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Exceptional Preservation of Eocene Vertebrates in the Lake Deposit of Grube Messel (West Germany)

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Exceptional preservation of Eocene vertebrates in the lake deposit of Grube Messel (West Germany)

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[Plate 1]

Less than 2% of Lagerstätten with fossil vertebrate remains have yielded anything more than fragments of jaw material and other bones. One such exceptional deposit is the former oil shale mine of 'Grube Messel', located about 30 km south east of Frankfurt am Main. Articulated skeletons of various fish, salamanders, frogs, turtles, lizards, snakes, crocodiles, birds and mammals, as well as several hundred insects and plant remains, have been recovered, particularly during the last decade.

The quality of preservation is truly exceptional. In many cases not only are the skeletons articulated, but the outlines of the entire body are preserved as black silhouettes. Sometimes even the contents of the digestive tract are available for investigation.

Apart from the fish that formerly lived in the lake, the most frequent fossils found are flying creatures such as birds, bats and insects. Clearly, the lake acted as some kind of trap for these animals.

The different modes of preservations are reviewed and the factors involved in this example of special preservation discussed.

1. Introduction

What did fossilized animals look like originally, how were they built, in what kind of biotope did they live, how did they move, on what and how did they feed? Answers to these questions are essential if one is trying to reconstruct the palaeobiology of extinct vertebrates. The possibilities of providing such answers in detail, however, are extremely slight. I have calculated that less than 2 out of 100 Lagerstätten of fossil vertebrates have yielded anything more than teeth and fragments of bones. An exceptional site is the former opencast oil shale mine of 'Grube Messel', located about 30 km southeast of Frankfurt am Main in West Germany (figure 1, plate 1).

The threat posed to this site by a projected refuse dump is one reason why an intensive excavation was begun by a variety of scientific institutes in 1975, which has led to a rich haul of finds and associated data. The broadest programme of excavation is being conducted by the Forschungsinstitut Senckenberg.

Based on the results of all of these excavations and on a drilling program carried out in the mine in 1980, a whole series of research projects has been developed with support from the Deutsche Forschungsgemeinschaft over the last few years. The spectrum of subjects range from geochemistry, geology and sedimentology to the special processing of the fauna and flora, and to the answering of questions regarding the factors controlling preservation of the fossils and the origins of such fossiliferous beds (Koenigswald & Michaelis 1984).

2. The fossil record

All classes of vertebrates have been discovered from the oil shale of the Messel Formation, which dates from the beginning of the Mid-Eocene, about 48 ± 1 million years ago. Most abundant are the former inhabitants of the lake itself, especially fish. But, at least from time to time, some turtles and crocodiles also lived in the lake. Animals that lived in the adjacent surroundings, for instance anura and snakes, are also relatively frequent. Exceptionally skeletons of mammals living in the forests of the hinterland are found, though those that were gregarious, such as early horses, are more common. Really puzzling is the fact that birds and bats, which are extremely rare in the fossil record, as a result of the fragile character of their skeletons, are among the most frequent vertebrates from the Messel Formation (figure 2). During 10 years of excavation no less than 150 more or less complete skeletons of each of these taxa have been recovered by the team from our institution alone.

3. The quality of preservation

As far as the quality of preservation is concerned, it is very fortunate that, at Messel, most of the fossil vertebrates are recovered as complete articulated skeletons, although isolated bones and scattered skeletons occur occasionally as well. However, the most remarkable fact is that in some cases the fossil vertebrates are not only preserved as skeletons but still display the outlines of their entire bodies as black shadows in the oil shale. Fish display the outline of their fins, and in anura it is possible even to distinguish the eye, the liver, and the veins on the inner side of their thighs. Birds show the detailed structures of their feathers (figure 2). Bats display their external ears and their flying membrane, and in other mammals the fur is exposed to the tips of the hairs (figure 4). Thus the palaeontologist who wants to reconstruct what these animals looked like during their life can rely upon direct evidence instead of vague assumptions and bold speculations.

Even more significant, so far as the reconstruction of ways of life and phylogenetic development is concerned, however, is the fact that in many cases at least part of the contents of the digestive system have been preserved and can be investigated. The early horses have provided us with the first, and a particularly good example, demonstrating that determinable remains of food from the intestinal tract have survived to the present day in an extraordinary state of preservation.

