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Notes on the Development of some Benthic Marine Macroalgae of King George Island, Antarctica

CHRISTIAN WIENCKE(1)

ABSTRACT

From a total number of 29 species of Antarctic macroalgae in 26 species reproductive tissue was found, release of viable spores or gametes was observed in 21 species during two expeditions to King George Island in January/ February 1986 and 1987. Germination and further development has been monitored in laboratory cultures under varied light conditions. Within one year of culture adult plants developed in ***Gigartina papillosa, Iridaea obovata, Leptosomia simplex, Adenocystis utricularis*** *and* ***Enteromorpha bulbosa.*** *In the latter two species spore release was observed after one year. In the former perennial species formation of reproductive tissue started after one year, maturation, however, is very slow and presumably may take additional five months or more. Growth in some developmental stages is light saturated at very low photon flux densities, total darkness is tolerated for several months.*

The gamethopyte of ***Leptosomia simplex,*** *which previously was unknown, is described and microscopic evidence of the mating and fusion process of* ***Ascoseira mirabilis*** *gametes, which previously were regarded as spores, is given.*

Key words: Antarctica, marine macroalgae, reproductive tissue, lab cultures.

Notas sobre el desarrollo de macroalgas marinas bentónicas de isla Rey Jorge, Antártica

CHRISTIAN WIENCKE(1)

RESUMEN

Durante los meses de enero y febrero de 1986 y 1987 se efectuaron recolecciones de macroalgas bentónicas en isla Rey Jorge. De un total de 29 especies de macroalgas antárticas, en 26 de ellas se encontró tejido reproductivo y en 21 se observó gametos o liberación de esporas viables.

La germinación y desarrollo se monitoreó en cultivo de laboratorio bajo diversas condiciones de luminosidad. En un año de cultivo se desarrollaron ejemplares adultos de ***Gigartina papillosa, Iridaea obovata, Leptosomia simplex, Adenocystis utricularis*** *y* ***Enteromorpha bulbosa.*** *En las últimas dos especies se observó liberación de esporas después de un año.*

En las primeras especies perennes la formación de tejido reproductivo se observó después de un año; sin embargo, la maduración es muy lenta y presumiblemente puede ocurrir después de cinco meses o más.

El crecimiento en algunos estados del desarrollo se saturan de luz a muy baja densidad de flujo de fotones, tolerando oscuridad total por muchos meses.

Además, se describe por primera vez el gametofito de ***Leptosomia simplex*** *y se entrega evidencia microscópica del proceso de apareamiento y fusión de gametos de* ***Ascoseira mirabilis,*** *los que antes eran considerados como esporas.*

Palabras claves: Antártica, macroalgas marinas, tejidos reproductivos, cultivo de laboratorio.

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(1) Alfred Wegener Institut für Polar und Meeresforschung, Sektion Biologie II, An Handelshafen 12, D-2850, Bremerhaven, F.R.G.

INTRODUCTION

In contrast to the large quantity of information on the development and life strategy of marine Antarctic phytoplankton (Horner 1985; Priddle *et al.* 1986) little comparable results exist on benthic marine macroalgae growing luxuriantly in the southern ocean. Data on the types and the structure of sporangia and gametangia of some of the encountered species are already known (cf. Gain, 1912; Hylmö 1919; Kylin and Skottsberg 1919; Lamb and Zimmermann 1977; Skottsberg 1907). However, little information is available about reproductive periodicities, in particular, on the actual season of spore and/or gamete release. Other unsolved questions are the fate of the released spores, their germination and further development. In this respect, the growth patterns of the different algal generations during the year and the duration of the total development until release of new spores is unknown. Moreover, the conditions for initiation of macroscopic generations in species with heteromorphic life-cycles have still to be determined. Many of these events are controlled by the prevailing environmental conditions, i.e., water temperature and photoperiod, as has been shown in algae of other biogeographic regions (for review see Lüning 1985). In Antarctica with its year-round nearly steady water temperatures (Knox 1960) most probably light conditions alone are responsible for control of algal growth and development.

In order to get more information about these questions algal spores were isolated during two expeditions to Antarctica in January/February 1986 and 1987 and their development followed during the expedition time and subsequently in laboratory cultures under varied light conditions. Some early data are given already in a technical report based on the experiences of the 1986 expedition (Clayton and Wiencke 1986).

MATERIALS AND METHODS

Microscopic studies were done either using a Zeiss Standard GF 525 or a Leitz Ortholux II microscope equipped with a Leica M1 for photography. In most studies seawater immersion objectives were used allowing microscopic observations of the algae in culture petridishes without transfer to microscopic slides. Macrophotography was done using a Minolta 101 camera equipped with a 50 mm macrolens.

The techniques used for setting up cultures of Antarctic macroalgae are described elsewhere (Clayton and Wiencke 1986). Culture conditions in the home laboratory were as follows: Generally a light - dark cycle of 18: 6 h was maintained throughout the year. Some algae, however, were cultivated under other light - dark cycles as indicated in the text. During the early stages of algal development (March - mid May) photon fluence rate was set to 15 μE m $^{-2}$ sec $^{-1}$, later on - (mid May to mid October) in order to approximate the conditions encountered in the Antarctic - to less than 5 μE m $^{-2}$ sec $^{-1}$. During the last two weeks of October photon fluence rate was increased at equal daily increments to 60 μE m $^{-2}$ sec $^{-1}$. Other treatments indicated in the text. For lighting OSRAM L 58/W 19 daylight 5000 de luxe cold light neon tubes were used. The temperature in the culture room was 5° Celsius. Light measurements were done using a Licor-Quanta meter LI-185B equipped with a LI 190 SB Quantum sensor.

As culture medium enriched seawater from the North Sea (35‰) was used (ES enrichment, Provasoli, 1968). For the microscopic stages the water was heat sterilized. The macroscopic stages were cultivated in membrane filtered medium (Sartorius Sartobran II, pore size 0.2 μm). Petri dishes were used for the cultivation of small algae, 1 - 3 l beakers with glass tops for the larger forms. The latter cultures were aerated vigorously with membrane filtered air (cellulose nitrate, pore size 0.2 μm) in order to maintain a permanent movement of the algae. By this way all parts of an algal thallus were exposed regularly to the light. The culture medium was changed every 4 weeks in the petri-dish cultures and every two weeks in the beaker cultures.

RESULTS

During the two expeditions to King George Island 29 species of macroalgae (Table 1) were collected at different sites of the Fildes Peninsula (Fig. 1). In 26 species of them reproductive tissue was found and 21 species released viable spores or gametes which could be used for setting up algal cultures. Note that in the red algae **Gigartina papillosa** and **Iridaea obovata** the release of only one type of spores - tetraspores or carpospores - could be observed although tetrasporangia and carposporangia, one of both obviously being immature, were present.

The development of the most important mainly subtidally growing red macroalgae **Iridaea obovata, Leptosomia simplex** and **Gigartina papillosa** starts with the formation of rhizoids. Fig. 2 shows the germination of the **Iridaea obovata** gametophyte. Within 5 months a small ball-shaped plantlet is formed, the winter stage. This stage is very similar in the different species, in Fig. 3 that of the **Leptosomia simplex** - gametophyte is shown. 6 to 8 months after spore release the organisms become susceptible to high photon fluence rates (60 μE m $^{-2}$ sec $^{-1}$), their volume increases and the differentiation of the phylloid starts. Fig. 4 shows the development of **Gigartina papillosa** as an example. The thalli grow slowly at first, then more rapidly to their final dimensions Fig. 5: **Iridaea obovata).** As in nature, thallus sizes of adult **Iridaea obovata** and **Gigartina papillosa** plants vary from one to several decimeters in length. Fig. 6 shows males and Fig. 7 female gametophytes of **Iridaea obovata.** Reproductive structures began to develop after one year of cultivation. Release of spores, however, could not be observed within the subsequent 4 months.

In **Leptosomia simplex** the tetraspores collected in the field developed into (bi-) furcate gametophytes with a total length of approx. 7.5 cm **(Fig. 8).** Development of reproductive structures started in the basal part of the thallus after one year of cultivation. Later on also in the phylloid sori were found. Spore release however, could not be detected within the subsequent 4 months. In **Gigartina papillosa** tetrasporophytes the formation of reproductive structures starts after 15 months of cultivation. However, their development is so slow that release of mature tetraspores cannot be expected before further 5 months.

The monospores of **Porphyra endiviifolium** from the upper intertidal zone (Fig. 9) develop in culture within three months after collection into 2 mm large plants of the parent generation (**Porphyra**-phase). The carpospores of this species form the typical **Conchocelis**-phase. The further development was not yet investigated, but the present results indicate, that during the Antarctic winter both phases of the **Porphyra** life-cycle are present.

In the brown macroalgae **Adenocystis utricularis** and in the different members of the Desmarestiales (cf. Table 1) an alternation of microscopic and macroscopic developmental stages occurs. The microthalli are filamentous; as examples the microthalli of **Adenocystis utricularis** (Fig. 10) and **Himantothallus grandifolius** (Fig. 14, 15) are given. The light requirements for growth are very low: e.g., the growth of the female gametophyte of **Phaeurus antarcticus** is light saturated at a photon fluence rate of 3 μE m $^{-2}$ sec $^{-1}$ (Fig. 17). Higher photon flux densities of more than 30 μE m $^{-2}$ sec $^{-1}$ have a growth inhibitory effect. Moreover these microthalli are characterized by a strongly expressed dark resistance. The microthallus of **Adenocystis utricularis** e. g. is able to withstand 4 months of total darkness and continues to grow after that time when placed in the light.

The formation of macrothalli may be initiated with or without sexual processes. In **Adenocystis utricularis,** growing in Antarctica in the lower intertidal zone and in the upper infralittoral belt macrothalli develop asexually on microthallic filaments, which become at first a nodular structure (Fig. 11, arrow). Subsequently these nodules develop into adult spore releasing plants (Fig. 11, 12; double arrows) which eventually form additional macrothalli at their base (Fig. 13; arrows). This special manner of vegetative propagation and the initiation of macrothalli in general is stimulated under high photon flux densities (30-60 μE m $^{-2}$ sec $^{-1}$).

In the members of the Desmarestiales which all grow subtidally the formation of macrothalli is linked to the prior fertilisation of the gametophytic microthalli. This process can be dependent on the light period. **Phaeurus antarcticus** develops antheridia and oogonia under long and short day conditions, whereas for fertilization of **Himantothallus grandifolius** short days are necessary, as preliminary experiments indicate. The growth of the sporophytes, initiated in this way, seems to be independent of daylength. Fig. 16 and Fig. 18 show young sporophytes of **Himantothallus grandifolius** and **Desmarestia ligulata** developed in culture. In the latter species fertile gametophytes were found under long day conditions (more than 14 h light; short days not yet tested).

