ARTHROPOD SYSTEMATICS
& PHYLOGENY

75 (2): 185–194
8.9.2017

SENCKENBERG

Eoplatypus jordali gen.n. et sp.n., the first described Platypodinae (Coleoptera: Curculionidae) from Baltic amber

David Peris*,1, Mónica M. Solórzano Kraemer2, Sarah M. Smith3 &
Anthony I. Cognato*,3

[1] Departament de Ciències Agràries i del Medi Natural, Universitat Jaume I (UJI), Campus del Riu Sec, Castelló de la Plana, E-12071, Spain; David Peris * [daperce@gmail.com] — [2] Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany; Mónica M. Solórzano Kraemer [monica.solorzano-kraemer@senckenberg.de] — [3] Department of Entomology, Michigan State University, 288 Farm Lane, room 243, East Lansing, MI 48824, U.S.A.; Anthony I. Cognato * [cognato@msu.edu], Sarah M. Smith [camptocerus@gmail.com] — * Corresponding authors

Accepted 20.iii.2017.

Editors in charge: Klaus-Dieter Klass & Christian Schmidt

Abstract

The first platypodine beetle from Baltic amber, *Eoplatytpus jordali* **gen.n. et sp.n.**, is described from two specimens. The species shares diagnostic characters with Tesserocerini and a phylogeny reconstructed with morphological and DNA data groups the species with *Mitosoma*, *Cenocephalus*, and *Chaetastus*. The species lacks mesepisternal and mesonotal carinae and has an antennal club wider than long, which is a unique combination of generic characters. Furthermore, the species provides an additional calibration point for dating of platypodine phylogenies. It corroborates the molecular dating of the *Mitosoma* + *Cenocephalus* + *Chaetastus* clade at approximately 50 mya. Finally, the rarity of platypodine Baltic amber inclusions is discussed.

Key words

Beetle, Polyphaga, Curculionidae, ambrosia beetle, Tesserocerini.

1. Introduction

Baltic amber has been known and valued for millennia (Grimaldi 1996). It was most often collected from Baltic Sea beaches of the Samland Peninsula until the early 1800's; where it was dredged and mined at industrial scale. These processes recovered over 1 million tons and most of it was rendered for varnish and industrial oils (Grimaldi 1996). However, a significant amount of amber yielded approximately 200,000 inclusions of flora and fauna which provided a detailed picture of an ancient ecosystem (Ley 1951). Although the original stratigraphic position of Baltic amber is unclear due to re-deposition as a consequence of glaciation events, most of it is considered of Lower Eocene age, approximately 45 Ma (Weitschat & Wichard 2010).

The origin of and inclusions within Baltic amber have a long history of study compared to all other known deposits. The botanical origin of Baltic amber has been discussed extensively, and several conifer families have been identified as taxa belonging to the Pinaceae or Araucariaceae (reviewed in Langenheim 2003). However, the latest chemical analyses and fossils suggested the Sciadopityaceae as the most likely source of Baltic amber (Wolfe et al. 2009; Sadowski et al. 2016). Plant specimens include a diversity of gymnosperms and angiosperms; a floral assemblage that indicates a tropical or subtropical Baltic amber forest (Larsson 1978; Poinar 1992). Nevertheless, recently discovered conifer and angiosperm inclusions of ecological relevance suggest the resin was produced in warm-temperate forests with a few subtropical and tropical species (Sadowski et al. 2016). Baltic amber also contains a menagerie of inclusions from spiders to lizards, and it has the most diverse assemblage of fossil insects of any geological age, representing 98% of all animal inclusions (Weitschat & Wichard 2010). It is particularly rich in bark beetle (Curculionidae: Scolytinae) inclusions, which are exclusively phloem feeders, and are represented by at least 21 species in eight genera (Hulcr et al. 2015). Several of the genera are extant pine-feeders occurring in subtropical and temperate regions of the northern hemisphere (Wood & Bright 1992). By contrast, subcortical ambrosia-feeding platypodines have not been reported so far. Here we describe the first ambrosia-feeding platypodine beetle.

Platypodinae are commonly known as flat-footed ambrosia beetles because of the characteristic flattened protibia and larvae that develop on ambrosia fungi cultivated in galleries bored in the wood. The group comprises almost 1500 mostly tropical and subtropical species (Wood & Bright 1992). The results of several phylogenetic analyses differ in the placement of platypodines in relation to other curculionoid subgroups and the position of Platypodinae is contentious (Kuschel et al. 2000; Farrell et al. 2001; Marvaldi et al. 2002; McKenna et al. 2009; Oberprieler et al. 2007; Jordal et al. 2011, 2014; Haran et al. 2013; Gillett et al. 2014; Jordal 2014). However, most consider platypodines as a subfamily of Curculionidae (Oberprieler et al. 2007; Bouchard et al. 2011; Jordal 2014).

Fossil platypodines are well documented. Currently, there are 15 described fossil species, a subfossil redescribed from copal with unknown origin, and an Oligocene fossil from Sicilian amber with a dubious assignment to an extant species (Table 1) (Peris et al. 2015; Legalov 2015). Dating of a molecular-based phylogeny estimates a Mid-Cretaceous (105 – 85 Ma) origin of the platypodines (i.e., time of first ingroup dichotomy; Jordal 2015) which is supported by an undescribed platypodine fossil from Cretaceous amber from Myanmar (~99 Ma) (Jordal & Cognato 2012). Platypodines are most commonly known from Dominican and Mexican amber (Miocene, 20 – 15 Ma) and are the most diverse paleoassemblage of species (Schedl 1962; Bright & Poinar 1994; Grimaldi & Engel 2005; Peris et al. 2015). Several authors' references to platypodines from Eocene Baltic amber (Scudder 1891; Klebs 1910; Larsson 1978; Poinar 1992; Bright & Poinar 1994; Davis & Engel 2007; Kirejtshuk et al. 2015; among others) represent misidentified provenance of the amber, are not present in existing collections, or are unstudied (Schedl 1947; Weitschat & Wichard 2002; Alekseev 2013; Cognato 2015).

Two specimens were recently located in a contemporary collection from Baltic amber in Germany, which we describe within the context of a generic level phylogeny based on morphological and molecular (for extant species) data. These fossils are significant because: 1) they provide a previously unknown calibration point for phylogenetic dating of the subfamily; and 2) their morphological similarities with recent taxa are useful for the analysis of the evolution and paleobiogeography of this taxon.

2. Material and methods

2.1. Specimens and their examination

The new genus and species are described from two inclusions in Baltic amber (SMF Be 2547 and SMF Be 2548), received from Christel and Hans Werner Hoffeins (Senckenberg Forschungsinstitut und Naturmuseum, Germany). As characteristic of Baltic amber inclusions, these pieces included stellate hairs and microscopic bubbles on parts of the beetle. Nevertheless, to confirm the provenance of the amber, Fourier Transform Infrared Spectroscopy (FTIR) was performed on a Thermo Scientific Nicolet iN10 MX using a transmitted infrared beam 100 × 100 µm aperture. The spectra are the sum of 64 scans at a resolution of 4 cm^{-1}, with a spectral range 4000 – 675 cm^{-1}.

