Entomologie heute 28 (2016): 127-142

The Fossil Insects of the Quercy Region: A Historical Review

Die fossilen Insekten der Quercy Region: eine historische Übersicht

Achim H. Schwermann, Michael Wuttke, Tomy dos Santos Rolo, Michael S. Caterino, Günter Bechly, Heiko Schmied, Tilo Baumbach & Thomas van de Kamp

Summary: At the end of the 19th century, numerous mineralized insects from the Paleogene were discovered during phosphorite mining in the former province of Quercy in France. Despite their unusual three-dimensional preservation, the Quercy insects received only minor attention from the scientific community. During the time of mining, the only detailed study on the subject was provided in 1890 by Karl Flach, who described two carrion beetle species. More than five decades later, the Swiss entomologist Eduard Handschin published the first and hitherto only comprehensive study on the Quercy insects. Unfortunately, his detailed work did not draw the attention of paleoentomologists to these fascinating fossils. More than 70 years after Handschin's study, recent examinations provided fascinating new insights into this almost forgotten fossil type. While the descriptions by the early researchers were largely restricted to the external shape of the specimens, X-ray microtomography now permits detailed non-destructive examination of their internal composition. The latest study revealed extraordinarily well-preserved anatomical characters in a fossil hister beetle (Histeridae: *Onthophilus intermedius* Handschin, 1944), which was largely hidden inside a stony matrix. This finding suggests that the Quercy specimens constitute a rich but yet largely unexploited source for anatomical data of fossil insects.

Keywords: Paleogene, phosphatization, mineralization, François Gervais, Henri Filhol, Armand Thévenin, Karl Flach, Eduard Handschin

Zusammenfassung: Gegen Ende des 19. Jahrhunderts wurden während des Phosphorit-Abbaus in der ehemaligen Provinz Quercy in Frankreich zahlreiche mineralisierte Insekten aus dem Paläogen gefunden. Trotz ihrer ungewöhnlichen dreidimensionalen Erhaltung haben die Quercy-Insekten jedoch nur wenig Beachtung in der wissenschaftlichen Welt erfahren. Karl Flach veröffentlichte 1890 die einzige während der Abbauphase entstandene Studie zu dem Thema, in der er zwei Aaskäferarten beschreibt. Mehr als fünf Jahrzehnte später publizierte der Schweizer Entomologe Eduard Handschin die erste und bisher einzige umfassende Studie über die Quercy-Insekten. Unglücklicherweise hat auch seine detaillierte Arbeit nicht die Beachtung der Paläoentomologen für diese faszinierenden Fossilien wecken können. Mehr als 70 Jahre nach Handschins Studie ermöglichten aktuelle Untersuchungen nun faszinierende neue Einsichten in einen fast vergessenen Fossilientyp. Während die Untersuchungen der ersten Bearbeiter weitgehend auf die äußere Form der Stücke beschränkt waren, erlaubt die Röntgen-Mikrotomographie heutzutage eine zerstörungsfreie Untersuchung ihres internen Aufbaus. Die jüngste Arbeit offenbarte außergewöhnlich umfassend überlieferte anatomische Merkmale eines Stutzkäfers (Histeridae: *Onthophilus intermedius* Handschin, 1944), der größtenteils im Gestein verborgen ist. Dieses Ergebnis verdeutlicht, dass die Quercy-Insekten eine reichhaltige und bislang weitgehend unerschlossene Quelle für anatomische Informationen fossiler Insekten darstellen.

Schlüsselwörter: Paläogen, Phosphatisierung, Mineralisation, François Gervais, Henri Filhol, Armand Thévenin, Karl Flach, Eduard Handschin

1. Introduction

Arthropod fossils occur in many varieties, e.g. as compressions and impressions, casts, embeddings, or inclusions in amber (Grimaldi et al. 1994; Martínez-Delclòs et al. 2004; Grimaldi & Engel 2005; Penney & Jepson 2014). While amber inclusions are most famous for their exquisite preservation of three-dimensional shape, sometimes even preserving soft tissues (Perreau & Tafforeau 2011; van de Kamp et al. 2014), 3D arthropod fossils are also known from concretions, hollow casts, encapsulations and mineral replications. In mineralized fossils, organic tissues are replaced by minerals like calcite (McCobb et al. 1998), silica (Miller & Lubkin 2001), pyrite (Grimaldi & Engel 2005), or phosphate (Duncan & Briggs 1996; Hellmund & Hellmund 1996; Waloszek 2003). These fossils are known from many localities and geological ages, but while there are several examples of mineralized arthropod fossils from marine deposits (e.g. Ma et al. 2013; Cong et al. 2014; Edgecombe et al. 2015; Siveter et al. 2007, 2013, 2014), mineralization within subaerial conditions are generally less known.

At the end of the 19th century numerous fossils were discovered in the former Quercy province in southwestern France. Whereas most vertebrates from that locality were represented merely by bones and teeth, a smaller number of body fossils of mineralized – or more precisely phosphatized – frogs, salamanders, and snakes were described (Filhol 1876a; Laloy et al. 2013; Tissier et al. 2015). Multiple phosphatized arthropods – most of them insects – were found alongside the vertebrate fossils. A fascinating feature of the Quercy arthropods is their three-dimensional preservation, while most fossil arthropods – with the exception of amber inclusions – are compressed to two-dimensional objects. However, despite their unusual properties, the insects of the Quercy received only minor attention in the scientific community.

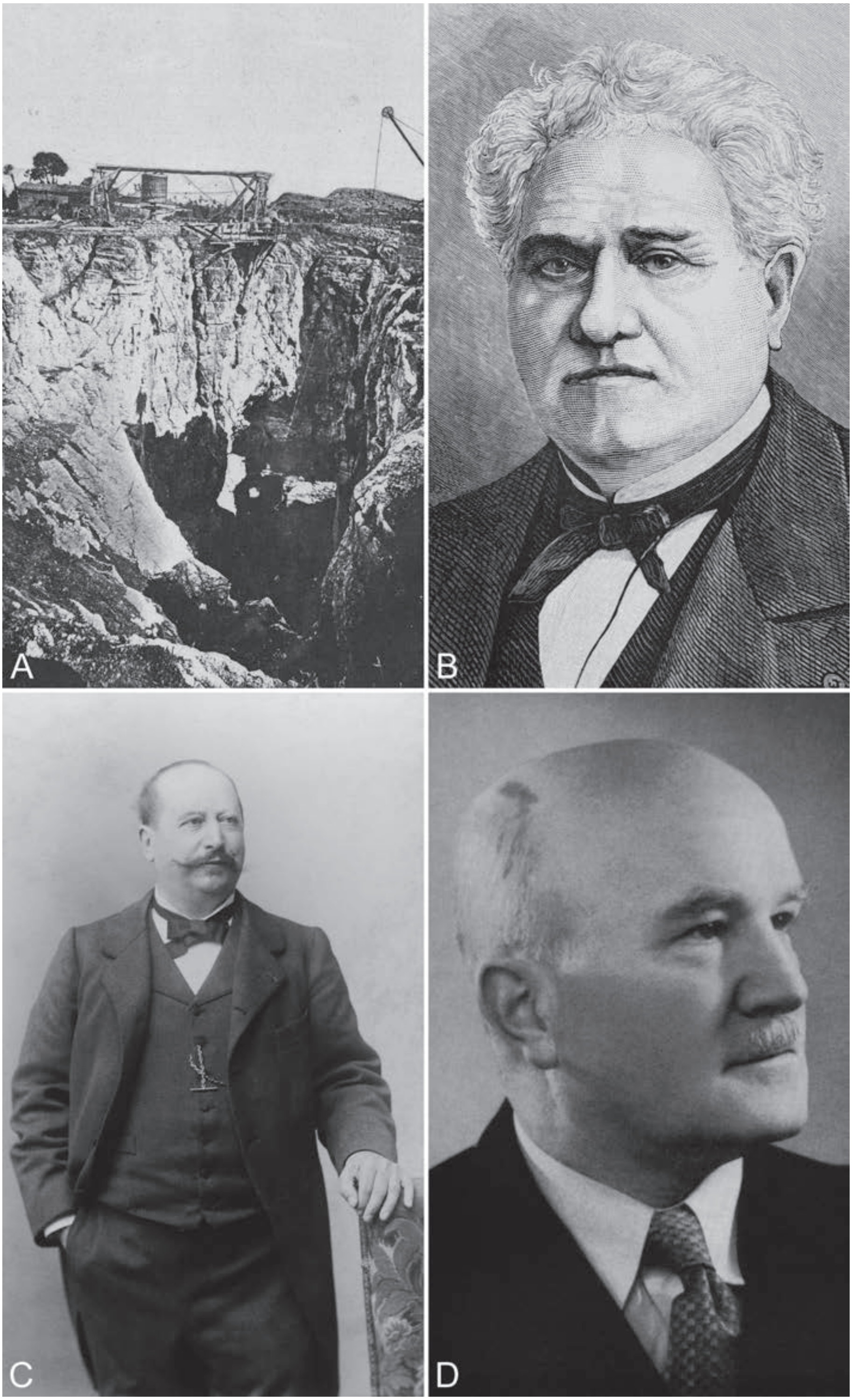
Here we highlight the scientific history of the Quercy insects, comment on their fossilization and demonstrate how state-of-the-art digital imaging techniques facilitate fascinating new insights into a fossil type that was largely neglected by paleoentomologists for more than a century.