Description of plate 1

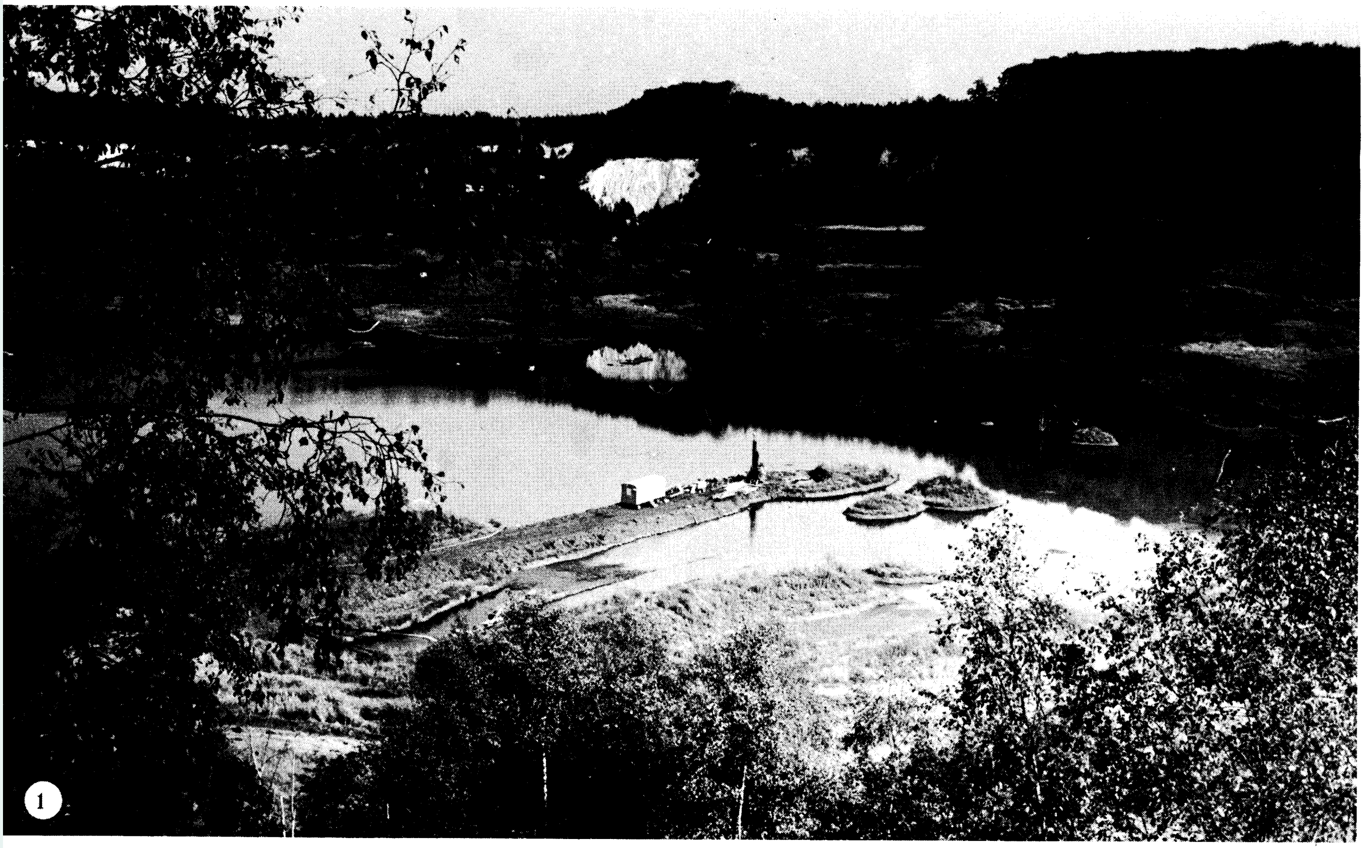
Figure 1. View eastward into the Grube Messel in 1980 showing drilling for research purposes in progress in the centre of the former open-cast mine. Photograph from Senckenberg-Museum, J. L. Franzen.

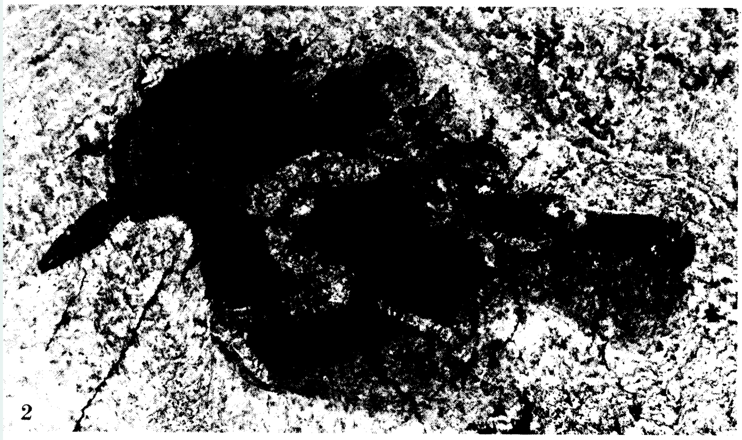
Figure 2. Eocene bird displaying the body outline as a black silhouette; natural size. Photograph from Senckenberg-Museum, U. Wegmann.

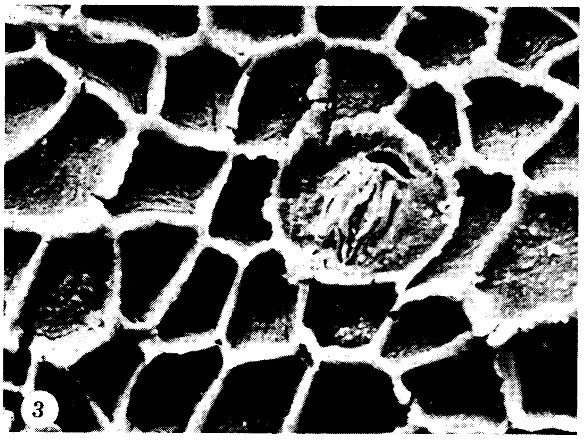
Figure 3. Fragment of a leaf out of the digestive tract of an Eocene horse (*Propalaeotherium* sp.); view of the underside displaying the cell walls and a stomatum. Scanning electron micrograph (*ca.* × 550), Senckenberg-Museum, G. Richter.