The pieces were cut, polished and embedded in a transparent polyester resin (Hoffeins 2001). The specimens were examined under Leica MS5 and MZ16 stereomicroscopes and an Olympus BX41 compound microscope. The photograph of the holotype (Fig. 4C) was taken using a Leica DFC 320 camera attached to the Leica MZ16 stereomicroscope, using the Leica FireCam 1.9.1 software. Photographs of the paratype (Figs. 4A, B) were taken using a Leica DFC 420 camera attached to the Leica MS5 stereomicroscope, using the Leica IM1000 software. A detailed photograph of the antenna (Fig. 4D) was taken using a ColorView IIIu camera attached to the Olympus BX41 compound microscope, using the software Olympus Cell A2. Drawings were made using a camera lucida attached to the Leica stereomicroscope. Photographs were merged using the software Combine ZP edited with Photoshop Elements 10 and CorelDraw X8. All measurements in the descriptions are in millimeters.

2.2. Taxonomy and phylogenetics

Taxonomic identification was based on a key to extant platypodine genera (Wood 1993) and nomenclature followed Alonso-Zarazaga & Lyal (2009). Based on the result of this initial identification, we reconstructed a phylogeny for representatives of extant Tesserocerini,

Table 1. Fossil ambrosia beetles (Coleoptera: Curculionidae: Platypodinae), modified after Davis & Engel (2007) and Peris et al. (2015). The provenance of *Periommatus severisee* is confirmed as copal (Nunberg 1959).

Species	Deposit	Age	Reference
Cenocephalus antillicus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus antiquus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus biconicus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus exquisitus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus hurdi Schedl	Mexican amber	Miocene	Schedl 1962
Cenocephalus quadrilobus Schedl	Mexican amber	Miocene	Schedl 1962
Cenocephalus quasiexquisitus Davis & Engel	Dominican amber	Miocene	Davis & Engel 2007
Cenocephalus rhinoceroide (Schawaller)	Dominican amber	Miocene	Schawaller 1981
Cenocephalus senectus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus spinatus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Cenocephalus succinicaptus Schedl	Mexican amber	Miocene	Schedl 1962
Cenocephalus tenuis Peris & Solórzano Kraemer	Mexican amber	Miocene	Peris et al. 2015
Periommatus severisee (Strohmeyer) Nunberg	Copal (origin unknown)	Holocene	Nunberg 1959
Platypodidaeum ferrarae Kohring & Schlüter	Sicilian amber	Oligocene	Kohring & Schlüter 1989
Platypus maravignae (Guérin-Méneville)	Sicilian amber	Oligocene	Guérin-Méneville 1838
Tesserocerus primus Bright & Poinar	Dominican amber	Miocene	Bright & Poinar 1994
Tesserocerus simojovelensis Peris & Solórzano Kraemer	Mexican amber	Miocene	Peris et al. 2015
Eoplatypus jordali **gen.n. et sp.n.** Peris, Solórzano Kraemer & Cognato	Baltic amber	Eocene	This work

the new fossil species, *Platypus sampsoni* Schedl, 1933 from Platypodinae-Platypodini, and the following non-platypodine outgroup taxa: *Coptonotus cyclops* Chapius 1869 and *Scolytus intricatus* Ratzeburg, 1837 (following Jordal 2015); using 22 external morphological characters and geography (Tables 2, 3). Unassignable characters for the specimens in amber were scored as missing.

DNA data, including sequences of ArgK, CAD, COI, and EF-1α, used in Jordal (2015), were included for the extant species. DNA sequence data was not available for all species and surrogate species (in parentheses) were used to represent *Mitosoma crenulatum* Chapuis, 1865 (*Mitosoma* sp. TsMit08), *Mitosoma rugosum* Schaufuss, 1905 (*Mitosoma* sp. TsMit09), *Chaetastus persimilis* Schedl, 1933a (*Chaetastus montanus* Schedl, 1957), *Cenocephalus thoracicus* Chapuis, 1865 (*Cenocephalus* sp. TsCen01), and *Tesserocerus rudis* Chapuis, 1865 (*Tesserocerus ericius* Blandford, 1895). Alignment of the DNA sequences was manually assembled as a NEXUS file and did not require the insertion of gaps. The alignment block consisted of 2946 base pairs (bp), which is slightly less than in Jordal (2015) and likely due to the inclusion of fewer taxa in our analyses. DNA data for the fossil species were scored as missing.

Using PAUP* 4.0 b10 PPC (Swofford 2002), we conducted a separate analysis of the morphological data and an analysis of all data using a heuristic search (with 100 random additions and default settings) for the most parsimonious trees using unordered character states. For the morphological data set, characters were reweighted based on the rescaled consistency index determined by the initial analysis. Character states were optimized with accelerated transformations. A bootstrap analysis of 500 pseudoreplicates was conducted. Character state transformations were mapped on the morphological tree and inspected with MacClade 4.0 PPC (Maddison & Maddison 2000).

A Bayesian analysis was also performed using Mr. Bayes 3.2.6 (Ronquist et al. 2012) with combined data partitioned into 13 sets including by gene and codon position, and by morphology. The molecular data were independently analyzed under a general time reversible model ($\mathrm{GTR}+\Gamma+\mathrm{I}$), which was determined as best fit by AIC in MrModeltest v.2 (Nylander et al. 2004). The morphological partition was analyzed using an equal rate model. Four Metropolis-Coupled Markov Chain Monte Carlo searches (one cold, three heated) were run in two simultaneous runs for 2 million generations, each with sampling of every 100th iteration. A burn-in was set after the first 25% of all saved trees. All parameters reached stability within 2 million generations and the split distribution between runs did not vary much (mean standard deviation between runs = 0.020187).

3. Results

3.1. Provenance of the amber

The FTIR analysis of the piece (SMF Be 2547) produced spectra containing bands that correspond to Baltic amber (Fig. 1) (Pakutinskiene et al. 2007). A characteristic peak attributed to the carbon-oxygen bond at 1158 cm^{-1} distinguished it as Baltic amber and the presence of the "Baltic shoulder" region between 1155 cm^{-1} and 1275 cm^{-1} confirmed its origin. Additional bands at 1737 cm^{-1} and 1715 cm^{-1} were assigned to the ester and carboxylic acid groups, whereas peaks located at 1643 cm^{-1} and 888 cm^{-1} were attributed to the exocyclic methylene group. A doublet for carbonyl C=O stretching peaks at 1739 cm^{-1} and 1714 cm^{-1} was characteristic of ester and acid groups. Bands at 1260 cm^{-1} and 1157 cm^{-1}

