

A new genus and species of Dermestidae (Coleoptera) from the Eckfeld Maar crater (Middle Eocene, Germany)

JIŘÍ HÁVA & TORSTEN WAPPLER



Eckfeldattagenus eocenicus gen. et sp. nov. is described from the Middle Eocene Eckfeld Maar (Germany) on the basis of completely preserved specimens, representing one of the rare reports of fossil skin beetles (Coleoptera: Dermestidae: Attageninae). The new genus and species differs from all other Dermestidae by the very flat body form and pronotum, and its unique structure of the antennal club and the wrinkled elytral surface. • Key words: taxonomy, new genus, new species, fossil, Coleoptera, Dermestidae, Germany.

HÁVA, J. & WAPPLER, T. 2014. A new genus and species of Dermestidae (Coleoptera) from the Eckfeld Maar crater (Middle Eocene, Germany). *Bulletin of Geosciences* 89(1), 67–74 (1 figure, appendix). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received July 24, 2013; accepted in revised form October 23, 2013; published online December 12, 2013; issued January 21, 2014.

Jiří Háva, Department of Forest Protection and Entomology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ-165 21, Prague 6 – Suchbátka, Czech Republic • Torsten Wappler (corresponding author), Steinmann Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany; twappler@uni-bonn.de

Dermestidae commonly referred to as skin, larder and carpet beetles are characterized by a variety of ecological habits and a fascinating biology. Most genera are scavengers that feed on dry animal or plant material such as skin or pollen, animal hair, feathers, dead insects or natural fibers. They are even widely used to clean bones during the preparation of skeletons for osteological studies and forensic entomological. In the literature, the traces left on skeletal remains by the family Dermestidae have been documented for dinosaurs (Paik 2000, Roberts *et al.* 2007, Britt *et al.* 2008, Chin & Bishop 2008, Bader *et al.* 2009) and extinct mammals (Martin & West 1995, Kaiser 2000, Laudet & Antoine 2004, Fejfar & Kaiser 2005).

The cosmopolitan beetle family Dermestidae comprises more than 1460 described species (Háva 2003, 2013). According to a cladistic-based analysis of higher categories within the family Dermestidae (Lawrence & Slipinski 2005, Kiselyova & McHugh 2006), six subfamilies could be recognized: Dermestinae (including Marioutinae), Thorictinae, Trinodinae (including Thylodriadiinae), Orphilinae, Attageninae and Megatominae; whereas only members of the Thorictinae are yet unknown from the fossil record. The geological history of the family was summarized by Háva & Prokop (2004) and Kirejtshuk *et al.* (2009), with new information appended in the present contribution (appendix). The earliest fossils assigned tentatively to Dermestidae are isolated elytra

from the Triassic deposits of Queensland, described by Dunstan (1923), but the assignment of these fossils was doubted by Háva & Prokop (2004). The first definitive remains of the family have been recorded from the Lower Cretaceous Lebanese amber (Kirejtshuk *et al.* 2009). However, the majority of fossil dermestids were described from inclusions in Baltic (40–35 Ma BP) and Dominican Amber (20–17 Ma BP) – most of these are representing relatively modern groups, thereby relating more to questions of Tertiary biogeography than to higher-level branching patterns (Kiselyova & McHugh 2006).

Herein we provide the description of a new Paleogene dermestid beetle from the Middle Eocene Eckfeld Maar. This deposit has produced a broad spectrum of fossils ranging from organic molecules, micro-organisms, aquatic invertebrates, plants and insects and their varied associations, to a wide range of vertebrates including articulated mammals exhibiting soft tissue preservation and gut contents (*e.g.*, Lutz *et al.* 2010). The new species belongs to the Attageninae of the Dermestidae and is placed in a new genus most probably closely related to the extant genus *Attagenus* Latreille, 1802.

Material and methods

The Fossilagerstätte of Eckfeld is a deposit of a maar lake, which was formed during the early middle Eocene. The

basin was initially formed by volcanic explosions, resulting in deep depressions on top of diatremes that was soon occupied by a lake. Following early stages with succeeding volcanoclastic and predominantly siliciclastic sedimentation, the lake became meromictic and the finely laminated bituminous claystone (“oilshale”) was formed in the quiet anoxic bottom layer of the lake. The oilshale contains biomarkers and lithified bacteria, algae, a great diversity of tracheophytes, numerous arthropods, few molluscs and a wide range of vertebrates, documenting a highly diverse terrestrial flora and fauna representing an ecosystem towards the end of the middle Eocene (*e.g.*, Neuffer *et al.* 1996; Lutz *et al.* 1998, 2010; Wilde & Frankenhäuser 1998; Lutz & Neuffer 2000; Wappler 2002, 2003a, b; Wappler & Engel 2003, 2006; Wappler & Andersen 2004; Wappler *et al.* 2004, 2005; Wappler & Heiss 2006; Wappler & Petrulevičius 2007; Petrulevičius *et al.* 2008; Dlusky *et al.* 2008, 2009). The Eckfelder Maar insect taphocoenosis contains a total of nearly 4700 fossil specimens. Most of them are in good condition with a potential for exceptional details of preservation. This fossil record documents a highly diverse terrestrial fauna and flora, while aquatic life is rather poorly represented. The insect taphocoenosis is predominantly composed of Coleoptera (84%) (*e.g.*, Lutz 1993, Wappler 2003a, b).

