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### Plant Fossils (Psilophytes) from the Devonian Trout Valley Formation of Baxter State Park

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PLANT FOSSILS (PSILOPHYTES) FROM THE DEVONIAN  
TROUT VALLEY FORMATION OF BAXTER STATE PARK

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INTRODUCTION

Although small in geographical extent, the Trout Valley Formation contains one of the richest early-land-plant deposits in the world. Dorf and Rankin first described the flora and defined the formation in 1962. Since then, Andrews (Biological Sciences, Univ. Connecticut) and his students in a series of papers over the years have reported numerous taxa from these strata. A recent paper with reconstructions and illustrations of both micro- and mega-plant fossils has summarized their work up to now (Andrews et al., 1977).

The Trout Valley Formation consists of relatively undeformed continental strata lying in the trough of a synclinorium whose axis strikes east-northeast in the Traveler Mountain Quadrangle, Maine. The formation contains the youngest sedimentary rocks in the area. Their maximum exposed thickness is about 1500 feet and they outcrop over an area 1.5 by 8 miles in the valley of Trout Brook northwest of Traveler Mountain in Baxter State Park (Dorf & Rankin, 1962). These clastic rocks are a heterogeneous assemblage of shale, siltstone, sandstone and conglomerate. The formation unconformably overlies the Traveler Rhyolite which, in turn, rests conformably on the Matagamon Sandstone (Dorf & Rankin, 1962). The marine fauna of the Matagamon Sandstone is of Becraft-Oriskany age (=Sieggenian of Europe, Lower Devonian; Rankin, 1965).

Dorf and Rankin (1962) date the Trout Valley Formation as Early Devonian based on the flora. Because of lithological similarities, Rankin (1961) had previously correlated the formation with the marine beds of the Tomhegan Formation to the southwest. Boucot et al. (1964, p. 94) date the Tomhegan Formation as Schoharie (=Emsian, Lower Devonian). A palynological analysis by Andrews et al. (1972) suggests an Emsian/Eifelian age (late Lower/early Middle Devonian). An absolute date for the underlying Traveler Rhyolite is given as 360±10 m.y. (Bottino et al., 1966) which suggests a much younger age, Givetian/Frasnian (late Middle/early Upper Devonian). In their summary paper based on both plant megafossils and paleopalynology, Andrews et al. (1977) suggest that the formation is Emsian (late Lower Devonian). Finally, the recent discovery of the hitherto Middle Devonian lycopod, Leclercqia complexa, in the formation adds to the dating problem and favors a Middle Devonian age (Kasper & Forbes, 1979).



The majority of species described in the Trout Valley Formation belong to a group of extinct plants which previously had been called 'psilophytes'. In 1968 Banks re-classified the psilophytes into three distinct Subdivisions, one of which, the Trimerophytina, is abundantly represented in the Trout Valley flora. In addition to this Subdivision, lycopods--well known from the 'scale trees' of the Carboniferous--are also present in the formation, however, only as small herbaceous forms.

### PSILOPHYTE CLASSIFICATION

Early land plants have been called 'psilophytes' after the genus, Psilophyton, described by J. W. Dawson in 1859 from the Gaspé Peninsula, Quebec. Dawson's historic Psilophyton princeps was one of the first-reported early land plants from North America. The name Psilophyton, i.e., naked-plant, correctly characterizes the group as plants without leaves. For many years after, paleobotanists assigned the numerous and varied early Devonian fossil plants to this single category, the psilophytes. It was becoming readily apparent, however, that the psilophytes were a heterogeneous assemblage and an artificial taxon. In 1968 and more recently, 1975, Banks re-classified the psilophytes into three major groups based on structural and reproductive features.

#### Subdivision Rhyniophytina:

The Subdivision name comes from the genus Rhynia described from the silicified Devonian peat beds near Rhynie, Scotland. The Subdivision Rhyniophytina contains small leaf-less plants a few decimeters in height with dichotomously forking stems and single sporangia borne at the branch tips. The sporangia or spore sacs are generalized as being spindle-shaped and splitting lengthwise. A cross-sectional view of 'rhyniophyte' stem anatomy shows a small centrally-located strand of conducting tissue round in outline with the first-formed cells in the center (centrarch).

The rhyniophytes are the most primitive vascular land plants known--primitive from both a botanical and geological standpoint. Morphologically and anatomically they are the smallest and simplest of plants. Geologically they contain the oldest unquestionable vascular plant genus, Cooksonia. Cooksonia was described by the paleobotanist, Lang, in 1937 from latest Silurian (=Downtonian) strata of Wales. Banks (1974, 1975) has discussed the controversial topic of the 'oldest land plant' in two recent papers.