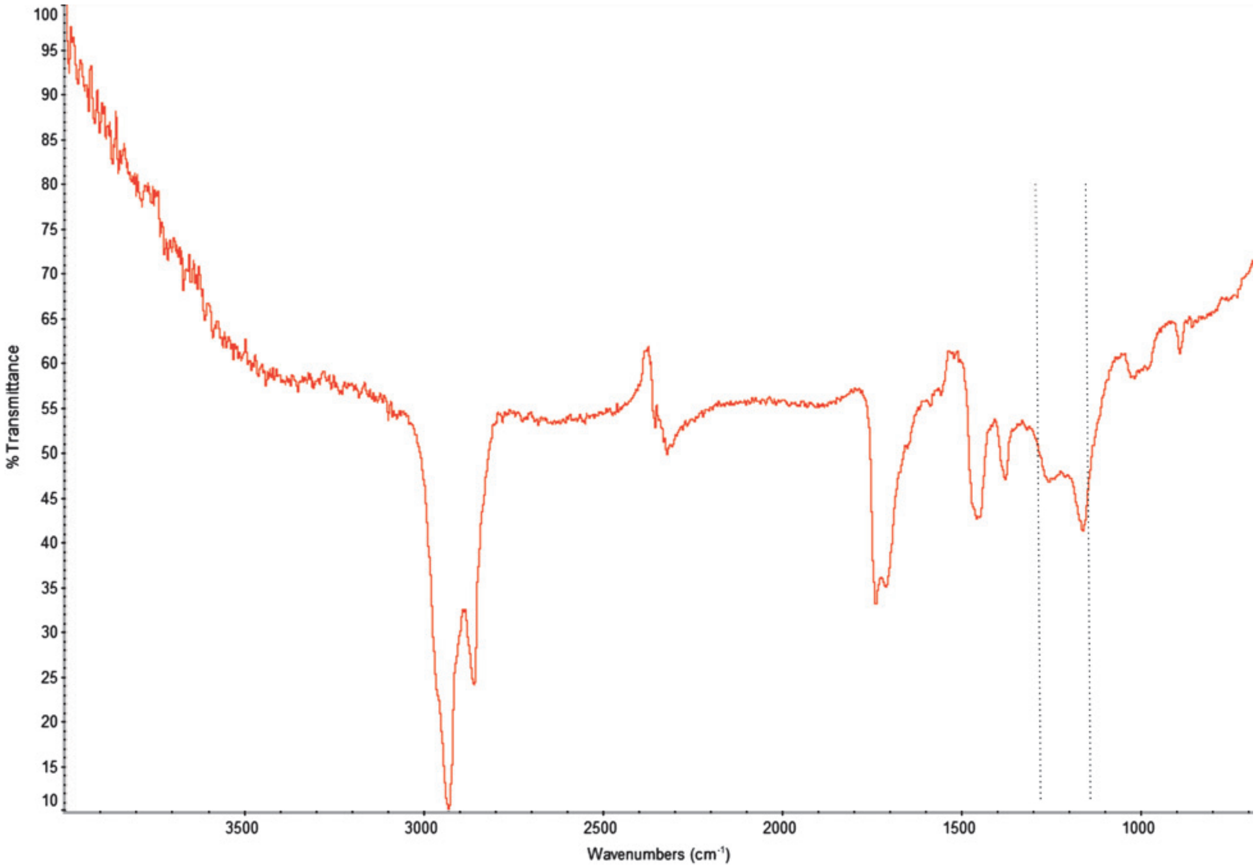

Fig. 1. Fourier Transform Infrared Spectroscopy (FTIR) analysis; "Baltic shoulder" region is indicated.

are assigned to CO-O- modes of the succinate group, whereas the C-H bending modes for the terminal olefins were located at 888 cm^{-1}. Peaks located at 1643 cm^{-1} and 888 cm^{-1} were attributed to the exocyclic methylene group. Also, the FTIR of this amber showed characteristic intense absorption bands at 2926 cm^{-1}, 2867 cm^{-1}, and 2849 cm^{-1} which were attributed to C-H stretching modes of the -CH2 and -CH3 groups.

3.2. Taxonomy and phylogeny

Visual inspection of the platypodine fossil specimens suggested their identity as a species of Tesserocerini given the following characters: posterior margin of prothorax strongly procurved in pleural area, pregula separated on each side from margin of oral fossa by a deep cleft, procoxae contiguous and scutellum small, slender and pointed (Wood 1993). The 4-segmented antennal funicle, pubescent club, subcircular eye, stouter pronotum and the abrupt elytral declivity suggested inclusion in *Mitosoma* Chapuis, 1865 (Wood 1993). However, *Mitosoma* is only distinguishable from *Cenocephalus* Chapuis, 1865, by geographic location (Madagascar versus Central and South America) (Wood 1993; Peris et al. 2015). The absence of characters to clearly differentiate the new Baltic fossils from extant genera required a phylogenetic analysis.

Parsimony analysis of the morphological data from 18 Tesserocerini species, one Platypodini species, and two outgroup taxa resulted in 79 most parsimonious trees which were unresolved in a strict consensus of these trees. Reanalysis with the characters reweighted based on the rescaled consistency index resulted in one parsimonious tree (Fig. 2). *Periommatus* Chapuis, 1865 was the only monophyletic genus. The Baltic amber species was sister to the clade consisting of *Mitosoma*, *Cenocephalus*, and *Chaetastus*. *Periommatus*, *Tesserocerus* Saunders, 1837, and *Tesserocranulus* Schedl, 1933b formed a clade which was sister to *Platypus* Herbst, 1793 (i.e., Tesserocerini were not obtained as monophyletic). *Notoplatypus* Lea, 1910, *Diapus* Chapuis, 1865 and *Genyocerus* Motschulsky, 1858 formed a clade which was sister to the remaining ingroup taxa. Bootstrap values were low for all clades. Most characters were phylogenetically informative (21/22) but most demonstrated some level of homoplasy (RI = 0.548). One of the most important generic level diagnostic characters, the mesepisterum carina, lacked homoplasy (Table 2; Wood 1993). Another generic level diagnostic character, the longitudinal carina on the mesonotum demonstrated some homoplasy (RI = 0.5).

The parsimony analysis of the combined data resulted in 19 most parsimonious trees. The strict consensus was unresolved for the relationships among *Mitosoma*, *Cenocephalus*, and *Chaetastus*. The resolved clades had bootstrap values > 50% (Fig. 3).

Bayesian analysis of combined data found all genera monophyletic except for *Cenocephalus.* This analysis did not resolve all species relationships and posterior prob-

Table 2. Characters and states scores for platypodine species. Measures of homoplasy given as retention index (RI) are based on the phylogeny (Fig. 2). Character weights (W) based on maximum value of rescaled consistency indices.

Nr	Character	State 0	State 1	State 2	State 3	State 4	RI	W
1	Geographical distribution	Ethiopian	Palearctic	Neotropical	Indo-Malayan	Australasian	0,125	0,5
2	Female frons	flat/convex	impressed/ concave	laterally impressed			1,00	1,00
3	Eye shape	ovoid	round	elongate	reniform		0,667	1,00
4	Antennal club shape	longer than wide	wider than long				0,00	1,00
5	Corneus area on club base	procurved, occupying less than1/3 of club	bisinuate	strongly procurved, occupying more than half of club	absent		0,111	0,24
6	Pronotal mycangia	dense, minute punctures	strigate	absent	large pores		0,714	1,00
7	Lateral margin of pronotum	emarginate	entire				0,00	0,086
8	Lateral margin of pronotum carinate	absent	at least basal 1/2	basal 1/3	entirely		0,20	0,2
9	Male pronotal base	straight, acuminate at scutellar notch	bisinuate				0,375	0,44
10	Posterior face of protibia	two rugae	at least four rugae	unarmed			0,455	0,41
11	Posterior face of protibia denticulate	absent	present				0,125	0,25
12	Anterior face of mesotibia	1 ruga	2 rugae	3 rugae	4 rugae	absent	0,333	0,38
13	Anterior face of metatibia	lacking transverse processes	crenulations	1 ruga	2 rugae	3 rugae	0,200	0,4
14	Mesepisternum carina	absent	present				1,00	1,00
15	Mesepisternum excavated for reception of mesofemur	absent	present				0,00	0,00
16	Mesonotum with longitudinal carina	absent	present				0,50	0,25
17	Female elytral base carinate	absent	present				0,714	1,00
18	Elytral discal interstriae elevated	present	absent				0,111	0,11
19	Male circumdeclivital ring	absent	present				0,429	0,43
20	Declivity punctures	confused	seriate	impunctate			0,40	0,28
21	Male declivital face sculpturing	unarmed	rugose	denticulate	reticulate		0,222	0,17
22	Declivital face bearing spines	absent	present				0,00	0,20

Table 3. Morphological character states scored for platypodine species.

