Durlachia striata gen. nov., spec. nov., a new beetle (Coleoptera) from the Upper Buntsandstein (German Lower Triassic) from Karlsruhe

Eberhard Frey, Samuel Giersch & Wolfgang Munk

Abstract

A fossil beetle from the Upper Buntsandstein (Röt-Folge, Lower Triassic) in Karlsruhe Durlach-Eisenhafengrund is described. The specimen is one of the oldest known beetle findings in Germany. According to its stratigrafic context, the finding layer can be correlated with the Voltzia-Sandstone (E-France), which also yielded fossil beetles. The silty matrix, in which the beetle occurs, is interpreted as seasonal playa sediment.

The beetle was fragmented during extraction. The lack of diagnostic features of elytra, scutellum and pronotum does not allow to assign the specimen to a family. However, the elytral humeral callus, the set off pronotum with caudolaterally concave margins combined with the size of almost 15 mm allows a diagnostic distinction from other coeval Coleoptera at least in Europe. Therefore, it is justified to refer the specimen from Durlach-Eisenhafengrund to a new genus and species: *Durlachia striata*.

Kurzfassung

***Durlachia striata* gen. nov., spec. nov., ein neuer Käfer (Coleoptera) aus dem Oberen Buntsandstein (Olenekian, Germanische Untertrias) aus Karlsruhe-Durlach (Südwestdeuschland)**

Ein Käfer-Fossil aus Durlach-Eisenhafengrund bei Karlsruhe (Oberer Buntsandstein, Röt-Folge, Untertrias) wird beschrieben. Das Stück ist eines der ältesten bekannten Käferfunde Deutschlands. Stratigraphisch ist die Fundschicht mit dem Voltziensandstein Ostfrankreichs parallelisierbar, in welchem ebenfalls fossile Coleopteren gefunden wurden. Die siltige Matrix, in die das Fossil eingebettet ist, wird als jahreszeitliche Playaablagerung interpretiert.

Die Coleoptere wurde bei der Bergung zerbrochen. Das Fehlen diagnostischer Merkmale an Elytren, Scutellum und Pronotum erlaubt keine zweifelsfreie Zuordnung des Stückes zu einer Familie. Die Schulterhöcker auf den Elytren, das angesetzte Pronotum mit seinen caudolateral konkaven Rändern in Verbindung mit der Größe von fast 15 mm ermöglicht eine diagnostische Trennung von anderen Coleopteren gleichen geologischen Alters, zumindest in Europa. Es ist daher gerechtfertigt, das Stück aus Durlach-Eisenhafengrund als neue Gattung und Art *Durlachia striata* gen. nov., spec. nov. zu beschreiben.

Autoren

Eberhard Frey, Samuel Giersch & Wolfgang Munk, Staatliches Museum für Naturkunde, Geowissenschaftliche Abteilung, Erbprinzenstraße 13, 76133 Karlsruhe, Germany. E-mail of corresponding author: dinofrey@aol.com.

1 Introduction

The earliest fossil Coleoptera are reported from the Early Permian of southern Siberia and the Ural Mountains (Ponomarenko 2003). They are referred to Tschekardocoleidae (Protocoleoptera, Rohdendorf 1944). Throughout the later Permian, beetle fossils are frequently found. These early beetles are referred to Archostemata with the families Permocupedoidea, Rhombocoleoidea and Asiocoleoidea. All Permian taxa comprise animals with elongate elytra with large pits between widely spaced striae (Ponomarenko 1969). Their body shape resembled that of extant elaterids or buprestids, but the body length scarcely exceeds 10 mm.

The fossil record of the Triassic Coleoptera is sparse compared with the Permian, while the diversity of major taxa slightly increases. Archostemata and Ademosyridae appear together with the obscure group of Schizophoriformia, while Rhombocoleoidea vanish from the fossil record. The Adephaga and Polyphaga finally appear during the Middle and Late Triassic and rapidly reach a large diversity throughout the Mesozoic.