2. The history of the Quercy locality

Phosphate was discovered to be a potent fertilizer by Justus von Liebig in 1840, triggering the search and mining of natural accumulations of phosphorite in the second half of 19th century. After phosphorite was found in the fissure fillings of Quercy in 1865 (Thévenin 1903), intensive mining took place from 1870 until the end of that century (Filhol 1876b; Handschin 1944; Fig. 1A). The fissure fillings originate mainly from the Paleogene (Legendre et al. 1997), when Mesozoic bedrocks of the region of the Quercy (Jurassic limestones and marls, Cretaceous calcareous sandstones and reefal clayey limestones) were subject to erosion and karstification. The environment was like a tropical rainforest, crossed by rivers

Fig. 1: The locality and related researchers. **A** Phosphorite mine in the Quercy region (photograph taken from Thévenin 1903). **B** François Louis Paul Gervais (1816-1879); public domain picture originally published in "Popular Science Monthly", August 1887. **C** Pierre Antoine Henri Filhol (1843-1902); source unknown; restored by Didier Descouens, Muséum de Toulouse. **D** Eduard Handschin (1894-1962); courtesy of W. Etter, Naturhistorisches Museum Basel.

Abb. 1: Der Fundort und seine Bearbeiter. **A** Phosphoritmine im Quercy (Foto aus Thévenin 1903). **B** François Louis Paul Gervais (1816-1879); gemeinfreies Bild, ursprünglich gedruckt in „Popular Science Monthly", August 1887. **C** Pierre Antoine Henri Filhol (1843-1902); Quelle unbekannt; restauriert von Didier Descouens, Muséum de Toulouse. **D** Eduard Handschin (1894-1962); freundlicherweise zur Verfügung gestellt von W. Etter, Naturhistorisches Museum Basel.


A
B
C
D

coming down from the Massif Central. Water, enriched with carbon dioxide, penetrated through fractures within the rocks, and dissolved and dug cavities into the subsurface of the Jurassic limestones (BRUXELLES et al. 2008). The tropical erosion at the surface led to an intense lateritization of the Jurassic and Cretaceous sediments, which partly were accumulated as limey clays and sands, rich in iron and phosphate (GÉZE 1938, 1949), within the karstic cavities. Additionally those cavities acted as traps for vertebrate remains like teeth and bones and invertebrates. Unfortunately, little attention was paid to the stratigraphic differences between the multiple localities during the excavations in the 19th century. As known nowadays, they cover mainly the time of the Middle and Late Eocene up to the beginning of the late Oligocene. But also fossils from the early Eocene (about 50 Ma) up to the lower Miocene (about 20 Ma) are known (SIGÉ et al. 1991; LEGENDRE et al. 1997; RAGE 2006). Thus, the fossils from the Quercy region cover about 30 Ma of natural history in Europe, including important faunal interchanges with Asia.

Massive accumulations of animal remains in the phosphorites of Quercy were reported to the Académie des sciences de Paris on October 30th 1871 (FILHOL 1876b) after the beginning of mining, initiating the paleontological collecting activities in the Quercy. Soon, several collections in different institutions worldwide were developed.

3. Early reports of insect fossils

In 1877 FRANÇOIS LOUIS PAUL GERVAIS (1816-1879; Fig. 1B), a French paleontologist holding the chair for comparative anatomy at the Paris Muséum national d'histoire naturelle, reported new *"Fossiles du Quercy"*, including a butterfly pupa from the fissure fillings. When this first fossil insect was published, mining in the Quercy region already persisted for more than ten years.

In 1890 the German entomologist KARL L. FLACH (1856-1920) documented four specimens from Caylus[1]: an ootheca of a cockroach species (genus *Blatta*), a larva of a cicada, and two carrion beetles (Silphidae), which he illustrated in detail (FLACH 1890; Fig. 2). He compared both beetle specimens with modern taxa, found most similarities with the genera *Necrodes* and *Ptomascopus*, and described them as new species (*Palaeosilpha Fraasii* [sic!] & *Ptomascopus aveyronensis*). Flach assumed a slow fossilization process involving adipocere, and hypothesized vertebrate bones as the primary phosphate source, which triggered the mineralization:

"Die Umwandlung scheint eine sehr langsame gewesen zu sein und nimmt man an, daſs der Versteinerung ein Zustand der Leichenwachsmetamorphose (Adipocire-Bildung) vorausgegangen sei. Die später sich einlagernden Phosphorsalze entstammen vorzüglich Thier- bezw. Knochenresten in der Umgebung und es ist nicht undenkbar, daſs die beiden Käfer (Aasfresser!) den Knochen desselben Thieres ihre Erhaltung verdanken, dessen Leichnam sie einst zu vertilgen bestrebt waren." (FLACH 1890, S. 105) [Transformation seems to have occurred very slowly, and a preceding process of an adipocerous metamorphosis is supposed. The later incorporated phosphoric salts probably originate from animal or bone remains in the vicinity and it is not unimaginable that both beetles (carrion eaters!) owe their preservation to the bones of the very same animal, whose corpse they were once eager to devour.] (Translated by the authors)

He recognized the extraordinary preservation of those specimens and encouraged further research:

[1] FLACH wrote "Caylux". This is a synonym of the modern commune Caylus, which is located about 40 km northeast of Montauban. The name Caylux was used by FLACH (1890) and also by THÉVENIN (1903) and is cited in that way by HANDLIRSCH (1907). HANDSCHIN (1944) also used the term "Caylux" and pointed also to the locality "Bach". This is the commune next to Caylus to the north.

