

VIII. JURASSIC INSECTS FROM SOLENHOFEN IN THE
CARNEGIE MUSEUM AND THE MUSEUM OF
COMPARATIVE ZOÖLOGY.

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Museum of Comparative Zoölogy

The lithographic limestone at Solenhofen, Bavaria, and vicinity, has long been famous as a source of Jurassic fossils. Although the reputation of the formation has depended largely upon the discovery of certain remarkable vertebrates, such as *Archæopteryx* and *Rhamphorhynchus*, invertebrates are far commoner. Most of these are marine types, the limestone being marine in its origin; but numerous insects, which undoubtedly fell into the water, have also been preserved. More publications have been devoted to these insects than to any other fossil insect-fauna of equivalent size, chiefly because the commercial working of the limestone has produced an almost continuous output of specimens.

In view of the extensive bibliography of the fossil insects of Solenhofen, one might conclude that all positive information about them has already been published. This would probably be true, were it not for the fact that, exclusive of Handlirsch's extensive compilation on fossil insects (1906-08), and a few papers of a general nature, or brief notes, all the literature was published prior to 1900, before the geological history of the insects as a whole was well enough known to enable a proper appreciation of the species contained in any one stratum. Handlirsch, of course, straightened out most of the taxonomic difficulties encountered by the older investigators, and was able to make the necessary comparisons with other extinct faunas; but he was not able to examine specimens of all the species from Solenhofen, and, with a few exceptions, took his figures without modification from the earlier writings.

Several years ago, while engaged in a rearrangement of the fossil insects in the Museum of Comparative Zoölogy, I was impressed by the large number of specimens from Solenhofen in that collection. Studies on other fossil insects already in progress prevented my immediate examination of these, but last year my attention was called

to another large collection in the Carnegie Museum. This material, although secured many years ago from Baron de Bayet,* the Private Secretary of King Leopold II of Belgium, when he sold his vast collection to Mr. Andrew Carnegie, had not been critically studied until 1930, when Mr. Stephen Herrick, a graduate student in the University of Pittsburgh, undertook its arrangement and description. Mr. Herrick, however, did not proceed far, and did not prepare any account for publication. Accordingly the entire collection was sent to me for detailed description. This is particularly desirable, not only because the Bayet Collection contains new material, but because the percentage of excellent specimens in it is unusually high. The present paper is essentially an annotated list of the specimens in the collection of the Carnegie Museum. I have, however, considered it opportune to mention and occasionally describe some of the important fossils in the Museum of Comparative Zoölogy. About half of the Harvard collection was secured from Krantz as far back as 1860, and was studied by Hagen; but many of the specimens have not been properly described.¹ The other half of the collection was purchased from Haberlein about 1883; it has not been studied, or at least published upon, except very briefly.² For the benefit of those who desire further discussion of the fossils of Solenhofen, I have included under each species the reference to the original description and to the important subsequent redescriptions; a more complete series of references will be found in Handlirsch (1906-08). In the bibliography I have listed the most useful papers on the fauna. The synonymy of these fossils is very confusing and uncertain. In the main I have followed Handlirsch, but I believe that he recognizes many more species than are actually valid. This is chiefly due to the inadequacy of the figures and descriptions published during the Eighteenth and early

*The Editor, who acted as the agent of Mr. Andrew Carnegie in the purchase of the Collection of Baron de Bayet, and spent many weeks in Brussels in 1908 packing it for shipment to Pittsburgh, recalls that the Baron informed him that the specimens from Solenhofen had been acquired at the quarries from the superintendents to whom the Baron had made an offer to recompense them for all fossils found by them in good condition as they proceeded with their work. This offer continued for a couple of years and it was thus that Baron de Bayet succeeded in amassing among other things the fine collection of insects from Solenhofen. W. J. H.

¹One of these I have already described in *Psyche*, Vol. XXXVI; No. 3, pp. 190-194, 1929.