Especially in Central Europe Early and Middle Triassic localities that yield fossil Coleoptera are exceedingly rare (for an overview see Grimaldi & Engel 2005, Brauckmann & Schlüter 1993). With the exception of a questionable record that has tentatively been referred to Coleoptera (Müller 1982), no fossil beetles have been reported from the lower Early Triassic of Central Europe. The most diverse Central European coleopteran fos-

sils come from strata transitional from the late Early to the early Middle Triassic, especially from the Voltzia Sandstone of the Vosgues (northeastern France; Papier *et al*. 2005). Additionally, a few coleopteran remains have been reported from the early Middle Triassic of Lower Frankonia (Brauckmann & Schlüter 1993). In the late Middle to Upper Triassic, the fossil record of Coleoptera in Central Europe becomes more abundant (e.g. Geyer & Kelber 1987, Hennig 1969, Handlirsch 1906-08).
Here we report on an fragmentary, hence articulated coleopteran fossil from the late Early Triassic (Upper Buntsandstein, Olenekian), which was found in 1959 during an excavation campaign near Durlach at Karlsruhe (southwestern Germany, Jörg 1969). It was recently rediscovered in the collections of the Staatliches Museum für Naturkunde Karlsruhe (SMNK) by one of us (W.M.).

2 Location and Geological Setting

At the time of excavation in 1958 the locality was an abandoned quarry in an area called "Eisenhafengrund" near Karlsruhe-Durlach. The quarry named "Rittershofer" was operated for the so-called Plattensandstein also known as Pfinztal Sandstone. Today the locality is buried by the garbage deposit "Karlsruhe Ost", which meanwhile is recultivated.
The excavation campaign in 1958 yielded an abundant but paucispecific fish assemblage (*Praesemionotus aculeatus* Jörg, 1969, *Pericentrophorus minimus* Jörg, 1969, *Dorsolepis virgatus* Jörg, 1970), numerous decapod crustaceans (e.g. *Aspidogaster durlachensis* Förster, 1967), masses of conchostacans, a large quantity of plant remains and a few tetrapod trackways (Jörg 1969). The fossil beetle was discovered in a part of the collection that comprised amongst other material "problematica". The fossil coleopteran presented here is preserved in a greenish-grey, slightly reddish flamed and thin layered mudstone. The fossil was labelled as "Käfer?", but it has never been studied since its integration into the collection.

Geology
According to Jörg (1969) the finding layers were exposed in a seven metres wide lentil of mudstone in the upper "Plattensandstein". The section is characterised by a 0.32 m thick bank consisting of partly reddish or greenish mostly sub-millimetrically laminated mudstone. The content of sand

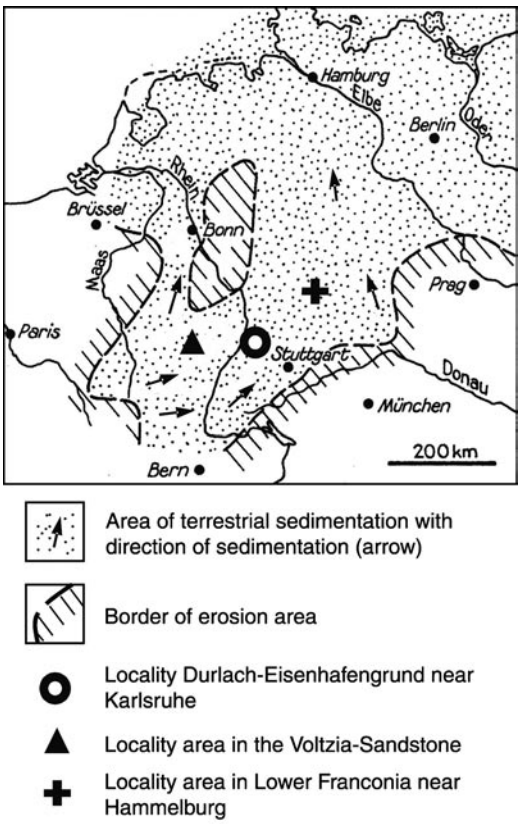

Figure 1. Palaeogeography of Middle European Lower Triassic (Buntsandstein) with localities of fossil Coleoptera (symbols), changed after Groschopf & Villinger 1998.

