



How long can insect species exist? Evidence from extant and fossil *Micromalthus* beetles (Insecta: Coleoptera)

THOMAS HÖRNSCHEMEYER^{1*}, SONJA WEDMANN² and GEORGE POINAR³

¹Johann-Friedrich-Blumenbach-Institut für Zoologie & Anthropologie, Georg-August-Universität Göttingen, Berliner Str. 28, D-37073 Göttingen, Germany

²Forschungsstation Grube Messel, Forschungsinstitut Senckenberg, Markstraße 35, D-64409 Messel, Germany

³Zoology Department, Oregon State University, Corvallis, OR 97331, USA

Received 19 September 2008; accepted for publication 17 November 2008

Six new fossils of *Micromalthus* (Coleoptera: Archostemata) from Dominican amber are compared with extant and previously described fossil micromalthid beetles. The amber inclusions are well preserved and all important morphological features are visible. Taking into account the morphological variability of the extant species *Micromalthus debilis* LeConte, 1878, it is not possible to find any morphological features that distinguish the fossils from the extant species. This also applies to the Dominican amber inclusion described as *Micromalthus anasi* Perkovsky, 2008, which therefore is considered a junior synonym of *M. debilis*. The lack of morphological change in *M. debilis* over time might possibly be explained by unusually stable environmental conditions, as this species occupies a very specialized ecological niche in decaying timber. A general survey of fossil insects indistinguishable from extant species is presented.

© 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2010, 158, 300–311. doi: 10.1111/j.1096-3642.2009.00549.x

ADDITIONAL KEYWORDS: Archostemata – Dominican amber – evolution – fossil record – Miocene.

INTRODUCTION

The minute archostematan beetle *Micromalthus debilis* LeConte, 1878 is a very special species. One of its most remarkable characteristics is a complex life cycle with a triungulin-like first instar, followed by paedogenetic, parthenogenetic, and viviparous stages, as well as the formation of haploid males (Barber, 1913a, b, Scott, 1936, 1938; Pringle, 1938, Costa, Vanin & Casari-Chen, 1988; see Discussion and Fig. 5). In addition, the habitus and some morphological details of this species are unusual and the phylogenetic position of *M. debilis* was fairly uncertain for some time. Today the affiliation of *Micromalthus* with Archostemata, the most ancient group of Coleoptera, can be regarded as relatively certain. Within Archostemata *M. debilis* is usually regarded as the only representa-

tive of Micromalthidae (Lawrence & Newton, 1995; Hörnschemeyer, 1998; Beutel & Haas, 2000; Beutel & Hörnschemeyer, 2002; Beutel, Gea & Hörnschemeyer, 2007).

Even though larval or adult specimens of extant *M. debilis* have been reported from China, Hawaii, South America, Central America, North America, South Africa, and Europe (Table 1), the natural range of extant *Micromalthus* seems to be restricted to North America. The other occurrences are most likely the result of human activity in the form of transport/export of lumber. The findings outside of North America are always singular incidences and there is no evidence that established populations exist anywhere else in the world.

The fossil record of Micromalthidae is still quite scarce. So far, first instar larvae have been found in Cretaceous Lebanese amber (Crowson, 1981: 668), Eocene Baltic amber (Lawrence & Newton, 1995),

*Corresponding author. E-mail: thoerns@gwdg.de

Table 1. Records of *Micromalthus*

Locality	Reference	Extant/fossil	Documented developmental stage
Northern Europe	Lawrence & Newton (1995)	Baltic amber (Eocene)	Larva
France, Europe	Kirejtshuk <i>et al.</i> (in press)	Paris amber (Eocene)	Imagines
Austria, Europe	Jäch & Komarek (2000)	Extant	Imagines
Lebanon, Asia minor	(Crowson, 1981: 668; Lawrence & Newton, 1995)	Lebanon amber (Early Cretaceous)	Larva
South Africa	(Paterson, 1938; Scholtz & Holm, 1985)	Extant	Imagines
Hong Kong, China	Marshall & Thornton (1963)	Extant	Larvae
Eastern United States, North America	Philips & Young (2001)	Extant	Larvae, imagines
British Columbia, Canada, North America	Borror, Triplehorn & Johnson (1992)	Extant	Imagines
New Mexico, USA, North America	Borror <i>et al.</i> (1992)	Extant	Imagines
Dominican Republic, Caribbean	Perkovsky (2008)	Dominican amber (Miocene)	Imago
Dominican Republic, Caribbean	Lawrence & Newton (1995)	Dominican amber (Miocene)	Larva, imago
Cuba, Caribbean	Lawrence (1982)	Extant	Imagines
Belize, Caribbean	Philips (2001)	Extant	Imagines
Chiapas, Mexico, Central America	Rozen (1971)	Mexican amber (Miocene)	Larva
Sao Paulo, Brazil	Costa <i>et al.</i> (1988)	Extant	Imagines
Hawaii, Western Pacific	Swezey (1940)	Extant	Imagines

Dominican amber (Lawrence & Newton, 1995), and Mexican amber (Chiapas) (Rozen, 1971). Dominican amber is dated as Early to Middle Miocene, corresponding to 20 to 15 Mya (Iturralde-Vinent & MacPhee, 1996; Iturralde-Vinent, 2001). The age of Mexican amber and Dominican amber is about the same, reaching an age of up to 20 million years (Solórzano Kraemer, 2007). Recently an imago from Dominican amber has been described as *Micromalthus anasi* Perkovsky, 2008, and two specimens from Eocene amber of the Paris Basin will be described soon as a new species by Kirejtshuk, Nell & Colomb (in press).

In the present study we address the questions of how many extinct and extant species of *Micromalthus* exist and how long insect species in general might exist. We were able to examine six new fossil adult specimens of *Micromalthus* from Dominican amber. Together with a detailed investigation of numerous extant specimens of *M. debilis*, the available material now provides enough data to assess these questions.

MATERIAL AND METHODS

MATERIAL EXAMINED

Fossil specimens of Micromalthus

Specimens from Dominican amber: one specimen (collection number MTEC226, Fig. 1A) housed in the entomological collection of Montana State University at Bozeman, USA.

Five specimens from the Poinar Amber collection (collection numbers C7-191A to C7-191E) maintained at Oregon State University, USA.

One specimen (coll. no. Do-632-K, holotype of *M. anasi*) from the amber collection of the Staatliches Museum für Naturkunde Stuttgart, Germany.

Extant specimens of Micromalthus debilis

Three specimens from Albuquerque, New Mexico, USA, collected in 1917 and now stored at the Staatliches Museum für Naturkunde Dresden, Germany.

