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RESEARCH PAPER

First record of the family Trogossitidae (Insecta, Coleoptera) in the Late Pliocene deposits of Willershausen (Germany)

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Abstract A new species of the genus *Peltis* (Coleoptera, Trogossitidae, Peltinae), *P. antehercynica* sp. nov., is described from the Pliocene lake sediments of the former clay pit of Willershausen (Lower Saxony, Germany). The clearly visible antennae and elytra sculpturing of fossil provide clear morphological information about generic position, and other features, some of them unique in the Peltinae, show that it is an independent new way. In addition, the importance, geology and stratigraphy of the Willershausen Fossil Lagerstätte is briefly discussed.

Keywords Coleoptera · Cleroidea · Trogossitidae · *Peltis* · Pliocene · Willershausen

Kurzfassung Eine neue Art der Gattung *Peltis* (Coleoptera, Trogossitidae, Peltinae), *P. antehercynica* sp. nov., wird aus den jungpliozänen Ablagerungen der ehemaligen Tongrube von Willershausen (Niedersachsen, Deutschland) beschrieben. Die deutlich erkennbaren Antennen und die Skulpturierung der Elytren des Fossils liefern klare morphologische Informationen zur generischen Stellung. Weitere Merkmale, einige davon einzigartig innerhalb der Peltinae, zeigen, dass es sich um eine selbständige neue Art handelt. Ferner wird eine kurze Übersicht über die Geologie, das mögliche Alter, aber auch die Bedeutung der ehemaligen Tongrube von Willershausen diskutiert.

Schlüsselwörter Coleoptera · Cleroidea · Trogossitidae · *Peltis* · Pliozän · Willershausen

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Introduction

Since the first geological description by Wegele (1914), the now abandoned clay pit of Willershausen has become internationally known as an important Fossil Lagerstätte situated in the western foreland of the Harz Mountains (Lower Saxony, Northern Germany). The exceptional importance of the Willershausen site is also mentioned in modern textbooks on palaeoentomology, as for example in Rasnitsyn and Zherikhin (2002: 443) and Grimaldi and Engel (2005). As already listed by Krüger (1979a, b), the fossils include diverse algae, fungi, lichens, numerous terrestrial plants (mainly leaves), and among the animals include Bivalvia, Gastropoda, Annelida, Arachnida, Insecta, Crustacea, Teleostei, Amphibia, Reptilia, Aves, and Mammalia. A modern analysis of the diversity of vertebrates has been elaborated by Gehler (2003). The total number of fossil specimens is estimated at about 50,000, with more than 500 described species distinguished thus far. Most abundant are leaves and insects. Plant/animal interactions are documented by a large number of galls, mines, and foliage damage by feeding activities (Straus 1977; Titchener 1999; Adroit and Wappler, pers. observ.).

In the present article, a hitherto unknown beetle family, the Trogossitidae, of the Late Pliocene (Piacenzian) age

from the Fossil Lagerstätte Willershausen is described. A number of other beetles from Willershausen have already been described by Korge (1967: Staphylinidae), Schmidt (1967: Cerambycidae), Gersdorf (1969, 1971, 1976: all remaining groups), and Schweigert (2003: Cerambycidae, Scarabaeidae). The rhinoceros beetle mentioned by Gersdorf (1971) has been revised by Brauckmann et al. (2013).

The evolutionary significance of the Pliocene for insects largely concerns the origins of modern species and sweeping changes in their distribution in the more recent past (e.g., Elias 2015; Rizzo et al. 2013; Su et al. 2015).