A development without formation of microthalli is found in the subtidal **Ascoseira mirabilis.** This alga develops isomorphic biflagellate gametes (Fig. 19, 20). Female gametes move slow and settle quickly after the release surrounded then by the quicker swimming males. Eventually male and female come into contact and fuse subsequently. The fusion process (Fig. 21, 22) can be very slow and may take some days. Gametes of **Ascoseira** are extremely heat sensitive. Temperatures above 5°C are lethal. Mating and fusion could be observed microscopically only under conditions in which temperatures could be kept between 0 and +2 centigrades. The zygotes germinate into racket-shaped plantlets (Fig. 23) within 3 months. Under the prevailing long-day conditions their further development is relatively slow, resulting in 30 - 60 mm large plants after one year of culture.

The spores of the intertidal green alga **Enteromorpha bulbosa** develop within three months into 2 mm long filaments, which are able to withstand up to one year of total darkness without any damage. Under the given light conditions adult spore releasing plants of a length of up to 30 cm were formed within one year of cultivation.

DISCUSSION

From Table 1 it is evident that the period of spore release in many of the studied macroalgae is the Antarctic summer and autumn. The occurrence of reproductive tissue alone cannot be used as a criterion for the determination of the actual propagation period as the development of reproductive organs especially in Antarctic algae is very slow as has been shown in this study for **Iridaea obovata, Gigartina papillosa** and **Leptosomia simplex.** In the authors opinion it may take at least 5 months from the first indication of sorus development to the actual time of spore release in these species. In **Gigartina papillosa** and **Leptosomia simplex** even more time may be required and in these algae the situation may be similar to the arctic kelp **Laminaria solidungula,** where sori are produced in autumn, spore release, however, does not occur before spring (Hooper, 1984).

At present, no general overview on the growth pattern of the different algae during the year can be given. However, it is certain that during winter time only small microscopic stages develop from the released spores. Under higher light intensities occurring in spring and summer growth rates increase as shown in **Iridaea obovata** (Fig. 5), representing also the performance of **Gigartina papillosa** and **Leptosomia simplex.** The result is the formation of adult plants in these three species. In the case of **Enteromorpha bulbosa** and **Adenocystis utricularis** adult spore releasing specimen are developed within one year, in culture as in nature (cf. Müller 1984). As discussed above in **Iridaea obovata, Gigartina papillosa** and **Leptosomia simplex** growth and maturation in the laboratory takes more than one year.

As can be deducted from the data given for the female gametophyte of **Phaeurus antarcticus** (Fig. 17) as example for brown algal microthalli these developmental stages are able to grow under conditions of very low light. Comparable to the microthalli of the Antarctic Desmarestiales are by reason of their structural similarity and of their position in the life-cycle those of the Laminariales occuring in all algal floras of the world except the Southern Ocean (Moe and Silva 1976). As has been shown for three **Laminaria** species from Helgoland, North Sea (Lüning 1980), their growth is light saturated at 20 - 30 μE m $^{-2}$ sec $^{-1}$, a nearly ten times higher value than that of **Phaeurus**

antarcticus. This feature is regarded as special adaptation to the prevailing light conditions in Antarctic waters. In this context, the ability to withstand long periods of absolute darkness without any damage, as shown for **Adenocystis utricularis** and **Enteromorpha bulbosa,** seems to be another important prerequisite for algae living in this type of environment.

Finally, details of the life-cycles of two antarctic algae are discussed. The first concerns the nature of the swarmers of **Ascoseira mirabilis.** As has been shown already during the first expedition in 1986 (Clayton and Wiencke, 1986) the swarmers are no spores as stated by Moe and Henry (1982) but isomorphic gametes. In this study microscopic evidence of the mating and fusion process in **Ascoseira** gametes is presented (Fig. 19 - 22).

A detailed description of the life history of **Ascoseira mirabilis** is given by Clayton (1987).

The second example concerns the gametophyte of **Leptosomia simplex** (Fig. 8) which previously was unknown. Its structure differs considerably from that of its circumpolar widely distributed tetrasporophyte which is rarely furcate and more flaccid in texture than the cultivated gametophyte. Moreover, there seems to be a considerable difference in the size of the thalli: The tetrasporophyte reaches in the field easily a length of 80 cm, whereas the largest gametophyte developed in culture had a length of only 7,5 cm. In the field specimen with a structure similar to the described gametophyte are quite often found. These plants generally are regarded as tetrasporophytic fronds proliferating in summer from overwintering basal portions (Lamb and Zimmermann, 1977). In the author's opinion they are probably no tetrasporophytes but gametophytes. This assumption, however, has yet to be proven by careful examination of field material.

From the present study it becomes clear that it is possible to cultivate even the larger of the Antarctic species in the laboratory. By this way many different kinds of investigations can be carried out which would be much more difficult or even impossible to perform in Antarctica itself.

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Table 1

LIST OF MACROALGAE STUDIED DURING THE TWO EXPEDITIONS TO KING GEORGE ISLAND, ANTARCTICA

Species	Reproductive tissue found	viable spores / gametes released
RED ALGAE		
Bangiales		
Porphyra endiviifolium (A. et E. Gepp) Chamberlain	Monosporangia	+
	Carposporangia	+
Porphyra sp. **	Monosporangia	+
	Carposporangia	+
Cryptonemiales		
Kallymenia antarctica Hariot	Carposporangia	—
Gigartinales		
Curdiaea racovitzae Hariot	Carposporangia	—
Gigartina papillosa (Bory) Setchel et Gardner	Carposporangia	+
	Tetrasporangia	—
Iridaea obovata Kützing	Carposporangia	—
	Tetrasporangia	+
Plocamium coccineum (Hudson) Lyngbye	—	—
Rhodymeniales		
Leptosomia simplex (A. et E.Gepp) Kylin	Tetrasporangia	+
Ballia callitricha (C.Agardh) Kützing	—	—
Georgiella confluens (Reinsch) Kylin	—	—
Myriogramme mangini (Gain) Skottsberg	Tetrasporangia	—
Myriogramme smithii (Hooker et Harvey) Kylin	Carposporangia	—
BROWN ALGAE		
Ectocarpales		
Geminocarpus geminatus (J.D. Hooker et Harvey) Skottsberg	pluriloc. sporangia	+
Chordariales		
Elachista antarctica Skottsberg	uniloc. sporangia	+
Dictyosiphonales		
Adenocystis utricularis (Bory) Skottsberg	uniloc. sporangia	+
Desmarestiales		
Desmarestia anceps Montagne	uniloc. sporangia	+
Desmarestia ligulata (Light.) Lamouroux	uniloc. sporangia	+
Desmarestia menziesii J. Agardh	uniloc. sporangia	+
Himantothallus grandifolius (A. et E.S. Gepp) Moe et Silva	uniloc. sporangia	+
Phaeurus antarcticus Skottsberg	uniloc. sporangia	+

(Tabla 1, cont.)

Species	Reproductive tissue found	viable spores / gametes released
Ascoseirales		
Ascoseira mirabilis Skottsberg	gametangia	+
Fucales		
Cystosphaera jacquinotii (Mont.) Skottsberg	antheridia	—
	oogonia	—
GREEN ALGAE		
Ulotrichales		
Ulothrix australis Gain	zoosporangia	+
Ulothrix flacca (Dillw.) Thuret	zoosporangia	+
Monostromatales		
Monostroma hariotii Gain	+*	+
Acrosiphoniales		
Acrosiphonia sp. **	+*	+
Urospora penicilliformis (Roth) Aresch.	zoosporangia	+
Ulvales		
Enteromorpha bulbosa (Suhr) Montagne	zoosporangia	+
Prasiolales		
Prasiola sp. **	+	+

** type of reproductive structure to be determined

** species name to be determined

Fig. 1: Map of the study area (redrawn after Barsch *et al.* 1985, collecting sites marked with rhombs). The exposed northeastern coast bears numerous rocky islets, the water is relatively shallow. Ardley Bay is more sheltered and characterized by deep waters (30 m and more). Certain brown algae (**Himantothallus grandifolius** and **Desmarestia anceps)** have been found only in Ardley Bay. On the other hand the northeastern coast is characterized by the occurrence of large red algal beds (mainly **Iridaea obovata, Gigartina papillosa** and **Myriogramme** sp.).