Fifteen specimens collected in 1994 in Cameron, Missouri, USA, but probably originating from Ohio or Kentucky, because the timber from which they emerged was probably milled there. The specimens are now deposited at the Wilbur R. Enns Entomology Museum, University of Missouri at Columbia, USA.

Six specimens collected in 2006 from a laboratory culture at the University of Wales at Bangor, UK. The founding specimens of this culture are from Wisconsin, USA.

METHODS

Fossil and extant specimens were studied, drawn, and photographed with a Leica MZ16 stereomicroscope with camera lucida attachment and a Nikon Coolpix 4500 digital camera.



Figure 1. A, photograph of *Micromalthus debilis* in Dominican amber (MTEC226, MSU Bozeman, USA), female specimen. B, extant female *M. debilis* in dorsal view. The abdomen appears comparatively short in the extant specimen because of (1) perspective distortion because the abdomen is bent downward and (2) because the segments are retracted. Arrows mark the protruding edges of two segments; in (A) the segments are fully extended.

SYSTEMATIC PALAEOONTOLOGY

COLEOPTERA LINNAEUS, 1758

ARCHOSTEMATA KOLBE, 1908

MICROMALTHIDAE BARBER, 1913

MICROMALTHUS DEBILIS LECONTE, 1878

Figures 1A, 2A–C

DESCRIPTION OF DOMINICAN AMBER SPECIMENS

A detailed description of specimen MTEC226 (Figs 1A, 2A–C) is given as representative of the Dominican amber specimens.

The fossil is embedded in a very clear piece of Dominican amber of light amber colour. There is a fissure running from one corner of the amber piece to the tip of the abdomen.

With a few restrictions, the beetle is completely visible from both dorsal and ventral surfaces. It is intact with the exception of both antennae, which are broken after the fifth (left) and fourth (right) antennomere. Both hind wings are outstretched. The left one lies flat and shows the complete venation, whereas the right one is unnaturally folded at the radial hinge. Both elytra are partially closed and translucent (Fig. 1A). Overall, the animal is 2.18 mm long. In comparison with the figured extant specimen (Fig. 1B), the amber inclusions seem to have a very long abdomen. The length of the abdomen is very variable both in extant and fossil specimens. The abdominal segments are often more contracted in

males than in females. For example, this may be because of physiological conditions, e.g. the developmental stage of eggs in the reproductive system of the female. Therefore, the overall length, especially of females, can be very variable. Further measurements are given in Table 2.

Head

The head is turned to the left and directed slightly upward. Of the mouthparts, only the protruding maxillary palps are visible. Each terminal palpomere is enlarged and bears a large sensory area with long rod-shaped sensilla. A white foggy substance covers the remaining mouthparts. Both antennae are complete but broken, the left antenna behind the fifth antennomere and the right antenna behind the fourth antennomere. The distal parts of the antennae are separated by the lengths of approximately three (right) to five (left) antennomeres from the more proximal segments. It is possible that the distal parts of the antennae stuck to the resin and were separated when the beetle attempted to free itself. The antennae are 11-segmented. The two basal antennomeres are distinctly larger than the third. Antennomeres 3 to 11 increase in size. The terminal antennomere is similar in size to the pedicel. The head is approximately 0.26 mm long and 0.38 mm wide. Each antenna is about 0.29 mm long without the gap.

Thorax

The pronotum is 0.27 mm wide at the anterior margin and 0.18 mm wide at the posterior margin. The

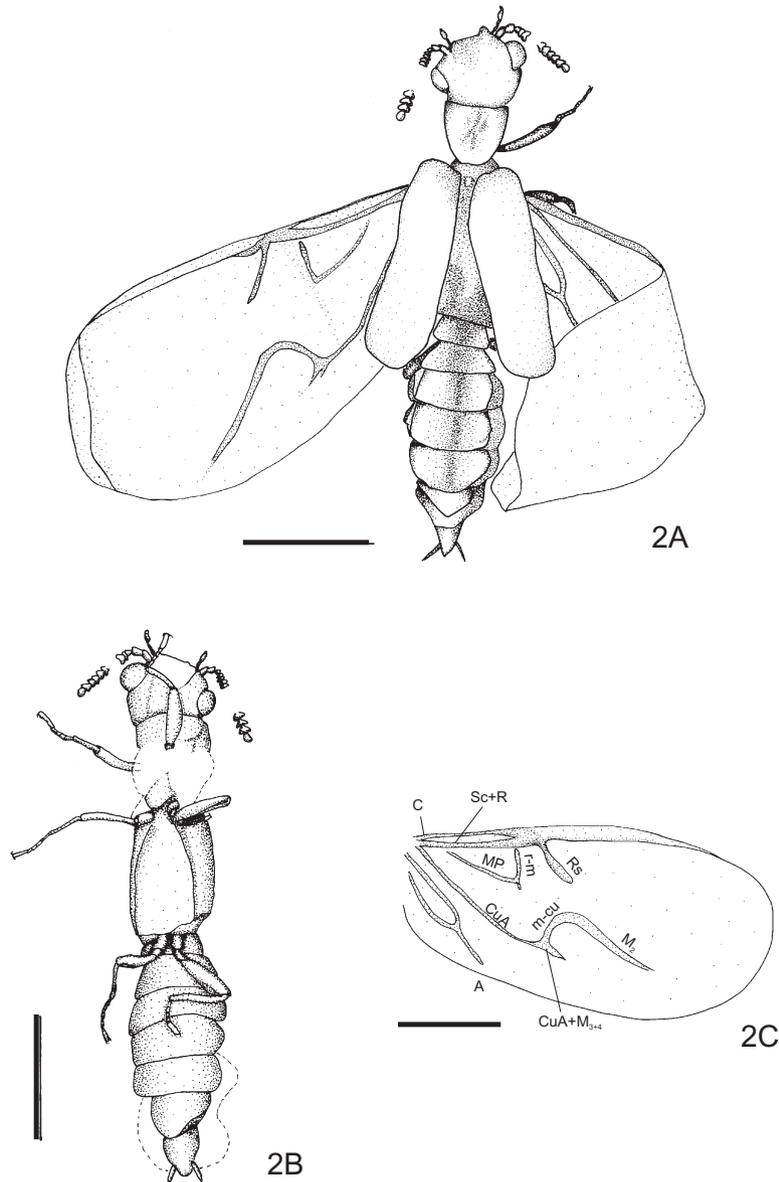


Figure 2. *Micromalthus debilis* from Dominican amber (MTEC226 MTU Bozeman, USA). A, dorsal view. B, ventral view, wings omitted, mouthparts and mesothorax obscured by white, foggy substance. A cloud of this substance also surrounds the last three abdominal segments. C, reconstruction of wing venation of fossil specimen. Nomenclature of wing veins after Wallace & Fox (1975). Scale bars = 0.5 mm.

