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RESEARCH PAPER

Have ladybird beetles and whiteflies co-existed for at least 40 Mya?

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Abstract

The beetle family Coccinellidae is rarely recorded from fossils. Most of the records come from the nineteenth and beginning of the twentieth century. A complete list of Coccinellidae records from Baltic amber is presented and discussed. Extensive literature research provided a surprising conclusion that not a single species of Coccinellidae has been formally described from Baltic amber till now. The first two species of ladybird beetles from Eocene Baltic amber are described and placed in the genus *Serangium*, namely *S. twardowskii* sp. nov. and *S. gedanicum* sp. nov. Their phylogenetic placement in the subfamily Microweiseinae is provided. A key to the fossil species of *Serangium* is given. Extant representatives of the genus are distributed mainly in tropical areas of Asia and Oceania, and are specialised predators of whiteflies. Current discovery shows that during the Middle Eocene, the genus *Serangium* was distributed wider in the Northern Hemisphere and the evolution of these ladybird beetles was probably influenced by the evolution of whiteflies which are also found in the Baltic amber.

Keywords Coccinelloidea · *Serangium* · Fossil · New species · Systematics

Introduction

Systematic background

Ladybird beetles (Coccinellidae Latreille, 1807) constitute a well-defined family within Coccinelloidea Latreille, 1807 (formerly part of Cucujoidea Latreille, 1802). Its monophyly is supported by morphological (Ślipiński 2007) and molecular data analyses (Seago et al. 2011; Robertson et al. 2015). Coccinellidae form a very diverse and species-rich group (ca. 6000 species worldwide) with numerous species important from an economical point of view. However, they have various food preferences (Giorgi et al. 2009); most of them are predators of sternorrhynchous hemipterans, such as whiteflies, aphids, and scale insects (Hemiptera: Sternorrhyncha).

Traditionally, based on morphological data, Coccinellidae were divided into several subfamilies (Sasaji 1968; Kovář 1996), but molecular analyses proved these classifications to be artificial (Giorgi et al. 2009; Magro et al. 2010; Seago et al. 2011; Robertson et al. 2015). Ślipiński (2007) proposed division of Coccinellidae into two subfamilies, Microweiseinae Leng, 1920 and Coccinellinae Latreille, 1807. Microweiseinae forms a small group including mostly cryptic, pubescent beetles that more closely resemble Endomychidae Leach, 1815 or Corylophidae LeConte, 1852, the 'true' lady beetles. Remaining taxa are included in the large subfamily Coccinellinae. This division into two subfamilies was confirmed by molecular data (Seago et al. 2011; Robertson et al. 2015). Subfamily Microweiseinae was recently revised by Escalona and Ślipiński (2012), and currently includes 25 genera (with about 150 species described) grouped in 3 tribes: Carinodulini Gordon, Pakaluk et Ślipiński, 1989, Microweiseini Leng, 1920 and Serangiini Pope, 1962 (Escalona and Ślipiński 2012; Wang and Ren 2012; Jałoszyński and Ślipiński 2014).

Serangiini Pope, 1962 consists of four extant genera: *Serangium* Blackburn, 1889, *Delphastus* Casey, 1899, *Serangiella* Chapin, 1940 and recently described *Pangia*

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Wang and Ren, 2012. The tribe is characterised by: prosternum elevated, forming a large triangular plate with its anterior covering anterior margin of clypeus in repose; ventral side, including epipleura deeply foveate, receiving folded legs; five-segmented abdomen with ventrite 5 as long as ventrites 2–4 combined; and antenna with flattened one-segmented antennal club. Currently, Serangiini representatives inhabit tropical regions mostly with a few taxa in more temperate regions: *Delphastus* (New World); *Pangia*, *Serangium* and *Serangiella* (Old World, mostly Asia and Australia). Serangiini are well-known whitefly (Aleyrodidae) predators. Some of them are used as biological agents against such pests like citrus blackfly *Aleurocanthus woglumi* Ashby, 1915, silverleaf whitefly *Bemisia* spp., citrus whitefly *Dialeurodes* spp. and many others (Escalona and Ślipiński 2012).

Fossil record of Coccinellidae

Recent molecular phylogenetic reconstructions nest the Coccinelloidea emergence at the Triassic/Jurassic turn (171 Mya, McKenna et al. 2015; 202 Mya, Hunt et al. 2007) or even earlier (252 Mya, Toussaint et al. 2017). The age of the family Coccinellidae is estimated at about 125 Mya (McKenna et al. 2015). Surprisingly, for such relatively old lineage, there is very poor evidence in the fossil record. Ladybird beetles are known only from some Cenozoic sedimentary deposits and recently described three species from Lowermost Eocene amber from Oise in France (Kirejtshuk and Nel 2012). Presence of ladybird beetles in Baltic amber has been mentioned several times (Hope 1836; Berendt 1845; Menge 1856; Helm 1896; Klebs 1910; Larsson 1978; Hieke and Pietrzeniuk 1984). Nevertheless, closer investigation of these records revealed that specimens were assigned to the extant genera of ladybird beetles without any formal description of the taxa. Moreover, all these materials have not been revised and its systematic position in modern beetle classification has not been tested. Below, we present a critical checklist of Baltic amber inclusions of Coccinellidae.

Apart from amber inclusions, an Eocene Coccinellidae fossil was described from Eckfelder Maar in Germany by Wappler (2003), but poor preservation of this specimen hindered its generic assignment.

Materials and methods

Systematic part

For critical checklist of fossil Coccinellidae records, open nomenclature has been applied following Matthews (1973) and Bengtson (1998).

