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## Fossil insects from the Tithonian „Solnhofener Plattenkalke“ in the Museum of Natural History, Vienna

### Die fossilen Insekten der Solnhofener Plattenkalke im Naturhistorischen Museum in Wien

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(With 6 text-figs. and 4 plates)

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#### Summary

The fossil insects from Solnhofen and Eichstätt (Lowermost Tithonian, Bavaria, FRG) in the collection of the Museum of Natural History, Vienna are listed and their systematic position discussed. *Malmagrion* (Odonata) is a possible protomyrmeleontid. *Chresmoda* neither a phasmid nor a water bug. *Procalasoma minor* HANDLIRSCH is transferred to Trachypachidae according to the structures of the holotype. A first record of a culicomorph midge in the locality is indicated. A new species of hydrophiloid beetle is described.

#### Zusammenfassung

Die fossilen Insekten aus Solnhofen und Eichstätt (Unterstes Tithon, Bayern, BRD) der Sammlung des Naturhistorischen Museums in Wien sind angeführt und ihre systematische Stellung wird diskutiert. *Malmagrion* (Odonata) zählt möglicherweise zu den Protomyrmeleontiden. *Chresmoda* ist weder ein Phasmodea noch eine Wasserwanze. *Procalasoma minor* HANDLIRSCH wird nach den Merkmalen des Holotypus den Trachypachidae zugeordnet. Eine culicomorphe Mücke wird für diesen Standort erstmals nachgewiesen. Es folgt die Erstbeschreibung einer neuen hydrophiloiden Käfer-Art.

The insects from the famous Tithonian „Lithographische Schiefer“ of Solnhofen and Eichstätt are among the best-studied and are usually considered as being typical for the Jurassic. However, virtually all these studies date from the previous century, with only one account of these insects from the present century (CARPENTER 1933). The author's research into the collections of beetles described by DEICHMÜLLER (1886) and OPPENHEIM (1888) has shown that the family position was correct for only one species (PONOMARENKO 1971, 1980). The same holds true for the collection under study. The oryctocoenosis composition cannot be taken as being characteristic for the Jurassic insect fauna because this fauna was biased by being bedded in marine deposits and by special selection for good flying capability. According to the classical model these insects inhabited islands along the north

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coast of the Tethys and their remains were found in the deposits of a lagoon. Only several insects in fact inhabited that lagoon; most were allochthonous. The reinvestigation of these insects is of great interest both for insect phylogeny and for the reconstruction of Mesozoic environments.

Acknowledgments: During my study at the Naturhistorisches Museum in Wien as a visiting scientist at the Österreichische Akademie der Wissenschaften I was able to reexamine the collection of insect remains from the Jurassic of Solnhofen and Eichstätt including some of A. HANDLIRSCH's (1906–1908) types. I am very grateful to Dr. Heinz KOLLMANN, Director of the Geologisch-Paläontologische Abteilung of the Museum for permission to study this interesting material and to the entire staff of the division, especially Dr. Ortwin SCHULTZ, for help and hospitality. I thank Mrs. H. SCHMITZ for help in compiling the bibliography and Mrs. A. SCHUMACHER for photographic work.

#### List of insects:

The collection consists of 103 specimens and includes nearly 50 species from 10 orders of Insecta as listed below:

#### Ephemeroptera

- Mesephemeridae: *Mesephemera procera* (HAGEN),  
*M. prisca* (GERMAR) (2 specimens),  
 ? *M. spp.* (2 specimens).  
 Paedephemeridae: *Paedephemera? oppenheimi* HANDLIRSCH.

#### Odonata

- Protomyrmeleontidae: ? *Malmagrion eichstaettensis* (HAGEN) (2 specimens)  
 Isophlebiidae: *Isophlebia aspasia* HAGEN (2 specimens)  
*Anisophlebia helle* (HAGEN)  
*Tarsophlebia eximia* HAGEN (3 specimens)  
 Stenophlebiidae: *Stenophlebia latreillei* (GERMAR) (2 specimens),  
*S. amphitrite* (HAGEN) (2 specimens)  
 Amphipterygidae: *Steleopteron deichmuelleri* HANDLIRSCH, holotype  
 Gomphidae: *Nannogomphus bavaricus* H. (2 specimens, syntypes)  
*Cymatophlebia longialata* (GERMAR) (5 specimens)  
 Petaluridae: *Mesuropetala koehleri* (HAGEN)  
*Aeschnogomphus intermedius* (HAGEN) (4 specimens)

- Aeschnidiidae: *Aeschnidium densum* (HAGEN) (2 specimens)

