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RESEARCH PAPER

First Triassic record of the beetle family Permocupedidae (Insecta: Coleoptera): a peculiar example of a Lazarus taxon

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Abstract

The first Mesozoic representative of the extinct archostematan beetle family Permocupedidae, *Frankencupes ultimus*, gen. et sp. nov., is described based on two isolated elytra from the Lower Anisian (Middle Triassic) Röt Formation of Lower Franconia, Germany. The new fossil occurrence extends the range of the family from the Lower Wuchiapingian (Upper Permian) up to the Anisian, and represents a fine example of a Lazarus taxon in the fossil record of beetles.

Keywords Permian–Triassic event · Lazarus effect · Coleoptera · Buntsandstein · Lower Franconia · Germany

Introduction

Coleoptera (beetles) is a mega-diverse insect order that accounts for nearly one-quarter of all known species on Earth and nearly 40% of all insects (Slipinski et al. 2011). It is generally assumed that the main taxonomic diversification of beetles took place in the Mesozoic (Ponomarenko 2002; Grimaldi and Engel 2005). However, some recent molecular phylogenetic studies indicate that all four living coleopteran suborders diverged as early as in the Permian (Hunt et al. 2007; McKenna and Farrell 2009; McKenna et al. 2015; Toussaint et al. 2017). These estimations are supported by recently obtained palaeontological data. The most ancient beetles identified as possible representatives of Polyphaga and Adephaga, or at least their closest ancestors (stem lineages), were found in the late Middle Permian of China (Ponomarenko et al. 2013) and in the Upper Permian of Australia (*Ponomarenkium belmontensis*: Yan et al. 2017, 2018a). The terminal-Permian insect assemblages of the Tunguska and Kuznetsk basins in Siberia were dominated by beetles that probably belonged to both of these suborders; among those were the oldest Trachypachidae (*Petrodromeus asiaticus* (Martynov 1936): Ponomarenko and Volkov 2013), Gyrinidae (*Tunguskagyrus planus*: Yan et al. 2018b), Triaplidae, and possible Haliplidae (Ponomarenko and Prokin 2015), etc. However, after the Permian–Triassic boundary (PTB), most of these beetles disappear from the fossil record only to reappear again in the Middle and Late Triassic, and can therefore be regarded as Lazarus taxa (sensu Flessa and Jablonski 1983; Jablonski 1984, 1986). Some of the typical Permian beetle groups, such as Asiocoleidae and Taldycupedidae, show similar gaps in their stratigraphic ranges extending from the terminal Permian until the Middle Triassic (Ponomarenko 1969, 2004, 2015). However, it is unknown whether this gap is attributable to biological or ecological causes in the context of the P/T biotic crisis, or whether it simply reflects the incompleteness of the fossil record and the dearth of Lower Triassic insect-bearing deposits.

A more unequivocal example of a Lazarus taxon, not attributed exclusively to the Early Triassic gap, is reported herein and concerns the Permian beetle family Permocupedidae. Permocupedidae belongs to Archostemata sensu Ponomarenko (1969), but, based on the non-numerical character analysis of Beutel (1997) and Beutel et al. (2008), members of this family are stem-group Coleoptera. Permocupedidae was dominant among beetles during the Middle Permian, especially during its first half, but it then abruptly decreased to become rare in the Late Permian, showing a typical extinction scenario (Ponomarenko 2004, 2013). It is not represented among the abundant coleopteran assemblages of the terminal Permian; the last findings were recorded from

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the latest Severodvinian of the Russian Platform (correlated to the Lower Wuchiapingian: for details see Aristov et al. 2013), well before the PTB (Ponomarenko 2013). Recently, two specimens of Permocupedidae were found in the Upper Buntsandstein (Lower Anisian) deposits in Germany. Based on this material, a new genus and species, *Frankencupes ultimus* gen. et sp. nov., is described. The new fossils represent the first record of this family in the Mesozoic and extend its known range for about 14 million years across the PTB into the Middle Triassic.