This study is based on a two Baltic amber pieces, of which one has been found in Quaternary amber deposits in the 'Przeróbka' mining area in Gdańsk (Poland); the other was bought from a commercial company. For opinions about Baltic amber age, history of its deposition, and origin, see discussion in supplementary material in Szwedo and Drohojowska (2016).

The material was polished manually with emery papers with different grain sizes and finally lustrated with polishing powder. The specimens were examined and photographed with a Leica M205A stereomicroscope with Leica DM6000 digital camera attached and working under Leica Application Suite LAS 3.7. Terminology used in this paper follows Ślipiński (2007) and Lawrence et al. (2011). Type specimens are deposited in the Museum of Amber Inclusions at the University of Gdańsk (MAIG).

For documentation of amber samples designated as type material and confirmation of their origin (Szwedo and Stroiński 2017), the Fourier transform infrared (FT-IR) spectra were obtained in the Laboratory of the International Amber Association, Gdańsk, Poland, with a Nicolet iS10 spectrometer with an attenuated total reflectance (ATR) accessory. Reference curve numbers in the collection archives serve as the registration number of the specimen, with suffix 'IR'.

Phylogenetic analysis

Taxon sampling and characters used for the phylogenetic analysis follow Escalona and Ślipiński (2012). Additionally, two recently described genera of Microweiseinae were added to the dataset: *Pangia* Wang and Ren, 2012 and *Ruthmuelleria* Jałoszyński and Ślipiński, 2014, with the two fossil species here described. Characters were scored and coded in Mesquite (Maddison and Maddison 2017). Unknown character states were coded with '?'. All characters were unordered and unweighted. The resulting data matrix is enclosed in Supplementary Table S1. Tree searches were conducted in NONA (Goloboff 1999) run within WinClada 1.00.08 (Nixon 2002). Parsimony analyses were performed using the parsimony ratchet (Nixon 1999), under the following settings: 1000 iterations, 10 trees held, 6 characters resampled and ambiguity set to polytomy, concavity (K) value fixed to 10.

Results and systematic palaeontology

Critical checklist of Coccinellidae inclusions in Baltic amber

Several authors mentioned Coccinellidae inclusions in Baltic amber. The first records came from nineteenth century published by Hope (1836), Berendt (1845), Menge (1856) and Helm (1896) and the beginning of the twentieth century by Klebs (1910). More recent publications by Larsson (1878) and Hieke and Pietrzeniuk (1984) mostly repeated previous reports. These authors recorded ladybird beetles from six extant genera: *Coelopterus* Mulsant, *Coccinella* Linnaeus, *Cynegetis* Dejean, *Pharus* Mulsant, *Platynaspis* Redtenbacher and *Scymnus* Kugelann. Additionally, some specimens were listed as Coccinellidae, but without determination of generic placement: Berendt (1845; 2 exx.), Klebs (1910; 2 exx.) Larsson (1974; 4 exx., Copenhagen), Kulicka and Ślipiński (Kulicka and Ślipiński 1996, 3 exx. Warsaw), Kubisz (2000; 1 ex., Kraków).

Order **Coleoptera** Linnaeus, 1758
Suborder **Polyphaga** Emery, 1886
Infraorder **Cucujiformia** Lameere, 1938
Superfamily **Coccinelloidea** Latreille, 1807
Family **Coccinellidae** Latreille, 1807

Genus ***Coccinella*** Linnaeus, 1758

Type species. *Coccinella septempunctata* Linnaeus, 1758.

1836 Coccinella?—Hope: 142 [Listed]; 3 exx.
1836 Coccinella?—Hope: 142 [Listed]; 1 ex.
1845 Coccinella?—Berendt: 56 [Listed]; 5 exx.
1856 *Coccinella*?—Menge: 21 [Short description]
1856 Coccinella—Menge: 23 [Listed, larva]; 1 ex.
1978 Coccinella: Berendt 1845—Larsson: 121 [Listed]
1978 Coccinella?: Menge 1856—Larsson: 121 [Listed, larva]
1984 Coccinella?—Hieke and Pietrzeniuk: 306 [Listed]
2012 Coccinella—Kirejtshuk and Nel: 132 [Listed]

Remarks. Hope (1836) indicated that these three specimens come from amber from India and should be deposited in the Hope collection. The other specimen mentioned separately comes from amber. All the specimens listed were attributed to Berendt as the authority who placed them in the genus *Coccinella*. Menge (1856) indicated that legs are hidden under the body, as in modern *Coccinella*. The other specimens were compared with the genus *Lycoperdina* Latreille, 1807, recently placed in the family Endomychidae Leach, 1815.

Genus ***Scymnus*** Kugelann, 1794

Type species. Scymnus nigrinus Kugelann, 1794.

1845 Scymnus?—?Berendt: 56 [Listed]
1896 Scymnus?—Helm: 230 [Listed]
1910 Scymnus?—Klebs: 238 [Listed]; 4 exx.
1978 Scymnus: Helm 1896—Larsson: 121 [Listed]
1978 Scymnus: Klebs 1910—Larsson: 122 [Listed]
1984 Scymnus?—Hieke and Pietrzeniuk: 306 [Listed]

Remarks. Helm (1896) discussed more the recent ladybird beetles, their feeding strategy, mentioning that the genus *Scymnus* is still present in spruce forests.

Genus ***Coelopterus*** Mulsant and Rey, 1853

Type species. Coelopterus salinus Mulsant and Rey, 1853.

1910 Coelopterus?—Klebs: 238 [Listed]; 2 exx.
1978 Coelopterus: Klebs 1910—Larsson: 122 [Listed]
2012 Coelopterus?—Kirejtshuk and Nel: 131 [Listed]

Genus ***Cynegetis*** Chevrolat in Dejean, 1837

Type species. *Coccinella impunctata* Linnaeus, 1767.

