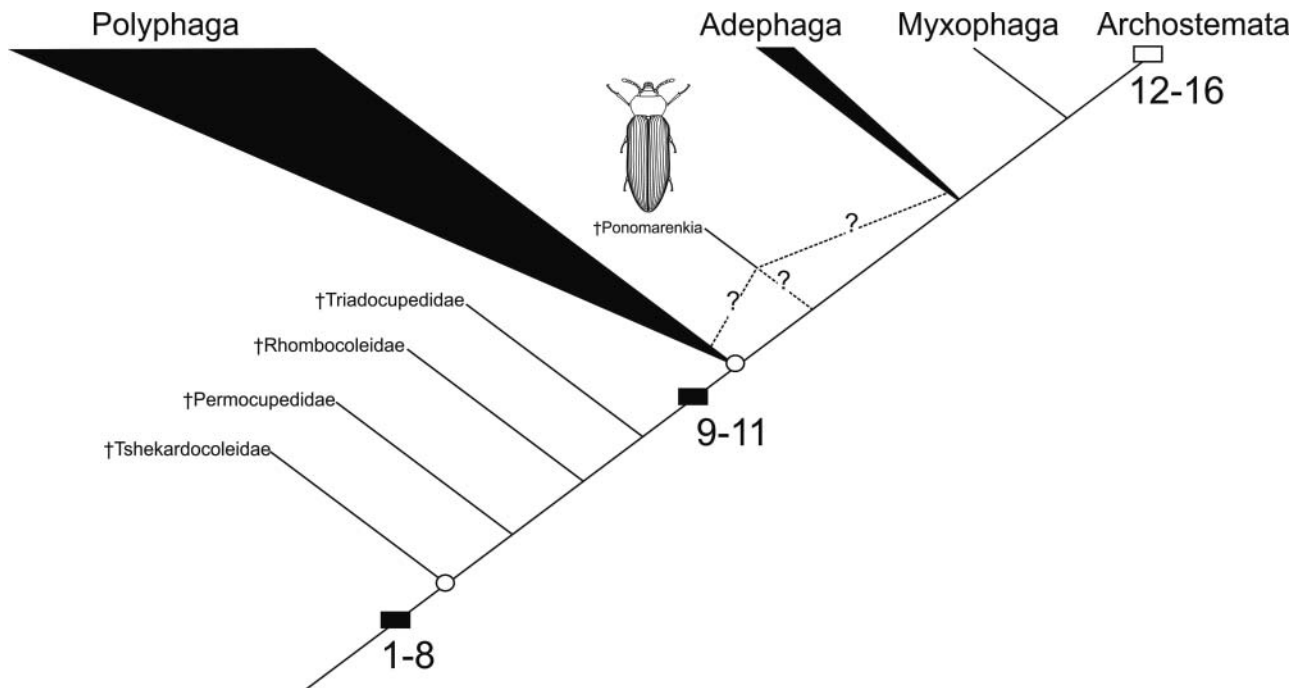


Figure 5. Phylogenetic diagram showing relationships between the extant suborders Archostemata (*c.* 40 spp.), Myxophaga (*c.* 120 spp.), Adephegata (*c.* 40,000 spp.) and Polyphaga (*c.* 320,000 spp.), and stem group Coleoptera. Based on Misof *et al.* (2014) and McKenna *et al.* (2015) (extant groups), and Beutel (1997) and Beutel *et al.* (2008) (extinct taxa). Full boxes indicate apomorphies; the empty box indicates retained plesiomorphies. Characters 1–8: Coleoptera *sensu lato*. (1) strongly sclerotized, without exposed membranes; (2) elytra; (3) wedge-shaped head; (4) wings with transverse folding mechanism; (5) posterior abdominal segments retracted; (6) closed prothoracic postcoxal bridge; (7) broad, apically truncate prosternal process; (8) tuberculate surface structure. Characters 9–11: Coleoptera *sensu stricto*. (9) procoxal cavities secondarily open (already in †Triadocupedidae); (10) prosternal process narrow; (11) larval urogomphi (?). Characters 12–16: plesiomorphies retained in Archostemata. (12) tuberculate surface structure; (13) cuticular scales (?); (14) transverse ridge of mesoventrite retained; (15) metatrochantin exposed; (16) thoracic muscle apparatus distinctly more complex than in other three suborders (Beutel & Hass 2000).

Similarly, new groups appear before the boundary event and then disappear from the fossil record in the Early Triassic, to re-surface beginning in the Middle Triassic. In the Lower Triassic, only scant fossil remains of beetles with smooth elytra are known, similar in body shape to water beetles. During the Permian–Triassic extinction event the abundance and distribution areas of many groups were temporarily reduced, but without distinctly affecting the course of the evolutionary process itself.

