

Systematics and age of the Dasycladales

The order Dasycladales of the green algae includes macroalgae which grow in the shallow waters of tropical and subtropical shores as far north as the Mediterranean Sea. They are rarely found in deep water but have been observed to a depth of 20 m.

Dasycladales are now classified as members of the Class Ulvophyceae (GRAHAM et WILCOX, 2000), although VAN DEN HOEK *et alii* (1993), due to their unique combination of features, placed them in a discrete class, the Dasycladophyceae.

Dasycladales are unicellular algae which can grow to a length of 200 mm in the major dimension. They may have been even larger in past geological times. This is an enormous size for a unicell. Multicellular organisms gain stability by constructing walls of differentiated cells to demarcate their several functional elements, while some of the huge unicellular organisms gain stability by surrounding themselves with a calcareous coating. This is how the long unicellular Dasycladales gain enough stability to grow upright. When a calcified alga dies the coating may be preserved in the sediment as an impression of a once-living structure. Consequently, fossils of these coated algae exist, sometimes in great numbers, over relatively long periods of time. One of these long-enduring groups is the algal order called Dasycladales. It had already been in existence a long time at the dawn of the Cambrian period, about 570 million years ago. The fact that the Dasycladales have survived for so long a time with but few changes in distinctive features has led us to call them "living fossils".

Five families with nearly 200 genera, some with a large number of species, have evolved but most have become extinct. They flourished in the Middle Permian, the Early Jurassic, at the Jurassic/Cretaceous boundary and during the Palaeocene. In the Holocene new genera developed which, together with the genus *Acetabularia* that originated in earliest Oligocene times and some persistent Cretaceous genera, constitute the present-day representatives of the Order Dasycladales. It comprises two families, the Dasycladaceae and Polyphysaceae, with

10 genera and 38 species. Some genera are represented by only one or two species, and some species are rarely observed today.

Systematic classification

Section: Chlorophyta

Class: Ulvophyceae (Dasycladophyceae)

Order: Dasycladales PASCHER 1931

Family: Dasycladaceae KÜTZING 1843

Genera: *Batophora* J. AGARDH 1854, *Bornetella* MUNIER-CHALMAS 1877, *Cymopolia* LAMOUROUX 1816, *Chlorocladus* SONDER 1871, *Dasycladus* C. AGARDH 1828, *Neomeris* LAMOUROUX 1816

Species: *Batophora occidentalis* (HARVEY 1858) S. BERGER et KAEVER ex M. J. WYNNE 1998

B. oerstedii J. AGARDH 1854

Bornetella nitida (HARVEY 1857) MUNIER-CHALMAS 1877

B. oligospora SOLMS-LAUBACH 1893

B. sphaerica (ZANARDINI 1878) SOLMS-LAUBACH 1893

B. capitata (HARVEY 1857) J. AGARDH 1886

Cymopolia barbata LAMOUROUX 1816

C. vanbosseae SOLMS-LAUBACH 1893

Chlorocladus australasicus SONDER 1871

Dasycladus densus WOMERSLEY 1955

D. ramosus CHAMBERLAIN 1958

D. vermicularis (SCOPOLI) KRASSER 1898

Neomeris annulata DICKIE 1875

N. bilimbata KOSTER 1937

N. cokeri HOWE 1904

N. dumetosa LAMOUROUX 1816

N. mucosa HOWE 1909

N. stipitata (CHURCH 1895) HOWE 1909

N. vanbosseae (SONDER 1871) HOWE 1909

Family: Polyphysaceae KÜTZING (1843: 302, 311)

[formerly Acetabulariaceae NÄGELI (1847: 158, 252)]

Genera: *Acetabularia* J.V. LAMOUREUX (1812: 185), *Chalmasia* SOLMS-LAUBACH (1895: 32), *Halicoryne* HARVEY (1859: 333), *Parvocaulis* S. BERGER *et alii* (2003: 559)

Species: *Acetabularia acetabulum* (LINNAEUS) P. C. SILVA (1952: 255)

A. caliculus J.V. LAMOUREUX *in* QUOY *et* GAIMARD (1824: 621, pl. 90, figs. 6, 7)

A. crenulata J.V. LAMOUREUX (1816: 249, pl. 8, fig. 1)

A. dentata SOLMS-LAUBACH (1895: 23, pl. 1, fig. 11)

A. farlowii SOLMS-LAUBACH (1895: 27, pl. 3, fig. 1)

A. kilneri J. AGARDH (1886: 171-172)

A. major MARTENS (1866: 25, pl. 4, fig. 3)

A. peniculus (R. BROWN *ex* TURNER) SOLMS-LAUBACH (1895: 27-28, pl. 2, figs. 2 & 6-7)

A. ryukyuensis OKAMURA *et* YAMADA *in* OKAMURA [1932:71(68), pl. 285, figs. 5-12]

A. schenckii MÖBIUS (1899: 318-320, pl. 10, figs. 8-12)

Chalmasia antillana SOLMS-LAUBACH (1895: 32, pl. 3, figs. 2-3 & 5)