Importance, geology and stratigraphy of the Willershausen Fossil Lagerstätte

As compiled by Meischner (2000), in the meantime, many details have become known concerning the Fossil Lagerstätte of Willershausen, e.g., its development, taphonomy, and hydrography. The Late Pliocene sediments were deposited in a pond which had its origin in a collapse sink in a strongly disturbed sequence of Triassic and Early Jurassic sediments above subaerial eroded Late Permian (Zechstein) evaporites. The salt ascended across a fault zone along the valley of the Leine river and intruded laterally into younger Triassic saliferous strata (Late Buntsandstein: Röt, and Middle Muschelkalk). A detailed compilation of the geology of the Willershausen area, as well as of the mountainous region in southern Lower Saxony, has been published by Vinken (1967), Meischner (2000), and Ferguson and Knobloch (1998). Sedimentological data indicate that the palaeobasin was ca. 200 m in diameter and some 10 m deep, with a narrow sandy shelf beyond which the sides sloped steeply towards the flat bottom of the lake (Meischner and Paul 1982; Meischner 2000). Nevertheless, the oligotrophic to eutrophic lake (Briggs et al. 1998a, b) was sheltered by a broad-leaved forest, rendering it ideal for the establishment of meromictic conditions. In the monimolimnion, anoxia coupled with alkaline conditions and the accumulation of dissolved minerals, as well as the occurrence of toxic gases (?), prevented bioturbation and led to the preservation of laminations (Briggs et al. 1998b), with an exceptionally well-preserved flora and fauna (e.g., Meischner 2000). Thus, the Willershausen Fossil Lagerstätte has recently even been taken into consideration in the analyses of several Pleistocene and Neogene chitin-yielding localities by Flannery et al. (2001) and for additional geochemical studies (Keely et al. 1994).

The flora from Willershausen is dominated by taxa typical of hilly mesophytic woodland; the rich assemblage of deciduous trees may have been concentrated close to the water. Typical elements are represented by *Fagus, Liriodendron, Sassafras, Cercidiphyllum, Tilia, Aesculus,* Betulaceae, Rosaceae, various lobed oaks, and species of *Acer* (e.g., Ferguson and Knobloch 1998; Knobloch 1998; Straus 1992). Other taxa such as *Parrotia* and *Liquidambar* were also characteristic elements in the Pliocene sediments from Willershausen (Mai 1995). Based on palaeoclimatological estimates, the Willershausen flora grew where mean annual temperature was 12.5–16.5 °C, with warm-month mean temperatures of 19.0 ± 1.8 °C and cold-month mean temperatures of 3.9 ± 2.5 °C (e.g., Thiel et al. 2012); with an average rainfall of >900 mm, the actual climate resembles more a humid warm temperate Cfa/b climate (Kovar and Gregor 1984). These climatic parameters are consistent with those of other coeval floras (Teodoridis et al. 2009). With decreasing temperatures throughout the course of the Pliocene, the dominant European vegetation changed gradually from highly diverse subtropical and warm-temperate forests to temperate deciduous forests with East Asian and North American affinities (Mai 1995).

The clay mining was abandoned in 1975. Since 1977, the locality is a nature sanctuary, and in 2012 it was included in the Geopark Harz, Braunschweiger Land, Ostfalen (Fig. 1). In addition to its importance as a Fossil Lagerstätte, it is now a special biotope with a number of rare plants and animals.

A Late Pliocene age of the Willershausen sediments has already been proposed by Wegele (1914), which was later confirmed by Mammalia-like *Anancus arvernensis* and remains of Cervidae, as well as by microfloral components (Mohr 1986), and was accepted in several publications in more recent years (see for example Kohring and Schlüter 1993; Meischner 2000; Brauckmann et al. 2001; Brauckmann and Gröning 2002; Popov 2007; Dlussky et al. 2011). After the current definition of the Pliocene/Pleistocene boundary (Hilgen et al. 2012), the absolute age of the Late Pliocene (Piacenzian) is considered to range approximately from 3.6 to 2.588 million years ago.