ventral sides of the prothorax and mesothorax are obscured by a white foggy substance so that neither the prosternal area nor the procoxae or trochanters are visible (Fig. 2B). The tibiae are about two-thirds as long and about half as wide as the femora. Only in the hind legs are the tibiae nearly as long as the femora. All tarsi are five-segmented. The terminal tarsomere bears two claws and is nearly as long as the remaining tarsomeres combined. The metathorax is slightly longer than the prothorax and mesothorax combined. The metacoxae are inserted at the poste-

rior margin of the metathorax. They stand close together and are somewhat cylindrical in shape. The elytra are very translucent and partially opened. Their surface is smooth and without recognizable pubescence. It is not possible to distinguish any details on the dorsal sides of the mesothorax and metathorax. The alae are nearly completely extended. The distal half of the right wing is turned upward and inward so that its tip is directed toward the abdomen. The left wing is nearly fully outstretched. Only the apex is slightly crumpled. Combining features from

Table 2. Measurements of fossil amber specimens in comparison with extant *Micromalthus debilis*

Preservation	<i>Micromalthus</i> from Paris amber Kirejtshuk et al., in press		Former <i>Micromalthus anasi</i> Perkovsky, 2008; Dominican amber		<i>Micromalthus debilis</i> this paper Dominican amber					<i>Micromalthus debilis</i> extant (N = 24)
	PA 7870, PA 1286 (N = 2)	Do-632-K	MTEC 226	C7-191A	C7-191B	C7-191C	C7-191D	C7-191E	Dry & ethanol	
Gender	Female	Female	Female	Unknown	Female	Female	Female	Female	Female	Male & female
Preservation		Left hind wing and tarsi of meso- & metathorax cut off (preparation artefact?)		Part of abdomen missing	Part of thorax missing		Abdomen contracted			Dried & alcohol
Preserved length (mm)	2.5; 2.9	2.07	2.18	1.32	1.78	1.8	1.64	1.70	1.6–2.2	
Number of antennomeres	11	11	11	11	11	11	11	11	11	
Antenna length (mm)	0.5 (?)	0.38	0.29	0.36	0.36	0.33	0.33	0.33	0.27–0.35	
head length (mm)	0.5 (?)	0.25	0.26	0.21	0.24	0.21	0.23	0.21	0.26–0.3	
Head width (over eyes) (mm)	0.6	0.32	0.38	0.33	0.35	0.30	0.38	0.35	0.38–0.42	
Pronotum width at anterior margin (mm)	0.58 (?)	0.23	0.27	0.26	0.26	0.23	0.30	0.24	0.27–0.33	
Pronotum length (measured in middle of pronotum) (mm)	0.4	0.25	0.24	0.23	Not measurable	0.21	0.23	Not measurable	0.24–0.27	
Ratio of maximum elytra length to middle elytra width	4.14	~4.2–4.3	~3.6	~3.9	~4.2	~4.3	~4.3	~4.4	~4.1–4.7	
No. of abdominal segments	7	7	7	Missing	7	7?	?	7	?	
No. of visible abdominal tergites	?	7?	?	Missing	7	?	?	?	7	
No. of visible abdominal sternites	?	?	?	Missing	7	?	7?	6	6	

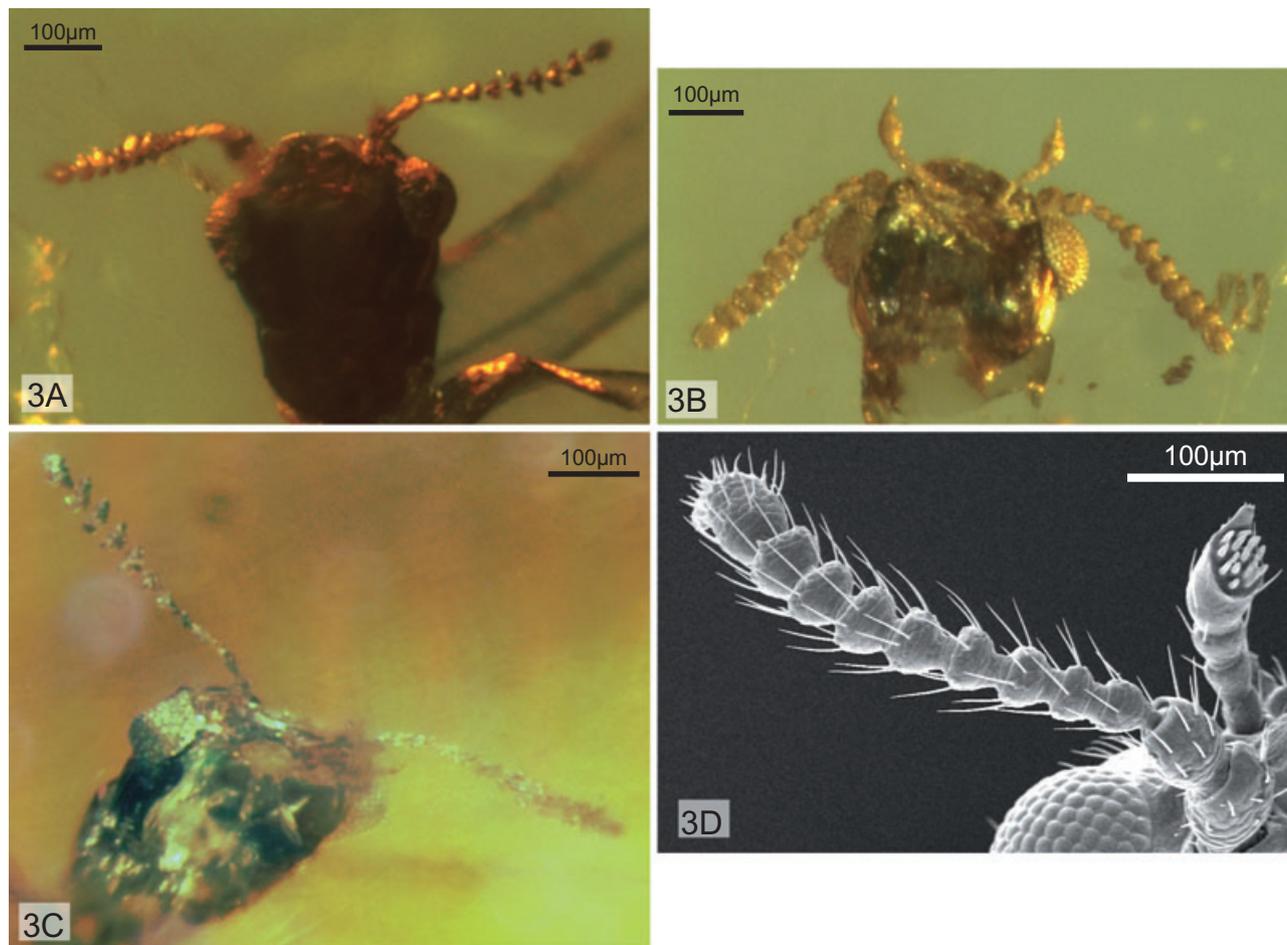


Figure 3. A–C, photographs of heads of Dominican amber specimens of *Micromalthus* from the Poinar collection. A, coll.no. C 7-191^a. B, coll.no. C 7-191B. C, coll.no. C 7-191C. D, scanning electron micrograph of left antenna of extant specimen of *Micromalthus debilis*, dorsal view.

both hind wings, it is possible to reconstruct the complete venation (Fig. 2C).

