†Peltosynidae, a new beetle family from the Middle–Late Triassic of Kyrgyzstan: its affinities with Polyphaga (Insecta, Coleoptera) and the groundplan of this megadiverse suborder

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†Peltosynidae, a new beetle family from the Middle–Late Triassic of Kyrgyzstan: its affinities with Polyphaga (Insecta, Coleoptera) and the groundplan of this megadiverse suborder

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Middle–Late Triassic fossil beetles previously assigned to Polyphaga *incertae sedis* and new material from this period are described and illustrated. †Peltosynidae fam. nov. is introduced to contain the type genus *Peltosyne*, and species *P. triassica* Ponomarenko, 1977, together with the new species *P. varyvrosa* sp. nov. Two new monospecific genera, *Gnathopeltos* gen. nov. and *Ofthalmopeltos* gen. nov., with type species *G. dixis* sp. nov. and *O. synkritos* sp. nov., are also included in †Peltosynidae. Morphological characters evaluated with respect to their phylogenetic significance confirm that the family belongs to the suborder Polyphaga, mainly supported by the apomorphic internalized propleura. †Peltosynidae is characterized by a large transverse head, long and prominent, strongly developed mandibles, a short prosternum with a narrow, relatively short prosternal process, an interlocking mechanism between this process and a groove of the anteromedian process of the mesoventrite, striated elytra, a short metakatepisternum, transverse coxae, and a short abdomen with five ventrites. The large and transverse head is a potential autapomorphy. †Peltosynidae do not fit into any of the seven extant major polyphagan infraorders (series). The presence of a mesothoracic transverse katepisternal ridge in †*Peltosyne* is a plesiomorphic feature distinguishing the new family from all other groups of the suborder and suggesting its placement in the stem-group of Polyphaga. The strongly prominent mandibles and the coarse body sculpture resemble features found in extant Archostemata. It is likely that the beetles were xylophagous and adapted to subcortical habitats, arguably maintaining plesiomorphies. The polyphagan groundplan is reconstructed based on recent phylogenies and features found in †Peltosynidae and other extinct and extant groups. A scenario for the evolution of non-archostematan beetles in the late Permian and early Mesozoic is presented.

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Keywords: Coleoptera; new family; †Peltosynidae; Polyphaga; phylogeny; early evolution

Introduction

The coleopteran suborder Polyphaga represents one of the most remarkable radiations among all groups of living organisms. With approximately 350,000 described species (Grimaldi & Engel 2005), and doubtlessly many more to discover (e.g. Stork *et al.* 2015), the group comprises about 90% of all known beetles (both fossil and recent) and more than 20% of all presently described organisms (Costello *et al.* 2012).

Despite this unparalleled diversification and numerous economically relevant species (Booth *et al.* 1990), many important questions concerning the higher level taxonomy, phylogeny and evolution of Polyphaga remain open. Recently, considerable progress has been made in reconstructing the phylogeny of the suborder, mainly based on morphological and molecular datasets of increasing size

(e.g. Lawrence *et al.* 2011; Bocak *et al.* 2014; McKenna *et al.* 2015). However, the placement of Polyphaga among the other three beetle suborders, Archostemata, Myxophaga and Adephaga, remains controversial, with various incongruent branching patterns (Kukalová-Peck & Lawrence 1993, 2004; Hunt *et al.* 2007; Beutel *et al.* 2008; Misof *et al.* 2014; McKenna *et al.* 2015). The origin of Polyphaga before the Permian–Triassic transition zone is also obscure, mainly due to the scarcity of well-preserved fossil material. Several fossil taxa of Permo-Triassic or even Jurassic age have been considered as close relatives or basal members of Polyphaga, for instance †Ademosynidae (Crowson 1975) and the genus †*Peltosyne* (Ponomarenko 1977: Polyphaga *incertae sedis*). However, at that time the investigation of possible ancestral polyphagans was impeded by various factors. Crucial insect-rich Lagerstätten (e.g. Kirejtshuk *et al.* 2010; Ponomarenko *et al.* 2014;

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Yan *et al.* 2013) were still unknown, and detailed morphological studies on potentially ancestral and more advanced beetles (e.g. Beutel *et al.* 2008; Friedrich *et al.* 2009; Lawrence *et al.* 2011) were much more limited.

The primary aim of the present study is the introduction and phylogenetic evaluation of a new extinct family, †Peltosynidae, which includes †*Peltosyne triassica* Ponomarenko, 1977 together with two new genera. Structural features are discussed with respect to their taxonomic and phylogenetic implications, especially with respect to the affinities of the fossils to the megadiverse Polyphaga. A groundplan for this suborder is suggested based on the evaluation of the extinct taxa assigned to †Peltosynidae and on recent phylogenetic studies founded on extensive morphological character sets (e.g. Beutel *et al.* 2008; Friedrich *et al.* 2009; Lawrence *et al.* 2011) and molecular data (McKenna *et al.* 2015). The new findings are also discussed with respect to their possible implications for the early evolution of this group of beetles.

Material and methods

The studied material comes from the Late Triassic Madygen Formation of the Dzhailyaucho site, Batken region, Osh Province, Southern Fergana, Kyrgyzstan (40° 04′ N, 70° 12′ E). The Madygen Formation unconformably overlies Upper Carboniferous marine limestones (Uchbulak Horizon) and is transgressively covered by Lower Jurassic terrestrial deposits. The age of the Madygen Formation is Ladinian or Carnian according to floristic analysis (Dobruskina 1995). Sedimentation took place within a tectonically active basin that accumulated several hundred metres of alluvio-fluvial and lacustrine deposits (Franeck *et al.* 2012).

Dzhailyaucho, one of the most insect-rich Triassic sites, has yielded many hundreds of fossil beetle remains belonging to Cupedidae, †Schizophoridae, †Catiniidae and †Ademosynidae (Ponomarenko 1969). The Madygen Formation is also unique in its rich fossil fishes, crustaceans (ostracods) and flying reptiles (Buchwitz 2011; Kogan *et al.* 2013).

Characters such as the elytral ultrastructure or proportions of different body parts should be used very cautiously in descriptions of compressed beetle fossils since they are often heavily affected by postmortal deformation of the compression and tectonic deformation of the host rock (Ponomarenko 1969). Beetles from the Dzhailyaucho site are especially exposed to these distortions: elytra of a single specimen can have different shapes and sizes (see Fig. 1C) and may be easily assigned to different taxa if found separately. This is also a common reason why the left and right side of the same imprint are often asymmetrical. Arrows in Figures 1C, 3B, 5A, and 7B indicate directions of tectonic deformation.

The 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. Fossil beetles in the Dzhailyaucho Lagerstätte are preserved as complete bodies with several collapsed layers of cuticle, so that the dorsal and ventral surfaces are often visible on the same imprint. For the convenience of morphological interpretation, the dorsal and ventral features for each specimen are presented as two separate figures (Fig. 5). Figure 3G was made using plasticine and subsequently coloured in Photoshop CS.

Drawing conventions are as follows: solid line, distinct margin; dashed line, indistinct margin and structures overlapping each other; dashed and dotted line, fold; dark grey, occipital foramen, posteriorly open procoxal cavities and wing veins; dotted filling, membranous area of mesometoventral connection; reconstructed characters in Figure 3E, F are red; dorsal characters often visible on fossils ventral aspect are grey in Figure 1A.

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 elytron, head, pronotum, abdomen; only the length was specified for legs (see Table 1). As membranous connections between different sclerites are not preserved (pronotum and abdomen usually somewhat detached, Fig. 1B), combined lengths of body parts are not equal to specimen overall length.

All fossils are deposited in Borissiak Paleontological Institute (**PIN**), Russian Academy of Sciences.

Phylogenetic analyses were based on 35 coded characters (Supplemental Appendix 1), mostly from Beutel & Haas (2000), Beutel *et al.* (2008) and Lawrence *et al.* (2011), with a main focus on features that can be observed in well-preserved fossils (e.g. head capsule, elytron, configuration of ventral thoracic and abdominal sclerites). The taxon sampling included two megalopteran outgroups (*Sialis*, *Chauliodes*), and 31 coleopteran ingroup taxa representing all four suborders, 18 extant and 13 extinct. Parsimony analyses were carried out with NONA (Goloboff 1995) (ratchet, 1000 replicates). All characters were equally weighted and unordered. Bremer support values were calculated with NONA.

Archostemata is used *sensu* Beutel *et al.* (2008), with the majority of extinct families regarded as 'stem-group Coleoptera'.

Systematic palaeontology

Class **Insecta** Linnaeus, 1758
Order **Coleoptera** Linnaeus, 1758
Suborder **Polyphaga** Emery, 1886
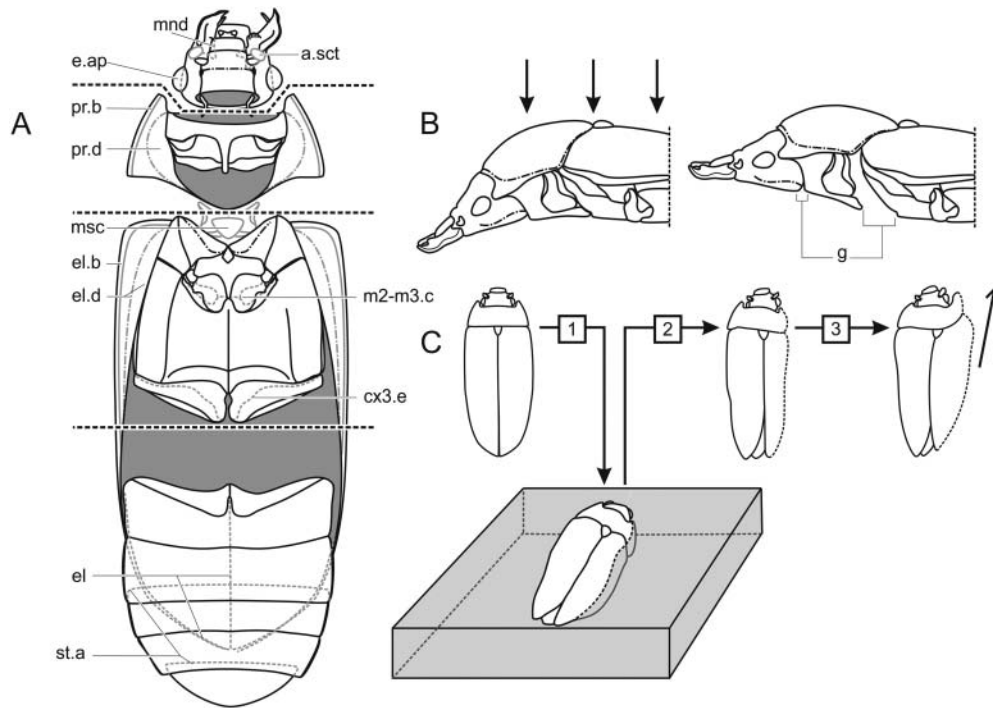Family †**Peltosynidae** fam. nov.