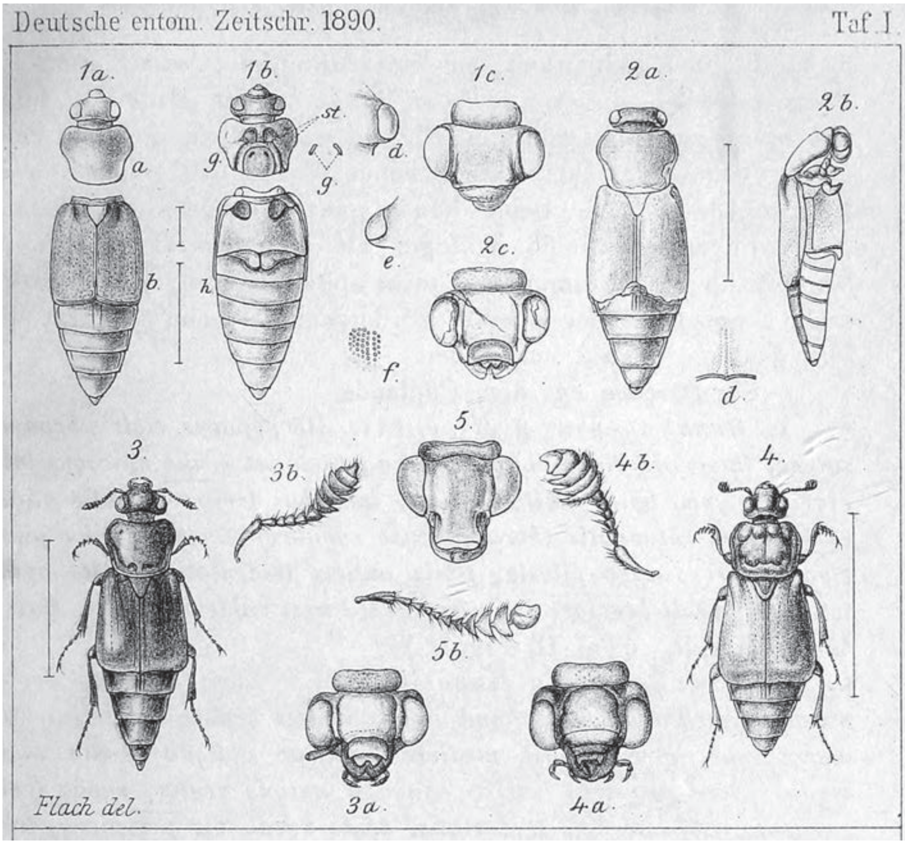


Fig. 2: FLACH's drawings of the two fossil carrion beetles (Silphidae) and two extant species, which he considered to be most closely related to them (FLACH 1890). His figure caption (translated from German): *"Fig. 1. Palaeosilpha Fraasii* [sic!] *m.; a. from top, b. from below, c. head from top, d. eye from top, e. from below, f. sculpture of the covers* [elytra – author's note]*, g. position of stigmata* [spiracles – a/n] *(st.). Fig. 2. Ptomascopus aveyronensis m.; a. from top, b. from the side, c. head from top, d. sculpture of the hind thorax* [metaventrite – a/n] *with both smooth stripes. Fig. 3. Ptomascopus morio Kraatz. ♂.; a. head from top, b. antenna. Fig. 4. Necrophorus* [now *Nicrophorus* – a/n] *vespilloides Herbst, without taking the line pattern into account; a. head from top, b. antenna. Fig. 5 Asbolus* [now *Necrodes* – a/n] *littoralis L. a. head from top, b. antenna."*
Abb. 2: FLACHS Zeichnungen zweier fossiler Aaskäfer (Silphidae) und zweiter rezenter Arten, die er für nah mit ihnen verwandt hielt (Flach 1890). Seine Bildlegende: *„Fig. 1. Palaeosilpha Fraasii* [sic!] *m.; a. von oben, b. von unten, c. Kopf von oben, d. Auge von oben, e. von unten, f. Sculptur der Decken* [Elytren – Anm. d. Verf.]*, g. Stellung der Stigmen (st.). Fig. 2. Ptomascopus aveyronensis m.; a. von oben, b. von der Seite, c. Kopf von oben, d. Skulputur der Hinterbrust* [Metaventrit – Anm. d. Verf.] *mit den beiden glatten Streifen. Fig. 3. Ptomascopus morio Kraatz ♂.; a. Kopf von oben, b. Fühler, Fig. 4. Necrophorus* [jetzt *Nicrophorus* – Anm. d. Verf.] *vespilloides Herbst, ohne Berücksichtigung der Bindenzeichnung; a. Kopf von oben, b. Fühler. Fig. 5. Asbolus* [jetzt *Necrodes* – Anm. d. Verf.] *littoralis L.; a. Kopf von oben, b. Fühler."*

„Eine gründliche Untersuchung der Schichten an Ort und Stelle Seitens der französischen Collegen in Hinsicht auf fossile Insekten wäre sehr erwünscht und dankenswerth." (FLACH 1890, S. 109) [A thorough examination of the layers at the locality by the French colleagues with respect to fossil insects would be very welcome and thanksworthy.]

PIERRE ANTOINE HENRI FILHOL (1843-1902; Fig. 2C) was engaged in paleontological research on the Quercy phophorites and wrote several articles about them (e.g. FILHOL 1876a, b, 1877, 1884). In 1894 he became chair for comparative anatomy at the Paris Muséum national d'Histoire Naturelle. He described the phosphatized fossil amphibians and reptiles, including preservation of soft tissue remains, and suspected a very rapid fixation of the organic material by hydrothermal solutions (FILHOL 1876a). In 1892 he presented a dynastine beetle to the Société philomathique de Paris. Without any published description he named it *Pseudopentodon blanchardi* (see HANDSCHIN 1944).

Eleven years later, ARMAND THÉVENIN (1870-1918), a French paleontologist employed at the Muséum National d'Histoire Naturelle, described the geology of the southwest Massif central (THÉVENIN 1903). At this time, mining had already significantly decreased. He provided a map with the former phosphorite localities of the Quercy region (THÉVENIN 1903; Pl. 13), including the locations of the arthropod discoveries. THÉVENIN reported millipedes (Julida and Polydesmida), an orthopteran – later, HANDSCHIN (1944) considered this specimen a *Gryllotalpa* –, and a large number of butterfly pupae and fly puparia from the Collection Rossignol at the Muséum d'Histoire Naturelle in Montauban. Contrary to FILHOL, THÉVENIN excluded a hypothermal origin of the phosphorites. Further, he suggested that the fossils do not represent the outer shapes of the original animals, but rather representing natural casts:

"Ils ont été englobés dans l'argile de remplissage de la poche et il y a eu ultérieurement moulage par le phosphate du creux formé ainsi dans l'argile." THÉVENIN 1903, p. 468) [They were embedded in the clay that was filling the pocket and there was subsequently a casting process by the phosphate from the cavity thus formed in the clay.]

It is evident that fossil arthropods – and especially insects – were frequently found in the fissure fillings of Quercy. Those findings were well-known to the paleontological community of that time, as indicated by citations in a couple of other contemporary studies (e.g. HANDLIRSCH 1907; GAILLARD 1908). With the end of mining activity, however, paleontological collecting stopped for decades (LEGENDRE et al. 1997) and the arthropods of the Quercy got more and more buried in oblivion. The detailed investigation encouraged by FLACH (1890) was never accomplished during the time of active mining of the Quercy phosphorites.

4. HANDSCHIN's study

In 1944, more than 50 years after FLACH's study, the Swiss entomologist EDUARD HANDSCHIN (1894-1962; Fig. 2D) published his article "Insekten aus den Phosphoriten des Quercy", which constitutes by far the most comprehensive work on the Quercy arthropods to date (HANDSCHIN 1944). HANDSCHIN was professor for entomology at the University of Basel and at the same time employed by the Naturhistorisches Museum Basel, whose director he became in 1946. He discovered several specimens in the collection of the museum and pointed out that they originated from three separate collections:

"In der geologischen Sammlung des Naturhistorischen Museums Basel befinden sich eine Anzahl fossiler Insekten, welche wegen ihres aussergewöhnlichen Erhaltungszustandes besondere Beachtung verdienen. Sie stammen aus den Phosphoriten des Quercy und sind zum Teil mit der Sammlung Rossignol erworben, zum Teil von H.G. Stehlin und H. Helbing gesammelt worden." (HANDSCHIN 1944, p. 1). [The geological collection of the Naturhistorisches Museum Basel contains a number of fossil insects, which, given their extraordinary preservation stage, deserve special attention. They originate from the phosphorites of Quercy and were partly acquired with the Rossignol collection and partly collected by H.G. Stehlin and H. Helbing.]

