

THE JURASSIC DISSEMINULES WITH PAPPUS AND THEIR BEARING ON THE PROBLEM OF ANGIOSPERM ANCESTRY

V. A. KRASSILOV

Institute of Biology and Pedology, Far-Eastern Scientific Center, Vladivostok

ABSTRACT

The morphology and cuticular structure of *Problematospermum ovale* Tur.-Ket. from the Upper Jurassic of Karatau (South Kazakhstan, USSR) are described. These disseminules resemble the achenes of several Compositae genera. It is suggested that *Problematospermum* belonged to some members of Bennettitales probably ancestral to the Compositae.

INTRODUCTION

In discussing the fascinating problem of the origin of flowering plants much attention has been paid to pre-Cretaceous angiosperm-like fossils. The majority of them were proved to have nothing to do with actual angiosperms (HARRIS, 1960; HUGHES, 1961; KRÄUSEL, 1956; STOCKMANS & WILLIERE, 1962). The fossil dealt with in this paper was not involved in these discussions despite its striking resemblance to the achene of a Compositae. It was described by TURUTANOVA-KETOVA (1930) from the dolomitic shales of Karatau (South Kazakhstan) under the name *Problematospermum* and attributed to Gymnospermae *incertae sedis*. The Late Jurassic age was established on the evidence of fairly abundant invertebrate as well as vertebrate (fishes, reptiles, etc.) fossils. The fossil flora of Karatau was rich in the bennettites and conifers of *Brachyphyllum-Pagiophyllum* group and comprised no leaf remains of the angiosperm type. New specimens of *Problematospermum* were obtained by courtesy of Dr. Maya Doludenko (Geological Institute, Moscow). They provided additional information on the external morphology, and the microscopical details were revealed by the maceration and transfer preparations.

According to Doludenko, *Problematospermum* is rather common in the Karatau shales. The pappus was evidently not very firmly attached to the disseminule body and there were many bodies deprived of pappus (though readily recognized by their characteristic form and dimensions) as well as isolated pappus remains.

DESCRIPTION

***Problematospermum* Turutanova-Ketova, 1930**

***Problematospermum ovale* Turutanova-Ketova**

Pl. 1, Figs. 1-12; Pl. 2, Figs. 13-22

1930 *Problematospermum ovale* Turutanova-Ketova, p. 160, pl. 4, fig. 30, 30a.

The body is elongate-elliptical, 5-8 mm long, 1.5-1.8 mm wide, apically passing into a tube ("micropylar tube" or "style") 1-1.5 mm long (Pl. 2, Figs. 15, 17-18). The opposite

end of the body is typically obtusely pointed or rounded, but sometimes tipped with a tube similar to the apical one (Pl. 1, Fig. 2). The body possesses a few longitudinal ribs (Pl. 1, Fig. 6) and fine longitudinal striations. In a few specimens there are basal swellings occupying from one fourth to one third the length of the body (Pl. 2, Fig. 14). Small hairs arranged in longitudinal files cover the body surface (Pl. 1, Figs. 11-12; Pl. 2, Fig. 19). When the body was transferred to balsam the hairs were left in the matrix. The enlargement of apical hairs up to 0.3 mm was observed in a single specimen. Such hairs probably might augment the pappus.

The outer cuticle is extremely delicate and the epidermal cells were observed only in transparencies of the body (Pl. 2, Figs. 15-16). The cells are irregular, elongate, 130-200 μ long, 45-55 μ wide and arranged in longitudinal files. The cell walls are undulate to sinuous. No stomata were observed. The inner cuticle is more resistant and readily obtainable by nitric acid maceration. This cuticle is longitudinally ridged. The cell outlines are generally obscure but where visible straight, forming files about 25 μ wide (Pl. 1, Fig. 9). The epidermis of the apical tube is composed of rectangular cells which are much smaller than those of the rest of the body, 20-40 μ long and 20-23 μ wide. The cell walls are straight or curved. The tube is filled with dark tissue composed of small cubical cells (Pl. 2, Fig. 18). Bands of elongated cells presumably belonging to sclerenchyma have been obtained by careful maceration (Pl. 1, Fig. 10).