#### Hemiptera-Homoptera

- Palaeontinidae: *Protopsyche braueri* HANDLIRSCH, holotype  
*Archipsyche eichstaettensis* HANDLIRSCH, holotype  
*Beloptesis oppenheimi* HANDLIRSCH, holotype

#### Hemiptera-Heteroptera

- Belostomatidae: *Mesobelostomum deperditum* (GERMAR) (4 specimens)  
*Mesonepa primordialis* (GERMAR)

- Geocorisae incertae familia: *Copidopus jurassicus* HANDLIRSCH, holotype
- Neuroptera  
 ?Osmyliidae: *Nymphites lithographicus* HANDLIRSCH, holotype  
*Gigantotermes excelsus* (HAGEN)
- Coleoptera  
 Cupedidae: *Omma brevipipes* (DEICHMÜLLER)  
*Notocupes tripartitus* (OPPENHEIM)  
 ?Schizophoridae: *Malmelater grossum* (WEYENBERGH)  
 Trachypachidae: *Procalasoma minor* (HANDLIRSCH) (2 specimens, includ. holotype)  
 Coptoclavidae: *Pseudohydrophilus avitus* (HEYDEN) (3 specimens)  
*Ditomoptera dubia* (GERMAR)  
*Actea sphinx* GERMAR  
 Hydrophilidae *Mesosperchus schultzi* sp. nov.  
 ?Elateridae gen. sp. incertae familia: 2 species, 2 specimens
- Diptera  
 Culicoidea incertae familia
- Hymenoptera  
 Myrmiciidae: *Myrmicium schroeteri* (GERMAR)  
*M. elongatus* (GERMAR), (2 specimens)  
*M. nanus* (HANDLIRSCH) (2 specimens, includ. holotype)  
 incertae familia propria Apocrita
- ?Ordo  
 Chresmodidae: *Chresmoda obscura* GERMAR (9 specimens)
- Orthoptera  
 Elcanidae: *Elcana lithophila* (GERMAR) (6 specimens, includ. holotypes)  
*E. bavarica* HANDLIRSCH, holotype  
*E. phyllophora* HANDLIRSCH) (3 specimens, includ. holotype)  
 Haglidae: *Pycnophlebia speciosa* (GERMAR) (5 specimens),  
*P. minor* HANDLIRSCH (3 specimens, syntypes)
- Blattodea  
 Mesoblattinidae: *Lithoblatta lithophila* (GERMAR) (8 specimens)  
 Blattodea or Orthoptera-Grylloidea: *Megalocerca longipes* HANDLIRSCH (2 specimens, syntypes)
- Insecta incertae sedis (7 specimens)

F. M. CARPENTER (1933) listed insects from these localities in the collections of the Carnegie Museum and the Museum of Comparative Zoology, Harvard, U.S.A. This material is more comprehensive than the collection under study and includes 432 specimens. Certain differences with regard to the range of insect orders in these two collections exist. Both are dominated by dragon-flies, but in CARPENTER's material they are followed by Coleoptera, Hymenoptera and Hemiptera; in the present collection dragon-flies are followed by Orthoptera, Coleoptera, *Chresmoda* and Hemiptera. The high percentage of Hymenoptera is quite atypical for Mesozoic localities and the percentage of Diptera is unusually low. This bias seems to be the result of the special selection involved in marine deposition.

The preservation of most of the material is not good, as is usually the case for insect remains from this locality. Very often only rough casts without any fine details exist. Only in several specimens of dragon-flies and elcanids is the fine wing venation preserved. The casts of the bodies are often filled with secondary calcite, and the large crystals do not permit the study of body structures. Due to this poor state of preservation, the systematic position of many forms cannot be accurately determined. It should be taken into account that the number of described species may exceed the actual number by two or three times and that many described species may be synonyms.

May-flies (Ephemeroptera), with the three families and four to six species, are unexpectedly numerous in this collection and in the oryctocoenosis as a whole. Only remains of adult insects were found, but one would not expect these to fly the long distance from the lakes and rivers inhabited by their larvae. A part of the species of *Mesephemera* and *Paedephemera* may be synonyms.