The crater structure at the Eckfeld Maar near Manderscheid, Eifel, Germany, originally had a diameter of 900 m and a depth of about 170 m. The depth of the maar lake initially exceeded 110 m and might have reached 150 m (Pirrung *et al.* 2001). Rapid sedimentation over a 250.000 year period combined with anoxic alkaline conditions resulted in the absence of bioturbation and explains the perfect preservation of fossils within the oil-shale laminae (Mingram 1998).

Biochronologically the biota of the Eckfeld Maar represent the late Geiseltalium of the European Land Mammal Ages (ELMA), which corresponds to the middle part of the Lutetian of the global geochronological time scale (Franzen 1993). Argon ^{40/39}Ar dating of basalt from the diatreme breccia underlying the lake sediments resulted in an age of 44.3 ± 0.4 Ma at Eckfeld (Mertz *et al.* 2000).

The specimens examined in the present work were gathered from the collection of the Naturhistorisches Museum Mainz, Landessammlung für Naturkunde Rheinland-Pfalz (NHMM). The type specimens are equipped with red, printed labels bearing the text as follows: “HOLOTYPE (or PARATYPE, respectively), *Eckfeldattagenus eocenicus* gen. et sp. nov. J. Háva & T. Wappler det. 2013”.

The specimens were studied by immersing the slab in glycerine to prevent oxidation. All metrics were made using an ocular micrometer and are given in millimetres. The nomenclature of dermestids is based on the interpretations of Lawrence & Slipinski (2005) and Háva (2007).

Systematic palaeontology

Family Dermestidae
Subfamily Attageninae

Eckfeldattagenus gen. nov.

Figure 1

Type species. – *Eckfeldattagenus eocenicus* sp. nov. (by monotypy).

Diagnosis. –

Adult female: Body length 5.5–6.3 mm. The antennae consist of the 11 antennomeres, antennal club consist of two antennomeres (Fig. 1D). Last antennal antennomere is long, oval. Pronotum is long trapezoidal, with a clear wrinkled surface structure. Elytra long, parallel, with a clear wrinkled structure.

Adult male: Externally similar to female, but differs by the structure of antennae, with the 10th segment being slightly more prolonged (Fig. 1F, G).

Remarks. – *Eckfeldattagenus* is similar to genera belonging to the Attageninae and in particular to the genus *Attagenus* according to a Prosternum not forming a “collar”, therefore, mouthparts are free, but on the other hand it differs from all other Dermestidae by the very flat body form, the outline of the pronotum, and its unique structure of the antennal club and the wrinkled elytral surface.

A key to the genera is given below:

- 1(5) antennomeres of antennal club compact
- 3(4) antennal club consist *Eckfeldattagenus* gen. nov.
of two antennomeres
- 4(3) antennal club consist *Attagenus* Latreille, 1802
of three antennomeres
- 5(1) antennomeres of antennal club loosely joined
- 6(7) cuticle bicolorous *Novelsis* Casey, 1900
or unicolorous with bicolorous pubescence
- 7(6) cuticle and pubescence unicolorous, terminal antennomere very long, arenicollis species
- 8(9) profemora stout *Araphonotos* Beal & Kadej, 2008
- 9(8) profemora slender *Sefrania* Pic, 1899

Eckfeldattagenus gen. nov. differs from the genus *Egidyella* Reitter, 1899 (tribe Egidyellini) by the five visible abdominal ventrites (in the genus *Egidyella* six ventrites are visible).

Etymology. – The new generic name is a combination of Eckfeld (type locality from were the specimens are found), and *Attagenus*, type genus for one of the most abundant pests in stored products. The gender is masculine.