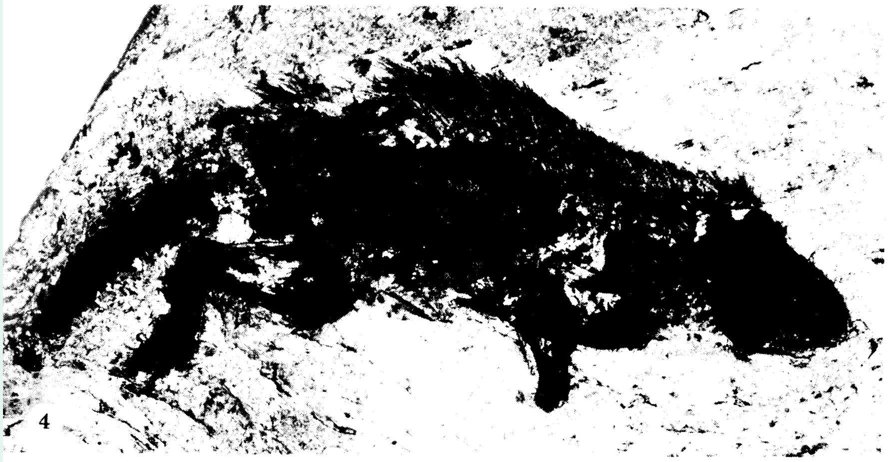
Figure 4. Eocene erinaceomorph mammal (*Pholidocercus hassiacus* Koenigswald & Storch 1983) displaying the silhouette of the original body outline extending to the tips of the hairs; about half natural size. Photograph from Senckenberg-Museum, U. Wegmann.

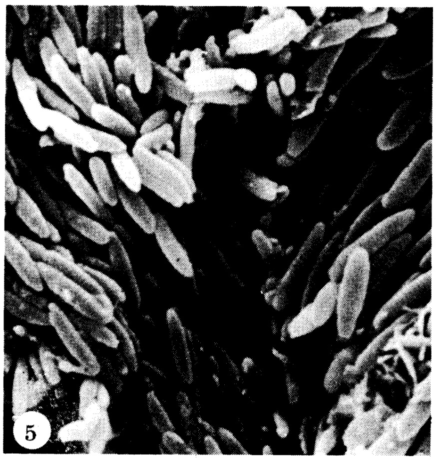
Figure 5. Bacteria preserving the body outline of an Eocene bat (*Palaeochiropteryx tupaiodon* Revilliod 1917). Scanning electron micrograph (*ca.* × 7000): Senckenberg-Museum, G. Richter.











FIGURES 1–5. For description see opposite.

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In nearly every textbook of biology or palaeontology the phylogenetic tree of the horse is presented as one of palaeontology's finest examples of evolution. A series of skeletal finds, almost without break in terms of either time or morphology, has enabled the evolution of the horse to be displayed with film-like clarity. Thus the evolution of intricately structured, high-crowned molar teeth, such as are found in the modern horse, from low-crowned molars of a simple cusp pattern had already been attributed to changes of environment and diet as long ago as the second half of the last century.

Two hypotheses have been proposed. That of Kowalevsky (1876) explained the primitive dentition of the earliest horses as that of omnivorous animals, whereas that of W. D. Matthew (1926), based upon a comparison with recent mammals having similar types of teeth, regarded the early horses of Eocene and Oligocene times as browsers.

The first horse unearthed by us in 1975 brought clarification, for a thick wad of leaves was found in its abdomen (Franzen 1976, 1977, 1984; figure 3). This discovery has since been confirmed on several occasions. A find made in 1980 by the team from the Hessisches Landesmuseum Darmstadt proved in addition that the diet of the Messel horses did not consist exclusively of leaves, but also included, at least intermittently, fruit, for in this case numerous grape pips were found in the region of its stomach (Koenigswald & Schaarschmidt 1983).

Another example of the far-reaching consequences of analysing the stomach contents is provided by the bats. Although the fossil bats from Messel belong among the earliest skeletons of the Chiroptera found so far in the world, they already broadly correspond in their physical construction to the present day representatives of that order. This is remarkable, as one would think that such extremely specialized flying mammals would represent rather a late stage in evolution. With respect to this problem, the stomach contents analyses have produced interesting evidence (Richter & Storch 1980): the very commonest species, *Palaeochiropteryx tupaiodon*, has proved to have had a highly specialized diet. It apparently fed exclusively on butterflies. Butterflies also formed a significant part of the diet of the other two species examined, but they also fed at different times on beetles. An interesting fact is that the scales of the wings of the butterflies show that they obviously came from primitive butterflies that were active in twilight or at night. If one considers that insectivorous bats catch their prey on the wing, then the results of the stomach contents analyses can only be explained if it is accepted that these Messel bats, like their modern counterparts, had already evolved an ultrasonic orientation system 50 Ma ago. This in turn leads to the assumption that it was this ability that permitted the insectivorous forebears of the bats to evolve rapidly into the niche of the nocturnally flying insect predators in which no other animal has so far been able to compete successfully with them.

Stomach contents analyses have in the meantime been conducted on a whole series of the fossilized mammals found in Messel. Taken in conjunction with the associated reconstructions of their skeletons and habits, they are furnishing us with a truly vivid picture of the fauna of that period.

Other contents of the body have also come to light. A skeleton of an early horse of the genus *Propalaeotherium*, for instance, included some unexpected bones when it was excavated by our team in 1980. My first idea was that the very fragmentary and tiny supernumerary bones were those of an embryo. Thus I tried to search for milk teeth to prove this assumption. The result was positive: a series of isolated cusps of lower deciduous molars allowed the identification of the skeleton as that of a pregnant female.