Figure 1. Peculiarities of preservation of fossil beetles and character interpretations. **A,** zones of body disarticulation (black dotted lines), dorsal characters and hidden structures, which are often observed on ventral imprints; **B,** compression during burial (vertical arrows). resulting in flattening of beetle body and formation of gaps (g) between head and anterior prosternal margin, and also between prosternum and mesoventrite; **C,** distortion of beetle during burial process and fossilization; body tilting and partial immersion (1) into sediment resulting in apparent body asymmetry (2); further tectonic deformation (oblique arrow) stretches and distorts body (3) in one or several directions. Abbreviations: a.sct, antennal socket; cx3.e, excavated metacoxae; e.ap, eyes apodeme; el, elytral apices overlapped by abdomen; el.b, elytral bead; el.d, elytral disk; mnd, mandibular base (usually very thick and visible through many other head structures); ms, mesoscutellar shield and parts of mesosternum; m3–m3.c, meso- metaventrite connection; pr. B, pronotal bead; pr.d, pronotal convex disk.

Type genus. *Peltosyne* Ponomarenko, 1977.

Diagnosis. †Peltosynidae have a completely internalized propleuron; they differ from other extant and extinct groups of Coleoptera by: large and broad head without defined neck region, strongly protruding mandibles with well-developed mesal teeth, very short prosternum with fairly short and narrow prosternal process, interlocking mechanism formed by this process and a distinct groove of anteromedian process of mesoventrite, striated elytron, short metakatepisternum, and short and broad abdomen.

Description (modified from Ponomarenko 1977). Medium-sized to small, 6–15 mm, elongate-oval beetles. Body surface covered with densely arranged and very distinct punctures, often rugose.

Head prognathous, large and transverse, as long as pronotum (excluding protruding part of mandible), deeply retracted into prothorax, without constricted neck region. Mandibles massive, very heavily sclerotized, making up more than half of head length, reaching far beyond anterior margin of labrum; located close to each other, bearing large denticle at midlength, with blunt apices and distinct molar areas. Frons and clypeus fused. Antennal sockets widely separated, close to the anterior margin of frons; antennal grooves often present on ventral side. Ocelli absent. Compound eyes rather small, rarely longer than half of mandibles, laterally placed and only slightly protruding. Posterior tentorial pits distinct, deep. Gular sutures almost parallel-sided, gular plate weakly or not narrowing anteriad.

Pronotum transverse, very weakly widening posteriorly, with distinctly protruding anterior angles and narrow hypomeres; posterior pronotal margin slightly bisinuate. Prosternum in front of procoxae short. Procoxae separated. Procoxal (= intercoxal) process rather narrow, parallel-sided, not widening at apex. Procoxal cavities posteriorly open. All coxae transverse, pro- and meso-coxae with exposed trochantins.

Mesoventrite short, not longer than middle coxae; anteromedian process with cavity always present and forming well-developed interlocking mechanism with prosternal process. Mesoventrite with longitudinal suture; transverse katepisternal suture also recognizable in some species. Procoxal rests broad, well developed. Mesocoxal cavity not partially bordered by metanepisternum.

Elytron fully developed and well adjusted to shape of abdomen, not projecting posteriorly beyond abdominal apex; without window punctures, deeply striated with distinct punctures, often with shortened stria and scutellar striae.

Metaventrite slightly widening posteriorly, its anterior intercoxal process well developed, distinctly separating mesocoxae. Longitudinal suture (discrimen) present, katepisternal suture usually shifted close to posterior margin of metaventrite. Metacoxae fairly short, medially contiguous, transverse, distinctly reaching beyond lateral margin of metaventrite; metacoxal plates completely lacking.

Abdomen rather short, as long as or slightly longer than combined length of meta- and mesoventrite, with five free and abutting exposed sternites III–VII (= sternites 1–5). Second sternite not visible lateral to metacoxa. Terminal sternite VII evenly rounded or semioval, with or without median incision. Aedeagus of trilobed type.

Occurrence. Three genera from the Middle–Late Triassic, Dzhailyaucho site.

Genus †*Peltosyne* Ponomarenko, 1977

Type species. *Peltosyne triassica* Ponomarenko, 1977; by original designation.

Revised diagnosis. Differs from all other peltosynid genera in: antennal sockets with oblique longitudinal grooves beneath them extending along temples; anterior process of metaventrite rather narrow, triangular.

Description. Medium-sized to relatively large beetles, 11–15 mm. Head exposed at least from midlength of eyes. Anterior angles of frons acute, distinctly protruding forward. Labrum free. Mandibles almost as long as head, with thickened outer margins; apices curved, blunt; denticles located close to mandibular midlength. Pronotum with thin lateral bead. Pronotal disc convex, with flat, thin lateral margins. Posterior angles reach beyond protruding middle portion of posterior pronotal margin. Elytral base flattened, disc convex; at least third stria from sutural margin shortened. Longitudinal suture of mesoventrite reaches mesoventral cavity.

Species included. *Peltosyne triassica* Ponomarenko, 1977, and *P. varyvrosa* sp. nov.

Occurrence. Lower Triassic, Kyrgyzstan, Southern Fergana, Osh Province, Batken region, Madygen area, Dzhailyaucho site.

†*Peltosyne triassica* Ponomarenko, 1977
(Figs 2, 3)

Diagnosis. Mesal mandibular denticle not smaller or narrower than apices; cutting edge indistinctly bisinuate, molar area absent. Elytral striae 2 and 3 shortened,
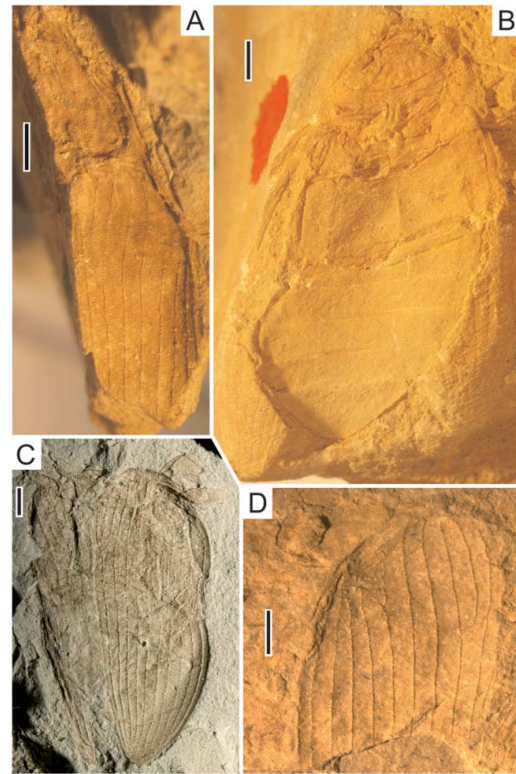

Figure 2. *Peltosyne triassica* Ponomarenko, 1977. **A, B,** habitus photographs of the holotype, PIN 2240/278, part and counterpart respectively; **C,** new specimen, PIN 2971/47; **D,** counterpart of paratype, PIN 2240/240. Scale bars = 1 mm.

reaching basal third of elytral length, other striae ending at elytral apex. Protrochanter very slender, elongate, half as long as procoxal width. Intercoxal process of mesoventrite very short, longitudinal suture of mesoventrite reaches half-length of cavity of anteromedian process; paracoxal suture present.

Material. Holotype: PIN 2240/278, impression of beetle without antennae and legs. Paratypes: PIN 1725/925, 2069/1340, 2070/1551, from the same locality. Additional new finding PIN 2971/47 is here identified as *Peltosyne triassica*.

Occurrence. Lower Triassic, Dzhailyaucho, Middle Asia.

Description. Moderately large beetles. Space between mandibular posterior condyle and inner ocular margin equal to half of eye length; mesal ocular margin on dorsal side with three shallow grooves. Antennal grooves oblique. Gular plate trapeziform. Submentum transverse, anterior margin roundly curved. Cardo rectangular, half as long as eye.

