Paläontol Z (2012) 86:175–185
DOI 10.1007/s12542-011-0119-8

RESEARCH PAPER

Insects from the Buntsandstein of Lower Franconia and Thuringia

Alexei Bashkuev · Jürgen Sell · Daniil Aristov · Alexandr Ponomarenko · Nina Sinitshenkova · Horst Mahler

Received: 22 February 2011 / Accepted: 31 August 2011 / Published online: 27 September 2011

Abstract Upper Buntsandstein deposits (mainly *Myophoria* beds, Röt Formation, Early Anisian) in Lower Franconia and Thuringia have yielded a rather rich insect fauna comprising ca. 300 insect specimens assigned to ten orders: Archaeognatha (Dasyleptidae), Ephemeroptera, Blattodea, Grylloblattida, Orthoptera, Hemiptera, Glosselytrodea, Coleoptera, Mecoptera and Diptera. The systematic list of recorded insects is provided. Two species are identified as *Triassodotes vogesiacus* Sinitshenkova, Marchal-Papier, Grauvogel-Stamm et Gall, 2005 (Ephemeroptera: Misthodotidae) and *Pseudopolycentropus triasicus* Papier, Nel et Grauvogel-Stamm, 1996 (Mecoptera), which were previously described from the "Grès à Voltzia" Formation of the Vosges, the stratigraphically closest insect fauna. All grylloblattid specimens are identified as *Chauliodites picteti* Heer, 1864 (Chaulioditidae), known previously from the Middle Buntsandstein of Gödewitz, Saxony-Anhalt. The new genus and species *Hammephemera pulchra* Sinitshenkova, gen. et sp. n. (Ephemeroptera: Sharephemeridae) is described.

Keywords Triassic insects · Coleoptera · Ephemeroptera · Grylloblattida · Mecoptera · Upper Buntsandstein · Lower Franconia · Thuringia

Kurzfassung Der Oberen Buntsandstein (hauptsächlich aus Myophorien-Schichten, Röt Formation, Unter-Anisium) in Unterfranken und Thüringen bringt ziemlich reiche Insektenfauna, in der ca. 300 Exemplare festgestellt wurden, die zu zehn Ordnungen gehören: Archaeognatha (Dasyleptidae), Ephemeroptera, Blattodea, Grylloblattida, Orthoptera, Hemiptera, Glosselytrodea, Coleoptera, Mecoptera und Diptera. Zwei Arten, *Triassodotes vogesiacus* Sinitshenkova, Marchal-Papier, Grauvogel-Stamm et Gall, 2005 (Ephemeroptera: Misthodotidae) und *Pseudopolycentropus triasicus* Papier, Nel et Grauvogel-Stamm, 1996 (Mecoptera) sind auch in der stratigraphisch nächsten Insektenfauna der "Grès à Voltzia" Formation der Vogesen verbreitet. Alle Grylloblattiden-Reste werden zu *Chauliodites picteti* Heer, 1864 (Chaulioditidae) gestellt. Neu aufgestellt werden eine neue Gattung und Art der Sharephemeridae (Ephemeroptera): *Hammephemera pulchra* Sinitshenkova, gen. et sp. n.

Schlüsselwörter Triassische Insekten · Coleoptera · Ephemeroptera · Grylloblattida · Mecoptera · Oberer Buntsandstein · Unterfranken · Thüringen

A. Bashkuev (✉) · D. Aristov · A. Ponomarenko · N. Sinitshenkova
Borissiak Paleontological Institute,
Russian Academy of Sciences, Moscow 117997, Russia
e-mail: fossilmec@gmail.com

D. Aristov
e-mail: danil_aristov@mail.ru

A. Ponomarenko
e-mail: aponom@paleo.ru

N. Sinitshenkova
e-mail: nina_sin@mail.ru

J. Sell · H. Mahler
Sammlung Mainfränkische Trias, 97717 Euerdorf, Germany
e-mail: SMTEuerdorf@t-online.de

H. Mahler
e-mail: SMTEuerdorf@t-online.de

Introduction

Brauckmann and Schlüter (1993) described the insect assemblage of Hammelburg, Unterfranken (Lower

Franconia), which is hitherto the richest occurrence from the European Buntsandstein except for the Vosges ("Grès à Voltzia" Formation of the Upper Buntsandstein, NE France; see for example Gall and Grauvogel-Stamm 2005). They mentioned 17 specimens from the *Myophoria* beds (uppermost Röt, Early Anisian), belonging to Blattodea (*Triassoblatta*? sp.), Coleoptera: Permosynidae (cf. *Ademosyne* sp., aff. *Meseumolpites* sp.), Hemiptera: Auchenorrhyncha (*Heseneuma hammelburgensis* Brauckmann et Schlüter, 1993; *Saaloscytina perreticulata* Brauckmann et Schlüter, 1993; Ipsviciidae gen. et sp. indet.), Hemiptera: Sternorrhyncha (*Dubiaphis curvata* Brauckmann et Schlüter, 1993), Heteroptera fam., gen. et sp. indet. and also Planipennia fam., gen. et sp. indet. The latter three are referred here to Diptera, Hemiptera indet. (determined by D.E. Shcherbakov), and Grylloblattida: *Chauliodites* Heer, 1864, respectively.

The number of fossil insects collected from Hammelburg to other Buntsandstein outcrops in Lower Franconia and Southern Thuringia has greatly increased in recent years owing to the activity of the working group "Mainfränkische Trias" from Markt Euerdorf, Unterfranken, headed by Jürgen Sell. This collection includes more than 300 specimens by now, assigned to ten orders: to the orders listed above, Ephemeroptera, Glosselytrodea, Orthoptera, Mecoptera, Diptera and Archaeognatha were added.

In addition, Ansorge and Brauckmann (2008) recorded a grylloblattid insect from the "Strohgelbe Kalke" of Gambach am Main, one of the localities considered here, and identified it as *Chauliodites picteti* Heer, 1864. The total list of insects recorded from the Upper Bundsandstein of Lower Franconia and Southern Thuringia adjusted for the redefining of Brauckmann and Schlüter's types is provided below.

Archaeognatha: Dasyleptidae: *Dasyleptus* sp.

Ephemeroptera: Misthodotidae:

Triassodotes vogesiacus Sinitshenkova, Marchal-Papier, Grauvogel-Stamm et Gall, 2005

Ephemeroptera: Sharephemeridae:

Hammephemera pulchra Sinitshenkova, gen. et sp. n.

Blattodea: Mesoblattinidae: *?Triassoblatta* sp.

Grylloblattida: Chaulioditidae:

Chauliodites picteti Heer, 1864

Orthoptera fam., gen. et sp. indet.

Hemiptera: Auchenorrhyncha: Saaloscytinidae:

Saaloscytina perreticulata Brauckmann et Schlüter, 1993

Hemiptera: Auchenorrhyncha incertae sedis:

Heseneuma hammelburgensis Brauckmann et Schlüter, 1993

Hemiptera: Auchenorrhyncha: Ipsviciidae gen. et sp. indet.