1

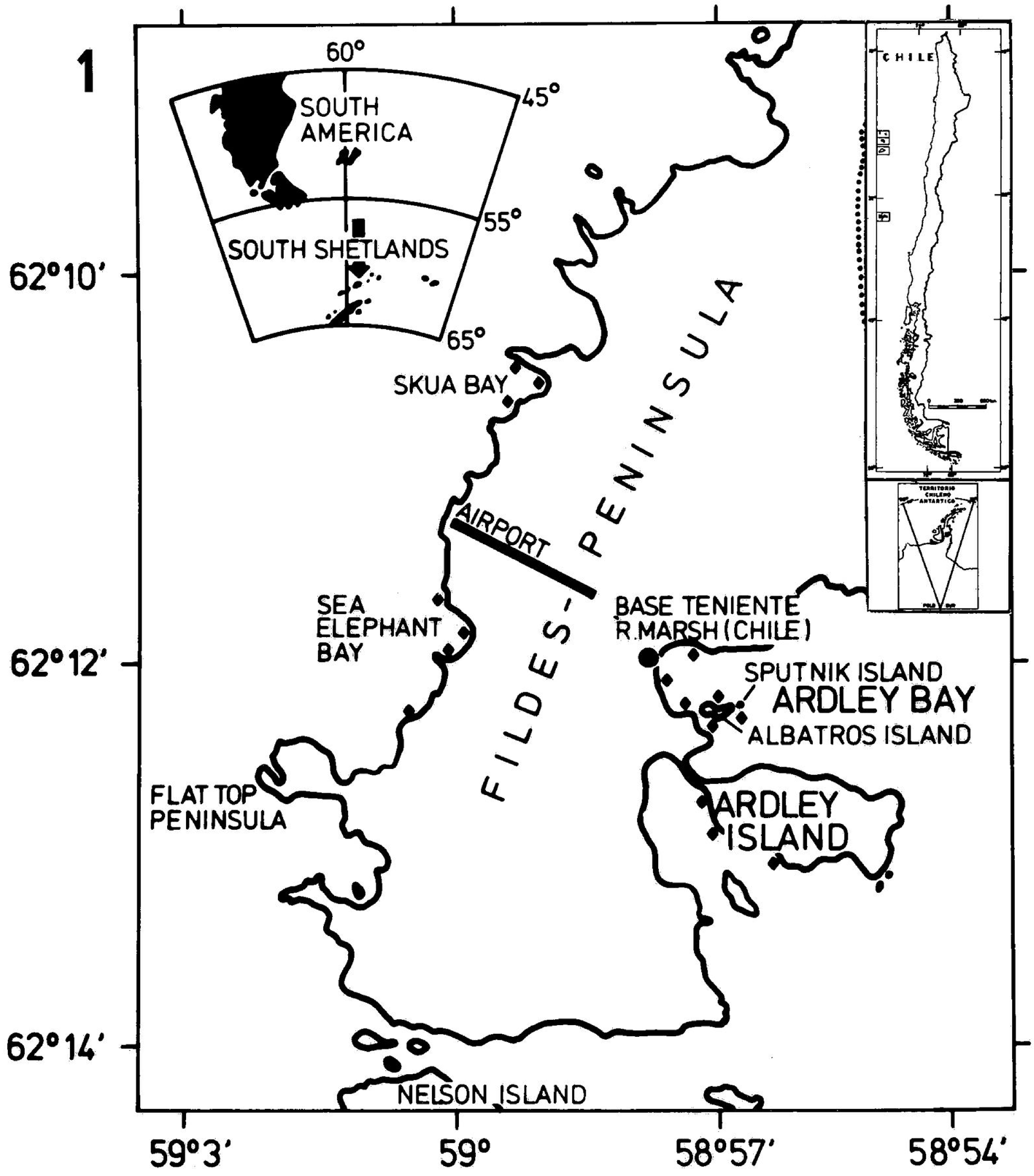

60°
SOUTH AMERICA
45°
55°
SOUTH SHETLANDS
65°
62°10'
62°12'
62°14'
SKUA BAY
AIRPORT
FILDES - PENINSULA
SEA ELEPHANT BAY
BASE TENIENTE R.MARSH (CHILE)
SPUTNIK ISLAND
ARDLEY BAY
ALBATROS ISLAND
FLAT TOP PENINSULA
ARDLEY ISLAND
NELSON ISLAND
59°3'
59°
58°57'
58°54'
CHILE
TERRITORIO CHILENO ANTARTICO

Fig. 1:

Fig. 2: Formation of a discoid rhizoid (arrows) in the gametophyte of **Iridaea obovata,** 48 days after spore release.

Fig. 3: Winter stage of the **Leptosomia simplex** gametophyte after 4 months of cultivation.

Fig. 4: Development of the phylloid in **Gigartina papillosa** tetrasporophytes after 9 months of cultivation.

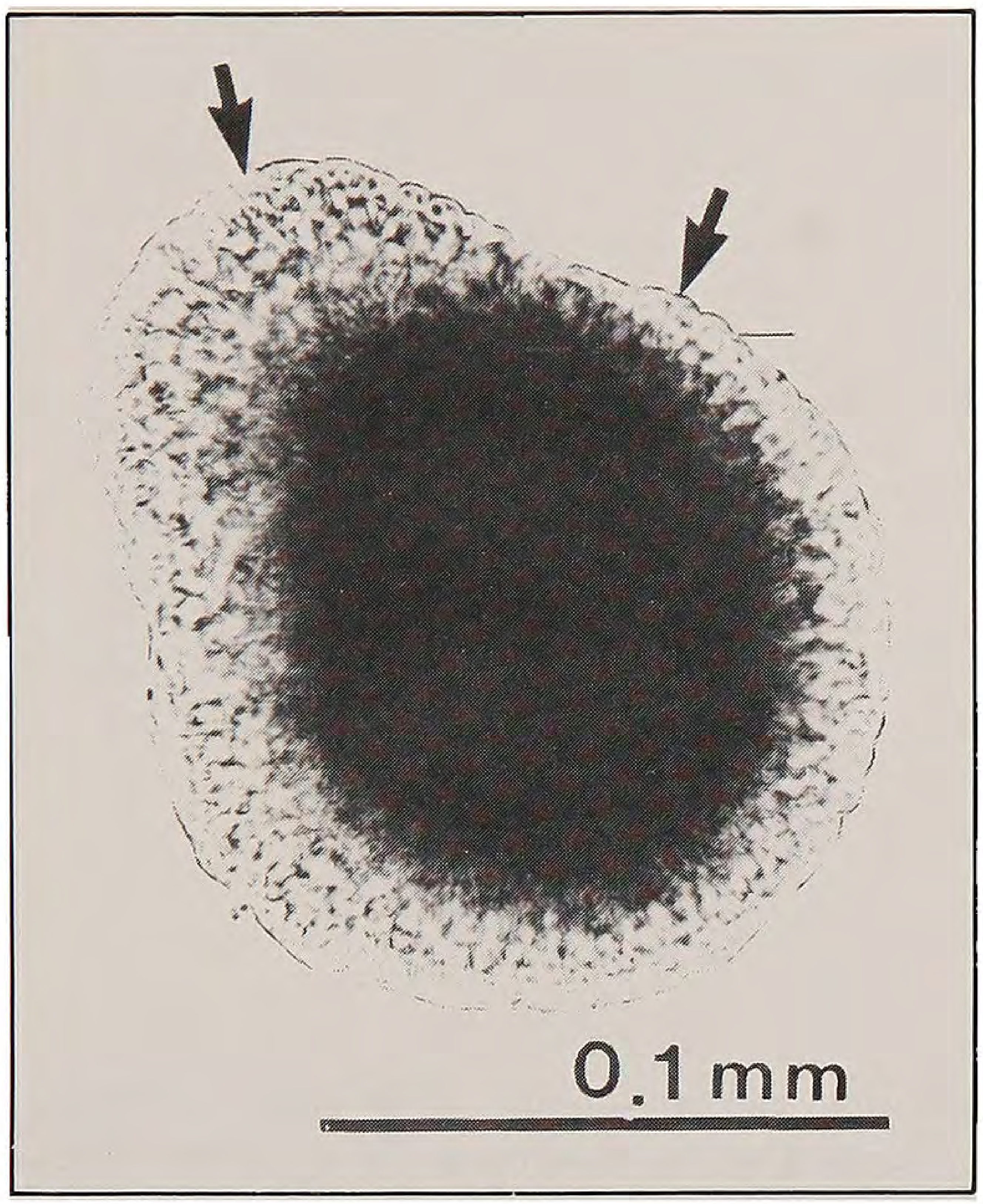
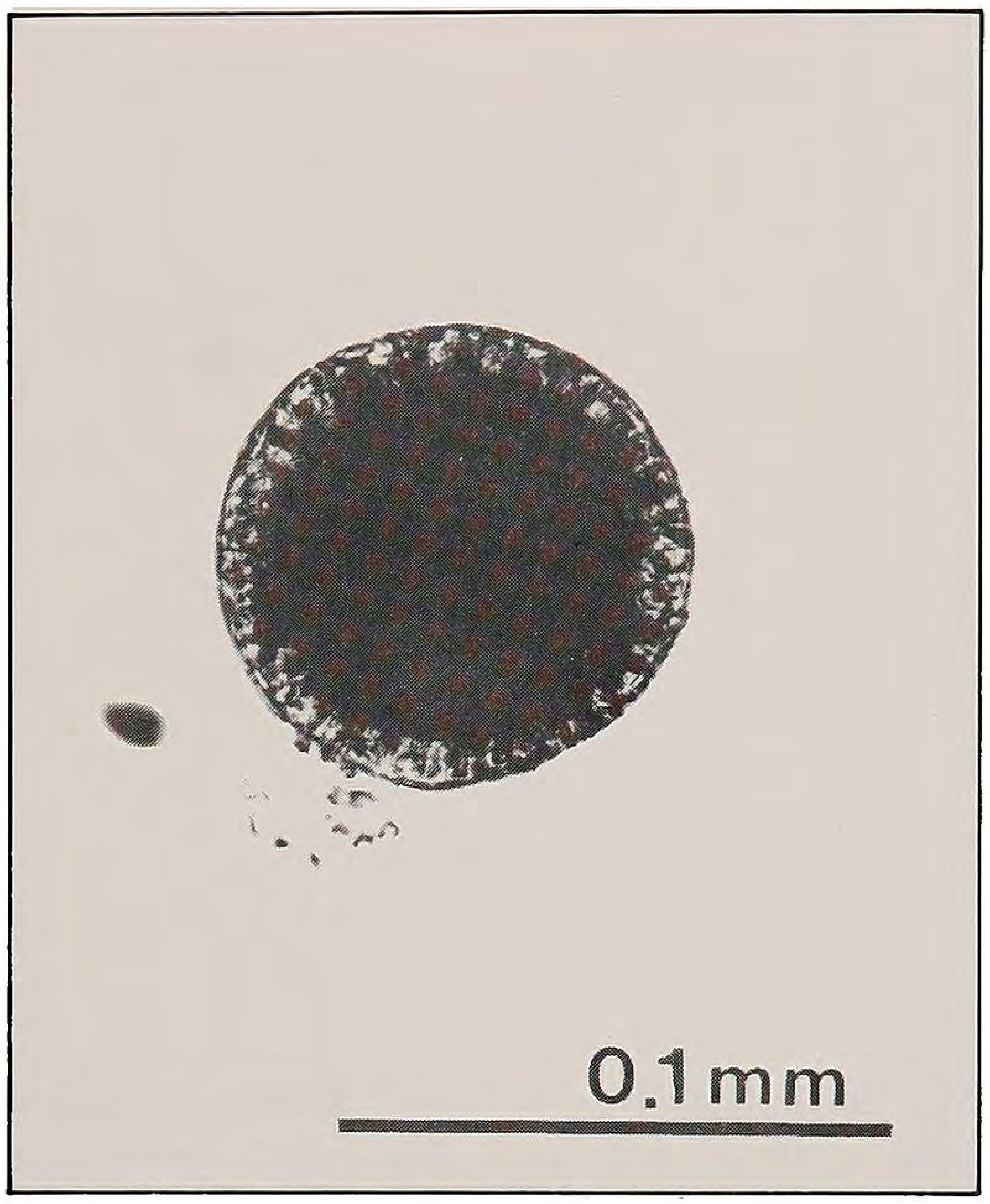


