

mind. No control samples, such as raw source material, are required. The artifacts tested varied widely in color from white to dark red to brown, and the TL results demonstrate the difficulty of making judgments based on visual appearance alone, at least for cherts from these sites. In the case of the seven Cibola artifacts, judgment based on visual appearance proved to be correct on six samples but incorrect on one. The Koster cherts were carefully selected to contain what were thought to be, based on appearance, both heated and unheated artifacts. Although the TL test showed cherts of both types, the results did not correspond to the visual assessment.

The reliability of the TL determination of heat treatment is dependent on the age of the archeologic site; the older the site, the nearer the reaccumulated dose of a heated chert to the saturation dose of an unheated chert. For example, the difference between the heated and unheated cherts is less distinct for the Koster site (Fig. 2B, 5000 to 8000 years old) than for the Cibola site (Fig. 2A, ~ 700 years old). For sites  $\approx$  10,000 years old, the archeologic dose is at least an order of magnitude less than the saturation dose and the detection of prehistoric heat treatment can be reliably based simply on a determination of the equivalent dose. For older sites, however, more detailed measurements must be made. The saturation level must be determined, the dose rate calculated from the radioactivity of the sample and its environ-

ment, and nonthermal ("anomalous") fading (12) must be measured.

Although we have used this technique exclusively on chert, other lithic materials such as obsidian and fireplace rocks often give suitable TL and could be tested by the same technique.

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3 March 1977; revised 23 May 1977

## Arthropod Invasion of Land During Late Silurian and Devonian Times

**Abstract.** *Fossil floras and faunas of a Lower Devonian black shale from Alken, Germany, include aquatic, amphibious, and terrestrial forms. The presence of these forms suggests conditions in favor of an invasion of the land. Various arthropod adaptations to terrestrial life are present, including the development of a preoral cavity.*

One of the most important events in the history of the earth was the invasion of the land by higher plants and animals. It probably took place some 400 million years ago at the transition from late Silurian to early Devonian time. Fossil terrestrial plants, mainly psilophytes, are well known from these times, but a more detailed knowledge of the morphology of the plant and animal groups, as well as their ecology, is known only in two cases.

The well-known Rhynie Chert in Scotland, now regarded as Lower Devonian (Emsian), has yielded exceptionally

well-preserved plants and arthropods belonging to the Crustacea, Arachnida, and Collembola, all very small and with appendages intact. Evidently the environment was some kind of a swamp.

The second occurrence, near the village of Alken in the Mosel Valley, Germany, does not present the same excellent preservation of the fossils, but the spectrum of forms is much wider. The fossil flora and fauna comprise marine, brackish, and freshwater forms as well as terrestrial ones. The aquatic fauna includes mostly arthropods, pelecypods, and ostracoderm fishes. The fossiliferous

black shale is of Lower Devonian (Lower Emsian) age and was probably deposited in a lagoon along the coast of a major island (1).

The more or less aquatic plants along the shores of the lagoon formed small "mangroves." This material and the wet plant debris on the beaches evidently constituted conditions very favorable for an invasion and gradual adaptation to a life on land.

A recently completed study of the arthropods (2) demonstrates that a mixture of forms, which belonged to different ecological niches, was present. Eurypterids with swimming legs, such as *Parahughmilleria* (Fig. 1), were probably also able to travel outside the lagoon. The lagoon was occasionally visited by huge and predaceous pterygotous eurypterids, known to be to 180 cm in length. Other eurypterids without swimming legs walked on the bottom and perhaps occasionally walked on land. This might have been possible primarily because the gills (Fig. 2a) were protected by the plate-shaped abdominal appendages and could be kept moist in a way similar to that used by the living horseshoe crab, *Limulus*, when it comes on land.

The gills of eurypterids have been studied in Silurian specimens from Estonia by Wills (3) and in specimens from the Lower Devonian of Scotland by Waterston (4). The respiratory surface of the elliptical gill areas is enlarged by close-set cones with a reticulate surface (Fig. 2a). The ribs surround small areas of very thin chitin through which the respiration probably took place. In several places invaginations between the cones lead into masses of spongy chitin possibly penetrated by five canals (Fig. 2, b through d). Wills assumed that the gas exchange from water to blood took place within the spongy masses. However, the invaginations seem to be too few and limited to be able to take care of the complete aquatic respiration; moreover, water, in contrast to air, has considerable difficulty passing in and out of long narrow passages. Several terrestrial isopods have pseudotrachea in addition to gills, and both kinds of respiratory organs may occur on abdominal legs in one and the same individual. One the basis of a comparison with the isopods, it seems natural to assume that at least some eurypterids might have had both gills and pseudotrachea, the latter represented by the invaginations and spongy masses. The Estonian species *Baltoeurypterus tetragonophthalmus* ("*Eurypterus fischeri*"), showing the structures mentioned, had swimming legs and was thus largely a swimming form, but a fossil eurypterid