Dragon-flies and damsel-flies (Odonata) are the most numerous insects in the collection and the oryctocoenosis. They compose a quarter of the collection (a third in CARPENTER 1933). The entire list includes approximately eight families and more than 50 species, although a part must be synonyms. Dragon-fly remains are much more common than damsel-flies. Dragon-flies possibly flew to the lagoon to hunt insects transported there by breeze. This is a common habit of recent dragon-flies, especially the large ones. The dragon-flies from the family Aeschnidiidae are the most characteristic for the marine Mesozoic localities, but they are not dominant under the Odonata of this locality. Larvae of dragon-flies occasionally inhabit recent lagoons, but none could be found in this locality. Three very rare small damsel-flies are contained in the collection. One of them is *Steleopteron*, which is known only from a single specimen. The second is a very well preserved specimen of a small (wing length 20 mm) damsel-fly. According to its size it may be the undescribed specimen of *Malmagrion eichstaettensis* HAGEN. The wing venation of the holotype of this species is not distinct enough to permit designation to the previously given systematic position of *Malmagrion*. The new specimen proves to belong to the Protomyrmeleontidae by venation (pl. 1, fig. 1).

Cicadas (Hemiptera-Homoptera) are very rare in this locality, much rarer than usual in the Jurassic. Six species of large cicadas from the family Palaeontinidae are known from the locality and the types of three of them are in the

collection. In none is the venation satisfactory enough for the study of details. Most of the bugs (Hemiptera-Heteroptera) are aquatic. Several belostomatids are present in the collection. They may be autochthonous because certain recent belostomatids live in lagoons. Other families of water bugs – Naucoridae, Notonectidae, Nepidae and Corixidae – are very rare in this locality and are not represented in the collection. *Copidopus* is the only terrestrial bug in this locality.

Neuroptera is not as rare here, but only two forms are present in the collection under study. Both specimens are poorly preserved. Neuropteroids with this type of wing venation were placed by PANFILOV (1980) into the extinct family Osmylidae. There is, however, one feature of both *Nymphites lithographicus* HANDLIRSCH and *Gigantotermes excelsus* (HAGEN) that is in contradiction to their osmylid affinities. These insects both have a stout body with very wide thorax as in itthonids (pl. 1, fig. 2).

Beetles (Coleoptera) are common and diverse in this locality. The water beetles (especially Coptoclavidae) are the most numerous. Coptoclavids were the most common Jurassic and Lower Cretaceous water beetles. Adults had pneustonic habits; they lived on the surface film of the water and collected insects that dropped into the water. Three genera of coptoclavids are known from this locality and all are represented in the collection (pl. 1, fig. 3, 4; text-fig. 1). The first plant-eating water beetle for the locality is found in the collection. It is a new species of hydrophilid from the common Jurassic genus *Mesosperchus*. The description of this new species will follow below. Among the terrestrial beetles there are both xylophilous and predaceous forms. The former include cupedids, buprestids and elaterids, the latter caraboid beetles from the family Trachypachidae. Cupedidae are very rare in recent times but were common in the Mesozoic and dominate among the terrestrial beetles in the locality (pl. 2, figs. 1,2; text-figs. 2,3). A single buprestid was found earlier (PONOMARENKO 1971), and a probable elaterid is found in the collection for the first time. The preservation of the specimen (pl. 3, fig. 1; text-fig. 4) is not satisfactory for a comparison with the numerous Jurassic elaterids

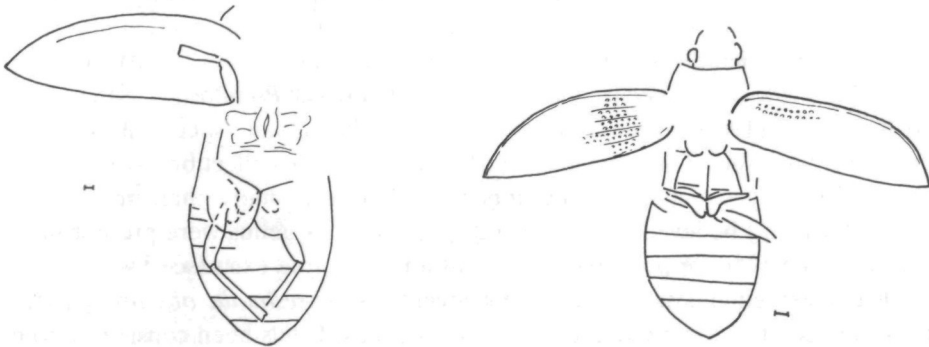


Fig. 1. *Pseudohydrophilus avitus* (HEYDEN). – NMW 1985/26/2. – Scale on all text-figures is 1 mm.

Fig. 2. *Omma brevipes* (DEICHMÜLLER). – NMW 1985/26/4.