### Subdivision Zosterophyllophytina:

The Subdivision Zosterophyllophytina is the second group to which a portion of the psilophytes have been assigned. The name comes from the early described genus, Zosterophyllum (Penhallow, 1892) from the Lower Devonian of Scotland. The 'zosterophylls' are larger plants than the rhyniophytes and may have attained heights up to a meter. They also had dichotomously forking stems, however, 'overtopping' was common. Overtopping occurs when one limb of a dichotomy continues as the main shoot and the other limb is restricted in growth as a side branch. Even though all parts of the plant are equivalent botanically speaking, the plant appears to have a 'main stem' and 'side branches'--the pseudomonopodial habit. Overtopping and an increase in size of the conducting tissue permitted plants to grow taller. The conducting tissue in cross-sectional view is much larger, elliptical in outline and has the first-formed cells at its periphery (exarch).

The key to identification of the zosterophylls is the location of their spore sacs, sporangia. The sporangia are attached along the stem--in a lateral position--rather than at the tips or terminal position as in the rhyniophytes. The spore sacs are kidney-shaped (reniform) and open by a distal suture. Finally, the zosterophylls may either be unornamented or their stems may display a variety of surface ornamentation or enations. Enations vary from species to species and are important in identification. They range in form from multicellular spines or glands to deltoid tooth-like emergences.

### Subdivision Trimerophytina:

The third group to which a portion of the psilophytes have been assigned is the Subdivision Trimerophytina (Banks, 1968, 1975). The majority of the Trout Valley specimens belong to this category. This Subdivision contains the largest plants of the three. The 'trimerophytes' were probably over a meter tall, with a robust stem in which overtopping was so pronounced that specimens display a distinct main stem and side branches. These plants had much more conducting tissue than members of the previous two groups. This, along with thick-walled outer cortical cells, supported these taller plants. The conducting tissue was circular in cross section and the first-matured cells were in the center (centrarch). The location, shape and dehiscence of the sporangia are diagnostic. The spindle-shaped or fusiform sporangia are located at the ends of the side branches and form dense clusters rather than being solitary as in the rhyniophytes or scattered as in the zosterophylls. The spore sacs opened by means of a longitudinal slit. Some of the trimerophytes were unornamented, while others bore hair-like, gland-like or spine-like processes on their stems--important characteristics in field



identification.

#### FLORA OF THE TROUT VALLEY FORMATION

Plant fossils from the Trout Valley Formation were first described and illustrated by Dorf and Rankin in 1962. These significant but fragmentary specimens were assigned to six taxa of early land plants. This initial report was important in making geologists aware of the presence of plant fossils in northern Maine and their potential use in dating and correlating the isolated continental deposits in the region.

In 1964 and 1965 Forbes (Univ. Maine, Presque Isle), Mencher (City College, C.U.N.Y.) and Schopf (U.S.G.S., Columbus) guided Andrews to several plant localities in northern Maine and encouraged him to study the plant fossils of the area. In 1968 Andrews et al. reported a new species of Psilophyton, P. forbesii, named after its discoverer.

In 1969 Gensel et al. described a new plant, Kaulangiophyton akantha, which appears to be intermediate between the zosterophylls and the lycopods. This is an important addition to the accumulating evidence that the lycopods arose from the zosterophyll line.

Six years after the initial introduction to the area, Andrews and Kasper (1970) published a summary report on the flora. The text was accompanied with illustrations of specimens and reconstructions of plants. The age of the formation, based on plant fossils, was given as middle or upper Lower Devonian.

In 1972 a new trimerophyte, Pertica quadrifaria, was described by Kasper and Andrews based on exceptionally complete compression/impression specimens. The material permitted an accurate reconstruction of the plant providing information on its size, arrangement of side branches on the stem and the branching patterns in both fertile--sporangium bearing--and sterile branches.

In 1974 Kasper et al. described two new species of Psilophyton, P. dapsile and P. microspinosum, besides presenting additional information on the previously reported species, P. forbesii and P. princeps. This paper illustrated for the first time trimerophyte remains from the Fish River Lake Formation in the Eagle Lake/Saint Froid Lake area (Winterville and Eagle Lake Quadrangles) of northern Maine.

A detailed review of the megaplant fossils along with the first illustrated analysis of the microflora was presented by Andrews et al. in 1977. This is the best summary article, to



date, containing numerous photographs and reconstructions. Again, an age of either "...late Early Devonian or earliest Middle Devonian...." is suggested (Andrews et al., 1977, p. 283).

Finally, Kasper and Forbes (1979) presented the first detailed report of a lycopod from the formation. Leclercqia complexa, although preserved in a fragmentary condition, is readily identified because of the unique morphology of its leaves. Up until now this lycopod has been known only from the Middle Devonian, so it adds to the controversy regarding the age of the Trout Valley Formation.

A revised list of plant mega- and microfossils is presented below. Each taxon is followed by one or two selected references recording its presence in the Trout Valley Formation and, if illustrated, by the plate and figure numbers. For comments on Dorf and Rankin's (1962) original determinations see Andrews et al. (1977, p. 272).

#### Megafossils:

##### Subdivision Rhyniophytina

Taeniocrada sp. -- Dorf & Rankin, 1962, Pl. 140, Fig. 9; Andrews et al., 1977, Pl. VI, Fig. 4.

##### Subdivision Zosterophyllophytina

Sawdonia ornata -- Dorf & Rankin, 1962, Pl. 140, Fig. 1-4.