Unfortunately, any details of these collecting sites are unknown, leaving some uncertainty in stratigraphic assignment of the specimens. Like Flach, Handschin immediately noticed the exceptional preservation of the fossils and was astonished that they were completely disregarded by paleontologists for more than five decades:

"Trotzdem dieser Erhaltungszustand zu Untersuchungen herausfordert und obschon Thévenin 1903 in seiner Monographie des Quercy auf die zahlreiche Insektenfauna der Phosphorite hingewiesen hat, hat sich erstaunlicherweise bis jetzt kein Bearbeiter derselben gefunden." (Handschin 1944, p. 1) [Despite the preservation state urging investigations, and despite Thévenin (1903) having pointed out the large insect fauna of the phosphorites in his monography of Quercy, amazingly no one has taken up the challenge.]

Handschin examined hundreds of specimens including: ca. 100 diplopod body parts he assigned to the new species *Protosilvestra sculptata* (Myriapoda: Juliadae; Fig. 3A); two oothecae of a *Blatta* (Blattodea; Fig. 3B); three abdomina of a mole cricket species he named *Gryllotalpa aveyronensis* (Orthoptera: Ensifera; Fig. 3C); one caterpillar and four pupae of a moth species (Lepidoptera: Tineidae; Fig. 3D); 25 beetles (Coleoptera) incl. 13 specimens of *Ptomascopus aveyronensis* (Silphidae), a pronotum of *Thanatophilus* sp. (Silphidae; Fig. 3E), an unidentified silphid larva, eight specimens of a hister beetle species he described as *Onthophilus intermedius* (Histeridae; Fig. 3F), one abdomen of *Aphodius* sp. (Scarabaeidae) and a pronotum of a longhorn beetle species he named *Dorcadion bachense* (Cerambycidae); multiple puparia of phorid flies (Phoridae) incl. 41 specimens of *Megaselia* (Fig. 3G), 22 of *Spiniphora* and several hundreds of a genus he described as *Eophora* (Fig. 3H).

Handschin created sections of some puparia, revealing a fly pupa inside an *Eophora* specimen (Fig. 4A). Moreover, he even reports a parasitoid braconid wasp ("Braconidarum gen. indet.") in an *Eophora* puparium. His study is accompanied by detailed drawings (Figs 4, 5) created for this purpose by the distinguished scientific illustrator Otto Garraux (1904 - 1989).

Like Flach, Handschin hoped to encourage other scientists to investigate the Quercy insect fauna:

"Ich hoffe, damit auch die Aufmerksamkeit der Fachgenossen auf diese so eigentümliche Insektenfauna zu lenken, die sicher weit reicher ist, als man bisher angenommen hat." (Handschin 1944, p. 2) [I hope to call my colleagues' attention to this peculiar insect fauna, which is certainly richer than expected.]

However, following Handschin's investigation, the arthropod fossils of the Quercy returned to their slumber. The next addition to their documented fossil record was another 60 years later, when Laudet & Antoine (2004) reported pupal chambers of skin beetles (Dermestidae) in rhinoceros bones from the late Oligocene/earliest Miocene of Quercy.

5. Recent investigations

While the early descriptions of the Quercy insects – with the exception of the thin or polished sections by Handschin – were based solely on their external morphology, state of the art imaging methods now permits the non-destructive examination of their internal structures.

Handschin described the hister beetle *Onthophilus intermedius* (Coleoptera: Histeridae) from eight specimens, and considered it closely related to the extant European species *O. striatus* (Forster, 1771). His description was based mainly on the two apparently best-preserved specimens, which he did not identify. More than 70 years after Handschin's study, we had the opportunity to reexamine all eight specimens of *O. intermedius* from his collection using synchrotron X-ray microtomography (Schwermann et al. 2016). This non-destructive imaging

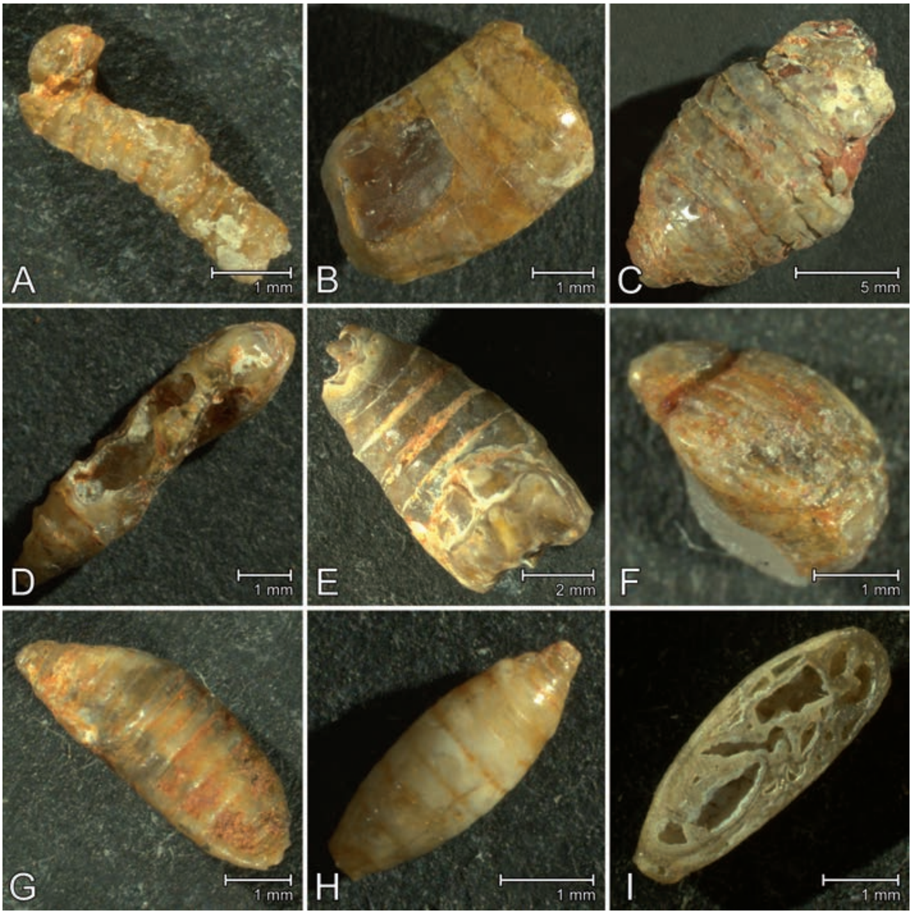
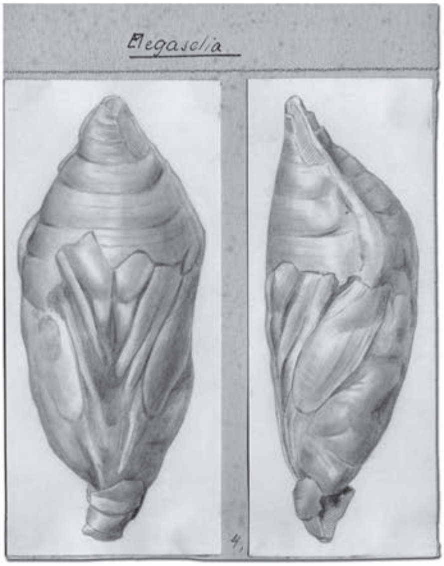