Fig.: 2



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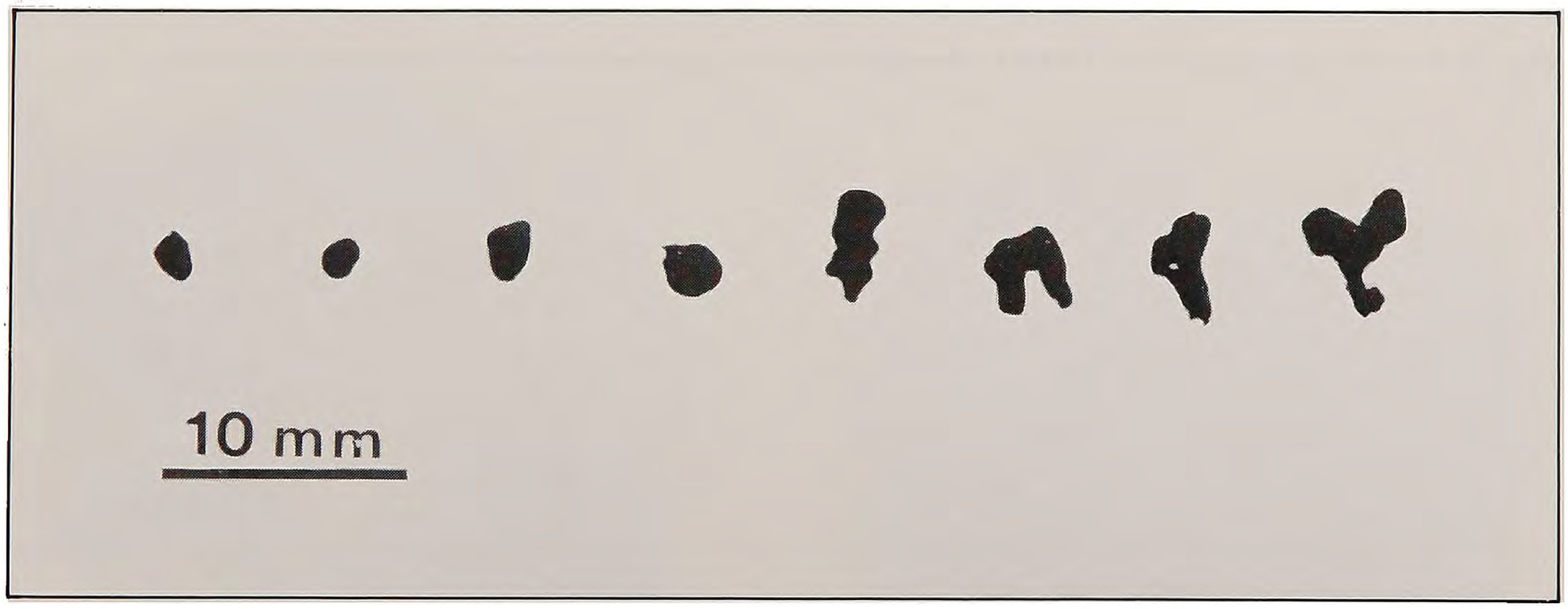
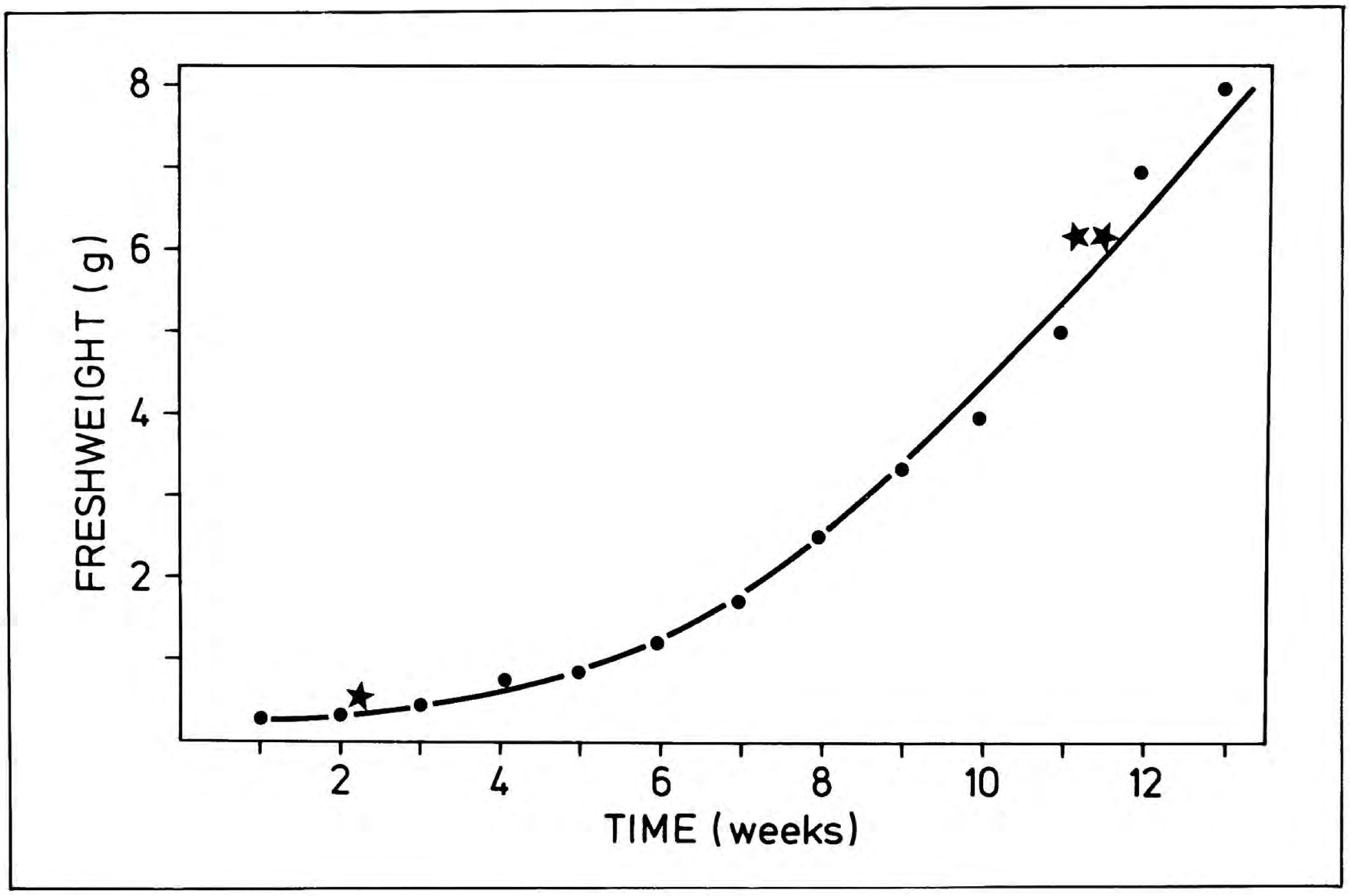


Fig.: 4

Fig. 5: Growth of an individual **Iridaea obovata** gametophyte from end of November 1986 to end of February 1987 at 60 µE m-2 sec-1. The specific growth rate at the beginning of the experiment (*) was 5,9% increase day-1 and 1.6% increase day-1 in the last weeks of the experiment (**).

Fig. 6: Male gametophyte of **Iridaea obovata** developed after 16 months of cultivation. Note the formation of antheridial sori (arrows).

Fig. 7: Female gametophyte of **Iridaea obovata** with sori developed after 16 months of cultivation.



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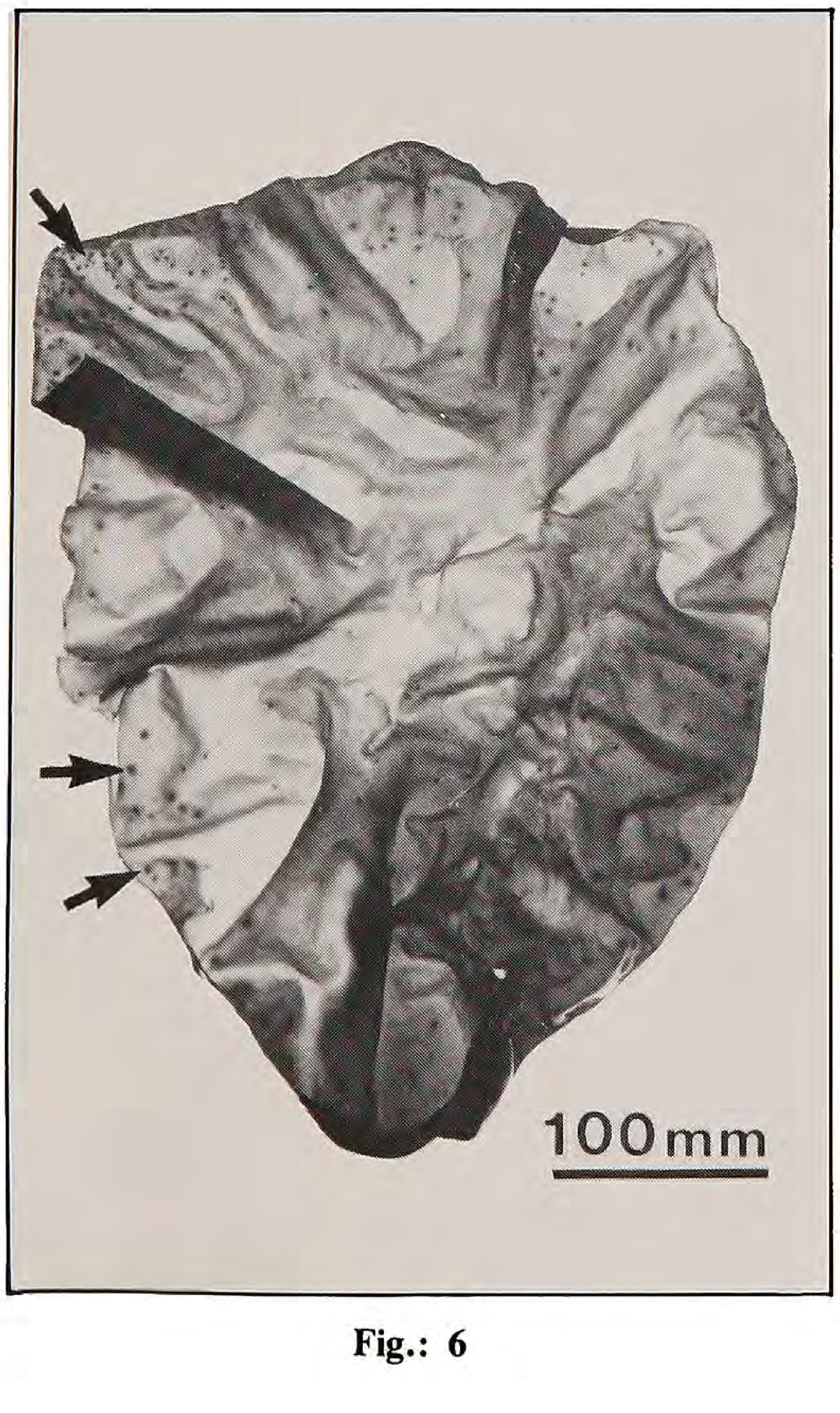