²See Tillyard, 1921, 1927; Needham, 1903, 1907.

Nineteenth Centuries. The authors of these accounts often made a new species for every specimen preserved in a different position.

It is surprising, that, although the shales of Solenhofen were used for building purposes in the time of the Roman Empire, no recognizable accounts of fossils were published, so far as I am aware, until 1705, when Rumphius described a fish from the formation. Knorr (1755) was the first to mention the presence of insects; in 1782 Schmidel figured a dragon-fly from the limestone; two years later Schröter published a description of a supposed Sphingid, which is now known to be a Siricoid wasp. During the first third of the Nineteenth Century a few isolated accounts were published, mostly on Dragonflies (Kœhler, Parkinson, Van der Linden); but after the discovery of lithography in 1834,³ large collections of the fossils were secured, which were first studied by Germar (1837, 1839, 1842), later by Hagen (1862, 1866, et seq.), and Weyenbergh (1869, 1873, et seq.). Deichmüller (1886) published a very complete account of the lithographic insects in the Dresden Museum; and Handlirsch made a comprehensive compilation and classification of the species (1906).

In the Carnegie Museum there are one hundred and forty-six specimens sufficiently well preserved at least to permit generic classification. In the Museum of Comparative Zoölogy there are two hundred and eighty-six such specimens. In the accompanying table I have listed the percentages of specimens falling into each order. The figures in the first column are based upon the four hundred and thirty-two specimens, which I have examined in these two collections; those in the second column are the percentages which Deichmüller found in his collection of two hundred and seventy-two specimens; and in the last column are the averages of these, based upon the seven hundred and four specimens in all three collections. This last computation probably represents a fairly accurate picture of the relative abundance of the several orders. From this it is apparent that the *Odonata* are far in the lead, followed by the *Hymenoptera*, *Coleoptera*, *Blattaria*, *Hemiptera*, *Orthoptera*, *Phasmodea*, *Plectoptera*, *Neuroptera*, and finally the *Trichoptera*. These figures do not, however, represent the composition of the insect-fauna, which existed in the region of Solenhofen during the Upper Jurassic; for the limestone is of such a nature that only the larger insects were capable of being preserved,

³See Crook, A. R., "The Lithographic Stone Quarries of Bavaria, Germany," Store, Oct., 1894.

the smaller ones having been decomposed, or devoured by fishes before fossilization took place.

Table I. Approximate percentages of specimens from Solenhofen in each order of insects.

	Carpenter (432 specimens)	Deichmüller (272 specimens)	Average (704 specimens)
Plectoptera.....	4. pr. ct.	.3 pr. ct.	2. pr. ct.
Odonata.....	33. pr. ct.	34. pr. ct.	34. pr. ct.
Blattaria.....	6. pr. ct.	11. pr. ct.	9. pr. ct.
Orthoptera.....	9. pr. ct.	5. pr. ct.	7. pr. ct.
Phasmodea.....	8. pr. ct.	5. pr. ct.	7. pr. ct.
Hemiptera.....	10. pr. ct.	6. pr. ct.	8. pr. ct.
Neuroptera.....	2. pr. ct.	1. pr. ct.	1.5 pr. ct.
Trichoptera.....	.2 pr. ct. pr. ct.	.1 pr. ct.
Coleoptera.....	13. pr. ct.	12. pr. ct.	13. pr. ct.
Hymenoptera.....	12. pr. ct.	24. pr. ct.	18. pr. ct.

Order PLECOPTERA.