Coleoptera: ?Adephaga: Triaplidae: *Triaplus* sp.

Coleoptera: Archostemata:

continued

Cupedidae: *Notocupes* sp.

Tricoleidae indet.

Permosynidae (formal taxa):

Ademosyne sp.

Ulomites sp.

Schizocoleidae (formal taxa):

Polysitum sp.

Pseudohydrophilites sp.

Strongulites sp.

Tillyardiopsis sp.

Adikia sp.

Metriorhynchus sp.

Wollastonia sp.

Shepherdia sp.

Mesolobites sp.

Glosselytrodea: Jurinidae (s.l.) gen. et sp.

Mecoptera: Pseudopolycentropodidae:

Pseudopolycentropus triasicus Papier, Nel et Grauvogel-Stamm, 1996

Diptera:

Dubiaphis curvata Brauckmann et Schlüter, 1993

Diptera gen. et sp.

All the new specimens referred to as SMTE are stored in the collection "Sammlung Mainfränkische Trias" in Markt Euerdorf, Unterfranken. Specimen MHI 1486 is deposited in the Dr. Hans Hagdorn's collection in the Muschelkalkmuseum Ingelfingen, Baden-Württemberg.

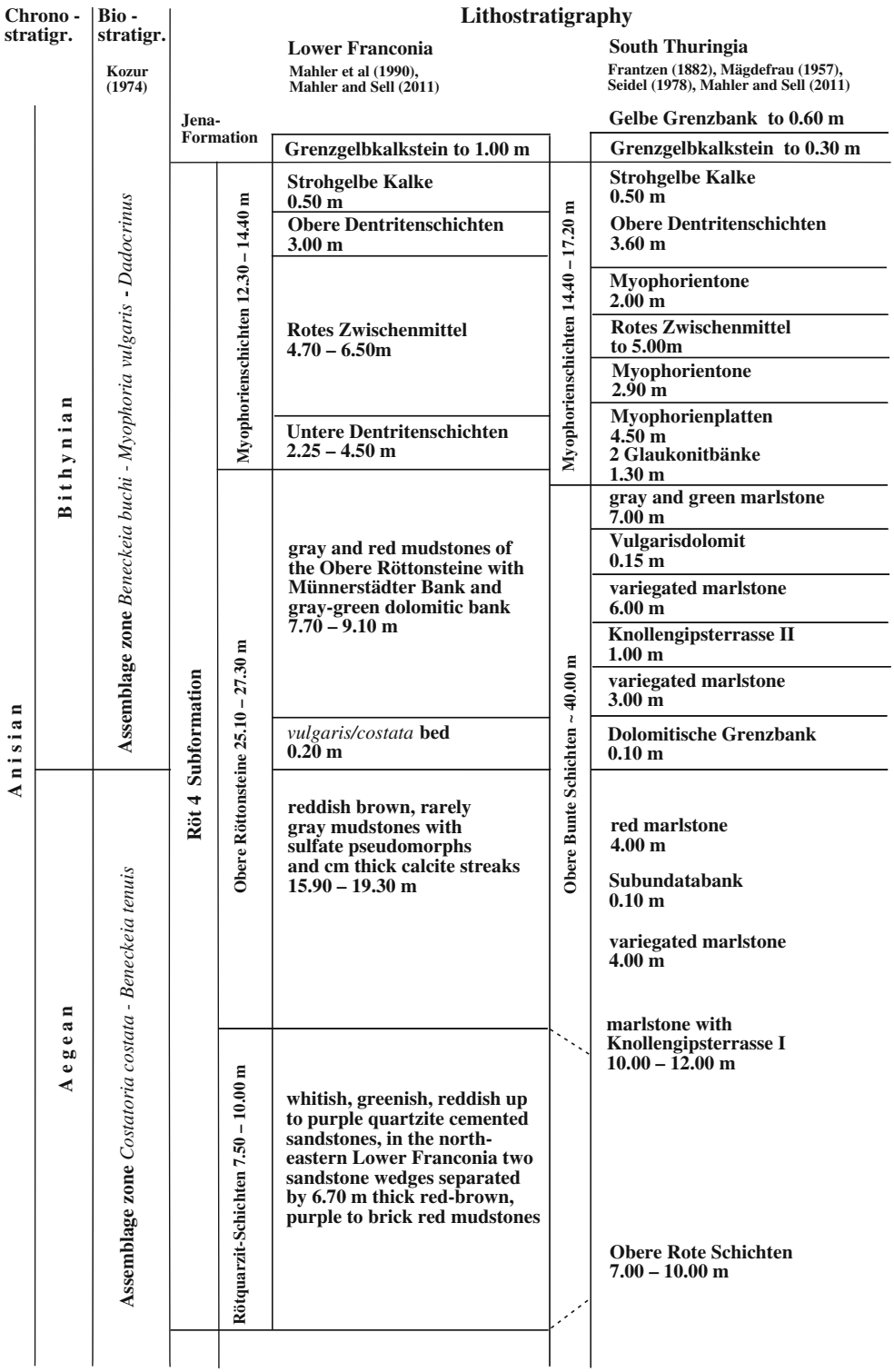
Geological and stratigraphical setting

After being classified as Formation s7, the Röt-Formation (Upper Buntsandstein), was divided into four subformations. Röt 4 Subformation (Table 1) consists of "Rötquarzitschichten," "Obere Röttonsteine" and "Myophorienschichten," and corresponds to the subformation s7–4 (resolution no. 61/66 of the Permian-Triassic Subcommission, 2006/2007).

"Rötquarzitschichten" are interpreted as having been developed in the tidal area (Geyer 2002) and correspond to the beginning of transgressive system tracts of Lower Muschelkalk (Aigner and Bachmann 1992).

The depositional environment of reddish silty clay marls of the "Obere Röttonsteine" is supposed to be similar to the recent playa/sabkha deposits, which were sometimes flooded by marine incursions. In the upper third section of the "Obere Röttonsteine" the *vulgaris/costata* bed (isochronous to the "Dolomitischen Grenzbank" in Thuringia)

Table 1 Stratigraphic division of the Upper Buntsandstein (Röt 4) in Lower Franconia and South Thuringia



forms the most important key horizon in the Upper Buntsandstein in Lower Franconia (Mahler and Sell 1993).

The layers above the "*vulgaris/costata*" bed are characterized by some distinctive green to grey-yellow reduced horizons separated by red-brown, silty, crumbly clay marls. The "Münnerstädter bank" with *Pseudocorbula subundata*, *Saurichthys* sp., vertebrate and insect remains along with the *vulgaris/costata* bed is the horizon with the richest content of fossils within the "Obere Röttonsteine."

The "Myophorienschichten" (Myophoria beds) form the uppermost part of the Buntsandstein section. In Lower Franconia they begin by the "Untere Dendritenschichten," an interbedding of green-grey mudstones and marls, at the base with glauconitic material (Mahler et al. 1990), which are overlaid by sandstones separated by thin clay marl layers. The terminal bed of grey-green mudstones of 0.20–0.80 m thickness ("Myophorien-Hauptbank": Schuster 1936) with bivalves, conchostracans, decapods and rare insect remains (beetle elytra) extends from southern Thuringia to northern Baden-Württemberg.