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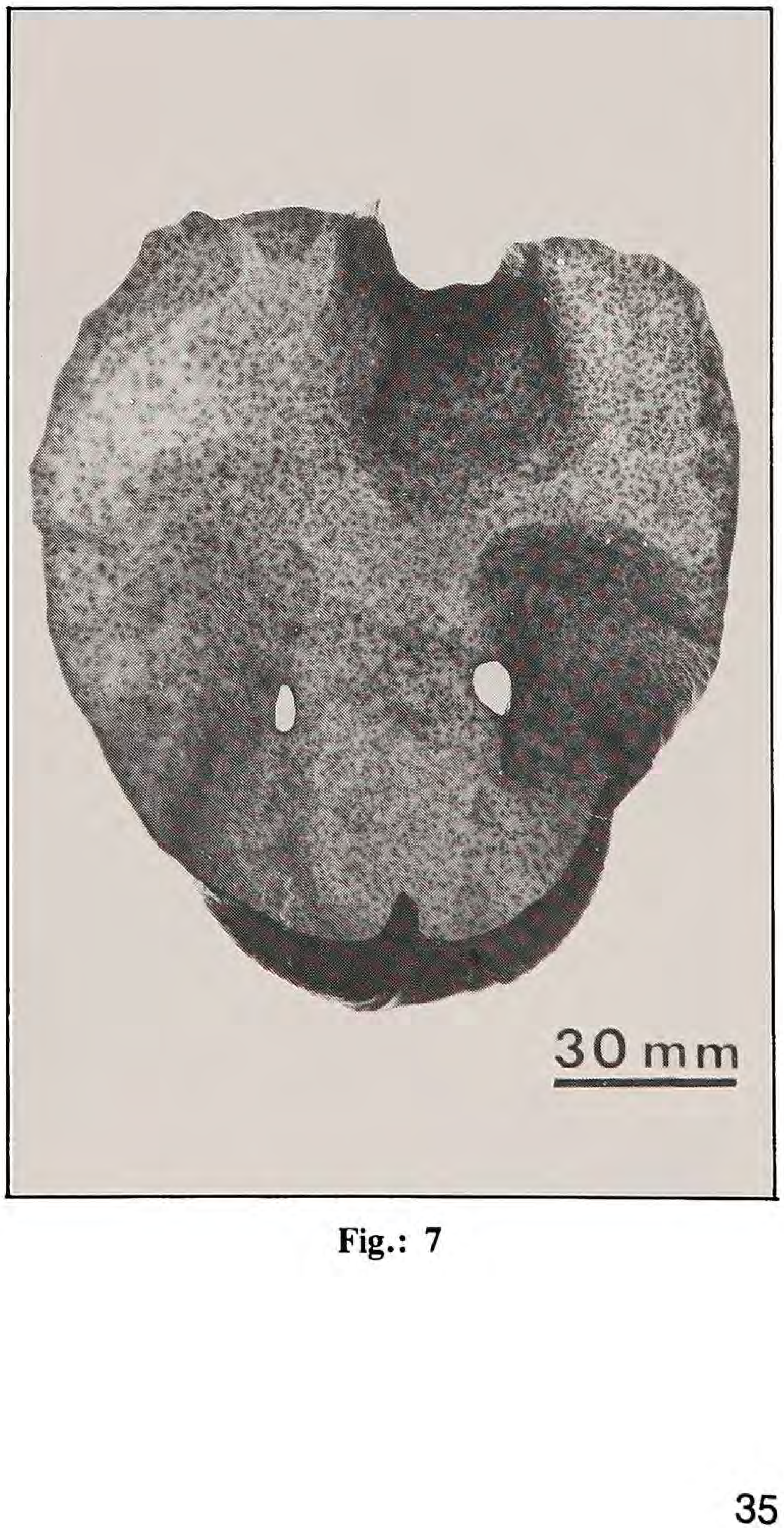


Fig.: 7

Fig. 8: Gametophyte of **Leptosomia simplex** with sori at the periphery of the cauloid (arrows) and in the phylloid (double arrows).

Fig. 9: Spermatia (arrow heads), carpospores (arrows) and monospores (double arrows) of **Porphyra endiviifolium** released in February 1987.

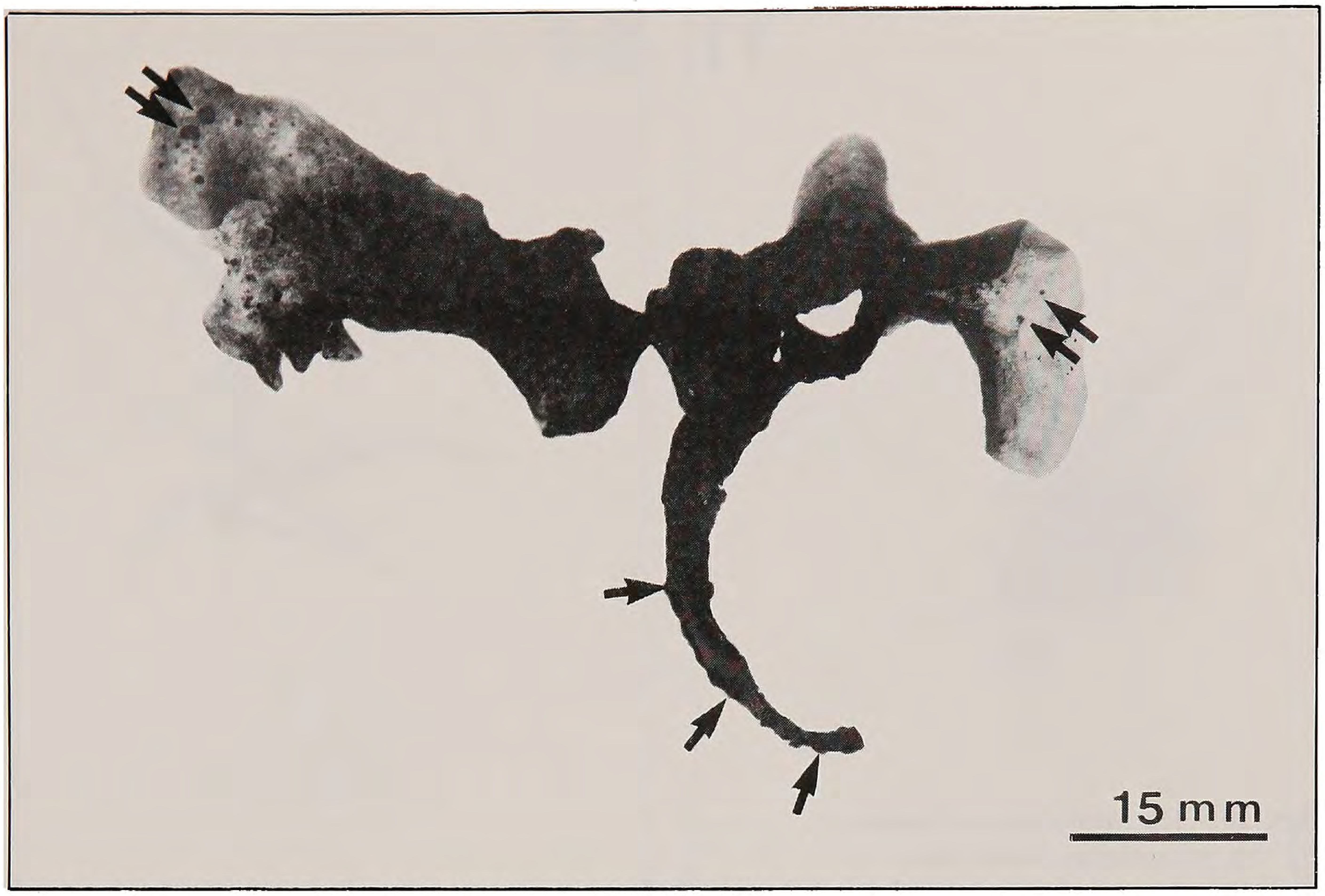


Fig.: 8

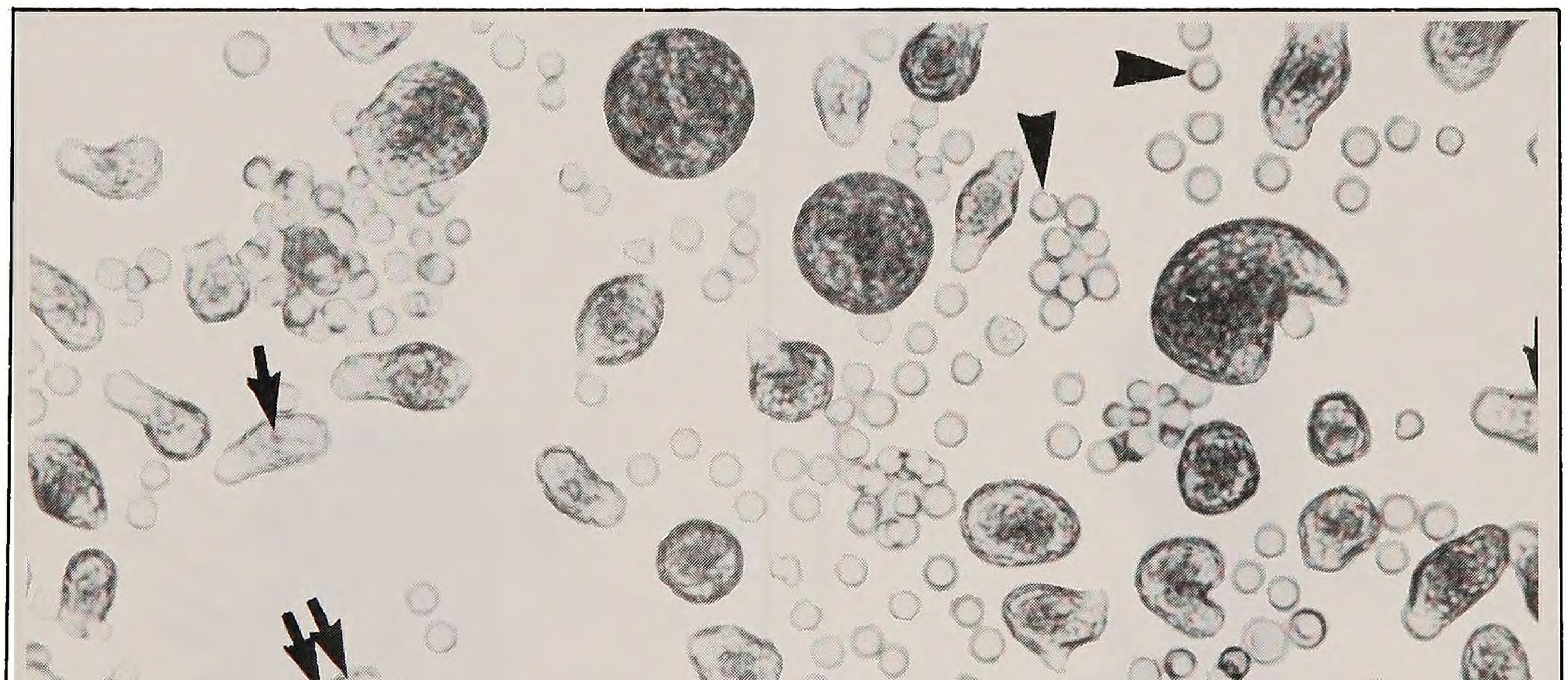


Fig.: 9

Figs. 10 - 13: Adenocystis utricularis.
Fig. 10: Microthallus, winter stage.
Figs. 11 - 12: Development of macrothalli on microthalli.
Fig. 13: Formation of young macrothalli at the base of older ones. For further information see text.