Halicoryne spicata (KÜTZING) SOLMS-LAUBACH (1895: 31-32, pl. 4, figs. 3, 7, 9 & 11)

H. wrightii HARVEY (1859: 333)

Parvocaulis clavata (YAMADA) S. BERGER *et alii*, *comb. nov.* (2003: 559)

P. exigua (SOLMS-LAUBACH) S. BERGER *et alii*, *comb. nov.* (2003: 559)

P. parvula (SOLMS-LAUBACH) S. BERGER *et alii*, *comb. nov.* (2003: 559)

P. polyphysoides (P. CROUAN et H. CROUAN *in* SCHRAMM et MAZE) S. BERGER *et alii*, *comb. nov.* (2003: 559)

P. pusilla (M. HOWE) S. BERGER *et alii*, *comb. nov.* (2003: 560)

Morphology

All Dasycladales have a similar and distinctive plan of construction. They are unicellular and radially symmetrical; although branching may occur and branched laterals are formed, no cell walls interrupt the continuity of the cytoplasm throughout the whole alga.

The main axis has a branched rhizoid at the base. This serves as a holdfast to a solid substratum. The main axis grows from its apical tip. The tip flattens periodically forming circularly arranged, branched laterals called whorls. The older whorls fall off leaving scars on the main axis. The length of time that the laterals persist varies according to species. Also the whorls may be modified in different ways according to species. In the genera *Bornetella*, *Cymopolia* and *Neomeris* of the family Dasycladaceae the laterals expand and fuse along their widened sides to form a cortex. Within the laterals, or in structures which develop from the laterals, gametangia may be formed. These structures are called gametophores and have a strict species-specific morphology.

The two living families of the Dasycladales are easy to distinguish by their gametophores or fertile whorls. In the Dasycladaceae the fertile whorls are branched laterals. Ovoid or spherical gametophores are attached to the branches by means of a short stalk. In the family Polyphysaceae the fertile whorls are composed of unbranched broad laterals with special basal parts, called *corona superior* and *corona inferior*, the latter being found only in the genus *Acetabularia*. In most species of the Polyphysaceae the fertile laterals are close together giving the impression of a cap composed of rays sited on the apex of the main axis.

Species may exhibit a certain amount of variability, primarily in size but also in color. These variations may be due in part to the amount of light and the availability of nutrients. Also in the family Polyphysaceae the number of cap rays may vary to a certain degree. In particular, *Acetabularia crenulata* is highly variable in the shape of the cap rays. This led to confusion when the species was described in the literature. Each of the cap rays of *A. crenulata* always has a spine

at its distal end. Cap rays of one cap may have spines that extend far out (one extreme) while the cap rays of another cap may have their spines embedded in the indented cap ray (the other extreme). However, there are many transitions. The variations are demonstrated in the several photographs of the cap rays of *A. crenulata*.

Life cycle

The life cycle starts with the growth of a diploid zygote. The zygote forms a branched rhizoid at the pole where the nucleus is located. Because the rhizoid fastens to a substratum this location of the nucleus ensures the possibility of regeneration when the rest of the cell is torn or grazed upon. At the opposite pole the zygote elongates and growth of the tip starts. After several days of growth, the tip flattens, and circularly arranged whorls of branched laterals are formed. Whorl formation is then followed by renewed tip growth. These events alternate periodically.

While calcium carbonate is deposited extracellularly around the main axis, the thin-walled tip and young laterals are free of calcification and thus exposed allow absorption of light and ingestion of nutrients.