Abdomen

The abdomen is completely collapsed with distinctly concave tergites, which are obliquely pressed against the sternites, so that the pleural membranes on the right side of the body can be seen in dorsal view. The abdomen has seven visible segments. None of the abdominal tergites have pubescent foveae, which, in combination with the long styli visible at the tip of the abdomen, indicates that the specimen is a female.

SPECIMENS FROM THE POINAR COLLECTION

The five specimens from the Poinar collection are morphologically nearly identical to the specimen MTEC226. Slight variations are present in the sizes

of the specimens and in some instances taphonomic deformations seem to have occurred. For example, in one specimen (Fig. 3A) the left and right antennae look significantly different with the segments of the left antenna appearing much thinner and further separated than in the right antenna. Similar effects are also visible in other specimens (Fig. 3B). This specimen (C7-191B) obviously is in an advanced state of decay with large areas of the thorax being completely transparent and featureless. Specimen C7-191C also shows strong signs of decay and/or deformation. The abdomen and head are distinctly compressed and deformed and the antennae look as if they were serrate (Fig. 3C). The comparison of the antennae of the different amber specimens supports the conclusion that the antennae are similar to those of extant specimens (Fig. 3D). The variable shapes of the antennae in the amber inclusions are obviously preservation artefacts.

COMPARISON WITH EXTANT SPECIMENS OF *MICROMALTHUS DEBILIS*

Twenty-four extant specimens originating from three different collections were measured to determine the morphological variability amongst extant specimens of *M. debilis*. The results are given in Table 2. Both dry and alcohol preserved specimens were measured to compare with the fossil specimens, which seem to have undergone some decay. It is apparent that there is quite a high degree of variability amongst extant specimens of this species.

DISCUSSION

How should fossils that are morphologically very similar to, or in fact indistinguishable from, extant representatives be treated taxonomically?

Obviously the biological species concept (e.g. Mayr, 1969; Willmann, 1985; Ax, 1988) is impossible to apply to fossil specimens and is often extremely problematic even with extant species. So, we are dependent on morphological characters in an attempt to discriminate amongst members of different species. One very important factor is the variability of extant specimens.

After comparing the fossil *Micromalthus* specimens from Dominican amber with 24 extant specimens (see description above and Table 2), we were not able to determine any morphological characteristics that distinguish the fossils from extant representatives of *M. debilis* considering the variability of extant species.

The two characters used by Perkovsky (2008) to distinguish *Micromalthus anasi* from *M. debilis* are either undeterminable or fall within the variability of fossil and extant specimens of *M. debilis*. Perkovsky (2008) stated that the fore and mid femora of *M. anasi* are more than 2.5 times longer than the associated coxae, whereas in *M. debilis* they are not more than 1.5 times longer. In fact, the femora of the fore and mid legs in both the extant and fossil specimens are approximately two times longer than the associated coxae. That also applies to the holotype of *M. anasi*.

According to Perkovsky (2008), the antennae are significantly longer in *M. anasi* than in *M. debilis*. He states that in *M. anasi* 'The antennae extend beyond the base of the prothorax.' (Perkovsky, 2008: 626), whereas in *M. debilis* '... the antennae extend only slightly beyond the apex of the prothorax...' (Perkovsky, 2008: 627). It is correct that the antennae of this amber specimen are comparatively long in absolute values. Nevertheless, they would not even reach the posterior margin of the pronotum in the holotype of *M. anasi* but the antennae do reach beyond the anterior margin of the pronotum in all other investigated specimens of *M. debilis*, fossil or extant.

If one also takes taphonomically induced deformations (Fig. 3A, C) into account that quite regularly

seem to occur in amber specimens, then these characters are not suitable to diagnose a new species.

Considering all preserved characters and the observable taphonomic deformations, the specimen Do-632-K from Dominican amber (Fig. 4; Perkovsky, 2008) falls within the variability of other Dominican