There are some variations in the organization of the pappus. Numerous thin bristles may arise from the apical tube (in this case the enlarged epidermal hairs may contribute to the pappus or they may fuse proximally into a single thread irregularly divided upwardly into more and more thin bristles (Pl. 1, Figs. 4-5). In one specimen (Pl. 1, Figs. 1, 3) the tube is directly extended by a straight and evidently rigid thread 20 mm long. The uppermost hairs just below the tube are enlarged up to 0.3 mm, however no bristles arise from the tube. The plumose pappus is produced 15 mm above the tube by the pinnate branching of the thread. The thread apex is free and undivided. The individual bristles are about 45 μ thick, with mottled surface.

No evidence of pollen chamber was found within the body. However, pollen grains were observed on the tube or immediately below it in three cases. The preservation of pollen grains is rather poor due to heavy mineralization. Some equatorial striations are just visible as well as a proximal circular area surrounded by a ridge. Pollen grain diameter 38-40.5 μ (Pl. 2, Figs. 20-22). There is no direct evidence of functional connection between the *Problematospermum* and pollen grains.

DISCUSSION

The external form of the body is comparable with that of Bennettitalean seed, the tube is similar to micropylar tube of the latter and the inner (nucellar?) cuticle is thicker than the outer which is also characteristic of the Bennettitales. The proximal tube-like appendage noticed in some specimens may represent a stalk of Bennettitalean "megasporephyll". Considerable diversity of Karatau Jurassic bennettites and the hairiness of their flowers also support the possibility of Bennettitalean affinities of *Problematospermum*. However the seeds with pappus have not been reported in Bennettitales. Although hairy seeds date back to the Devonian (*Archaeosperma*, *Thysanotesta*, etc.), the parachute apparatus of the pappus type is entirely alien not only to the Bennettitales but also to Gymnosperms as a whole. At the same time it is characteristic of some families of flowering plants. The *Problematospermum* body with its longitudinal ribs and upwardly enlarged hairs closely

resembles the achenes of such Compositae genera as *Taraxacum* or *Hieracium*, and the capillary pappus contributes to this resemblance. The uniovulate ovary in the Compositae is thought to be derived from multiovulate one. However, SUNDARA RAJAN (1972) has shown that at least in some members of the Compositae biovulate condition is derived. The pappus of a Compositae has been interpreted as a modified calyx. According to CRONQUIST (1955) "once the genetic tendency toward a capillary pappus is well established, the pappus may even be augmented by enlarging the uppermost hairs of the achene. . . . Thus, although in an evolutionary sense the pappus is a modified calyx, it may not always, in its more modified states, be strictly so in a morphological sense". If the achene nature of *Problematospermum* is accepted, then the basal swelling may be interpreted as an ovule not filling the ovary cavity like in the most primitive members of Compositae.

The Compositae are thought to be a highly advanced group of flowering plants, "the very extreme culmination of the angiosperm evolutionary series" (SCHAFFNER, 1932, p. 376). However, there are several independent lines of evidence indicating a great antiquity of these plants. According to CRONQUIST (1955) they form a group so distinct "as to render their affinities doubtful". However, *Palaeanthus problematicus* Newberry from the Cretaceous of New Jersey was compared by STEBBINS (1939) with *Wyethia*, and CRONQUIST (1955) confirmed its assignment to the Heliantheae. Thus, the Compositae dates back at least to the Cretaceous. BOULTER *et al.* (1972) argued against the derivation of Compositae from Rosidae. Cytochrome *c* studies suggest their divergence from ancestral stock prior to the Rosidae.

STEBBINS and MAJOR (1965) claimed that "although the Compositae are a highly specialized family, they nevertheless show signs of great age. In addition to somewhat doubtful fossil evidence, phytogeographic evidence for age exists in the form of genera with widely disjunct patterns of distribution on different continents, and of isolated genera with doubtful affinities, like *Fitchia* of the South Sea Islands. . . . In addition, VAN DER PIJL (1961) has pointed out that Compositae are basically adapted to pollination by *Coleoptera* which is the most primitive form of insect pollination. . . . This suggests that the origin of the family antedated the rise of these (*Hymenoptera*, *Lepidoptera*—V. K.) more specialized pollinators".