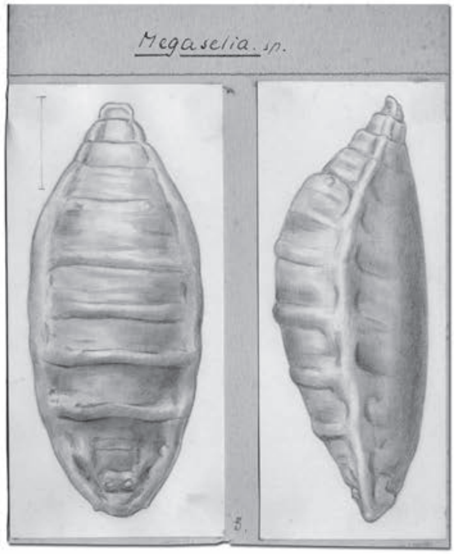
Fig. 3: Photographs of specimens described and determined by Handschin. **A** Fragment of a myriapod (*Protosilvestria sculpta*). **B** Ootheca of a cockroach (*Blatta* sp.). **C** Abdomen of a mole cricket (*Gryllotalpa averonensis*). **D** Pupa of a moth (family Tineidae). **E** Abdomen and parts of the metathorax of a silphid beetle (*Ptomascopus aveyronensis*). **F** Hister beetle (*Onthophilus intermedius*). **G, H** Puparia of phorid flies (G: *Megaselia* sp.; H: *Eophora* sp.). **I** Sliced puparium of *Eophora* sp.; note the fly pupa inside (compare with Fig. 5).

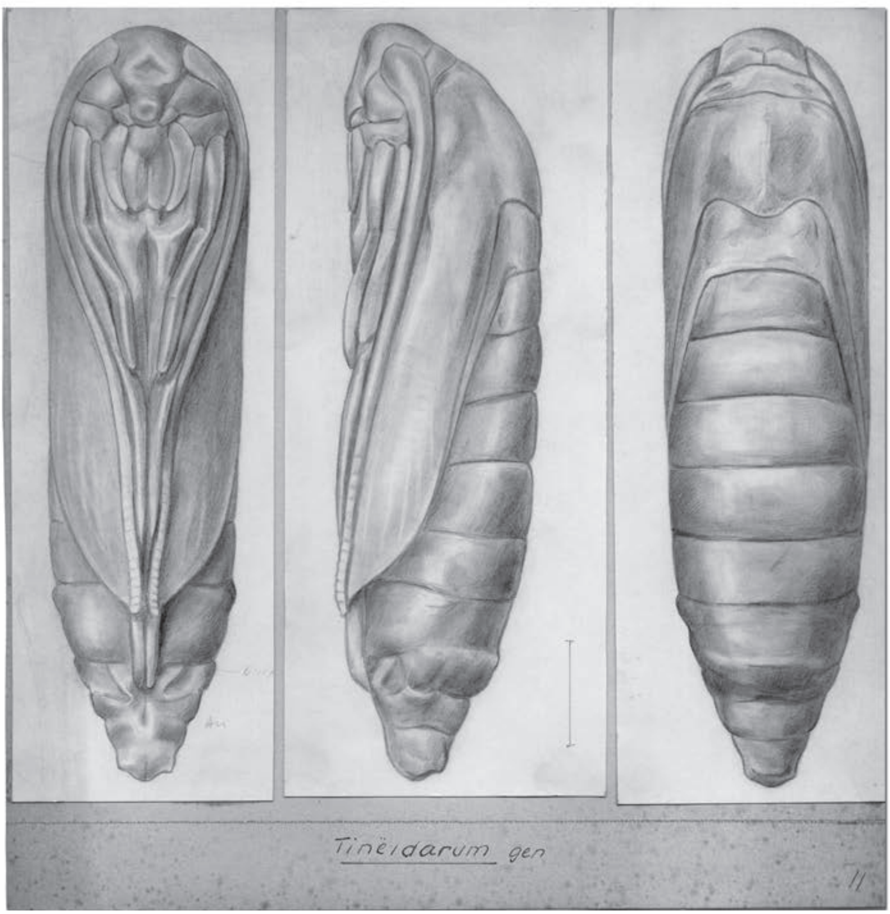
Abb. 3: Fotos einiger von Handschin beschriebener Stücke. **A** Fragment eines Tausendfüßers (*Protosilvestria sculpta*). **B** Oothek einer Schabe (*Blatta* sp.). **C** Abdomen einer Maulwurfgrille (*Gryllotalpa averonensis*). **D** Puppe einer Motte (Familie Tineidae). **E** Abdomen und Teile des Methathorax eines Aaskäfers (*Ptomascopus aveyronensis*). **F** Stutzkäfer (*Onthophilus intermedius*). **G, H** Puparien von Buckelfliegen (G: *Megaselia* sp.; H: *Eophora* sp.). **I** Aufgeschnittenes Puparium von *Eophora* sp.; man beachte die Fliegenpuppe im Innern (vgl. Fig. 5).

Fig. 4: Drawings of *Megaselia* puparia (top) and a moth pupa (bottom) created by GARRAUX for HANDSCHIN's study.

Abb. 4: Von GARRAUX für HANDSCHIN erstellte Zeichnungen von *Megaselia*-Puparien (oben) und einer Mottenpuppe (unten).


Megaselia.
4.


Megaselia. sp.
5.


Tinëidarum gen
11

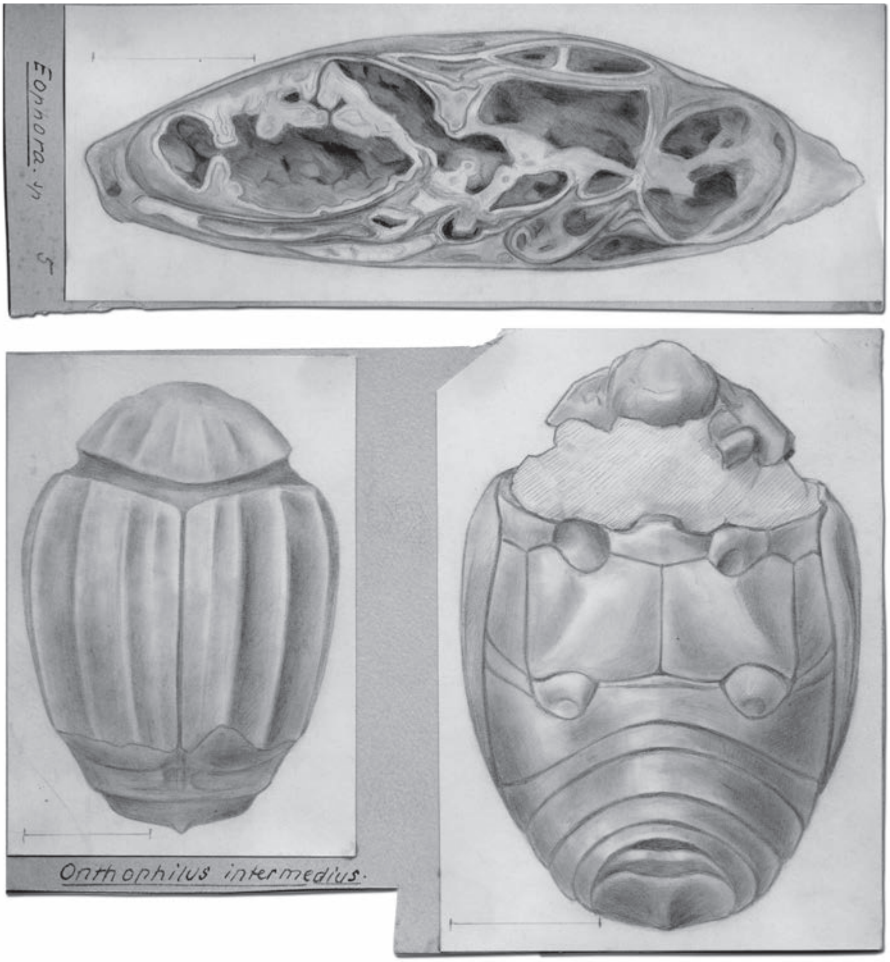


Fig. 5: Drawings of a section of an *Eophora* puparium (top) and a hister beetle (*Onthophilus intermedius*; bottom) created by GARRAUX for HANDSCHIN's study. Compare with Fig. 3F, I.
Abb. 5: Von GARRAUX für HANDSCHIN erstellte Zeichnungen eines angeschnittenen *Eophora*-Pupariums (oben) und eines Stutzkäfers (*Onthophilus intermedius*; unten; vgl. Abb. 3F, I).