trail has indicated that the swimming paddles might also be used in walking. Apart from the large pterygotids with reduced legs, most eurypterids were probably able to walk and stay on land to

some extent. The possible development of pseudotrachea might be regarded as an adaptation that makes possible survival during dry periods and during the desiccation of lagoons, estuaries, and

lakes. A similar adaptation is found in the Lower Devonian crossopterygians and lungfishes.

Another more successful approach to terrestrial life is seen in the arachnids.

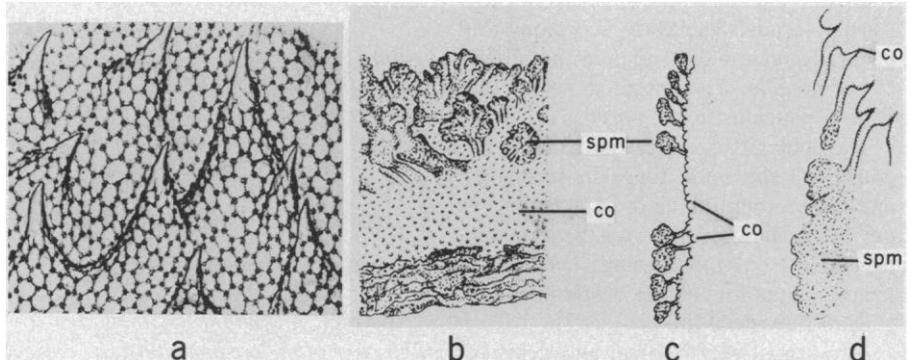
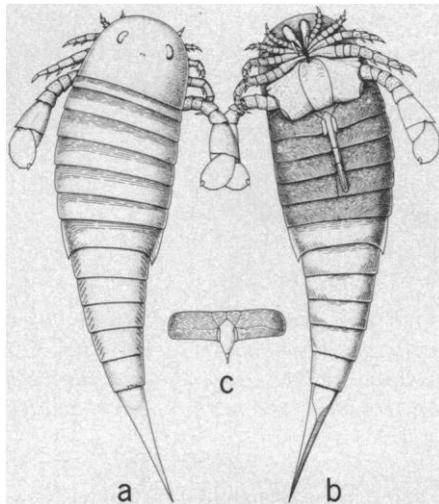


Fig. 1 (left). The eurypterid *Parahughmilleria hefteri* from the Lower Devonian of Alken, Germany. Length about 7 cm. (a and b) Dorsal and ventral views of the male (?). (c) Genital segment of the female (?). Fig. 2 (right). Respiratory structures in the eurypterid *Baltoeurypterus tetragonophthalmus* from the Silurian of Estonia. (a) Reconstruction of parts of the presumed gill surface. (b) Parts of the gill area seen from the inside. The invaginations with the spongy masses (*spm*) appear as mushrooms, and the cones (*co*) as pits. (c and d) Reconstructions of the invaginations which might have been some kind of pseudotrachea [highly magnified after Holm in Wills (3)].

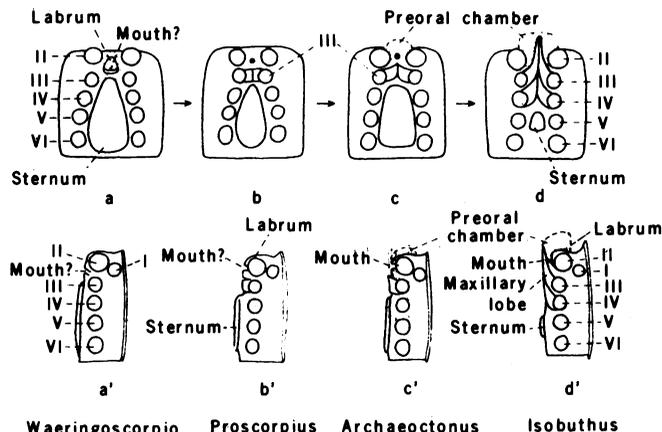
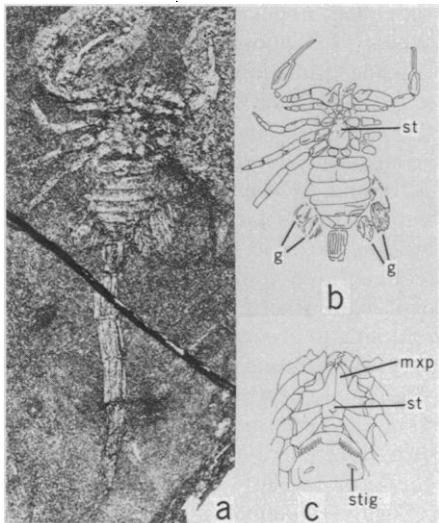