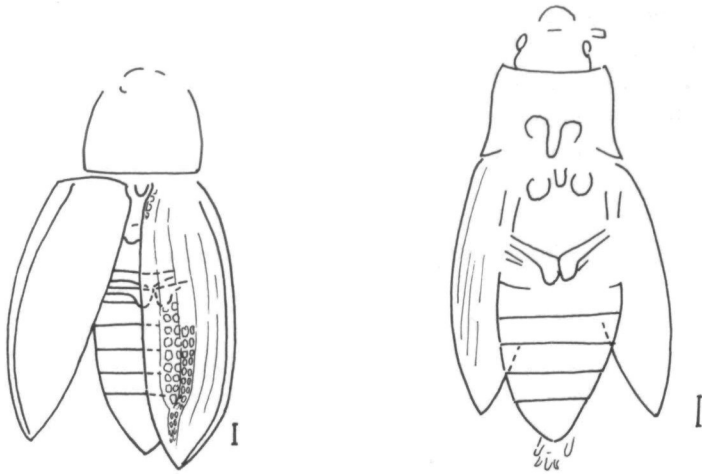
Fig. 3. *Notocupes tripartitus* (OPPENHEIM). – NMW 1985/26/5.

Fig. 4. ?Elateridae gen. sp. – NMW 1985/26/7.

described by V. G. DOLIN (1980) from the well known locality Karatau in South Kazakhstan, USSR. Two species of trachypachids were designated for the locality (PONOMARENKO 1971) and two specimens of the same species were found in the collection. The first is the holotype of *Procalasoma minor* HANDLIRSCH (pl. 3, fig. 2; text-fig. 5a), the second an undescribed beetle which resembles the first with regard to the structures of head, prothorax and elytra (pl. 3, fig. 3; text-fig. 5b). *Procalasoma minor* seems to be related to *Karatoma* PONOMARENKO, 1977 (Upper Jurassic of Asia) or the new genus *Evertus* (PONOMARENKO, in press) from the Lower Cretaceous of Mongolia. These genera had mouth parts and prothorax similar to recent snail-eating carabids and their habits may possibly be the same. *Procalasoma* was previously thought to be a cupedid (PONOMARENKO 1980). This is incorrect in the case of *P. minor* and further species of the genus should be studied.

Most Mesozoic localities are dominated by Diptera, but these insects are very rare in the oryctocoenosis of Solnhofen. Only several specimens of nemestrinids were known earlier. The collection contains a specimen of a culicomorphous midge (pl. 4, fig. 1), but its preservation is unsatisfactory for the study of details.

The large siricoid wasps (Hymenoptera) are not rare in this locality, although they all belong to a few species of a single genus known as *Pseudosirex*. MAA (1949) and RASNITSYN (1969) considered these insects to be a single species *Myrmiceum schroeteri* (GERMAR). The specimens of *Myrmiceum* in the collection vary greatly in size and in body structures. They appear to belong to more than one species. CARPENTER (l. c.) believed that two valid species of this genus were present in the locality. It seems more probable to this author that three exist (see list).

The most enigmatic insect in this locality is *Chresmoda obscura* GERMAR (pl. 4, fig. 2). It is a large insect with very long legs. It has been considered to be both an aquatic and terrestrial bug, a mantid and a phasmid (see discussion in POPOV 1980). One specimen in the collection bears five tarsomers, and I can detect