The overlaying, maximally 6.5 m thick, "Rotes Zwischenmittel" is an equivalent of Myophorientone of the Thuringian Basin. It is formed mainly by red clay marls, in which spreite burrows (*Rhizocorallium* sp.) are rarely to be found.

The "Rotes Zwischenmittel" are followed by the "Obere Dendritenschichten," a sequence of interbedded gray-gray-green and yellow clay marls, mudstones and sandstones. At the top there are intraformational mudstone/marlstone breccias up to 0.50 m thickness, penetrated by calcite veins, often with halite crystals. In contrast to the "Untere Dendritenschichten," bivalves here are rare and small sized. Most commonly lingulids, vertebrate remains (particularly *Saurichthys* sp.), crustaceans (*Triops* sp., conchostracans), and plant and insect remains are found.

The "Strohgelbe Kalke" form the top of the *Myophoria* beds. Yellow-grey to straw-yellow dolomitic marls to mudstones contain mainly conchostracans, plant and insect fossils.

After Kozur (1974) the *Myophoria* beds are considered to be the biostratigraphic equivalent of the "Grès à Voltzia" Formation in the southwest and of the lower Gogoliner Schichten Formation in the east. However, the biostratigraphic correlation of the "Grès à Voltzia" Formation is based only on the occurence of *Myophoria vulgaris*, which confirms at best the Bithynian age.

Localities and paleogeography

In the early Triassic the Germanic Basin resembled to a great extent that of the Zechstein sea. Due to tectonic processes at the beginning of the Anisian, a connection to the Tethys basin was established via the East Carpathian Gate (Fig. 1).

The marine sediments of the lower "Rötkalk" (equivalent of the "Dolomitischen Grenzbank" of Thuringia) with crinoids, *Costatoria costata* and *M. vulgaris* were deposited in areas of the East Carpathian Gate. In contrast, from the time of the formation of the *vulgaris/costata* bed, the region between Jena and Würzburg was situated within an area characterized by the frequent change of playa-,

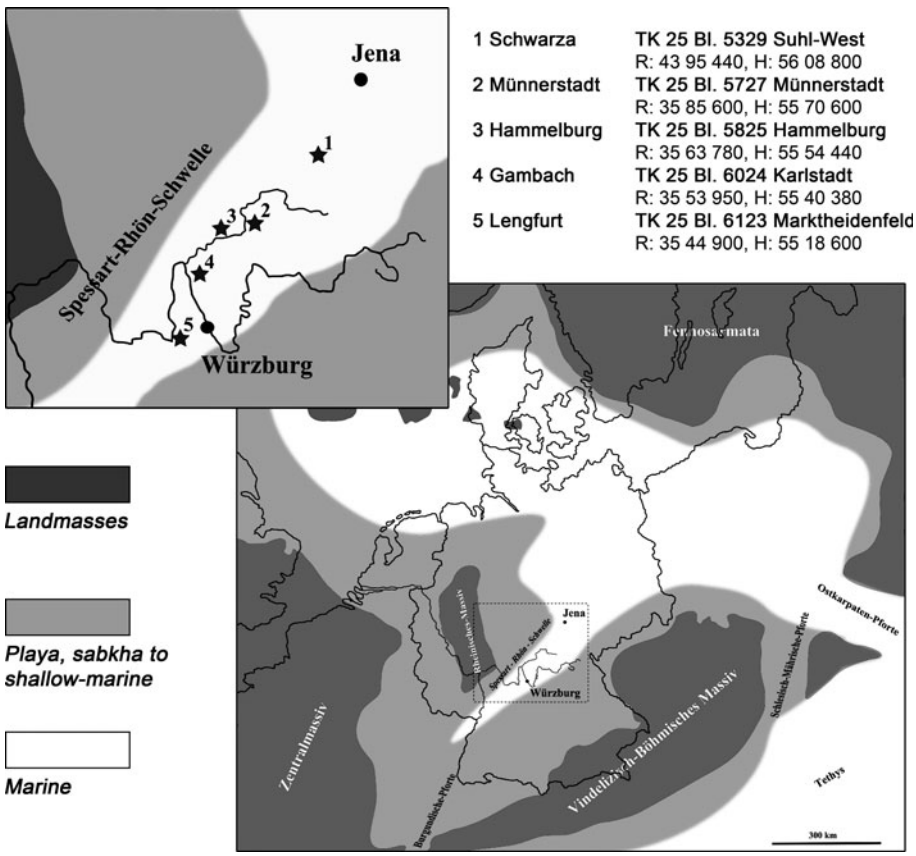


Fig. 1 Paleogeography of the Germanic Basin during the Upper Buntsandstein (Röt 4). Modified after Ziegler (1990). 1–5, insect localities

sabkha- and shallow-marine settings. This assumption, hitherto predominantly justified lithologically, is confirmed particularly by the frequent co-occurrence of terrestrial/freshwater, brackish and marine organisms.

Composition and taphonomy of insect assemblages

The ordinal composition of the insect collections from Upper Buntsandstein localities housed at the SMTE is summarized in the Table 2. The incomplete or poorly preserved specimens that cannot be definitely assigned to any particular order are listed as *incertae sedis* and excluded from percentage counts.

All assemblages are strongly biased, with the Coleoptera comprising from 48 to 78% of collected material. They are represented mainly by isolated elytra (or rarely by isolated thoracic fragments); among other insects the strongly sclerotized elements such as tegmina or their parts (isolated clavi) of Auchenorrhyncha and Blattodea also prevail. Wings of other insects, as well as whole insects including beetles, are very rare.

Assemblages enriched with robust elytra of beetles, cockroaches, and cicadas, are typical for allochthonous taphocoenoses with a long transportation of remains by flowing water (Zherikhin 2002). Though some schizocoleid coleopterans are presumed to be surely aquatic, they are taphonomically similar to other beetles and are apparently allochthonous as well. The only possibly autochthonous elements in the assemblage are quite numerous *Dasyleptus* fossils (Fig. 2) found in the "Obere Dendritenschichten" of Hammelburg. They are mostly completely preserved (not as molting casts), including a number of specimens buried clustered on a small piece of rock. The data available imply at least a semiaquatic lifestyle of *Dasyleptus* (Rasnitsyn 1999; Rasnitsyn et al. 2004). There is no evidence of other aquatic insects, e.g., mayfly nymphs, which in contrast are very abundant in the Vosges.

The insect assemblage of the Schwarza locality rather differs from other regions: Here three rather complete grylloblattid wings (in other localities grylloblattids are represented mostly by wing fragments) and a fragment of large orthopteran wing are found among a total of ten insect fossils. The fossil content of the Buntsandstein section of Schwarza has not yet been prospected in detail, but owing to these finds it looks to be the most promising locality for fossil insects.