1978 Cynegetis?:—Hieke and Pietrzeniuk: 306 [Listed]

Genus ***Pharus*** Mulsant, 1850

Type species. *Coccinella sexguttata* Gyllenhal, 1808.

1910 cf. *Pharus*?—Klebs: 238 [Listed]; 2 exx.
1978 cf. *Pharus*: Klebs 1910—Larsson: 122 [Listed]
2012Pharus?—Kirejtshuk and Nel: 131 [Listed]

Remarks. In the original list of Klebs (1910), two specimens are mentioned as being similar to *Pharus* or *Coelopterus*. Kirejtshuk and Nel (2012) listed separately both genera as present among Baltic amber inclusions.

Genus ***Platynaspis*** Redtenbacher, 1843

Type species. *Coccinella luteorubra* Goeze, 1777.

1910 cf. *Platynaspis*?—Klebs: 238 [Listed]; 2 exx.
1978 cf. *Platynaspis*: Klebs 1910—Larsson: 122 [Listed]
2012 Platynaspis?—Kirejtshuk and Nel: 131 [Listed]

This extensive literature investigation come up with the surprising conclusion that not a single species of Coccinellidae has been formally described from Baltic amber. Authors just assigned specimens found in Baltic amber to currently existing genera without giving any description or characters. Frequently, these records were copied and multiplied by subsequent authors. The original specimens have never been revised and, without reinvestigation, the taxonomic placement should be treated as rather doubtful. Generic names, mentioned by previous authors, were attributed by Kirejtshuk and Nel (2012) to currently recognised tribes of the

Coccinellidae family based only on its present taxonomic placement. In the light of present investigation, this treatment seems to be premature.

New Coccinellidae from Baltic amber

Order **Coleoptera** Linnaeus, 1758
Suborder **Polyphaga** Emery, 1886
Superfamily **Coccinelloidea** Latreille, 1807
Family **Coccinellidae** Latreille, 1807
Subfamily **Microweiseinae** Leng, 1920
Tribe **Serangiini** Pope, 1962
Genus ***Serangium*** Blackburn, 1889

Type species. Serangium mysticum Blackburn, 1889, by monotypy.

Serangium twardowskii sp. nov.
Figures 1a–g; 3a, c

Etymology. The species is dedicated to Mr. Piotr Twardowski who collected the type specimen.

Holotype. MAIG, no. 5670. Reference IR curves no. MAIG 5670 IR (Fig. 4a, b) and deposited in MAIG. Piece of Baltic amber, transparent yellow, anterior and anterior left part of the inclusion covered with a milky veil. Cuticule black, without any trace of maculation. Amber piece sorted from the amber deposit in 'Przeróbka' in Gdańsk, Poland, collected by Piotr Twardowski, sorted by Błażej Bojarski.

Locality and horizon. Eocene, Lutetian, Baltic amber, Gulf of Gdańsk area (secondary deposit).

Diagnosis. Serangium twardowskii sp. nov. can be distinguished by its elytral margins visible from above throughout (similarly as in *S. magna* Ślipiński and Burckhardt, 2006, but narrower) and glabrous elytral disc with a row of sparse, short setae at the outer margin.

Description. Total length = 1.40 mm, total width = 1.23 mm, elytral length = 1.12 mm, pronotal length = 0.38 mm, pronotal width = 0.88 mm, body width = 0.70 mm. Body oval (Fig. 1b), strongly convex, hemispherical (Fig. 1c); pronotal margins visible from above (Fig. 1b); elytral margins entirely visible. Wings not visible.

Head hypognathous, retracted, not clearly visible. Antenna not visible except antennal club; antennal club one-segmented, elongate oval (Fig. 1d).

Pronotum transverse, covered with punctures, glabrous, shiny; base and lateral margins bordered. Prothoracic hypomeron posteriorly with deep delimited fovea for reception of folded antennae and covering legs. Prosternum large, elevated and prominent anteriorly, forming a broad triangular chin piece concealing mouthparts from below, anteriorly rounded; prosternal process smooth. Mesoventrite with mesoventral process strongly transverse and very short (Fig. 1e), anterior margin with complete raised border; meso-metaventral junction with suture visible, broader than a mesocoxal diameter. Metaventrite transverse, shorter than ventrites 1–4 combined (Fig. 1a); metaventral postcoxal lines joined medially, complete and extending to metanepisternum (Fig. 1g). Scutellar shield small, triangular, glabrous.

Elytral surface covered with punctures, with a row of sparse setae at outer margin (Fig. 1a), elytral disc glabrous, sutural line not present. Epipleura incomplete apically, inclined throughout, reaching about half length of the 5th abdominal ventrite, with foveae to accommodate apices of mid and hind femora, foveae for hind femora shallowly marked.

Abdomen with five ventrites: ventrites 1 and 5 each much longer than ventrites 2 and 3 combined, ventrite 5 rounded, not crenulated, not grooved laterally. Postcoxal lines incomplete, reaching lateral margin of ventrite.

Legs short, not reaching outer margin of elytra; coxae large, about half length of femora; femora, especially profemur, broad, flattened and closely fitting into depression on meso- and metaventrite; tibiae externally angulate medially (Fig. 1g); tarsi four-segmented; tarsal claws toothed at base (Fig. 1f). Sex undetermined. Genitalia not visible.

Serangium gedanicum sp. nov.
Figures 2a–g; 3b, d

Etymology. The specific name is derived from *Gedanum*, the Latin name of Gdańsk.