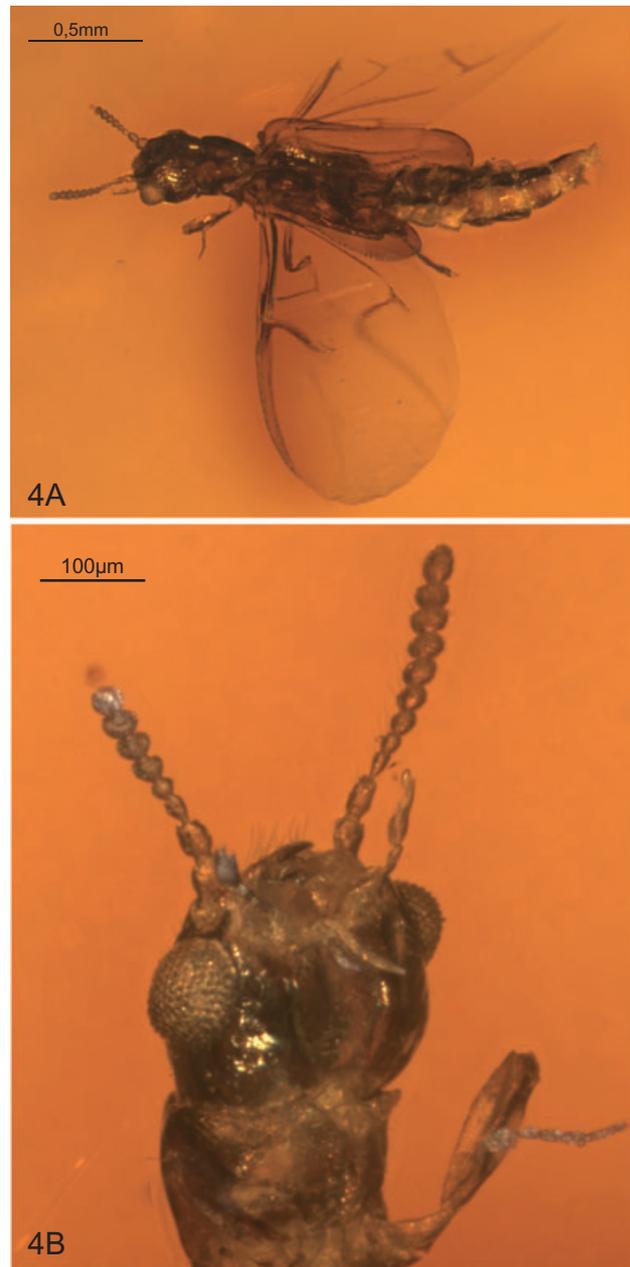


Figure 4. Photographs of holotype of *Micromalthus anasi* Perkovsky, 2008, now considered a junior synonym of *Micromalthus debilis*. A, dorsolateral view. Distal half of right wing missing. (Courtesy of Karin Wolf-Schwenninger, Staatliches Museum für Naturkunde, Stuttgart, Germany.) B, ventrolateral view of prothorax and head. Three apical antennomeres of the right antenna missing.

amber specimens, as well as extant species. Therefore there is no justification for establishing a new species for any known Dominican amber fossils of *Micromalthus*. We therefore consider *M. anasi* Perkovsky, 2008 a junior synonym of *M. debilis* LeConte, 1878.

With the species of *Micromalthus* from Eocene French amber that will be described by Kirejtshuk *et al.* (in press) the situation is slightly different. Even though the morphological characteristics are extremely similar to extant and Dominican amber specimens, the two available Paris amber specimens are significantly larger. Although size differences alone do not necessarily indicate a separate species, it is possible the French amber specimens are different and therefore we suggest that this species be retained.

FOSSIL RECORDS OF MORPHOLOGICALLY UNCHANGED INSECT SPECIES

Without morphological differences between extant and fossil specimens, and accepting the present age determination, the question arises: how long can insect species survive?

The record for morphological stasis is apparently held by the living crustacean species, *Triops cancriformis* (Bosc, 1801), which is known from morphologically indistinguishable fossils dating from the Upper Triassic more than 200 Mya (Eldredge, 1984; Kelber, 1999).

Although insect species can exist for several million years, the average duration has been suggested to range from two to three million years (Poinar & Milki, 2001) or three to ten million years (Grimaldi & Engel, 2005). Records much older than this hitherto have been suspected to be the result of imprecise comparisons of fossil and living specimens or of incorrect age determination of the fossils. However, insufficiently detailed comparison is a factor that can be excluded in the case of the Dominican amber specimens of *M. debilis*.

A literature survey reveals that a number of fossil insect specimens, mostly from amber, have been described as morphologically indistinguishable from and consequently conspecific with extant species. The age of these fossils ranges from 10 000-year-old Ice Age specimens to amber and sediment fossils dated between 15 and 45 Mya (Table 3).

One example is the extant staphylinid beetle *Micropeplus dokuchaevi* Rjaburkhin, 1991. Extant populations occur in Siberia, whereas subfossil and fossil specimens also occur in middle Pleistocene (c. 1.5 Mya) Britain to upper Miocene (c. 5.7 Mya) Alaska (Coope, 1995). It is obvious that the Ice Age and even younger pre-Ice Age specimens, belong to the same extant species, but the older fossils are more controversial. The re-analysis of a tiger beetle (Cicindelinae)

inclusion in Baltic amber recorded by Horn (1906) as belonging to the extant species *Tetracha carolina* (Linnaeus, 1767) is most likely not the case. Röschmann (1999) compared the fossil in question with several extant specimens of the supposed species and found significant differences, which indicate that the fossil should not be considered as an extant species. Perhaps some of the records of extant species listed in Table 3 would be untenable after careful revision, but this is beyond the scope of this paper.

However, if environmental conditions remain stable, morphologically well adapted species could retain a reproductive advantage over genetically modified offspring, thereby keeping the modified genes constantly low in the gene pool of the species. This might have been the scenario with *M. debilis*.

CONSTANT ENVIRONMENTAL CONDITIONS FOR *MICROMALTHUS DEBILIS*

In the case of *M. debilis*, the critical environmental conditions might have been constant for an extended period. This beetle occupies a very special ecological niche. The peculiar and complex life cycle of *M. debilis* occurs in dead wood of a wide range of trees decayed by red-rot fungi (Pollock & Normark, 2002; Hörnschemeyer, 2005). The mature timber habitat is an important component of forest ecosystems and offers ecological niches for a wide range of species (e.g. Grove, 2002). It can be assumed that this habitat remained more or less unchanged since the existence of deciduous and coniferous forests; i.e. since the middle Cretaceous for deciduous trees and significantly earlier for conifers (e.g. Nabors, 2007). In the life cycle of *M. debilis* (Fig. 5), there are two different types of parthenogenesis ('virgin birth'), both of which have their origin in the so-called paedogenetic larva. In one pathway, the larva lays one egg, which then develops into a male beetle. In the other cycle a paedogenetic larva gives birth to about ten small larvae of the triungulin type, which are very agile and can disperse easily in the decaying wood. The triungulin larva passes through an unknown number of moults to become the cerambycoid larva, which may develop into a female beetle. But more often, this cerambycoid larva moults into a paedogenetic larva, and the cycle of larval reproduction starts anew.

To date it is not known for certain whether the adult beetles can reproduce successfully. It may be that reproduction and also dispersal of *M. debilis* is completely dependent on the larval stages. In this case, the very small triungulin larva could cling to other larger flying insects as a means of transport to another decaying log, a behaviour known as phoresy (Wheeler, 1919; Clausen, 1976; Hörnschemeyer, 2005). Confirmation that this type of development

Table 3. Records of fossil insects considered to be conspecific with extant species (this list probably is not exhaustive)