Coleoptera

Beetles are mostly represented by diverse Schizocoleidae and Permosynidae. Among the beetles determined as cf. *Ademosyne* sp. by Brauckmann and Schlüter, only two specimens may actually belong to this genus (SMTE, 5825/2-43, 5825/2-31), while most others are rather similar to *Ulomites* Dunstan, 1924 (in Tillyard and Dunstan 1924), and one specimen is referable to *Shepherdia* Dunstan, 1924 (in Tillyard and Dunstan 1924) (Schizocoleidae). The specimen identified as aff. *Meseumolpites* sp. by Brauckmann and Schlüter belongs most probably to the genus

Table 2 Distribution of insect orders in Upper Buntsandstein localities

Site	Lengfurt		Gambach		Hammelburg**				Münnerstadt		Schwarza	
Stratum	Strohgelbe Kalke		Strohgelbe Kalke		Ob. Dendritenschichten		Strohgelbe Kalke		Münnerstädter bank		Ob. Dendritenschichten	Strohgelbe kalke
Order	Expl.	%	Expl.	%	Expl.	%	Expl.	%	Expl.	%	Expl.	Expl.
Archaeognatha	–	–	–	–	>20	–	–	–	–	–	–	–
Ephemeroptera	1	2.2	–	–	1	2.1	–	–	–	–	–	–
Blattodea	3	6.7	10	8.7	3	6.3	6	10	4	17.4	–	–
Grylloblattida	5	11.1	1	0.9	–	–	3	5	–	–	3	1
Orthoptera	–	–	–	–	–	–	–	–	–	–	1	–
Hemiptera	1	2.2	17	14.8	8	16.7	20	33.3	1	4.3	–	–
Glosselytrodea	–	–	–	–	–	–	1	1.6	–	–	–	–
Coleoptera	34	75.6	87	75.6	36	75.0	29	48.3	16	78.3	4	–
Mecoptera	–	–	–	–	–	–	1	1.6	–	–	–	–
Diptera	1	2.2	–	–	–	–	–	–	–	–	–	–
All identifiable*	45	100	115	100	48	100	60	100	23	100	8	1
Incertae sedis	2		2		4		10		1		1	

* Except Dasyleptidae (Archaeognatha)

** In addition, two specimens of Coleoptera are found in the "Untere Dendritenschichten" of Hammelburg

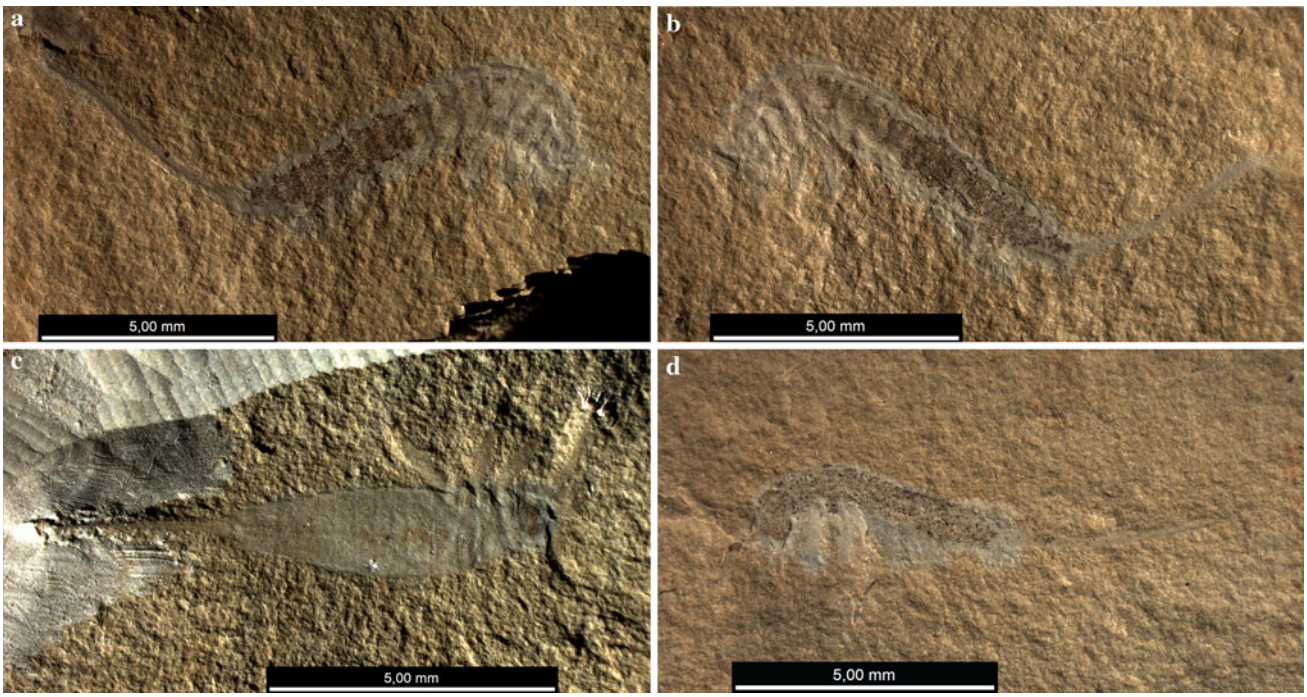


Fig. 2 *Dasyleptus* sp.; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Strohgelbe Kalke", Lower Anisian); Hammelburg, Lower Franconia. **a**–**b** Part and counterpart of specimen SMTE, 5825/2-436, *lateral view*. **c** Specimen SMTE, 5825/2-364, *dorsal view*. **d** Specimen SMTE, 5825/2-417, *lateral view*

Triaplus Ponomarenko, 1977 (in Arnoldi et al. 1977) (Triaplidae): no other known Triassic beetles had their opistognathous head so deeply bent under the prothorax.

Other coleopterans are represented by rare Cupedidae (single specimen of *Notocupes* sp.) and indeterminable Tricoleidae. There are not any Polyphaga as well as true Adephaga. Most determined genera are common in the Middle-Late Triassic and Early Jurassic.

The list of determined genera is provided in the Introduction section. But since many specimens are represented by poorly preserved isolated elytra, their further specification as well as the comprehensive systematic study of the beetle assemblage is needed.

Ephemeroptera

The finds of the fossil mayfly wings are quite rare. Therefore, the two complete wings with clear venation, recorded from the Upper Buntsandstein of Lower Franconia, are of great interest.

One wing (SMTE, 6123/1-28; Fig. 3), from "Strohgelbe Kalke" of Lengfurt, is referred to the family Misthodotidae and may be identified to the species level as *Triassodotes vogesiacus* Sinitshenkova, Marchal-Papier, Grauvogel-Stamm et Gall, 2005 from the Vosges in northeastern France (Sinitshenkova et al. 2005).

In the deposits of the "Grès à Voltzia" Formation in the Vosges, a rich mayfly fauna has been found. Two mayfly species, based on wings, belong to the families Misthodotidae and Toxodotidae (Sinitshenkova et al. 2005). Up to now this is the only case in which the typical Permian family Misthodotidae still occurs in Triassic deposits. The representatives of Misthodotidae and Toxodotidae are characterized by the presence of oval and almost homonomous wings.