Holotype. MAIG, no. 5674. Reference IR curves no. MAIG 5674 IR (Fig. 4c, d) and deposited in MAIG. Piece of Baltic amber transparent yellow. Cuticle probably covered with a thin air layer with darker spots imitating true maculation. Inclusion laying in the crack junction. Material from Mr. Jonas Damzen company, www.amberinclusions.eu (Vilnus, Lithuania).

Locality and horizon. Eocene, Lutetian, Baltic amber, Gulf of Gdańsk area (secondary deposit).

Diagnosis. *Serangium gedanicum* sp. nov. can be separated from previous species by its dorsal surface covered with long sparse setae and very narrow lateral margin of elytra.

Description. Total length = 1.23 mm, total width = 1.11 mm, elytral length = 1.04 mm, pronotal length = 0.35 mm, pronotal width = 0.76 mm, body width = 0.68 mm. Body oval,

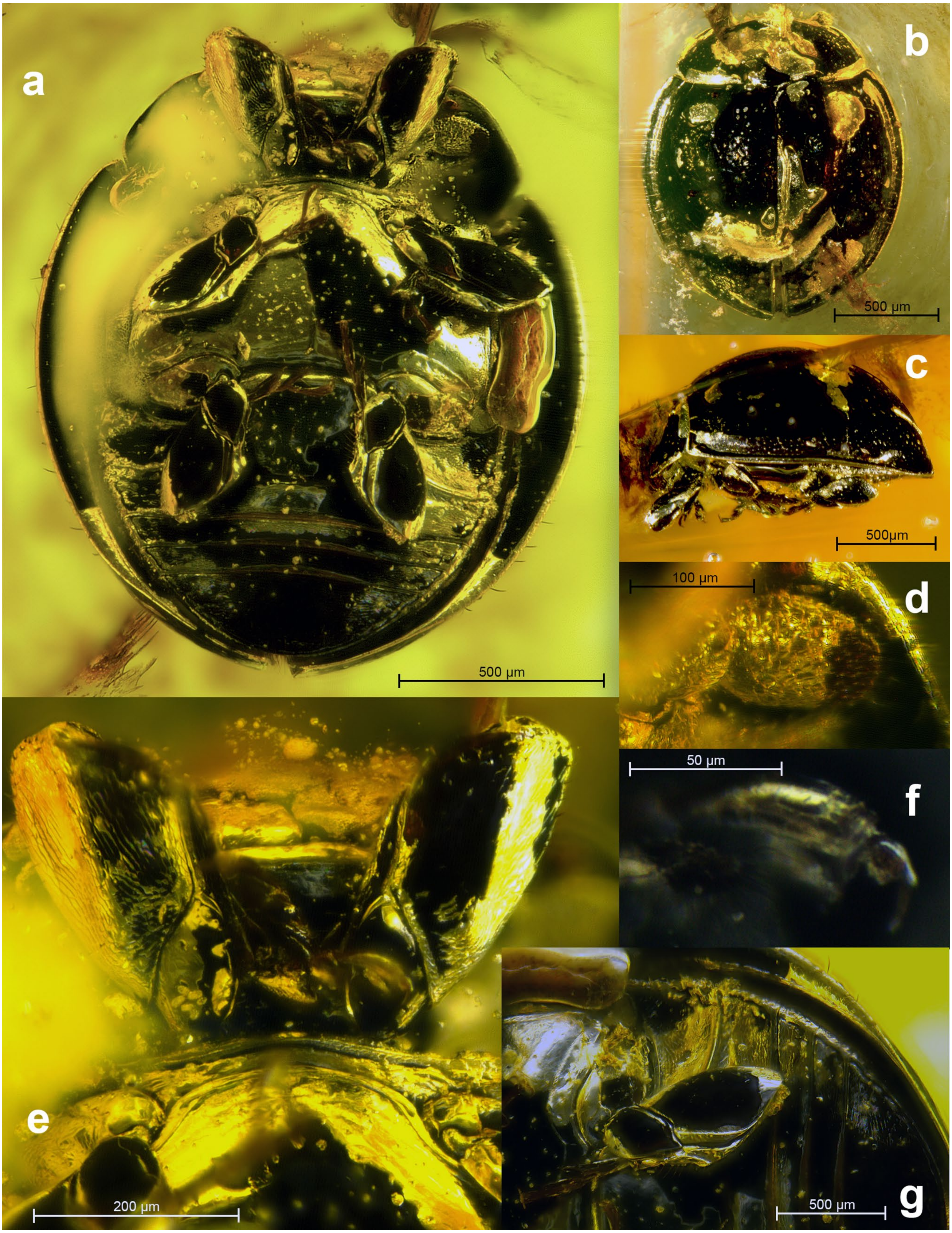

Fig. 1 *Serangium twardowskii* sp. nov., holotype MAIG 5670. **a** Ventral view, **b** dorsal view, *c* lateral view, **d** antennal club, **e** prosternum and mesoventrite, **f** tarsal claw, **g** hind leg and abdominal postcoxal line