Taxa	Source or fossil site	Age (million years)	Reference
Various beetles	Great Britain	0.1 to ~1	Coope (1995)
Various ants and beetles	Peary Land (Greenland)	~2	Böcher (1989)*
Odonata: Aeshnidae: probably <i>Sarasaeschna pryeri</i> (Martin, 1909)	Kazusa (Japan)	~2	Esaki & Asahina (1957)
Coleoptera: Staphylinidae: <i>Micropeplus tessera</i> Curtis, 1828; <i>Micropeplus dokuchaevi</i> Rjaburkhin, 1991; possibly <i>Kalissus nitidus</i> LeConte, 1874	Lava Camp (Alaska, USA)	5.7	(Matthews 1970*, 1977; Coope 1995, 2004)
Odonata: Aeshnidae: possibly <i>Anax imperator</i> Leach, 1815, possibly <i>Anax parthenope</i> Selys, 1839	Monte Castellaro (Italy)	6	Gentilini & Peters (1993)
Coleoptera: Carabidae: <i>Asaphidion alaskanum</i> Wick, 1919; Staphylinidae: <i>Micropeplus sculptus</i> LeConte, 1863	Meighen Island, Banks Island (Canada)	~6 to 8	Matthews (1977)
Sternorrhyncha: Aphidoidea: <i>Longistigma caryae</i> (Harris, 1841)	Mókollsdal (Iceland)	~5 to 10	Heie & Friedrich (1971)*
Coleoptera: Dytiscidae: <i>Hydaticus laevipennis</i> Thomson, 1867; <i>Hydaticus transversalis</i> (Pontoppidan, 1763)	Przeworno (Poland)	~10	Galewski & Glazek (1973, 1977)
Strepsiptera: <i>Bohartilla megalognatha</i> Kinzelbach, 1969	Dominican amber	~20	Kathirithamby & Grimaldi (1993)
Coleoptera: Tenebrionidae: <i>Lorelus wolcottii</i> Doyen, 1993	Dominican amber	~20	Doyen & Poinar (1994)
Trichoptera: <i>Ochrotrichia aldama</i> (Mosely, 1937)	Dominican amber	~20	Wells & Wichard (1989)
Coleoptera: <i>Micromalthus debilis</i> LeConte, 1878; Larvae	Mexican amber	~20	Rozen (1971)*
Psocoptera: <i>Belaphotroctes ghesquierei</i> Badonnel, 1949	Mexican amber	~20	Mockford (1972)*
Hymenoptera: Scelionidae: <i>Paleogryon muesebecki</i> Masner, 1969	Mexican amber	~20	Masner (1969)*
Hymenoptera: Mymaridae: <i>Alaptus psocidivorus</i> Gahan, 1927; possibly <i>A. globosicornis</i> Girault, 1912	Mexican amber	~20	Doutt (1973)
Coleoptera: Chrysomelidae: possibly <i>Plateumaris nitida</i> (Germar, 1811)	Florissant (USA)	35	Askevold (1990)*
Diptera: Nemestrinidae: possibly <i>Neorhynchocephalus volaticus</i> (Williston, 1883)	Florissant (USA)	35	Bequaert & Carpenter (1936)
Hymenoptera: Mymaromatidae: <i>Petiolaria anomala</i> Blood & Kryger, 1922	Baltic amber	~45	Bakkendorf (1948)
Hymenoptera: Mymaridae: <i>Palaeomyrmar duisburgi</i> (Stein, 1877)	Baltic amber	~45	Doutt (1973)*
Diptera: Chironomidae: <i>Buchonomyia thienemanni</i> Fittkau, 1955	Baltic amber	~45	Murray (1976)
Ephemeroptera: Heptageniidae: <i>Heptagenia (Kageronia) fuscogrisea</i> (Retzius, 1783)	Baltic amber	~45	Klyuge (1986)
Coleoptera: Leiodidae: <i>Nemadus colonoides</i> (Kraatz, 1851)	Baltic amber	~45	Jeannel (1942)
Hemiptera: Gerridae: <i>Limnopus rufoscutellatus</i> species group	British Columbia (Canada)	50	Möller Andersen, Spence & Wilson (1993)

(*also mentioned in Grimaldi & Engel, 2005: 642).

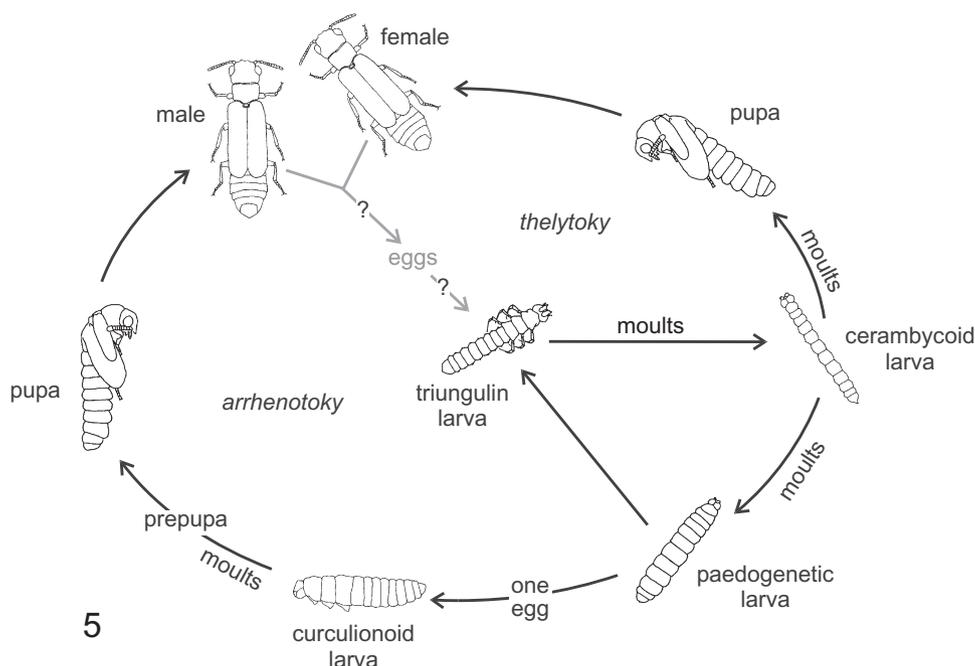


Figure 5. Life cycle of *Micromalthus debilis*.

is ancient is shown by *Micromalthus* larvae from Miocene Mexican amber (Rozen, 1971) and Eocene Baltic amber (Lawrence & Newton, 1995). The larvae most likely feed on fungi in the rotten wood. This remarkable life cycle entails a very efficient usage of resources and the species is well protected against potential predators. Obviously, *M. debilis* was able to survive with this life style for millions of years.

ACKNOWLEDGEMENTS

Our study was supported by Klaus Klass (Staatliches Museum für Naturkunde, Dresden, Germany) and Kristin B. Simpson (Wilbur R. Enns Entomology Museum, University of Missouri, Columbia, USA) through the loan of extant specimens of *M. debilis*, and by M. Alejandra Perotti (University of Wales at Bangor, UK) who relinquished valuable specimens from her laboratory culture. We also thank Mike Ivy (Montana State University at Bozeman, USA) for the loan of a Dominican amber fossil, Günther Bechly (Staatliches Museum für Naturkunde, Stuttgart, Germany) for allowing the study of the holotype of *M. anasi*, and David Haas (Museum of Paleontology, University of California at Berkeley, California, USA) for the loan of the Mexican amber *Micromalthus* larvae. Many thanks to Alexander G. Kirejtshuk for providing us with information from a manuscript in press. We also would like to thank two anonymous referees for their comments and suggestions.

