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ARTICLE



Archaeomalthus-(Coleoptera, Archostemata) a 'ghost adult' of Micromalthidae from Upper Permian deposits of Siberia?

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ABSTRACT

Archaeomalthus synoriacos gen. et sp. nov. from the Upper Permian Babiy Kamen' locality indicates a remarkable evolutionary stability. Herein we report the oldest record of the family Micromalthidae, *Archaeomalthus synoriacos* gen. et sp. nov., which demonstrates several plesiomorphic character states, but generally retains most of the apomorphies of Micromalthidae. *Archaeomalthus* suggests that a distinct simplification of the morphology of adults already evolved in the late Paleozoic, suggesting an early reduction of the role of adults in the life cycle of the group. Despite the marked differences between *Archaeomalthus* and *Micromalthus*, the former already show a distinct and apparently very stable degree of deviation from the ground plan of Coleoptera s.str. and s.l. The remarkable series of reductional features shared by the Permian fossil and the extant species include a lightly sclerotized body without distinct surface sculpture, a head lacking dorsal protuberances, shortened and apparently thin elytra, exposed membranous areas behind the procoxae and between at least two basal visible abdominal sternites, and the reversal of the invagination of the terminal abdominal segments. It is likely that the reduced role of adults of Micromalthidae was a syndrome of simplified, vestigial adult morphology characters acquired at least 255 million years ago.

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Introduction

The insect order Coleoptera (beetles) is by far the most species-rich group of living organisms, with approximately 380,000 described extant species (Zhang 2011, 2013) and an estimated number of 1.5 million that presently exist (Stork et al. 2015). The bulk of beetle diversity, more than 91%, is in the suborder Polyphaga, with the remaining occupied by Adephaga, Myxophaga and Archostemata suborders (Costello et al. 2012).

Despite controversies concerning its systematic placement (e.g. Beutel and Haas 2000; Misof et al. 2014; McKenna et al. 2015), Archostemata are doubtlessly the extant subgroup among beetles with the maximum number of preserved ancestral features (e.g. Beutel and Haas 2000; Beutel et al. 2008; Friedrich et al. 2009). Therefore, they are clearly a key taxon for understanding early evolutionary processes in the order, which finally led to a diversification unparalleled among all groups of eukaryotic organisms. Stem group Coleoptera (Beutel et al. 2008): Tshcardocoleidae, Permocupedidae, Rhombocoleidae or Archostemata s.l. (Ponomarenko 1969) and Cupedidae (Triadocupedinae), were among the first beetles appearing in the geological record and flourished during the Late Permian, 251–254 million years ago (Ponomarenko 1969). Archostemata were still the dominant group of beetles

in the Triassic (e.g. Ponomarenko 1995). However, in recent faunas, they are a tiny relict taxon, comprising only about 45 species (Hörnschemeyer 2016).

Most of the recent diversity of archostematans is in two families (Hörnschemeyer 2016): Cupedidae and Ommatidae, with the remaining three each represented by a single extant species: Jurodidae (only holotype known), Crowsoniellidae (only type series known) and Micromalthidae. Grimaldi and Engel (2005) stated that what is described as *Micromalthus debilis* LeConte, 1878 may comprise several cryptic species. However, sufficient evidence confirming this assumption is lacking presently.

Micromalthus debilis is mainly known from the eastern part of the USA (Philips and Young 2001), and was also collected in Belize (Philips 2001). Both areas are likely part of the original area of distribution (Philips 2001). However, recently the species was introduced with timber into many parts of the world, including for instance Hong Kong, South Africa and Austria (e.g. Philips 2001; Hörnschemeyer 2016). The beetles differ strikingly from the relatively large species of Cupedidae and Ommatidae, which have preserved many ground plan features of Coleoptera (e.g. Beutel and Haas 2000; Beutel et al. 2008; Friedrich et al. 2009). The adults of *Micromalthus debilis* are very small, elongated, and weakly

sclerotized, with shortened elytra, superficially resembling those of some staphylinids (Coleoptera; Polyphaga). The larvae develop and burrow in the wood of oaks, hemlock, acacias or eucalypts (Grimaldi and Engel 2005) infested by red-rotting fungus (Pollock and Normark 2002; Hörnschemeyer 2016). *Micromalthus* is also known for having ‘one of the most bizarre life cycles of any metazoan’ (Pollock and Normark 2002: 105), including thelytoky, arrhenotoky, vivipary, paedogenesis, matriphagy and hypermetamorphosis with several distinctly different types of larvae (Hörnschemeyer 2016).