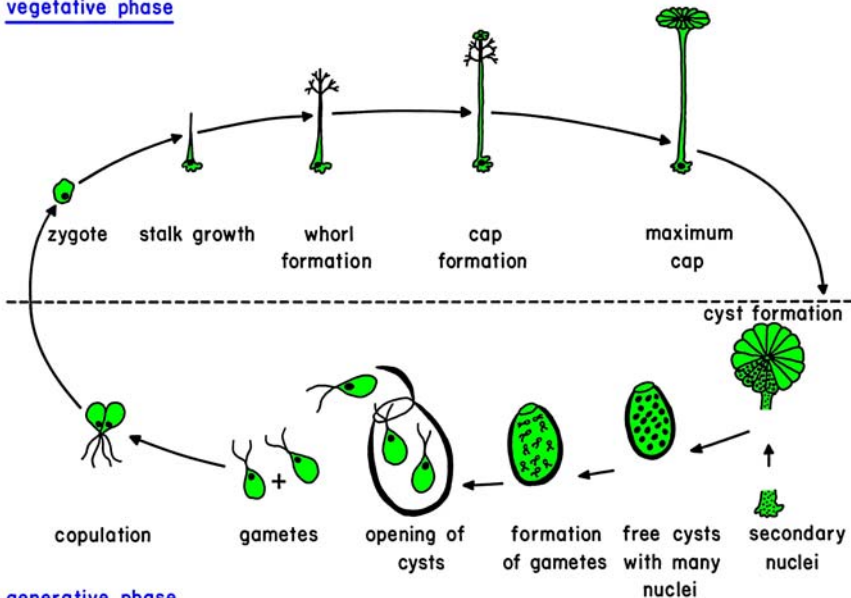
These first stages of development are identical for all Dasycladales. Differences occur during the morphogenesis, particularly during reproduction. Ovoid or spherical, short-stalked gametophores are formed on the laterals of the species belonging to the family Dasycladaceae. In the family Polyphysaceae the gametophores have the shape of cap-like structures formed by broad laterals. As soon as the gametophores are fully grown, the diploid (primary) nucleus in the rhizoid undergoes meiosis followed by many mitoses which result in a large number of haploid secondary nuclei. These secondary nuclei together with the cytoplasm containing plastids migrate up the main axis into the gametophores where each nucleus along with some cytoplasm is enclosed by a cell membrane and a cell wall to form the gametangium. An exception exists in the genera *Cymopolia* and *Dasycladus* where no gametangia form in the gametophores, for the gametophores themselves serve as gametangia.

The secondary nucleus in the gametangium undergoes many mitoses. At this point the bleached mother cell is nearly devoid of cytoplasm and disintegrates, so the gametangia tumble out and sink to the substrate.

The gametangia are very thick-walled, operculate cysts that can

survive a long time. When environmental conditions are favourable, a final division of the secondary nuclei occurs and gametes are formed with the nucleus located beneath the flagellar pole. The thick-walled cysts open by mean of a preformed lid, and the gametes swim out. Each gamete has two flagella of identical length and an eyespot which enables it to swim toward light (positively phototactic). The gametes look identical but are of different mating types. One gametangium releases gametes of only one type (+ or -), but one cell releases both types of gametes. Attracted by light, one + and one - gamete copulate at their flagellar poles and then fuse along their sides. The phototactically negative zygote swims to a dark place and settles with the flagellar pole on a solid substratum. The nuclei of the two gametes are located at the flagellar poles. This ensures that the nucleus of the zygote is at the pole selected for the formation of the rhizoid. The zygote starts to grow immediately.

vegetative phase



generative phase

Example of a life cycle: *Acetabularia* sp.

Significance of Dasycladales to paleontologists and biologists

Paleontologists appreciate the calcification of the Dasycladales. Many of the periods during which large quantities of calcareous sediments were produced were also times when calcareous algae flourished. And many calcareous coats preserved morphology well enough to enable paleontologists to follow the evolution of the Dasycladales through geologic time.

Existing Dasycladales live in littoral and sublittoral zones of warm-temperate and tropical oceans. As the environmental conditions of dasycladalean habitats are known, the preserved calcareous coats of fossils of these algae indicate the environment of the sediments of the large number of geological formations in which they have been found. Due to continental drift and changes of sea level dasycladalean fossils are found far from the present-day oceans, *e.g.* in the Alps and Carpathians. The fossils from these and other marine sediments now exposed contribute to the knowledge of paleoclimate and paleoecology (salinity, temperature, water depth, *etc.*). Some genera lived only during very restricted geological epochs, and consequently are used as indicator fossils for fine stratigraphic classification.

Contemporary Dasycladales attracted the attention of observers in ancient times. Pedianus DIOSCORIDES, who served as surgeon in the army of the Roman emperor NERO (37-68 A. D.), wrote a treatise in Greek describing the properties of about 600 medical plants. Among these was *Acetabularia* from the Mediterranean Sea which he called *Androsaces*. His treatise was copied many times throughout the centuries and designated in Latin as *De Medica Materia*.

The species *Acetabularia acetabulum* was especially admired due to its fragile beauty. It was called by the fishermen "mermaid's wineglass". Species were collected and described by scientific globetrotters in the 16th, 17th, 18th and 19th century. However, their taxonomic classification and body plan were recognized only at the end of the 19th and in the first half of the 20th century.