REFERENCES

- Askevold IS. 1990.** Classification of Tertiary fossil Donaciinae of North America and their implications about evolution of Donaciinae (Coleoptera: Chrysomelidae). *Canadian Journal of Zoology* **68**: 2135–2145.
- Ax P. 1988.** *Systematik in der Biologie*. Stuttgart: Gustav Fischer Verlag.
- Bakkendorf O. 1948.** A comparison of a Mymarid from Baltic Amber with a recent species, *Petiolaria anomala* (Micro-Hym.). *Entomologische Meddelelser* **25**: 213–218.
- Barber HS. 1913a.** The remarkable life-history of a new family (Micromalthidae) of beetles. *Proceedings of the Biological Society of Washington* **26**: 185–190.
- Barber HS. 1913b.** Observations on the life history of *Micromalthus debilis* Lec. (Coleoptera). *Proceedings of the Entomological Society of Washington* **15**: 31–38.
- Bequaert JC, Carpenter FM. 1936.** The Nemestrinidae of the Miocene of Florissant, Colorado, and their relations to the recent fauna. *Journal of Palaeontology* **10**: 395–409.
- Beutel RG, Gea S, Hörnschemeyer T. 2007.** On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. *Cladistics* **23**: 1–29.
- Beutel RG, Haas F. 2000.** Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* **16**: 102–141.
- Beutel RG, Hörnschemeyer T. 2002.** Larval morphology and systematic position of *Micromalthus debilis* LeConte, 1878 (Coleoptera, Micromalthidae). *Systematic Entomology* **27**: 169–190.
- Böcher J. 1989.** Boreal insects in northernmost Greenland: palaeontological evidence from the Kap Kobenhavn

- Formation (Plio-Pleistocene), Peary Land. *Fauna Norvegica, Series B* **36**: 37–43.
- Borror DJ, Triplehorn CA, Johnson NF. 1992.** *An introduction to the study of insects*. Fort Worth, TX: Harcourt Brace College Publishers.
- Bosc LAG. 1801.** *Histoire naturelle des coquilles, contenant leur description, les mœurs des animaux qui les habitent et leurs usages*. Paris: Deterville.
- Clausen CP. 1976.** Phoresy among entomophagous insects. *Annual Review of Entomology* **21**: 343–368.
- Coope GR. 1995.** Insect faunas in ice age environments: why so little extinction? In: Lawton JH, May RM, eds. *Extinction rates*. Oxford: Oxford University Press, 54–74.
- Coope GR. 2004.** Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability? *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences* **359**: 209–214.
- Costa C, Vanin SA, Casari-Chen SA. 1988.** *Larvas de Coleoptera do Brazil*. Sao Paulo: Muse de Zoologia, Univ. de Sao Paulo.
- Crowson RA. 1981.** *The biology of Coleoptera*. London: Academic Press.
- Doutt RL. 1973.** The Fossil Mymaridae (Hymenoptera: Chalcidoidea). *The Pan-Pacific Entomologist* **49**: 221–228.
- Doyen JT, Poinar GO. 1994.** Tenebrionidae from Dominican amber (Coleoptera). *Entomologica Scandinavica* **25**: 27–51.
- Eldredge N. 1984.** Simpson's inverse: bradytely and the phenomenon of living fossils. In: Eldredge N, Stanley SM, eds. *Living fossils*. New York: Springer Verlag, 272–277.
- Esaki T, Asahina S. 1957.** On two tertiary dragonfly species from the Ôya-formation in Kazusa, Nagasaki Prefecture. *Kontyu* **25**: 82–86.
- Galewski K, Glazek J. 1973.** An unusual occurrence of the Dytiscidae (Coleoptera) in the siliceous flowstone of the Upper Miocene cave at Przeworno, Lower Silesia, Poland. *Acta Geologica Polonica* **23**: 445–461.
- Galewski K, Glazek J. 1977.** Upper Miocene Dytiscidae (Coleoptera) from Przeworno (Lower Silesia) and the problem of Dytiscidae evolution. *Bulletin de L'Academie Polonaise des Sciences, Série des sciences biologiques Classe II* **25**: 781–789.
- Gentilini G, Peters G. 1993.** The upper Miocene Aeshnids of Monte Castellaro, Central Italy, and their relationships to extant species (Anisoptera: Aeshnidae). *Odonatologica* **22**: 147–178.
- Grimaldi D, Engel MS. 2005.** *Evolution of the insects*. Cambridge, New York: Cambridge University Press.
- Grove SJ. 2002.** Saproxyllic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* **33**: 1–23.
- Heie OE, Friedrich WL. 1971.** A fossil specimen of the North American hickory aphid (*Longistigma caryae* Harris), found in tertiary deposits in Iceland. *Entomologica Scandinavica* **2**: 74–80.
- Horn W. 1906.** Ueber das Vorkommen von *Tetracha carolina* L. im preussischen Bernstein und die Phylogenie der *Cicindela*-Arten. *Deutsche Entomologische Zeitschrift* **2**: 329–336.
- Hörschemeyer T. 1998.** Morphologie und Evolution des Flügelgelenks der Coleoptera und Neuropterida. *Bonner Zoologische Monographien* **43**: 1–126.
- Hörschemeyer T. 2005.** Archostemata. In: Beutel RG, Leschen R, eds. *Handbook of Zoology Coleoptera*, Vol. 1. Berlin: de Gruyter, 29–42.
- Iturralde-Vinent MA. 2001.** Geology of the amber-bearing deposits of the Greater Antilles. *Caribbean Journal of Science* **37**: 141–167.
- Iturralde-Vinent MA, MacPhee RDE. 1996.** Age and paleogeographical origin of Dominican amber. *Science* **273**: 1850–1852.
- Jäch MA, Komarek A. 2000.** Bemerkenswerte Käferfunde aus Österreich (IX) (Coleoptera: Micromalthidae et Dytiscidae). *Koleopterologische Rundschau* **70**: 223–224.
- Jeannel R. 1942.** *La Genèse des Faunes terrestres*. Éléments de Biogéographie. Paris: Presses Universitaires de France.
- Kathirithamby J, Grimaldi D. 1993.** Remarkable stasis in some Lower Tertiary parasitoids: descriptions, new records, and review of Strepsiptera in the Oligo-Miocene amber of the Dominican Republic. *Entomologica Scandinavica* **24**: 31–41.
- Kelber K-P. 1999.** *Triops cancriformis* (Crustacea, Notostarcia): Ein bemerkenswertes Fossil aus der Trias Mitteleuropas. In: Hauschke N, Wilde V, eds. *Trias. Eine ganz andere Welt*. München: Verlag Dr. Friedrich Pfeil, 355–370.
- Kirejtshuk AG, Nel A, Colomb FA.** in press. New Archostemata (Insecta, Coleoptera) from the French Palaeocene and Early Eocene, with a note on composition of the suborder. *Annales de la Société Entomologique de France* **45**.
- Klyuge NY. 1986.** A recent mayfly species (Ephemeroptera, Heptageniidae) in Baltic amber. *Paleontological Journal* **20**: 106–107.
- Lawrence JF. 1982.** Coleoptera. In: Parker SP, ed. *Synopsis and classification of living organisms*, Vol. 2. New York: McGraw-Hill, 482–553.
- Lawrence JF, Newton AF. 1995.** Families and subfamilies of Coleoptera. In: Pakaluk J, Slipinski SA, eds. *Biology, phylogeny, and classification of Coleoptera*, Vol. 1. Warszawa: Muzeum i Institut Zoologii PAN, 779–1006.
- LeConte JL. 1878.** The Coleoptera of Michigan. 1. Descriptions of new species. *Proceedings of the American Philosophical Society, Philadelphia* **17**: 593–648.
- Linnaeus C. 1767.** *Systema naturae*. Tom. I. Pars II. Editio duodecima, relormata. Stockholm: Laurentii Salvii.
- Marshall AT, Thornton WB. 1963.** *Micromalthus* (Coleoptera: Micromalthidae) in Hong Kong. *Pacific Insects* **5**: 715–720.
- Masner L. 1969.** A Scelionid wasp surviving unchanged since Tertiary (Hymenoptera: Proctotrupoidea). *Proceedings of the Entomological Society of Washington* **71**: 397–400.
- Matthews JV. 1970.** Two new species of *Micropeplus* from the Pliocene of western Alaska with remarks on the evolution of Micropeplinae (Coleoptera: Staphylinidae). *Canadian Journal of Zoology* **48**: 779–788.
- Matthews JV. 1977.** Tertiary Coleoptera fossils from the North American Arctic. *The Coleopterists Bulletin* **31**: 297–308.