Previously it was stated, that micromalthids have minimal chances to occur in the paleontological record as impression fossils due to their small size and weak sclerotization, and would at least be restricted to amber produced by dicots (Mexican amber) and conifers (Baltic and Lebanese amber) (Grimaldi and Engel 2005). The oldest described finding of Micromalthidae was the triungulin larvae, *Cretomalthus* (Kirejtshuk and Azar 2008) from Lower Cretaceous Lebanese amber. Consequently, it was estimated that they appeared not later than in the Lower Cretaceous, while the genus *Micromalthus* appeared in the Early Eocene or earlier (Kirejtshuk and Azar 2008). Compression fossils of poor preservation quality were reported from the Kazakhstani Middle-Upper Jurassic locality Karatau (Kirejtshuk and Azar 2008). However, no detailed information is available and the fossils were never formally described. Micromalthids became rather abundant in amber starting from the Eocene, and two species attributed to the type genus were described: *M. eocenicus* Kirejtshuk et al. 2010 (Kirejtshuk et al. 2010) and *M. priabonicus* Perkovsky 2016 (Perkovsky 2016). Inclusions from Miocene Mexican amber (Rozen 1971) and Dominican amber were identified as representatives of *M. debilis* Hörnschemeyer et al. 2010.

The Babiy Kamen' locality is one of the most complete sections of the Maltsevo Formation (sometimes spelled as ‘Mal'tseva’ or ‘Maltsevskaya’) intertrappean deposits in the Kuznetsk Basin. The formation lies within a hidden nonconformity on Permian coal-bearing deposits of the Tailuganskaya Formation. It consists of tuffaceous argillites, siltstones and sandstones, with two remarkable basalt units at the top, the latter of which is known as Ryaby Kamen' Cliff. (references for this information??)

The Maltsevo Formation is traditionally subdivided into Tarakanikhinsky, Barsuchiy, Kedrovsky, and Ryabokamensky biostratigraphic horizons which were accepted as subformations (Saks et al. 1981) but usually are simply referred to as ‘Beds’. These beds have yielded numerous fossil insects (Aristov et al. 2013). Most of them, including the specimen under study, were collected from the upper part of Kedrovsky (=Kedrovka) Beds, about 50 m below the lower basalt unit.

The age of the Babiy Kamen' deposits is still debatable: Maltsevo Formation Beds are well correlated with the regional horizons of the Tunguska Basin, based on floristic, faunal, and palynological assemblages. Depending on two opposite points of view, these horizons in Tunguska and Kuznetsk Basins are considered to be either Lower to Middle Triassic, which is traditional and adopted in the regional stratigraphic chart (Betehtina et al. 1986; Mogutcheva and Krugovykh 2009), or terminal-Permian (Sadovnikov 1981, 2008; Gomankov and

Meyen 1986; Gomankov 2005). In the former case, Kedrovsky Beds are dated as upper Induan to lower Olenekian. In recent years, more evidence has emerged for the Permian age of those deposits (Kozur and Weems 2001, 2010; see also Sadovnikov 2015). A detailed correlation of the uppermost Changhsingian to lowermost Triassic conchostracan zones of the Germanic and Tunguska plus Taimyr Basins with the marine conodont scale strongly supports Permian age of the Siberian Trap flood basalts and intertrappean beds. The latest Permian age of the Tunguska and Kuzbass vulcanites are also supported by recent radiometric data (Reichow et al. 2009). Particularly, 40Ar/39Ar plagioclase ages from basaltic units that occur in the upper horizon of the Maltsevo Formation are 250.3 ± 0.7 Ma (Reichow et al. 2009) or ~ 252 Ma (recalculated by Svetlitskaya and Nevolko 2016). According to BuslovClarke and Chatzimanolis (2009) and Davies et al. (2010), Permian–Triassic boundary in the Kuznetsk Basin should be placed above the basalts, suggesting the Permian (Changhsingian) age for the insect beds (Shcherbakov 2015). A Late Permian age for Babiy Kamen' is also adopted in the present study.

Material and methods

The fossil specimens were examined dry using a Leica M165C microscope. The photographs were taken with VEGA TESCAN, Zeiss DSM 940 scanning electron microscopes and a Nikon D90 digital single-lens reflex camera. The photomicrograph of an extant specimen in glycerine 3A was made using a Dino-Eye AM4023XC Eyepiece camera attached to a Leitz Wetzlar compound microscope (100X) and DinoCapture 2.0 software. Line drawings were prepared based on photographs using image-editing software: CorelDRAW X8 and Adobe Photoshop CC.

Drawing conventions are as follows: a solid line represents a distinct margin; a dashed line represents an indistinct margin and structures overlapping each other; dashed and dotted lines represent a fold.