Species	Character number																					
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
Cenocephalus epistomalis	2	1	1	0	3	0	0	1	1	1	0	1	0	0	0	1	1	1	0	2	1	0
Cenocephalus exquisitus	2	1	1	0	0	0	1	0	1	0	1	0	0	?	0	1	1	0	1	0	3	1
Cenocephalus pulchellus	2	1	1	0	3	0	1	0	0	1	0	1	3	0	0	1	1	1	0	2	0	0
Cenocephalus robustus	2	1	1	0	3	0	1	2	1	1	0	0	2	0	0	1	1	0	0	2	2	0
Cenocephalus thoracicus	2	1	1	0	1	0	0	0	0	0	1	1	2	0	0	1	1	1	1	0	3	1
Chaetastus persimilis	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	2	2	0
Chaetastus tuberculatus	0	1	1	0	0	0	0	0	1	1	1	0	2	0	0	1	1	0	0	1	3	0
Diapus unispineus	3	0	0	0	2	3	0	0	1	2	1	4	0	0	0	0	0	1	1	2	0	0
Eoplatypus jordali	1	1	1	1	0	0	0	0	?	0	?	1	0	0	0	0	0	1	?	1	?	0
Genyocerus exilis	3	0	1	0	3	3	0	0	1	2	1	4	0	0	0	0	0	1	1	2	0	1
Mitosoma crenulatum	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	2	3	0
Mitosoma rugosum	0	1	1	0	0	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	0
Notoplaytus elongatus	4	0	1	0	2	2	1	0	1	2	1	4	0	0	0	1	0	0	1	0	2	1
Periomatus bispinus	0	0	2	0	2	1	0	2	0	0	0	2	3	1	1	1	0	0	1	1	2	1
Periomatus sp.	0	0	2	0	2	1	0	1	0	0	0	1	3	1	0	0	0	0	1	1	0	0
Platypus sampsoni	0	0	0	0	3	0	0	2	0	1	0	2	0	0	0	1	0	0	1	2	1	1
Tesserocerus dewalquei	2	0	0	0	0	1	1	0	0	1	1	2	0	1	0	0	0	0	1	1	0	0
Tesserocerus rudis	2	0	0	0	0	1	1	0	0	1	0	1	3	1	0	0	0	0	1	1	0	0
Tesserocranulus nevermanni	2	2	0	0	3	1	0	1	0	1	0	3	4	1	1	0	0	1	1	1	?	0
Coptonotus cycops	2	0	3	0	3	2	0	3	0	2	0	4	0	0	1	0	0	0	0	1	1	0
Scolytus intricatus	1	0	3	0	0	2	1	3	0	2	0	4	0	0	0	0	0	1	0	1	0	0

abilities of clades were mostly low with the exception of the relationships concerning *Diapus*, *Genyocerus*, *Periommatus*, *Tesserocerus*, and *Tesserocranulus* (Fig. 3). Despite the low resolution, the Bayesian and parsimony analyses of the combined data did not completely conflict with species relationships compared to each other, although they differed from the parsimony analysis of the morphology data (Figs. 2, 3). The Bayesian phylogeny

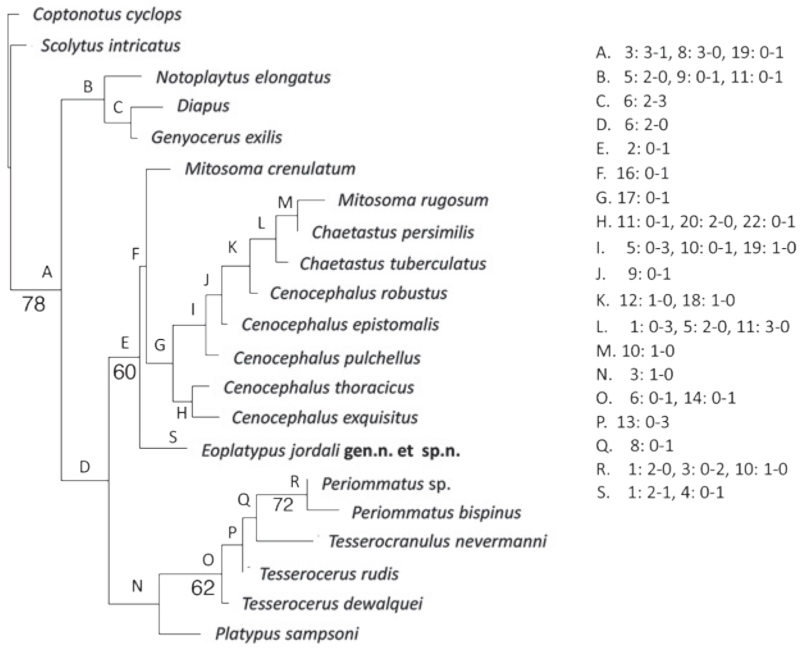

Fig. 2. The most parsimonious tree found in a heuristic search based on the reweighted analysis of 22 morphological characters. Numbers or letters at nodes indicate unambiguous morphological character state changes (character number: state number to state number), see Table 2 for character and state details. Numbers below the branches are bootstrap values.