The particular characters of the second wing make it possible to erect a new genus and species, named *H. pulchra* Sinitshenkova, gen. et sp. n. Due to the presence of a long CuA with intercalary veins forming a triad, it is included in the family Sharephemeridae Sinitshenkova, 2002. This family was originally established for the single species *Sharephemera cubitalis* Sinitshenkova, 2002, based on a unique find of a forewing from the Late Jurassic insect-bearing deposits in the Shar Teg locality in Mongolia (Sinitshenkova 2002). The new specimen renders a review of the family and the nominate genus *Sharephemera*, showing that the diagnosis of the family as given in the original paper was right. The new genus differs from *Sharephemera* in many features.

In the new species *H. pulchra* sp. n. the wing has an obviously expressed tornus, which is characteristic for a heteronomous flying apparatus. This means that hind wings

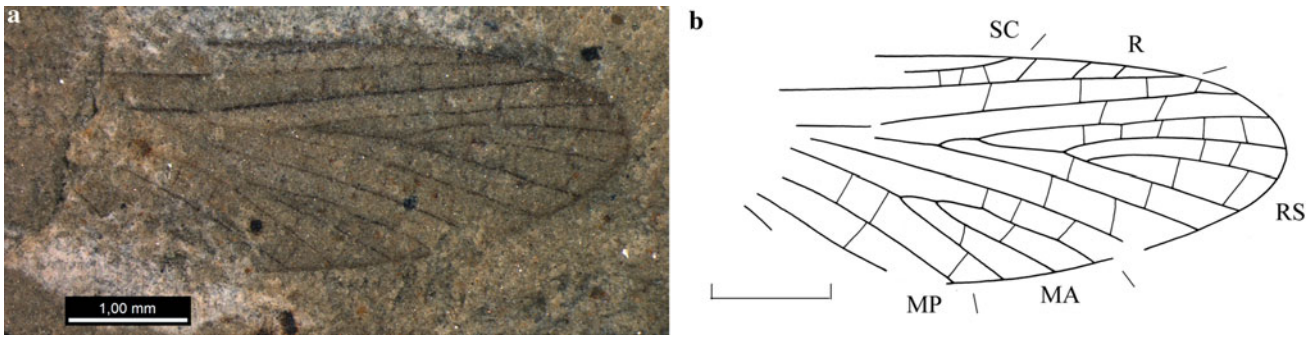


Fig. 3 *Triassodotes vogesiacus* Sinitshenkova, Marchal-Papier, Grauvogel-Stamm et Gall, 2005; specimen SMTE, 6123/1-28; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Strohgelbe Kalke," Lower Anisian); Lengfurt, Lower Franconia. **a** Photograph, **b** drawing

of *H. pulchra* sp. n. were considerably shortened in comparison with the forewings. This feature is typical for an advanced state of the flying apparatus. However, the venation with CuA branching and forming a triad is pleiomorphic.

Order Ephemerida Latreille, 1810
(=Ephemeroptera Hyatt and Arms, 1890, s.l.)
Family Sharephemeridae Sinitshenkova, 2002

Emended diagnosis: Small mayflies, forewing two times as long as wide. Base of forewing broad with developed anal area, cubital area narrow, CuA fork long with intercalary vein, CuP long and simple, anal veins long, cubital and anal veins straight and slightly curved.

Comparison: The new family sharply differs from known families by the shape of the forewing with wide basal part, narrow cubital area, long CuA fork with intercalary vein, almost straight and slightly curved cubital and anal veins.

Genus *Sharephemera* Sinitshenkova, 2002

Type species: *Sh. cubitalis* Sinitshenkova, 2002, from the Upper Jurassic lacustrine insect-bearing deposits from west of Shar Teg Mountain to southeast of Adzh-Bogdo in Gobi-Altai aymak of Mongolia.

Emended diagnosis: Forewing. Anterior margin slightly concave, costal area wider at wing base than on its top. Anterior RS branch simple, posterior one branching. Forks of MA and CuA longer than their stems correspondingly. CuP straight, A1 branching, with a long intercalary longitudinal vein between its branches. Anal area obviously widened, tornus poorly expressed.

Genus *Hammephemera* Sinitshenkova, gen. n.

Etymology: from Hammelburg.

Type species: *Hammephemera pulchra* Sinitshenkova, n. sp.

Diagnosis: Forewing. Anterior margin slightly convex, its top rounded. RS system with seven longitudinal veins, posterior branch of RS simple, anterior one branching. Forks of MA and CuA not longer than their stems correspondingly, CuP almost straight. Anal veins simple, A1 smoothly curved, A2 almost straight, moderately seen simple short A3. Anal area narrowed, tornus expressed and moved towards the middle of wing.

Comparison: *Hammephemera* gen. n. differs well from *Sharephemera* by the convex anterior wing margin, branching of the anterior RS branch, shorter forks of MA and CuA, simple anal veins in more narrow anal area and by tornus moved towards the middle of the wing.

Hammephemera pulchra Sinitshenkova, sp. n.

Etymology: from Latin *pulchra,* beautiful.

Holotype: SMTE, 5825/2-365; negative impression of complete forewing with well-preserved longitudinal venation, crossveins not visible (Fig. 4).

Locality and Horizon: Herolds-Berg N'Hammelburg, Lower Franconia; Myophoria beds ("Obere Dendritenschichten"), Röt Fm, Early Anisian, Bythinian, Middle Triassic.

Diagnosis: as for the genus by monotypy.

Description: Forewing length, 8.75 mm, maximum width, 4.06 mm. Costal area obviously wider than subcostal one at the wing base and in its top. Anterior RS branch forking twice and entering wing margin by seven branches. MA fork situated restrictedly proximal than third RS fork, MA fork shorter than its stem. MP branching near wing base slightly distad of first RS fork, its posterior branch running from MA with curve. CuA branching in the

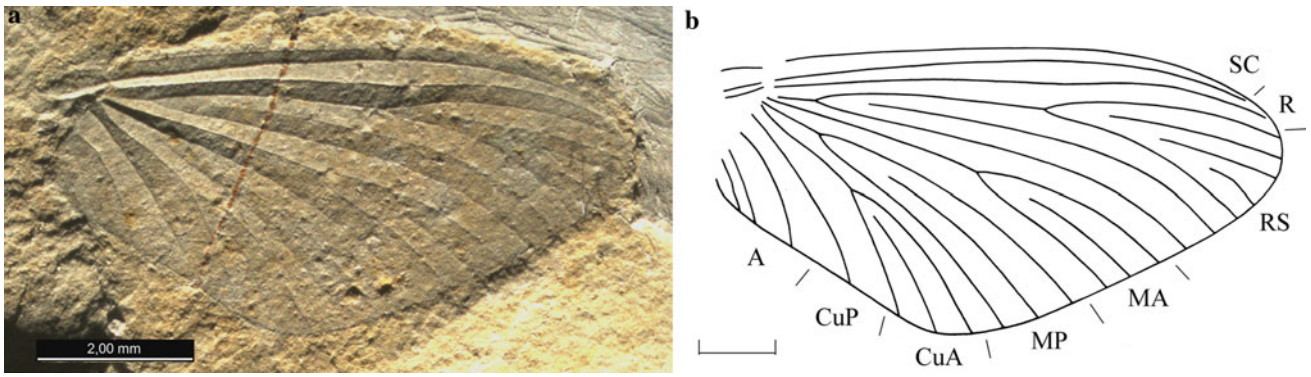


Fig. 4 *Hammephemera pulchra* Sinitshenkova, gen. et sp. n., holotype SMTE, 5825/2-365; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Obere Dendritenschichten", Lower Anisian); Hammelburg, Lower Franconia. **a** Photograph, **b** drawing

middle, CuP slightly curved near wing margin. Tornus situated almost at middle of wing.