The unique characteristics of the body plan and the reproductive methods of the Dasycladalean cells make them favourable subjects for biological research:

They

- are extremely large unicellular organisms (depending on the species 2 – 200 mm long)
- show a pronounced morphogenesis forming rhizoid (holdfasts), branched laterals (nutrition) and species-specific gametophores (reproduction)
- reveal a pronounced polarity
- tolerate extensive surgical manipulations, recover from and heal wounds in a short time
- have a high capability to regenerate
- allow transplantation of cell segments between different individuals of the same or different species
- possess only one cell nucleus (during the vegetative phase of their life cycle) which, taking into account the volume of the cell's cytoplasm, has an enormous size (up to 200 μm in diameter)
- have this nucleus always located in the rhizoid, so production of anucleate cells is easy (by cutting off the rhizoid)
- allow easy manual isolation of the nucleus which may be kept alive outside the cell for more than 24 hours, microinjected or subjected to other treatments
- permit implantation of nuclei into anucleate fragments
- are easy to cultivate in the laboratory

Contribution of Dasycladales to knowledge of cell biology

It is to the credit of Joachim HÄMMERLING that *Acetabularia* flourished as a model subject for cell biological research. He succeeded in growing *Acetabularia* in laboratory cultures and discovered that through the entire vegetative phase of its life cycle this large unicell has only one nucleus and that this primary nucleus is always located in the rhizoid. HÄMMERLING made use of these features, as well as of the well-defined morphogenesis and of the high tolerance to surgery. By carrying out very clever and well-designed experiments he pioneered the knowledge in cell biology:

Long before the basis of the expression of genetic information was understood HÄMMERLING demonstrated that the nucleus is responsible for species-specific morphogenetic patterns. Based on the results which he obtained from growing cell fragments and anucleate cells, and by transplanting cell parts and implanting nuclei he postulated the existence of "morphogenetic substances". He showed that these substances are distributed with strict polarity.

Today we know that the morphogenetic substances are mRNPs (messenger RNA bound to proteins) and that their life-time is extended by protein binding. The polarity of HÄMMERLING's morphogenetic substances was eventually confirmed by the demonstration of a gradient of rRNA, mRNA and protein synthesis from the base to the apex of the cell. Morphogenetic substances have also been proven by the existence of a cap-specific mRNA. This RNA is produced early during growth of the cell but its translation is regulated by the cell nucleus which produces an inhibitor of cap formation for a certain time.

On the other hand, the cytoplasm too regulates activities of the nucleus. For example, only after the cap is mature will the nucleus undergo meiosis, but removal of the cap will inhibit nuclear division. A combination of an "old" nucleus close to meiosis with young cytoplasm returns the nucleus to its early state so meiosis is deferred until the cell is mature. *Vice versa* a combination of a young nucleus with

cytoplasm of a fully grown cell results in rapid meiosis.

Due to the open morphology of the Dasycladales it is easy to isolate chloroplasts devoid of any nuclear debris to study their autonomy. For example, it was shown for the first time in *Acetabularia* that while chloroplasts synthesize their own rRNA it is the nuclear genome that codes for their ribosomal proteins. This fact demonstrates an evolutionary loss of autonomy of these organelles. Another loss of chloroplast autonomy was demonstrated by considering Dasycladales as cell biological systems: the gene coding for dTMPkinase is located in the nucleus in *Acetabularia* while in *Batophora* it is located in the chloroplasts. In their evolutionary development the two genera separated 300 million years ago. An additional example of loss of organellar autonomy was given by a gene's involvement in the expression of circadian rhythmicity. Although this gene is located in the nucleus of higher plants, it is part of the chloroplast genome in the evolutionarily ancient *Acetabularia*.

Acetabularia also provided knowledge basic to the understanding of circadian rhythmicity. Anucleate cells keep their free-running circadian rhythm over several weeks. However, if a nucleus is implanted they change the phase of the rhythm to that of the mother cell of the nucleus. This observation together with other experiments making use of the implantation of the nucleus led to the detection that the nucleus initiates the circadian rhythm and determines its phase. However, the cytoplasm is capable of storing this information and regulating it on the level of translation. The observations of the circadian rhythm in *Acetabularia* led to the development of a "coupled translation membrane model". It postulates an "essential clock protein (ECP)". This protein was isolated from *Acetabularia*.

Acetabularia is also well suited for the study of cytoskeletal processes involved in the regulation of morphogenesis. And the fact that *Acetabularia* may be grown uncalcified in laboratory culture makes the cell transparent and allows investigations in cytoplasmic streaming which promotes the migration of chloroplasts and secondary nuclei. Elaborate morphogenetic models have been developed and tested experimentally in *Acetabularia*.

