References and Notes

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5. The Joint Prehistoric Project of Istanbul University and of the Oriental Institute of the University of Chicago returned to southeastern Turkey in 1968 to resume research begun in 1963 (*1*). Supported in part by NSF grant GS-1968 and by a student training grant from the Ford Foundation. We thank B. Lawrence, R. B. Stewart, R. A. Watson, G. A. Wright, and our graduate student trainees for their assistance.

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Oldest Known Terrestrial Arachnids

Abstract. *New finds of nonscorpionid arachnids in the Lower Devonian Nellenköpfchen Shale of Alken an der Mosel, Germany, give valuable information on the first appearance of terrestrial arachnids.*

Fossil arachnids are fairly abundant in Upper Carboniferous (Pennsylvanian) deposits, but from earlier formations very little is known of this important group. The first arachnids to appear in the geological record are the scorpions, which occur both in the Silurian and Devonian and continue up to recent time. When the Silurian scorpions were first discovered, scientists generally regarded them as the first arthropods to appear on land. However, more recent finds and an increased knowledge of the morphological structures of the early scorpions indicate that they were aquatic forms breathing with gills like the contemporaneous eurypterids (*1*).

Devonian nonscorpionid arachnids have been described from the Rhynie Chert in Scotland. The arachnids belong to the orders Acarida (*Protacarus*) and Anthracomarti (*Palaeocharinoides* and *Palaeocharinus*), and possibly to the order Araneida (*Palaeocteniza*) (*2*). The Acarida and Anthracomarti are very small, only 0.3 to 3.5 mm long. Because marine fossils are lacking in the Old Red sequence at Rhynie, the age of the chert has been difficult to determine. In general the beds have been regarded as Middle Devonian, but more recently a late Lower Devonian (Emsian) age has been suggested (*3*).

Our find of fossil arachnids gives valuable information on the first appearance of nonscorpionid arachnids. The fossils occur in the so-called Nellenköpfchen Shale in a quarry near the town of Alken an der Mosel in the Western part of Germany. The age of the beds is upper Lower Devonian or Emsian. The dark grey shale, which probably was deposited under more or less anaerobic conditions, has yielded an important fossil flora and fauna, the former with algae and other plants (*Chaetocladus hefteri, Dawsonites jebachensis* a.o.) (*4*), the latter with eurypterids (*Parahughmilleria* n. sp. a.o.) and some mollusks and ostracoderms [*Pteraspis* (*Rhinopteraspis*) *dunensis a.o.*] (*5, 6*). During my studies of the eurypterids, I have noticed several arthropod specimens which I recognized as arachnids similar to those known from the Upper Carboniferous of Europe and North America.

The well-preserved large specimen (Fig. 1) as well as its counterpart in the shale has been cleaned, and the different structures exposed in the two pieces are combined in the reconstruction (Fig. 2). Only the dorsal surface of the body is demonstrated. The elongate body (12.5 mm long) has a large, nearly triangular prosoma (cephalothorax) which is attached to the opisthosoma (abdomen) along a broad juncture. The inflated median portion of the prosoma has transverse furrows indicating a primitive segmentation present also in certain Carboniferous forms such as *Trigonomarthus* (*7*). Four of the five pairs of legs of the arachnid are more or less preserved. They are nearly uniform in shape and size, and the surface is covered by minute tubercles. Each leg has a blunt distal joint (tarsus) which apparently was provided with a pair of small claws similar to those found in related Devonian species from Scotland, and in most Recent arachnids. This type of leg is characteristic of terrestrial forms. In the aquatic eurypterids the distal joint of the legs had a strong terminal claw or spine, often flanked by two spines evidently homologous with the two arachnids claws (*8*).

The oblong opisthosoma (abdomen) is transversally divided into nine segments, and longitudinally by two furrows into one median and two lateral areas. The opisthosoma and parts of the prosoma are provided with prominent knobs or tubercles.

The present species, which is characterized by its elongate body and broad juncture between the prosoma and opisthosoma, probably belongs to the extinct order Trigonotarbida of which one family is known from the Devonian and four from the Carboniferous. Our species seems to belong to the family Palaeocharinidae which is represented by two genera in the Devonian of the Rhynie. However, the German form differs considerably from the Scottish ones and evidently belongs to a separate genus.