varies in the different laminae. The underlying *Corophioides*-Bank probably represents remains of a big playa lake and is characterised by the ichnotaxon *Corophioides luniformis* Blanckenhorn. The *Corophioides*-Bank laterally expands throughout the regional outcrop. The facies of this horizon is uniform and represents the most important key layer of this sections.
According to Villinger (1995) the entire section between the paleosol VH 2 at the top of the Hardegsen Formation (Ortlam 1974) and the "*Rötton"* (Clays in the Röt-Folge) is referred to as "Plattensandstein", which represents the lower part of the Röt-Folge in the northern Black Forest (German Stratigraphic Commission 2002). The upper "Plattensandstein" and the overlying "*Rötton"* are coeval with the Voltzia-Sandstone

(Grés á Voltzia) from the Northern Vosgues (PERRIAUX 1961, GALL 1971, TRUNKÓ 1984). In the international stratigraphical system (GRADSTEIN & OGG 2004) the Röt-Folge marks the border between Early (Olenekian) and Middle Triassic (Anisian).
Lenticular mudstone deposits are abundant in the entire "Pattensandstein". They are interpreted as sediments of occasionally flooded oxbow lakes. Some coarse-grained layers might indicate short termed fluvial events. Probably, after seasonal heavy rain fall, flow channels and ponds became stagnant with the end of the flood and clay sedimentation set in. During the dry season most ponds rapidly became shallow and finally desiccated. With the evaporation, the pond water became hypersaline, which is proved by halite crystals and salt pseudomorphs on surfaces of many laminae. The Durlach-Eisenhafengrund section was probably part of an extensive braided river system. Its channel fillings laterally interdigitate with playa clays. The remains of fossil fishes and decapod crustaceans indicate an at least seasonal connection to a larger river system, which allowed these animals to invade the channels and ponds, where they became trapped during the dry seasons.
In the entire Buntsandstein of the German Basin fossils are rare due to the predominantly coarse, clastic sediments. Moreover, the rare fossil remains often suffered from a complex metasomatism (decalcification, silification etc.), which leads to severe structural damage or even complete destruction. The mudstone layers of Durlach-Eisenhafengrund yielded unidentified plant fragments, the conchostracan *Euestheria albertii* (VOLTZ) and a variety of ichnofossils. These represent the most abundant fossils of an apparently oligospecific assemblage. Occasionally, the plant fragments are concentrated in layers of debris. The floral taphocoenosis is predominated by equisetes and conifers indicating different habitats in the vicinity of the stream, which were not necessarily water dependant.

3 Systematic Palaeontology

Order Coleoptera LINNAEUS, 1758
Family incertae sedis
Genus *Durlachia* gen. nov.
Derivation of name: *Durlachia*, referring to the town of Durlach near Karlsruhe (Southwest Germany).
Type species: *Durlachia striata* spec. nov.
Diagnosis: Same as for the only known species

Durlachia striata spec. nov.
Text-figures 2A-B, 3
Derivation of name: Latin *striata,* striped, referring to the striae on the surface of the elytra.

Holotype: Slab and counterslab with articulated pair of elytra, scutellum and caudal fragment of pronotum. The specimen is housed in the palaeontology collection of the Staatliches Museum für Naturkunde Karlsruhe under the collection number SMNK-PAL 6098 a + b (slab and counter-slab).

Biometry:

Total length of elytra:	13.4 mm
Maximum width of elytra:	9.3 mm
Width of pronotum:	4.25 mm
Width of scutellum:	1.0 mm
Length of scutellum:	0.65 mm

Locus typicus: Former Rittershofer Quarry („Hochstädt"), Eisenhafengrund, Karlsruhe-Durlach (Southwestern Germany, Topographical Map 1:25000, sheet 7016 Karlsruhe Süd (German grid), right: 34 62 700, high: 54 27 500).

stratum typicum: "Plattensandstein", also known as "Pfinzsandstein" or "Pfinztäler Sandstein", Upper Buntsandstein, late Early Triassic.

Diagnosis of genus and species: Sclerotisation of pronotum, scutellum and elytra massive, as concluded from the nearly three-dimensional preservation. Width of caudal margin of pronotum ca. 4/5 of cranial margin of elytra. At least caudal part of lateral margin of pronotum concave. Sulcus running subparallel to caudal margin of pronotum. Scutellum regularly triangular. Outline of elytra suboval with distinct humeral calli. Elytral lateral margin with slightly convex rim. At least central part of external surface of elytra with an oblique striation with rows of pits between the striae. Striae of contralateral elytra converging caudally at angle of ca. 10°. Surface of pronotum and scutellum pitted.