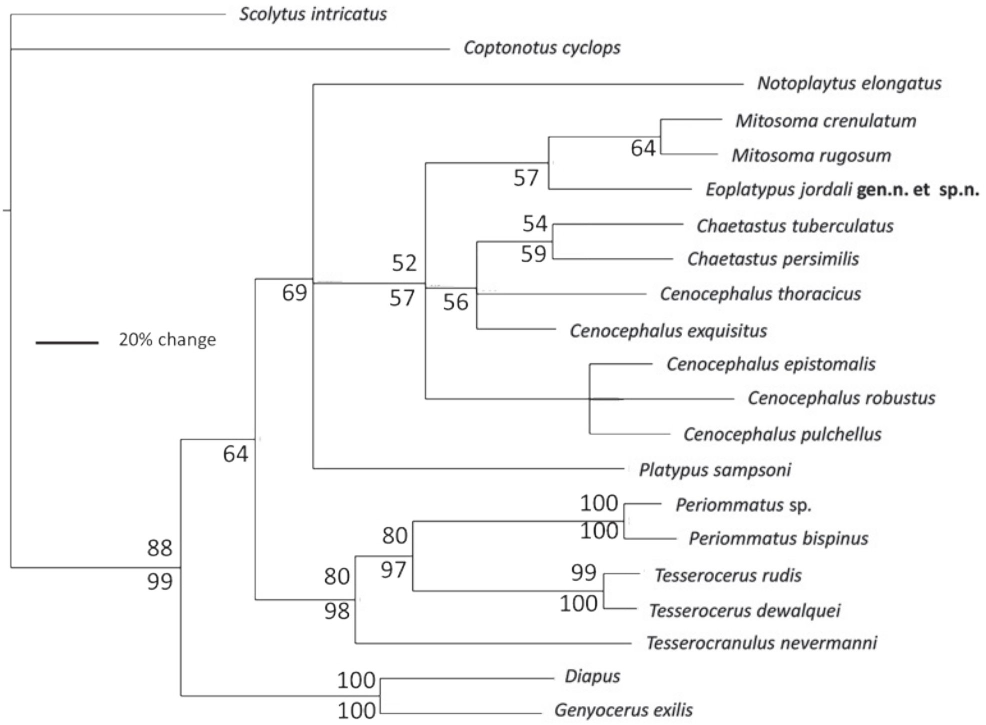

Fig. 3. Majority-rule consensus tree for 40002 trees kept from the Bayesian analysis of 2 million generations using the morphological and DNA data. Numbers below branches are posterior probabilities and the numbers above are bootstrap values determined via a parsimony analysis of the same data.

differed most notably by the placement of *Notoplatypus* and *Platypus* with *Mitosoma*, *Cenocephalus*, and *Chaetastus*. Also the Baltic amber species was sister to *Mitosoma*, *Cenocephalus*, and *Chaetastus* in the parsimony analysis of morphological characters but it was sister to *Mitosoma* in the Bayesian phylogeny (Figs. 2, 3).

Overall these data and analyses suggest that the new species belongs in a clade with *Mitosoma*, *Cenocephalus*, and *Chaetastus*. It is also distinguished by a unique combination of character states. These states include the absence of both mesepisterum carina, and longitudinal carina on the mesonotum and the presence of an antennal club that is wider than long. These results validate the recognition of a new genus.

4. Description

Order: Coleoptera Linnaeus, 1758
Suborder: Polyphaga Emery, 1886
Superfamily: Curculionoidea Latreille, 1802
Family: Curculionidae Latreille, 1802
Subfamily: Platypodinae Shuckard, 1840
Tribe: Tesserocerini Strohmeyer, 1914

Eoplatypus gen.n. Cognato & Smith

(Fig. 4)

Type species. *Eoplatypus jordali* **sp.n.**
Etymology. *Eo* (G) = Dawn, *platy* (G) = flat, *pus* (G) = foot.
Diagnosis. A combination of characters including the wider than long antennal club, and the absence of the mesepisternal and mesonotal carinae distinguishes this genus from other Tesserocerini. Although *Eoplatypus* **gen.n.** appears similar to *Mitosoma* and *Cenocephalus*, these genera have mesonotal carinae and antennal clubs that are longer than wide.
Description. Frons concave, setose. Eyes round. Antennal funicle with four antennomeres (Fig. 4D); club wider than long, pubescent, with a corneous base less than a third of club length. Pronotum longer than wide, lateral margin emarginate, carina absent, posterior lateral margin rounded (Fig. 4A), dorsal mycangia present medially on basal half, comprised of two groups of dense, minute punctures. Procoxae contiguous. Protiba posterior face with two rugae. Mesonotal longitudinal carina absent, mesepisterum carina absent. Mesotibia anterior face with two rugae. Metatibia anterior face transverse processes absent. Eytral base with tubercle-like expansions. Discal interstriae not elevated above striae. Declivital punctures seriate; declivity without spines.

Eoplatypus jordali sp.n. Peris, Solórzano Kraemer & Cognato

(Fig. 4)

Material. ***Holotype***. Eocene amber from Baltic region (SMF Be 2548); housed in the public collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany. A complete specimen, ♀ (likely), partly covered by small bubbles. ***Paratype***. Eocene amber from Baltic region (SMF Be 2547); housed in the public collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany. A complete specimen, unknown gender, partly covered by small bubbles. It is in syninclusion with “stellate hairs”, from an oak tree.
Etymology. The species epithet honors Dr. Bjarte Jordal, University of Bergen, Norway, specialist on Platypodinae beetles.
Diagnosis. No other species of *Eoplatypus* are known. This species is diagnosed from other playtypodine amber inclusions by the generic characters referred to in the generic diagnosis and by the structure of the elytral declivity described below.
Description. Body length 3.8 – 4.0 mm, maximum width around 1.1 at elytral apex, 3.5 × longer than wide. Body cylindrical in section. Setae present dorsally on head and elytra, ventrally in the whole body; pronotum glabrous. Head distinctly longer than wide, about 3 × longer than eye diameter. Eyes lateral, relatively small, round, visible dorsally, very finely faceted (Fig. 4D). Vertex divided by a median carina (Fig. 4A). Frons depressed, setose. Antennae very short, reaching to cephalic insertion but not extending beyond; scape straight; funicle 4-segmented; pedicel robust, inserted at the scape apex, as wide as long; antennomere 3 conical, narrower at base and wider at apex, shorter than long; antennomeres 4 and 5 strongly transverse; antennomere 5 slightly wider than and half the length of 4 (Fig. 4D); club compressed, wider than long (Fig. 4C), base flat, setose from a corneous base to apex. Mandibles short and rounded, with one large tooth at the apex. Pregula separated on each side from margin of oral fossa by deep cleft (Fig. 4B).

Pronotum stout, 1.2 × longer than wide, sides subparallel (Fig. 4A); anterior angles obtusely pointed; posterior angles rounded; basal margin sequentially narrower, pointed at middle. Disc smooth except basally, with two groups of dense minute mycetangial pores left and right of the medial line. Posterior margin of pronotum strongly procurved in pleural area. Scutellum very small, apically pointed. Procoxae contiguous (Fig. 4B).

Elytra 1.8 × longer than wide (length measured from base to apex of first tubercle-like expansion; width measured at the wider, apical portion); 1.5 × longer than pronotum. Elytra subparallel, becoming wider apically, base emarginate at suture, as wide as pronotal base. Discal striae punctate (Fig. 4A); interstriae seriate, shallowly sparsely punctured, ~3 × wider than striae. Declivity occupying apical fifth, obliquely truncate beyond tubercle-like expansions of the base (Fig. 4A). Base of interstriae 2 – 4 together posteriorly expanded, triangulate, acutely tipped; interstriae 5 – 6 together posteriorly expanded, rounded, serrate; interstriae 7 – 8 together posteriorly expanded, rounded, serrate; interstriae 9 continued on declivital face terminating as a tubercle. Basal edge lined with hair-like setae longer than interstrial width. Declivital face with seriate punctures. Apical margin rounded.

Mesosternum with mesepisternum convex, unarmed, without a carina. Metasternum long, with distinct femoral impression; metacoxae contiguous. Legs long; femora wide, compressed; protibiae with two transverse rugae and a long weakly hooked inner mucro. Tarsi slender, longer than tibia (Fig. 4B); tarsomere 1 as long as the following tarsomeres combined; tarsomeres 2 and 3 equal in length; tarsomere 4 the shortest, 0.5 × the length of tarsomere 3, tarsomere 5 as long as the previous three combined, slender. Long, slender claws.