Grylloblattida

All of the nine identifiable grilloblattid fossils found in the Upper Buntsandstein of Lower Franconia and Thuringia (including the specimen MHI 1486, deposited in the Muschelkalkmuseum Ingelfingen) belong to *C. picteti* Heer, 1864 (Chaulioditidae) (argumentation is given below in Remarks). In addition, there are four wing fragments belonging apparently to Chaulioditidae and possibly to *Chauliodites* as well. Thus, the grylloblattid assemblage is in contrast to that of the Vosges, where Blattogryllidae dominate (about 70% of all grylloblattids), while Chaulioditidae are rare (as well as Megakhosaridae and Mesorthopteridae) (Aristov et al. 2011).

Also, grylloblattids are relatively more abundant in Lower Franconia (Table 2) than in the Vosges: 5–11% in Hammelburg and Lengfurt; 4 specimens of 10 in Schwarza, versus 2 or <1% (Shcherbakov 2008; Aristov et al. 2011, respectively).

The family Chaulioditidae was erected by Handlirsch (1906) for *C. picteti* Heer, 1864 from the Middle Buntsandstein of Gödewitz near Salzmünde in Saxony-Anhalt. As it proved later, Chaulioditidae (especially the most widespread genus *Chauliodites*) are among the most important insect index fossils of the Late Permian-Early Triassic, which numerically dominated most of the Early Triassic insect assemblages. The most ancient findings of the family are known from the Middle and Late Permian of European Russia, and the youngest ones from the Middle Triassic of France (Vosges) and China (Aristov 2003, 2004, 2005, 2008, 2009; Aristov et al. 2011).

Order Grylloblattida Walker, 1914
Suborder Grylloblattina Walker, 1914
Family Chaulioditidae Handlirsch, 1906
Genus *Chauliodites* Heer, 1864
Chauliodites picteti Heer, 1864

Holotype: (Heer 1864: Fig. 11; Handlirsch 1906: pl. 39, Fig. 16); Gödewitz near Salzmünde (S Wettin), Saxony-Anhalt; Middle Buntsandstein, Lower Triassic.

New material: specimens SMTE, 5329/1-12 (Fig. 5) and 5329/1-39 (Fig. 6), each presented by part and counterpart of well-preserved forewing without anal area; Myophoria beds ("Obere Dendritenschichten"), Röt Fm, Lower Anisian, Bythinian, Middle Triassic; Schwarza, Thuringia;

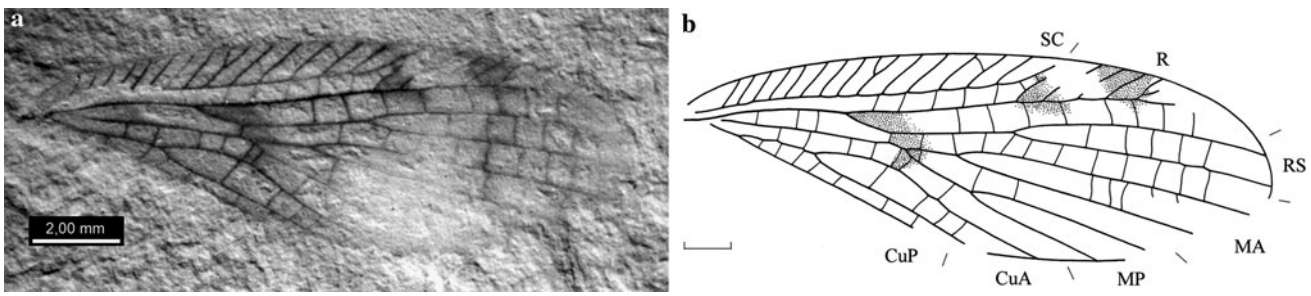


Fig. 5 *Chauliodites picteti* Heer, 1864, specimen SMTE, 5329/1-12; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Obere Dendritenschichten", Lower Anisian); Schwarza, Thuringia. **a** Photograph, **b** drawing

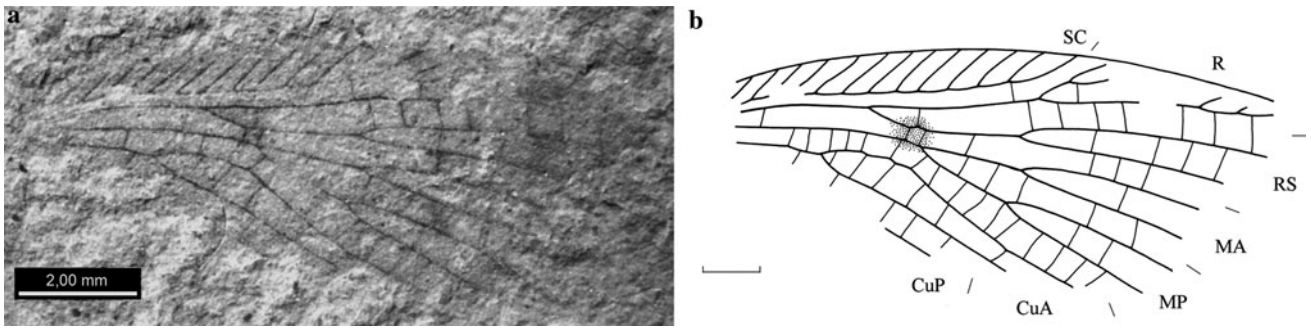


Fig. 6 *Chauliodites picteti* Heer, 1864, specimen SMTE, 5329/1-39; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Obere Dendritenschichten", Lower Anisian); Schwarza, Thuringia. **a** Photograph, **b** drawing