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4. The factors of preservation

Let us now ask what the reasons were for such exceptional preservation. What kind of factors were involved in the processes leading to the preservation of articulated skeletons and silhouettes of entire vertebrate bodies (figures 2, 4 and 6)?

First, the lake was only a few square kilometres in area, but more than 10 m deep. The lake was of tectonic origin as is indicated by its faulted boundaries.

Second, the climate at that time was tropical to subtropical with mean annual temperatures of more than 20 °C at least, as is demonstrated by the existence of alligators and palm trees, as well as by oxygen isotope palaeotemperatures taken from molluscs of the Tertiary North Sea basin (Buchardt 1978). According to the classification of Hutchinson & Löffler (1956: p. 85, figure 1) the Eocene lake of Messel must have been of a warm-monomictic subtropical type (Franzen *et al.* 1982: pp. 6–7).

The lake was evidently integrated into a river system as is indicated by the existence of large specimens of crocodiles, garfish, and bowfin, and by the occurrence near a reconstructed inflow of certain insect larvae typical of running water (Lutz 1985). The pattern of distribution of certain fossils within the lake points towards the existence of at least two inflows at different times and one outlet (Franzen *et al.* 1982: pp. 29–33).

Within the river system the lake acted like a settling tank (Franzen 1977*b*). The currents decreased considerably, and the carcasses drifting downstream were embedded in argillaceous sediments that were accumulating at the bottom of the lake. Most of the land-dwelling vertebrates were drowned by occasional floods, as is demonstrated by their relaxed position, typical for such a kind of death. Those cadavers that were deposited at a depth of more than about 10 m did not rise again to the surface of the lake because the pressure of the water column was too high to permit an inflation of the bodies as a result of the generation of gas (M. Wuttke, personal communication).

In this more or less stagnant lake, under tropical to subtropical climatic conditions, there was an abundant production of microorganisms, particularly algae. Chemical analyses suggest that the occurrence of dinoflagellates is indicative of occasional blooms (Habermehl & Hundrieser 1983), which in turn led to an exhaustion of oxygen near the bottom of the lake. Thus reducing conditions appeared, and the oxides produced by decomposing anaerobic bacteria (Wuttke 1983*a*) were at least partly reduced to hydrides such as hydrocarbons and other poisonous substances like hydrogen sulphide (H_2S), and ammonium (NH_4), which prevented the development of any benthic macro-organisms. Hence there was no bioturbation. The cadavers buried completely at the bottom of the lake were neither destroyed by any scavengers nor disturbed by palaeocurrents, and thus became fossilized as articulated skeletons.

Annual turnover of the lake on the other hand led to poisoning of vertebrates dwelling in the epilimnion such as fish, turtles, crocodiles, and occasionally semiaquatic piscivorous mammals.

But why do flying animals, such as birds and bats, occur so abundantly in the Messel oil shale? There must have been a special trap for them. We believe that a layer of air near the water surface was polluted by carbon dioxide (CO_2). As is known from accidents today, such a pollution cannot be detected in advance, and it leads immediately to a loss of consciousness. Hence, flying animals that get into such a situation crash and drown. The carbon dioxide could have originated from the lake itself, but as we did not detect any signs of degassing from the