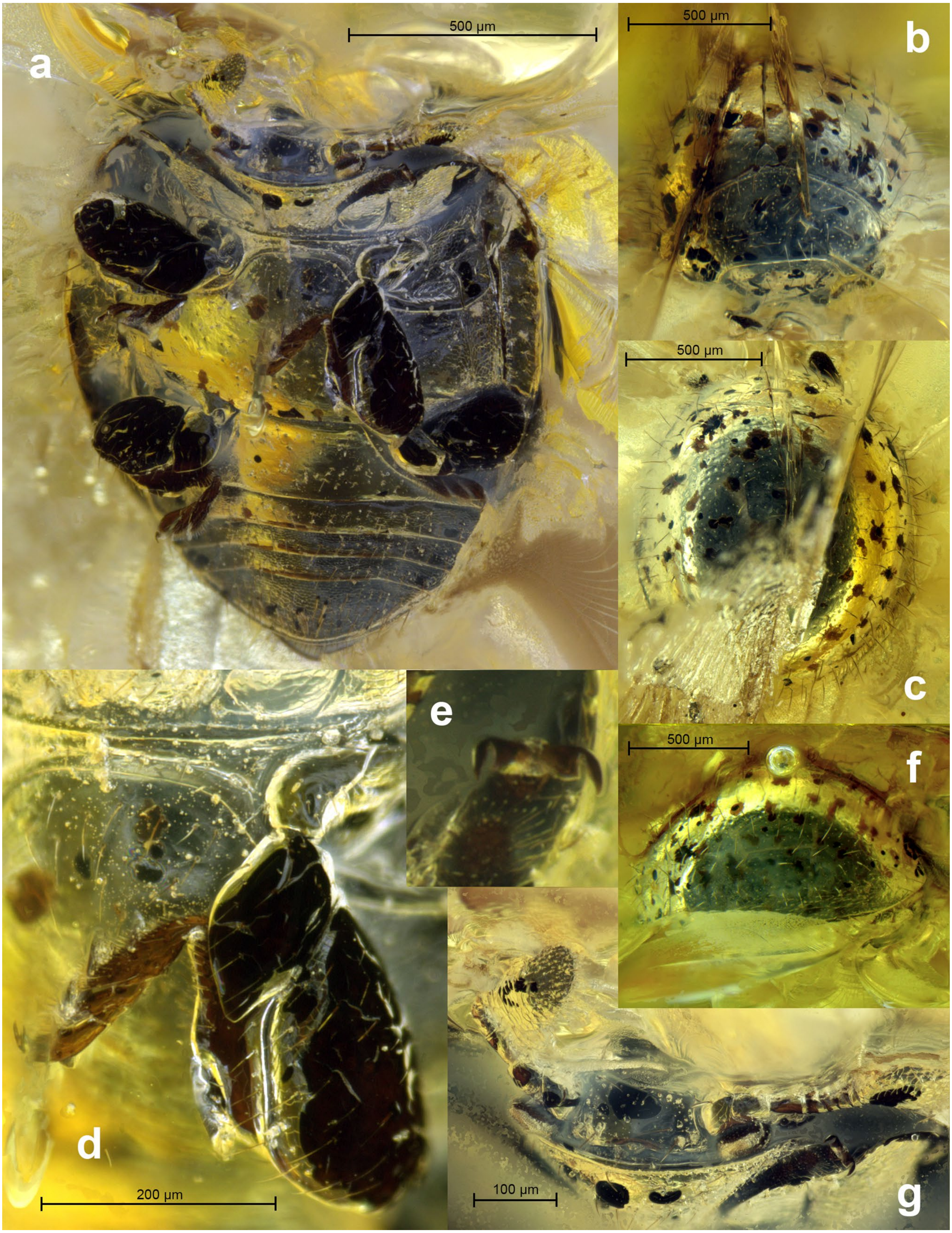

Fig. 2 *Serangium gedanicum* sp. nov. holotype MAIG 5674. **a** Ventral view, **b** pronotum, frontal view, **c** dorsal view, **d** mid-leg, **e** tarsal claw of a foreleg, **f** lateral view, **g** antennae