The May-flies of Solenhofen, although few in number, are particularly interesting, since they are the first representatives of members of the order in rocks above the Permian. Aside from a few fragments from the Lower Cretaceous of Mongolia (Cockerell, 1924, 1927) they are the only Ephemeroidea known in the whole Mesozoic. However, because of the delicacy of the wings and their tendency to fold together in such a way that the venation is badly confused, good specimens of these fossils are extremely rare. Thirteen species of May-flies from Solenhofen have been described, but many of these are undoubtedly synonymous. Handlirsch has separated most of these species into two genera, *Mesephemera* and *Paedephemera*, the former including species with nearly homonomous wings, and the latter species with the hind wings more reduced in size, about two-thirds the length of the fore wings. Although the general shape of the wings is known in *Mesephemera*, the details of the venation have not been determined. But in *Paedephemera* the venation is known in two species, *multinervosa* Oppenheim, and *schwertschlagerei* Handlirsch. The latter, which was based upon a fine specimen, is in all probability synonymous with one of the other species of the genus, but in view of the obscurity of these other species, I believe we should retain a separate name for Handlirsch's specimen. The single remaining genus,

Hexagenites Scudder is probably synonymous with *Mesephemera*, but because the hind wing is unknown and for another reason given below, I believe Scudder's genus should be regarded as valid.

Inasmuch as the existing Ephemerids have now been divided into recent families, I propose the name *Mesephemeridæ* for these forms from Solenhofen. At present, because of our lack of knowledge of their tarsal and other body-structures, I do not believe we can assign them to existing families or even superfamilies.

Family MESEPHEMERIDÆ.

Genus MESEPHEMERA Handlirsch.

1. *Mesephemera procera* (Hagen).

Ephemera procera Hagen, 1862, Palæontogr., X, 116; pl. 15, f. 2.
Mesephemera procera Handlirsch, 1906, Foss. Ins.: 600.

I consider *speciosa* Oppenheim (1888) and *weyenberghi* Handlirsch (1906) as synonyms of this species. *Lithophila* Germar (1842) is probably the same insect also, although it was considered by its author to be a Lepidopteron; but Germar's figure and descriptions do not serve as sufficient identification of the species. In the Bayet Collection in the Carnegie Museum there are five specimens of *M. procera*; Nos. 3835, 3836-3837,* 3838-3839, 5083-5084, 5085-5086. In the Museum of Comparative Zoölogy there are four specimens, of which one (No. 6280a, b) is marked "type" by Krantz. In none of these is the venation distinct, and I can add nothing to Hagen's description.

2. *Mesephemera cellulosa* (Hagen).

Ephemera cellulosa Hagen, 1862, Palæontogr., X, 115; pl. 15, f. 3.
Mesephemera cellulosa Handlirsch, 1906, Foss. Ins.: 601.

In the Bayet Collection (Carn. Mus.) there are two specimens: Nos. 3840 and 5087. In the Museum of Comparative Zoölogy there are four specimens, one (No. 6281a, b) being the type figured by Hagen.

*In this paper all the figures connected with a dash indicate the reverse of the first numbered specimens.

Genus PAEDEPHEMERA Handlirsch.

3. *Paedephemera mortua* (Hagen).

Ephemera mortua Hagen, 1862, Palæontogr., X, 117; pl. 15, f. 5.
Paedephemera mortua Handlirsch, 1906, Foss. Ins.: 602.

I consider Handlirsch's *oppenheimi* a synonym of this species. There are no representatives in the Bayet Collection of the Carnegie Museum, but in the Museum of Comparative Zoölogy, there is the type figured by Hagen (No. 6283).

Genus HEXAGENITES Scudder.

4. *Hexagenites weyenberghi* Scudder. (Fig. 1)

Ephemerida, Eaton, 1871, Trans. Ent. Soc. Lond., p. 158; pl. 1, f. 10.
Hexagenites weyenberghi Scudder, 1880, Anniv. Mem. Bost. Soc. Nat. Hist., 6.

Length of fore wing, 15 mm.