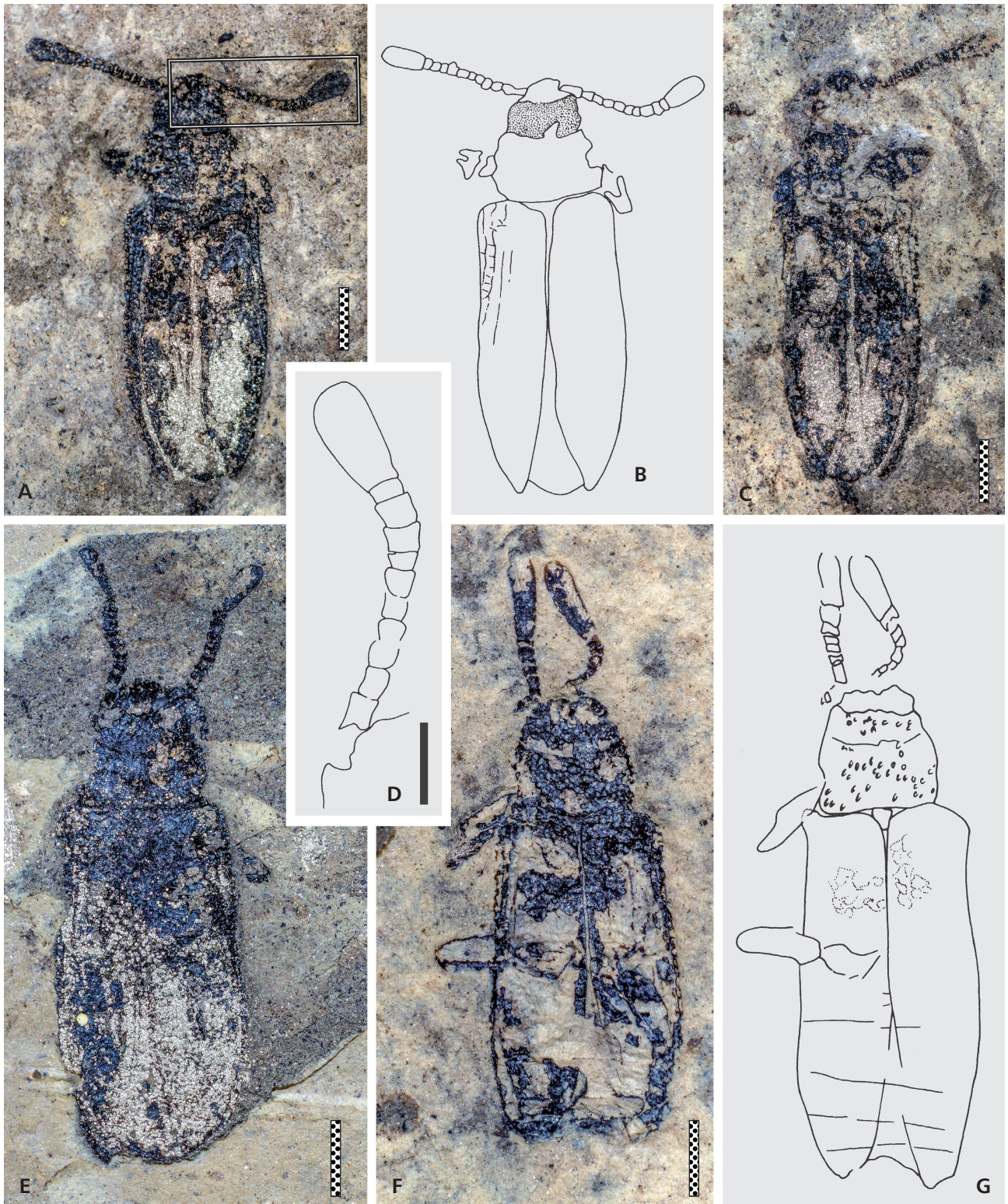


Figure 1. *Eckfeldattagenus eocenicus* gen. et sp. nov. • A – holotype (PE 2000/995a, LS). • B – habitus diagram of A. • C – counterpart of holotype (PE 2000/995b, LS). • D – detail of antennae in A. • E – paratype (PE 2000/996a, LS). • F – paratype (PE 2000/997a, LS), arrows indicating the presences of relatively short and thin hairs. • G – habitus diagram of F. Dotted scale bar = 1 mm; solid scale bar = 0.5 mm.

***Eckfeldattagenus eocenicus* sp. nov.**

Figure 1

2003a *Attagenus?* sp. indet. Wappler; p. 95, abb. 64, pl. 11, fig. h, i.

2003b *Attagenus?* sp. indet. Wappler; p. 95, abb. 64, pl. 11, fig. h, i.

Type material. – Holotype (female) (PE 2000/995 a+b). Paratype: 1 spec. (female) (PE 2000/996 a+b), 1 spec. (male) (PE 2000/997 a+b). The type material is deposited in the Naturhistorisches Museum Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany.

Type locality. – Eckfeld Maar near Manderscheid, Eifel Mountains, Germany.

Stratigraphic occurrence. – Middle Eocene (ELMA Geiseltalian, MP13, 44.3 ± 0.4 Ma).

Diagnosis. – As for the genus (*vide supra*).

Description. – Holotype measurements: total length 6.3 mm, pronotum length 0.9 mm, elytra length 4.1 mm, antennae length 4.2 mm, terminal antennomere length 0.7 mm. The antennae consist of the 11 antennomeres, with a two-segmented antennal club. Last antennal antennomere is long, oval, and covered with dark, relatively short and thin subrecumbent hairs. Pronotum is long trapezoidal, with a clear wrinkled surface structure. Elytra long, parallel, with a clear structure wrinkled surface.

Etymology. – *Eocenicus* in reference to the Eocene age of the fossil.

Discussion. – Because of the preservation style, compression fossils cannot be easily compared to amber fossils or extant genera and species. Nonetheless, they can be diagnosed moderately well and differentiated with reasonable certainty from other extinct and extant genera. In some aspects, *Eckfeldattagenus* resembles members of the related genus, *Attagenus* Latreille, 1802 (*vide supra*). The latter contains about 180 recent species. Only eight fossil species are known worldwide; two species from Early Oligocene deposits in Colorado (*A. aboriginalis* Wickham, 1913 and *A. sopitus* Scudder, 1900), one species from Middle Miocene deposit in Germany (*A. extinctus* Heyden & Heyden, 1865), four species from the Eocene Baltic amber (*A. hoffeinsorum* Háva, Prokop & Herrmann, 2006a, *A. obesus* Háva, Prokop & Herrmann, 2008, *A. balticus* Háva, Prokop & Herrmann, 2008 and *A. yantarnyi* Háva & Bukejs, 2012), and one species from Dominican amber (*A. ambericus* Háva & Prokop, 2004). The newly described species differs from all fossil and recent species by the presence of

very flat form of the body, a unique structure of the antennal club, indicating even some sexual dimorphism expressed by the length of the 10th antennomere, and a more elongated, trapezoidal outline of the pronotum.