Materials and methods

Fossil specimens described herein originate from a bed of yellow-grey to straw-yellow dolomitic marls and mudstones called "Strohgelbe Kalke", which crop out at Gambach am Main, Lower Franconia, Germany (for details, see Ansorge and Brauckmann 2008; Bashkuev et al. 2012; Mahler and Sell 2015). The bed represents the uppermost unit of the Myophorienschichten (Röt Formation, Upper Buntsandstein), and is dated to the Lower Anisian, Middle Triassic (Bachmann and Kozur 2004).

Specimens are housed in the collection "Sammlung Mainfränkische Trias" in Markt Euerdorf, Lower Franconia (SMTE). Photographs were taken using a Leica DFC 425 digital camera attached to a Leica M165C stereomicroscope. Scanning electron micrographs were taken from uncoated specimens using a Tescan Vega XMU electron microscope. Line drawings were processed using CorelDRAW 12 software, and photographs were assembled in Adobe Photoshop CS3. Drawing conventions are as follows: double lines filled with a texture, main and additional veins; simple solid lines of various thickness, distinct margins of elytron and cells; dotted lines, indistinct margins.

Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758
Suborder **Archostemata** Kolbe, 1908
Family **Permocupedidae** Martynov, 1933

New specimens, represented by isolated elytra, share the main diagnostic character of the Permocupedidae: a short additional vein in the middle of the elytral base. Additional characters are as follows: principal veins are higher than intermediate ones; all principal veins extend into the elytral apex; the epipleural rim is wide; and broadened fields with rows of small cells are present at the elytral base.

Genus ***Frankencupes*** gen. nov.

Etymology. Generic name is derived from the German name for Franconia—Franken, and -*cupes*, a common suffix for cupedid-like elytra.

Type species. F. ultimus sp. nov.

Diagnosis. Very small, flattened beetles. Elytron about twice as long as wide. Epipleural rim wide, with irregular rows of small polygonal cells. Main veins of elytron clearly wider and higher than intermediate ones, not confluent in apical part of elytron, extending into elytral apex. Cells polygonal, becoming smaller toward the basal parts of all fields. External (subcostal) field with two rows of cells. Cubital field (third counting from sutural margin) with four rows of small cells and short high vein at the base, two rows of wide cells in middle part. All veins bear small, dense tubercles.

Remarks. The new genus differs from all other genera in its very small size and the presence of numerous small cells at the elytral base.

Frankencupes ultimus sp. nov.
Figure 1

Etymology. Specific name is derived from Latin *ultimus*—latest, referring to the relic nature of the new species as the youngest and apparently 'ultimate' representative of this family to be known.

Type material. Holotype, SMTE 6024/4–77, right elytron, part and counterpart; Gambach am Main, Lower Franconia, Germany; Myophorienschichten (Strohgelbe Kalke), upper Röt Formation (Röt-4 Subformation); Lower Anisian, Middle Triassic; paratype, SMTE 6024/4–88, left elytron, part and counterpart, from the same locality and stratum.

Description. Elytron weakly dilated from the base and narrowed in the apical quarter, maximal width after middle part, with subsymmetrical apex, twice as long as wide. Principal veins mainly straight, very distinctly different from intermediate ones. Two principal veins closest to sutural margin run into elytral margin before apex. Intermediate veins of elytra zigzagging. Cells of elytra wide and polygonal on disc and several times smaller on elytral base, with about 25–30 cells in a row. Epipleural rim with 4–5 rows of cells. More than ten cells present posterior to scutellar vein. All veins bear small tubercles.

Measurements. Length of elytra 1.7 mm (holotype)—1.8 mm (paratype), width—0.8 mm.