The fossil specimen is deposited in Borissiak Paleontological Institute (PIN), Russian Academy of Sciences.

Systematic paleontology

Herein we report the oldest record of the family Micromalthidae, *Archaeomalthus synoriacos* gen. et sp. nov., which demonstrates several plesiomorphic character states, but generally retains most of the apomorphies of Micromalthidae.

Archaeomalthus gen. nov. is placed within Archostemata based on exposed propleura and characters used below for familial affiliation. *Archaeomalthus* gen. nov. is attributed to the family Micromalthidae on the basis of the following features: slightly depressed anterior portion of head with frontoclypeal and clypeolabral sutures obliterated (Figures 1(b) and 2(c)); mesothoracic spiracles on conspicuous elevations (Figures 1(b) and 2(g,m)); shortened elytra, truncated apically, not covering posterior half of abdominal dorsum; mesocoxae widely separated medially by large, triangular anterior process of metaventrite (Figure 1(b)); absence of exposed metatrochantins;

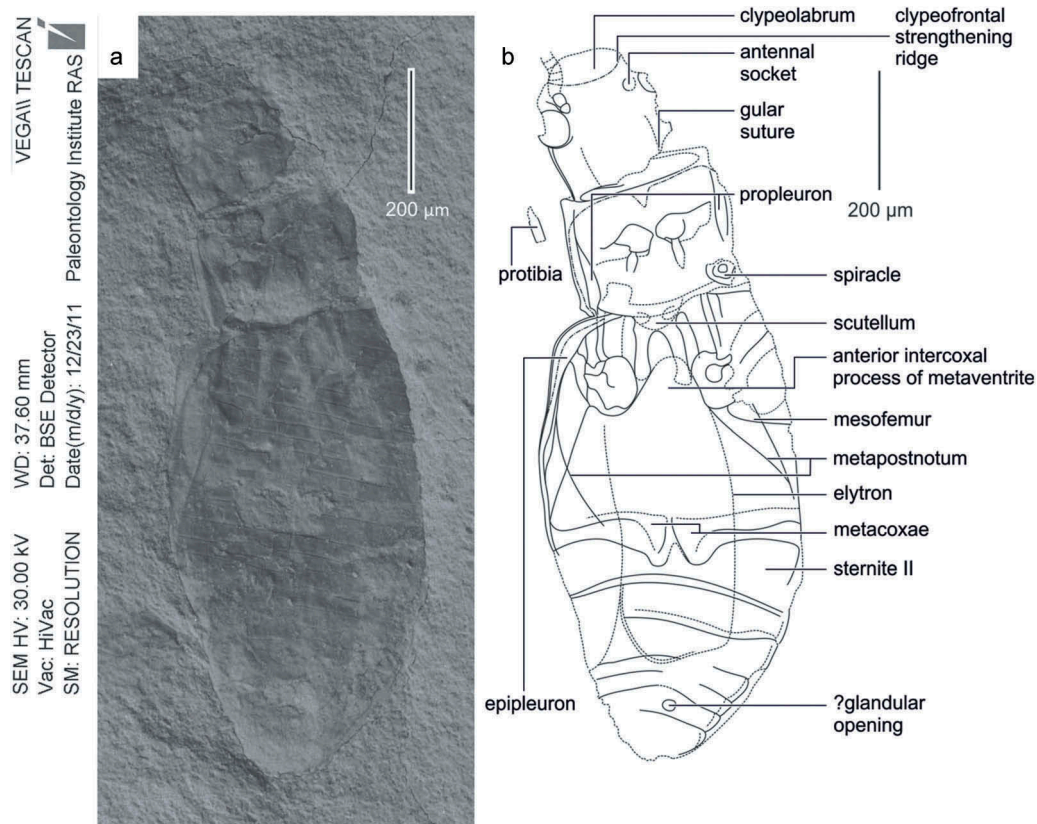


Figure 1. *Archaeomalthus synoriacos* sp. nov., Habitus. (a) Scanning electron micrograph of the holotype 5381/32. (b) Interpretative drawing.

presence of seven abdominal sternites with glandular opening on sixth segment (Figures 1(b) and 2(c) ?glandular opening).

Class **Insecta**, Linnaeus, 1758
 Order **Coleoptera**, Linnaeus, 1758
 Suborder **Archostemata** Kolbe, 1908
 Family **Micromalthidae**, Barber, 1913

Genus †**Archaeomalthus** gen. nov.

Type species. *Archaeomalthus synoriacos* Yan et al., sp. nov., by monotypy.