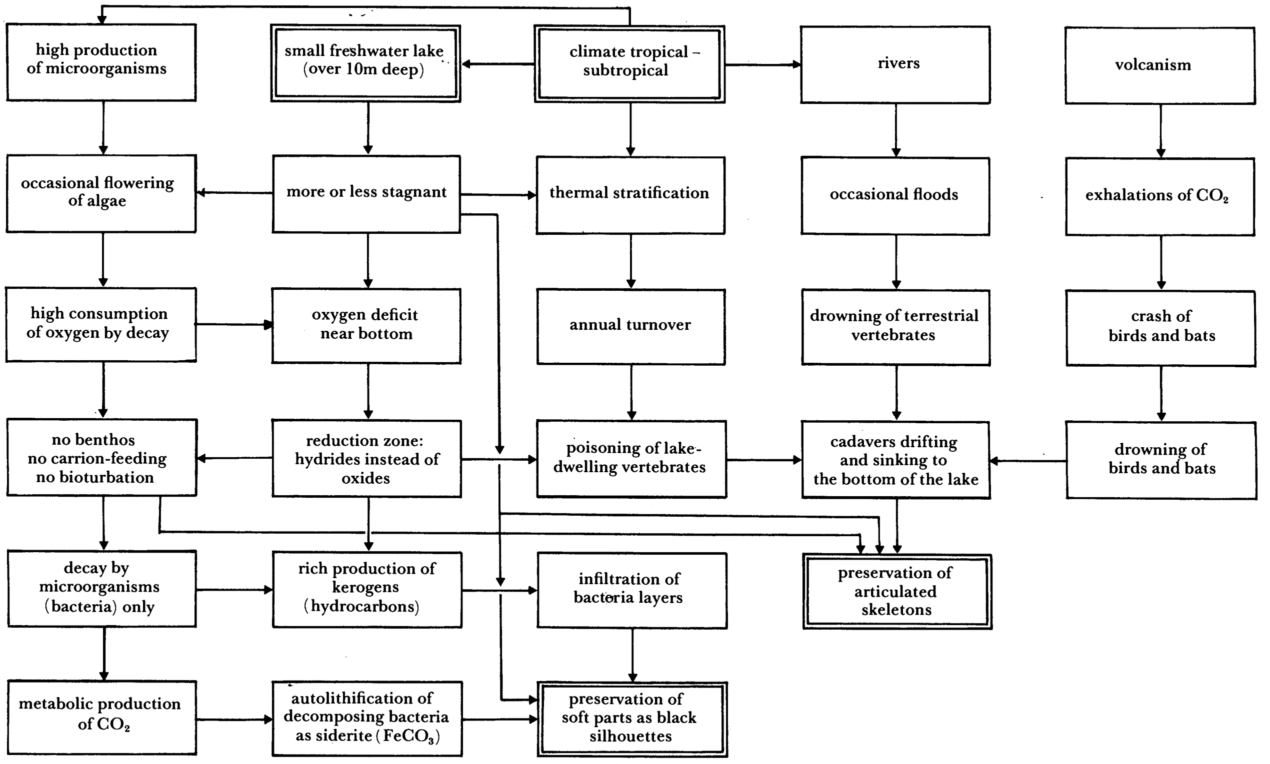

FIGURE 6. Factors involved in the exceptional preservation of articulated skeletons and so-called soft-parts of Eocene vertebrates from the Grube Messel (West Germany).

oil shale we prefer the idea of volcanic exhalations taking place at that time in the neighbourhood of the Eocene lake of Messel (Franzen *et al.* 1982: p. 8).

What were the processes that resulted in the preservation of the body outline of vertebrates as black silhouettes? Attempts by a student working on the fossil anura from Messel who was trying to discover the fine structure of the epidermis, had a surprising result (Wuttke 1983*b*). Scanning electron microscope studies revealed no histological details, but instead, minute bodies in the form of rods or grains consisting of siderite ($FeCO_3$) were observed (figure 5). This could only be explained as originating from a dense covering of bacteria, such as must have formed on the underside of the body when putrefaction had begun soon after the carcass had been deposited on the bottom of the Messel lake. Apparently the bacteria had then been petrified in the sedimentary milieu through the production of carbon dioxide (CO_2) and precipitation of iron (Fe), the latter present in the lake water as a result of weathering of igneous rocks and Permian red-beds in the surrounding region.

Only later was this thin 'lawn' of lithified bacteria changed into a black silhouette by infiltration and cementation by organic material derived from plants. In this way the soft-part contours of the Eocene vertebrates have been handed to us not directly but by a kind of a natural 'photographic' process!

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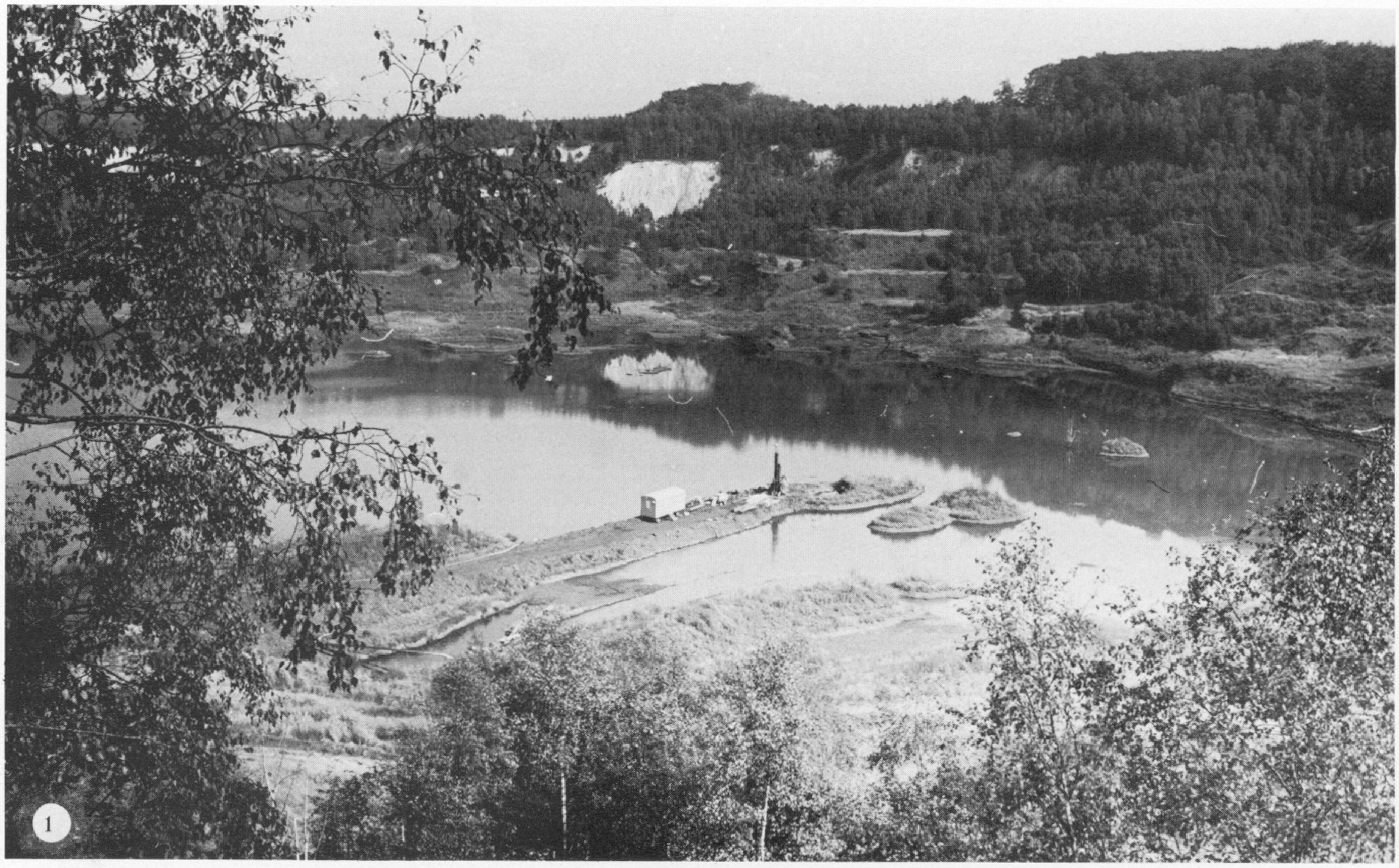