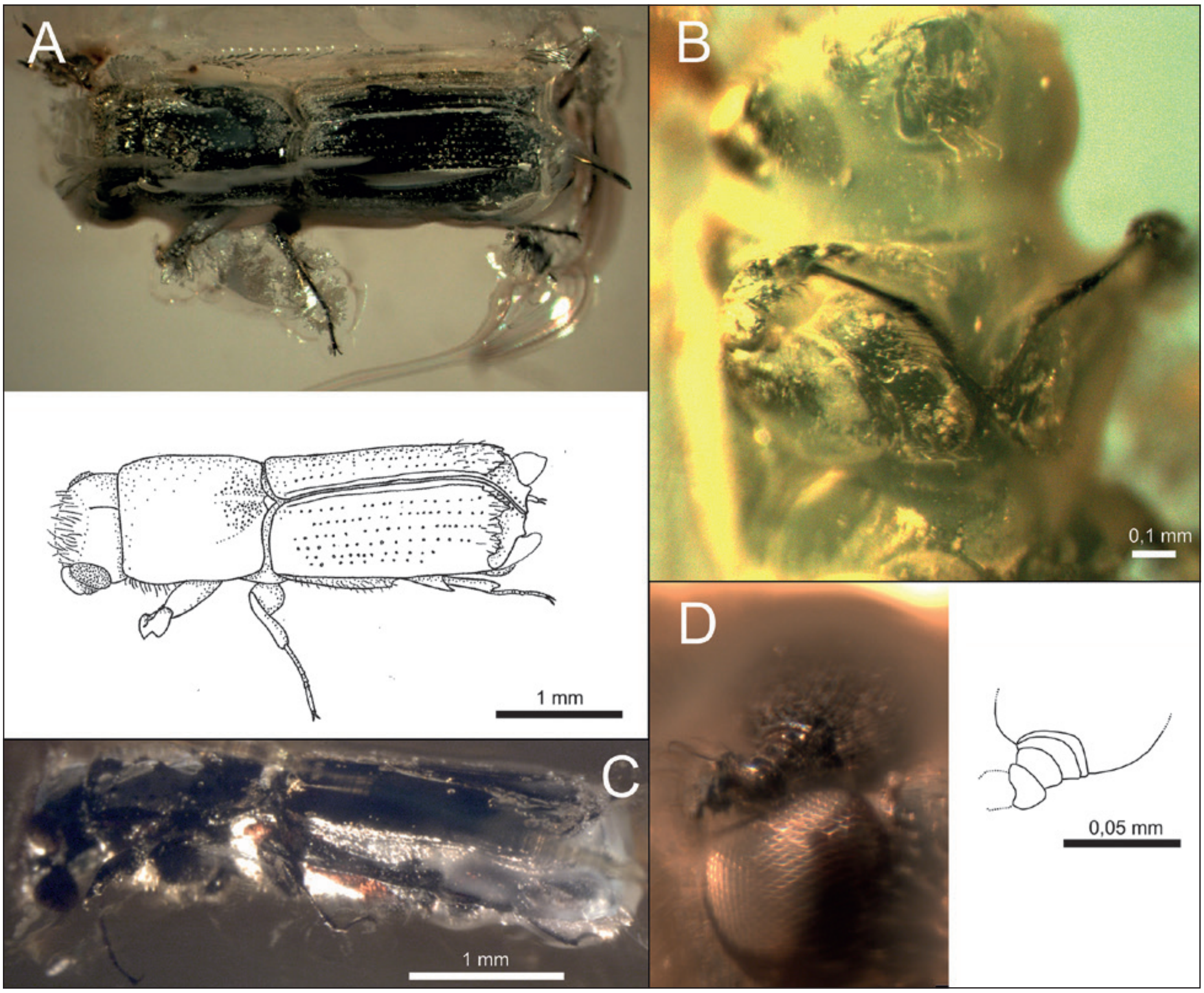

Fig. 4. *Eoplatypus jordali* **gen.n. et sp.n. A**: Dorsal habitus of the holotype SMF Be 2548, ♀ (likely). **B**: Ventral habitus of the head and pronotum of the holotype. **C**: Lateral habitus of the paratype SMF Be 2547. **D**: Antenna of the holotype.

5. Discussion

Insects whose life cycles are closely tied to amber producing trees occur in higher numbers in amber (Solórzano Kraemer et al. 2015). Thus the scarcity of platypodine inclusions in Baltic amber is inconsistent with platypodine biology. Given the subfamily's subcortical lifestyle, multiple specimens, as observed with scolytines, are expected because these beetles are attracted to injured or dying trees which may ooze resin. Of the thousands of insect specimens (Poinar 1992) found in angiosperm derived Dominican amber (*Hymenaea* spp.), approximately 7% are scolytines and platypodines (Cognato & Grimaldi 2009). These species have extant relatives which all use angiosperm hosts. If the conifer that produced the Baltic amber served as a host for *Eoplatypus jordali* **gen.n. et sp.n.**, specimens would be more common. As consequence, their scarcity in Baltic amber suggests that Eocene platypodines mainly used angiosperm hosts for their brood sites as it is known from the vast majority of extant platypodines. Cognato & Grimaldi (2009) observed a similar pattern with conifer derived Burmese amber inclusions: among 4200 animal inclusions only one scolytine was found and its extant relatives are angiosperm feeders.

Eoplatypus jordali **gen.n. et sp.n.** represents the first platypodine described from Baltic amber. Phylogenetic analyses group this species with the extant genera *Mitosoma*, *Cenocephalus*, and *Chaetastus* although supporting values are low. The low support values will likely persist for this relationship in future analyses because of the limited number of variable morphological characters observed for these taxa and a lack of DNA data for the fossil specimens. Despite the poor support, *E. jordali* **sp.n.** and these genera are united by characters which exhibit low homoplasy (i.e. 2, 3, and 6). Furthermore, the monophyly of the extant genera is well-supported in a more comprehensive study of platypodines and not disputed (Jordal 2015). This Baltic amber species is superficially similar to *Cenocephalus* and *Mitosoma* but it differs by the lack of mesepisternal and mesonotal carinae, two characters important for generic placement in platypodine taxonomy. The variation of these characters and the autapomorphy of the antennal club (character 4) provide more justification for the recognition of *Eoplatypus* **gen.n.** than previously described genera *Cenocephalus* and *Mitosoma,* which were based only on geographic location and without reference to a phylogeny (Wood 1993).

The phylogenetic placement of *E. jordali* **sp.n.** with *Mitosoma*, *Cenocephalus*, and *Chaetastus* provides an additional calibration for phylogenetic divergence. Prior to these specimens, platypodine fossils were known for two time periods, the Cretaceous (~100 mya) (Cognato & Grimaldi 2009) and the Miocene (~20 mya) (Table 1). Jordal (2015) used these calibration points to date a phylogeny of platypodine genera. Bayesian analysis of evolutionary rates suggested a stem age of 80.3 mya and a crown age of 51 mya for the *Mitosoma*, *Cenocephalus*, and *Chaetastus* clade (Jordal 2015: fig. 4). The Baltic amber fossil, aged at approximately 45 mya, fits well with the molecular dating estimate and given the overall similarity of *Eoplatypus* **gen.n.** to the extant genera, association with the crown age seems appropriate (Jordal 2015). Inclusion of this calibration point in future studies of platypodine phylogeny will help to refine the dating of the origin of biological features and ecological events such as the long distance dispersals among continents for platypodine lineages (Jordal 2015; Peris et al. 2015).