A comparison with the three described compression fossils *Attagenus aboriginalis* Wickham, 1913 [Colorado (Early Oligocene: Florissant)], *Attagenus extinctus* C. Heyden & L. Heyden, 1865 [Germany (Middle Miocene)] and *Attagenus sopitus* Scudder, 1900 [Early Oligocene: Florissant]), reveals that *E. eocenicus* gen. et sp. nov. differs mainly by the following characters: (1) body maximum length 5.5–6.3 mm, long, parallel; (2) antennae very long, antennal club composed of two antennomeres in male and two in female (*Attagenus* antennal club consists of three antennomeres).

Conclusions

1. Tertiary fossils of dermestid beetles are clearly more related to the extant fauna even though the two Cretaceous records represent members of extant families (comp. appendix). Interestingly, basalmost members of the Thorictinae, sister group to the remainder of Dermestidae are completely absent from the fossil record yet.

2. Although cosmopolitan in distribution, dermestid beetles species are most active during warmer climate conditions (*e.g.*, Klok & Harrison 2013, fig. 5).

3. The temperature requirements of dermestids did not conflict with the interpretations of Middle Eocene climatic conditions in the Eifel region based on the macrobotanical record. Grein *et al.* (2011) and Wappler *et al.* (2012) concluded that during middle Eocene climate at the Central European locality the mean annual temperature was in the order of above 20 °C, probably around 22 °C. The summers were rather hot with temperatures of the warmest month between 24.7 °C and 27.9 °C. It is interesting, therefore, that the majority of insect species from the Eckfeld Maar are today found in the Southern Hemisphere but are known from Cenozoic fossils in Europe and other parts of the Northern Hemisphere (*e.g.*, Wappler 2003a, p. 181ff).

Acknowledgements

We are very indebted to Herbert Lutz (Naturhistorisches Museum Landessammlung für Naturkunde Rheinland-Pfalz, Mainz, Germany) for providing to the interesting material for study and to Thomas Engel for taking photos of the specimens. The authors also thank the reviewers Bo Wang, Nanjing, and André Nel, Paris, for their critical reading of the manuscript and constructive suggestions. This is “Fossilfundstätte Eckfelder Maar (Mittel-Eozän)” contribution No. 137.