Fig. 3 (left) Fossil and Recent scorpion. (a and b) *Waeringoscorpio hefteri* without maxillary processes but with a large sternum (*st*) and possible gills (*g*); this specimen is from the Lower Devonian, Alken, Germany. (c) Recent scorpion with well-developed maxillary processes (*mxp*), small sternum (*st*), and respiratory openings or stigmata (*stig*). Fig. 4 (right). Diagram showing the development of a preoral cavity in four Paleozoic scorpions. The preoral cavity developed gradually beginning in the Silurian.

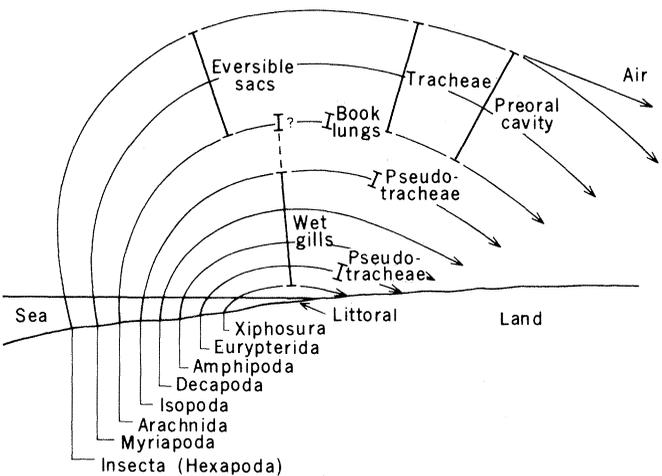
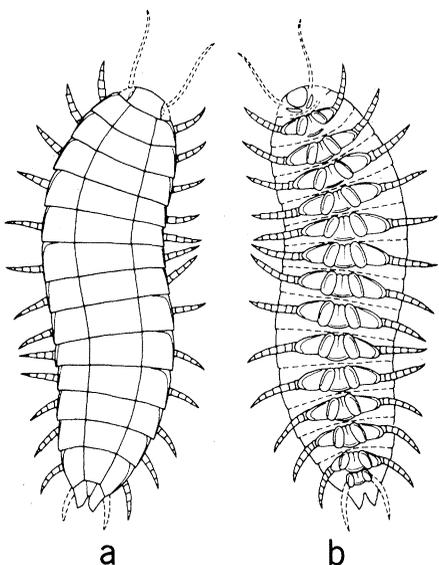


Fig. 5 (left). *Eoarthropleura devonica*, a Lower Devonian myriapod from Alken, Germany. Reconstruction of the dorsal (a) and ventral (b) surface. The number of segments is unknown. Fig. 6 (right). Diagram suggesting the more or less successful invasion of land by different arthropods. The respiratory adaptations are indicated.

The Alken fossils include a fossil scorpion, *Waeringoscorpio hefteri*, which possibly had gills (Fig. 3, a and b). In most Paleozoic scorpions the absence of internal book lungs is indicated by the lack of ventral respiratory openings or stigmata, a feature first appearing in the Carboniferous. The early scorpions are generally regarded as aquatic, breathing by book gills (?) concealed above the ventral plates as in *Limulus*.

The book gills are regarded as homologous with the book lungs in scorpions and many other arachnids. The embryology of spiders demonstrates the probable transition from gills to lungs, which is a major adaptation of the respiratory organs to terrestrial life.

In my opinion, the final and decisive adaptation to terrestrial life seems to have been the development of a preoral cavity from which fluid containing digestive enzymes could pass to the prey. This assumption is based on paleontological and embryological evidence.

The paleontological evidence for this assumption is demonstrated in scorpions. In Recent forms (Fig. 3c) a preoral cavity is formed by the basal portions of the anterior appendages and by the maxillary lobes of the coxae of the two first pairs of walking legs. As indicated in Fig. 4, the preoral cavity developed gradually from the Silurian to the Carboniferous, a time span which largely corresponds to the time of transition from water to land in these animals. A further phylogenetic support for this idea is derived from the fact that in Recent arachnids a preoral cavity is feebly developed in primitive forms (*Palpigrada*) and well developed in the advanced forms.