Thanks to Joachim HÄMMERLING and Hans-Georg SCHWEIGER, who recognized the importance of an extensive collection of Dasycladales, other species became available for experiments. Twenty-six species were ultimately maintained in laboratory cultures under standard conditions of light and temperature. They were originally housed in Germany at the Max-Planck-Institut für Zellbiologie where they were used for research and sent to scientists working in various countries on the fundamentals of cell biology. Now they are included in the Culture Collection of Algae at the University of Texas, Austin, in the USA. From there they are available to scientists all over the world:

Culture Collection of Algae (UTEX)

The University of Texas at Austin
MCDB Biology (A 6700)
205 W. 24th Street
Austin, TX 78712 - U. S. A.

[utalgae@uts. cc. utexas. edu](mailto:utalgae@uts.cc.utexas.edu)

[http://www. zo. utexas. edu/research/utex/](http://www.zo.utexas.edu/research/utex/)

Concluding remarks

As they are such favorite organisms in paleontological and cell biological research it is not surprising that an immense body of literature has accumulated covering the different fields of dasycladalean research. Three scientists who devoted many years to these fascinating organisms collected this literature and made the references available to other scientists interested in Dasycladales. Thousands of references on Dasycladales are listed on a CD:

BERGER S., GRANIER B. & BONOTTO S. (2004). - Dasycladales. Research publications from the beginning until the year 2000. - 2 illustr., 373 p., CD-ROM, ISBN 3-906166-12-0, A.R.G. Gantner Verlag K.-G., FL 9491 Rugell (distributed by Koeltz Scientific Books, D 61462 Königstein)

During the time that I devoted my scientific life to research on Dasycladales, I collected a large number of photographs of these beauties. The selection of these photographs presented here is intended to provide information about the diverse species, make work with the Dasycladales easier and no less importantly to provide a means to enjoy their aesthetics.

Acknowledgments

The photographs were taken during my many years of research in the Max-Planck-Institut für Zellbiologie in Wilhelmshaven and later in Ladenburg (both in Germany). I highly appreciate the theoretical and practical help of everyone who had a share in my work with the Dasycladales. I am indebted to Larry LITTLE and Nestor SANDER for critical reading of the English manuscript. My particular thanks go to Bruno GRANIER, whose highly motivated participation made the publication of these photographs first possible.

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Photo-Atlas

Dasycladaceae

Batophora

B. occidentalis

1. upper part of a gametophore-bearing cell
2. isolated whorls with gametophores
3. isolated whorl with gametophores

B. occidentalis var. *largoensis*

4. part of a field-collected cell with gametangia-bearing gametophores
5. part of a field-collected cell with gametangia-bearing gametophores
6. part of a field-collected cell with gametangia-bearing gametophores
7. upper part of a cell grown in the laboratory, f1 generation. The gametophores bear gametangia
8. upper part of a cell grown in the laboratory, f2 generation
9. isolated whorl with gametangia-bearing gametophores
10. gametangia shortly before release of gametes
11. chloroplasts of *B. oerstedii* (upper micrograph) and *B. occidentalis* var. *largoensis*

B. oerstedii

12. young cell
13. young cell
14. young cell
15. young cell
16. young cell with condensed cytoplasm around the nucleus
17. young cell with condensed cytoplasm around the nucleus
18. beginning of gametophore formation

19. beginning of gametophore formation
20. beginning of gametophore formation
21. beginning of gametophore formation
22. upper part of a cell with gametophores
23. upper part of a cell with gametophores
24. upper part of a cell with gametophores
25. part of a cell with gametophores
26. part of a cell with gametophores
27. part of a cell with gametangia-bearing gametophores
28. one whorl with gametangia-bearing gametophores

Bornetella

B. oligospora

29. young cell
30. two young cells with pseudocortex
31. young cell with pseudocortex
32. young cell with pseudocortex
33. immature cell

B. sphaerica

34. a cluster of young cells
35. a cluster of young cells
36. young cells
37. young cells
38. young cells
39. two young cells just after cortex formation
40. growing cell
41. growing cell
42. cell
43. cell
44. cell

45. faceted cortex of a cell shortly before formation of gametophores
46. enlarged faceted cortex of a cell shortly before formation of gametophores
47. a cluster of young and mature cells
48. two grown cells in a cluster of young cells
49. a cluster of young and mature cells
50. three cells with gametophores
51. cell with gametophores
52. cell with gametophores
53. longitudinal section through a cell with gametophores
54. longitudinal section through a cell with gametophores
55. cross section through a cell with gametophores