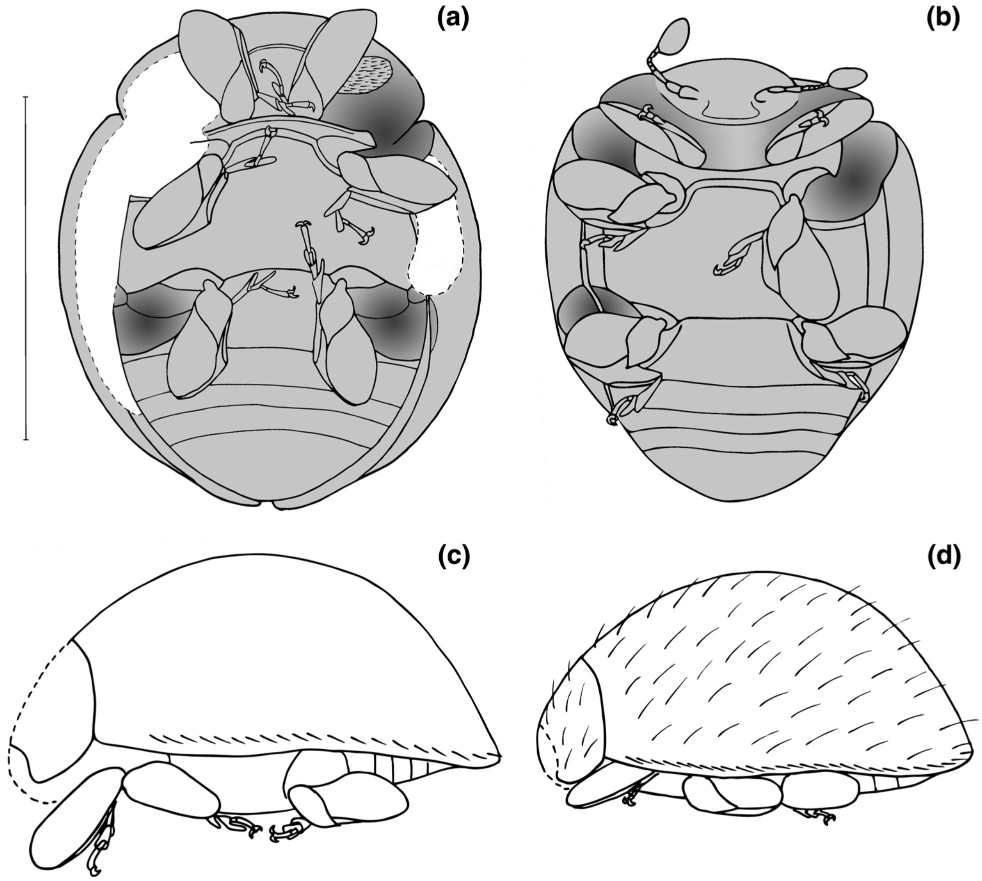

Fig. 3 Drawings of the holotypes of fossil *Serangium* species. **a** *S. twardowskii* sp. nov. ventral, **b** *S. twardowskii* sp. nov. lateral, **c** *S. gedanicum* sp. nov. ventral, **d** *S. gedanicum* sp. nov. lateral

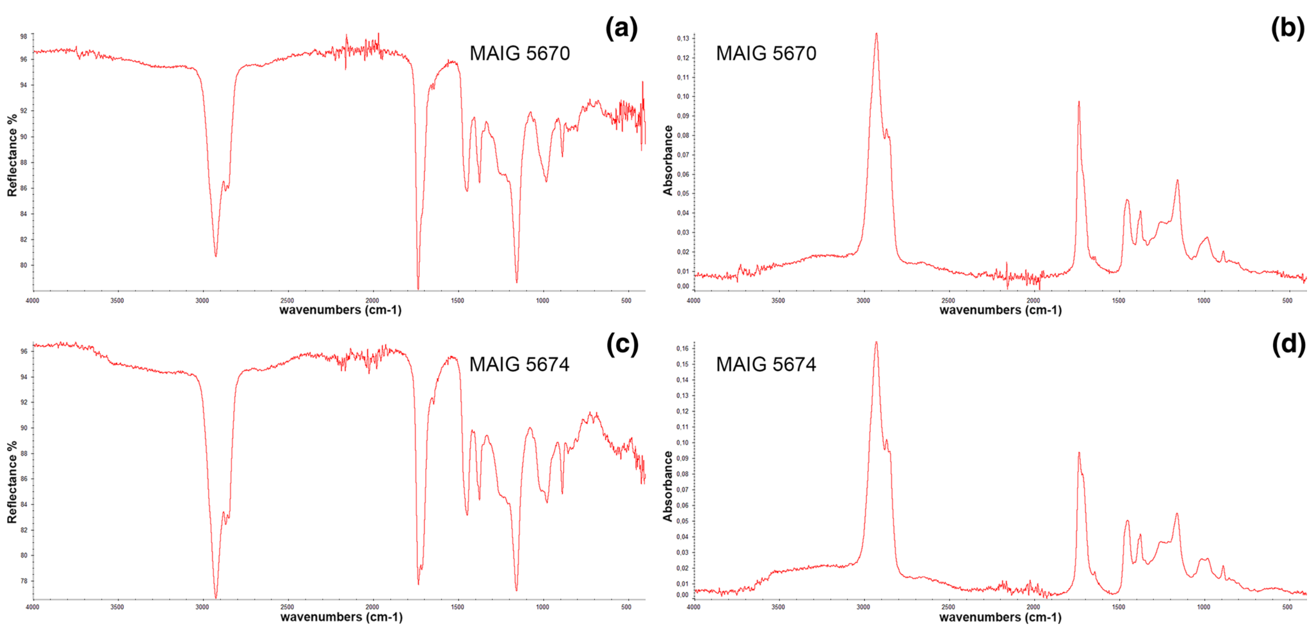

Fig. 4 FT-IR spectra of analysed amber pieces. MAIG 5670: **a** reflectance spectrum, **b** absorbance spectrum, MAIG 5674: **c** reflectance spectrum, **d** absorbance spectrum