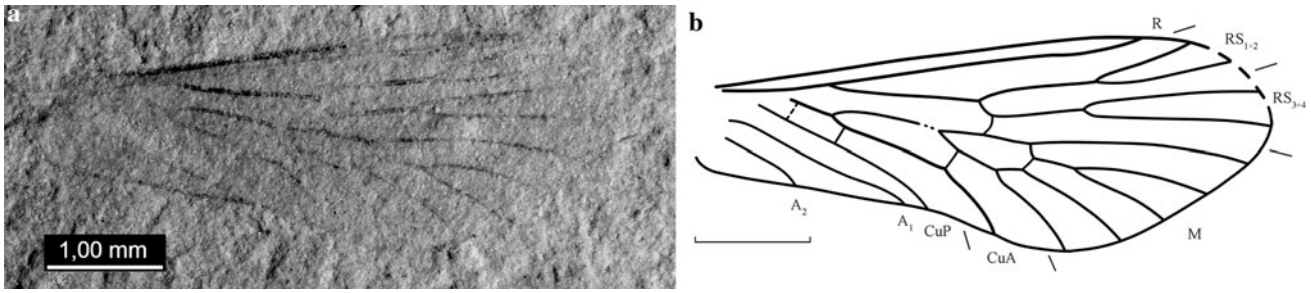


Fig. 7 *Pseudopolycentropus triasicus* Papier, Nel et Grauvogel-Stamm, 1996, specimen SMTE, 5825/2-199; early Middle Triassic (Upper Buntsandstein, Röt Fm, "Strohgelbe Kalke", Lower Anisian); Hammelburg, Lower Franconia. **a** Photograph, **b** drawing

SMTE, 5329/1-1, forewing with apical and basal parts being destroyed; Myophoria beds ("Strohgelbe Kalke"), Röt Fm, Lower Anisian, Bythinian, Middle Triassic; Schwarza, Thuringia; SMTE, 5825/2-198, fragment of central part of forewing; Myophoria beds ("Strohgelbe Kalke"), Röt Fm, Lower Anisian, Bythinian, Middle Triassic; Herolds-Berg N'Hammelburg, Lower Franconia.

Specimens SMTE, 5825/2-21 (Brauckmann and Schlüter 1993: Fig. 10, described as Planipennia, fam., gen. et sp. indet.), from "Strohgelbe Kalke" of Hammelburg, and SMTE, 6123/1-26, 6123/1-31 and 6123/1-32 from "Strohgelbe Kalke" of Lengfurt, Lower Franconia, all represented by forewing fragments, also belong most likely to the same species.

Description: Forewing length about 14; length/width ratio about 3:1. Anterior margin convex. Costal space at the beginning of RS is 2.5–3 times as wide as subcostal space. SC terminating before distal wing third. Fore branches of SC and R simple or dichotomous. R curving towards before beginning of RS. RS beginning in basal wing third, forked before the SC apex. M forked distally to base of RS. MA and MP two-branched. Space between the CuA branches narrowed in its distal half. CuA_1 kinked at joints with crossveins. Interradial space at wing base narrow. Crossveins simple. Color pattern formed by dark spots in wing base, at base of RS and at pterostigma.

Remarks: The described material is indistinguishable from the holotype of *Ch. picteti* as figured by Ansorge and Brauckmann (2008, Fig. 3b) and referred here to this species despite of the stratigraphic difference. Since the holotype of *Ch. picteti* is missing (Ansorge and Brauckmann 2008, p. 256), the final decision of the specific attribution of the described material should be deferred until new finds of conspecific wings in the type locality.

The specimen MHI 1486 from "Strohgelbe Kalke" of Gambach, described as *Ch.* cf. *picteti* by Ansorge and Brauckmann (2008), is only distinguished by the simple (or forking very late) MP and falls apparently within the observed intraspecific variability.

Mecoptera

The only specimen of Mecoptera from German Buntsandstein occurs from "Strohgelbe Kalke" of Hammelburg and is referred to the Vosges species *P. triasicus* Papier, Nel, et Grauvogel-Stamm, 1996. The family Pseudopolycentropodidae includes three genera, of which the most widespread, nominate genus *Pseudopolycentropus* is known from the Middle Triassic to Late Jurassic of Europe und Asia (Grimaldi et al. 2005), comprising only the minor component of the mecopteran fauna in almost all localities. The only exception is for the Vosges, where 19 of 22

mecopteran specimens belong to *P. triasicus*, while the rest fall within Permochoristidae (*Prochoristella pilosa* Papier, Nel et Grauvogel-Stamm, 1996), Liassophilidae [*Laurentiptera gallica* (Laurentiaux et Grauvogel, 1953) (in Laurentiaux 1953)] and Parachoristidae (Bashkuev, personal observation). In consideration of the shared species, it can be assumed that the Mecoptera assemblage of Lower Franconia was generally similar to the Vosges.

Order Mecoptera Packard, 1886
Family Pseudopolycentropodidae Handlirsch, 1925
Genus *Pseudopolycentropus* Handlirsch, 1906
Pseudopolycentropus triasicus Papier, Nel et Grauvogel-Stamm, 1996

Holotype: Papier et al. (1996): Fig. 1; Northern Vosges Mountains, NE France; "Grès à Voltzia" Formation, Lower Anisian, Middle Triassic.

New material: SMTE, 5825/2-199; complete forewing, part and counterpart (Fig. 7); Herolds-Berg N'Hammelburg, Lower Franconia; Myophoria beds ("Strohgelbe Kalke"), Röt Fm, Early Anisian, Bythinian, Middle Triassic.

Remarks: Wing length, 5 mm, and maximum width 1.9. SC, pterostigma, free base of CuA and crossveins in anal area are not traceable because of poor preservation. The described specimen slightly differs from the holotype of *P. triasicus* in the narrow costal space and shorter CuA, reaching just the wing midlength. These deviations apparently fall within the range of intraspecific variability shown in the material from the Vosges.

Acknowledgments We are deeply grateful to Dr. Dmitry Shcherbakov [Borissiak Palaeontological Institute, Russian Academy of Sciences (PIN)] who excited his interest in the problem, reviewed the manuscript and proposed some important revisions, and in addition redetermined Brauckmann and Schlüter's types of Hemiptera; to Prof. Alexandr Rasnitsyn (PIN) for providing the determination of Dasyleptidae and Glosselytrodea, and for further helpful comments; to Prof. C. Brauckmann (Clausthal University of Technology), Dr. Jean-Claude Gall (Louis Pasteur University, Strasbourg) and Prof. Jörg Schneider (Freiberg University, Geological Institute) for the critical reading of the manuscript and valuable information; to Lea Grauvogel-Stamm (Louis Pasteur University, Strasbourg) for providing access to the insect collections of the Vosges. Finally, we wish to thank to Michael and Larissa Henz, Bernd Neubig (SMTE) and Elena Bashkueva for their comprehensive aid in the study. The research was supported by the Russian Foundation for Basic Research, project 09-04- 01241, and by the Program 15 of the Presidium of the Russian Academy of Sciences "The Origin of the Biosphere and Evolution of the Geo-Biosystems".

References

Aigner, T., and G.H. Bachmann. 1992. Sequence-stratigraphic framework of the German Triassic. *Sedimentary Geology* 80: 115–135.

Ansorge, J., and C. Brauckmann. 2008. Chaulioditidae from Germany, with description of a new specimen from early middle Triassic of Gambach/main, Bavaria (Insecta, Grylloblattida). *Entomologia Generalis* 31(3): 251–260.