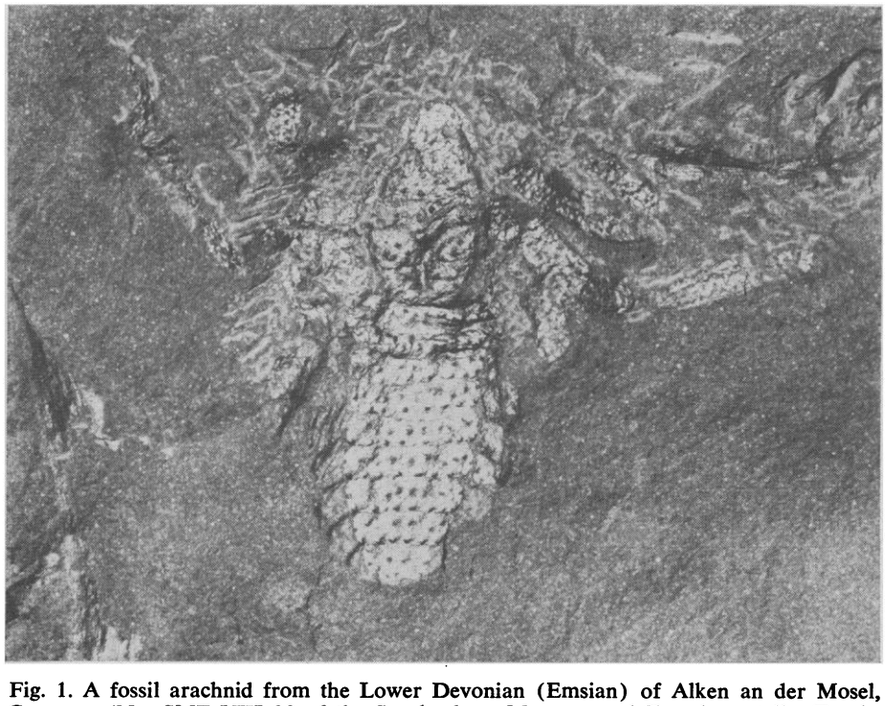

Fig. 1. A fossil arachnid from the Lower Devonian (Emsian) of Alken an der Mosel, Germany (No. SMF VIII 30 of the Senckenberg Museum und Forschungstelle, Frankfurt am Main, Germany)

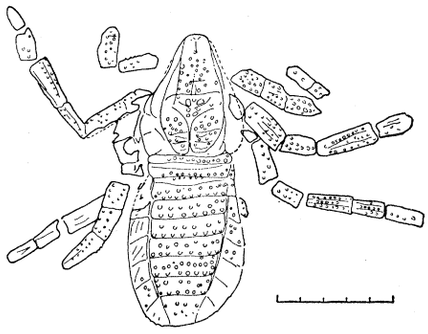

Fig. 2. A restoration of the arachnid based on the structures shown in the specimen (Fig. 1) and its counterpart. Scale is 5 mm.

Besides the rather complete specimen a few abdominal shields have been found (Fig. 3) which evidently belong to a different species. The moderately inflated shields (3.8 to 5.6 mm long) have a nearly circular outline. A median axis has seven segments, the frontal one being rather broad. The lateral portions of the shield are divided into eight pairs of segments, the hind ones forming a single plate behind the axis.

The eight segments of the abdomen are characteristic of the family Trigonotarbidae of the order Trigonotarbida. However, with its subcircular opisthosoma and an axis not reaching the hind border, the species does not fit into previously described genera. The shape of the opisthosoma might recall species of the Carboniferous order Anthracomarti, which, however, have an extra row of plates outside the lateral ones. The present forms may possibly have been related to the ancestors of the Anthracomarti.