technique has become established for the three-dimensional examination of both extant (e.g. BETZ et al. 2007; BOSSELAERS et al. 2010; VAN DE KAMP et al. 2011, 2014, 2015; BREHM et al. 2015; SOMBKE et al. 2015) and extinct (SUTTON, 2008; SUTTON et al. 2014) arthropods, including fossils preserved in amber (PERREAU & TAFFOREAU 2011; LAK et al. 2009; POHL et al. 2010; SORIANO et al. 2010; RIEDEL et al. 2012). In addition to the fossils, we performed tomographic scans of the extant *O. striatus* for a direct comparison. Scans were done at the TOPO-TOMO beamline (RACK et al. 2009) of the ANKA Synchrotron Radiation Facility (VAN DE KAMP et al. 2013) at Karlsruhe Institute of Technology.

One specimen strikingly differs from all other specimens of the collection by the presence of a stony matrix covering the ventral part of the beetle; its dorsal part and head are exposed (Fig. 6A, B). The elytra are missing, the exposed surface is partly eroded and no appendages are visible from the outside.

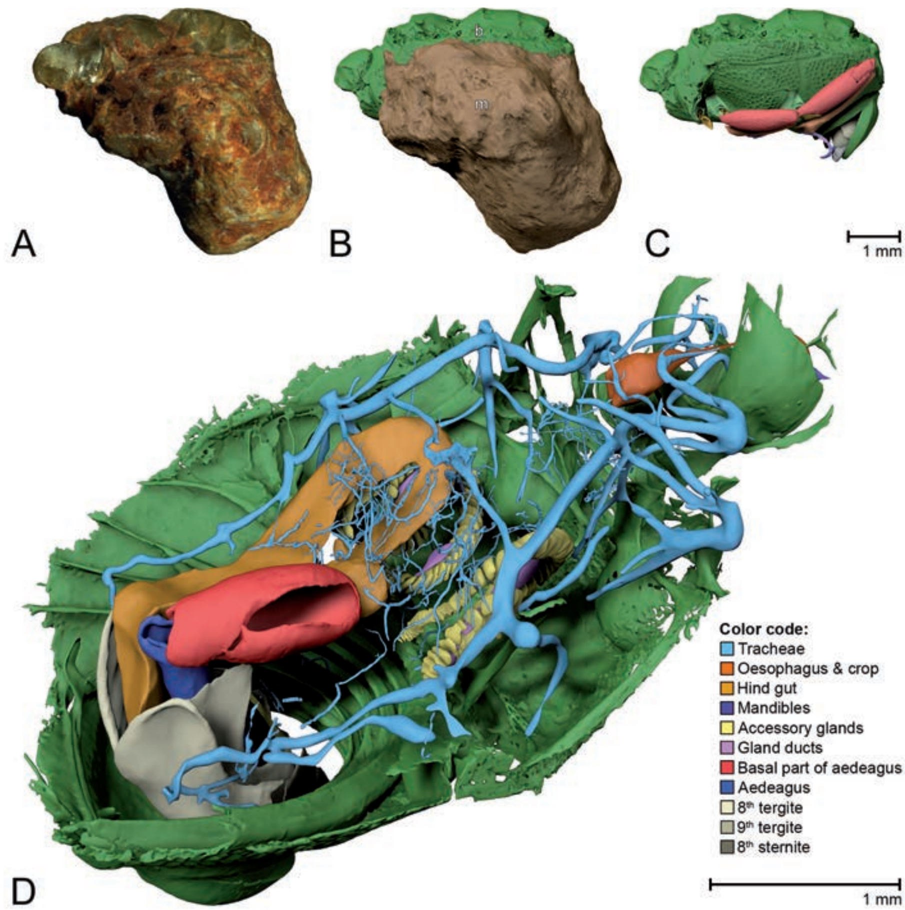


Fig. 6: Digital reconstruction of *Onthophilus intermedius* (from SCHWERMANN et al. 2016). **A** Photograph of the fossil ventrally embedded in a stony matrix. **B** Digital reconstruction showing fossilized beetle (b) and matrix (m). **C** Beetle digitally isolated from the stone, revealing well-preserved morphology hidden by the matrix. **D** Perspective view of the fossil showing parts of exoskeleton, tracheal network, alimentary canal and genitals.

Abb. 6: Digitale Rekonstruktion eines *Onthophilus intermedius* (aus SCHWERMANN et al. 2016). **A** Foto des Fossils, das ventral in eine Steinmatrix eingebettet ist. **B** Digitale Rekonstruktion mit Käfer (b) und Matrix (m). **C** Der digital vom Stein befreite Käfer offenbart gut erhaltene, in der Matrix verborgene morphologische Strukturen. **D** Die perspektivische Ansicht des Fossils zeigt Teile von Exoskelett, Tracheennetzwerk, Verdauungstrakt und Genitalien.

Ironically, this very specimen – apparently the worst from the collection – proved to be the most completely preserved fossil and revealed remarkable details. Hidden by the matrix and invisible to HANDSCHIN, large parts of the beetle's exoskeleton and internal anatomy are extraordinarily preserved, including detailed ornamentation, fragile appendages, tracheal system, alimentary canal and genitals (Fig. 6C, D). Our results facilitated a redescription of the species based on modern standards and allowed a phylogenetic analysis, which placed *O. intermedius* into a different evolutionary lineage from *O. striatus*.

Further, we found that the sclerotized exoskeletal parts are largely missing and represented by voids inside a stony marix. Thus, the external surface of the beetle fossils is actually a natural cast of the inner surface of the original exoskeleton and the characteristic surface pattern of the outer cuticle, as well as appendages (antennae, legs) are missing (except in the single specimen that was embedded in a stony matrix). The same condition may apply for the two silphid beetles described by Flach (1890; Fig. 2). He noticed missing appendages and mentioned missing characteristic structures on the outer exoskeleton, which are present in Recent relatives. Therefore, we can partially verify Thévenin's (1903) natural cast theory.

6. Concluding remarks

In retrospect, it may appear strange that the insects of the Quercy region have received so little attention by the scientific community. However, three-dimensionally preserved insects in amber are much more famous and certainly more attractive to the naked eye. It is therefore easy to imagine that comparatively shabby mineralized specimens – despite their unusual 3D preservation – were likely considered inferior in quality. Moreover, while amber inclusions are widely available, the Quercy insects are confined to only a handful of museum collections.

Most information on the internal morphology of fossil insects was so far obtained from amber inclusions, which causes a representational bias toward generally arboreal taxa (Martínez-Delclòs et al. 2004). In contrast, the Quercy insects represent an assemblage more typically associated with forest floor communities (Handschin 1944), which are less commonly preserved than those of many other environments (Kidwell & Flessa 1996). Modern 3D imaging techniques now enable us to appreciate the true value of these almost forgotten fossils, which indeed may provide a rich complementary source for anatomical data of fossil insects. Whereas Handschin (1944) was forced to create polished or thin sections of selected specimens to examine their inner structures, we are now able to investigate a large quantity of fossils by non-destructive methods. Our latest results illustrate that one should not merely rely on the outer shape of a fossil to estimate its worth, as even those specimens that appear poorly preserved on the outside can provide invaluable new insights.