Chlorocladus

Chlorocladus australasicus

56. young cell
57. upper part of a cell with gametophores
58. upper part of a cell with gametophores
59. upper part of a cell with gametophores
60. part of a cell with cyst-bearing gametophores
61. part of a cell with cyst-bearing gametophores
62. part of a cell with cyst-bearing gametophores
63. one whorl with gametophores containing gametangia

Cymopolia

C. barbata

64. upper part of a cell
65. upper part of a cell
66. upper parts of two cells
67. upper parts of two cells

68. young cells growing out of a mature cell
69. *Cymopolia barbata* in its natural habitat (by courtesy of Larry B. LIDDLE, Long Island University, New York, USA)
70. *Cymopolia barbata* in its natural habitat (by courtesy of Larry B. LIDDLE, Long Island University, New York, USA)

C. vanbosseae

71. cell
72. cell
73. cross section
74. longitudinal section

Dasycladus

D. vermicularis

75. young cell
76. upper part of a young cell
77. beginning of gametangia formation
78. beginning of gametangia formation
79. part of a mature cell
80. part of a mature cell
81. most gametangia have released gametes
82. gametangia close to release of gametes

Neomeris

N. annulata

83. mature cell grown in laboratory culture
84. five mature cells as they appear in their natural habitat
85. mature cells collected in their natural habitat
86. gametophores made coherent by thick calcareous encrustation
87. *Neomeris annulata* in its natural habitat (by courtesy of Ikuko SHIHARA-ISHIKAWA, Institute of Physical and Chemical Research (RIKEN), Japan)

N. dumetosa

88. young cells
89. young cells, one with pseudocortex
90. young cell with pseudocortex
91. three cells
92. upper part of a cell
93. upper part of a cell
94. mature cell as it appears in its natural habitat
95. mature cell as it appears in its natural habitat
96. upper part of a mature cell as it appears in its natural habitat
97. upper part of a cell collected in its natural habitat
98. isolated laterals with gametophores

Polyphysaceae

Acetabularia

A. acetabulum

99. cell
100. cell
101. cell
102. three fully grown cells
103. fully grown cap
104. fully grown cap
105. upper part of a fully grown cell
106. upper part of a fully grown cell
107. cell with gametangia (cysts)
108. upper part of a cell with gametangia
109. cap with gametangia
110. cap with gametangia
111. cap with gametangia
112. field-collected rock with *A. acetabulum*
113. upper part of a cell growing in its natural habitat
114. upper parts of two cells growing in their natural habitat
115. cap of a cell growing in its natural habitat
116. cap of a cell growing in its natural habitat
117. cap of a cell growing in its natural habitat

A. caliculus

118. young cell with persistent whorls
119. cell with a young cap
120. cell with a young cap
121. cell with a young cap
122. upper part of a cell with a young cap

- 123. upper part of a cell with a gametangia (cyst)-bearing cap
- 124. mature cell opening to release gametangia

A. crenulata

- 125. cell
- 126. cap
- 127. cell
- 128. cell
- 129. cell
- 130. cell
- 131. cell
- 132. cell
- 133. young cap
- 134. young cap
- 135. cap
- 136. cap
- 137. cap of a cell as it appears in its natural habitat, seen from below
- 138. cap of a cell as it appears in its natural habitat
- 139. cap rays of a cell as it appears in its natural habitat
- 140. cap rays of a cell as it appears in its natural habitat
- 141. cap rays of a cell as it appears in its natural habitat
- 142. cap rays of a cell as it appears in its natural habitat
- 143. cap rays of a cell as it appears in its natural habitat
- 144. cap rays of a cell as it appears in its natural habitat. Rays open at their tips to release gametangia (cysts)
- 145. part of a gametangia-bearing cap collected in the natural habitat

A. dentata

- 146. *A. dentata* growing in its natural habitat (by courtesy of Ikuko SHIHIRA-ISHIKAWA, Institute of Physical and Chemical

Research (RIKEN), Japan)

147. *A. dentata* (right) and *P. parvula* in their natural habitat
148. cap of a cell in its natural habitat
149. upper part of a cell in its natural habitat
150. cap of a cell as it appears in its natural habitat
151. cap of a cell collected in its natural habitat seen from below
152. cell with gametangia (cysts)
153. cap
154. cap

A. farlowii

155. one cell
156. cap with gametangia (cysts) seen in the natural habitat
157. cap with gametangia as it appears in the natural habitat
158. several calcified caps as they appear in the natural habitat
159. young cap
160. upper part of a cell with gametangia
161. cap with gametangia

A. kilneri

162. cell with very young cap
163. cell with immature cap
164. cell with immature cap
165. cell with not fully grown cap
166. cell
167. cell
168. cell
169. cell
170. cap with gametangia (cysts)