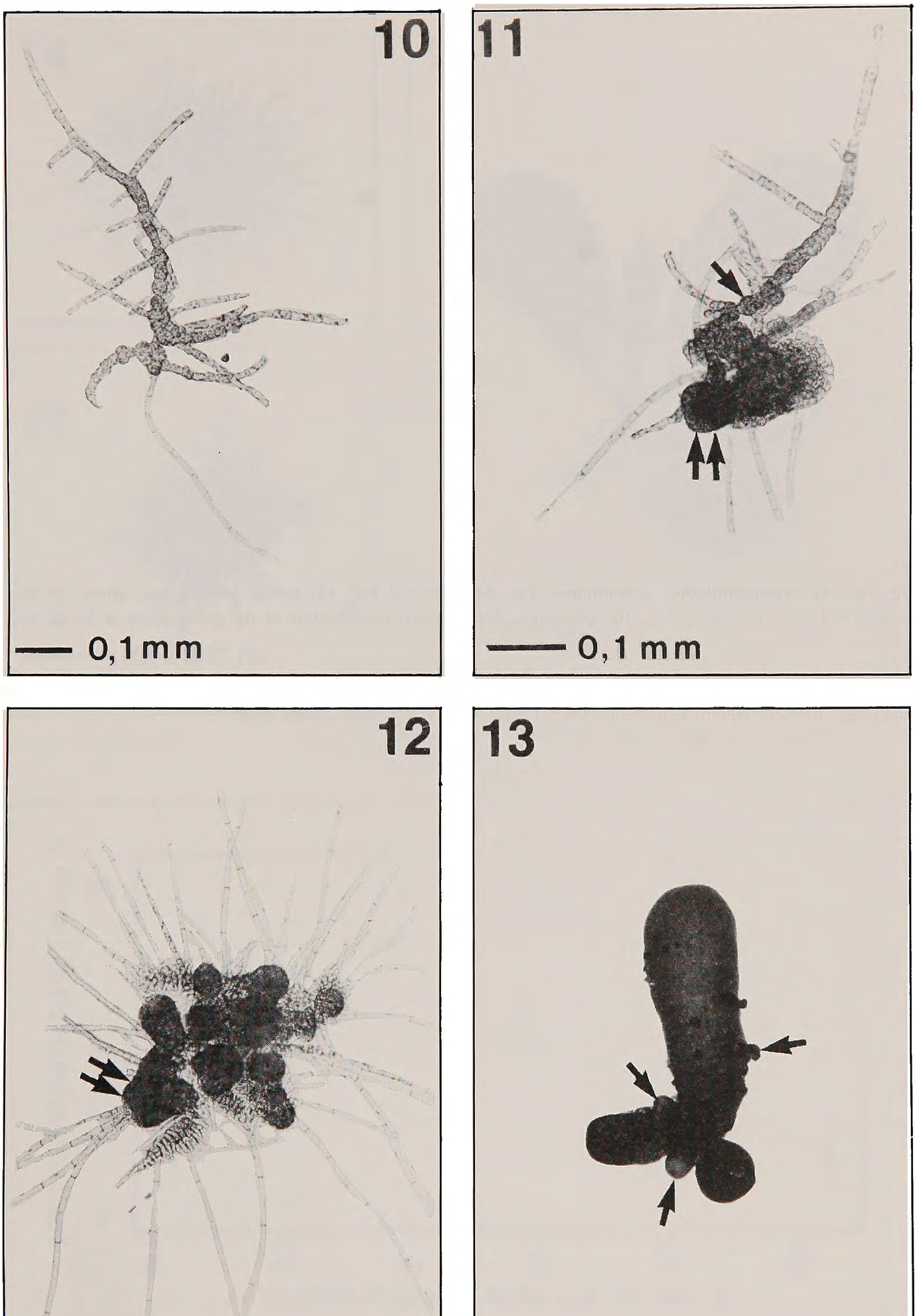
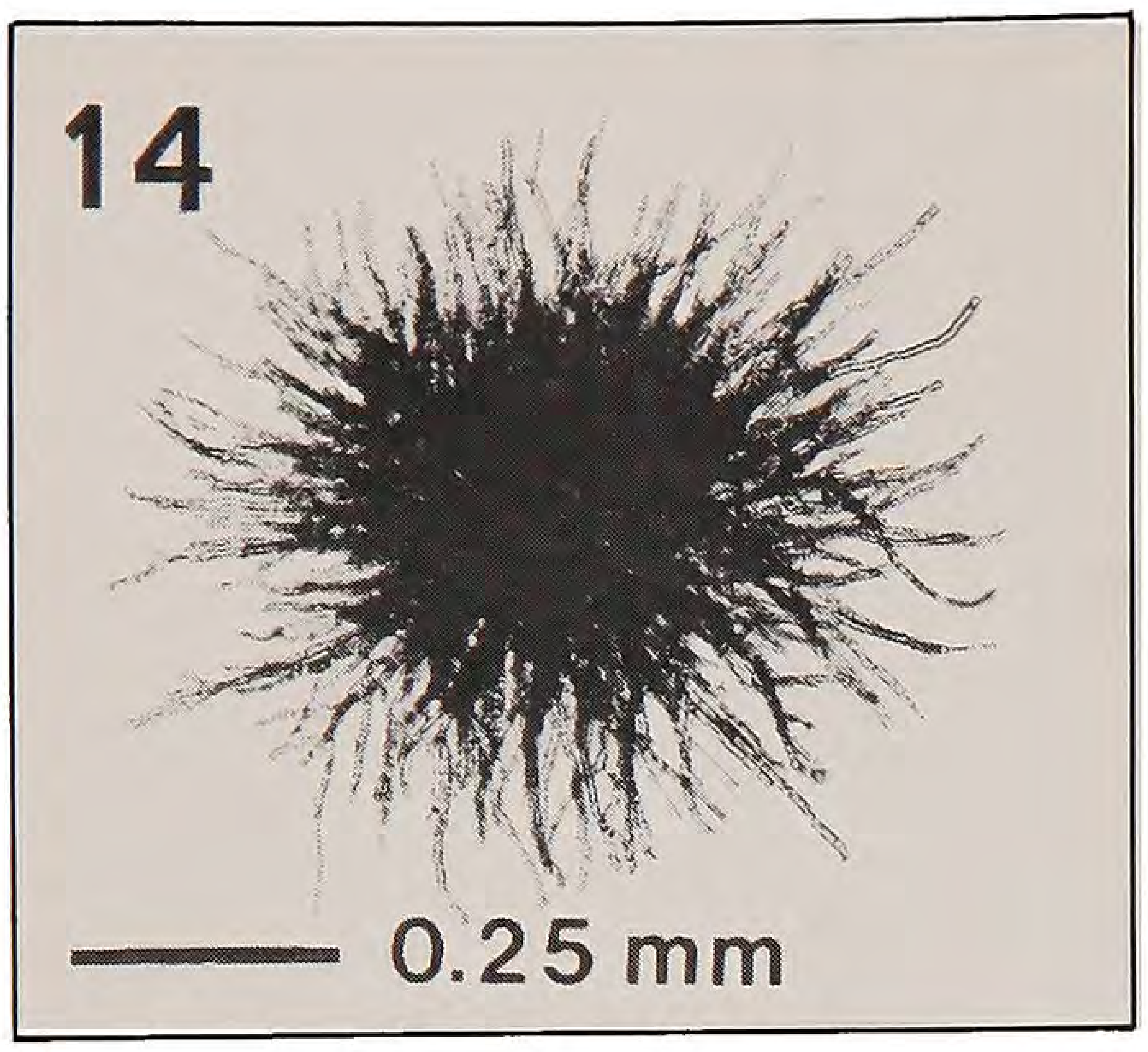
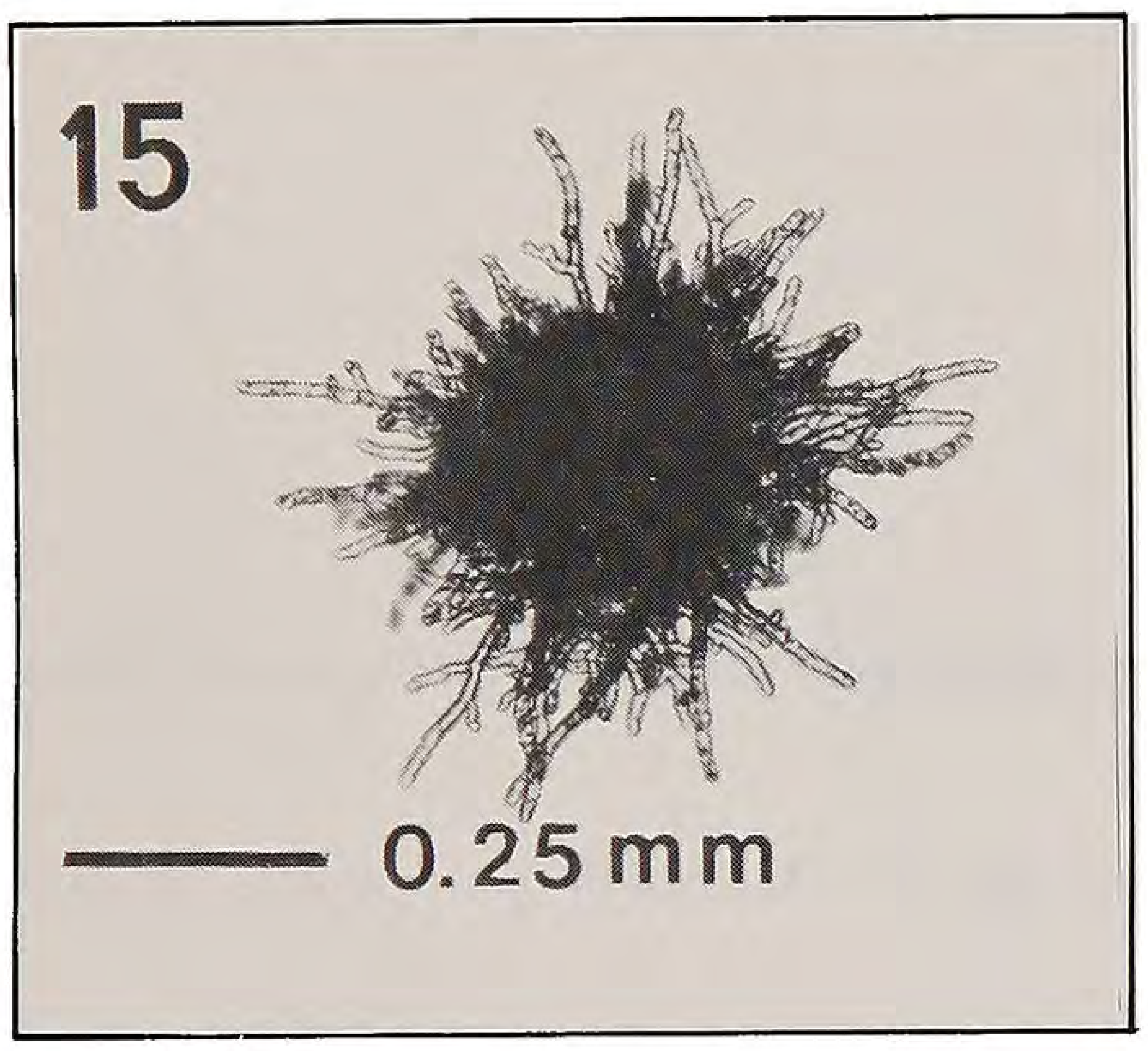