References

- BADER, K.S., HASIOTIS, S.T. & MARTIN, L.D. 2009. Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Morrison Formation, northeastern Wyoming. *Palaios* 24, 140–158. DOI 10.2110/palo.2008.p08-058r
- BEAL, R.S. 1972. A new fossil *Cryptorhopalum* (Dermestidae: Coleoptera) from Tertiary amber of Chiapas, Mexico. *Journal of Palaeontology* 46, 317–318.
- BRITT, B.B., SCHEETZ, R.D. & DANGERFIELD, A. 2008. A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA. *Ichnos* 15, 59–71. DOI 10.1080/10420940701193284
- CHIN, K. & BISHOP, J.R. 2008. Exploited twice: bored bone in a theropod coprolite from the Jurassic Morrison Formation of Utah, U.S.A., 379–387. In BROMLEY, R.G., BUATOIS, L.A., MÁNGANO, G., GENISE, J.F. & MELCHOR, R.N. (eds) *Sediment-organism Interactions: A Multifaceted Ichnology*. *SEPM Special Publication* 88.
- COCKERELL, T.D.A. 1917. Arthropods in Burmese Amber. *Psyche* 24, 40–45. DOI 10.1155/1917/83242
- DLUSSKY, G.M., WAPPLER, T. & WEDMANN, S. 2008. New middle Eocene formicid species from Germany and the evolution of weaver ants. *Acta Palaeontologica Polonica* 53, 615–626. DOI 10.4202/app.2008.0406
- DLUSSKY, G.M., WAPPLER, T. & WEDMANN, S. 2009. Fossil ants of the genus *Gesomyrmex* Mayr (Hymenoptera, Formicidae) from the Eocene of Europe and remarks on the evolution of arboreal ant communities. *Zootaxa* 2031, 1–20.
- DUNSTAN, B. 1923. Mesozoic Insects of Queensland. Part I. Introduction and Coleoptera. *Queensland Geological Survey Publication* 273, 1–88.
- FEJFAR, O. & KAISER, T.M. 2005. Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in the Doupov Mountains, northwestern Bohemia. *Palaeontologia Electronica* 8(8A), <http://palaeo-electronica.org>, 1–11.
- FRANZEN, J.L. 1993. Das biostratigraphische Alter der Fossilagerstätte Eckfelder Maar bei Manderscheid (Eifel). *Mainzer Naturwissenschaftliches Archiv* 31, 201–214.
- GREIN, M., UTESCHER, T., WILDE, V. & ROTH-NEBELSICK, A. 2011. Reconstruction of the middle Eocene climate of Messel using palaeobotanical data. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 260, 305–318. DOI 10.1127/0077-7749/2011/0139
- HÁVA, J. 2003. World Catalogue of the Dermestidae (Coleoptera). *Studie a zprávy Oblastního muzea Praha-východ v Brandýse nad Labem a Staré Boleslavi, Supplementum* 1, 1–196.
- HÁVA, J. 2007. Dermestidae, 57, 299–320. In LÖBL, I. & SMETANA, A. (eds) *Catalogue of Palaearctic Coleoptera. Volume 4. Elateroidea – Derodontoidea – Bostrichoidea – Lymexyloidea – Cleroidea – Cucujoidea*. Apollo Books, Stenstrup.
- HÁVA, J. 2008. *Globicornis rakovici* n. sp., a new fossil species (Coleoptera: dermestidae: Megatomini) from Baltic amber. *Alavesia* 2, 3–5.
- HÁVA, J. 2013. Description of *Sodaliatoma konvickai* gen. et sp. nov. (Coleoptera: Dermestidae: Megatominae) from Peru. *Boletín de la Sociedad Entomológica Aragonesa* 52, 113–115.
- HÁVA, J. & BUKEIS, A. 2012. *Attagenus yantarnyi* sp. nov., a new species from Baltic Amber (Coleoptera: Dermestidae). *Baltic Journal of Coleopterology* 12, 155–158.
- HÁVA, J. & PROKOP, J. 2004. New fossil dermestid-beetles (Coleoptera: Dermestidae) from the Dominican amber, with an appendix listing known fossil species of this family. *Acta Societatis Zoologicae Bohemicae* 68, 173–182.
- HÁVA, J. & PROKOP, J. 2006. *Trinodes puetzi* sp. nov., a new fossil species described from the Baltic Amber (Coleoptera: Dermestidae). *Acta Societatis Zoologicae Bohemicae* 69, 277–279.
- HÁVA, J., PROKOP, J. & HERRMANN, A. 2006a. New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber. *Acta Societatis Zoologicae Bohemicae* 69, 281–287.
- HÁVA, J., PROKOP, J. & HERRMANN, A. 2008. New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber – III. *Acta Societatis Zoologicae Bohemicae* 71, 151–157.
- HÁVA, J., PROKOP, J. & KADEJ, M. 2006b. New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber – II. *Studies and Reports of Regional Museum Prague-East, Taxonomic Series* 2, 1–14.
- HEER, O. 1847. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Erste Abteilung: Käfer. *Neue Denkschriften Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften* 9, 1–222.
- HIEKE, F. & PIETRZENIUK, E. 1984. Die Bernstein-Käfer des Museum für Naturkunde, Berlin (Insecta, Coleoptera). *Mitteilungen des Zoologischen Museum Berlin* 60, 297–326.
- HEYDEN, C. & HEYDEN, L. VON 1865. Fossile Insekten aus der Braunkohle von Salzhausen. *Palaeontographica* 14, 31–35.
- KAISER, T.M. 2000. Proposed fossil insect modification to fossil mammalian bone from Plio-Pleistocene hominid-bearing deposits of Laetoli (Northern Tanzania). *Annals of the Entomological Society of America* 93, 693–700. DOI 10.1603/0013-8746(2000)093[0693:PFIMTF]2.0.CO;2
- KIREJTSHUK, A.G., AZAR, D., TAFFOREAU, P., BOISTEL, R. & FERNANDEZ, V. 2009. New beetles of Polyphaga (Coleoptera, Polyphaga) from Lower Cretaceous Lebanese amber. *Denisia* 86, 119–130.
- KIREJTSHUK, A.G., HÁVA, J. & NEL, A. 2010. New genus and species of subfamily Trinodinae (Coleoptera, Polyphaga, Dermestidae) from Lowermost Eocene French amber. *Zoosystematica Rossica* 19, 54–69.
- KISELYOVA, T. & MCHUGH, J. 2006. A phylogenetic study of Dermestidae (Coleoptera) based on larval morphology. *Systematic Entomology* 31, 469–507. DOI 10.1111/j.1365-3113.2006.00335.x
- KLOK, C.J. & HARRISON, J.F. 2013. The Temperature Size Rule in Arthropods: Independent of Macro-Environmental Variables but Size Dependent. *Integrative and Comparative Biology* 53(4), 557–570. DOI 10.1093/icb/ict075
- LARSSON, S.G. 1978. Baltic amber – a palaeobiological study. *Entomograph* 1, 1–192.
- LAUDET, F. & ANTOINE, P.-O. 2004. Des chambres de pupation de Dermestidae (Insecta: Coleoptera) sur un os de mammifère tertiaire (phosphorites du Quercy): implications taphonomiques et paléoenvironnementales. *Geobios* 37, 376–381. DOI 10.1016/j.geobios.2003.04.005
- LAWRENCE, J.F. & ŚLIPINSKI, A. 2005. Three new genera of Indo-Australian Dermestidae (Coleoptera) and their phylogenetic significance. *Invertebrate Systematics* 19, 231–261. DOI 10.1071/IS04033
- LUTZ, H. 1993. Zur Taphonomie der aquatischen und terrestrischen Fauna des “Eckfelder Maares” (Mittel-Eozän;