Thus *Problematospermum ovale* probably belonged to some peculiar Bennettitalean plant which either displayed the high grade convergence with the Compositae in respect to disseminule morphology or were ancestral to this group of flowering plants. The latter possibility seems at first improbable since the Bennettitales are not supposed to be the angiosperm ancestors "unless all modern ideas concerning angiosperm morphology are in error" (DELEVORYAS, 1968, p. 145). However, this opinion depends largely on the interpretation of interseminal scales of bennettites. These organs are viewed either as modified megasporophylls or as perianth lobes (SHARMA, 1970). The latter interpretation being correct the difference between floral structures of bennettites and angiosperms appears not so formidable. The adnation of interseminal scales may result in "cupule" (HARRIS, 1954) which is analogous to angiospermous ovary.

REFERENCES

- BOULTER, D., RAMSHOW, J. A. M., THOMPSON, E. W., RICHARDSON, M. & BROWN, R. H. (1972). A phylogeny of higher plants based on the amino acid sequences of cytochrome *c* and its biological implications. *Proc. R. Soc.* **181B** (1065): 441-455.
- CRONQUIST, A. (1955). Phylogeny and Taxonomy of the Compositae. *Am. Midl. Nat.* **53**(2): 478-511.

- DELEVORYAS T. (1968). Some aspects of cycadeoid evolution. *J. Linn. Soc. (Bot.)*. **61** (384): 137-146.
- HARRIS, T. M. (1954). Mesozoic seed cuticles. *Svenk. bot. Tidskr.* **48**(2): 281-291.
- HARRIS, T. M. (1960). The origin of Angiosperms. *Advmt. Sci.* **67**:1-7.
- HUGHES, N. F. (1961). Fossil evidence and angiosperm ancestry. *Sci. Progr. Lond.* **49**(193): 84-102.
- KRÄUSEL, R. (1956). Zur Geschichte der Angiospermen. *Bot. Mag., Tokyo.* **69**(822): 537-544.
- SCHAFFNER, J. H. (1932). Ontogenetic evolution of degree of divergence between carpel and foliage leaf. *Ohio J. Sci.* **32**: 367-378.
- SHARMA, B. D. (1970). On the structure of a *Williamsonia* cf. *W. scotica* from the Middle Jurassic rocks of the Rajmahal Hills India. *Ann. Bot.* **34**: 289-296.
- STEBBINS, G. L. (1939). Additional evidence for a holarctic dispersal of flowering plants in the Mesozoic era. *Proc. Sixth Pac. Sci. Congr.* **3**: 649-660.
- STOCKMANS F. & WILLIERS Y. (1962). Que sait-on de l'apparition des angiospermes ? *Naturalistes. belg.* **43**(6): 237-256.
- SUNDARA RAJAN, S. (1972). Embryological studies in Compositae, 3. *Proc. Indian Acad. Sci.* **85B**: (4): 167.
- TURUTANOVA-KETOVA, A. I. (1930). Jurassic flora of the Chain Kara Tau. *Trudy geol. Muz.* **6**: 131-172.

EXPLANATION OF PLATES

PLATE 1

Problematospermum ovale Tur.-Ket.

1. Disseminule with pappus. × 1.
2. Body of the same specimen, note a tube-like basal projection. × 7.
3. The same specimen, enlarged. × 3.
- 4-5. Isolated pappus. × 3 and 7.
6. Body showing longitudinal ribs. × 7.
7. Body deprived of pappus. × 7.
8. Disseminule with pappus bristles arising from the body apex. × 1.
9. Nucellar (?) cuticle. × 146.
10. Cells of Sclerenchyma. × 146.
11. Files of hairs, transfer preparation. × 146.
12. Outer cuticle with hairs. × 146.

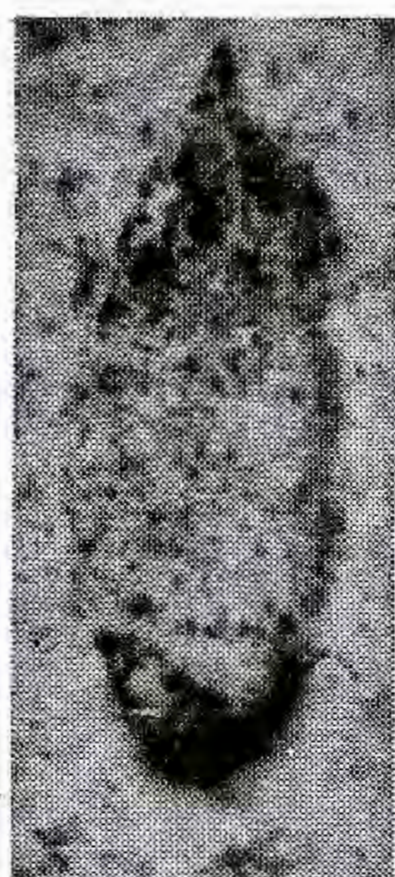
PLATE 2.