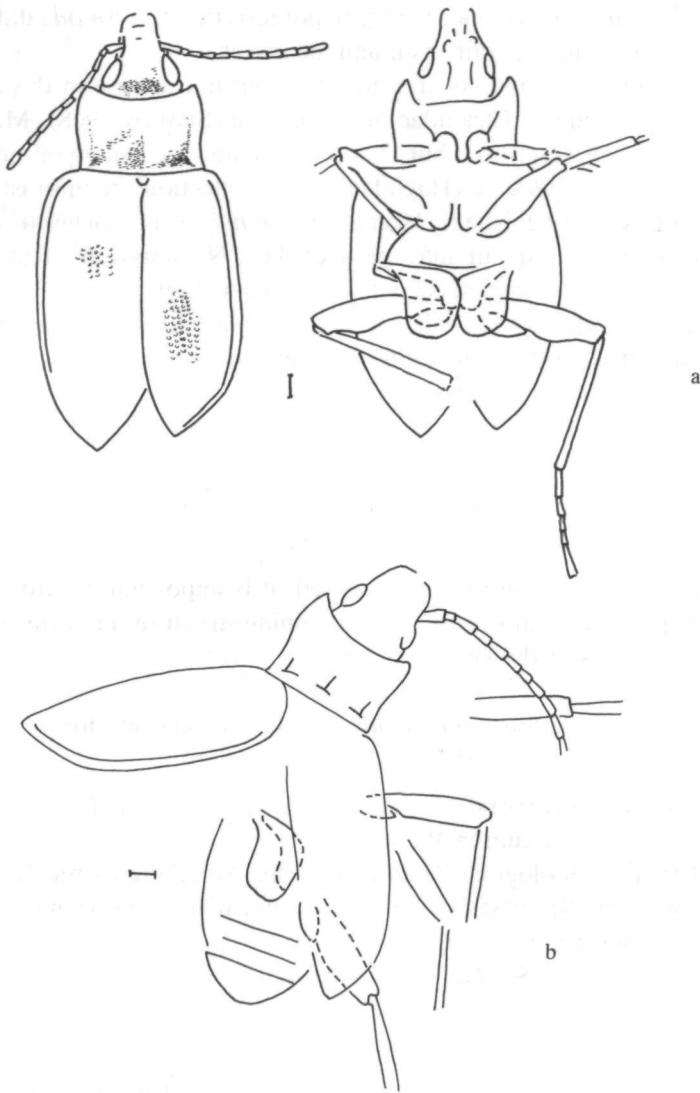


Fig. 5. *Procalasoma minor* HANDLIRSCH. – a – Holotype, NMW 1985/10, b – NMW 1985/26/8.

no precostal field on the others. According to these structures, *Chresmoda* can be neither a bug nor a phasmid. The third type of *Chresmoda* are hemimetabolous larvae; *Chresmoda* therefore cannot be a holometabolous insect. Only one group comes to mind for this strange insect: *Chresmoda* may be an anomalous paraplecopterid living on the water surface. *Chresmoda obscura* is the most common species of insects in this locality as is usually characteristic for aquatic forms. Certain unmistakable terrestrial insects are numerically as significant as *Chresmoda* in the oryctocoenosis (cockroach *Lithoblatta*, orthopteroids). *Lithoblatta* was very often found with outspread wings, while *Chresmoda* was never found in this

position. This may be evidence for the hypothesis that *Chresmoda* did not reach the lagoon by flying but was rather an aquatic insect.

The orthopterous insects are numerous but not diverse in this locality. They belong to two families: Elcanidae and Haglidae (SHAROV 1968). Many species of *Elcana* have been described, but they may possibly be synonymized to only two. All species of *Pycnophlabia* (Haglidae) in the collection are unsatisfactory and no veins could be distinguished. *Megalocerca longipes* HANDLIRSCH was originally described as a blattoid but may be a cricket. No important features could be distinguished from the two specimens in the collection.

A single, numerically well represented blattoid species is present in this locality. In certain other Mesozoic localities cockroaches, which were probably coastal insects, are very abundant.

### Description of a new species of beetle

Family Hydrophilidae LATREILLE, 1802

Genus *Mesosperchus* PONOMARENKO, 1977

As antennae have not been preserved, it is impossible to prove formally the systematic position of this beetle; the remaining structures are principally the same as in other species of the genus.

*Mesosperchus schultzi* PONOMARENKO, sp. nov.

(Plate 2, fig. 3; text-fig. 6)

Derivatio nominis: the species is named after Dr. Ortwin SCHULTZ, Naturhistorisches Museum in Wien.

Holotype: Geologisch-Paläontologische Abteilung of the Naturhistorische Museum in Wien, Nr. 1985/20; positive and negative impression of beetle without antennae and most parts of legs.

Locus typicus: Solnhofen, Bayern, BRD.

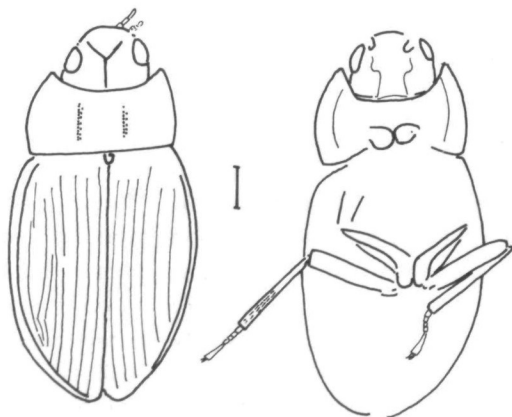


Fig. 6. *Mesosperchus schultzi* sp. nov. – Holotype, NMW 1985/26/6.