- Deutschland): Ergebnisse aus den Grabungen 1990–1992. *Mainzer Naturwissenschaftliches Archiv* 31, 85–113.
- LUTZ, H., FRANKENHÄUSER, H. & NEUFFER, F.O. 1998. *Fossilfundstätte Eckfelder Maar – Archiv eines mitteleozänen Lebensraumes in der Eifel*. 51 pp. Landessammlung für Naturkunde, Mainz.
- LUTZ, H., KAULFUS, U., WAPPLER, T., LÖHNERTZ, W., WILDE, V., MERTZ, D.F., MINGRAM, J., FRANZEN, J.L., FRANKENHÄUSER, H. & KOZIOL, M. 2010. Eckfeld Maar: Window into an Eocene Terrestrial Habitat in Central Europe. *Acta Geologica Sinica* 84, 984–1009. DOI 10.1111/j.1755-6724.2010.00237.x
- LUTZ, H. & NEUFFER, F.O. 2000. The middle Eocene fossil-lagerstätte Eckfeld Maar. *GFF* 122, 95–96. DOI 10.1080/11035890001221095
- MARTIN, L.D. & WEST, D.L. 1995. The recognition and use of dermestid (Insecta, Coleoptera) pupation chambers in paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 113, 303–310. DOI 10.1016/0031-0182(95)00058-T
- MERTZ, D.F., SWISHER, C.C., FRANZEN, J.L., NEUFFER, F.O. & LUTZ, H. 2000. Numerical dating of the Eckfeld maar fossil site, Eifel, Germany: a calibration mark for the Eocene time scale. *Naturwissenschaften* 87, 270–274. DOI 10.1007/s001140050719
- MINGRAM, J. 1998. Laminated Eocene maar-like sediments from Eckfeld (Eifel region, Germany) and their short-term periodicities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 140, 289–305. DOI 10.1016/S0031-0182(98)00021-2
- NEUFFER, F.O., GRUBER, G., LUTZ, H. & FRANKENHÄUSER, H. 1996. *Das Eckfelder Maar – Zeuge tropischen Lebens in der Eifel*. 102 pp. Landessammlung für Naturkunde, Mainz.
- PETRULEVICIUS, J.F., WAPPLER, T., WEDMANN, S., RUST, J. & NEL, A. 2008. New megapodagrionid damselflies (Odonata: Zygoptera) from the Paleogene of Europe. *Journal of Paleontology* 82, 1173–1181. DOI 10.1666/07-091.1
- PAIK, I.S. 2000. Bone chip-filled burrows associated with bored dinosaur bone in floodplain paleosols of the Cretaceous Hasandong Formation, Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 157, 213–225. DOI 10.1016/S0031-0182(99)00166-2
- PIERCE, W.D. 1960. Fossil arthropods of California. 23. Silicified insects in Miocene nodules from the Calico Mountains. *Bulletin of the Southern California Academy of Sciences* 59, 40–49.
- PIRRUNG, M., BÜCHEL, G. & JACOBY, W. 2001. The Tertiary volcanic basins of Eckfeld, Enspel and Messel (Germany). *Zeitschrift der Deutschen Geologischen Gesellschaft* 152, 27–59.
- ROBERTS, E.M., ROGERS, R.R. & FOREMAN, B.Z. 2007. Continental insect borings in dinosaur bone: Examples from the Late Cretaceous of Madagascar and Utah. *Journal of Paleontology* 81, 201–208. DOI 10.1666/0022-3360(2007)81[201:CIBIDB]2.0.CO;2
- ROSS, A.J. & YORK, P.V. 2000. A list of type and figured specimens of insects and other inclusions in Burmese amber. *Bulletin of the Natural History Museum (Geology)* 56, 11–20.
- SCUDDER, S.H. 1900. Adepagous and Clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado, with description of a few other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America. *Monography of the United States Survey Washington* 40, 3–148.
- SPAHR, U. 1981. Bibliographie der Bernstein- und Kopal-Käfer (Coleoptera). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 72, 1–21.
- WAPPLER, T. 2002. *Dicranoptycha* (Insecta: Nematocera: Limoniidae) aus der mitteleozänen Fossilagerstätte Eckfelder Maar bei Manderscheid / Eifel (Deutschland). *Mainzer Naturwissenschaftliches Archiv* 40, 129–134.
- WAPPLER, T. 2003a. Systematik, Phylogenie, Taphonomie und Paläoökologie der Insekten aus dem Mittel-Eozän des Eckfelder Maars, Vulkaneifel. *Clausthaler Geowissenschaften* 2, 1–241.
- WAPPLER, T. 2003b. Die Insekten aus dem Mittel-Eozän des Eckfelder Maars, Vulkaneifel. *Mainzer Naturwissenschaftliches Archiv, Beiheft* 27, 1–234.
- WAPPLER, T. & ANDERSEN, N.M. 2004. Fossil water striders from the Middle Eocene fossil sites Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift* 78, 41–52. DOI 10.1007/BF03009129
- WAPPLER, T. & ENGEL, M.S. 2003. The Middle Eocene bee faunas of the Eckfeld Maar and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* 77, 908–921. DOI 10.1666/0022-3360(2003)077<0908:TMEBFO>2.0.CO;2
- WAPPLER, T. & ENGEL, M.S. 2006. New record of *Mastotermes* from the Eocene of Germany (Isoptera: Mastotermitidae). *Journal of Paleontology* 80, 380–385. DOI 10.1666/0022-3360(2006)080[0380:ANROMF]2.0.CO;2
- WAPPLER, T., ENGEL, M.S. & HAAS, F. 2005. The earwigs (Dermaptera: Forficulidae) from the middle Eocene Eckfeld maar, Germany. *Polskie Pismo Entomologiczne* 74, 227–250.
- WAPPLER, T. & HEISS, E. 2006. Flatbugs from Paleogene limnic sediments. II. Eckfeld maar (Heteroptera: Aradidae). *Mainzer Naturwissenschaftliches Archiv* 44, 53–60.
- WAPPLER, T., LABANDEIRA, C.C., RUST, J., FRANKENHÄUSER, H. & WILDE, V. 2012. Testing for the effects and consequences of mid Paleogene climate change on insect herbivory. *PLoS ONE* 7, e40744. DOI 10.1371/journal.pone.0040744
- WAPPLER, T. & PETRULEVICIUS, J.F. 2007. Priscalestidae, a new damselfly family (Odonata: Lestinoidea) from the Middle Eocene Eckfeld maar of Germany. *Alavesia* 1, 69–73.
- WAPPLER, T., SMITH, V.S. & DALGLEISH, R.C. 2004. Scratching an ancient itch: an Eocene bird louse fossil. *Proceedings of the Royal Society of London B (Suppl.)* 271, 255–258. DOI 10.1098/rsbl.2003.0158
- WICKHAM, H.F. 1912. A report on some recent collections of fossil Coleoptera from the Miocene shales of Florissant. *Bulletin from the Laboratory National History University, Iowa* 6, 3–38.
- WICKHAM, H.F. 1913. The Princeton collection of fossil Beetles from Florissant. *Annals of the Entomological Society of America* 6, 359–366.
- WILDE, V. & FRANKENHÄUSER, H. 1989. Vorläufige Mitteilungen zur Flora aus dem Alttertiär von Eckfeld-Ergebnisse einer ersten Durchsicht des Fundmaterials aus den Grabungen von 1987 und 1988. *Mainzer Naturwissenschaftliches Archiv* 27, 23–31.
- ZHANTIEV, R.D. 2006. New Species of Late Eocene Dermestid Beetles (Coleoptera, Dermestidae) from the Rovno and Baltic Ambers. *Paleontological Journal* 40(5), 560–563. DOI 10.1134/S0031030106050108
- ZHERIKHIN, V.V. & ROSS, A.J. 2000. A review of the history, geology and age of Burmese amber (Burmite). *Bulletin of the Natural History Museum* 56, 3–10.