Future examinations of the Quercy arthropod fauna may also reveal the reconstruction of the different taphonomic processes yielding those fossils. Unequal kinds of preservation (simple natural casts or complex internal characters) within the arthropod fauna may reflect different stages of decomposition at the beginning of the phosphatization process. Such investigations will yield critical data testing the adipocere-hypothesis of Flach (l.c.) and the hydrothermal-solution-hypothesis of Filhol (l.c.) and compare them with a diagenetic driven fossilization by originally phosphate rich cave sediment. An improved understanding of the taphonomy of those arthropods, plus the mode of phosphate enrichments in lateritic sediments, is critical to testing pioneering reconstructions of phosphatization of the Quercy arthropods and to facilitate future interpretations.

Like Flach (1890) and Handschin (1944) before, we would like to call the attention of paleo-entomologists to the fascinating Quercy insects – we sincerely hope, this time it will not take decades until the next study on the subject.

Acknowledgments

We are exceptionally grateful to Walter Etter (Naturhistorisches Museum Basel), who instantly answered all of our questions regarding the Quercy fossils housed in Basel. Furthermore he kindly provided the scans of Garraux's original drawings and the portrait of EDUARD HANDSCHIN. Last but not least he and OLIVIER SCHMIDT enabled the loaning of the specimens for CT scanning. CLAUDE ANTONY, RUTH HEINE (both KIT, Eggenstein-Leopoldshafen), SERGE LEGENDRE (French National Centre for Scientific Research, Paris), and BASTIAN MÄHLER (Steinmann Institute, University of Bonn) are thanked for their help with translations from French, explanation of the historical Quercy collections, and fruitful discussions.

Literature

BETZ, O., WEGST, U., WEIDE, D., HEETHOFF, M., HELFEN, L., LEE, W.-K., & CLOETENS, P. (2007): Imaging applications of synchrotron X-ray phase-contrast microtomography in biological morphology and biomaterials science. I.General aspects of the technique and its advantages in the analysis of millimetre-sized arthropod structure. Journal of Microscopy 227: 51-71.

BOSSELAERS, J., DIERICK, M., CNUDDE, V., MASSCHAELE, B., VAN HOOREBEKE, L., & JACOBS, P. (2010): High-resolution X-ray computed tomography of an extant new *Donuea* (Araneae: Liocranidae) species in Madagascan copal. Zootaxa 2427: 25-35.

BREHM, G., FISCHER, M., GORB, S., KLEINTEICH, T., KÜHN, B., NEUBERT, D., POHL, H., WIPFLER, B., & WURDINGER, S. (2015): The unique sound production of the Death's-head hawkmoth (*Acherontia atropos* (Linnaeus, 1758)) revisited. The Science of Nature 102: 43.

BRUXELLES, L., MARCHET, P., & TARRISSE, A. (2008): Excursions en Quercy – Livret Guide. Journées AFK/AGSO/CFH 11, 12, 13 et 14 Septembre 2008.

CONG, P., MA, X., HOU, X., EDGECOMBE, G.D., & STRAUSFELD, N.J. (2014): Brain structure resolves the segmental affinity of anomalocaridid appendages. Nature 513: 538-542.

DUNCAN, I.J., & BRIGGS, D.E.G. (1996): Three-dimensionally preserved insects. Nature 381: 30-31.

EDGECOMBE, G.D., MA, X., & STRAUSFELD, N.J. (2015): Unlocking the early fossil record of the arthropod central nervous system. Philosophical Transactions of the Royal Society B: Biological Sciences 370: 2015-2038.

FILHOL, H. (1876a): Sur les reptiles fossiles des phosphorites du Quercy. Bulletin de la Société des Philomathique de Paris 11: 27-28.

FILHOL, H. (1876b): Recherches sur les phosphorites du Quercy; étude des fossiles qu'on y rencontre et spécialement des mammifères. Annales Science Géologique 7: 1-220.

FILHOL, H. (1877): Recherches sur les phosphorites du Quercy; étude des fossiles qu'on y rencontre et spécialement des mammifères. Masion; Paris.

FILHOL, H. (1884): Observations relatives à des mammifères fossiles nouveaux provenant des depots de phosphate de chaux du Quercy. Bulletin de la Société des Sciences Physiques et Naturelles de Toulouse 5: 159-203.

FLACH, K. (1890): Ueber zwei fossile Silphiden (Coleoptera) aus den Phosphoriten von Caylux. Deutsche Entomologische Zeitschrift 34: 105-109.

GAILLARD, C. (1908): Les oiseaux des phosphorites du Quercy. Annales du L'Université de Lyon, Nouvelle Série 23: 1-100.

GERVAIS, P. (1877): Fossiles du Quercy. Journal de Zoologie 6: 67-68.

GÉZE, B. (1938): La genèse des phosphorites du Quercy. Comptes Rendus de l'Académie des Sciences 206: 759-761.

GÉZE, B. (1949): Les gouffres à phosphate du Quercy. Essai de paléospéléologie. Annales de Spéléologie IV: 89-107.

GRIMALDI, D., BONWICH, E., DELANNOY, M., & DOBERSTEIN, S. (1994): Electron microscopic studies of mummified tissues in amber fossils. American Museum Novitates 3097: 1-31.

GRIMALDI, D., & ENGEL, M.S. (2005): Evolution of the insects. Cambridge University Press, Cambridge.

HANDLIRSCH, A. (1907): Die fossilen Insekten. IV. Tertiäre Insekten. Wilhelm Engelmann; Leipzig.

HANDSCHIN, E. (1944): Insekten aus den Phosphoriten des Quercy. Schweizerische Paläontologische Abhandlungen 64: 1-23.

HELLMUND, M., & HELLMUND, W. (1996): Phosphoritisierte Insekten- und Annelidenreste aus der mitteloligozänen Karstspaltenfüllung „Ronheim 1" bei Harburg (Bayern, Süddeutschland). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 241: 1-21.

KIDWELL, S.M., & FLESSA, K.W. (1996): The quality of the fossil record: populations, species, and communities. Annual Review of Earth and Planetary Sciences 24: 433-464.

Lak, M., Fleck, G., Azar, D., Engel, M.S., Kaddumi, H.F., Neraudeau, D., Tafforeau, P., & Nel, A. (2009): Phase contrast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae). Zoological Journal of the Linnean Society 156: 913-923.

Laloy, F., Rage, J.C., Evans, S.E., Boistel, R., Lenoir, N., & Laurin, M. (2013): A reinterpretation of the Eocene anuran *Thaumastosaurus* based on microCT examination of a 'mummified' specimen. PLoS ONE 8: e74874.

Laudet, F., & Antoine, P.-O. (2004): Des chambres de pupation de Dermestidae (Insecta : Coleoptera) sur un os de mammifère tertiaire (phosphorites du Quercy): implications taphonomiques et paléoenvironnementales. Geobios 37: 376-381.

Legendre, S., Sigé, B., Astruc, J.G., Bonis, L., Crochet, J.-Y., Denys, C., Godinot, M., Hartenberger, J.-L., Leveque, F., Marandat, B., Mourer-Chauviré, C., Rage, J.-C., Remy, J.A., Sudre, J., & Vianey-Liaud, M. (1997): Les phosphorites du Quercy: 30 ans de recherche. Bilan et perspectives. Geobios 20: 331–345.

Ma, X., Cong, P., Hou, X., Edgecombe, G.D., & Strausfeld, N.J. (2014): An exceptionally preserved arthropod cardiovascular system from the Early Cambrian. Nature Communications 5: 3560.

Martínez-Delclòs, X., Briggs, D.E.G., & Peñalver, E. (2004): Taphonomy of insects in carbonates and amber. Palaeogeography, Palaeoclimatology, Palaeoecology 203: 19-64.