6. Acknowledgements

We are grateful to Christel und Hans Werner Hoffeins for the loan of the Baltic amber specimens. We thank Dr. Lourdes Chamorro (United States Department of Agriculture) for facilitating a loan of extant platypodine specimens, Dr. Xavier Delclòs (University of Barcelona) for his help with FTIR analysis, and three anonymous reviewers for their comments. Dr. Bjarte Jordal kindly reviewed the characters and scored character states for some taxa. This research received support from the SYNTHESYS Project http://www.synthesys.info/ which is financed by the European Community Research Infrastructure Action under the FP7 "Capacities" Program. M.M.S.K. has been supported by VolkswagenStiftung (Project N. 90946), Germany. It is also a contribution to the project CGL2014-52163, from the Spanish Ministry of Economy and Competitiveness.

7. References

Alekseev V.I. 2013. The beetles (Insecta: Coleoptera) of Baltic amber: the checklist of described species and preliminary analysis of biodiversity. – Zoology and Ecology **23**: 5–12.

Alonso-Zarazaga M.A., Lyal C.H.C. 2009. A catalogue of family and genus group names in Scolytinae and Platypodinae with nomenclatural remarks (Coleoptera: Curculionidae). – Zootaxa **2258**: 1–138.

Blandford W.F.H. 1895. Fam. Scolytidae. – Biologia Centrali-Americana **4**: 115.

Bouchard P., Bousquet Y., Davies A.E., Alonso-Zarazaga M.A., Lawrence J.F., Lyal C.H., Newton A.F., Reid C.A.M., Schmitt M., Ślipiński S.S., Smith A.B.T. 2011. Family-group names in Coleoptera (Insecta). – ZooKeys **88**: 1–972.

Bright D.E., Poinar Jr. G.O. 1994. Scolytidae and Platypodidae (Coleoptera) from Dominican Republic amber. – Annals of the Entomological Society of America **87**: 170–194.

Chapuis F. 1865. Monographie des Platypides. – H. Dessain, Liege. 344 pp.

Cognato A.I. 2015. *Platypus cylindricus* Burmeister, 1831, in reference to a Baltic amber fossil, is an unavailable name (Coleoptera: Curculionidae: Platypodinae). – The Coleopterist Bulletin **69**: 176–177.

Cognato A.I., Grimaldi D. 2009. One hundred million years of morphological conservation in a bark beetle (Coleoptera: Curculionidae: Scolytinae). – Systematic Entomology **34**: 93–100.

Davis S.R., Engel M.S. 2007. A new ambrosia beetle in Miocene amber of the Dominican Republic (Coleoptera: Curculionidae: Platypodinae). – Alavesia **1**: 121–124.

Edgar R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. – Nucleic Acids Research **32**: 1792–1797.

Emery C. 1886. Ueber Phylogenie und Systematik der Insekten. – Biologisches Centralblatt **5**: 648–656.

Farrell B.D., Sequeira A.S., O'Meara B., Normark B.B., Chung J.H., Jordal B.H. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). – Evolution **51**: 2011–2027.

Grimaldi D.A. 1996. Amber: Window to the Past. – Harry N. Abrams, Inc., New York. 216 pp.

Grimaldi D.A., Engel M.S. 2005. Evolution of the Insects. – Cambridge University Press: Cambridge. 755 pp.

Guérin-Méneville F.E. 1838. Note sur la lettre de M. Maravigna sur les insectes trouvés dans l'ambre de la Sicile. – Revue Zoologique, par la Société Cuverienne **1838**: 168–170.

Gillett C.P.D.T., Crampton-Platt A., Timmermans M.J.T.N., Jordal B.H., Emerson C., Vogler A.P. 2014. Bulk de novo mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). – Molecular Biology & Evolution **31**: 2223–2237.

Haran J., Timmermans M.J.T.N., Vogler A.P. 2013. Mitogenome sequences stabilize the phylogenetics of weevils (Curculionoidea) and establish the monophyly of larval ectophagy. – Molecular Phylogenetics & Evolution **67**: 156–166.

Hoffeins H.W. 2001. On the preparation and conservation of amber inclusions in artificial resin. – Polskie Pismo Entomologiczne **70**: 215–219.

Hulcr J., Atkinson T.H., Cognato A.I., Jordal B.H., McKenna D.D. 2015. Morphology, taxonomy and phylogenetics of bark beetles. Pp. 41–84 in: Vega F., Hofstetter R. (eds), Bark Beetles: Biology and Ecology of Native and Invasive Species. – Academic Press, Oxford.

Jordal B.H. 2014. Platypodinae. Pp. 358–364 in: Beutel R., Leschen R.A. (eds), Handbook of Zoology, Band IV Arthropoda: Insecta Part 38: Coleoptera, Beetles, V. – de Gruyter Press: Berlin.

Jordal B.H. 2015. Molecular phylogeny and biogeography of the weevil subfamily Platypodinae reveals evolutionary conserved range patterns. – Molecular Phylogenetics and Evolution **92**: 294–307.

Jordal B.H., Cognato A.I. 2012. Molecular phylogeny of bark and ambrosia beetles reveals multiple origins of fungus farming during periods of global warming. – BMC Evolutionary Biology **12**: 133.

Jordal B.H., Sequeira A.S., Cognato A.I. 2011. The age and phylogeny of wood boring weevils and the origin of subsociality. – Molecular Phylogenetics & Evolution **59**: 708–724.

Jordal B.H., Smith S.M., Cognato A.I. 2014. Classification of weevils as a data-driven science: leaving opinion behind. – ZooKeys **439**: 1–18.

Kirejtshuk A.G., Ponomarenko A.G., Zherikhin V.V. 2015. Taxonomic list of fossil beetles of the suborder Scarabaeina (part 4). – URL http://www.zin.ru/Animalia/Coleoptera/eng/paleosy3.htm [accessed 07 July 2016].

Klebs R. 1910. Über Bernsteinschlüsse im Allgemeinen und die Coleopteren meiner Bernsteinsammlung. – Schriften der Physikalisch-Ökonomischen Gesellschaft Königsberg, Prussia **51**: 217–242. (http://www.biodiversitylibrary.org/bibliography/14682).

Kohring R., Schlüter T. 1989. Historische und palaontologische des Simetits, eines fossilen Harzes mutmasslich mio/pliozanen Alters aus Sizilien. – Documenta Naturae **56**: 33–58.

Kuschel G., Leschen R.A.B., Zimmerman E.C. 2000. Platypodidae under scrutiny. – Invertebrate Taxonomy **14**: 771–805.

Langenheim J.H. 2003. Plant Resins: Chemistry, Evolution, Ecology and Ethnobotany. – Timber Press: Portland. 612 pp.

Larsson S. 1978. Baltic amber – a palaeobiological study. – Entomonograph **1**: 1–192.

Latreille P.A. 1802. Histoire Naturelle, Générale et Particuliére des Crustacés et des Insectes. Familles Naturelles des Genres. – F. Dufart: Paris. 387 pp.