Materials and methods

The holotype of *Peltis antehercynica* sp. nov., collection no. RE 551.782.200 A 0083, was recovered from the Willershausen Fossil Lagerstätte. The specimen is part of a collection of Willershausen fossils donated to the Ruhr Museum Essen (RE) (former collection of Ernst Edinger, Leverkusen) in 2001, and was lent, together with other fossil insects from this locality, to one of us (CB) for documentation. All measurements were made using an ocular micrometer and are given here in millimeters. Body length was measured along the midline from the anterior margin of the frons to elytral apex, and width measured across the broadest part of the elytra. The specimen was examined using a Leica MZ95 stereomicroscope. Photographs were taken using a Canon EOS 350D camera with a Canon EF-S 60-mm f/2.8 macro lens or a Nikon Coolpix

Fig. 1 The location of the Willershausen quarry. **a** The location of the Willershausen in Germany. **b** The location of the quarry in the neighborhood of Northeim (district in Lower Saxony, Germany). **c** The location of the protected site (vertical hatching) to the northeast of Willershausen. After Ferguson and Knobloch (1998), strongly modified

E4500. All photographs were optimized using Adobe Photoshop CS6 and Adobe Lightroom 5.

Systematic palaeontology

Family **Trogossitidae** Latreille, 1802
Subfamily **Peltinae** Latreille, 1806
Genus ***Peltis*** O.F. Müller, 1764

Type species Silpha grossa Linnaeus 1758 [designated by Hope 1840].

Diagnosis Adults of *Peltis* are characterized by flat, oval body; eyes not exceeding contour of head; antennae with large scape and distinct 3-segmented weakly asymmetric club; procoxae conspicuously transverse; procoxal cavities externally widely open; transverse pronotum with anterior corners projecting forwards; elytra with several longitudinal carinae and rows of punctures among them; mesocoxae oval; metacoxae reaching elytral epipleuron; all coxae narrowly separated; abdomen with five ventrites.

Remarks The newly recorded fossil fits perfectly with this characterization. Considering its body size larger than 10 mm and three distinct elytral carinae, it is probably related to the species classified within the former subgen. *Zimioma* (*P. grossa* Linnaeus, *P. gigantea* Reitter) (Kolibáč 2013). Representatives of Peltinae and Lophocaterinae living under bark are often easily recognizable by their elytral carinae and punctation; therefore, differences in these characters in three relevant species (Table 1) can be

Table 1 Differences among *Peltis antehercynica* sp. nov., *P. grossa* Linnaeus and *P. gigantea* Reitter

Character	*P. antehercynica* sp. nov.	*P. grossa*	*P. gigantea*
Antennal club	Antennomeres 9, 10 asymmetric	Antennomeres 9, 10 weakly asymmetric	Antennomeres 9, 10 weakly asymmetric
Prosternal process	Parallel sided, apex probably sharpened	Weakly dilated at apex	Apex widely dilated
Elytral carinae, number	3 primary + 3 or 4 secondary carinae	Only 3 primary carinae	Only 3 primary carinae
Elytral carinae, size	Primary carinae moderately, secondary carinae weakly developed	Carinae moderately developed	Carinae distinctly elevated
Elytral punctation	4 regular rows of punctures between pairs of primary carinae	Punctation among pairs of primary carinae coarser and irregular (4–6 punctures between carinae)	Punctation between pairs of primary carinae finer and irregular

considered a valuable species-rank feature of the newly described *Peltis antehercynica* sp. nov.

Peltis antehercynica sp. nov.
Figures 2, 3

Etymology The specific epithet is based on that region of Lower Saxony, Germany (western Harzvorland) from which the fossil originates.

Holotype Fairly complete specimen, RE 551.782.200 A 0083.

Type locality Late Pliocene (Piacenzian) deposits of Willershausen am Harz (Lower Saxony, northern Germany).

Diagnosis The new species can be distinguished from modern *Peltis* by differences in the elytra sculpturing and the asymmetric form of the antennal clubs.

Description Body length (from elytral apex to clypeus): 16.5 mm. For other measurements see Table 2.