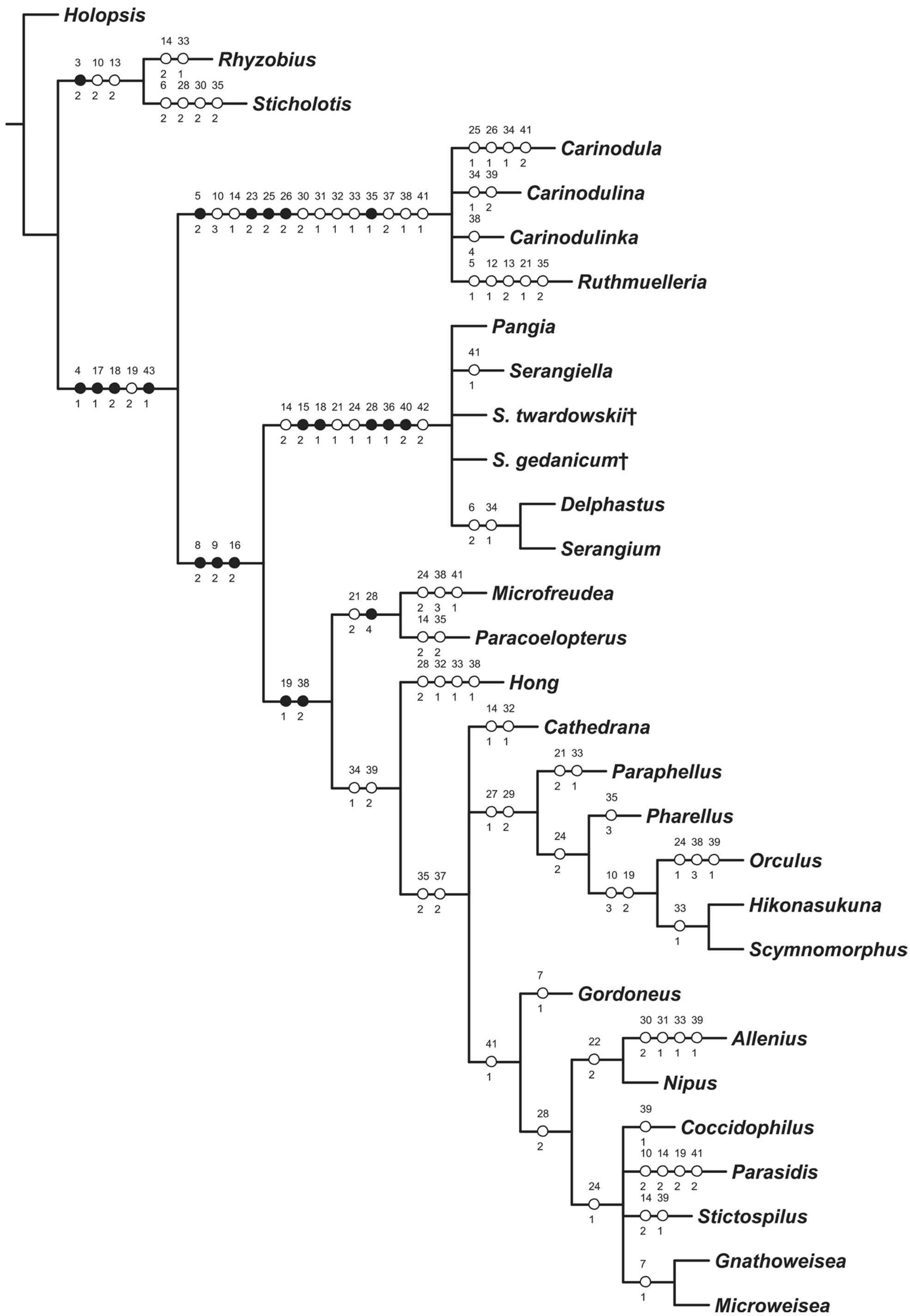

Fig. 5 Morphology-based parsimony analysis of Microweiseinae showing positions of investigated fossil species, (strict consensus tree, L = 121, Ci = 47, Ri = 74), † = extinct

strongly convex, hemispherical (Fig. 2b, c, f); pronotal margins not visible from above (Fig. 2c); elytral margins hardly visible. Wings visible apically.

Head hypognathous, retracted, not clearly visible. Anterior edge of clypeus margined. Antenna with nine antennomeres, antennomere three simple, elongate; antennal club one-segmented, elongate oval (Fig. 2g).

Pronotum transverse, covered with punctures, with sparse, long hair, shiny; base and lateral margins bordered (Fig. 2b). Prothoracic hypomeron posteriorly with deep delimited fovea for reception of folded antennae and covering legs. Prosternum large, elevated and prominent anteriorly, forming a broad triangular chin piece concealing mouthparts from below, anteriorly rounded; prosternal process smooth.

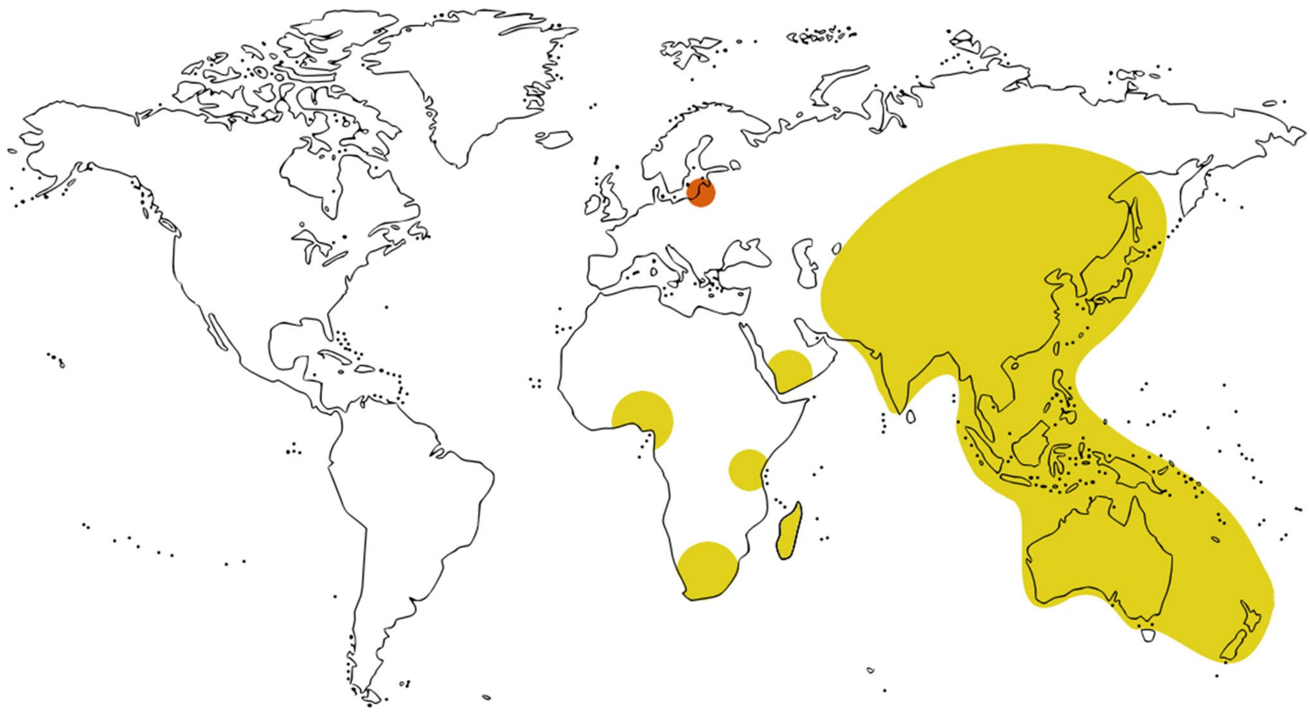

Fig. 6 Current distribution of the genus *Serangium* (yellow) and fossil records from Baltic amber (orange)