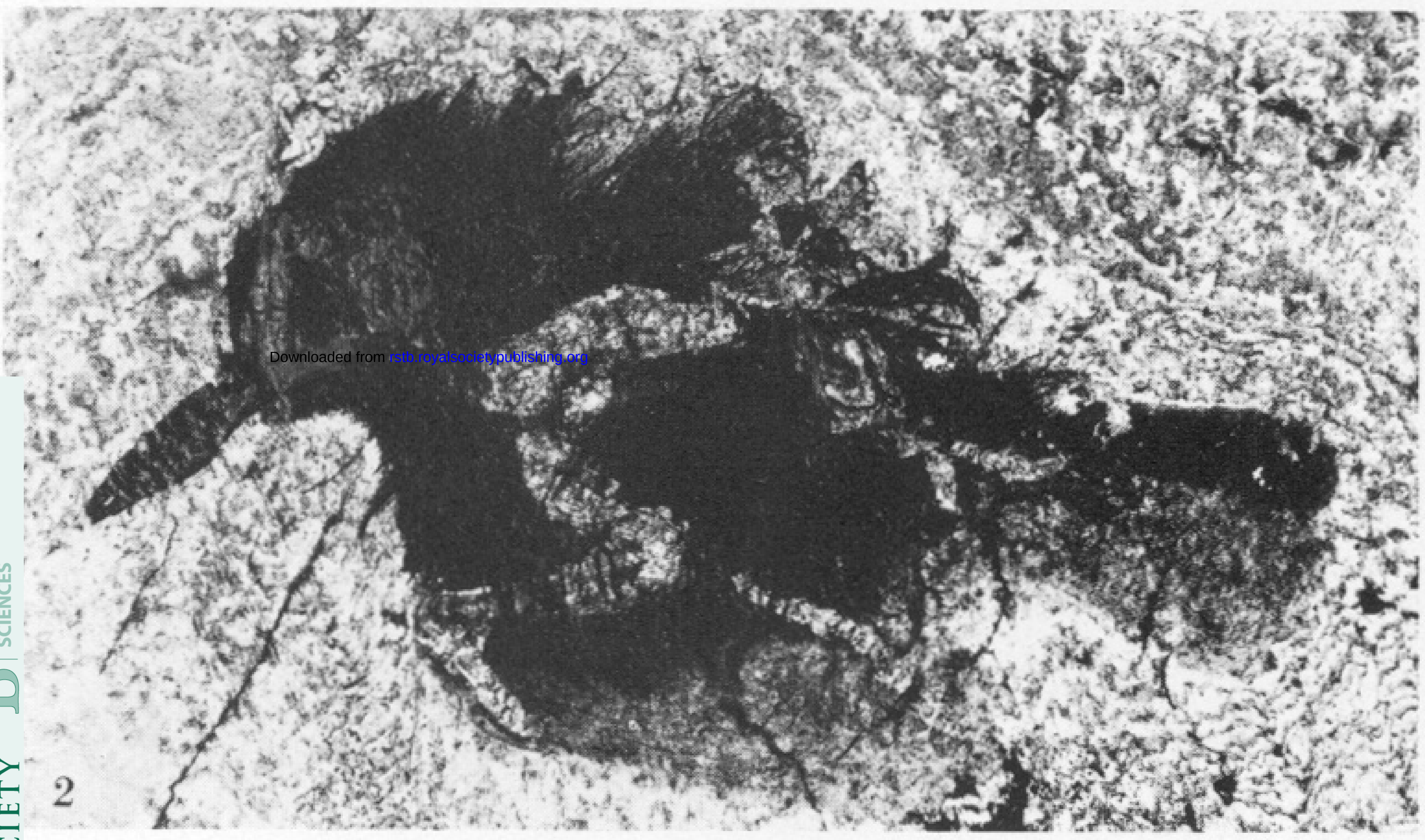

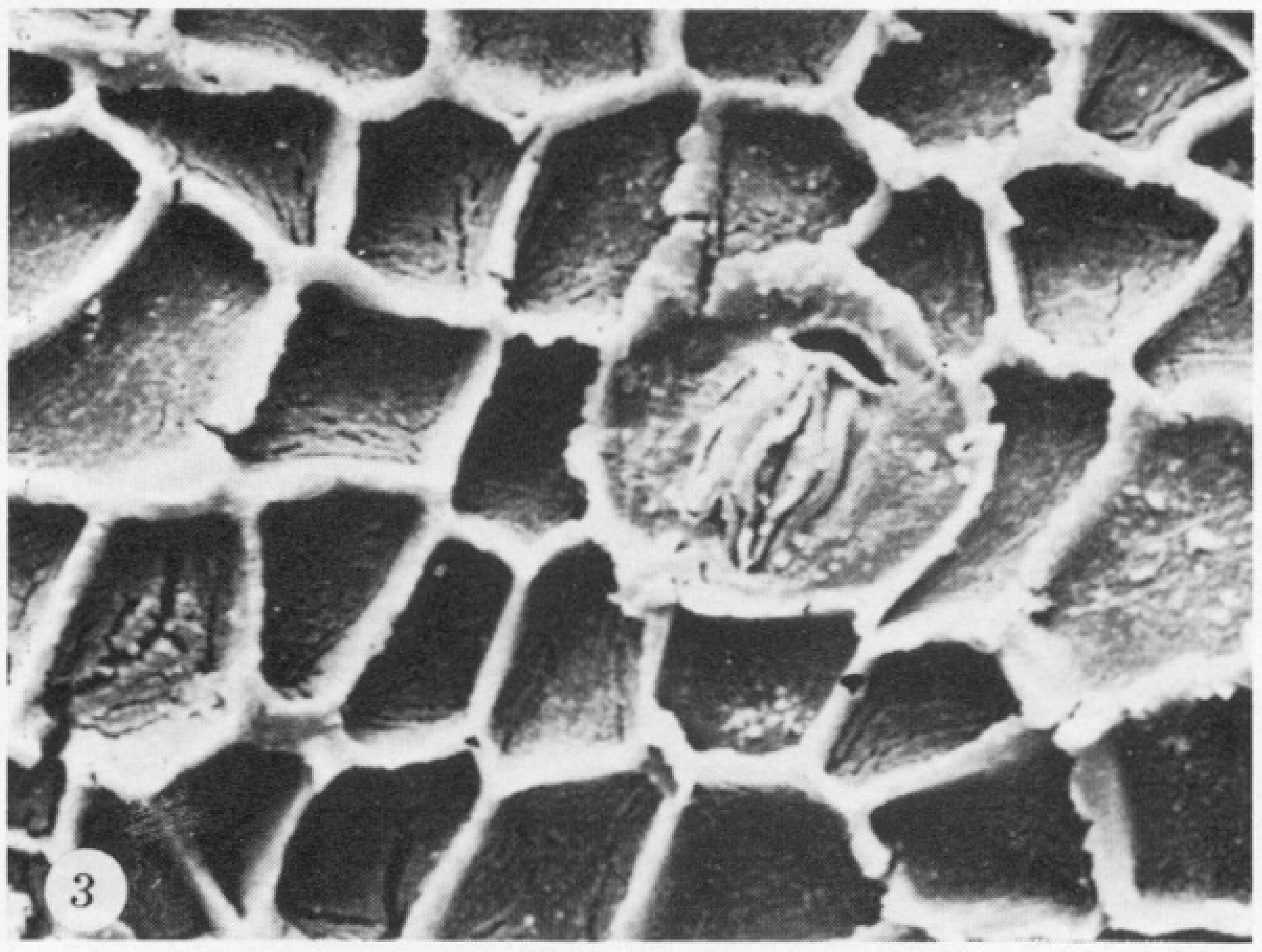