Diagnosis

Antennal sockets visible from above; propleuron exposed, narrow, not reaching anterior pronotal margin; procoxae slightly widened, almost contiguous medially; metanotum with metascutum delimited by very distinct longitudinal bulges (alacrista) (Figures 1(b) and 2(i,k,l)); anterior intercoxal process of metaventricle strongly developed, completely separating mesocoxae. Abdomen with seven visible sternites.

Derivation of name

Generic name from Greek ‘archaios’ – ‘ancient’ and *Micromalthus* LeConte, 1878, type genus of family Micromalthidae.

Description

Body elongated, slender, probably slightly flattened, with distinct shoulder region, slightly rounded laterally posterior to

prothorax. Total length ca. 1.18 mm, maximum width at posterior metathoracic region ca. 0.4 mm.

Cuticular surface largely smooth on all body regions, without recognizable scales, punctures or tubercles.

Head large, as long as pronotum, rectangular, slightly narrower than anterior pronotal margin; with widely separated well-developed compound eyes, inner margins of eyes are finely bordered; ocelli not recognizable, probably absent. Labrum not articulated, apparently fused with clypeus. Concave transverse line present on anterior head capsule, possibly indicating clypeofrontal strengthening ridge. Antennae inserted dorsally but still widely separated, articulatory area close to anteromesal edge of eyes. Mandibles sickle-shaped, with distal halves curved inwards. Maxillae not recognizable. Proximal elements of labium not visible as separate structures, submentum apparently fused with gula and ventral wall of head capsule (Figure 2(a,b)). Temporal region posterior to eyes very long, more than half as long as the length of head; narrowed neck region absent. Dorsal protuberances missing. Gular plate present, large.

Pronotum almost quadrangular, as long as wide, with distinct lateral carina; anterior and posterior angles distinct, triangular; anterior pronotal margin at the same level as the anterior prosternal edge. Prosternal intercoxal process not visible, apparently missing; wide membranous area present posterior to procoxae. Large spiracle recognizable in prothoracic-mesothoracic intersegmental region.

Elytral bases distinctly wider than maximum pronotal width; pronoto-elytral angle, i.e. humeral bulges, very distinct, rounded. The shape of elytra roughly quadrangular, with