Kaulangiophyton akantha -- Gensel et al., 1969.

##### Subdivision Trimerophytina

Psilophyton forbesii -- Andrews et al., 1968; Kasper et al., 1974, Fig. 21-26.

P. dapsile -- Kasper et al., 1974, Fig. 5-9.

P. microspinosum -- Kasper et al., 1974, Fig. 13-19.

P. princeps -- Kasper et al., 1974, Fig. 28-33.

P. sp. -- Andrews et al., 1977, Pl. II.

Pertica quadrifaria -- Kasper & Andrews, 1972.

##### Subdivision Lycopytina

Drepanophycus sp. -- Andrews & Kasper, 1970, Fig. 2B; Andrews et al., 1977, Pl. VI, Fig. 3.

Leclercqia complexa -- Kasper & Forbes, 1979, Pl. Fig. 1-12.



## Incertae Sedis

- Prototaxites sp. -- Andrews & Kasper, 1970, p. 12.  
Sciadophyton sp. -- Kasper et al., 1974, p. 358.  
Thursophyton sp. -- Andrews et al., 1977, Pl. VI,  
 Fig. 1-2.

## Microfossils:

## Spores (Andrews et al., 1977)

- Deltoidospora sp., cf. D. priddyi -- Pl. VII, Fig. 1.  
Apiculiretusispora sp. -- Pl. VIII, Fig. 1-2.  
Emphanisporites rotatus -- Pl. VII, Fig. 5; Pl. VIII,  
 Fig. 5.  
E. annulatus -- Pl. VII, Fig. 6-7.  
 cf. Clivosisporites verrucata -- Pl. VII, Fig. 3.  
Tholisporites sp., cf. T. chulus -- Pl. VII, Fig. 2.  
Grandispora sp., cf. G. douglastownense -- Pl. VIII,  
 Fig. 3-4.  
Grandispora sp. -- Pl. VII, Fig. 4.

## Chitinozoa (Andrews et al., 1977)

- Sphaerochitina sp. -- Pl. VIII, Fig. 6.

## LOCALITY 1

Psilophyton dapsile  
 ?Psilophyton sp.  
Kaulangiophyton akantha  
Taeniocrada sp.  
Thursophyton sp.  
Sciadophyton sp.

This locality was first reported by Dorf and Rankin in 1962 and has turned out to be the most productive fossil site in the Trout Valley Formation. The best-preserved plant here is the trimerophyte, Psilophyton dapsile (Kasper et al., 1974). P. dapsile was small, a few decimeters tall, with unornamented dichotomous or, occasionally, pseudomonopodial (overtopped) axes. The ultimate branchlets bore dense clusters of small sporangia. Specimens can be identified by their 2 mm wide axes, dichotomous branching and numerous elliptical paired sporangia about 2 mm long.

Also abundant at this site are specimens of a much larger plant tentatively assigned to the trimerophytes as ?Psilophyton



sp. (Andrews et al., 1977, Pl. II). Overtopping (pseudomonopodial habit) is quite evident in this plant with its distinct main axis and dichotomous laterals. The stems are 3 mm wide and are readily distinguished by the presence of longitudinal grooves and ridges probably resulting from supporting tissues revealed by compression. Specimens appear similar to those illustrated by Dorf and Rankin (1962, Fig. 6, 8) as Hostimella sp. (now: Hostinella) and Aphylopteris sp. Hostinella and Aphylopteris are both form genera--genera which are not readily assignable to any higher category because of the limited information provided by the specimens. The plant in question is referred to Psilophyton because of its overall habit. However, since sporangia have not been found as yet, a definite assignment to this genus cannot be made.

Kaulangiophyton akantha (Gensel et al., 1968) as reconstructed was a small plant with horizontal and erect axes up to 9 mm wide. Large (8 mm in diameter) ovoid sporangia on short stalks were borne attached along the erect axes. Small (2 mm long) spines were scattered along both prostrate and upright portions. K. akantha is important because of its intermediate position between the zosterophylls and the lycopods. It is tentatively classified here under the Zosterophyllophytina.

Taeniocrada (Andrews et al., 1977, Fig. 4) is a common Devonian plant genus described from around the world, however little is known about the plant itself. It is easily recognized by its broad (1½-2 cm) ribbon-like axes bearing a central strand 2 mm wide and dichotomizing infrequently. It is abundant at this locality.

Thursophyton (Andrews et al., 1977, Pl. VI, Fig. 1, 2) is another genus that is not known well, botanically speaking. In fact some authors use it as a form genus for fragmentary remains of axes densely covered with small, delicate, spine-like or hair-like enations. These 'leafy' axes branch pseudomonopodially or dichotomously, are about 5-6 mm wide and are clothed with emergences about 2 mm long. They are easily recognized but specimens are scarce. Sciadophyton has been found at this locality only once in the many years of collecting, so it too is rare.