Problematospermum ovale Tur.-Ket.

13. Body deprived of pappus. × 7.
14. Body showing the proximal swelling. × 7.
15. Upper part of the body, balsam transfer. × 58.
16. Epidermal cells × 146.
17. Apical tube, balsam transfer. × 58.
18. Epidermis of apical tube. × 146.
19. Balsam transfer of the body showing the hairs arranged in files. × 10.
- 20-22. Pollen grains from the tube surface. × 562.



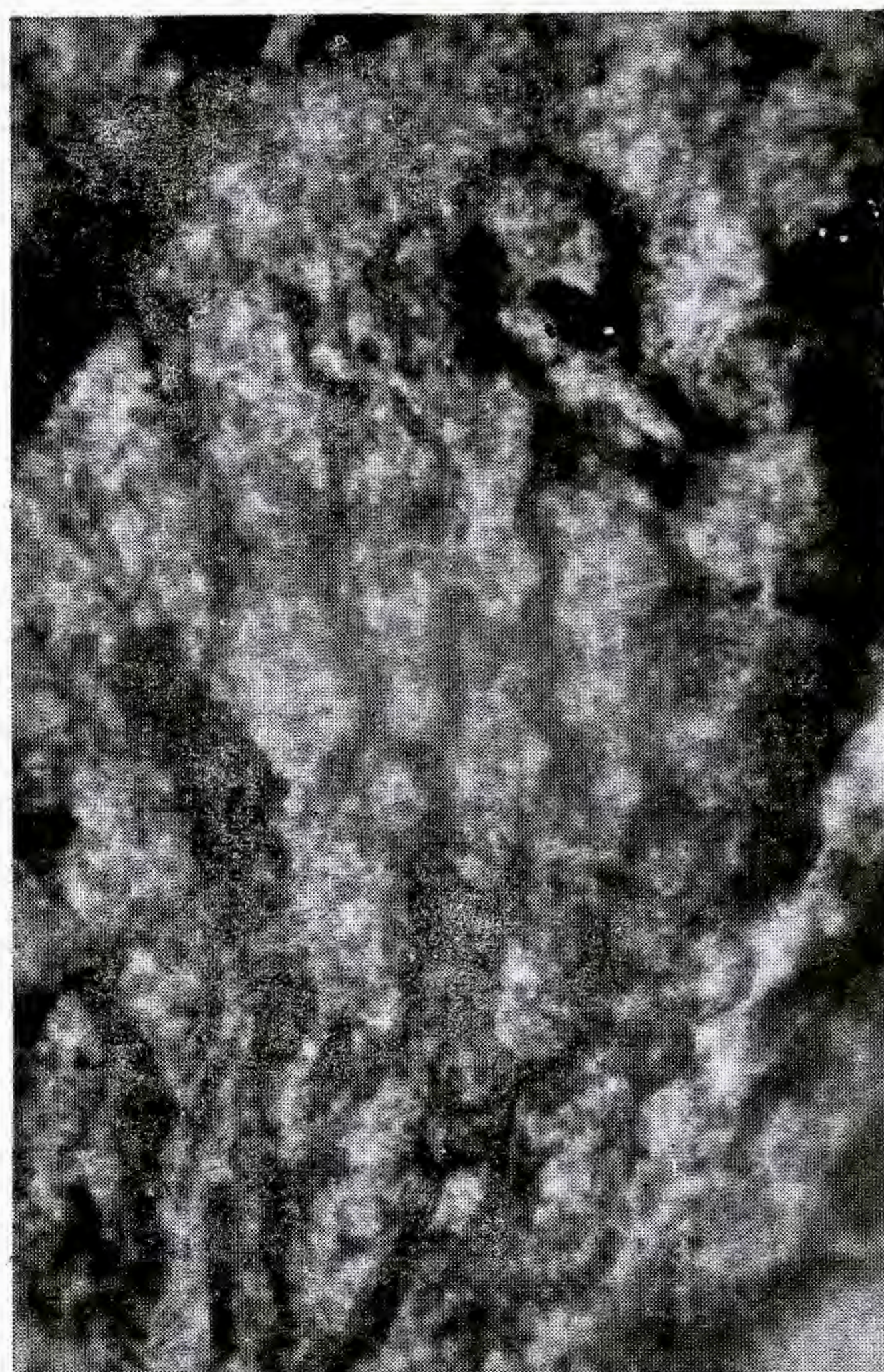
13



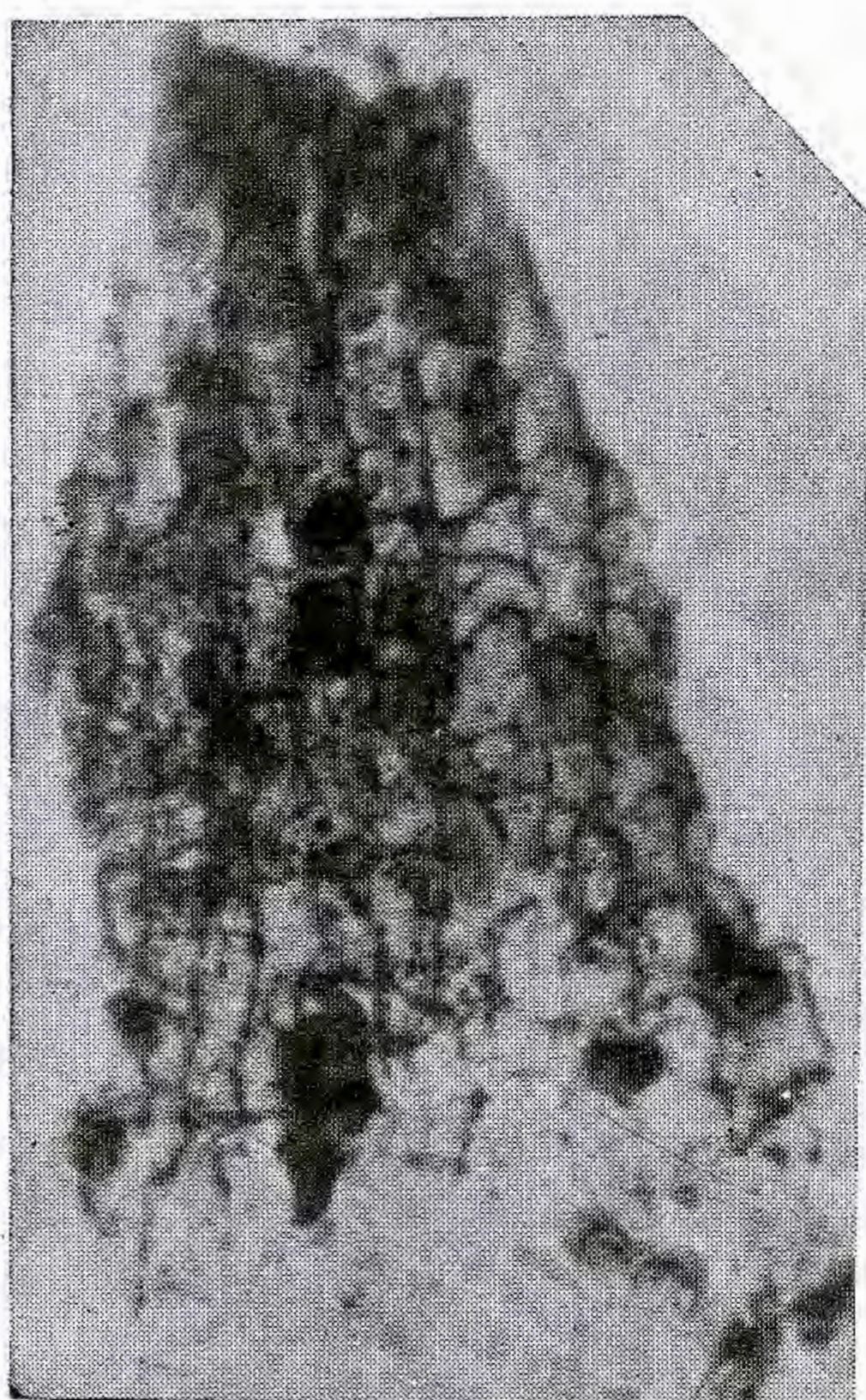