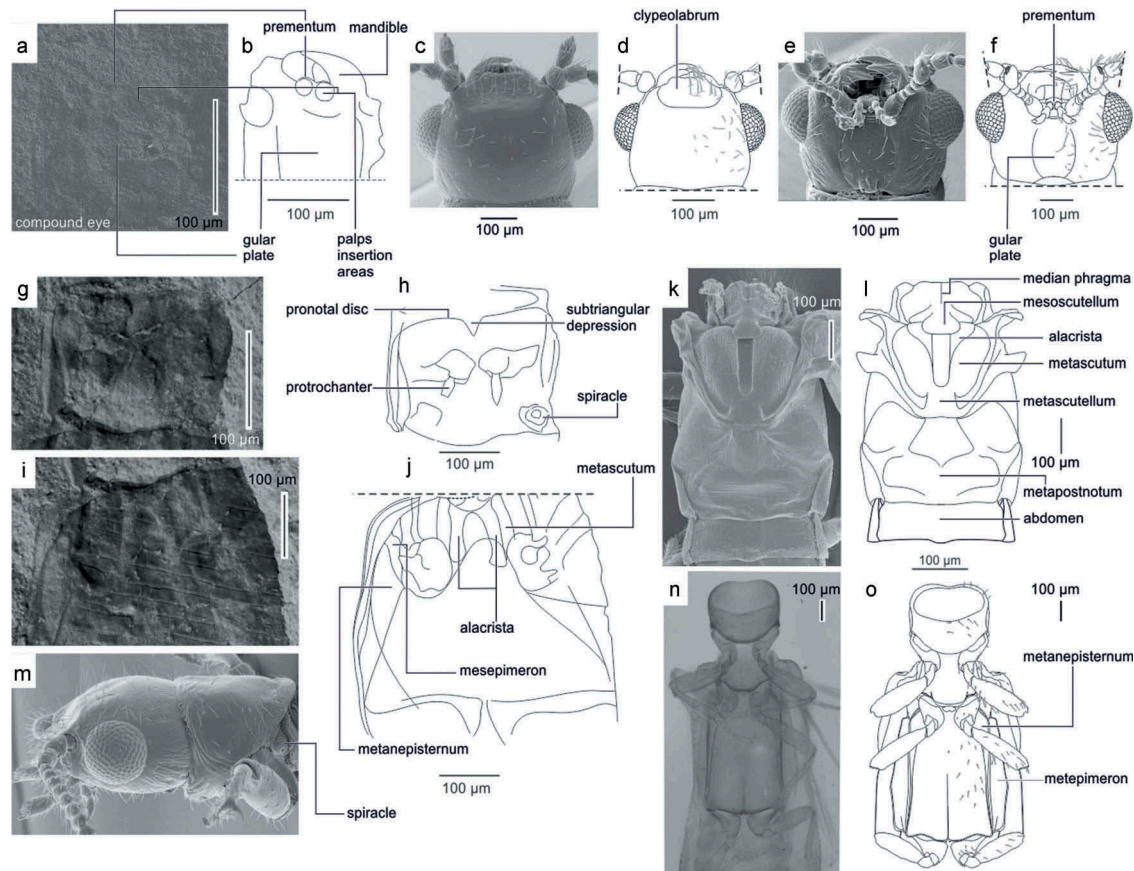


Figure 2. Details of the organization in extinct and recent Micromalthidae. (a) *Archaeomalthus synoriacos* sp. nov. head, scanning electron micrograph. (b) *A. synoriacos* sp. nov. head interpretative drawing. (c) *Micromalthus debilis*, head dorsal aspect, scanning electron micrograph. (d) *M. debilis* interpretative drawing of head dorsal aspect. (e) *M. debilis*, head ventral aspect, scanning electron micrograph. (f) *M. debilis* interpretative drawing of head ventral aspect. (g) *A. synoriacos* sp. nov. pronotum, scanning electron micrograph. (h) *A. synoriacos* sp. nov. pronotum interpretative drawing. (i) *A. synoriacos* sp. nov. metathorax, scanning electron micrograph. (j) *A. synoriacos* sp. nov. metathorax interpretative drawing. (k) *M. debilis*, thoracic dorsal aspect, scanning electron micrograph. (l) *M. debilis* interpretative drawing of thoracic dorsal aspect. (m) *M. debilis* prothoracic lateral aspect, scanning electron micrograph. (n) *M. debilis* photograph of thoracic ventral aspect. (o) *M. debilis* interpretative drawing of thoracic ventral aspect.

truncated apices. Mesal base enclosed by the semioval scutellar shield. Window punctures and other patterns of surface sculpture absent, degree of sclerotization uniform.

Metanotum with distinct longitudinal median groove delimited with strongly developed alacrissa; additional longitudinal bulges visible laterally. Mesocoxae widely separated, more or less rounded, nearly triangular, not transverse. Mesocoxal cavities laterally closed by mesepimeron and metanepisternum.

Metaventrite large, distinctly narrowed anteriorly, with large triangular, apically rounded anterior intercoxal process; separating mesocoxae completely. Transverse suture of metaventrite not recognizable, probably absent. Metatrochantin not exposed. Metacoxae short, transverse, reaching the lateral edge of ventrite, without recognizable metacoxal plates.

Abdomen of parabolic shape, evenly narrowing posteriorly, with rounded apex, as long as meso- and metaventrite combined; at least basal sternites separated by externally visible intersegmental membranes. Four distal abdominal tergites not covered by the elytra.

Species included

Monotypic.

Occurrence

Babiy Kamen` locality, Tom` river, Kuznetsk Basin, S. Siberian, in the upper part of the Maltsevo Formation.

Remarks

Generally, size alone does not justify a placement of a beetle in a specific supraspecific taxon. However, after taking into consideration all the characters mentioned in the Diagnosis and Description, a length of only slightly more than 1 mm should be seen as an additional argument for keeping *Archaeomalthus* in Micromalthidae. All other archostematan beetles with the exception of the strongly flattened *Crowsoniella relict*a (Pace 1975) are much larger.

The degree of cuticular sclerotization can rarely be adequately estimated on fossil imprints. Therefore, it cannot be used as a solid diagnostic character, even though some surface features such as tubercles, large punctures, etc., can be used for species identification and also in a phylogenetic context (e.g. Beutel et al. 2008; Hörschemeyer 2009). In the case of *Archaeomalthus*, the visibility of metathoracic fine details (including metapostnotum) on mostly ventral imprint and elytra (Figure 2(i,k)), preserved only as faint lines, suggests that *Archaeomalthus*

was overall weakly sclerotized. Elytra of most fossilized beetles, in contrast, are hard structures overlapping the body and usually retaining many structural details (Ponomarenko 1969). Beetle fossils previously known from Babiy Kamen` locality, *Petrodromeus* Ponomarenko et Volkov, 2013 and *Permunda* Ponomarenko et Volkov 2013 (Adephaga; Trachypachidae) both have finely preserved elytra with well-defined longitudinal striae (Ponomarenko and Volkov 2013).