**Stratum typicum:** Solnhofener Plattenkalke, lowermost Tithonian, Jurassic.

**Description:** Small oval beetle. Head transversal, its width one and a half times greater than its length, clypeus stout, eyes large, stalk of epicranial “suture” shorter than branches. Pronotum transversal, tapered anteriorly, rounded before anterior angles, width of pronotum twice its length, anterior margin sinuated, anterior angles sharp, posterior ones rectangular. Fore-coxae contiguous. Elytra convex, apex rounded, length of elytra three times greater than its width, disc with seven thin, finely punctuated furrows, all flowing into outward ones just before elytral apex. Hind legs thin and long, femur and tibia lineal in shape, length of femur equal to that of tibia, tibia with many small bristles.

**Dimensions:** length of beetle 10.0 mm, width – 4.5 mm, length of elytra – 7.0 mm.

The new species is distinguished from others by the form of the prothorax and by characters of elytral striae in addition to its size, which is larger than in all other species. The remaining species of this genus were found in the Jurassic of Siberia (PONOMARENKO 1977).

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## Explanation of plates

## Plate 1

- Fig. 1. ?*Malmagrion eichstaettensis* (HAGEN). – NMW 1985/26/1 (x 4,6), Eichstätt.  
 Fig. 2. *Nymphites lithographicus* HANDLIRSCH. – Holotype NMW 1985/9, (x 1,5), Eichstätt.  
 Fig. 3. *Pseudohydrophilus avitus* (HEYDEN). – NMW 1985/26/2 (x 1,5), Eichstätt.  
 Fig. 4. *Malmelater grossum* (WEYENBERGH). – NMW 1985/26/3 (x 2,1), Solnhofen.

## Plate 2

- Fig. 1. *Omma brevipes* (DEICHMÜLLER). – NMW 1985/26/4 (x 2,5), Solnhofen.  
 Fig. 2. *Notocupes tripartitus* (OPPENHEIM). – NMW 1985/26/5 (x 4,6), Solnhofen.  
 Fig. 3. *Mesosperchus schultzi* sp. nov. – Holotype, NMW 1985/26/6 (x 7,9), Solnhofen.

## Plate 3

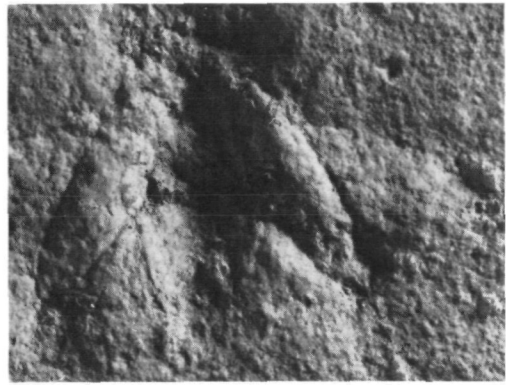
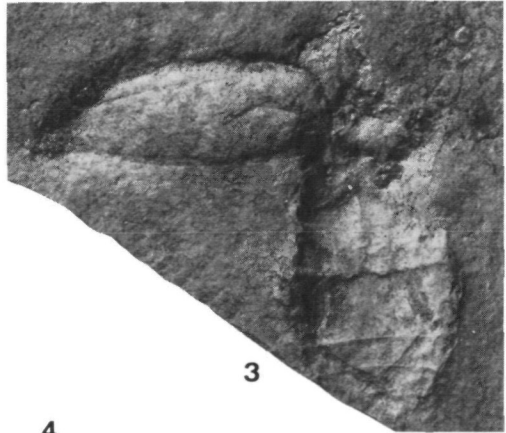
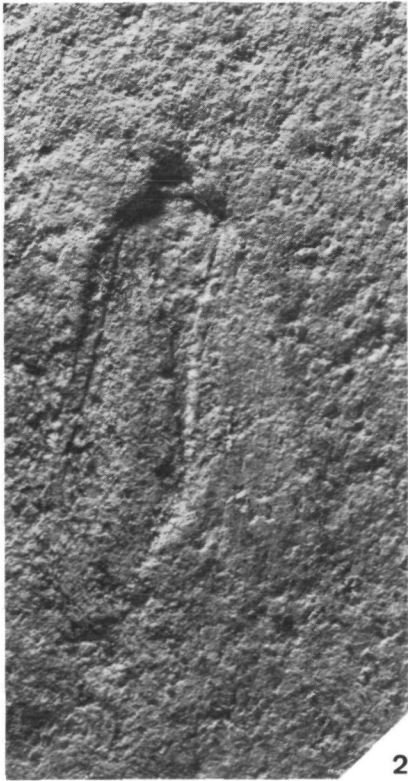
- Fig. 1. ?Elateridae gen. sp. – NMW 1985/26/7 (x 5,1), Solnhofen.  
 Fig. 2. *Procalasoma minor* HANDLIRSCH. – Holotype, NMW 1985/10, (x 3,3), Solnhofen.  
 Fig. 3. *Procalasoma minor* HANDLIRSCH. – NMW 1985/26/8 (x 3,0), Solnhofen.