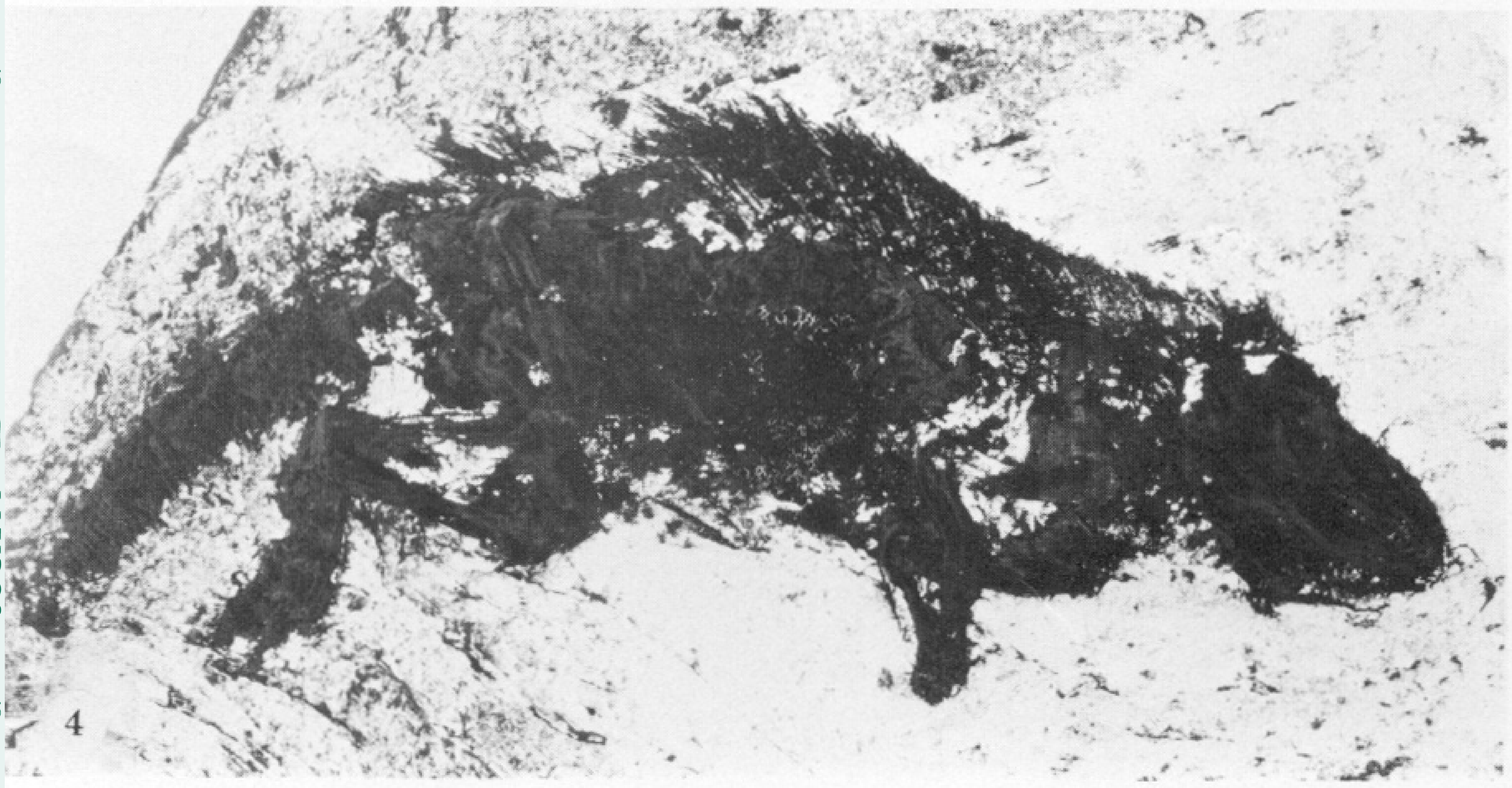