Scudder's description of this fossil was based entirely upon Eaton's published figure of a specimen in the British Museum. In the Museum of Comparative Zoölogy I find a very fine specimen of a May-fly, to which is attached the following note, in Hagen's characteristic writing: "*Ephemera cellulosa* Hagen, front wings and outline of body and setæ." On the reverse side of this label, written in a hand unfamiliar to me, is the following: "The counterpart was described by Scudder as *Palin. Weyenberghi*." Although this note is incorrect in its reference to the genus in which Scudder placed the species, there can be no doubt that this fossil (No. 6277) in the Museum of Comparative Zoölogy is the reverse of the specimen examined by Eaton in the British Museum. A comparison of the venation of our

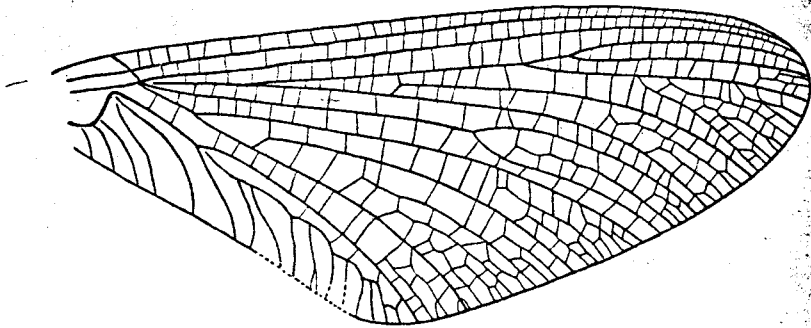


FIG. 1. *Hexagenites weyenberghi* Scudder, fore wing. Type (No. 6277), Mus. Comp. Zoöl. Magnified.

fossil and the figure given by Eaton shows that not only do all the cross-veins and cells correspond, but also the various breaks and imperfections in the wing occur in the same places, although our half of the fossil has been chipped out of the matrix, so that the whole wing is exposed. The specimen before me is therefore the counterpart of the type of Scudder's *weyenberghi*. Hagen's determination of this species as *cellulosa* perhaps indicates that *weyenberghi* is synonymous with *cellulosa*; but in view of the fact that *cellulosa* is a very obscure species, and is closely involved with the synonymy of the several species of *Mesephemera*, I believe that *weyenberghi* should be regarded as a separate species of a distinct genus. Figure 1, showing the fore wing of this May-fly, is based on the specimen in the Museum of Comparative Zoölogy. The entire wing is preserved with remarkable clearness. This is the only known complete wing of a Mesozoic May-fly. The figure shows more clearly than can be depicted in words the characteristics of the wing, but I wish to call attention to the similarity of this wing to that of recent May-flies, even to the formation of the third auxiliary vein at the base of the wing (3 Ax). The triad forking of *CuA* and the peculiar branching of *ICuA* are very distinctive features. As Scudder pointed out, the nearest approach to this *CuA* is found in the recent genus *Hexagenia*.

Order ODONATA.

As previously noted, the *Odonata* are the commonest insects in the shales of Solenhofen and they are usually well preserved. This fact, together with the importance of venational features in classifying the members of the order, has made the species of Solenhofen particularly valuable in studies of the evolution of the order. Unlike the May-flies, the dragon-flies are well represented in the Mesozoic strata. The Triassic of Australia, Liassic of England and Germany, and the Upper Jurassic of Turkestan have contributed many fossils of this order. The beds of Solenhofen, however, are the oldest rocks to yield fossils of the *Anisoptera*, which is now the predominant suborder. The *Zygoptera* are known as far back as the Upper Permian; and the *Anisozygoptera* from the Triassic to the Upper Jurassic and perhaps the Tertiary.⁴

⁴Some students of the *Odonata* consider that the recent Japanese *Epiophlebia* is a member of the *Anisozygoptera*. For an account of this subject, see my discussion in the American Journal of Science, (Ser. 5), Vol. XXXI, p. 97-139, 1931.

tive in its origin and perhaps 3A is also; but the venation is remarkably modern for a Jurassic species, especially for one which is the oldest record of the *Hymenoptera*.

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