## Plate 4

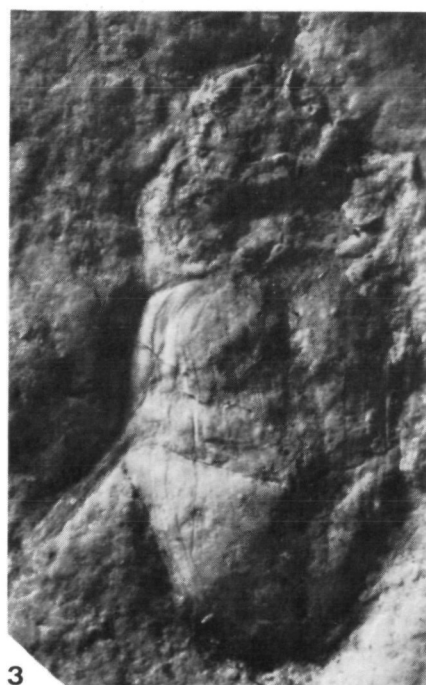
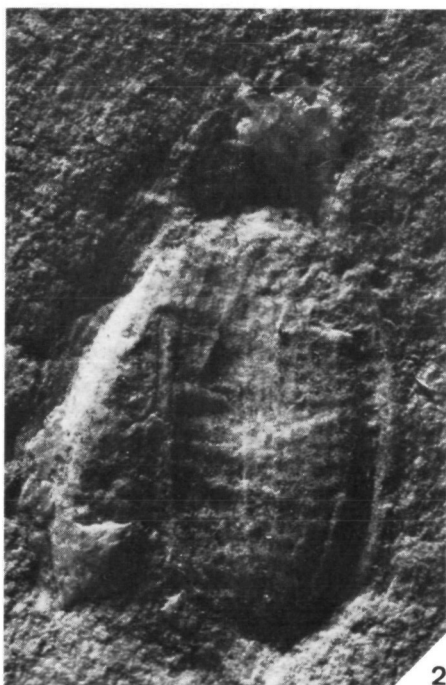
- Fig. 1. Diptera-Culicomorpha inc. fam. – NMW 1984/26/9 (x 5,0), Solnhofen.  
 Fig. 2. *Chresmoda obscura* GERMAR. – NMW 1985/26/10 (x 1,2), Eichstätt.

Locality resp. age: „Lithographische Schiefer“, Bayern, BRD, Lower Tithonian, Jurassic.

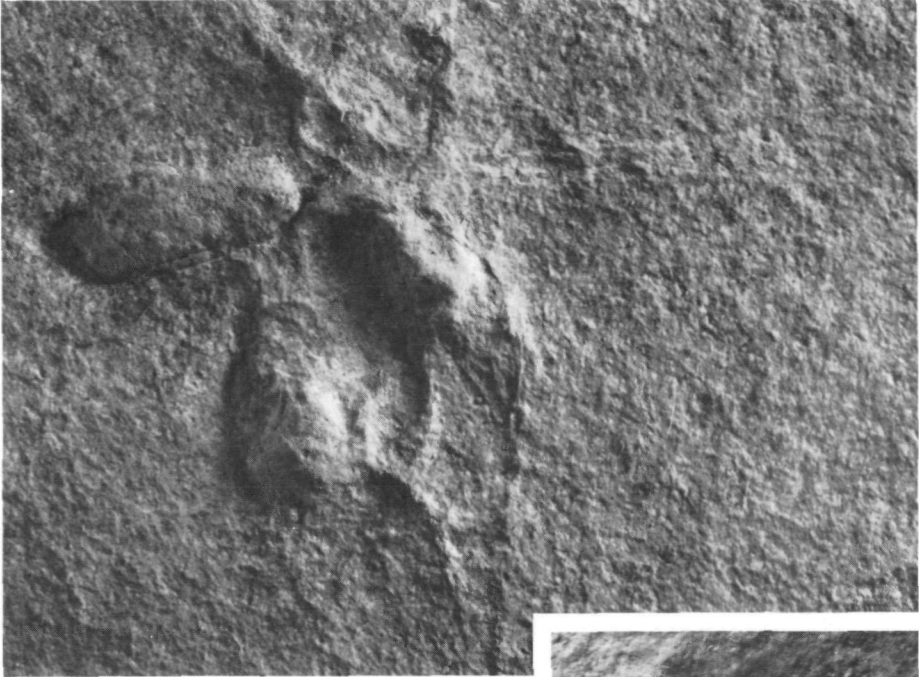
All specimens on the plates 1–4 from the Geologisch-Paläontologische Abteilung, Naturhistorisches Museum Wien (NMW).