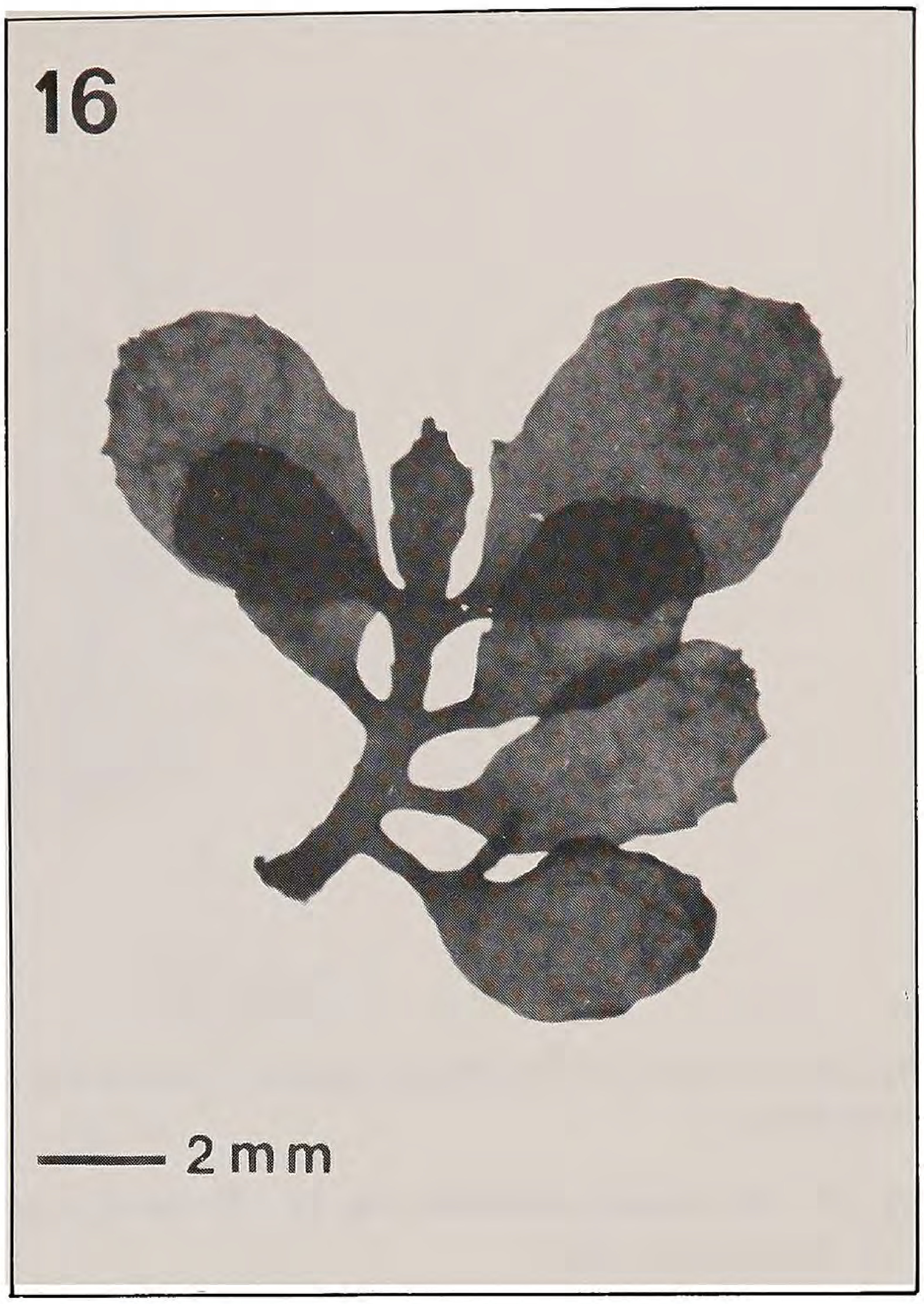
Fig.: 10 - 11 - 12 - 13

Fig. 14 - 16: Himantothallus grandifolius: Fig. 14: male and **Fig. 15:** female gametophyte, grown for two months at 10 µE m-2 sec-1. Fig. 16: sporophyte, 3 months after fertilization of the gametophyte at 30 µE m-2 sec-1.

Fig. 17: Growth of the female gametophyte of **Phaeurus antarcticus** at different photon fluence rates (measured parameter: filament length; temperature 0°C; 12 1/2 - 11 1/2 h light - dark cycle).







Figs.: 14 - 15 - 16.

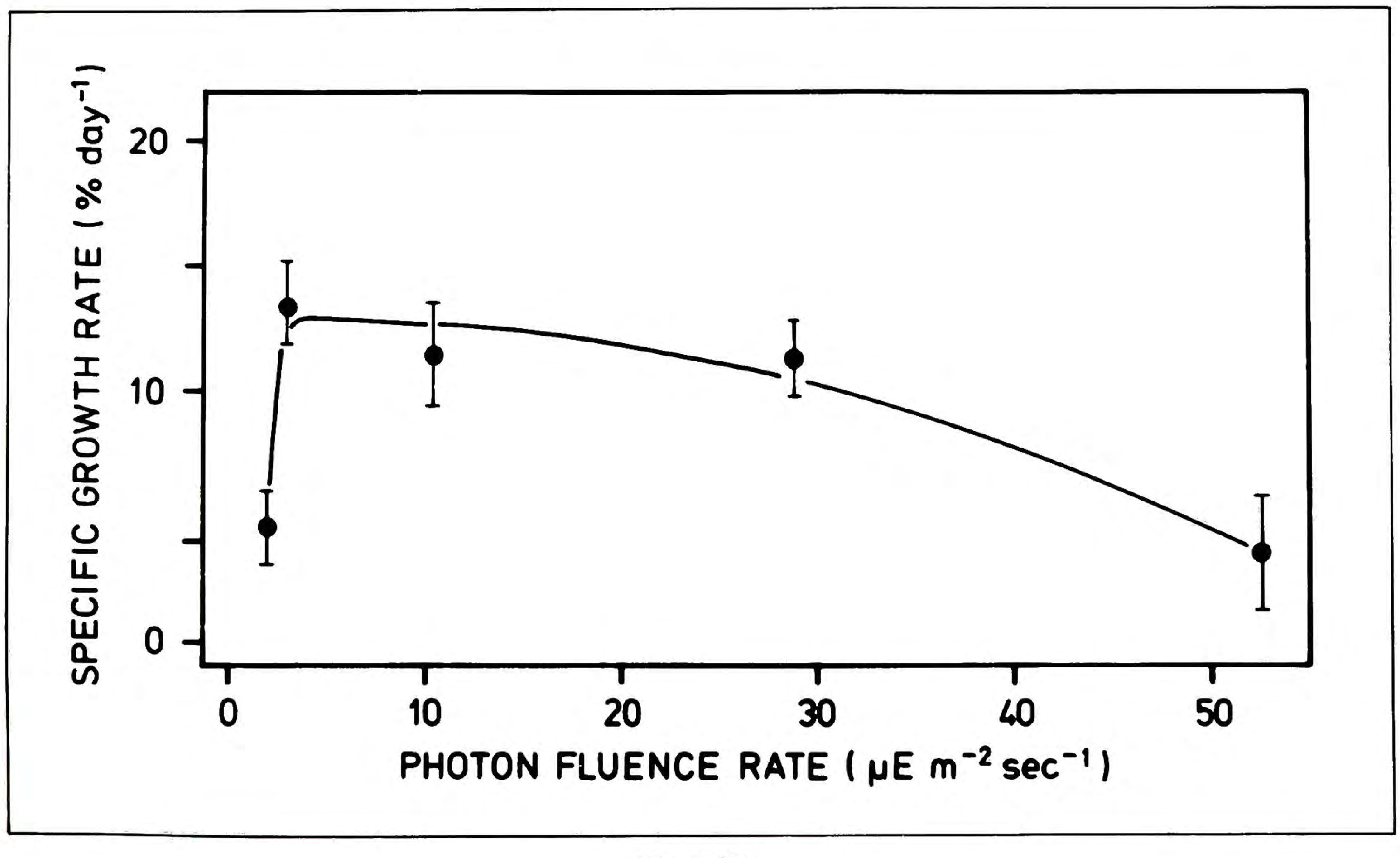


Fig.: 17.

Fig..18: Sporophyte of **Desmarestia ligulata,** 3 months after spore release and subsequent development of fertile gametophytes.

Fig. 19 - 22: Ascoseira mirabilis: Fig. 19 - 20: mating isogametes, **Fig. 21 - 22:** fusion of isogametes 72 resp. 90 h after gamete release.