Anterior margin of pronotum straight; anterior angles acute, reaching midlength of eye; posterior angles
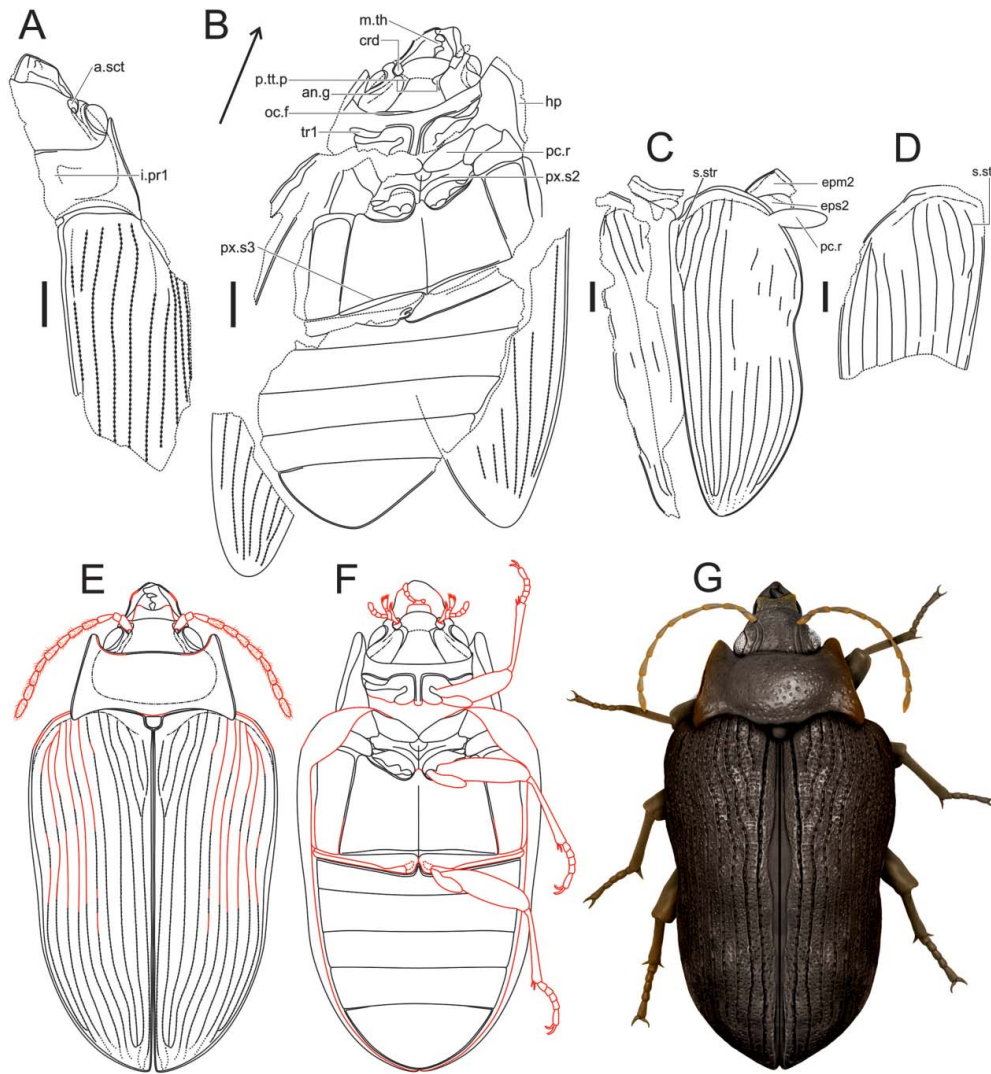
Figure 3. *Peltosyne triassica* Ponomarenko, 1977, line drawings. **A, B,** holotype, PIN 2240/278 part and counterpart; **C,** pair of elytra and ventral sclerites of new specimen PIN 2240/240; **D,** elytral base of paratype, PIN 2971/47; **E–G,** reconstruction of dorsal and ventral aspects. Abbreviations: a.sct, antennal socket; an.g, antennal groove; crd, cardo; i.pr1, intercoxal process of prosternum; m.th, mesal tooth; oc.f, occipital foramen; pc.r, procoxal rest; hp, hypomere; p.tt.p, posterior tentorial pits; px.s2, 3, paracoxal suture of meso- and metaventrites; tr1, protrochantin. Scale bars = 1 mm.

strongly protruding posterolaterally. Hypomeres thin, not wider than prosternal intercoxal process. Prosternum not narrower than head; posterior margin and intercoxal process with bead.

Mesoscutellar shield semioval, small, its width equal to space between adjacent stria. Elytron with fine bead; outer margin incised at midlength; scutellar stria one-fifth as long as entire elytron; third stria only slightly longer than sutural stria; striae 1–4, 5–6 and 11–12 merged pairwise near elytral apex.

Anterior process of mesoventrite short and acute. Mesepimeron with glabrous areas lacking coarse punctate sculpture. Metaventrite slightly widening posteriorly; anterior angles as long as anterior intercoxal process. Metanepisterna not widening posteriorly, as wide as

mesocoxae, with thickened anterior margin. Metacoxae with thin excavations on posterior margins; very short; laterally reaching beyond metanepisterna.

Abdomen conical, uniformly narrowing towards apex. Ventrites 2–4 of equal length; first ventrite one-third narrower at midlength; intercoxal process short, triangular; apical ventrite (sternite VII) triangular, twice as long as each of ventrites 2–4, with fine bead along posterior margin. For measurements, see Table 1.

†*Peltosyne varyvrosa* sp. nov.
(Figs 4, 5)

Diagnosis. Mesal mandibular denticle weakly developed, scarcely protruding; molar area semioval, occupying one-

Table 1. Body measurements (mm) of Peltosynidae species.

	Peltosyne triassica Ponomarenko, 1977		*Peltosyne varyvrosa* sp. nov.	*Gnathopeltos dixis* sp. nov.	*Ofthalmopeltos synkritos* sp. nov.
	PIN 2240/278 print	PIN 2971/47	PIN 2785/2655	PIN 2070/1620	PIN 2785/2888
Body length	11		14.3	8.8	5.3
Body width	5.6		5.2	≈3.2	2.1
Head length	2.1		2.3	1.4	1.2
Head width	2.6		1.7	1.6	1.2
Elytron length	8.5	11	9.3	7	
Elytron width	≈3.2	4.3	2.8	2.3	
Pronotum length	2.1		2.8	1.5	
Pronotum width	4.2		2.9	2.3	
Abdomen length	5.3			2.6	
Abdomen width	5			2.3	
Foreleg femur length			≈1.7		
Foreleg tibia length			1.8		
Foreleg length					
Midleg femur length				1.2	

quarter of basal length. Elytral striae 2 and 3 shortened, reaching elytral midlength, other striae ending at elytral apex. Intercoxal process of mesoventrite elongate-triangular, with longitudinal suture reaching its apex.
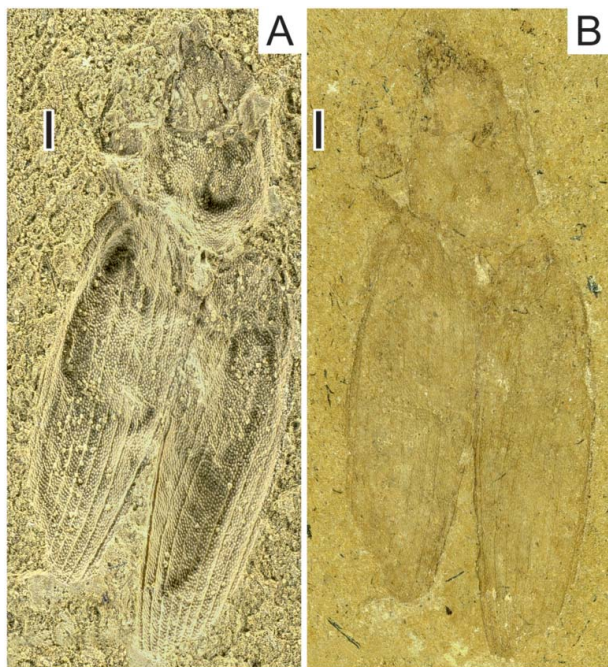

Figure 4. *Peltosyne varyvrosa* sp. nov. **A, B,** habitus photographs of the holotype, PIN 2785/2655, with different lighting. Scale bars = 1 mm.

Derivation of name. After the Greek βαρυβρώς, gnawing, biting, due to its large mandibles with molar areas. The species epithet is an adjective.

Material. Holotype: PIN 2785/2655, impression of beetle without antennae.

Occurrence. Lower Triassic, Dzhailyaucho, Middle Asia.

Description. Medium-sized beetles. Clypeal region semioval, recognizable as shallow impression. Antennal sockets ovoidal. Scapus elongate-rectangular, 3 times as long as wide, widening towards apex, almost as long as eye, with pair of fine sulci. Antennomeres 2–7 uniform, subtrapezoidal, one-third shorter than scapus. Submentum not longer than eye.

Profemur half as wide as head, narrowing towards slightly bent apex. Protibia 1.5 times longer than mandibles, bent at base, widening anteriad, bearing pair of conical spurs; spurs as long as antennomeres 2–7. For measurements, see Table 1.

Genus †**Gnathopeltos** gen. nov.

Type species. *Gnathopeltos dixis* sp. nov.