Description
Preservation: The specimen comprises a pair of fully preserved elytra and a scutellum and the basal part of the pronotum. Despite compaction, pronotum, scutellum and elytra are slightly vaulted and of brownish, coppery colour, which con-

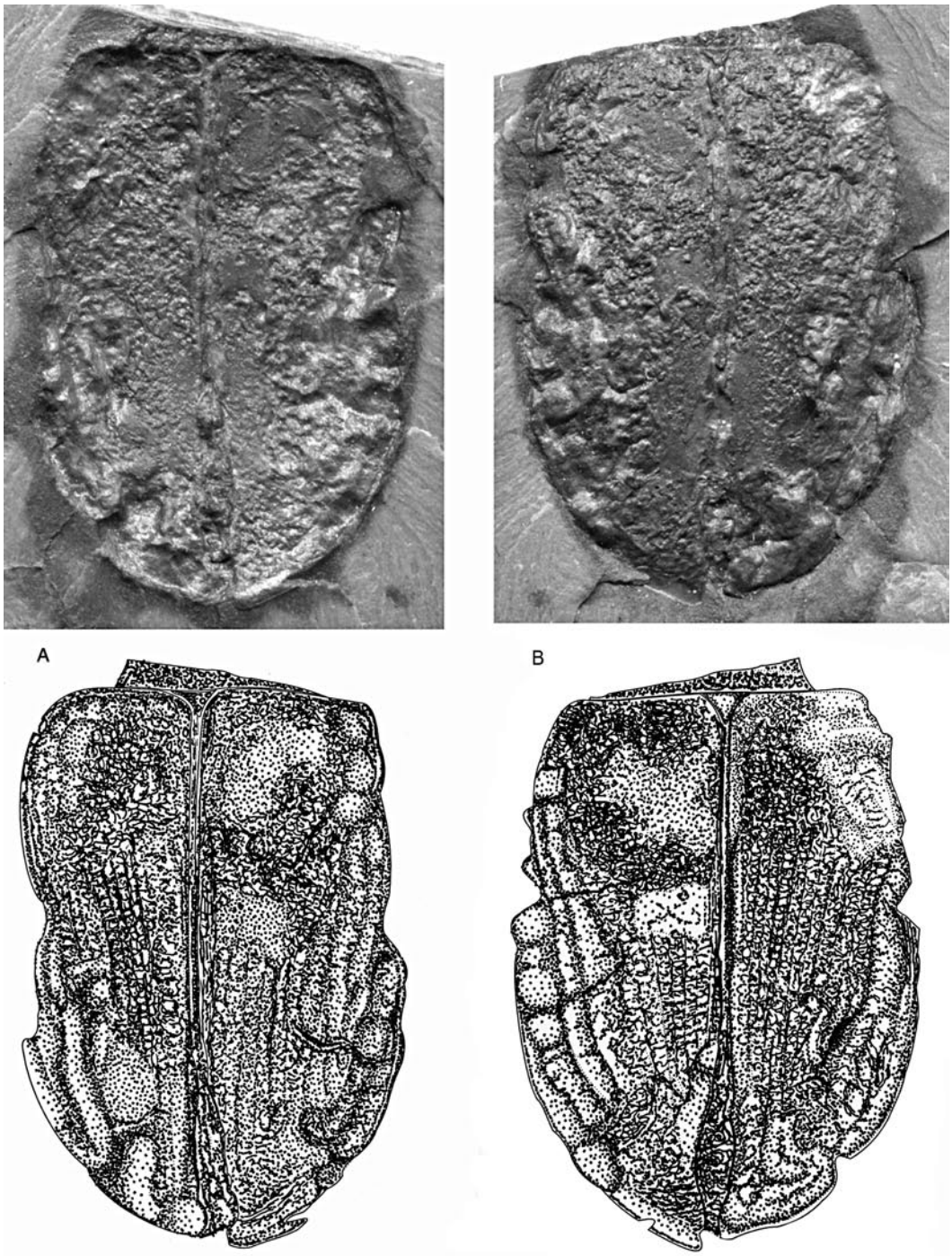

Figure 2. *Durlachia striata* gen. et sp. nov., SMNK-PAL 6098 a + b, holotype and single specimen: slab (A) and counter slab (B) from the Early Triassic (Buntsandstein, Olenekian) from Durlach-Eisenhafengrund (SW Germany).