Appendix

Geological records of Dermestidae (updated from Háva & Prokop 2004, Kirejtshuk *et al.* 2009).

Taxon	Fossil type	Epoche	Locality	References
Subfamily Dermestinae				
Tribe Dermestini				
<i>Dermestes</i> Linnaeus				
<i>Dermestes larvalis</i> Cockerell (larvae)	Inclusion	Cretaceous (Albian)	Myanmar	Cockerell (1917), Ross & York (2000), Zherikhin & Ross (2000)
<i>Dermestes pauper</i> Heer	Compression	Early Miocene	Radoboj	Heer (1847)
<i>Dermestes progenior</i> Zhantiev	Inclusion	Eocene (Lutetian)	Rovno	Zhantiev (2006), Háva (2008)
<i>Dermestes tertiaris</i> Wickham	Compression	Eocene–Oligocene	Florissant, CO	Wickham (1912)
<i>Dermestes vetustus</i> Zhantiev	Inclusion	Eocene (Lutetian)	Rovno	Zhantiev (2006), Háva (2008)
<i>Dermestes</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Dermestes</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
Subfamily Attageninae				
Tribe Attagenini				
<i>Attagenus</i> Latreille				
<i>Attagenus aboriginalis</i> Wickham	Compression	Eocene–Oligocene	Florissant, CO	Wickham (1913)
<i>Attagenus ambericus</i> Háva & Prokop	Inclusion	Miocene (Burdigalian)	Dominican Republic	Háva & Prokop (2004)
<i>Attagenus balticus</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2008)
<i>Attagenus extinctus</i> C. Heyden & L. Heyden	Compression	Middle Miocene	Salzhausen, Germany	Heyden & Heyden (1865)
<i>Attagenus hoffeinsorum</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006a, 2008)
<i>Attagenus obesus</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2008)
<i>Attagenus sopitus</i> Scudder	Compression	Eocene–Oligocene	Florissant, CO	Scudder (1900)
<i>Attagenus yantarnyi</i> Háva & Bukejs	Inclusion	Eocene (Lutetian)	Baltic	Háva & Bukejs (2012)
<i>Attagenus</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Attagenus</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
<i>Eckfeldattagenus eocenicus</i> gen. et sp. nov.	Compression	Eocene (Lutetian)	Eckfelder maar	this study
Subfamily Megatominae				
Tribe Anthrenini				
<i>Anthrenus</i> O.F. Müller				
<i>Anthrenus</i> sp. (larvae)	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Anthrenus</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
<i>Anthrenus (Nanthrenus) ambericus</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006a, 2008)
<i>Anthrenus (N.) electron</i> Háva, Prokop & Kadej	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006b)
<i>Anthrenus (N.) groehni</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006a)
<i>Anthrenus (N.) kerneggeri</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2008)
Tribe Megatomini				
<i>Amberoderma</i> Háva & Prokop				
<i>Amberoderma beali</i> Háva & Prokop	Inclusion	Miocene (Burdigalian)	Dominican Republic	Háva & Prokop (2004)
<i>Cryptorhopalum</i> Guérin-Méneville				
<i>Cryptorhopalum americum</i> Háva & Prokop	Inclusion	Miocene (Burdigalian)	Dominican Republic	Háva & Prokop (2004)
<i>Cryptorhopalum dominicanum</i> Háva & Prokop	Inclusion	Miocene (Burdigalian)	Dominican Republic	Háva & Prokop (2004)
<i>Cryptorhopalum electron</i> Beal	Inclusion	Miocene (Burdigalian)	Mexico, Dominican Republic	Beal (1972), Háva & Prokop (2004)
<i>Cryptorhopalum jantarcum</i> Háva & Prokop	Inclusion	Miocene (Burdigalian)	Dominican Republic	Háva & Prokop (2004)
<i>Globicornis</i> Latreille				
<i>Globicornis ambericus</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006a, b)