Diagnosis. Parietalia with single groove. Abdominal sternites 1–4 of similar length; posterior angles of sternites 2–4 acute, weakly protruding posteriorly; apical abdominal sternite VII transverse, not distinctly longer than other sternites, with evenly rounded posterior margin with median incision. Scutellar shield as large as cavity of
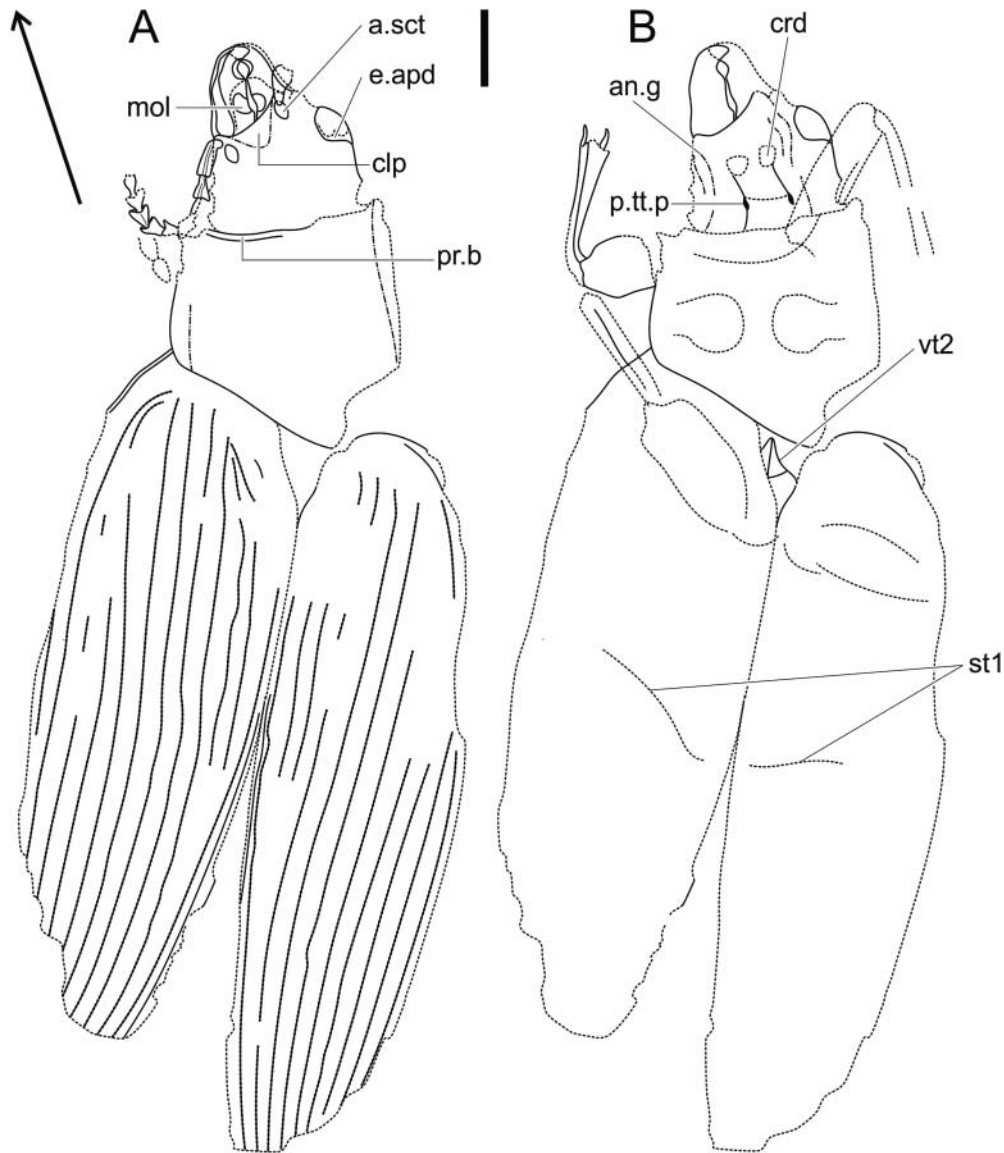
Figure 5. *Peltosyne varyvrosa* sp. nov., holotype, PIN 2785/2655, part, line drawings. **A,** dorsal view; **B,** ventral view. Abbreviations: a. sct, antennal socket; an.g, antennal groove; clp, clypeus; crd, cardo; e.apd, eye apodeme; mol, molar area; pr.b, pronotal bead; p.tt.p, posterior tentorial pit; st1, anterior margin of the first visible abdominal sternite; vt2, mesoventrite. Scale bars = 1 mm.

anterior process of mesoventrite. Differs from all other peltosynid genera in: mandibles shorter than head; cutting edge almost straight, with small preapical teeth separated by one-quarter of mandibular length from apex; anterior process of metaventrite wide, with straight apex.

Derivation of name. From the Greek γνάθος, jaw and πελτασ, shield, due to its prominent mandibles and the shield-like habitus; masculine.

Description. Medium-sized beetles. Antennal sockets located at anterior angles of frons. Temples as long as eyes. Gular plate weakly narrowing anteriad. Hypomeres narrow. Protruding median portion of posterior pronotal margin reaches beyond posterior angles. Mesoscutellar

shield triangular. Mesoventral cavity rhomboidal. Longitudinal suture of mesoventrite not reaching mesoventral cavity. Metanepisterna with thickened margins. Intercoxal process of first abdominal sternite well developed, triangular. Aedeagus of trilobate type.

Species included. Monotypic.

Occurrence. Lower Triassic, Dzhailyaucho site, Madygen area, Batken region, Osh Province, Southern Fergana, Kyrgyzstan.

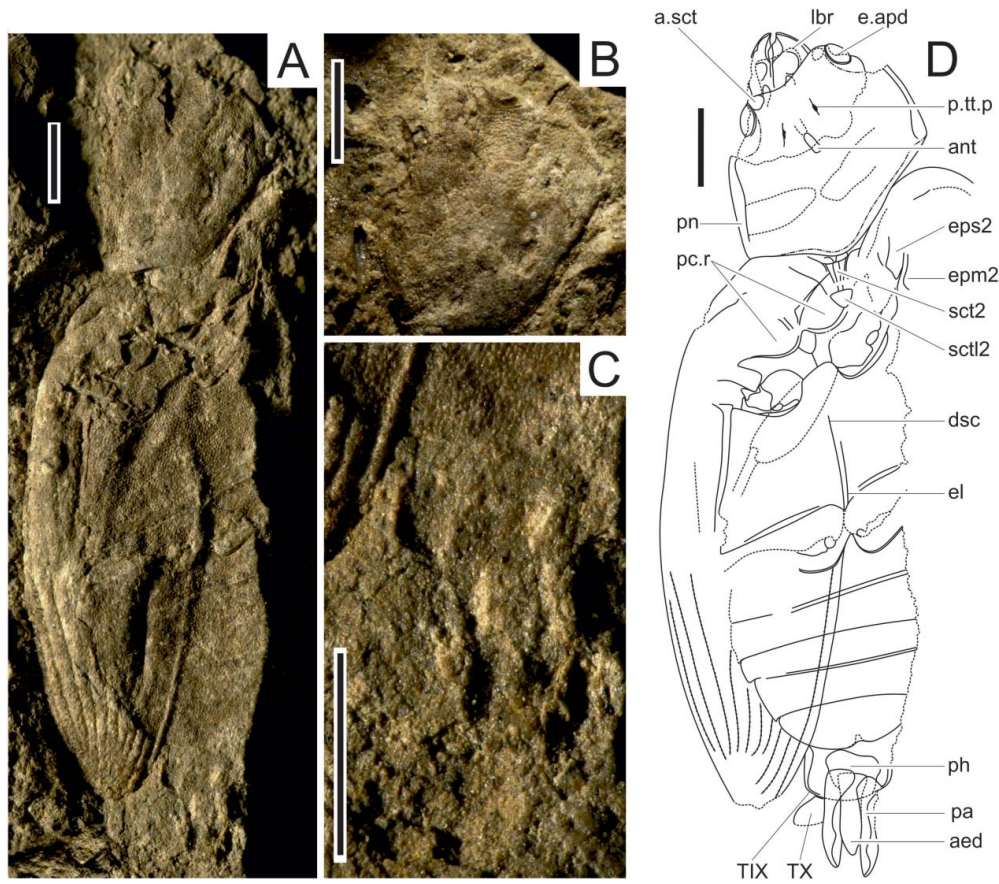<center>†<i>Gnathopeltos dixis</i> sp. nov.
(Fig. 6)</center>

Figure 6. Habitus photograph, morphological details and line drawing of *Gnathopeltos dixis* sp. nov., holotype, PIN 2070/1620. **A,** habitus photograph; **B,** head and pronotum; **C,** male genitalia; **D,** line drawing. Abbreviations: aed, aedeagus; a.sct, antennal socket; dsc, discrimen of the metaventrite; el, sutural margin of the left elytron; epm2, mesepimeron; eps2, mesepisternum; e.apd, eye apodeme; lbr, labrum; pa, paramere; ph, phallobase; hp, hypomere; sct2, mesoscutum; sctl2, mesoscutellar shield; T, XI, X, tergites 9 and 10. Scale bars = 1 mm.

Diagnosis. As for genus.

Derivation of name. From the Greek δῆξις, bite, due to its massive, prominent mandibles. The species epithet is a noun in apposition.

Material. Holotype: PIN 2070/1620, impression of beetle without antennae and distal parts of most legs.

Occurrence. Lower Triassic, Dzhailyaucho, Middle Asia.

Description. Mandibular outer margin with fine bead. At least two antennomeres elongate-rectangular, length 3 times exceeding width. Mesal margin of eyes with fine bead. Posterior pronotal margin slightly depressed. Elytron with at least 10 striae with punctures reaching elytral apex. Anterior process of metaventrite wider than half of mesocoxal width, located at level of acute anterior angles of metaventrite. Apical abdominal sternite VII with medially incised posterior margin. Tergite IX rectangular, two-thirds as wide as apical abdominal sternite, with lateral margins thickened. Aedeagus as long as combined length of abdominal sternites IV–VI; parameres with scoop-like apices, one-quarter longer than penis. For measurements, see Table 1.

Genus †*Ofthalmopeltos* gen. nov.

Type species. *Ofthalmopeltos synkritos* sp. nov.

Diagnosis. Differs from all other peltosynid genera in: eyes large, almost half as long as head; pronotal anterior angles with widely rounded apices; mesoventrite with very thin lateral arms.