- Mayr E. 1969.** The biological meaning of species. *Biological Journal of the Linnean Society* **1**: 311–320.
- Mockford EL. 1972.** New species, records, and synonymy of Florida *Belaphotroctes* (Psocoptera: Liposcelidae). *Florida Entomologist* **55**: 153–163.
- Murray DA. 1976.** *Buchonomyia thienemanni* Fittkau (Diptera, Chironomidae), a rare and unusual species recorded from Killarney. *Ireland Entomologist's Gazette* **27**: 179–180.
- Möller Andersen N, Spence JR, Wilson MVH. 1993.** 50 Million Years of Structural Stasis in Water Striders (Hemiptera: Gerridae). *American Entomologist* **39**: 174–176.
- Nabors MW. 2007.** *Botanik*. Munich: Pearson Studium.
- Paterson NF. 1938.** Note on the external morphology of South African specimens of *Micromalthus* (Coleoptera). *Transactions of the Royal Entomological Society of London* **87**: 287–290.
- Perkovsky EE. 2008.** On the find of adult *Micromalthus* (Coleoptera, Micromalthidae) in Dominican Amber. *Paleontological Journal* **41**: 626–628.
- Philips TK. 2001.** A record of *Micromalthus debilis* (Coleoptera: Micromalthidae) from Central America and a discussion of its distribution. *Florida Entomologist* **84**: 159–160.
- Philips TK, Young DK. 2001.** Micromalthidae Barber, 1913. In: Ross HA Jr, Thomas MC, eds. *American beetles*, Vol. 1. Washington: CRC Press, 22–23.
- Poinar GO, Milki R. 2001.** *Lebanese amber: the oldest insect ecosystem in fossilized resin*. Corvallis: Oregon State University Press.
- Pollock DA, Normark BB. 2002.** *Micromalthus debilis* LeConte (Coleoptera: Micromalthidae): life cycle and evolutionary considerations. *Journal of Zoological Systematics and Evolutionary Research* **40**: 105–112.
- Pringle JA. 1938.** A contribution to the knowledge of *Micromalthus debilis* LeC. (Coleoptera). *Transactions of the Royal Entomological Society of London* **87**: 271–287.
- Rjaburkhin AS. 1991.** A new species of *Micropeplus* (Coleoptera, Micropeplidae) from the North-East of the USSR. *Zoologičeskij žurnal* **70**: 151–153.
- Rozen JG. 1971.** *Micromalthus debilis* Leconte from amber of Chiapas, Mexico (Coleoptera: Micromalthidae). *University of California Publications in Entomology* **63**: 75–76.
- Röschmann F. 1999.** Revision of the evidence of *Tetracha carolina* (Coleoptera, Cicindelidae) in Baltic amber (Eocene-Oligocene). *Estudios del Museo de Ciencias Naturales de Álava* **14**: 205–209.
- Scholtz CH, Holm E. 1985.** *Insects of Southern Africa*. Pretoria: University of Pretoria.
- Scott AC. 1936.** Haploidy and aberrant spermatogenesis in a Coleoptera, *Micromalthus debilis* LeConte. *Journal of Morphology* **59**: 485–509.
- Scott AC. 1938.** Paedogenesis in the Coleoptera. *Zeitschrift für Morphologie und Ökologie der Tiere* **33**: 633–653.
- Solórzano Kraemer MM. 2007.** Systematic, palaeoecology, and palaeobiogeography of the insect fauna from Mexican amber. *Palaeontographica A* **282**: 1–133.
- Swezey OH. 1940.** *Micromalthus debilis* LeConte in Hawaii. (Coleoptera: Micromalthidae). *Proceedings of the Hawaiian Entomological Society* **10**: 459.
- Wallace FL, Fox RC. 1975.** A comparative morphological study of the hindwing venation of the order Coleoptera, Part I. *Proceedings of the Entomological Society of Washington* **77**: 329–354.
- Wells A, Wichard W. 1989.** Caddisflies of Dominican Amber VI. Hydroptilidae (Trichoptera). *Studies on Neotropical Fauna and Environment* **24**: 41–51.
- Wheeler WM. 1919.** The phoresy of *Antherophagus*. *Psyche* **26**: 145–152.
- Willmann R. 1985.** *Die Art in Raum und Zeit. Das Artkonzept in Biologie und Paläontologie*. Berlin: Parey.