A. major

- 171. one cell
- 172. upper part of a cell
- 173. cap from above

A. peniculus

- 174. cell
- 175. cell with gametangia (cysts)
- 176. upper part of a cell
- 177. upper part of a cell starting to form gametangia
- 178. upper part of a cell
- 179. upper part of a cell with gametangia
- 180. cap with gametangia
- 181. cap with gametangia
- 182. isolated gametangia (cysts)

A. ryukyuensis

- 183. *A. ryukyuensis* in its natural habitat (by H.G. SCHWEIGER, Max-Planck-Institut, Ladenburg, Germany)
- 184. *A. ryukyuensis* in its natural habitat (by H.G. SCHWEIGER, Max-Planck-Institut, Ladenburg, Germany)
- 185. *A. ryukyuensis* in its natural habitat (by H.G. SCHWEIGER, Max-Planck-Institut, Ladenburg, Germany)
- 186. *A. ryukyuensis* in its natural habitat (by H.G. SCHWEIGER, Max-Planck-Institut, Ladenburg, Germany)
- 187. cells on a rock collected in their natural habitat (by courtesy of Ikuko SHIHIRA-ISHIKAWA, Institute of Physical and Chemical Research (RIKEN), Japan)
- 188. *A. ryukyuensis* and *Halicoryne* spec. growing in their natural habitat (by courtesy of Ikuko SHIHIRA-ISHIKAWA, Institute of Physical and Chemical Research (RIKEN), Japan)
- 189. cell grown in laboratory culture
- 190. cell grown in laboratory culture

191. upper part of a cell grown in laboratory culture

192. cap of a cell grown in laboratory culture

A. *schenckii*

193. cell

194. cell

195. cell

196. upper part of a cell

197. upper part of a cell

198. upper part of a cell

199. upper part of a cell with gametangia (cysts)

200. cap of a cell grown in laboratory culture

201. cap with gametangia (cysts) of a cell grown in laboratory culture

202. cap revealing the calcification of gametangia

203. cap revealing the calcification of gametangia

204. cap revealing the calcification of gametangia

205. part of a cap revealing the calcification of gametangia seen from below

206. part of a cap revealing the calcification of gametangia

207. part of a cap revealing the calcification of gametangia

Chalmasia

C. *antillana*

208. cell

209. upper part of a cell

210. upper part of a cell with gametangia (cysts)

211. upper part of a cell with gametangia

212. cap with gametangia

213. part of a gametangia-bearing cap grown in laboratory culture, partially calcified, especially the lids of the gametangia

- 214. gametangia-bearing cap as it appears in its natural habitat
- 215. gametangia-bearing cap as it appears in its natural habitat
- 216. gametangia-bearing cap as it appears in its natural habitat
- 217. gametangia-bearing cap as it appears in its natural habitat
- 218. gametangia-bearing cap as it appears in its natural habitat
- 219. gametangia-bearing cap collected in its natural habitat
- 220. gametangia-bearing cap collected in its natural habitat

Halicoryne

H. spicata

- 221. young cell
- 222. young cell
- 223. upper part of a young cell
- 224. upper part of a cell, in part with gametangia
- 225. upper part of a cell with gametangia (cysts) growing in its natural habitat
- 226. upper parts of two cells growing in their natural habitat
- 227. upper parts of two cells, in part with gametangia, grown in their natural habitat
- 228. upper part of a cell with gametangia growing in its natural habitat
- 229. part of a cell with calcareous-spicule embedded gametangia growing in its natural habitat
- 230. lime spicules collected in the field
- 231. upper part of a cell, SEM micrograph

Parvocaulis

P. clavata

- 232. a cluster of entangled cells

- 233. a cluster of entangled cells
- 234. a cluster of very young and cap-bearing cells
- 235. cell
- 236. three cells
- 237. cap prior to gametangia (cyst) formation
- 238. cap prior to gametangia formation
- 239. two gametangia-bearing caps
- 240. gametangia-bearing cap

P. exigua

- 241. cells in several stages of development, growing on a rock
- 242. cells in several stages of development, growing on a rock
- 243. several cells, growing on a rock
- 244. several cells growing on a rock
- 245. cap of a cell, growing on a rock
- 246. caps of cells, growing on a rock
- 247. cap with gametangia (cysts), growing on a rock
- 248. cell with gametangia in cap and stalk, growing on a rock
- 249. cell with immature cap
- 250. cap with gametangia

P. parvula

- 251. cell
- 252. cell
- 253. cell
- 254. cell
- 255. cell with gametangia (cysts)
- 256. cell with gametangia
- 257. cell with gametangia
- 258. cell with gametangia
- 259. four cells in different stages of development