14



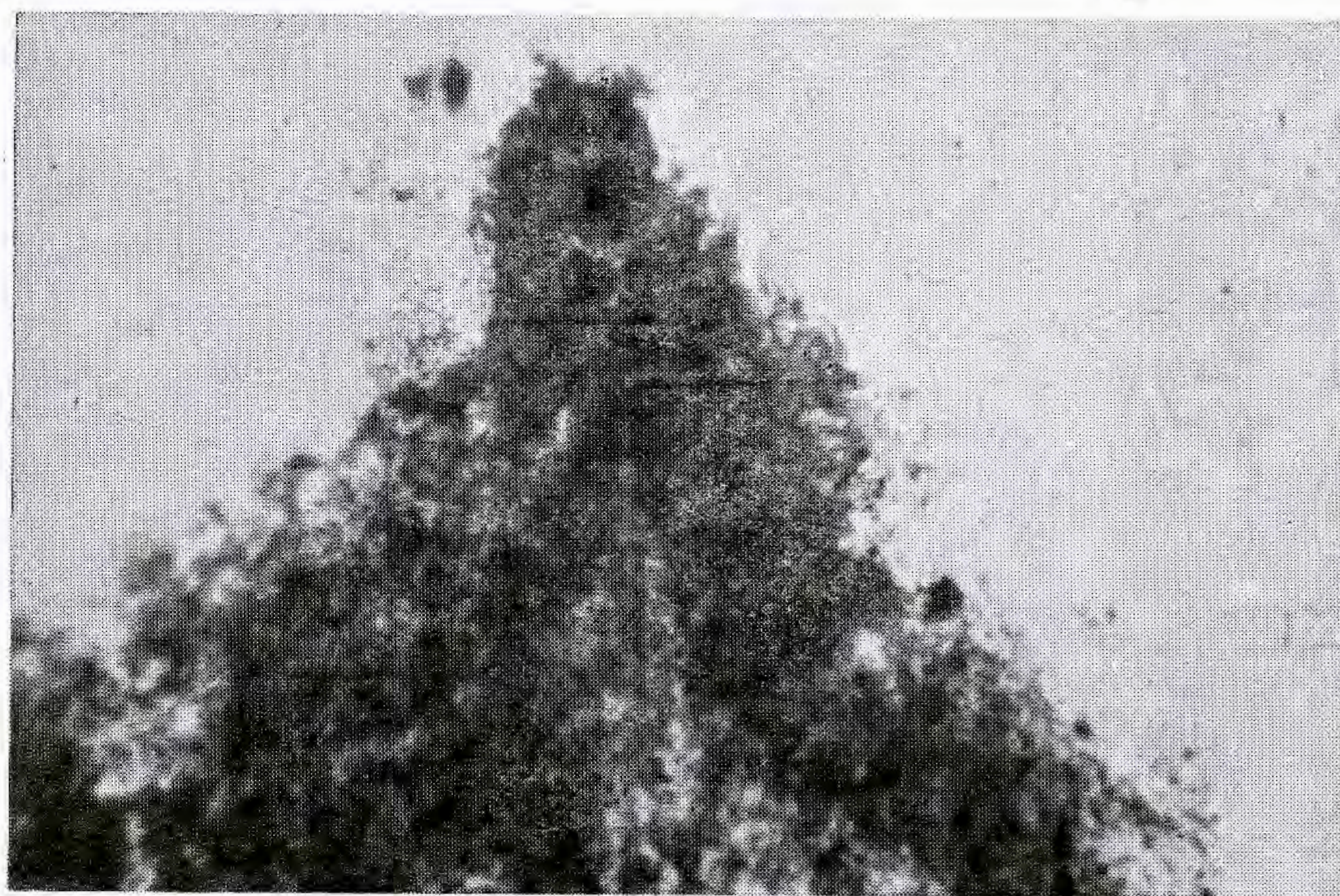
15



16



18



17



22



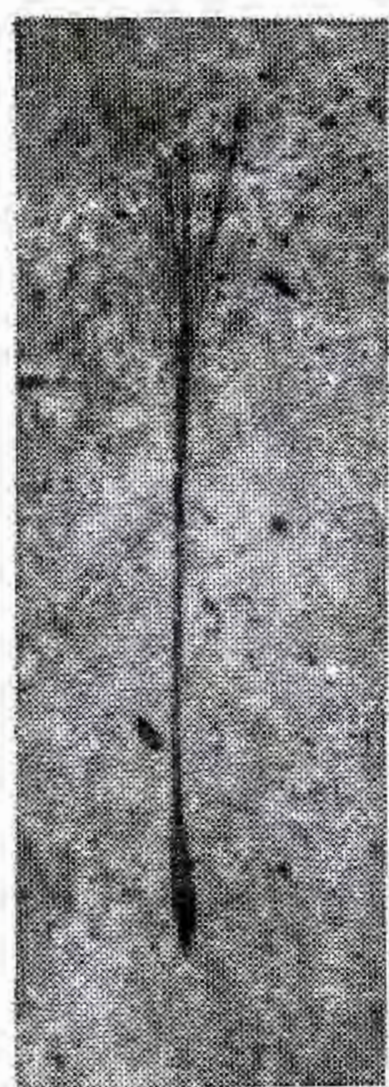
21



20



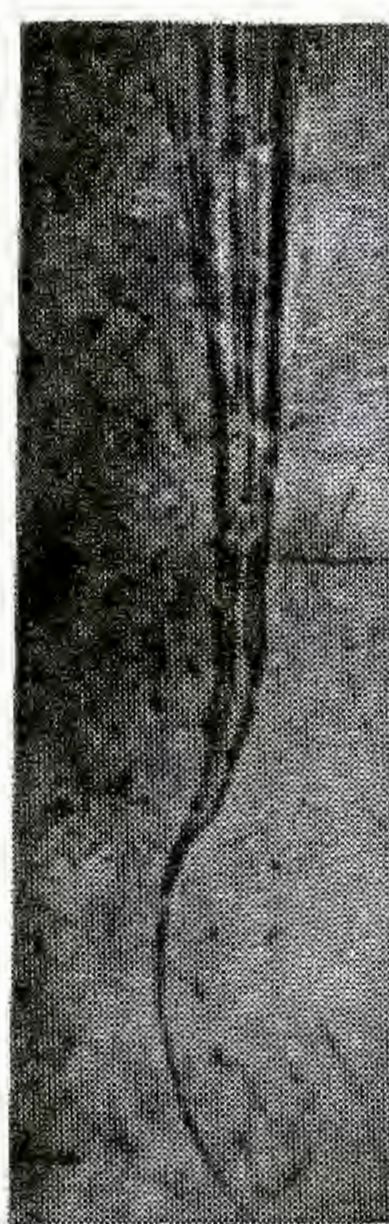