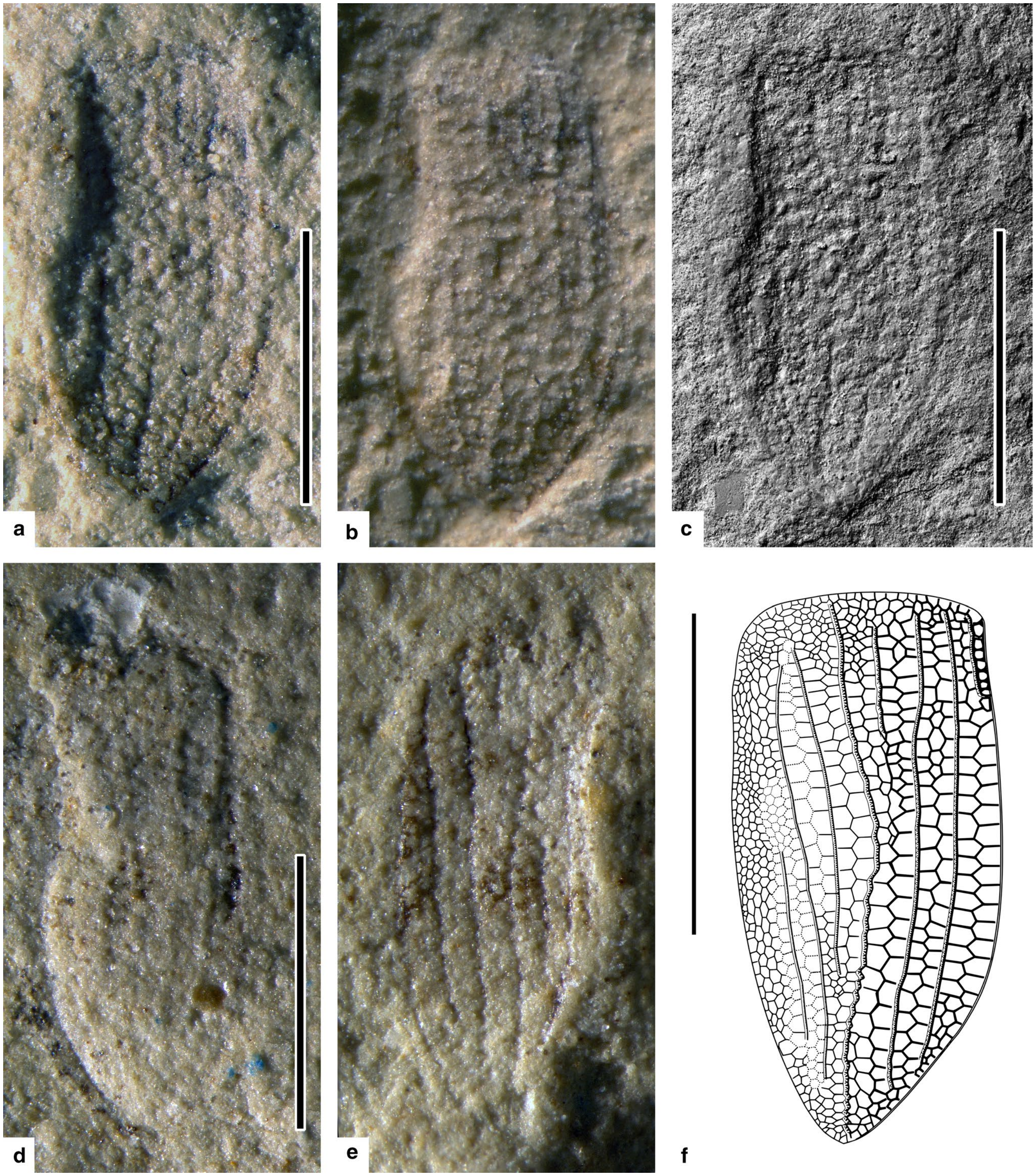

Fig. 1 *Frankencupes ultimus* gen. et sp. nov. **a**, **b** Holotype SMTE 6024/4–77 (counterpart), photographs taken in different illumination settings. **c** The same specimen, SEM photomicrograph. **d**, **e** Paratype SMTE 6024/4–88 (part and counterpart). **f** Interpretative drawing of elytron. *Scale bars* 1 mm (all except **f** to the same scale)