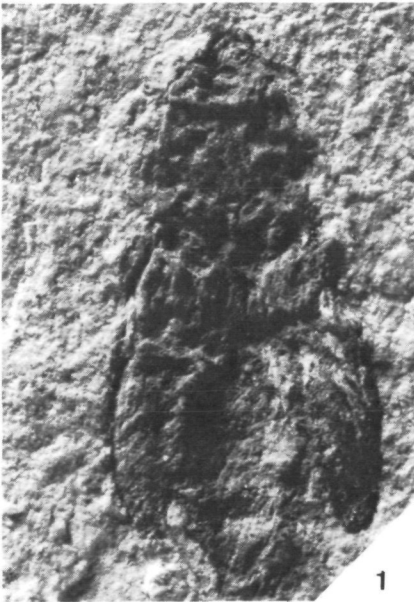




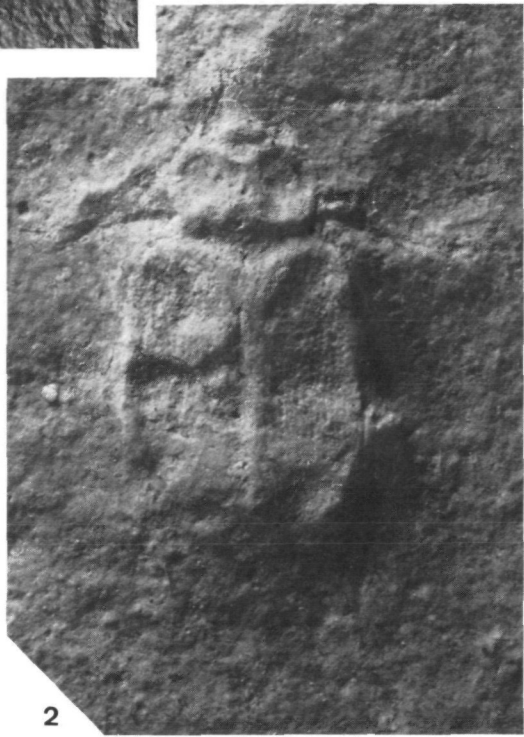




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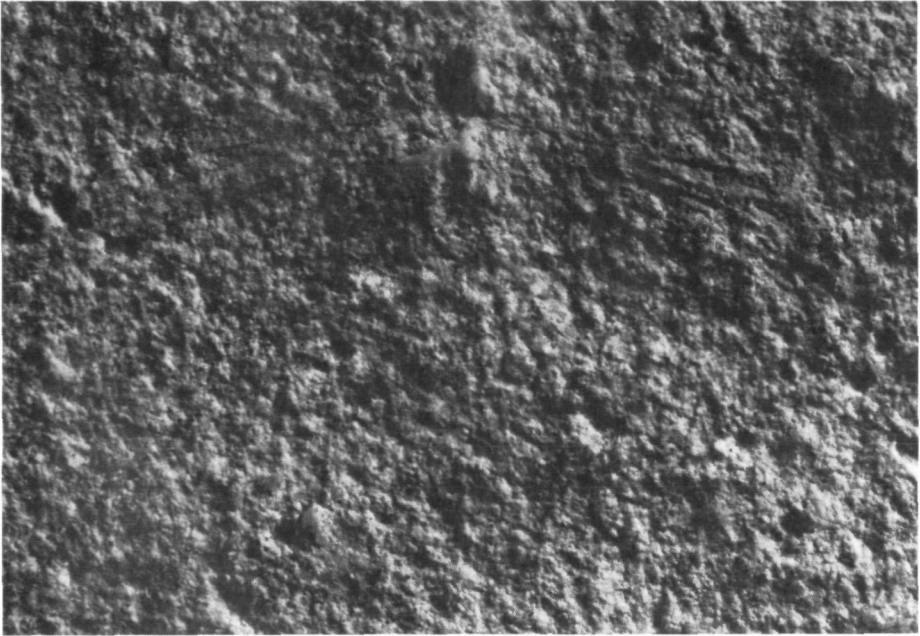
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