trasts the buff reddish matrix. The fossil has split in slab and counter slab both containing organic matter. Apparently, the chitin shell ruptured more or less in the middle, so that the concave part, here referred to as counter slab, also contains parts of the cuticula and does not represent an internal mould. Therefore the external structure of the elytra is camouflaged by matrix. The sculptures visible on the slab most likely represent internal structures of elytra, scutellum and pronotum, but are still indicative for the type of external sculpturing. This holds especially true for the margins of the elytra and the central area of the right elytron, where only a thin layer of the external cuticular cortex is missing. While the preserved parts of pronotum and scutellum are entire, the pair of elytra show sub-radial compaction cracks especially along the margin of the left elytron and deformation humps running sub-parallel to the lateral and caudal margins of both elytra. In the caudal third the elytral suture diverges, revealing organic matter, which is preserved as a mass of dark coppery substance. The caudolateral margin of the right elytron is flattened along the border of the abdomen. This is best visible on the counter slab. After the slab has been split, the specimen was neither prepared nor treated chemically.

Morphology: The nearly three-dimensional preservation of the elytra, scutellum and the base of the pronotum indicates a strong sclerotisation of these parts and of the abdomen. The basal margin of the pronotum has about four fifth the width of the elytra and is slightly concave. The preserved basal part of the lateral margin of the pronotum is strongly concave until the transverse break. The sculpture of the pronotum comprises a pattern of fine confluent pits, which is interrupted along a transverse sulcus visible on the left. This sulcus runs transversely sub-parallel to the base of the pronotum and is only preserved on the counter slab.

The scutellum is equilaterally triangular. Its slightly convex apical margin exactly matches the adjacent basal margin of the pronotum. The basolaterally facing margins are slightly concave and fit with the rounded elytral humeri. Its sculpture is identical to that of the pronotum. Probably, the central part of the external surface of the scutellum is smooth as can be seen on the counter slab.

The articulated elytra are suboval in outline. Their basal margin is straight, expanding laterally beyond the caudal corners of the pronotum. The elytral humeri are regularly rounded anteriorly and apically continue into the straight medial margin which stands at right angle to the basal margin. The craniolateral margins of the elytra are rounded and show humeral calli. The lateral margin of the elytra apparently was regularly convex in its caudal half. At the apical end of the humeral callus there is a shallow notch in the lateral margin of the elytron, which is best visible on the slab.

The apical of the medial margin of the elytra has been pressed open. The convexity of the apical sutural margins of the elytra hint to a strongly vaulted apical part of the elytra. Basal to the

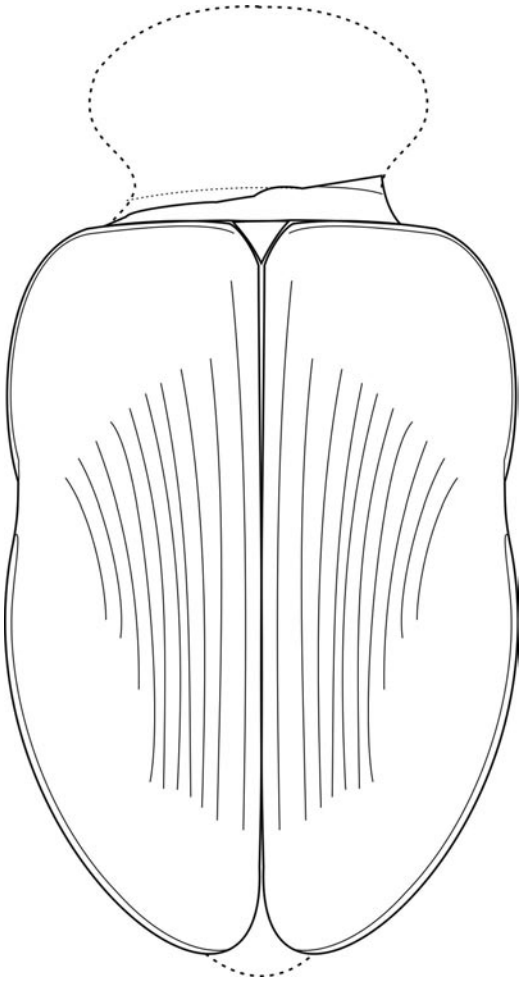

Figure 3. *Durlachia striata* gen. et sp. nov., reconstruction. Length of elytra: 13,4 mm.