## LOCALITY 2

Pertica quadrifaria  
Leclercqia complexa

This second locality was discovered by Forbes and I in July, 1971 (Kasper & Andrews, 1972); in later publications it is referred to as Locality # 7 (Andrews et al., 1977). Sev-



eral different plants are present at this site, two of which have been published: the trimerophyte, Pertica quadrifaria, and the lycopod, Leclercqia complexa.

As reconstructed, P. quadrifaria was a plant a meter or more tall with marked overtopping giving the appearance of a distinct main stem and side branches (Kasper & Andrews, 1972). The branches were arranged in a spiral and in four ranks or rows 90° apart (quadriseriate). The laterals were either fertile, i.e., sporangium-bearing, or sterile. Both types of branches were dichotomous and three dimensional. The sporangia are elliptical, 2-3 mm long and were aggregated into spherical masses. The specimens are easily identified by the large main stems (1½-2 cm wide) with dichotomously forking side branches to which are often attached the sporangial clusters.

At this locality but preserved in a very fragmentary manner is the lycopod, Leclercqia complexa (Kasper & Forbes, 1979). Identification of Devonian lycopods rests in large part on their leaf morphology. L. complexa is distinguished from other lycopods by its five-tipped leaves. The distal part of the blade is divided into a long tapering median segment with two shorter pointed segments on either side. Maceration of rock samples in HF acid frees large quantities of nearly complete leaves from the matrix. L. complexa can be recognized at the site by examining rock specimens with a hand lens. The highly coalified leaves are very reflective and readily show the five distal segments. L. complexa was first described from the late Middle Devonian Panther Mountain Formation of New York State (Banks et al., 1972). The implications of this as regards the age of the Trout Valley Formation are discussed in Kasper and Forbes (1979).

#### CONCLUSION

Although there is still much information to be obtained from the plant fossils of the formation, several important benefits have already accrued from studies to date. Botanically speaking, with the description of new genera and species the flora has provided a better understanding of the diversity of forms present during early Devonian times. Secondly, the remarkable preservation of some specimens--having large portions of the stem with fertile and sterile branch systems intact--has given us an opportunity to accurately reconstruct the plants in a true-to-life manner. Finally, the presence of several species of the genus, Psilophyton, displaying a wide variety of morphological features, has allowed us to speculate on possible evolutionary trends within the group (Kasper et al., 1974). It is a rather uncommon circumstance in early Devonian paleobotany to have several species of a single genus preserved within the limits of a geographically restricted formation.



Geologically speaking, accurate dating of the formation will probably rest on the plant megafossils. The spores, unfortunately, are poorly preserved "... showing a high degree of coalification ... as might have been expected from the high degree of diagenesis evident from the lithology ...." (Andrews et al., 1977, p. 275). Other paleontological data is scarce or yet to be discovered. Secondly, the morphological completeness of the plants of the Trout Valley flora permit identification and comparisons with isolated and fragmentary remains in other deposits in the region. At present, Forbes and I are working on two very small, geographically isolated and fragmentary floras in Nova Scotia. We are able to make identifications based on comparisons with the wider variety and more completely preserved plants of the Trout Valley Formation. Finally, it is hoped that after a thorough description, the flora of the Trout Valley Formation may serve as the basis along with other floras for a mega-plant biostratigraphic scheme for the region. Such a scheme would satisfy the initial request of the geologists working in the area who introduced us to the plant fossils with the hope that we could date the rocks and aid in correlating the numerous isolated intermontane continental deposits in the northern Appalachians. This is our ultimate goal and, at the same time, this demonstrates the important role to be played by the Trout Valley flora.

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### ITINERARY

Assembly point is Shin Pond Lodge, Shin Pond, on State Route 159 about 10 miles northwest of Patten, Maine. Assembly time is 8:30 A.M. Topographic Maps: Traveler Mountain and Shin Pond Quadrangles.

#### Mileage

- 0.0 At Shin Pond Lodge take Grand Lake Road north out of Shin Pond (Shin Pond Quadrangle).
- 5.9 Cross bridge over the Seboeis River.
- 10.4 Note Forest Service Camp and side road (right) to Hay Lake.
- 14.7 Cross bridge over East Branch of Penobscot River (Traveler Mountain Quadrangle).
- 15.7 Baxter State Park entrance; Horse Mountain on left.
- 19.0 Pass through Trout Brook Farm area.
- 20.0 Road turns sharply left (south); enter Trout Valley Formation shortly.
- 22.9 Cross over Dry Brook.
- 23.4 LOCALITY 1: The Crossing--a picnic area on the right and before the bridge over Trout Brook; park cars here and take path along the southeast bank of Trout Brook for about 200 yards upstream to outcrop; refer to text for information on plant fossils.

AT NOON RETURN TO CARS and take South Branch Ponds road to South Branch Ponds Campsite (2.2 miles south of The Crossing) to eat lunch; AT 1:00 P.M. RETURN TO THE CROSSING and continue itinerary; cross bridge and continue on Grand Lake Road.