The abdomen of *Archaeomalthus* is distinctly shorter than the head and pronotum combined; however, this character is variable in the extant *Micromalthus* due to varying degrees of extension of the intersegmental membranes. Thus it is not used in the generic diagnosis. The abdominal segments are often more contracted in males than in females, possibly due to different physiological conditions (e.g. development stage of eggs). The length of the abdomen, especially of females, varies in *M. debilis* Hörnschemeyer et al. 2010.

†*Archaeomalthus synoriakos* Yan et al., gen. et sp. nov.
(Figs. 1 and 2)

Diagnosis

As for the genus.

Derivation of name

The Greek-specific name ‘synoriakos’ – ‘borderline’, refers to the proximity of Babiy Kamen` locality to Permian-Triassic boundary.

Material

Holotype: PIN 4887/102, single specimen, counter print of the complete body impression with antennae and all legs missing. Repository: Paleontological Institute, Russian Academy of Sciences (curator Prof. Dr A.P. Rasnitsyn).

Occurrence

Babiy Kamen` locality, Tom` river, Kuznetsk Basin, S. Siberian, in the upper part of the Maltsevo Formation.

Description

Head slightly, ca. 0.23 mm, long and about as wide at the ocular region. Compound eyes round, located at anterior third of head, half as long as temporal region. Antennal insertion areas round, with outer margin bordered by fine carina. Antenna with small scapus, larger pedicellus with slightly rounded edges, and stout flagellomeres, apparently moniliform. The arrangement of apical mandibular teeth not recognizable. Prementum rather large, at least as wide as eye.

Anterior angles of pronotum blunt, not protruding forward; pronotal disc distinctly convex; anterior pronotal margin with median subtriangular depression; posterior angles slightly protruding laterally. Propleuron narrow, triangular, obliterating on anterior third of prothorax.

Elytra with fine lateral carina; epipleuron widest near humeral bulge, moderately wide on basal half, strongly narrowed posteriorly.

Mesepimeron oblique, with slightly sinuated anterior and posterior margins. Mesocoxal pits closed laterally by mesepimeron and metanepisternum. Metanotum with distinct alar cristae. Metanepisternum parallelogram-shaped. Metaventricle about as long as width between anterolateral edges, posterior edge about 1.5 times as wide.

Procoxae transverse, mesocoxae almost globular, with inconspicuous lateral extension. Metacoxae short, with mesal part posteriorly rounded and extending through approximately two-thirds of first abdominal ventrite, only slightly narrowing laterally.

Sternites II-IV distinctly longer than V-VII, gradually narrowing towards the abdominal apex. Short sternite VII with round median structure with unclear homology (apparently glandular opening). Terminal sternite VIII as long as VI and VII combined, with rounded hind margin. At least posterior abdominal sternites with narrow laterosternites. .

Discussion

Taxonomic position of *Archaeomalthus*

In contrast to specimens of *Micromalthus* described from Miocene amber, which were not very different from the recent *M. debilis* Hörnschemeyer et al. 2010, Permian *Archaeomalthus* shows distinct differences compared to the Recent species and Cenozoic fossils of the family. Nevertheless, the affinities of extant Micromalthidae are sufficient for justified placement in this family. This includes a number of diagnostic features: a small and slender body, the large relative size of the head capsule, and well-developed, round compound eyes. Clear apomorphies shared with fossil and extant *Micromalthus* are shortened, quadrangular and posteriorly truncated elytra, leaving abdominal tergites V-VIII exposed, and the increased number of abdominal sternites, in contrast to five in ancestral Permian species (Stem group Coleoptera) and the vast majority of extant beetles (Ponomarenko 1969; Beutel et al. 2008; Lawrence et al. 2011). Additional potential apomorphies are the fusion of the labrum and clypeus, the long subparallel temporal region, the stout antennal flagellomeres, the semioval scutellar shield (Figure 1(b)), and probably, weak sclerotization of the body. Considering the placement in Archostemata and the ground plan of this suborder (and Coleoptera s.l. (Beutel 1997; Beutel et al. 2008; Friedrich et al. 2009)), additional apomorphies shared with *Micromalthus* are the absence of cuticular tubercles and scales, the complete lack of dorsal cephalic protuberances, the absence of a constricted neck region, evenly sclerotized elytra lacking window punctures, the absence of the transverse ridge on the mesoventrite, the concealed metatrochantins (Beutel et al. 2008; Hörnschemeyer 2009) (Figures 1 and 2(m,n)) and abdominal glands (Figures 1(b) and 3)