The composition of beetles in the Early Triassic changed dramatically compared to that of the terminal Permian. For instance, the Induan locality Entala and Olenekian locality Tikhvinskoe included only beetles with elytra of the schizocoleid morphotype, almost exclusively representing the genus †*Pseudochrysomelites*, typical of the crisis interval (Ponomarenko 2016). Such changes in the faunal composition give evidence of considerable changes in landscapes and ecosystems. Some elements of the Permian diversity which largely disappeared from the fossil record began re-surfacing only in the basal Middle Triassic.

The character combination of †*Ponomarenkia* suggests a key position in coleopteran evolution in the

Permian–Triassic transition zone (Fig. 6). Several features clearly place it in Coleoptera *sensu stricto* as defined by Beutel (1997), i.e. Coleoptera excluding †Protocoleoptera (†Tshekardocoleidae, †Oborocoleidae, †Moravocoleidae), †Permocupedidae, †Rhombocoleidae and †Triadocupedinae (Beutel 1997; Beutel *et al.* 2008, fig. 14). In contrast to †Tshekardocoleidae and its relatives, it lacks the plesiomorphic elytral pattern with longitudinal veins not arranged in a regular parallel pattern (e.g. Ponomarenko 1969; Kukulová-Peck & Beutel 2012, fig. 8), elytral window punctures, a tuberculate surface structure, a subdivided propleuron, a very broad and apically truncate prosternal process, closed procoxal cavities with a broad postcoxal bridge, and a broad and straight contact between the meso- and metaventrite (Ponomarenko 1969, fig. 29a, b). The tips of the abdomen of †*Ponomarenkia* seem to reach slightly beyond the elytral apices. However, this is clearly different from the ancestral condition found in †Protocoleoptera, and likely an artefact due to a slightly deformed abdomen of the paratype. The terminal abdominal region superficially resembles the condition found in †Protocoleoptera. However, whereas an apically

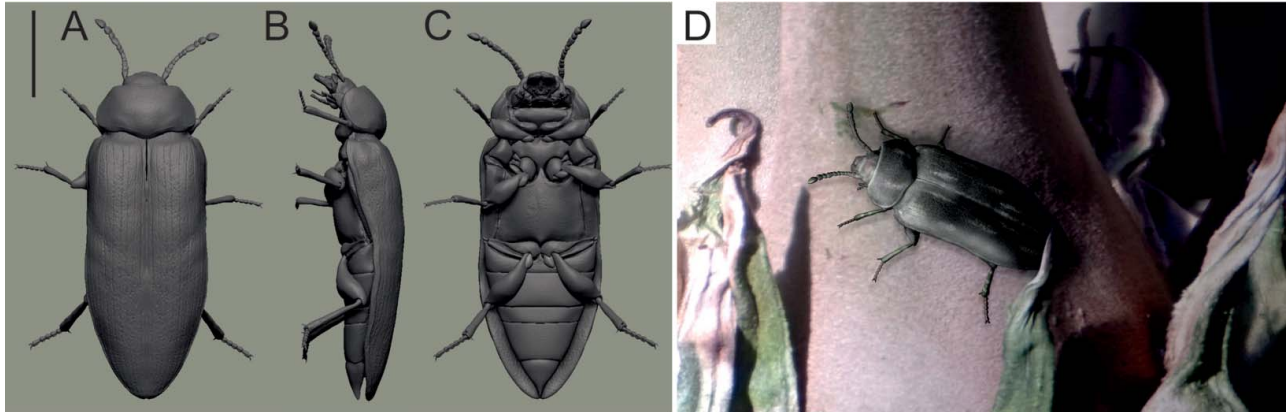


Figure 6. Three-dimensional reconstruction of †*Ponomarenkia belmonthensis* sp. nov. in **A**, dorsal, **B**, lateral and **C**, ventral views. **D**, environmental reconstruction. Scale bar = 1 mm.

pointed ovipositor is present in the former according to current interpretations (e.g. Ponomarenko 1969; Kukulová-Peck & Beutel 2012), the condition in the Australian fossil is apparently due to an apically pointed terminal sternite VII, arguably an apomorphy of the genus. The ancestral tuberculate body surface, the elytral window punctures, and a very broad and truncate prosternal process are still preserved in †Permocupedidae, †Rhombocoleidae and †Triadocupedinae (Ponomarenko 1969; Beutel 1997; Beutel *et al.* 2008, fig. 14), and the closed procoxal cavities in the former two taxa. These conditions are not only lacking in †*Ponomarenkia*, but also in the extinct †Ademosynidae (Yan *et al.* 2017), the Permian †*Archosyne*, the Mesozoic †*Jurodes* (Yan *et al.* 2014), †Schizophoridae and in †Catiniidae (Ponomarenko 1969).