- 24.8 Cross 'first' Town Line between T6N, R9W and T5N, R9W.
- 25.7 Cross 'second' Town Line between T5N, R9W and T5N, R10W.
- 26.4 LOCALITY 2: Park along road, walk to Trout Brook about 75 yards south of road; large blocks of indurated bluish shale with maroon-colored impression/compression plant fossils are present in the stream bed; the origin of this material is the south bank of Trout Brook about 40 yards upstream.

AT 4:00 P.M. RETURN TO CARS and drive back to Shin Pond Lodge.

END OF TRIP.



## FIGURES

Fig. 1. Psilophyton microspinosum. The pseudomonopodial habit, i.e., main stem and side branches, of this trimerophyte is evident. The side branches are either fertile (sporangium-bearing) or sterile. The sporangia are erect and borne in clusters. Note the small spines (=microspinosum). The scale bar is 1 cm.

Fig. 2. Psilophyton dapsile. This small trimerophyte is unornamented and branches dichotomously. The numerous sporangia are small, pendant, and in dense clusters. Plants were about 30 cm tall; scale bar is 1 cm.

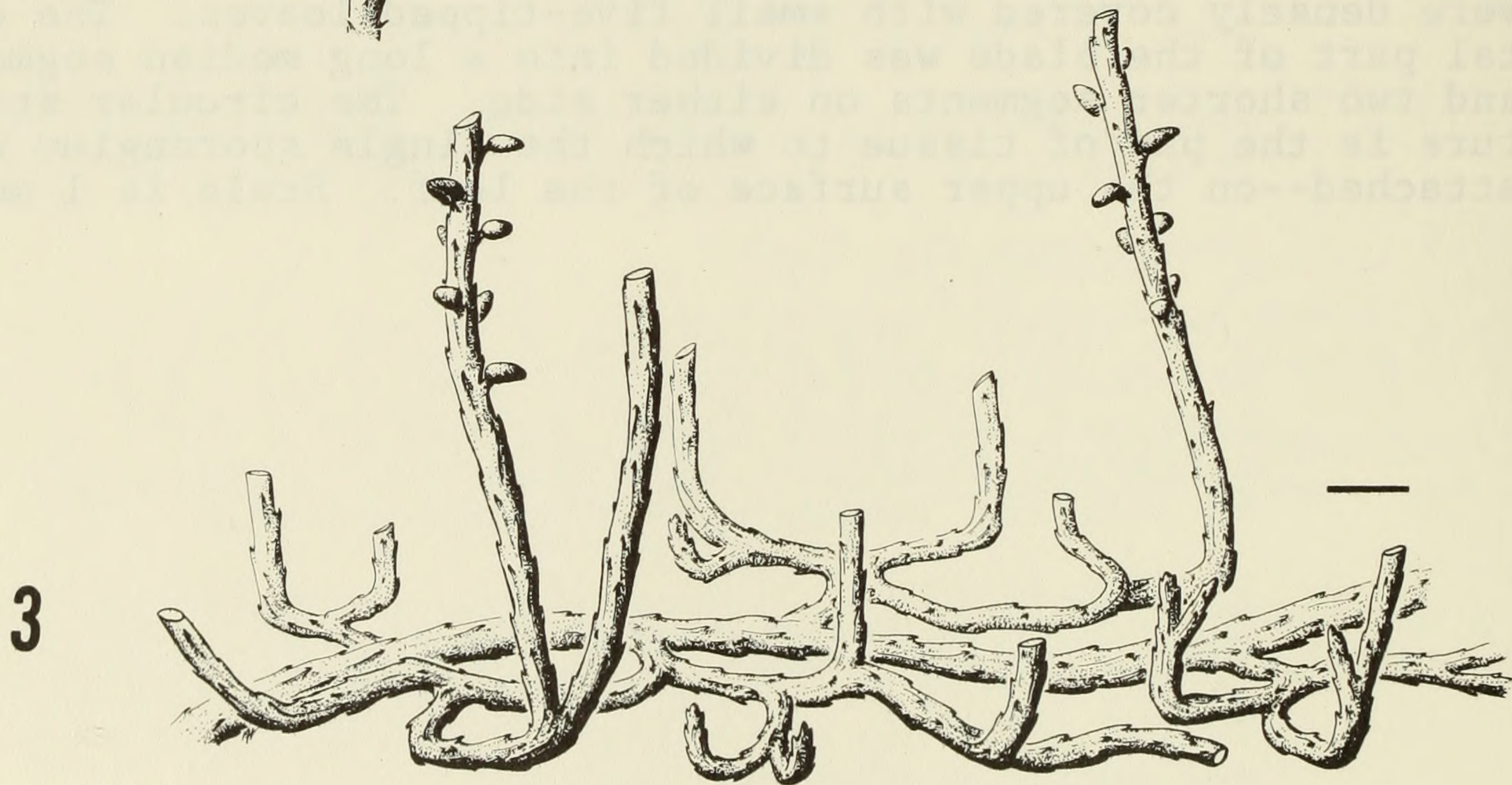
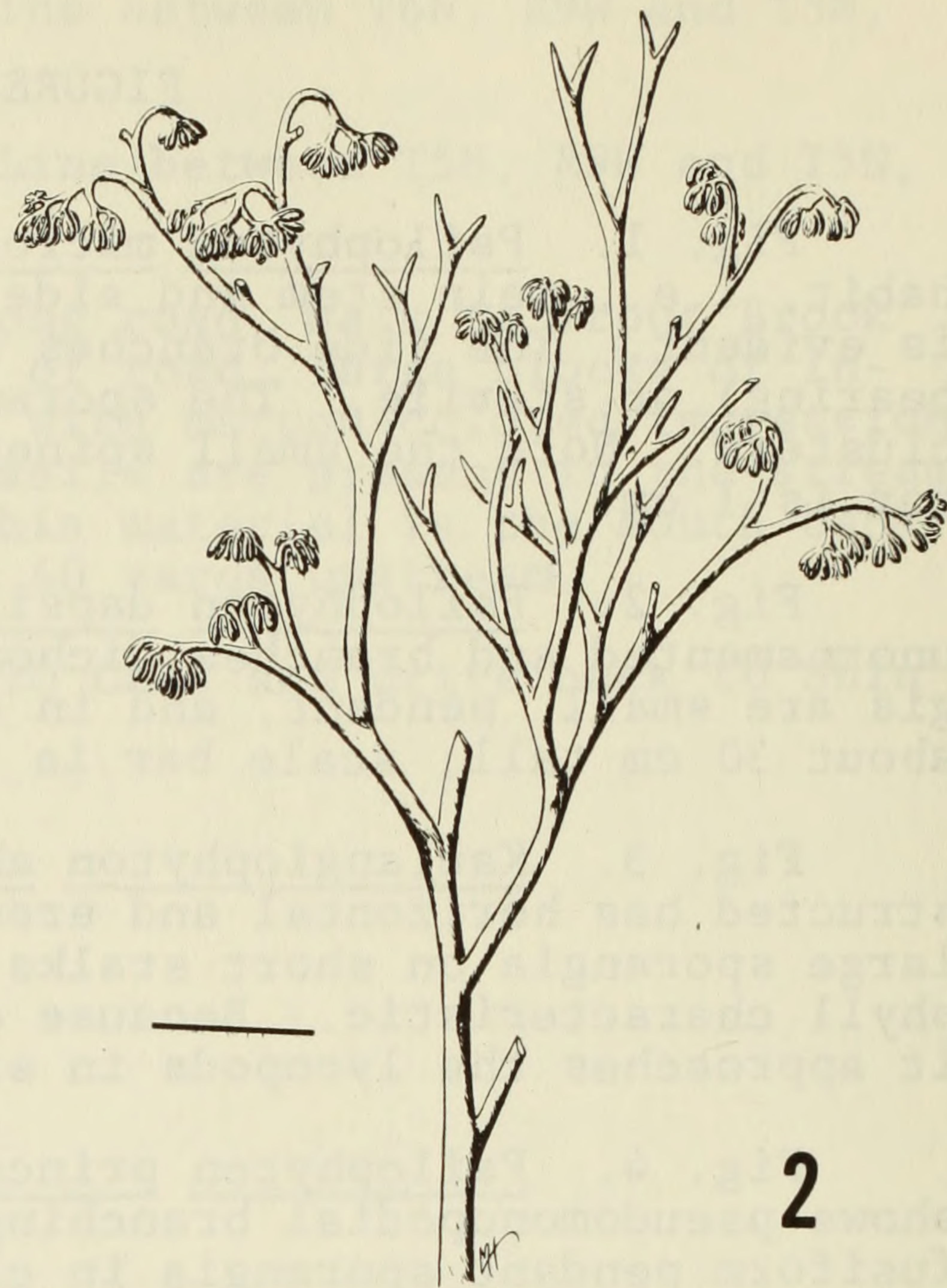
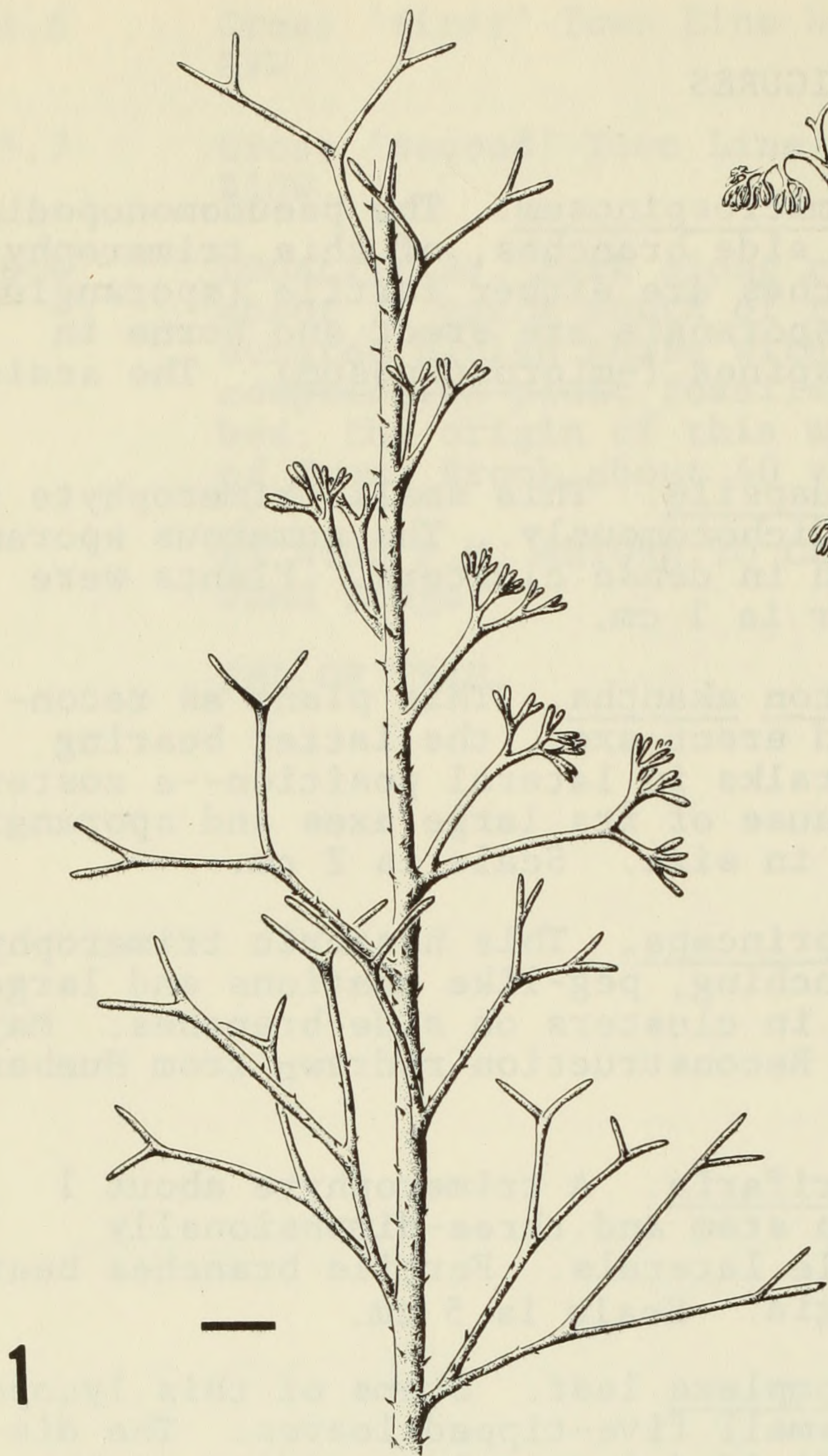
Fig. 3. Kaulangiophyton akantha. This plant as reconstructed has horizontal and erect axes, the latter bearing large sporangia on short stalks in lateral position--a zosterophyll characteristic. Because of its large axes and sporangia it approaches the lycopods in size. Scale is 2 cm.