Description. Mandibles elongate, 2.5 times as long as wide, with bidentate apices. Protrochantins shorter than one-third of procoxal width; procoxal anterior margin incised. Distance between katepisternal suture and posterior margin of metaventrite not less than half the length of anterior process of metaventrite. Metacoxae longer than first abdominal sternite. Apical abdominal sternite VII twice as long as preceding two.
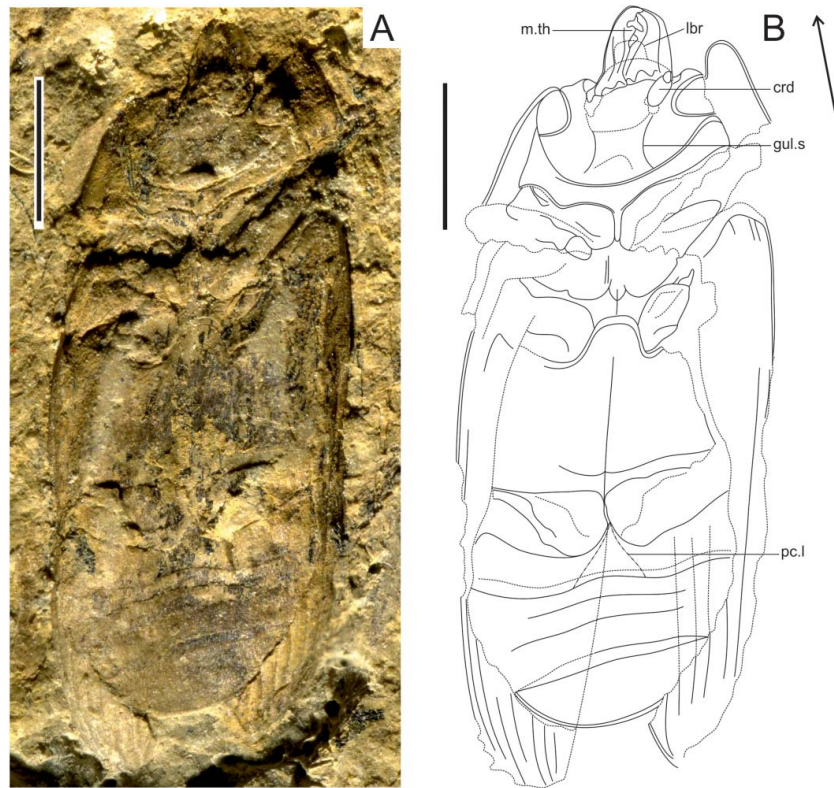
Figure 7. *Ofthalmopeltos synkritos* sp. nov., holotype, PIN 2785/2888. **A,** habitus photograph; **B,** line drawing. Abbreviations: crd, cardo; gul.s, gular suture; lbr, labrum; m.th, mesal tooth; pc.l, paracoxal lines. Scale bars = 1 mm.

Derivation of name. From the Greek όφθαλμός, eye and πελτασ, shield, referring to the large eyes partly concealed by a shield-like transverse pronotum. Neuter gender.

Species included. Monotypic.

Occurrence. Lower Triassic, Dzhailyaucho site, Madygen area, Batken region, Osh Province, Southern Fergana, Kyrgyzstan.

†*Ofthalmopeltos synkritos* sp. nov.
(Fig. 7)

Diagnosis. As for genus.

Derivation of name. From the Greek σύγκριτος, compact, referring to the compact habitus. Neuter gender.

Material. Holotype: PIN 2785/2888, impression of beetle without antennae and distal parts of most legs.

Occurrence. Lower Triassic, Dzhailyaucho, Middle Asia.

Description. Eyes, pronotum, prosternum and metaventrite with marginal bead. Mandibles with rectangular mesal teeth. Cardo elongate-oval, twice as long as wide. Longitudinal suture of mesoventrite reaches midlength of mesosternal cavity. Abdominal sternites loosely connected; first sternite with paired postcoxal lines, second and third of equal length and one-third shorter than first; apical abdominal sternite with semioval posterior margin, with fine marginal bead. For measurements, see Table 1.

Phylogenetic analysis

The cladistic analysis of 34 characters (Supplemental Appendix 1) yielded 847 minimum length trees with 66 steps (consistency index 0.57) (Supplemental Appendix 2). The resolution of the strict consensus tree is low, with only the following clades confirmed: Coleoptera *s.l.* (Bemer support [bs] 3), Coleoptera *s. str.* (excluding the Permian stem-group families †Tshekardocoleidae, †Permocupedidae, †Rhombocoleidae) (bs 2), Adephaga (bs 2), Adephaga excluding Gyrinidae (Bs 1), Jurodidae (bs 1), Ommatidae + Cupedidae (bs 1), Cupedidae (bs 2). The placement of the fossil taxa including the genera of †Peltosynidae was unstable. †Peltosynidae was confirmed as a clade in 67% of all minimum length trees and placed in an unresolved polytomy with the included terminals of Adephaga, Myxophaga and Polyphaga in the strict consensus tree.
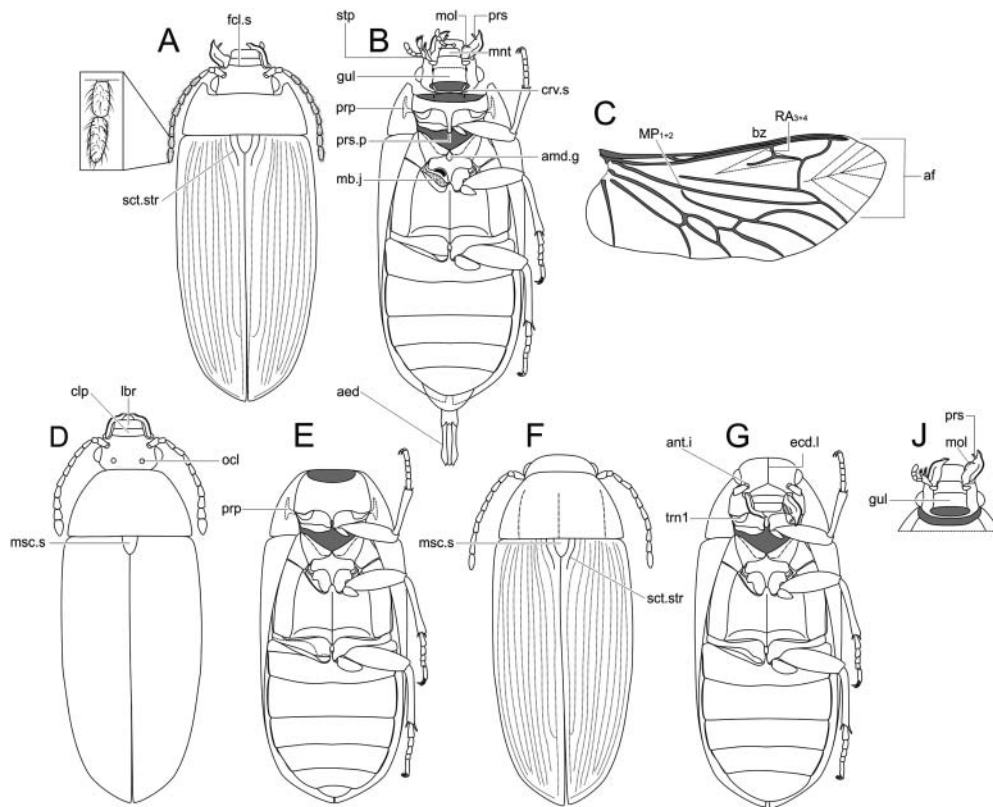
Figure 8. Reconstructions of ancestral Polyphaga beetles as suggested in the current paper. **A–C,** after Lawrence & Newton (1982); **D, E,** after Ponomarenko (1983). **A, D, F,** dorsal aspects, **B, E, G, J,** ventral aspects. Additional inset showing antennal pubescence. **C,** generalized polyphagan hind wing. Abbreviations: aed, aedegaus; amd.g, anteromedial groove; ant.i, antennal insertion; clp, clypeus; crv.s, cervical sclerite; ecd.l, ecdysial line; fcl.s, frontoclypeal suture; gul, gular plate; msc.s, mesocutellar shield; mol, molae; prp, propleuron; mb.j, membranous joint; mnt, mentum; ocl, ocellus; prs, prostheca; prs.p, prosternal process; sct. str, scutellar striole; stp, stipes; trn1, procoxal trochantin; wing structures: af, apical field; bz, bending zone; MP1+2, media posterior 1+2; RA3+4, radius anterior 3+4.

Discussion

The origin and systematic placement of †Peltosynidae

The appearance of †Peltosynidae is corroborated in the Late Middle–Early Late Triassic, when Archostemata were still diverse and very abundant, while Polyphaga were rare. Redescription of the type genus †*Peltosyne* and new findings from the type locality confirm that there was no external pleuron, procoxal cavities were posteriorly open, and mesocoxal cavities were not partially closed laterally by metanepisternum. These characters support the original assignment of †*Peltosyne triassica* to Polyphaga (Ponomarenko 1977), at that time as 'Polyphaga *incertae sedis*' due to the lack of information in the original description. The type of mesocoxal closure, with the metanepisternum not forming a significant part of the mesocoxal pit, also separates †*Peltosyne* from †Ademosynidae and other Mesozoic groups assigned to Archostemata by Ponomarenko (1969). An apomorphy shared with all non-archostematan beetles is the absence of an exposed metatrochantin, a potential synapomorphy of Adephaga, Myxophaga and Polyphaga (Beutel & Haas 2000; Beutel *et al.* 2008). The presence of a mandibular mola is another feature distinguishing †Peltosynidae from Archostemata (and Adephaga) but linking it with Polyphaga (and Myxophaga).