Aristov, D.S. 2003. Revision of the family Tomiidae (Insecta: Grylloblattida). *Paleontological Journal* 37(1): 31–38.

Aristov, D.S. 2004. Grylloblattids of the family Chaulioditidae (=Tomiidae syn. nov.) (Insecta: Grylloblattida) from the Upper Permian of Orenburg region. *Paleontological Journal* 38(Suppl 2): 146–149.

Aristov, D.S. 2005. New Grylloblattids (Insecta: Grylloblattida) from the Triassic of Eastern Europe, Eastern Kazakhstan, and Mongolia. *Paleontological Journal* 39(2): 173–177.

Aristov, D.S. 2008. New Tatarian representatives of the subfamily Chaulioditinae (Insecta: Grylloblattida: Chaulioditidae) from European Russia. *Paleontological Journal* 42(1): 32–35.

Aristov, D.S. 2009. New Permian grylloblattids (Insecta: Grylloblattida) from Isady locality (Severodvinian stage of Vologda region). *Russian Entomological Journal* 18(1): 17–22. (In Russian).

Aristov, D.S., L. Grauvogel-Stamm, and F. Marchal-Papier. 2011. New Grylloblattida (Insecta) from the Grès à Voltzia of the Vosges (Middle Triassic of the France). *Paleontological Journal* 45(2): 159–166.

Arnoldi, L.V., V.V. Zherikhin, L.M. Nikritin, and A.G. Ponomarenko. 1977. Mezozoyskie zhestkokrylye. Nauka: Moscow. (English translation: 1992. Mesozoic Coleoptera. Washington: Smithsonian Institution Libraries).

Brauckmann, C., and Th. Schlüter. 1993. Neue Insekten aus der Trias von Unter-Franken. *Geologica et Palaeontologica* 27: 181–199.

Frantzen, W. 1882. *Übersicht der geologischen Verhältnisse bei Meiningen*. Berlin: J.F. Starcke.

Gall, J.-C., and L. Grauvogel-Stamm. 2005. The early middle Triassic 'Grès à Voltzia' formation of Eastern France: A model of environmental refugium. *Comptes Rendus Palevol* 4: 637–652.

Geyer, G. 2002. *Geologie von Unterfranken und angrenzenden Regionen*. Stuttgart: Klett Perthes.

Grimaldi, D., J. Zhang, N.C. Fraser, and A. Rasnitsyn. 2005. Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea). *Insect Systematics and Evolution* 36(4): 443–458.

Handlirsch, A. 1906. *Die fossilen Insekten und die Phylogenie der rezenten Formen: Ein Handbuch für Paläontologen und Zoologen*. Leipzig: Verlag Wilhelm Engelmann.

Handlirsch, A. 1925. Palaeontologie. In *Handbuch der Entomologie*, ed. Schröder, Ch., 3: 117–306.

Heer, O. 1864. Über die fossilen Kakerlaken (Blattidae). *Vierteljahresschrift der Naturforschenden Gesellschaft, Zürich* 9: 273–302.

Kozur, H. 1974. *Biostratigraphie der germanischen Mitteltrias*. Freiberg: Freiberger Forschungshefte.

Laurentiaux, D. 1953. Classe des Insectes (Insecta Linné, 1758). In *Traité de Paléontologie, 3,* ed. Piveteau J., 397–527. Paris: Masson et Cie.

Mägdefrau, K. 1957. *Geologischer Führer durch die Trias um Jena*. Jena: Verlag von Gustav Fischer.

Mahler, H., and J. Sell. 1993. Die "vulgaris/costata-Bank"(Oberer Buntsandstein, Mitteltrias)—ein lithostratigraphisch verwertbarer biostratigraphischer Leithorizzont mit chronostratigraphischer Bedeutung. In *Muschelkalk. Schöntaler symposium 1991*, eds. Hagdorn, H., and A. Seilacher. Sonderbände der Gesellschaft für Naturkunde in Württemberg 2: 187–192.

Mahler, H., and J. Sell. 2011. Profile im Oberen Buntsandstein—Röt 4 von Unterfranken und Südthüringen. *Naturwissenschaftliches Jahrbuch Schweinfurt* (in press).

Mahler, H., J. Sell, M. Henz, and B. Neubig. 1990. Ein Beitrag zur Feinstratigraphie und Fossilführung der Myophorien-Folge (Trias) im nördlichen Unterfranken. *Naturwissenschaftliches Jahrbuch Schweinfurt* 8: 1–22.

Papier, F., A. Nel, and L. Grauvogel-Stamm. 1996. Deux nouveaux insectes Mecopteroidea du Buntsandstein superieur (Trias) des Vosges (France). *Paleontologia Lombarda* 5: 37–45.

Rasnitsyn, A.P. 1999. Taxonomy and morphology of *Dasyleptus* Brongniart, 1885, with description of a new species (Insecta: Machilida: Dasyleptidae). *Russian Entomological Journal* 8(3): 145–154.

Rasnitsyn, A.P., D.S. Aristov, A.V. Gorochov, J.M. Rowland, and N.D. Sinitshenkova. 2004. Important new insect fossils from Carrizo Arroyo and the Permo-Carboniferous faunal boundary. *New Mexico Museum of Natural History and Science Bulletin* 25: 215–246.

Schuster, M. 1936. Die Gliederung des Unterfränkischen Buntsandsteins. II. Der Obere Buntsandstein oder das Röt, c. Das Obere Röt oder die Die Stufe der Röt-Tone (2. Die Oberen Röt-Tone mit den Myophorien-Schichten). *Abhandlungen der Geologischen Landesuntersuchung am Bayerischen Oberbergamt* 15: 1–53.

Seidel, G. 1978. *Das Thüringer Becken. Geologische Exkursionen*. Leipzig: Kartographische Anstalt Gotha.

Sinitshenkova, N.D. 2002. New late Mesozoic mayflies from the Shar-Teeg locality, Mongolia (Insecta, Ephemerida = Ephemeroptera). *Paleontological Journal* 36(3): 270–276.

Sinitshenkova, N.D., F. Marchal-Papier, L. Grauvogel-Stamm, and J.-C. Gall. 2005. The Ephemeridea (Insecta) from the Grès à Voltzia (early Middle Triassic) of the Vosges (NE France). *Paläontologische Zeitschrift* 79(3): 377–397.

Shcherbakov, D.E. 2008. On Permian and Triassic insect faunas in relation to biogeography and the Permian–Triassic crisis. *Paleontological Journal* 42(1): 15–31.

Tillyard, R.J., and B. Dunstan. 1924. Mesozoic insects of Queensland. *Geological Survey of Queensland* 273: 1–74.

Zherikhin, V.V. 2002. Pattern of insect burial and conservation. In *History of Insects*, ed. A.P. Rasnitsyn, and D.L.J. Quicke, 17–63. Dordrecht: Kluwer Academic Press.

Ziegler, P.A. 1990. *Geological atlas of western and central Europe*, 2nd ed. The Hague: Shell Internationale Petroleum Maatschappij BV, and Geological Society of London.