Shortened antennae, wings and legs of a Miocene micromalthid (lately *Micromalthus anansi* was synonymized with *M. debilis* by (Hörnschemeyer et al. 2010)) were considered as a step of progressing morphological simplification of adults (Perkovsky 2007). However, this term is problematic, as these features have obviously nothing to do with

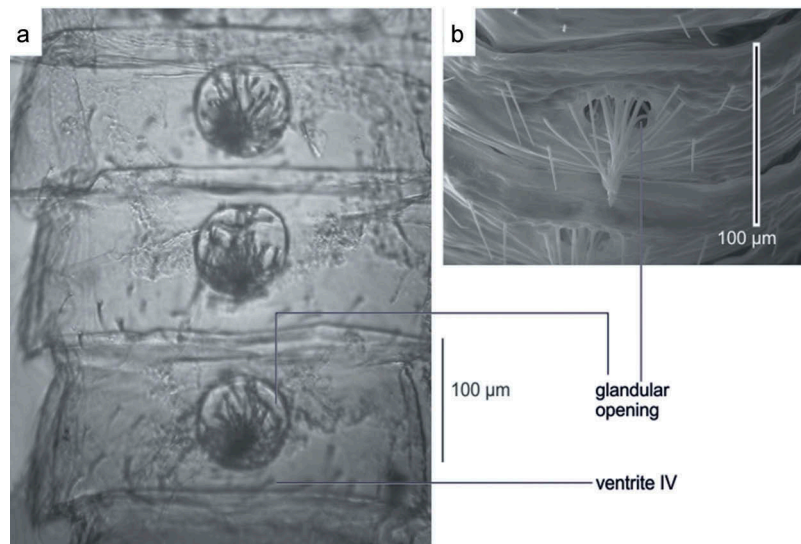


Figure 3. Abdominal glands of *Micromalthus debilis*. (a) Ventrites III – V with median glandular pits. (b) Scanning electron micrograph of the glandular opening.

regressive character conditions occurring in beetles (e.g. Rempel and Church 1965, 1969, 1971; Kühne 1972; Kobayashi et al. 2013). It appears likely that small size, shortened elytra, and weakly sclerotized cuticle are related to the short lifespan and sporadic occurrence of adults, and their ‘vestigial’ status in the context of reproduction (Pollock and Normark 2002; Hörnschemeyer et al. 2010). Relatively short legs are also common in other extant archostematan beetles including Permian forms (e.g. Ponomarenko 1969; see also Yan et al. 2017a) and moniliform antennae characterized as a plesiomorphic character by Perkovsky (2007).

One of several distinct features of *Archaeomalthus* differing from *Micromalthus* is the presence of an exposed propleuron separated by distinct sutures. This is clearly a plesiomorphy corresponding to the autapomorphic fusion of all prothoracic sclerites in extant or Cenozoic species (e.g. Beutel et al. 2008; Friedrich et al. 2008). Two other conspicuous features are the presence of a very distinctly delimited groove on the mesoventrite and a corresponding anteromedian process of the meta-ventrite. Both features resemble conditions commonly found in Adephaga, notably the aquatic groups (excluding Gyrinidae) and basal grade Carabidae (Beutel 1992). However, a placement of *Archaeomalthus* in these suborders can be clearly excluded based on the short metacoxae without enlarged coxal plates, the lack of a prosternal process, and the increased number of abdominal sternites (e.g. Beutel 1992; Beutel and Haas 2000). The strongly developed process of the metaventrite, which widely separates the mesocoxae, is uncommon in recent Archostemata, even though it occurs in some extinct groups of this suborder, such as Schizophoridae (e.g. *Tersus* Martynov, 1926) or Ademosynidae (Yan et al. 2017b). It is likely that this condition has evolved several times independently, in scattered groups of Archostemata including Micromalthidae, and also in Adephaga (e.g. Beutel 1986, 1992; Beutel and Haas 2000). In contrast to *Archaeomalthus*, the thoracic venter of *Micromalthus* appears distinctly simplified (Figures 2(g–j,m,n)). It is conceivable that this is a reduction linked with the very limited role of the adults in the life cycle of the extant species.

Despite the marked differences between *Archaeomalthus* and *Micromalthus*, the former already show a distinct and apparently very stable degree of deviation from the ground plan of Coleoptera s.str. and s.l. (e.g. Beutel 1997). The remarkable series of reductional features shared by the Permian fossil and the extant species include a lightly sclerotized body without any distinct surface sculpture, a head lacking dorsal protuberances, shortened and apparently thin elytra, exposed membranous areas behind the procoxae and between at least two basal visible abdominal sternites, and the reversal of the invagination of the terminal abdominal segments. It is likely that the reduced role of adults of Micromalthidae (Perotti et al. 2016) was a syndrome of vestigial characters acquired at least 255 million years ago.