The distinct elytral striation is a diagnostic feature shared with ademosynid genera. As this also occurs in different extant groups of Adephaga (e.g. Gyrinidae (e.g. *Gyrinus*, *Heterogyrus*), Dytiscidae (Copelatinae), Carabidae (major part) and Polyphaga (e.g. Hydrophilidae, Elateridae)), it is likely that it evolved early in the crown-group of Coleoptera. The presence in †*Peltosyne* and all species presently assigned to †Ademosynidae suggests that striated elytra were present in the groundplan of Polyphaga and reduced or transformed into more or less regular patterns of puncture rows in different subgroups. If Adephaga and Polyphaga are indeed sister taxa as suggested by transcriptomic data (Misof *et al.* 2014), it would be conceivable that this is a groundplan apomorphy of a clade comprising these two suborders and †Peltoysynidae
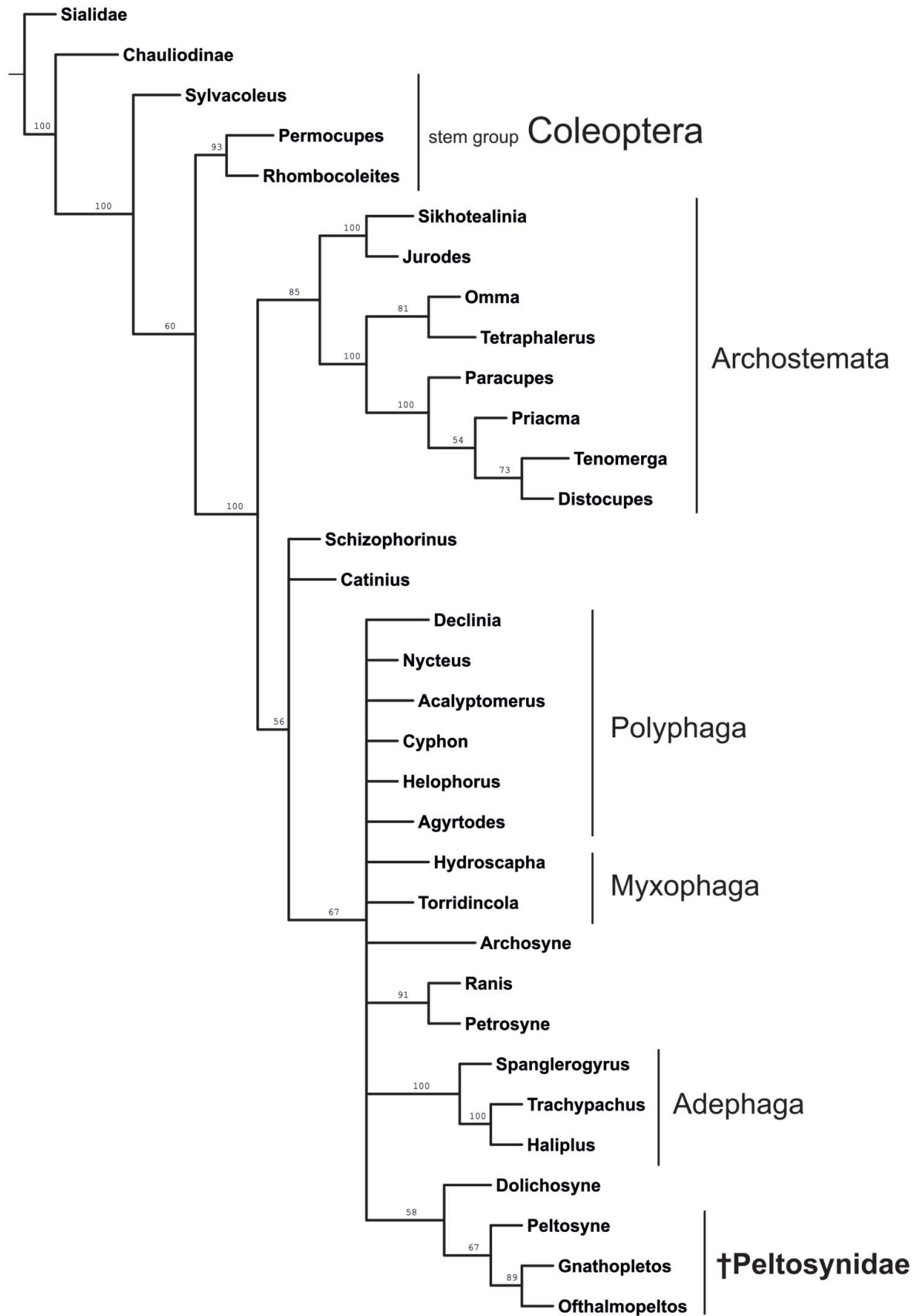
Figure 9. Majority rule consensus tree using 34 coded characters, mostly from Beutel & Haas (2000), Beutel *et al.* (2008) and Lawrence *et al.* (2011), two megalopteran outgroups (*Sialis*, *Chauliodes*) and 31 coleopteran ingroup taxa representing all four suborders, 18 extant and 13 extinct. Parsimony analysis with NONA (ratcheted, 1000 replicates) (Goloboff 1995), 847 minimum length trees with 66 steps, consistency index (CI) 0.57, retention index (RI) 0.82.

and †Ademosynidae, with multiple secondary modifications. Striation is absent in Myxophaga and extant and extinct groups of Archostemata *s. str.*, and also in the extinct families †Schizophoridae and †Catiniidae. An alternative interpretation would be several independent formations of an elytral striation.

A noteworthy plesiomorphic character state preserved in †*Peltosyne* but otherwise unknown in non-archostematan beetles (Friedrich *et al.* 2009) is the presence of a distinct mesoventral transverse suture separating a katepisternum from the anterior preepisternum (e.g. Baehr 1975; Friedrich *et al.* 2009). This ancestral feature places †Peltosynidae in the stem-group of Polyphaga, which implies the erection of a new family. The complete absence of the suture characterizes all extant groups included in the suborder. A feature observed in *Gnathopeltos dixis* (Fig. 6) – a simple trilobed aedeagus with a basal piece and not rotated when reposed and during copulation – is shared with many groups of Polyphaga. The occurrence of this type of genitalia in †Peltosynidae indicates that it is an ancestral feature of the suborder (Lawrence *et al.* 2011).

None of the features observed in †Peltosynidae suggests placement in one of the seven polyphagan series (Scirtiformia, Staphyliniformia, Scarabaeformia, Elateriformia, Derodontiformia, Bostrichiformia, Cucujiformia), which conforms its assignment to the stem-group of the suborder (Fig. 9). The transverse coxae with external pro- and mesotrochantins, the sutures on the meso- and metaventrites, and the unmodified aedeagus of the trilobed type excludes †Peltosynidae from Bostrichiformia and Cucujiformia. The lack of various derived features characterizing Derodontiformia (= Derodontidae) makes close affinities with this problematic taxon unlikely, aside from the peltosynid features of the prothorax and the type of mesocoxal closure with the metanepisternum not forming a considerable portion. The position of Derodontidae among scirtoid subgroups was suggested by the phylogenetic analyses of McKenna *et al.* (2015), but a reliable placement of the family is still pending. Comparisons with supposedly 'basal' polyphagan lineages, such as Scirtiformia, Staphyliniformia, Scarabaeiformia and Elateriformia, are more complicated, as most apomorphies defining these groups cannot be observed in the fossils (e.g. internal or larval characters). However, the known species of †Peltosynidae do not display any of the features characterizing the staphyliniform-scarabaeiform lineage (e.g. Beutel & Leschen 2005), such as for instance shortened elytra (often present in Staphylinoidea), missing sutures of the metaventrite (Staphylinoidea), short antennae with a symmetrical (Hydrophiloidea) or asymmetrical club (Scarabaeoidea), or a stout body with a small head and a freely rotatable prothorax (most Scarabaeoidea). The characteristic feeding apparatus with epi- and hypopharyngeal brushes interacting with the mandibular base cannot be observed in

†Peltosynidae. However, the strongly prominent mandibles clearly do not support placement in the staphyliniform-scarabaeoid lineage.

As more generalized beetles with a broad and rather flattened straight body, peltosynids can be excluded from Scirtiformia. Even though they also possess a short prosternum, the general configuration of the body indicates that they entirely lack compaction adaptations, with a strongly declined head fitting against the procoxae, as typical found in scirtoid beetles (e.g. Anton *et al.* 2016). Moreover, the large and prominent mandibles also exclude a placement in this small lineage. Due to the streamlined body and striated elytra, peltosynids look superficially similar to some members of the Elateriformia. However, the lack of interlocking devices on the posterior pronotal margin refutes placement in this series of Polyphaga.

The monophyletic origin of †Peltosynidae is mainly supported by the transverse and laterally rounded head. Another characteristic feature, the coarse surface structure of the cuticle, is ambiguous. A similar condition also occurs in †Ademosynidae. Moreover, it is conceivable that the rugose surface is a less distinct variation of the tuberculate surface of Archostemata, and therefore an intermediate condition and plesiomorphic compared to the smooth surface of many extant beetles. The genera of †Peltosynidae introduced here are mainly defined by differences of the anteromedian process of the mesoventrite, which is strongly broadened in *Gnathopeltos*, and the presence or absence of an incision at the posterior margin of the terminal abdominal sternite.

Groundplan of Polyphaga

As a basal branch mostly characterized by plesiomorphic features, †Peltosynidea is obviously important for the reconstruction of the groundplan of Polyphaga. The ancestral morphology of this suborder and the apomorphies defining it are crucial for understanding the early evolution, macrotaxonomy and phylogeny of Coleoptera. The discussion of this issue started long before reliable palaeontological material was obtained.