The embryological evidence for a secondary development of a preoral cavity is well demonstrated in the ontogeny of myriapods and insects, the arthropods best adapted to terrestrial and even aerial life. In the Chilopoda (*Myriapoda*) the primary mouth is situated behind a broad labrum. The anterior part of the sternal area and the limb buds on either side of it gradually sink into the head capsule, forming a preoral cavity with a secondary mouth in front. In Crustacea on the whole, a preoral cavity is lacking in aquatic forms but is indicated in terrestrial isopods by a strong development of the basal portions of head appendages.

The Alken fauna also contains a primitive myriapod, *Eoarthropleura* (Fig. 5), which might have had a ventral labrum instead of a secondary mouth opening in front of a preoral cavity. *Eoarthropleura* might have been only about 10 cm long but is evidently related to the Upper Carboniferous *Arthropleura*, a giant which

apparently had a length of up to 180 cm (5). Strangely enough, terrestrial arachnids from Alken also seem to be more closely related to the Upper Carboniferous species 70 million years younger (6). The main arthropod adaptations to terrestrial life are suggested in Fig. 6.

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25 March 1977

## Temperature Exposure Measured by the Use of Thermoluminescence

**Abstract.** *A method has been developed to measure temperature exposure based on the use of the temperature-dependent property of thermoluminescence fade. This property provides a relatively simple and inexpensive method for measuring both average and accumulated temperature exposure without the need for sophisticated temperature-recording equipment.*

Thermoluminescence (TL) has been used as a research tool in numerous analytical problems ranging from mineral identification to archeological dating (1). Thermoluminescent radiation dosimetry (TLD) is one application that has been widely accepted with the result that techniques have been standardized and various TLD phosphors have been developed (2). We report here a new application of TL in which the temperature-sensitive properties of TLD phosphors irradiated prior to use are utilized to measure temperature exposure. This application provides a simple and inexpensive method for measuring both average and accumulated temperature exposure over extended time periods and at remote locations, as is often re-

quired in environmental research such as oceanography and fisheries biology.

The relationship between TL and temperature exposure is apparent from a simplified explanation of TL theory. When TLD phosphors are exposed to ionizing radiation, electrons are dislodged and some become trapped within the crystalline lattice. The probability of an electron's escaping from a trap varies according to trap depth (energy gap), trap frequency factor, and temperature. Heating the material provides the energy to free these trapped electrons, which emit light (thermoluminescence) while returning to ground state. The TL signal is easily determined with a TL analyzer that rapidly heats the phosphor at a uniform rate and measures the light produced. Temperature exposures that occur prior to the TL measurement can prematurely empty the traps and cause a reduction or "fade" in the TL signal.

Fade is generally viewed as an undesirable interference for most TL applications; however, the temperature-dependent characteristics of fade are ideal for measuring temperature exposure. Since fade rate varies with temperature, the total accumulated fade (total signal loss over time) is a direct measure of the past accumulated temperature exposure. The basic procedures for using this relationship are as follows: (i) a TLD phosphor is irradiated to fill a large number of electron traps; (ii) the phosphor is then allowed to fade for a known time period at the thermal conditions of interest; (iii) upon retrieval, the remaining TL signal is measured; (iv) this value is compared with the value that would have been obtained initially after irradiation; and (v) the total signal loss is used in con-

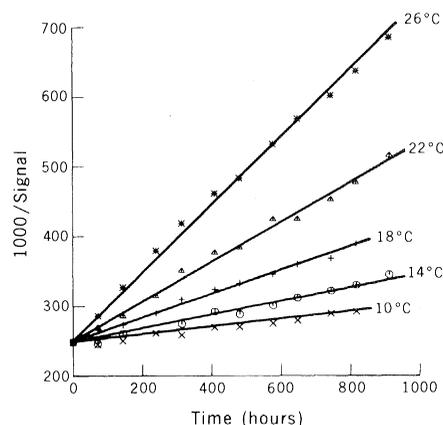


Fig. 1. Isothermal fade response observed for  $\text{CaSO}_4:\text{Mn}$  tags at the five temperatures indicated. Data points are the mean TL signal for one tag and have a 3 percent standard error at the 95 percent confidence level. Lines were fitted to the data by a combined computer analysis that specified both a hyperbolic fade response and a fixed relationship between fade rate and temperature.