gap, the interelytral suture is scarcely visible. Probably, the contralateral elytra were firmly connected with each other.
The lateral margins of the elytra were marked by a narrow frill separated from the central part by a shallow sulcus. At least the mid surfaces of the elytra are striated. On the left elytron, there is a minimum of eleven striae. The medial striae run sub-parallel to the medial margin of the elytron. The laterally the striae are, the more they diverge towards basally. Between the striae, there are lines of sub-circular pits. Fine punctures are visible between and along the pits, especially in the lateral pit rows. The unstriated parts of the elytra show a surface of irregular smooth plaques and rugosities, most likely a result of early diagenesis.
The gap between the elytra reveals organic matter with a wrinkled surface and a little bit darker colour than the elytra, but bears no anatomical details. Thus, its nature cannot be identified.

4 Discussion

Comparisons
The specimen described herein comprises the fragment of a medium sized beetle (length of elytra: 13.4 mm), which is characterised by longitudinally striated elytra, humeral calli and a basally constricted pronotum with concave lateral margins. Head, legs and the cranial part of pronotum is missing; the ventral side is not visible. Despite the good preservation, the lack of diagnostic features does not allow to assort the specimen to suborder or family. However, the specimen clearly differs from those of all other coleopteran families known from the Late Permian and the entire Triassic (c.f. Grimaldi & Engel 2005, Arnol´di 1992, Ponomarenko 1969).
Most of all Late Permian and Triassic beetles belong to Archostemata (Ponomarenko in Arnol´di 1992). Within the suborder Archostemata, the Protocoleoptera (Tscherkadocoleidae), Taldycupedidae, Tricoleidae, Asiocoleidae, Permocupedidae and Rhombocoleidae are characterised by a "strong, netlike or grid shaped sculpture of elytra" (Ponomarenko 1969: 47). With the fine striation on the elytra *Durlachia striata* differs from those families and from the extant families, too:
Micromalthidae are characterised by elytra shorter than the abdomen. The pronounced humeral calli, the faint sculpturing of the elytra showing flat and sub-circular pits mostly arranged in longitudinal rows and the basally constricted pronotum exclude *D. striata* from Cupedidae and Ommatidae. Furthermore, Archostemata from coeval localities are significantly smaller than *D. striata*.
The members of the ancestral myxophagid families Catiniidae and Schizophoridae (Grimaldi & Engel 2005) show "smooth or irregularly dotted elytra" (Ponomarenko 1969: 48), a feature which separates these two families from *D. striata.* Furthermore, in Catinidae and Schizophoridae the craniolateral margin of the elytra are rounded and flat and the pronotum shows diverging basolateral margins (Ponomarenko 1969).
Another coeval family with highly diverse members are Ademosynidae with seven described Permotriassic genera. Ademosynidae share many similarities with extant Polyphaga and therefore have been considered as their ancestors (Ponomarenko 1969, Grimaldi & Engel 2005). The elytra of Ademosynidae show "9-10 dotted furrows whereas the dots almost invisible" (Ponomarenko 1969: 125). *D. striata* also shows striated elytra. However, all known Ademosynidae are longitudinally oval beetles, whereby the base of pronotum and elytra are equally wide. In *D. striata* the pronotum base is only half the width of the elytra.
In Triassic times, the suborder Adephaga is only represented by the family Triaplidae (Arnol´di 1992). The genera of this family are characterised by small cylindrical beetles with smooth elytra without a trace of humeral calli. Among Geadephaga humeral calli and a basally constricted pronotum are common among fossil Carabidae e.g. in *Cretorabus* and *Carabites* from the Cretaceous (Ponomarenko in Arnol´di 1992).
The sparse records of beetles described from the Middle European Triassic do not share any diagnostic features with *D. striata*. The three specimens from the Upper Buntsandstein and the Lower Keuper from Lower Franconia are only half the size of *D. striata* and are referred to Permosynidae and Crysomelidae (Brauckmann & Schlüter 1993).
Within the 32 beetles from the Vosgian Voltzia Sandstone (north-eastern France), there are two specimens (espèce 8 and espèce 28), who are as big as *D. striata*. These two specimens have significantly narrower elytra similar to Archostemata (cf. Papier et al. 2005: 194, Fig. 2, E, F and 198, Fig. 6, D). The specimen „espèce 31" (Spécimen-Arzviller, Moselle, France, 6634/6635 in Papier et al. 2005: 199, Fig. 7, A) has humeral calli and a caudally constricted pronotum similar to *D. stri-*