An early concept of a polyphagan groundplan (Crowson 1960) was dominated by information from studies on extant beetles, resulting in a character syndrome unverifiable in the fossil record. This included, for instance, the loss of the original nutritive cells in the ovarian follicles, cryptonephric Malpighian tubules, features of the metendosternite, and also larval characters. Other characters, such as the loss of a hind wing cross vein, non-functional spiracles VIII and an aedeagus with a tegmen of the cucujoid type (or derived from it), are rarely sufficiently preserved in fossils. One of the few suggested ancestral characters that can be verified in fossil imprint

are hind coxae lacking a posterior excavation. Crowson (1960) suggested that ancestral polyphagans were small or very small, like extant myxophagans or scirtoids (Clambidae). This is consistent with the small or very small size of beetles from the oldest localities of Middle–Late Permian age, where possible polyphagan ancestors might be preserved (Volkov 2012; Ponomarenko *et al.* 2014). However, most of the characters suggested by Crowson (1960) are today recognized as derived features of 'higher Polyphaga', for instance, cryptonephridism as an autapomorphy of Cucujiformia (e.g. Lawrence & Newton 1982).

In the 30 years following Crowson's study, considerable progress was made in accumulating palaeontological material and analysing characters of hypothetical ancestral polyphagans. Lawrence & Newton (1982) and Ponomarenko (1983) suggested a character combination for the oldest polyphagan beetles including, for example, almost homonomous antennomeres, a propleuron completely or largely invaginated, transverse procoxae inserted in posteriorly open cavities, and a metaventrite transverse with distinct discrimen and katepisternal suture. Some additional ancestral features suggested by Lawrence & Newton (1982) are found in beetles of the family Jurodidae (Archostemata): paired ocelli, weakly clubbed antennae, transverse roughly rectangular head, lack of an interlocking device between the prosternum and mesoventrite, and the preservation of abdominal sternite II as lateral remnants.

In contrast to Crowson (1960) and Lawrence & Newton (1982), the concept of Ponomarenko (1983) was largely based on palaeontological investigations, depicting ancestral beetles as similar to representatives of Scirtiformia or partly also staphyliniform beetles. His groundplan included an orthognathous head with retained Y-shaped ecdysial sutures, mandibles with a distinct mola and separate prostheca, exposed pro- and mesotrochantins, elytra with 10 stria and a scutellar striole, a short mesoventrite without sutures, mesocoxal cavities laterally not closed by the metanepisternum, laterally extended metacoxae separating the metanepisterna from the abdomen, and a membranous second abdominal ventrite covered by the metacoxae.

The detailed groundplan reconstruction of Polyphaga proposed here (Supplemental Appendix 3) is based on palaeontological evidence and recent morphological and phylogenetic studies (Beutel & Haas 2000; Beutel *et al.* 2008; Friedrich *et al.* 2009; Lawrence *et al.* 2011; McKenna *et al.* 2015).

The structural features of the new family and presumably basal groups of Polyphaga *s. str.* (e.g. Scirtoidea, Derodontidae (McKenna *et al.* 2015)) suggest that ancestral representatives of the suborder (see Fig. 8 reconstruction) were relatively small beetles with a body length of less than 10 mm. In contrast to Ponomarenko (1983), the head was almost certainly prognathous and lacked ecdysial sutures, which would have no function in adult beetles. Both features are clearly recognizable in †Peltosynidae and also found in extant beetles with very few (orthognathous head) or no exceptions (ecdysial lines). Distinct anterior pronotal angles were present, as in †Peltosynidae (but not in †Ademosynidae). The body was more or less streamlined with an obsolete pronoto-elytral angle and an interlocking device between the posternal process and the mesoventrite was present. Other ancestral features documented in the observed fossils are striated elytra with a sutural striole, a moderately long parallel-sided prosternal process, a completely internalized propleura, adjacent but loosely connected meso- and metaventrites, an internalized metatrochantin, unmodified cursorial legs, an abdomen with five free and exposed ventrites corresponding with sternites III–VII, and a simple trilobed aedeagus with a basal piece. Additional features based on morphological data from recent studies are of predictive value. Even though they may not be visible in most presently available fossils, they may be preserved in new findings. Among these are the vestiture of the antennae, structural details of the feeding apparatus including mandibular grinding devices or endite lobes and palps of the ventral mouthparts, cervical sclerites, details of the wing venation, the meso-metaventral connection, and details of the male genitalia (see Supplemental Appendix 1 for the list of characters).

Lifestyle and evolutionary trends in the Permian–Triassic

The lifestyle of beetles during the Permian–Triassic periods cannot be reconstructed based on direct evidence. As suggested by Ponomarenko (2003) and the basal branching pattern in Coleoptera in the widest sense (Beutel 1997; Beutel *et al.* 2008), an association with wood and a preference of adults for subcortical spaces was ancestral for beetles (e.g. †Tshekarcocoleidae, †Permocupedidae). Independent of their placement among the extant suborders, extant Archostemata have maintained this lifestyle, along with a maximum number of preserved plesiomorphies including a tuberculate body surface, long and prominent mandibles, a relatively complete pterothoracic muscle system (Beutel & Haas 2000), incompletely sclerotized elytra with window punctures, a mesoventrite with a separate katepisternum, and distinctly exposed metatochantins.

A moderately flattened body, a (relatively) coarse surface sculpture, large prominent mandibles with blunt apices and strong mesal teeth, and cephalic antennal grooves are structural affinities with archostematan beetles, which tentatively suggest that species of †Peltosynidae were associated with wood, like all known extant species of the suborder. They may have been adapted for tight spaces

such as subcortical habitats and were probably xylo- or xylomycetophagous, which is considered as an ancestral feeding habit (e.g. †Tshekarcocoleidae and †Permocupedidae). A complex feeding apparatus involving mandibular bases with grinding molae and hairy epipharyngeal and hypopharyngeal lobes (Fig. 8B) is found in different groups of Polyphaga (Anton & Beutel, 2012) and also in Myxophaga (Anton & Beutel 2004, 2006). It is likely that this configuration of mouthparts evolved early in the crown-group of beetles. However, this character is generally inaccessible in fossils (see above). Moreover, a reliable interpretation of this complex feature, which is likely related with saprophagous or microphagous feeding habits, is not possible as long as the interrelationships of the coleopteran suborders remain uncertain.

Abundant conifers, pteridosperms, cycadophytes and cordaites of the Dzhailyaucho riverbank oases (Buchwitz 2011; Franeck *et al.* 2012) provided microhabitats where peltosynids could have lived and fed. Such oases were surrounded by xeromorphic valleys experiencing a hot continental climate and seasonal temperature fluctuations (Sikstel 1962, 1965; Ponomarenko 1969).

Structural features of †Ademosynidae, †Schizophoridae and †Catiniidae, which are interpreted as aquatic or semi-aquatic groups (Ponomarenko 1983), suggest that the ancestral wood-associated lifestyle was abandoned by many groups at about the Permian–Triassic boundary. This is suggested by a smooth body surface without tubercles and scale-like setae, the lack of cephalic protuberances (though preserved in †*Archosyne*), a more or less obsolete pronoto-elytral angle resulting in a streamlined body shape, and schizae as specific elytral locking in the case of †Schizophoridae (e.g. Crowson 1975; Ponomarenko 2003). This new evolutionary tendency in beetles was accompanied by extinction events survived by comparatively few lineages (e.g. McKenna *et al.* 2015).

Whereas a close association with wood was likely retained in †Peltosynidae and 'primitive' crown-group Archostemata, which were still successful in the Jurassic (e.g. Crowson 1975), other habitats and microhabitats apparently played an increasing role in the evolution of beetles. Unlike †Peltosynidae and extant Archostemata, different crown-group coleopterans developed a preference for riparian habitats in the earliest Mesozoic, similar to the extant *Omophron* (Adephaga: Carabidae), *Lepicerus* and *Sphaerius* (Myxophaga: Lepiceridae, Sphaeriusidae), and *Georissus* and *Heterocerus* (Polyphaga: Hydrophiloidea, Dryopoidea). Equipped with a closed subelytral space (Beutel 1997), at least 10 groups of the three non-archostematan extant suborders could successfully invade aquatic environments from this starting point (Beutel 1997). It is documented in the fossil record that different invasions of aquatic habitats had already taken place in the early Triassic (Ponomarenko 1983). Very early aquatic radiations of Adephaga are documented by

fossils belonging to Gyrinidae and †Triaplidae (and possibly the Permian †*Permosialis*; Beutel 1997), and the successful aquatic Dytiscoidea emerged in the Jurassic (Beutel *et al.* 2013).

Conclusions

†Peltosynidae are the first group placed in the polyphagan stem-group based on specific apomorphies and plesiomorphic features compared to extant lineages. Consequently, they play an essential role in interpreting early evolutionary developments in crown-group Coleoptera and Polyphaga. It is expected that further findings from the Dzhailyaucho site will yield specimens with more preserved structural features, and new fossils can also be expected from several other key localities, including Yinping (Middle–Upper Permian Yinping Formation, Anhui Province, China), Anakit (Upper Permian, East Siberia, Russia), and Babiy Kamen (Lower Triassic Maltsevskaya Formation, West Siberia, Russia). New morphological information combined with reliably established interrelationships of the extant suborders will help to develop a well-founded evolutionary scenario for the most successful insect order in the Permian–Triassic transition zone.