The fossils described reveal the existence of advanced nonscorpionid arachnids in the Lower Devonian. The previously known arachnids from Rhynie in Scotland may possibly have been of the same early age, but the accurate dating is uncertain. The German arachnids are much bigger than the Scottish

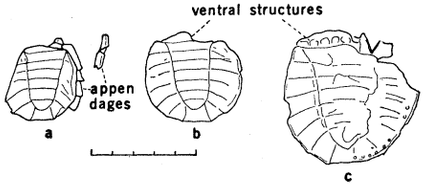

Fig. 3 (a–c). Specimens of the abdominal shield (opisthosoma) of another arachnid from the Lower Devonian (Emsian) of Alken and der Mosel, Germany (Nos. SMF VIII 32–34 of the Senckenberg Museum und Forschungstelle, Frankfurt am Main, Germany). Scale is 5 mm.

ones, and the morphological structures, notably the strong ornamentation of the integument of the large form (Fig. 1), indicate specialized and advanced features. The general structure of the legs conforms well with that of Carboniferous arachnids, which in turn correspond to recent terrestrial forms. The same terrestrial type of legs is found in the minute arachnids from the Devonian Rhynie Chert. This indicates that the German forms were terrestrial as mentioned above.

When did the arachnids become permanent land dwellers? They probably had their first development in aquatic environments, and it is reasonable to assume that before they invaded the land, members of the group passed a transition stage in which the aquatic forms were able to spend a short time on land. This is to some extent the case in the living horseshoe crabs, which can spend a short while on dry land because the gills are kept moist under the cover of the plate-shaped abdominal appendages. Among the Silurian and Devonian eurypterids, the Stylonuracea with their long and powerful legs might also have been able to crawl about on the tidal flats, perhaps taking advantage of the primitive swamps and land vegetation. As in the horseshoe crabs the gills were protected by the ventral plates. As shown by Wills and Kjellesvig-Waering (*9*) the early scorpions had similar ventral plates, which here too probably protected softer gills between the body and the plates. Also the legs of the primitive scorpions were eurypterid-like, the tarsal region of the legs not being so well adapted to carry the larger weight of the body on land (*8*). The first scorpion with stigmata, corresponding to those in recent forms, is known from the Carboniferous (*10*), a fact which suggests that the majority of the scorpions went on land in Devonian, perhaps late Devonian time, more or less at the same time as the first vertebrates. The nonscorpion arachnids seem to have been well established on land already in Lower Devonian time. The same may have been the case with the insects (*11*). Terrestrial forms of both these groups developed contemporaneously with the early land plants and probably depended on their presence. We do not know which of the various arthropod groups was the first to produce terrestrial forms, nor do we know when this happened. Certain forms described as diplopods (Myriapoda) have been described from the Silurian (Wenlockian) (*12*), but knowledge of these forms is too limited for one to decide whether or not they were terrestrial animals.

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3. Dr. C. D. Waterston, Royal Scottish Museum, Edinburgh, informs me that the age of the Rhynie Chert of the Scottish Old Red is still uncertain, ranging from Givetian down to Emsian (Middle and Lower Devonian). See *The Fossil Record, a Symposium with Documentation* (Geological Society of London, London, 1967), p. 500.
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8. L. Størmer, *Norske Vid. Akad. Skr. I. Mat. Nat. Kl. (new ser.)* No. 8, 86 (1963).
9. "Eurypterid" ventral plates in Carboniferous scorpions have been described by R. J. Pocock [*Quart. J. Microscop. Sci.* **44**, 291 (1901)] and by L. J. Wills [*Palaeontology* **3**, part 3, 330 (1960)]. A probable aquatic habitat of the early scorpions has been advocated by Kjellesvig-Waering (*1*) and Størmer (*8*).
10. B. R. Vogel and C. J. Durdon, *J. Paleontol.* **40**, 655 (1966).
11. Apterygote insects of the Order Collembola are known from the Rhynie Chert (Lower-Middle Devonian), the first pterygote insects probably from the Upper Devonian. [*The Fossil Record, a Symposium with Documentation* (Geological Society of London, London, 1967), p. 515.]
12. *Ibid.*, p. 507.

14 January 1969; revised 25 April 1969

Nitrogen Fixation in Some Anoxic Lacustrine Environments

Abstract. *Low rates of acetylene reduction to ethylene in water samples from two dystrophic lakes indicate the presence of nitrogenase and* in situ *nitrogen fixation. Highest rates were found in anoxic water from the aphotic zone. Environmental conditions in these lakes suggest the agents of fixation were bacteria.*

Nitrogen fixation in the surface waters of lakes and oceans is well documented (*1–4*). Numerous studies on ^{15}N have reported rates of fixation and have associated fixation with the presence of certain blue-green algae, primarily in the order Nostocales. Possible nitrogen fixation in aphotic zones of natural waters appears to have been either neglected or considered insig-