Coloration and sculpture Body broadly oval, flat. Probably unicolorously brown, without patches or stripes. Dorsal and ventral surface as well as antennae without distinct pubescence (no setae or hairs observed). Pronotum densely punctate (interspaces approximately the same as diameter of punctures), punctures probably finer than those on head (interspaces among punctures less than their diameter). Elytra with regular rows of large punctures (interspaces among punctures distinctly less than their diameter) between carinae: always 2 rows separated with primary or secondary carinae plus approximately 4 rows of punctures between third primary carina and lateral margin.

Head Situated between extended anterior corners of pronotum. Eyes medium-sized, not distinctly elevated but rather evenly rounded and not exceeding contour of cranium. Mandibles bidentate. Antennae with 11 antennomeres and distinct 3-segmented club; scape robust, distinctly larger than pedicel; antennomeres 9–10 weakly asymmetric (3 terminal antennomeres apparently sharply triangular on the right side but rather rounded on the left).

Prothorax Pronotum conspicuously transverse; anterior margin deeply emarginate (arcuate); anterior corners projecting, but not acute (their tips rather rounded); lateral margins convergent forwards, nearly straight, probably explanate from dorsal view; lateral edge distinct, even. Prosternal process not dilated at apex, relatively wide; sides convergent behind base, parallel-sided in front of apex; apex probably sharpened. Procoxal cavities narrowly separated, externally widely open, closed only to one quarter or one-third by postcoxal projections; trochantin poorly visible, probably exposed but slender and small.

Fig. 2 *Peltis antehercynica* sp. nov., holotype specimen, RE 551.782.200 A 0083. **a** Complete specimen in dorsal view. **b** Right antenna. **c** Enlargement and reconstruction of antennal club. **d** Detail of mesonotum and mesocoxae and sculpturing of the elytra. *Scale bars* striped, 5 mm; *back slashed* 0.5 mm; *dotted* 0.1 mm

Mesothorax Mesocoxal cavities narrowly separated; mesoventral process shorter than coxal diameter, reaching behind half of mesocoxae, acute; projection of metaventrite reaches approximately towards basal quarter of mesocoxae; tips of intercoxal processes touch each other; mesotrochantin not observed; scutum relatively wide, scutellum rounded at apex.

Elytra (Artificially compressed in fossil) Regularly punctate, with 3 conspicuous longitudinal (primary) carinae and 3 finer (secondary) carinae between each pair of them; lateral margin of elytra widely explanate from above. Elytral epipleure very wide in anterior third, then narrowed to half of width but distinct up to elytral apex.

Hind wing Well-developed, wing membrane visible; veins not observed.

Metathorax Metaventrite flat and wide, only slightly narrowed towards anterior portion; discrimen not visible (it coincides with elytral suture in semitransparent fossil); no other details visible.

Legs Procoxae not projecting, widely transverse; mesocoxae oval; metacoxae extended to lateral margin of metathorax; trochanters relatively small, triangular; femora rather clavate; tibiae and tarsi not observed.

Abdomen Five ventrites distinctly visible; remains of copulatory organs visible at apex (sex unrecognizable).

Remarks The newly described fossil is similar to the two recent species but easily recognizable by the difference in the elytra sculpture. The antennal club of the right antenna seems to be distinctly asymmetric but the state is likely specious. Although the left antenna is poorly visible, it can be estimated that the asymmetric look of the right club is given by its position during fossilization.

Conclusions

The Holarctic genus *Peltis* O.F. Müller consists of seven extant species, and to date only three fossils have been assigned to the genus described from Miocene and Oligocene deposits of Europe and the USA (see also Table 3). A list of species was given by Kolibáč (2013), and the biogeography of Palaearctic species was treated by Kolibáč in Löbl and Smetana (2007). Systematics and nomenclature of the genus were confusing in the past, as the generic