†Peltosynidae are unknown from Lower Triassic deposits, and beetles of the Dzhailyaucho location were apparently not the most ancient representatives of Polyphaga. Early members of the suborder probably existed long before the Triassic, even though they were rare. An origin around the end of the Middle Permian is conceivable, even though unambiguous fossil evidence is still lacking (Ponomarenko 2016). This is tentatively supported by the wide distribution of isolated elytra (which are much more common than complete bodies) with striate-punctate pattern, probably mainly or exclusively belonging to the family †Permosynidae (Ponomarenko 2003). In Western Europe, permosynid fossils became dominant among other isolated elytra beginning from the Aristovo locality (Lower Changsingian, lowermost Upper Vyatkian), with a 2 myr time gap before the Permo-Triassic mass extinction (Ponomarenko 2016). However, the interpretation remains ambiguous as elytra of the striate type can occur in different major groups of beetles (see above). †*Archosyne permiana* Ponomarenko *et al.*, 2014 with similar elytra known from the Yinping locality (terminal Capitanian of Eastern China, about 7 myr prior to the Permo-Triassic boundary) was assigned to Ademosynidae, traditionally considered as a family of Archostemata. Due to the lack of specific diagnostic features of presumptive permosynid elytra, comparisons with beetle body fossils or recent forms remain uninformative. A reliable system of elytral characters may help to elucidate the relationships of fossils from the Permian and Triassic periods.

Moreover, the search for fossils of †Permosynidae with preserved body should have high priority. A better knowledge of this obscure group could greatly improve our understanding of the evolutionary history of †Peltosynidae, Polyphaga and Coleoptera.

Acknowledgements

Supplemental data

Supplemental material for this article can be accessed at https://doi.org/10.1080/14772019.2017.1313789

References

Anton, E. & Beutel, R. G. 2004. On the head morphology and systematic position of *Helophorus* (Coleoptera: Hydrophiloidea: Helophoridae). *Zoologischer Anzeiger*, **242**, 313–346.

Anton, E. & Beutel, R. G. 2006. On the head morphology of Lepiceridae (Coleoptera: Myxophaga) and the systematic position of the family and suborder. *European Journal of Entomology*, **103**, 85–95.

Anton, E. & Beutel, R. G. 2012. The head morphology of *Dascillus* (L.) (Dascilloidea: Dascillidae) and *Glaresis* Erichson (Scarabeoidea: Glaresidae) and its phylogenetic implications. *Arthropod Systematics and Phylogeny*, **70**, 3–42.

Anton, E., Yavorskaya, M. I. & Beutel, R. G. 2016. The head morphology of Clambidae and its implications for the phylogeny of Scirtoidea (Coleoptera: Polyphaga). *Journal of Morphology*, **277**, 615–633.

Baehr, M. 1975. Skelett und Muskulatur des Thorax von *Priacma serrata* Leconte (Coleoptera, Cupedidae). *Zeitschrift für Morphologie der Tiere*, **81**, 55–101.

Beutel, R. G. 1997. Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg NF*, **31**, 1–164.

Beutel, R. G. & Haas, F. 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics*, **16**, 103–141.

Beutel, R. G. & Leschen, R. A. B. 2005. Phylogenetic analysis of Staphyliniformia (Coleoptera) based on characters of larvae and adults. *Systematic Entomology*, **30**, 510–548.

Beutel, R. G., Ge, S. Q. & Hörnschemyer, T. 2008. On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. *Cladistics*, **24**, 270–298.

Beutel, R. G., Wang, B., Tan, J.-J., Ge, S.-Q., Ren, D. & Yang, X.-K. 2013. On the phylogeny and evolution of Mesozoic and extant lineages of Adephaga (Coleoptera, Insecta). *Cladistics*, **29**, 147–165.

Bocak, L., Barton, C., Crampton-Platt, A., Chesters, D., Ahrens, D. & Vogler, A. P. 2014. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. *Systematic Entomology*, **39**, 97–110.

Booth, R. G., Cox, M. L. & Madge, R. B. 1990. *IIE guides to insects of importance to man. 3. Coleoptera*. International Institute of Entomology, London, 384 pp.

Buchwitz, M., 2011. *Taxonomy, phylogeny, and palaeobiology of the Madygen Tetrapod Fauna*. Unpublished thesis, TU Bergakademie, Freiberg.

Costello, M. J., Wilson, S. & Houlding, B. 2012. Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, **61**, 871–883.

Crowson, R. A. 1960. The phylogeny of Coleoptera. *Annual Review of Entomology*, **5**, 111–134.

Crowson, R. A. 1975. The evolutionary history of Coleoptera, as documented by fossil and comparative evidence. *Atti del X Congresso Nazionale Italiano di Entomologia Sassari*, **1975**, 47–90.

Dobruskina, I. A. 1995. Keuper (Triassic) flora from Middle Asia (Madygen, Southern Fergana). *New Mexico Museum of Natural History and Science Bulletin*, **5**, 1–49.

Emery, C. 1886. Über Phylogenie und Systematik der Insekten. *Biologische Zentralblatt*, **5**, 648–656.

Franeck, F., Schneider, J. W., Fischer, Kogan, I., Buchwitz, M., Spindler, F. & Voigt, S. 2012. Mircovertebrate remains from the non-marine Triassic Madygen Formation of Kyrgyzstan. *Thesis of Centenary Meeting of the Paläontologische Gesellschaft: Programme, abstracts, and field guides. Berlin, Alfred-Wegener Stiftung*, **3**, 57–58.

Friedrich, F., Farrell, B. D. & Beutel, R. G. 2009. The thoracic morphology of Archostemata and the relationships of the extant suborders of Coleoptera (Hexapoda). *Cladistics*, **25**, 1–37.

Goloboff, P. 1995. *NONA Version 1.5*. Tucuman: Fundación e Instituto Miguel Lillo.

Grimaldi, D. & Engel, M. 2005. *Evolution of the Insects*. Cambridge University Press, New York, 755 pp.

Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O. S., Wild, R., Hammond, P. M., Ahrens, D., Balke, M., Caterino, M. S., Gómez-Zurita, J., Ribera, I., Barraclough, T. G., Bocakova, M., Bocak, L. & Vogler, A. P. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science*, **318**, 1913–1916.

Kirejtshuk, A. G., Chang, H. Ren, D. & Kun, Sh. Ch. 2010. Family Lasiosynidae n. fam., new palaeoendemic Mesozoic family from the infraorder Elateriformia (Coleoptera, Polyphaga). *Annales de la Société entomologique de France*, **46**, 231–247.

Kogan, I., Fischer, J., Voigt, S. & Spindler, F. 2013. The ichthyofauna of the non-marine Triassic Madygen Formation (Southwest Kyrgyzstan, Central Asia). *Conference paper. 6th International Meeting on Mesozoic Fishes,* Vienna, 38–39.

Kukalová-Peck, J. & Lawrence, J. F. 1993. Evolution of the hind wing in Coleoptera. *The Canadian Entomologist*, **125**, 181–258.

Kukalová-Peck, J. & Lawrence, J. F. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. *European Journal of Entomology*, **101**, 95–144.

Lawrence, J. F. & Newton, A. F. 1982. Evolution and classification of beetles. *Annual Review of Ecology and Systematics*, **13**, 261–290.

Lawrence, J. F., **Ślipiński, S. A.**, **Seago, A. E.**, **Thayer, M. K.**, **Newton, A. F.** & **Marvaldi, A. E.** 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Annales Zoologici*, **61**, 1–271.

Linnaeus, C. 1758. *Systema Naturae per regni tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th edition. Laurentius Salvius, Stockholm, iv + 824 pp.

McKenna, D. D., **Wild, A. L.**, **Kanda, K.**, **Bellamy, C. L.**, **Beutel, R. G.**, **Caterino, M. S.**, **Farnum, C. W.**, **Hawks, D. C.**, **Ivie, M. A.**, **Jameson, M. L.** & 11 others. 2015. The beetle tree of life reveals Coleoptera survived end Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology*, **40**, 835–880.

Misof, M., **Liu, S.**, **Meusemann, K.**, **Peters, R. S.**, **Donath, A.**, **Mayer, C.**, **Frandsen, P. B.**, **Ware, J.**, **Flouri, T.**, **Beutel, R. G.** & 35 others. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Ponomarenko, A. G. 1969. Historical development of archostematan beetles. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, **125**, 1–240.

Ponomarenko, A. G. 1977. Composition and ecological characteristics of Mesozoic Coleoptera. *Trudy Paleontologicheskogo Instituta Akademiya Nauk SSSR*, **161**, 1–116. [In Russian with English translation.]

Ponomarenko, A. G. 1983. The historical development of Coleoptera. Extended abstracts of doctoral dissertation in biology. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR*, **167**, 1–47.

Ponomarenko, A. G. 2003. Ecological evolution of beetles (Insecta: Coleoptera). *Acta Zoologica Cracoviensia*, **46** (Suppl.), 391–328.

Ponomarenko, A. G. 2016. Insects during the time around the Permian-Triassic Crisis. *Paleontological Journal*, **50**, 174–186.

Ponomarenko, A. G., **Yan, E. V.** & **Huang, D.** 2014. New beetles (Coleoptera) from the terminal Middle Permian of China. *Paleontological Journal*, **48**, 191–200.

Sikstel, T. A. 1962. Flora of Late Permian and Early Triassic of South Fergana. Pp. 284–414 in *Stratigraphy and palaeontology of Uzbekistan and neighboring regions. Volume 1*. Publishing House of AS Uzb, SSR, Toshkent.

Sikstel, T. A. 1965. Triassic higher plants of Soviet Asia. *Conference thesis of interdepartmental meeting on continental deposits of Asia, Leningrad*, 19–20.

Stork, N. E., **McBroom, J.**, **Gely, C.** & **Hamilton, A. J.** 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences*, **112**, 7519–7523.

Volkov, A. N. 2012. Fossil beetles of the locality Babiy Kamen' locality (Permian – Triassic of the Kuzbass). Pp. 49–54 in A. Yu Rozanov, A. V. Lopatin & P. Yu Parkhaev (eds) *Modern paleontology: classical and new methods – 2012*. PIN RAS, Moscow.

Yan, E. V., **Wang, B.** & **Zhang, H.** 2013. First record of the beetle family Lasiosynidae (Insecta: Coleoptera) from the Lower Cretaceous of China. *Cretaceous Research*, **40**, 43–50.