ata, but with an elytra length of 6 mm it is only half the size. Furthermore, the lateral margins of "espèce 31" are converging and not subparallel as in *D. striata*. Unfortunately, the comments on the Voltzia Sandstone beetles (PAPIER et al. 2005) do not provide detailed anatomical descriptions of the specimens, which make a thorough morphological comparison with *D. striata* impossible. Compared to beetles of the Cretaceous, there is a striking similarity of *D. striata* and the Adephaga, especially Carabidae. These similarities refer mainly to the size of *D. striata*, the humeral calli, shallow lateral recess of the elytra, faint longitudinal striation separated by rows of pits and, especially the basally constricted pronotum. Because the diagnostic features for Carabidae are invisible in *D. striata* it would be too speculative to refer the specimen to Carabidae.

Taphonomy

As was shown above, the extremely fine grained sediment matrix, in which the coleopteran is embedded, was deposited under low energy or stagnant shallow water conditions, probably after rain induced floods. The abundance of nicely preserved leafs indicate that the sedimentation persisted for short while. These leafs either were washed or blown into the shallow temporary ponds and deposited together with the silts in suspension. The transport prior to embedding must have been short, which indicates, that the leaves must have arrived in the ponds after the actual floods. The same holds true for the insects, which are much rarer than the plant remains. While the other insect remains consist of single elements, the coleopteran must have been almost articulated when it became embedded. Probably, only some legs got lost during a short phase of floating. Then, the body sank and was rapidly covered by silty sediments. It appears highly likely that the beetle inhabited the flood plain, searching for food in the flood seams, which are food concentrations in the playa plains. Due to the excellent preservation it appears highly unlikely that the beetle was washed in with a flood or blown in by strong winds. A long floating period under high energy conditions would have rapidly destroyed the small insect. Furthermore, beetles normally do not fly under stormy and rainy conditions. It is much more likely that the beetle fell into one of the temporary ponds while searching for food in the flood seam. The insect drowned after a while and floated a short time on the water surface due to the air inside the tracheae and below the elytra. With the beginning of the decomposition some legs might have fallen off, the intersegmental or pleurotergal membranes disrupted and allowed the air to escape. Then the small carcass sank to the ground, where it got stuck in the mud and rapidly covered with silt.

5 Conclusions

The beetle from the Buntsandstein of Karlsruhe-Durlach died in a flood plain residual pond and was rapidly buried with silty sediments. The preservation is in three dimensions and the specimen must have been complete or at least sub-complete prior to excavation. Despite its excellent preservation, the specimen does not show features sufficient for reliable determination to family level. Hence, *D. striata* represents one of the oldest evidences for modern Coleoptera in Middle Europe and, at the same time, shows that the carabid habitus already existed in the Early Triassic.

Acknowledgements

We thank U. GEBHARDT (Karlsruhe) for fruitful discussions on the geological setting. We gratefuly acknowledge the careful review of the manuscript by A. RIEDEL (Karlsruhe), T. WAPPLER (Bonn) and an anonymous reviewer.

References

ARNOLDI, L. V., ZHERIKHIN, V. V., NIKRITIN, L. M. and PONOMARENKO, A. G. (1992): Mesozoic Coleoptera. – Smithsonian Institution Libraries and the NSF. Washington D.C.: 255 pp.