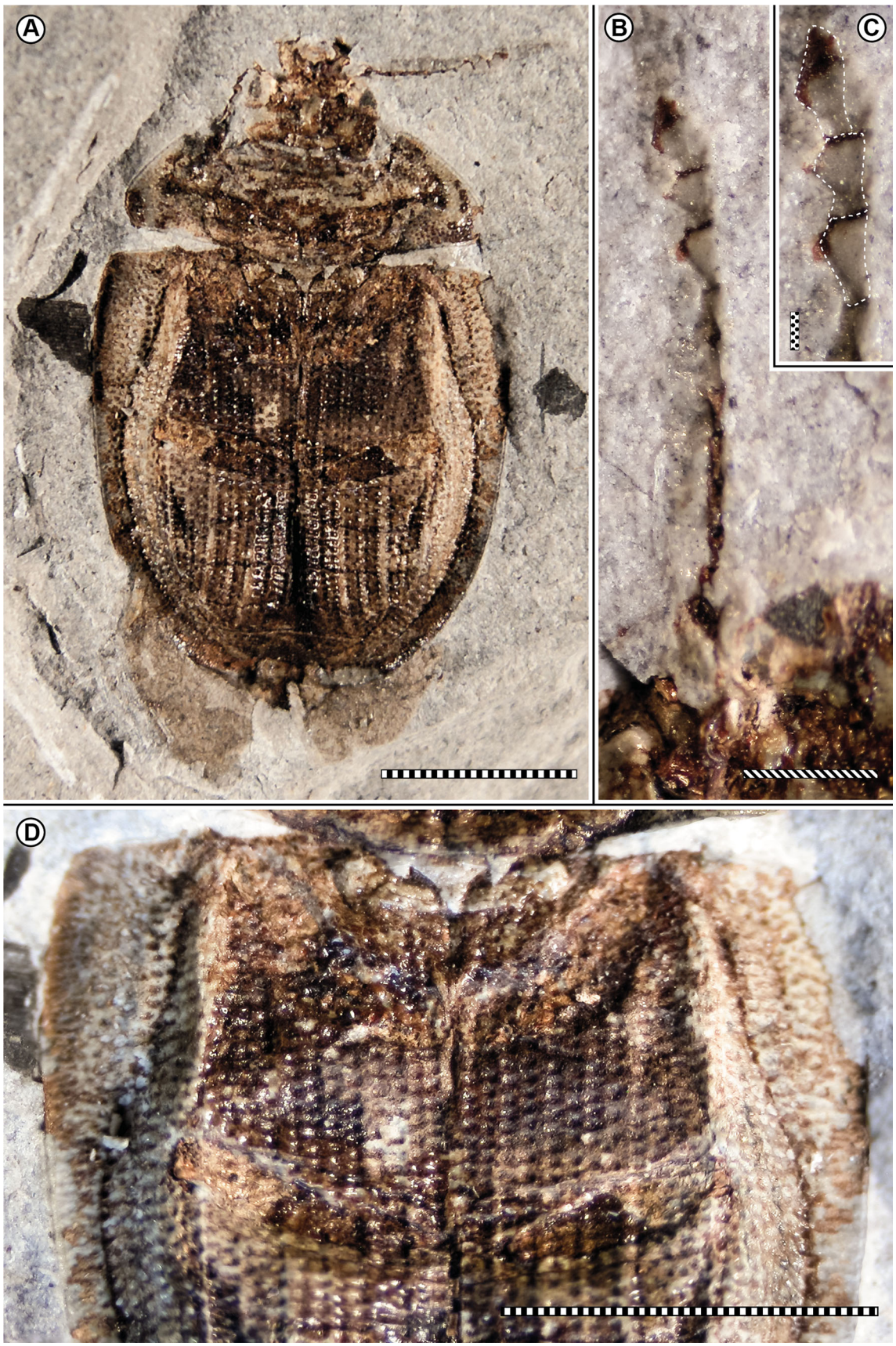
A
B
C
D

Fig. 3 *Peltis antehercynica* sp. nov. Reconstruction of the dorsal habitus

Table 2 Measurements of *Peltis antehercynica* sp. nov. As the fossil is compressed, the measurements are approximate and given in millimeters