Evolutionary stability of Micromalthidae

There are two main competing hypotheses to explain clades that accumulate phenotypic variation at a slow rate: the first one invokes genetic and developmental constraints that restrict the production of phenotypic variation (Smith 1981; Raff 1996; Gould 2002). The second explanation is that stasis is a result of stabilizing selection (Charlesworth et al. 1982; Kirkpatrick 1982; Estes and Arnold 2007). Exceptional evolutionary stability, bradytely, or ‘arrested evolution’ (Simpson 1944) of Micromalthidae, resulted in very slow morphological change over time, which characterizes ‘living fossils’. On principle, this could be due to very long periods of stable environmental conditions (Hörnschemeyer et al. 2010, see historical analysis of bradytely in Clarke and Chatzimanolis 2009). In the case of Micromalthidae this is the subcortical space of fungus-infested wood, which may have been one factor that buffered micromalthids from strong selection for morphological change (BuslovClarke and Chatzimanolis 2009). Almost any change, but particularly a major change, of the phenotype in such a well-balanced system will be deleterious. Although minor gene substitution may be frequent, the well-buffered system of developmental canalizations shields the phenotype from major changes. There is an

opportunity for speciation, but a major alteration of the morphotype is impossible as long as the epigenotype is intact (Mayr 1970).

Association with prokaryotic endosymbionts or parasites can result in genome reduction and also an overcomplicated lifecycle including hypermetamorphosis and parthenogenesis. A long co-evolution with *Wolbachia* Hertig, 1936 is assumed in the case of *M. debilis* (Grimaldi and Engel 2005; Perkovsky 2012). One of the results is apparently the ‘ghost sex life’, linked with a marginalization and vestigialization of the ‘ghost adults’ (Perotti et al. 2016). It is likely that the distinctly simplified adult morphology of *Micromalthus* is closely linked with the obsolete role in the life cycle, and that this applies also to the lesser but already distinct reduction in *Archaeomalthus*. The apparent stability of morphological simplification in the adult stage suggests a very old origin of a specialized mode of reproduction and possibly an equally old association with endosymbiotic organisms. Selective pressure on mechanical protection and a highly efficient locomotor apparatus in ‘ghost adults’ is likely minimal. Apparently, the resulting structural simplifications are irreversible once accomplished, even though the sex-life of adults can be revived as shown by Perotti et al. (2016). In the case of Micromalthidae, the increasing degree of reduction from the Permian to the Miocene is likely a matter of reduced investment in adult structures, and therefore a result of ‘evolutionary economy’.

A side effect of an association with symbionts can be a reduced ability to survive overheating (Dunbar et al. 2007; Perkovsky 2012). It is likely that the immediate ancestors of extant micromalthid species were also confined to extratropical areas, while the climate of Western Europe in the Ypresian (Early Eocene) was undoubtedly macrothermal, which is confirmed by, among other things, the absence of any Holarctic elements in the amber, in particular, in the myrmecofauna of Oise (Aria et al. 2011; Perkovsky 2016).

There are no specific paleoclimatic studies on Babiy Kamen` locality. However, some conclusions about climate during sediment accumulation could be made on the basis of paleofloristic analyses. The Kuznetsk Basin is mostly coal bearing, comprising industrial reserves of hard and brown coal. The process of coal-forming occurred on the former territory of a Carboniferous shallow marine bay, which was replaced by rather swampy lowland plains during the Permian. Alteration of coal and paleosols indicate sediment accumulation in rather humid environments, necessary for the increased accumulation of coal-forming biomass. For the upper part of the section, in which the fossil insects have been found (Dr E. Karasev PIN RAS, 2018 pers. comm. to DV), it is possible to assume alteration of humid and arid climatic conditions. Temperatures were not yet reconstructed for Babiy Kamen` locality. However, significant abundance of conifers (e.g. *Quadrocladus*, *Elatocladus*, *Voltzia*) is reported from the upper part of the Maltsevo Formation (including insect-bearing layers) (Betehtina et al. 1986). It was shown for Permian-Triassic deposits of the Severodvian Basin that climatic cooling was also characterized by an increased proportion of conifers in Babiy Kamen` locality (Krassilov and Karasev 2009).

Conclusions

Archaeomalthus is interpreted as an early representative of the aberrant archostematan family Micromalthidae. It suggests that a distinct simplification of the morphology of adults already evolved in the late Paleozoic, suggesting an early reduction of the role of adults in the life cycle of the group.

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