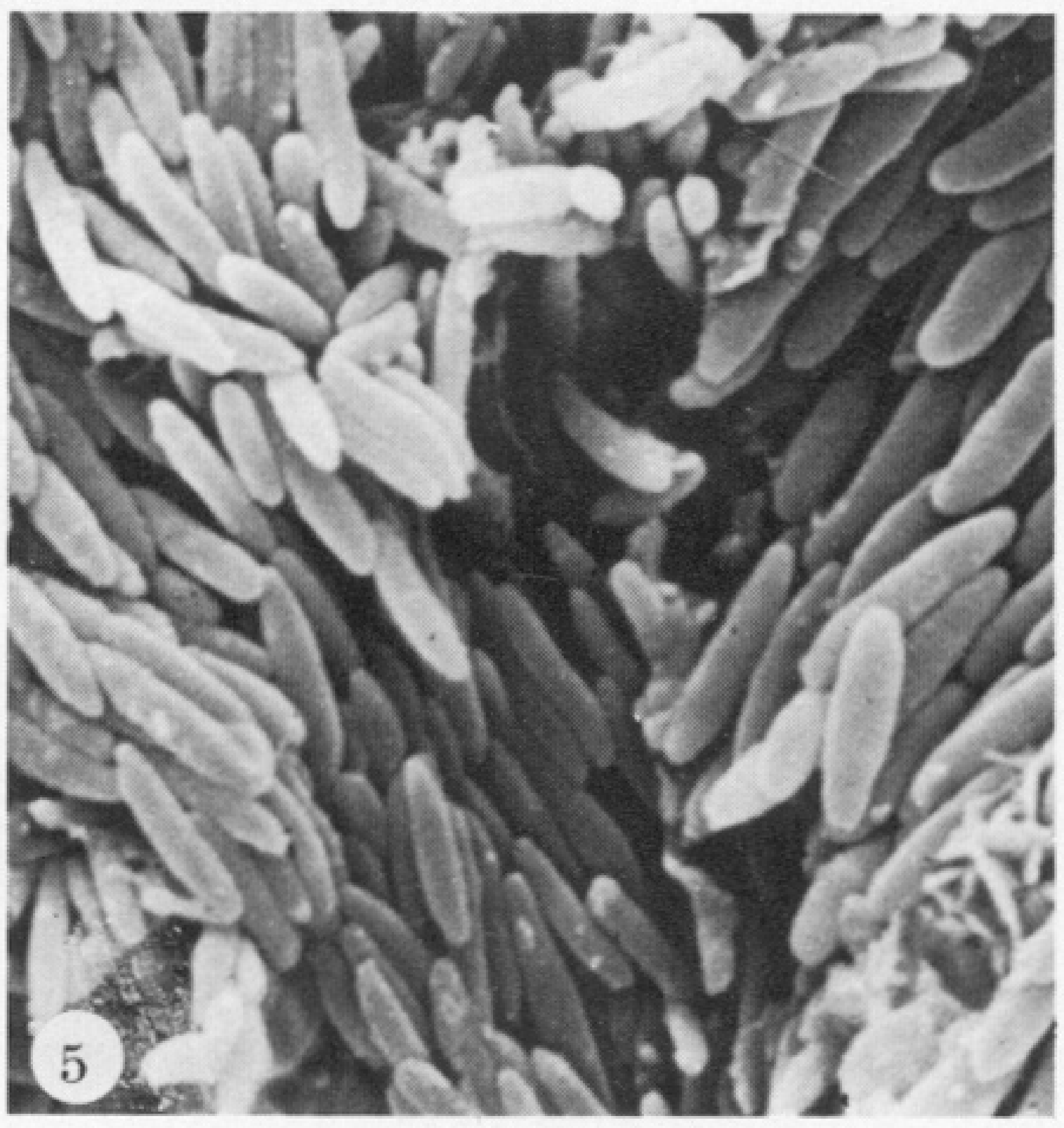

FIGURES 1–5. For description see opposite.