BRAUCKMANN, C. & SCHLÜTER, T. (1993): Neue Insekten aus der Trias von Unterfranken. – Geologica et Palaeontologica, **27**: 181-199.

Deutsche Stratigraphische Kommission (Hrsg.; 2002): Stratigraphische Tabelle von Deutschland 2002.

FÖRSTER, R. (1967): Die reptanten Dekapoden der Trias. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **128**(2): 136-194.

GALL, J.-C. (1971): Faunes et paysages du Grés á Voltzia du Nord des Vosges. Essai paléoécologique sur le Buntsandstein supérieur. – Mémoires du service de la carte géologique d'Alsace et de Lorraine, **34**: 318 pp.

GEYER, G. & KELBER, K.-P. (1987): Flügelreste und Lebensspuren von Insekten aus dem Unteren Keuper Mainfrankens. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **174**(3): 331-355.

GRADSTEIN, F. M. & OGG, J. G. (2004): Geologic Time Scale 2004 – why, how, and where next! Lethaia, **37**(2): 175-181.

GRIMALDI, D. & ENGEL, M. S. (2005): Evolution of the Insects. – 722 pp.; (Cambridge University Press)

GROSCHOPF, R. & VILLINGER, E. (1998): Erläuterungen zur Geologischen Schulkarte von Baden-Württemberg. – 12. überarbeitete und erweiterte Aufl., 142 S.; Freiburg i. Br. (Landesamt für Geologie, Rohstoffe und Bergbau, Baden-Württemberg).

HANDLIRSCH, A. (1906-1908): Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. – 1430 pp.; (Wilhelm Engelmann, Leipzig)

HENNIG, W. (1969): Die Stammesgeschichte der Insekten. – Senckenberg-Buch 49**:** 436 pp.; Frankfurt a. M.

JÖRG, E. (1969): Eine Fischfauna aus dem Oberen Buntsandstein (Unter-Trias) von Karlsruhe-Durlach (Nordbaden). – Beiträge zur naturkundlichen Forschung Südwestdeutschlands, **28**(2): 87-102.

JÖRG, E. (1970): Fischfunde im Oberen Buntsandstein (Untertrias) von Karlsruhe-Durlach. – Zeitschrift der deutschen Geologischen Gesellschaft, **121**: 105-110.

MADER, D. (1985): Entstehung des germanischen Buntsandsteins. - Carolinea, **43**: 5-60.

MÜLLER, A. H. (1982): Ein Problematikum (*Elytromorpha robusta* n.gen. n.sp.) aus dem Unteren Buntsandstein von Mitteleuropa. – Freiberger Forschungshefte, **C 366**: 85-88.

ORTLAM, D. (1974): Inhalt und Bedeutung fossiler Bodenkomplexe in Perm und Trias von Mitteleuropa. – Geologische Rundschau, **63**: 850-884.

PAPIER, F., NEL, A., GRAUVOGEL-STAMM, L. & GALL, J.-C. (2005): La diversité des Coleoptera (Insecta) du Trias dans le nord-est France. – Geodiversitas, **27**(2) : 181-199.

PERRIAUX, J. (1961): Contribution à la géologie des Vosges Grèseuses. – Mémoires du service de la carte géologique d'Alsace et de Lorraine, **18**: 236 S.; Strasbourg.

PONOMARENKO, A. G. (1969): Historical Development of Coleoptera, Archostemata. – Trudy paleontologitscheskovo Instituta Akademiya Nauk SSSR, **125**: 1-240 [in russian].

PONOMARENKO, A. G. (2003): Paleontological discoveries of beetles. – http://www.zin.ru/Animalia/Coleoptera/eng/syst4.htm.

SINITSHENKOVA, N. D., MARCHAL-PAPIER, F., GRAUVOGEL-STAMM, L. & GALL, J.-C. (2005): The Ephemeridea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges. – Paläontologische Zeitschrift, **79**(3): 377-397.

VILLINGER, E. & FLECK, W. (1995): Symbolschlüssel Geologie (Teil I) und Bodenkunde Baden-Württemberg. – Geologisches Landesamt Baden-Württemberg, Informationen, **5/95**: 67 pp.

TRUNKÓ, L. (1984): Karlsruhe und Umgebung. – Sammlung geologischer Führer, **78**: 227 pp.