19



1



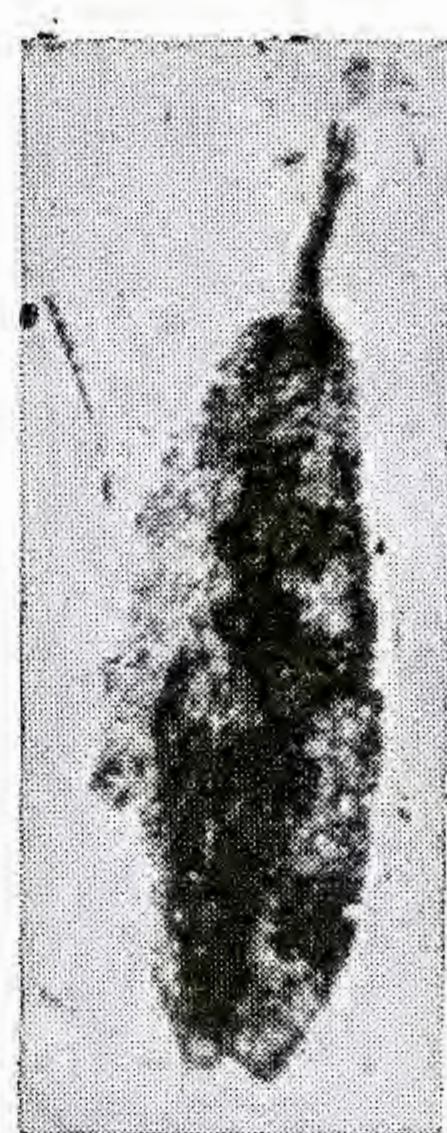
3



4



6



7



8



2



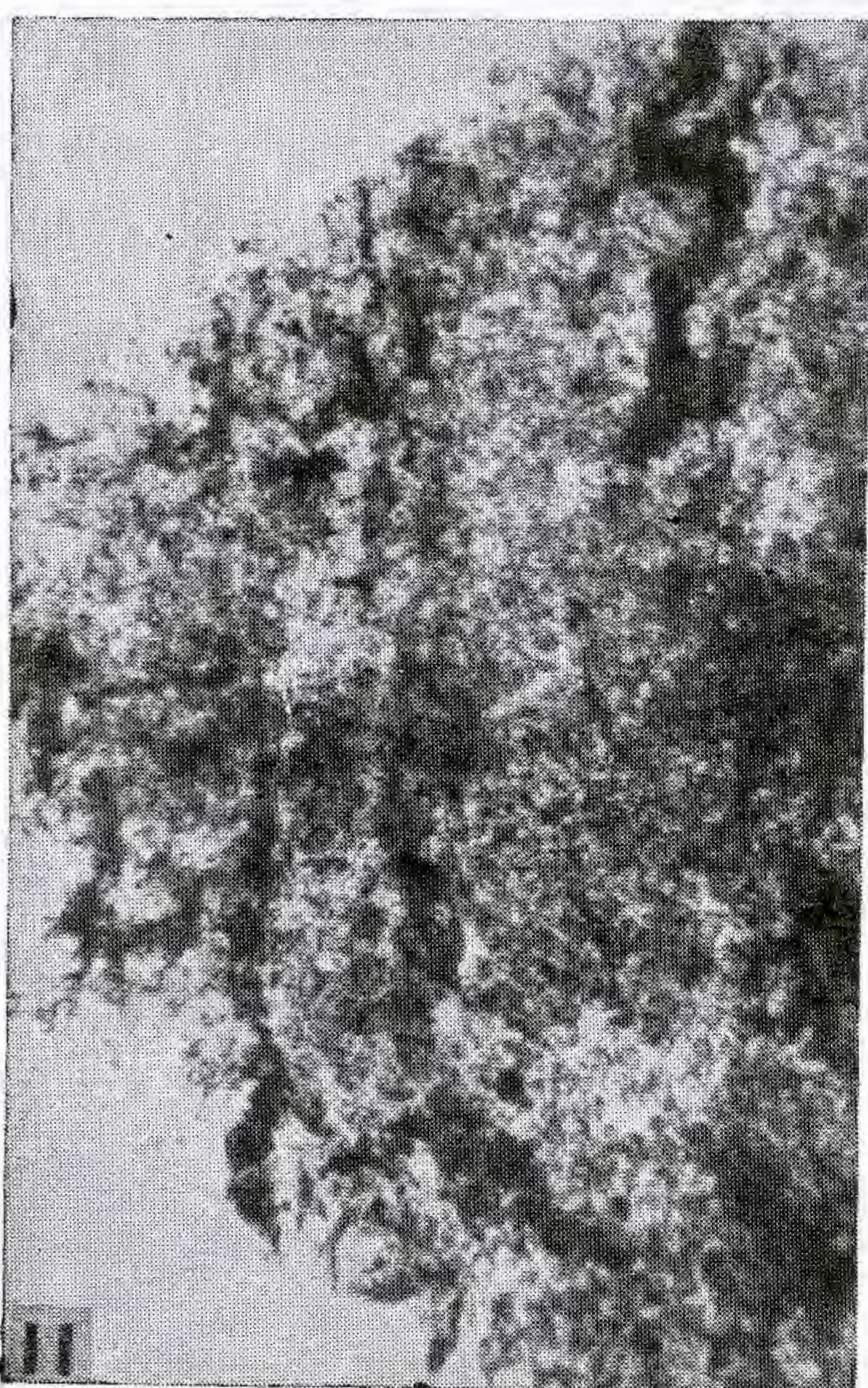
5



10



9



11



12