Mesoventrite with mesoventral process strongly transverse and very short (Fig. 2a, d), anterior margin with complete raised border; meso-metaventral junction with suture visible, broader than a mesocoxal diameter. Metaventrite transverse, longer than ventrites 1–4 combined (Fig. 2a); metaventral postcoxal lines joined medially, complete and extending to metanepisternum. Scutellar shield small, triangular, glabrous.

Elytra covered with distinct punctures, entirely covered with long sparse hairs (Fig. 2b, c), lateral margin with a row of short, evenly spaced setae, sutural line not present. Epipleura incomplete apically, reaching about 1/3 length of the 5th abdominal ventrite, with foveae to accommodate apices of mid and hind femora, foveae for hind femora deeply marked, reaching outer margin of epipleuron.

Abdomen with five ventrites: ventrites 1 and 5 each much longer than ventrites 2 and 3 combined, ventrite 5 rounded, not crenulated, not grooved laterally. Postcoxal lines incomplete, reaching lateral margin of ventrite.

Legs moderately long, reaching outer margin of elytra; coxae large, about half the length of femora; femora, especially profemur, broad, flattened and closely fitting into depression on meso- and metaventrite; tibiae externally not angulate (Fig. 2d); tarsi four-segmented; tarsal claws toothed at base (Fig. 2e). Sex undetermined. Genitalia not visible.

Key to *Serangium* species from the Baltic amber

1. Elytral margins broad, well visible from above throughout, elytral disc glabrous with a row of short and sparse setae at outer margin (Fig. 3c), metaventrite shorter than ventrite 1–4 combined, epipleuron with foveae for reception of hind femora shallowly marked (Fig. 3a).
   Serangium twardowskii sp. nov.
2. Elytral margins narrow, not well visible from above, elytral disc covered with long and sparse setae with a row of short and sparse setae at outer margin (Fig. 3d), metaventrite longer than ventrite 1–4 combined, epipleuron with foveae for reception of hind femora deeply marked, reaching outer margin of epipleuron (Fig. 3b).
   Serangium gedanicum sp. nov.

Discussion

Cladistic analysis places newly described taxa within the tribe Serangiini (Fig. 5). Due to limited character availability, relationships between Serangiini taxa and two Eocene species are not recovered. The classification of the extant genera of Serangiini is based on just a few characters such as number of tarsomeres, number of antennomeres, shape of mandibles, presence or absence of wings, and can fluctuate within genus. Moreover, generic concepts vary among the authors (Chapin 1940; Miyatake 1994; Ślipiński and

Burckhardt 2006; Escalona and Ślipiński 2012; Wang and Ren 2012). It makes systematics of this group somewhat complicated. The whole set of these characters is not clearly visible for any of the analysed fossils, which makes it quite difficult to assess if these taxa belong to an extant genus or new extinct genus. Nevertheless, broad profemora, four segmented tarsi, angulate tarsal claws, and antennae with nine antennomeres (*S. gedanicum*) allow to place both fossil species within type genus *Serangium*.

Recent species of *Serangium* are distributed in tropical and subtropical regions of the Old World, with most diverse faunas in Asian and Australian regions, with just a few species in the temperate areas (Fig. 6). Currently, no ladybird beetles from the tribe Serangiini occur in Europe. During the mid-Eocene period, the climate was much warmer and subtropical forests covered European land masses (Szwedo 2012), and genus *Serangium* was probably much more widely distributed.

Species described here from the Baltic amber are the oldest records of the tribe Serangiini as well as whole subfamily Microweiseinae. Most recent estimations about the age of Baltic amber place it in mid-Eocene about 44.1 ± 1.1 Mya (Szwedo and Drohojowska 2016; supplementary information). Very good preservation of the specimens allowed detailed diagnosis, making *S. twardowskii* sp. nov. and *S. gedanicum* sp. nov. the first ladybird beetles from the Baltic amber to be properly described and assigned to genus taxon.

Serangiini are specialised whitefly (Aleyrodoidea) predators (Giorgi et al. 2009). Several species are used as biological control agents (Booth and Polaszek 1996). Interestingly Aleyrodidae are also found in Baltic amber. However, they are not frequently found, and currently only four species are recognised (one with doubtful position; Drohojowska and Szwedo 2011; Szwedo and Drohojowska 2016). Probably in the Middle Eocene, epoch members of Serangiini had been preying on representatives of whiteflies as well. It cannot be excluded that the evolution and diversification of tribe Serangiini, which is one of the most basal lineages in ladybird beetles' evolution (Ślipiński 2007; Escalona and Ślipiński 2012), could be related to whiteflies' divergence influenced by a 'mid-Cretaceous biocoenotic crisis' (Krassilov 2003)—great change from gymnosperm-dominated biomes to angiosperm-dominated biomes. The most recent molecular hypotheses about the age of the ladybird beetles family show that the origin of Coccinellidae should be nested somewhere in the early Cretaceous (125 Mya; McKenna et al. 2015), which supports this opinion.

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