Legalov A.A. 2015. Fossil Mesozoic and Cenozoic weevils (Coleoptera, Obrienioidea, Curculionoidea). – Paleontological Journal **49**: 1442–1513.

Ley W. 1951. Dragons in Amber. – The Viking Press: New York. 328 pp.

Linnaeus C. 1758. Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentis, synonymis, locis. – Laurentii Salvii: Holmiae. 824 pp.

Maddison D.R., Maddison W.P. 2000. MacClade 4: Analysis of Phylogeny and Character Evolution. Version 4.0. – Sinauer Associates, Sunderland, Massachusetts.

Marvaldi A.E., Sequeira A.S., O'Brien C.W., Farrell B.D. 2002. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): Do niche shifts accompany diversification? – Systematic Biology **51**: 761–785.

McKenna D.D., Sequeira A.S., Marvaldi A.E., Farrell B.D. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. – Proceedings of the National Academy of Sciences **106**: 7083–7088.

Nunberg M. 1953. A new subfamily, genus and species of the family Platypodidae (Coleoptera). – Annales Musei Zoologici Polonici **15**: 43–53.

Nunberg M. 1959. Eine fossile Kernkaeferart aus der Gattung *Periommatus* Chap. (Platypodidae). – Annales Musei Zoologici Polonici **18**: 127–138.

Nylander J.A.A., Ronquist F., Huelsenbeck J.P., Nieves-Aldrey J.L. 2004. Bayesian phylogenetic analysis of combined data. – Systematic Biology **53**: 47–67.

Oberprieler R.G., Marvaldi A.E., Anderson R.S. 2007. Weevils, weevils, weevils everywhere. In: Zhang Z.-Q., Shear W.A. (eds), Linnaeus tercentenary: Progress in invertebrate taxonomy. – Zootaxa **1668**: 1–766.

Pakutinskiene I., Kiuberis J. Bezdicka P., Senvaitiene J., Kareiva A. 2007. Analytical characterization of Baltic amber by FTIR, XRD and SEM. – Canadian Journal of Analytical Sciences and Spectroscopy **52**: 297–242.

Peris D., Solórzano Kraemer M.M., Peñalver E., Delclòs X. 2015. New ambrosia beetles (Coleoptera: Curculionidae: Platypodinae) from Miocene Mexican and Dominican ambers and their paleobiogeographical implications. – Organisms Systematics & Evolution **15**: 527–542.

Poinar Jr. G.O. 1992. Life in Amber. – Stanford University Press: Standford. 368 pp.

Ratzeburg J.T.C. 1837. Die Forst-Insecten oder Abbildung und Beschreibung der in den Wäldern Preussens und der Nachbarstaaten als schädlich oder nützlich bekannt gewordenen Insekten. – Königliche Akademie der Wissenschaften: Berlin. 202 pp.

Ronquist F., Teslenko M., Van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice across a Large Model Space. – Systematic Biology **61**: 539–542.

Sadowski E.M., Schmidt A.R., Kunzmann L., Gröhn C., Seyfullah L.J. 2016. *Sciadopitys cladodes* from Eocene Baltic amber. – Botanical Journal of the Linnean Society **180**: 258–268.

Saunders S.S. 1837. Descriptions of some new species of coleopterous insects lately received from Monte Video. – Transactions of the Entomological Society of London **1**: 149–157.

Schaufuss C.F.C. 1905. Borkenkäferstudien, II. – Insektenborse **12**: 12.

Schawaller W. 1981. Pseudoskorpione (Cheliferidae) phoretisch auf Käfern (Platypodidae) in Dominikanischem Bernstein (Stuttgarter Bernsteinsammlung: Pseudoscorpionidea und Coleoptera). – Stuttgarter Beiträge zur Naturkunde, Serie B **71**: 1–17.

Schedl K.E. 1933a. Revue de Zoologie et de Botanique Africaines 23. – Hayez: Bruxelles.

Schedl K.E. 1933b. New Platypodidae from Central and South America. – Revista de Entomologia, Rio de Janeiro **3**: 163–177.

Schedl K.E. 1947. Die Borkenkäfer des baltischen Bersteins. – Zentralblatt für das Gesamtgebiet der Entomologie **2**: 12–45.

Schedl K.E. 1957. Scolytoidea nouveaux du Congo Belge. II. Mission R. Mayné – K. E. Schedl 1952. – Annales du Musée Royal du Congo Belge, Série in 8º, Sciences Zoologiques **56**: 1–162.

Schedl K.E. 1962. New Platypodidae from Mexican amber. – Journal of Paleontology **36**: 1035–1038.

Scudder S.H. 1891. Index to the known fossil insects of the world including myriapods and arachnids. – Bulletin of the United States Geological Survey **71**: 1–744.

Shuckard W.E. 1840. The British Coleoptera delineated, consisting of Figures of all the Genera of British Beetles, drawn in outline by W. Spry, M. E. S. W. – Crofts: London. 339 pp.

Solórzano Kraemer M.M., Kraemer A.S., Stebner F., Bickel D.J., Rust J. 2015. Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in Chiapas, Mexico. – PLoS ONE **10**: e0118820.

Strohmeyer H. 1912. Dreizehn neue Arten der afrikanischen Platypodiden-Gattung *Periommatus* Chap. – Entomologische Blätter **8**: 17–28.

Strohmeyer H. 1914. Coleoptera. Fam. Platypodidae. In: Wytsman P.A.G. (ed.), Genera Insectorum **163**: 1–55.

Swofford D.L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), s4.0b10. – Sinauer Associates, Sunderland, Massachusetts.

Weitschat W., Wichard W. 2002. Atlas of the Plants and Animals in Baltic Amber. – München: Verlag Dr. Friedrich Pfeil. 256 pp.

Weitschat W., Wichard W. 2010. Baltic amber. Pp. 80–115 in Penney D. (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. – Siri Scientific Press: Manchester.

Wolfe A.P., Tappert R., Muehlenbachs K., Boudreau M., McKellar R.C., Basinger J.F., Garrett A. 2009. A new proposal concerning the botanical origin of Baltic amber. – Proceedings of the Royal Society B **276**: 3403–3412.

Wood S.L. 1993. Revision of the genera of Platypodidae (Coleoptera). – The Great Basin Naturalist **53**: 259–281.

Wood S.L., Bright D.E. 1992. Catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: taxonomic index. – Great Basin Naturalist Memoirs **13**: 1–1553.

Zoobank registrations
at http://zoobank.org

Present article: http://zoobank.org/urn:lsid:zoobank.org:pub:C3023E65-BB07-44D0-BCD0-83259C57A782

***Eoplatypus* Cognato & Smith, 2017:** http://zoobank.org/urn:lsid:zoobank.org:act:F07BDB52-85A1-4803-AEA6-8226C29471AC

***Eoplatypus jordali* Peris, Solórzano Kraemer & Cognato, 2017:** http://zoobank.org/urn:lsid:zoobank.org:act:2D2841A2-5B23-4468-8836-2187390BE97C

Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2017

Band/Volume: 75

Autor(en)/Author(s): Peris David, Kraemer Monica M. Solorzano, Smith Sarah M., Cognato Anthony I.

Artikel/Article: Eoplatypus jordali gen.n. et sp.n., the first described Platypodinae (Coleoptera: Curculionidae) from Baltic amber 185-194