Taxon	Fossil type	Epoche	Locality	References
<i>Globicornis rakovici</i> Háva	Inclusion	Eocene (Lutetian)	Baltic	Háva (2008)
<i>Globicornis</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Globicornis</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
<i>Megatoma</i> Herbst				
<i>Megatoma electra</i> Zhantiev	Inclusion	Eocene (Lutetian)	Baltic	Zhantiev (2006), Háva (2008)
<i>Megatoma</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Hieke & Pietrzyński (1984)
<i>Miocryptorhopalum</i> Pierce				
<i>Miocryptorhopalum kirkbyae</i> Pierce (larvae)	Compression	Miocene	Calico Mts, CA	Pierce (1960)
<i>Orphinus</i> Motschulsky				
<i>Orphinus</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Orphinus</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
<i>Phradonoma</i> Jacquelin du Val				
<i>Phradonoma americum</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2008)
<i>Trogoderma</i> Dejean				
<i>Trogoderma larvalis</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2006a)
<i>Trogoderma</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Hieke & Pietrzyński (1984)
Subfamily Orphilinae				
Tribe Orphilini				
<i>Orphilus</i> Erichson				
<i>Orphilus dubius</i> Wickham	Compression	Eocene–Oligocene	Florissant, CO	Wickham (1912)
Subfamily Trinodinae				
Tribe Trinodini				
<i>Evoineia</i> Beal				
<i>Evoineia americana</i> Háva, Prokop & Herrmann	Inclusion	Eocene (Lutetian)	Baltic	Háva <i>et al.</i> (2008)
<i>Oisenodes</i> Kirejtshuk, Háva & Nel				
<i>Oisenodes azari</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Oisenodes clavatus</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Oisenodes gallicus</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Oisenodes metepisternalis</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Oisenodes oisensis</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Oisenodes transversus</i> Kirejtshuk, Háva & Nel	Inclusion	Lowermost Eocene	Chevrière, France	Kirejtshuk <i>et al.</i> (2010)
<i>Trinodes</i> Dejean				
<i>Trinodes puetzi</i> Háva & Prokop	Inclusion	Eocene (Lutetian)	Baltic	Háva & Prokop (2006), Háva <i>et al.</i> (2006a)
<i>Trinodes</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Larsson (1978)
<i>Trinodes</i> sp.	Inclusion	Eocene (Lutetian)	Baltic	Spahr (1981)
Tribe Cretonodini				
<i>Cretonodes</i> Kirejtshuk & Azar				
<i>Cretonodes antounazari</i> Kirejtshuk & Azar	Inclusion	Aptian	Lebanon	Kirejtshuk <i>et al.</i> (2009)
GENERA INCERTAE SEDIS				
<i>Reeveana</i> Dunstan				
<i>Reeveana intermedia</i> Dunstan	Compression	Late Triassic	Queensland, Australia	Dunstan (1923)
<i>Reeveana major</i> Dunstan	Compression	Late Triassic	Queensland, Australia	Dunstan (1923)
<i>Reeveana minor</i> Dunstan	Compression	Late Triassic	Queensland, Australia	Dunstan (1923)
<i>Tryoniopsis</i> Dunstan				
<i>Tryoniopsis granulata</i> Dunstan	Compression	Late Triassic	Queensland, Australia	Dunstan (1923)
<i>Tryoniopsis punctata</i> Dunstan	Compression	Late Triassic	Queensland, Australia	Dunstan (1923)