Fig. 4. Psilophyton princeps. This historic trimerophyte shows pseudomonopodial branching, peg-like enations and large fusiform pendant sporangia in clusters on side branches. Major axes are about 1 cm wide. Reconstruction redrawn from Hueber (1967).

Fig. 5. Pertica quadrifaria. A trimerophyte about 1 meter tall with robust main stem and three-dimensionally branched sterile and fertile laterals. Fertile branches bear spherical masses of sporangia. Scale is 5 cm.

Fig. 6. Leclercqia complexa leaf. Stems of this lycopod were densely covered with small five-tipped leaves. The distal part of the blade was divided into a long median segment and two shorter segments on either side. The circular structure is the pad of tissue to which the single sporangium was attached--on the upper surface of the leaf. Scale is 1 mm.

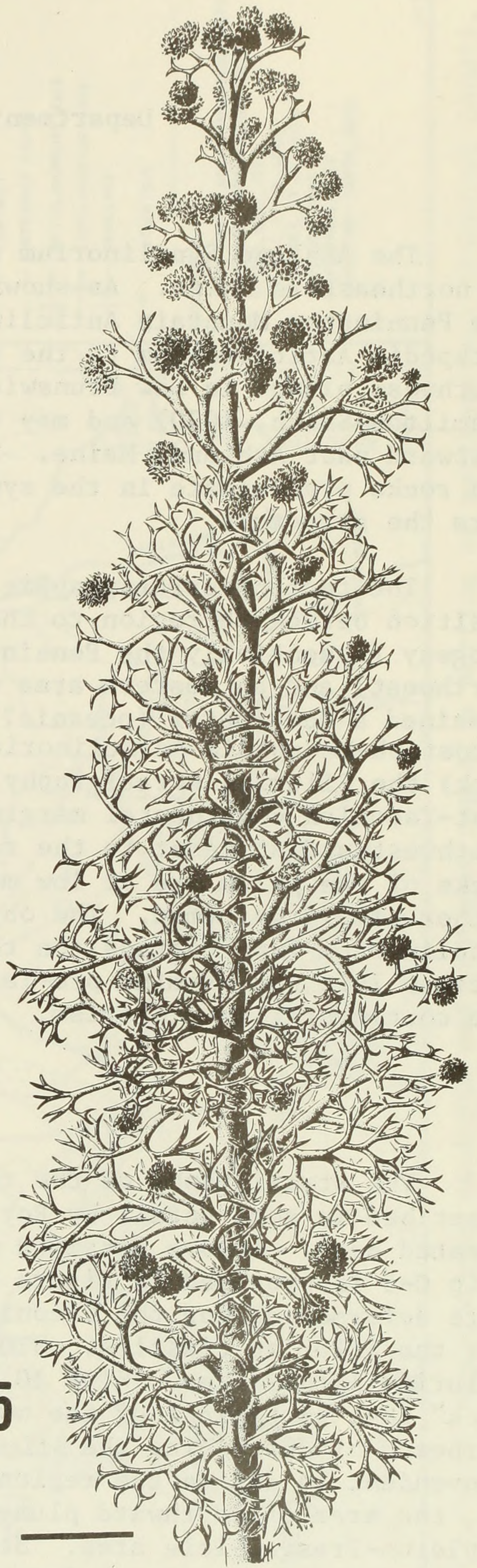




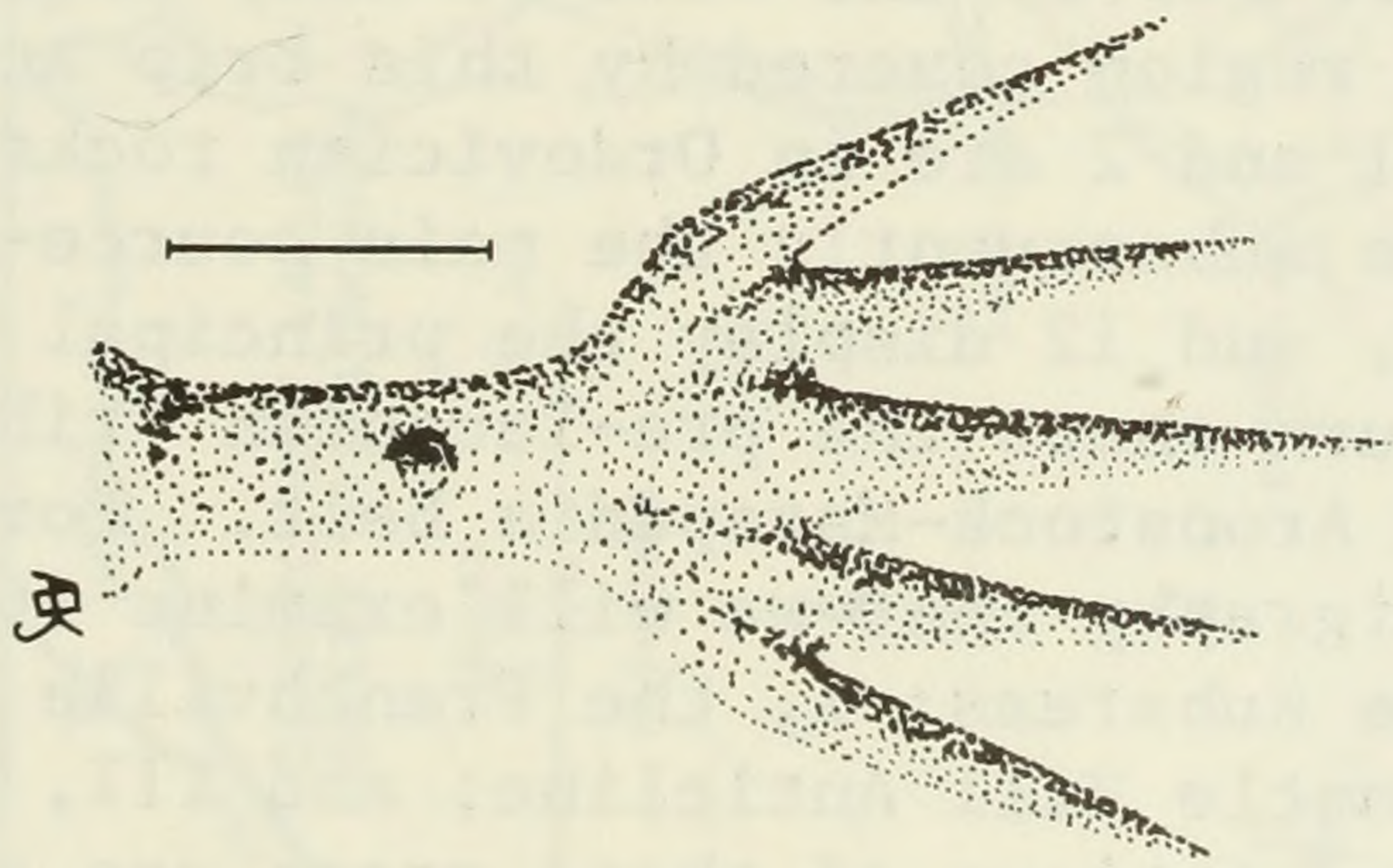




4



5



6