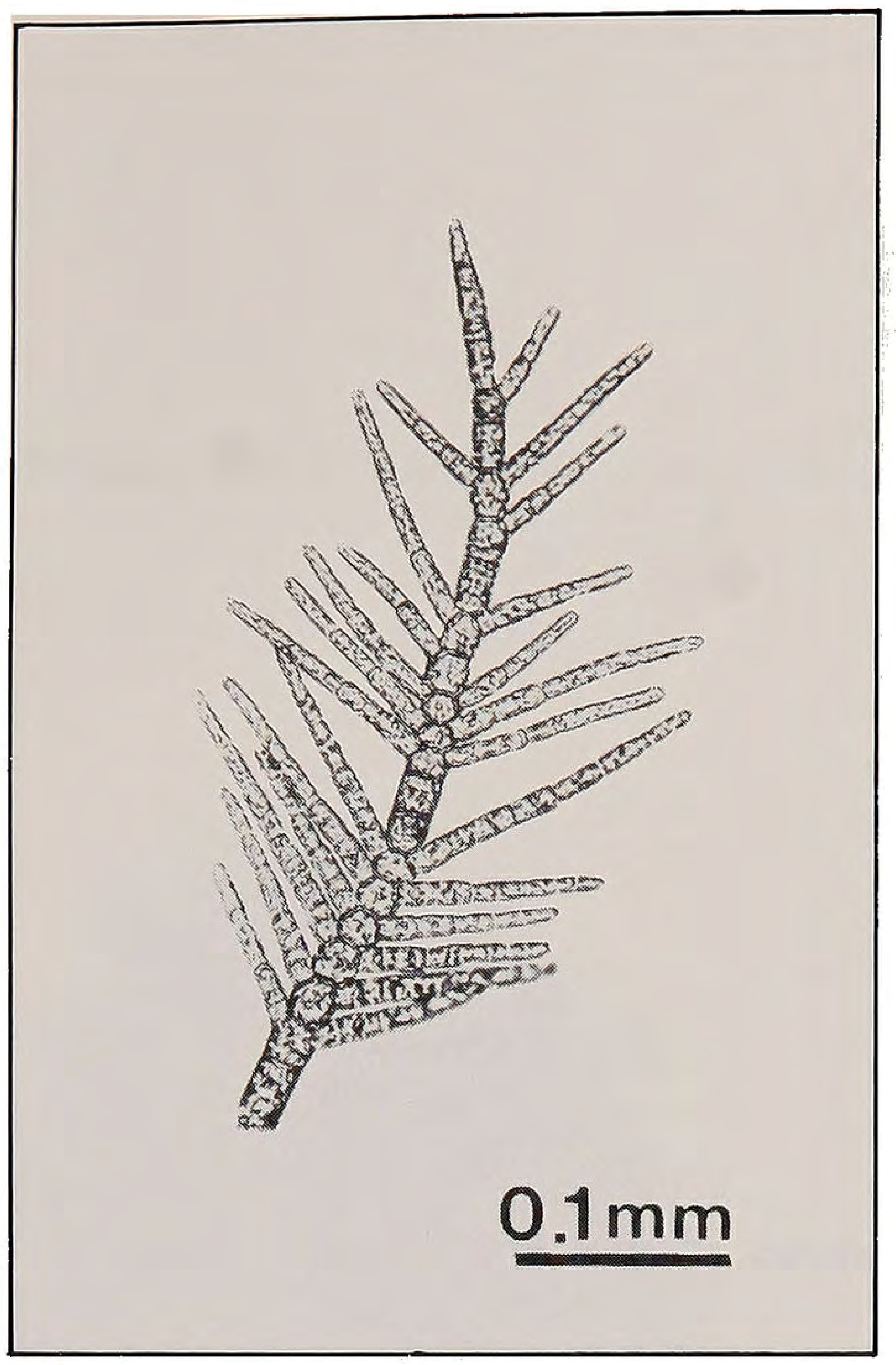
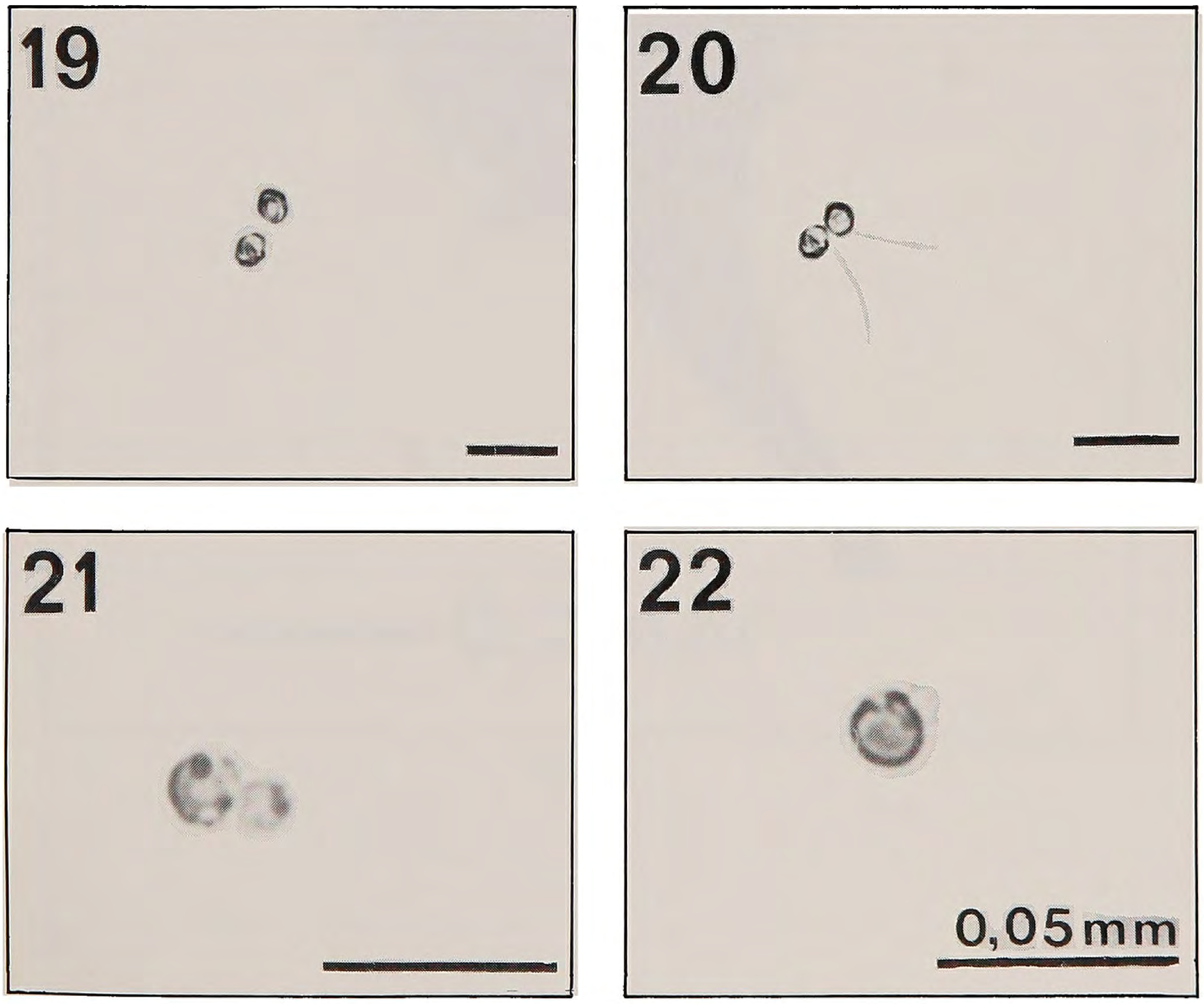


Fig. 18



Figs. 19 - 20 - 21 - 22

Fig. 23: Diploid plantlet of **Ascoseira mirabilis** after 3 months of cultivation.

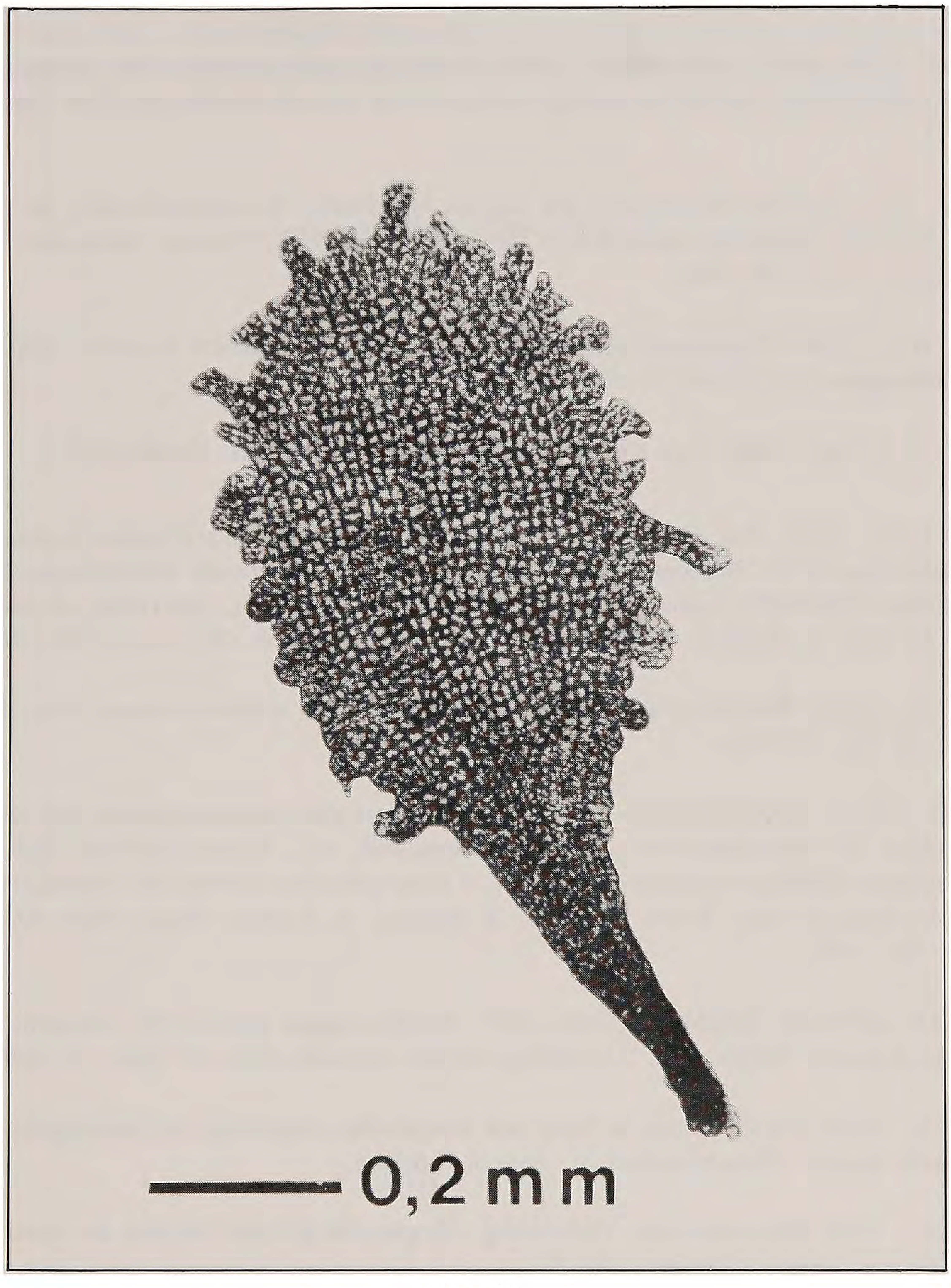


Fig.: 23

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