Within Coleoptera *sensu stricto*, defined by elytra closely fitting with the abdomen, a parallel elytral pattern, primarily open proximal cavities, a narrowed prosternal process (Beutel 1997), and a maximum number of 11 antennomeres, †*Ponomarenkia* does not fit into any of the four extant suborders. The well-developed transverse ridge of the mesoventrite is a symplesiomorphy with Archostemata (*sensu stricto*). However, aside from this, the Australian fossil differs strongly from extant or extinct representatives of that suborder with respect to the internalized metatrochantin, the metanepisterum being only marginally part of the closure of the mesocoxal cavity, the lack of elytral window punctures, and the moniliform antennae. †*Ponomarenkia* lacks archostematan apomorphies such as a constricted neck region or a distinct median ridge of the first abdominal ventrite, and also diagnostic features like a body parallel sided in ventral view and a comparatively long abdominal sternite VII.

†*Ponomarenkia* differs very clearly from Adephaga by the transverse ridge of the mesoventrite, short metacoxae not reaching the hind margin of abdominal sternite III, lacking coxal plates (also missing in Gyrinidae), and also

by the moniliform antennae, which occur only very rarely in the family Carabidae (Rhysodini). The relatively small body size may be seen as part of a tendency shared with extant Myxophaga (e.g. Beutel 1999), but a conspicuous myxophagan apomorphy, the very broad contact between the firmly connected meso- and metaventrite (e.g. Beutel & Haas 2000), is clearly lacking in the new taxon, which instead displays a triangular anteromedian process of the metaventrite connecting with the mesokatepisternum. Moreover, a transverse ridge of the mesoventrite is lacking in all extant Myxophaga, as in Polyphaga. †*Ponomarenkia* also differs from Polyphaga (including †*Peltosyne*, which likely belongs to the stem lineage of this megadiverse suborder; Yan *et al.* 2017) by the exposed propleuron. The ancestral condition of the mesoventrite, a symplesiomorphy shared with †*Peltosyne*, excludes it from Polyphaga *sensu stricto*. The moniliform antenna represents, at best, vague evidence for a phylogenetic affinity with Polyphaga. Filiform antennae as found in Scirtidae (part.; Lawrence 2016) and some other polyphagan groups are probably a groundplan feature of this suborder.

A feature shared with several extinct groups, like †*Peltosyne*, †*Ranis* and †Ademosynidae, and also some groups of Adephaga (e.g. Gyrinidae part., Carabidae part.) and Polyphaga (e.g. Hydrophilidae part., Elateridae part.), is the striation of the elytra. However, this character is apparently prone to parallel evolution and secondary loss. Phylogenetic affinities with †Ademosynidae are possible. Unfortunately, the pronotum of †*Ponomarenkia* is not well preserved. However, it is likely that anterolateral angles are present and that the anterior margin is not convex as in ademosynids (Yan *et al.* 2017). Moreover, the prosternal process of †*Ponomarenkia* is narrow and parallel sided, with a rounded apex, whereas it is usually relatively broad and apically extended in †Ademosynidae (Yan *et al.* 2017). Even though †*Ponomarenkia* shares

some plesiomorphic (or diagnostic) features with †Schizophoridae (e.g. shape of prosternal process and metacoxae), it lacks the elytral schizae and smooth elytral surface structure characteristic of this family. As in the case of †Ademosynidae, affinities with †Catiniidae, possible relatives of the extant Myxophaga (e.g. Crowson 1975), cannot be excluded. However, †*Ponomarenkia* differs from fossils assigned to this family by the distinctly developed prosternal process, the anteromedian process of the metaventrite, and the striated elytra.

The placement of †*Ponomarenkia* is clearly impeded by a character combination which is apparently close to the groundplan of Coleoptera *sensu stricto*, and also by the uncertain relationships of the extant suborders (Crowson 1955, 1960; Kukalová-Peck & Lawrence 1993, 2004; Beutel & Haas 2000; Beutel *et al.* 2008; Friedrich *et al.* 2009; Lawrence *et al.* 2011; Bocak *et al.* 2014; Misof *et al.* 2014; McKenna *et al.* 2015). The new taxon could belong to the stem group of either Polyphaga or Myxophaga, or more likely the stem group of a clade comprising more than one of the extant suborders. For now, †*Ponomarenkia* should be viewed as a representative of a coleopteran evolutionary stage typical for the Permian–Triassic transition zone. The discovery of new well-preserved fossils from this period and new data on subordinal relationships may help to clarify the precise placement of this key coleopteran taxon.

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