Measurement	*P. antehercynica* sp. nov.
Body without mandibles	16.5
Head, length of visible part	2
Head, max. width incl. eyes	4
Head, mean width between eyes	2.5
Antenna, length	4
Antenna, 3-segmented club	1.5
Pronotum, max. length	3
Pronotum, length in middle	2.5
Pronotum, max. width	10
Elytron, max. width	6
Elytron, max. length	12

name *Ostoma* Laicharting (type species: *Silpha ferruginea* Linnaeus, 1758) was used instead of *Peltis* (type species: *Silpha grossa* Linnaeus, 1758), and three subgenera were recognized within the genus: *Ostoma* s.str., *Zimioma* Gozis, and *Grynocharis* Thomson (Léveillé 1910). The latter has been classified within the Lophocaterinae (or Lophocateridae) since Crowson's (1970) review. *Ostoma* was synonymized with *Peltis* by Kolibáč et al. (2005; for complete synonymy of *Peltis* see Kolibáč 2007, 2013). The subgenus *Zimioma* (sometimes used in a rank of a genus) was established for two Palaearctic species (*P. grossa* Linnaeus is distributed in Europe, *P. gigantea* Reitter from East Siberia to Japan and NE China). They are distinctly larger in size (always >13 mm); their ratio of pronotum length/width is about 3. Species of *Peltis* s.str. are lesser than 12 mm, with a pronotum length/width ratio of about 2. Because of lack of other known morphological and biological differences among the species of *Peltis* s.str. and *Zimioma*, the latter name was put into synonymy by Kolibáč (2007). Considering the body size of about 16 mm and a distinctly transverse pronotum (length/width ratio >3), *P. antehercynica* sp. nov. is unambiguously related to the two species of the former subgenus *Zimioma*.

Adults of Palaearctic species are highly adapted to a hidden way of life under bark of dying or dead deciduous and coniferous trees, while larvae live in rotten or decaying wood. Both stages are slow moving; adults are distinctly flattened, with robust mandibles; larvae have a reduced number of stemmata and minute urogomphi. Species are fungivorous in both stages and inhabit old woods with conditions similar to virgin forests. Therefore, species are generally scarce in Europe, although they can be relatively common in old autochthonous forests (Kolibáč et al. 2005). All extant Palaearctic species of *Peltis* today live in colder climatic conditions than *P. antehercynica* sp. nov. They are distributed in Central Europe as well as Fennoscandia and Siberia with cold, long winters.

Today, two species of *Peltis* (*P. ferruginea* Linnaeus and *P. grossa* Linnaeus) are among the most abundant representatives of Trogossitidae in Central Europe; however, there is still much to do in a systematics and phylogeny of the monotypic tribe Peltini, even the subfamily Peltinae (Bocák et al. 2014; Hunt et al. 2007; Kolibáč 2008; Lawrence et al. 2011).

Table 3 Review of Cenozoic fossils classified within the genus *Peltis*

Species	Reference	Type locality	Period	Body size
Peltis costulata	Heyden (1862)	Germany	Upper Oligocene	Only elytron known: 3 mm
Peltis laminata	Wickham (1910)	USA: Colorado	Lower Oligocene	Body 12.5 mm, elytron 6.6 mm
Peltis minuscula	Piton (1935)	France	Upper Miocene	Only elytron known: 4 mm
Silpha[a] *tricostata*	Heer (1847)	Germany	Upper Miocene	Body 18 mm, elytron 12 mm

Based on data obtained directly from The Paleobiology Database Classic and Fossilworks: Gateway to the Paleobiology Database

[a] The fossil *Silpha tricostata* Heer (1847 from the Miocene of Oehningen is classified within *Peltis* in some palaeobiological databases (e.g., Paleobiology Database Classic, Fossilworks: Gateway to the Paleobiology Database). However, Heer (1847, 1865) considered the specimen as belonging to Silphidae (Heer 1847, 1865). The specimen is not well preserved, but its body shape, large size, and pronotum without extended anterior corners certainly do not allow its classification within *Peltis*. A placement within the carrion beetles (Silphidae) is more probable

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