Discussion

The Permian–Triassic environmental event, often referred to as the greatest mass extinction or the Great Dying, was one of the most important episodes in the evolution of life on Earth and the greatest ecological crisis in the entire Phanerozoic. At the same time, the large-scale analysis of the dynamics of the Middle Permian to Early Triassic insect taxonomic diversity revealed that insects as a whole underwent no catastrophic extinction at the Permian–Triassic boundary (Rasnitsyn et al. 2013a, b). Instead, a certain preceding depletion in their diversity took place before the PTB, in the Late Permian (Vyatkian = Changhsingian). This was caused by a deceleration of diversification rather than by actual extinction. However, this phenomenon, referred to as "Rasnitsyn's curve" (by analogy with the widely known Sepkoski's diversity curve), deals only with the taxonomic diversity (at the family level) and does not actually reflect the changes in population abundance of taxa, nor the changes in structure of insect communities. It therefore does not contradict the current hypothesis of a global biotic crisis coupled with a dramatic reorganization of continental ecosystems, which is based on vast evidence from many other groups of terrestrial and freshwater organisms, including plants and tetrapods (see e.g. Benton 2003).

Meanwhile, the earliest Triassic remains one of the most remarkable blank spots in the fossil record of insects, and we still know very little about the true abundances and distributions of insect taxa in terrestrial communities of that time. Beetle fossils known so far from Lower Triassic (pre-Anisian) deposits can be counted on fingers and are entirely represented by isolated smooth elytra of the schizocoleid morphotype attributed to the genus *Pseudochrysomelites*, which could possibly belong to Adephaga according to Ponomarenko (2004, 2008, 2015, 2016). These beetles were supposedly aquatic or at least semi-aquatic and therefore had a better chance of being buried and fossilized than terrestrial forms, especially woodland inhabitants such as cupedoid beetles. Alternatively, *Pseudochrysomelites* might have been a "disaster taxon" (sensu Sahney and Benton 2008), i.e. an opportunistic genus that flourished against a background of a genuinely scarce entomofauna in the aftermath of the Permian–Triassic crisis.

Starting with the latest Olenekian/earliest Anisian, the diversity of Coleoptera rapidly recovered to its pre-crisis levels and continued to increase in the Mesozoic (Ponomarenko 2016). In the Anisian insect faunas, such as those from the Grès à Voltzia Formation of the Vosges Mountains and the Röt Formation of Germany, Coleoptera is the dominant order in terms of species richness and/or in numbers of individuals (Papier et al. 2005; Bashkuev et al. 2012). The beetles of these fossil sites include both Permian and novel taxa.

Possible explanations for the Lazarus effect include three alternative hypotheses (Wignall and Benton 1999; Twitchett et al. 2000; Fara 2001): (1) a reduction in the quality of the fossil record; (2) a migration of taxa into undiscovered refugia; and (3) a critically low abundance of taxa during the episodes of biotic crises, such as mass extinctions, dramatically reduces the chance of taxa becoming fossilized. The first and the third hypotheses are plausible in the case of the Permian–Triassic gap, but they struggle to explain the causes of the Lazarus effect affecting Permocupedidae in the Late Permian. The fossil record of beetles in the interval from the Middle Permian up to the PTB is well documented: beetles are quite abundant or they dominate most of the insect assemblages (Aristov et al. 2013; Ponomarenko 2004, 2013, 2015, 2016, 2017). Thus, we suppose that the most possible scenario was a migration of at least some Permocupedidae in the late Middle Permian into some refugia or landscapes remote from the taphonomic window (see Fara 2001), where they successfully persisted over the next 14 million years and survived the Permian–Triassic crisis.

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