McCobb, L.M.E., Duncan, I.J., Jarzembowski, E.A., Stankiewicz, B.A., Wills, M.A., & Briggs, D.E.G. (1998): Taphonomy of the insects from the Insect Bed (Bembridge Marls), late Eocene, Isle of Wight, England. Geological Magazine 135: 553-563.

Miller, K.B., & Lubkin, S.H. (2001): *Calicovatellus petrodytes*, a new genus and species of primitive vatelline diving beetle (Coleoptera: Dytiscidae: Hydroporinae: Vatellini) from the Miocene Barstow Formation, Southern California, USA. Journal of Paleontology 75: 890-894.

Penney, D., & Jepson, J.E. (2014): Fossil insects – an introduction to palaeoentomology. Siri Scientific Press; Castleton.

Perreau, M., & Tafforeau, P. (2011): Virtual dissection using phase-contrast X-ray synchrotron microtomography: reducing the gap between fossils and extant species. Systematic Entomology 36: 573-580.

Pohl, H., Wipfler, B., Grimaldi, D., Beckmann, F., & Beutel, R.G. (2010): Reconstructing the anatomy of the 42-million-year-old fossil *Mengea tertiaria* (Insecta, Strepsiptera). Naturwissenschaften 97: 855–859.

Rack, A., Weitkamp, T., Bauer Trabelsi, S., Modregger, P., Cecilia, A., dos Santos Rolo, T., Rack, T., Haas, D., Simon, R., Heldele, R., Schulz, M., Mayzel, B., Danilewsky, A.N., Waterstradt, T., Diete, W., Riesemeier, H., Müller, B.R., & Baumbach, T. (2009): The micro-imaging station of the TopoTomo beamline at the ANKA synchrotron light source. Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms 267: 1978-1988.

Rage, J.C. (2006): The lower vertebrates from the Eocene and Oligocene of the phosphorites du Quercy (France): an overview. Strata 13: 161-173.

Riedel, A., dos Santos Rolo, T., Cecilia, A., & van de Kamp, T. (2012): Sayrevilleinae Legalov, a newly recognised subfamily of fossil weevils (Coleoptera, Curculionoidea, Attelabidae) and the use of synchrotron microtomography to examine inclusions in amber. Zoological Journal of the Linnean Society 165: 773-794.

Schwermann, A.H., dos Santos Rolo, T., Caterino, M.S., Bechly, G., Schmied, H., Baumbach, T. & van de Kamp, T. (2016): Preservation of three-dimensional anatomy in phosphatized fossil arthropods enriches evolutionary inference. eLife 5: e12129.

Sigé, B., Aguilar, J.-P., Marandat, B., & Astruc, J.-G. (1991): Extension au Miocène inférieur des remplissages phosphatés du Quercy. La faune de vertébrés de Crémat (Lot, France). Geobios 24: 497-502.

Siveter, D.J., Fortey, R.A., Sutton, M.D., Briggs, D.E.G., & Siveter, D.J. (2007): A Silurian 'marrellomorph' arthropod. Proceedings of the Royal Society B: Biological Sciences 274: 2223-2229.

Siveter, D.J., Sutton, M.D., Briggs, D.E.G., & Siveter, D.J. (2007): A new probable stem lineage crustacean with three-dimensionally preserved soft parts from the Herefordshire (Silurian) Lagerstätte, UK. Proceedings of the Royal Society B: Biological Sciences 274: b2099-2108.

Siveter, D.J., Tanaka, G., Farrell, U.C., Martin, M.J., Siveter, D.J., & Briggs, D.E. (2014): Exceptionally preserved 450-million-year-old Ordovician ostracods with brood care. Current Biology 24: 801-806.

Soriano, C., Archer, M., Azar, D., Creaser, P., Delclòs, X., Godthelp, H., Hand, S., Jones, A., Nel, A., Néraudeau, D., Ortega-Blanco, J., Pé rez-de la Fuente, R., Perrichot, V., Saupe, E., Kraemer, M.S., & Tafforeau, P. (2010): Synchrotron X-ray imaging of inclusions in amber. Comptes Rendus Palevol 9: 361-368.

Sutton, M.D. (2008): Tomographic techniques for the study of exceptionally preserved fossils. Proceedings of the Royal Society B: Biological Sciences 275: 1587-1593.

Sutton, M.D., Rahman, I.A., & Garwood, R. (2014): Techniques for virtual palaeontology. Wiley-Blackwell; Chichester.

Sombke, A., Lipke, E., Michalik, P., Uhl, G., & Harzsch, S. (2015): Potential and limitations of X-ray micro-computed tomography in arthropod neuroanatomy: a methodological and comparative survey. Journal of Comparative Neurology 523: 1281-1295.

Thévenin, A. (1903): Etude géologique sur la bordure sud-ouest du Massif central. Bulletin des services de la carte géologique del a France et des topographies souterraines 14: 353-548.

Tissier, J., Rage, J.-C., Boistel, R., Fernandez, V., Pollet, N., Garcia, G., & Laurin, M. (2015): Synchrotron analysis of a 'mummified' salamander (Vertebrata: Caudata) from the Eocene of Quercy, France. Zoological Journal of the Linnean Society 177: 147-164.

van de Kamp, T., Vagovič, P., Baumbach, T., & Riedel, A. (2011): A biological screw in a beetle's leg. Science 333: 52.

van de Kamp, T., Ershov, A., dos Santos Rolo, T., Riedel, A., & Baumbach, T. (2013): Insect imaging at the ANKA Synchrotron Radiation Facility. Entomologie heute 25: 147-160.

van de Kamp, T., dos Santos Rolo, T., Baumbach, T., & Krogmann, L. (2014): Scanning the past – Synchrotron X-ray microtomography of fossil wasps in amber. Entomologie heute 26: 151-160.

van de Kamp, T., dos Santos Rolo, T., Vagovič, P., Baumbach, T., Riedel, A., & Evans, A.R. (2014): Three-dimensional reconstructions come to life – interactive 3D PDF animations in functional morphology. PLoS ONE 9: e102355-102357.

van de Kamp, T., Cecilia, A., dos Santos Rolo, T., Vagovič, P., Baumbach, T., & Riedel, A. (2015): Comparative thorax morphology of death-feigning flightless cryptorhynchine weevils (Coleoptera: Curculionidae) based on 3D reconstructions. Arthropod Structure & Development 44: 509-523.

Waloszek, D. (2003): The "Orsten" window – a three-dimensionally preserved Upper Cambrian meiofauna and its contribution to our understanding of the evolution of Arthopoda. Paleontological Research 7: 71-88.

Dr. Achim H. Schwermann
Dr. Heiko Schmied
University of Bonn
Steinmann Institute for Geology, Mineralogy and Paleontology
Nussallee 8
D-53115 Bonn
E-Mail: achim.schwermann@uni-bonn.de

Dr. Michael Wuttke
Department of Palaeoanthropology and Messel Research
Section Palaeoclimate- and Palaeoenvironment Research
Senckenberganlage 25
D-60325 Frankfurt am Main

Dr. Michael S. Caterino
Clemson University
Department of Plant and Environmental Sciences
Clemson, South Carolina 29634-0310, USA

Dr. Günter Bechly
Staatliches Museum für Naturkunde Stuttgart
Rosenstein 1
D-70191 Stuttgart

Dr. Thomas van de Kamp
Dipl.-Ing. (FH) Tomy dos Santos Rolo
Prof. Dr. Tilo Baumbach
Karlsruhe Institute of Technology (KIT)

Institute for Photon Science and Synchrotron Radiation (IPS)
& Laboratory for Applications of Synchrotron Radiation (LAS)
Hermann-von-Helmholtz-Platz 1
D-76344 Eggenstein-Leopoldshafen
E-Mail: thomas.vandekamp@kit.edu