260. *P. parvula* growing on a rock

261. *P. parvula* growing on a rock

P. polyphysoides

262. cap with gametangia (cysts) and very young cap in a cluster of entangled young cells

263. cap

264. cap with gametangia

265. cap with gametangia

266. immature cap of a cell growing in its natural habitat

P. pusilla

267. a cluster of entangled cells, three of which are cells with gametangia (cyst)-bearing caps

268. cap with gametangia

269. several cells

270. several cells

271. cell with cap

272. three cells, two with gametangia

273. cap

274. cap

275. cap with gametangia

276. cap with gametangia

277. cap with gametangia

Velum of *Parvocaulis*

278. velum of *P. pusilla*

279. velum of *P. pusilla*

280. velum of *P. polyphysoides*

281. velum of *P. polyphysoides*

282. velum of *P. clavata*

283. velum of *P. clavata*

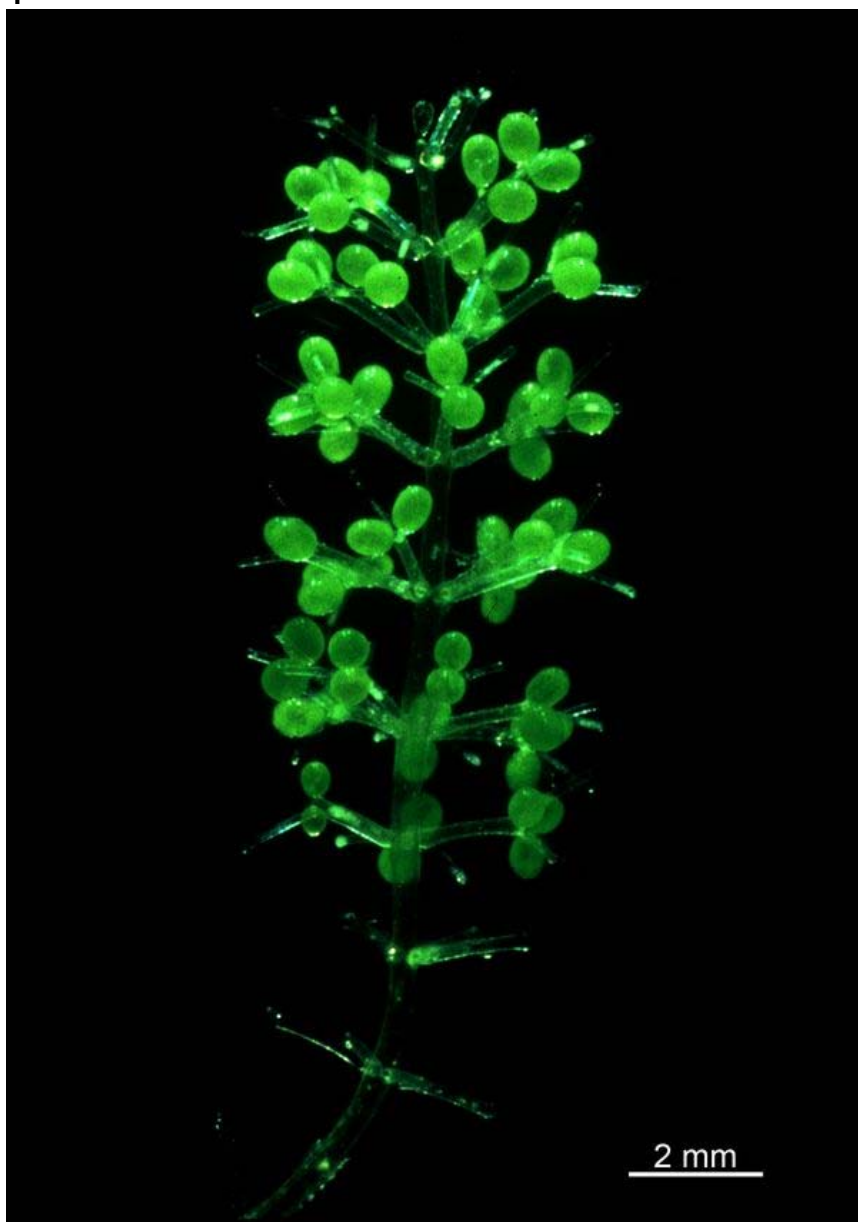
- 284. velum of *P. clavata*
- 285. velum of *P. clavata*
- 286. velum of *P. exigua*
- 287. velum of *P. exigua*
- 288. velum of *P. exigua*

Example of a life cycle: the Polyphysaceae

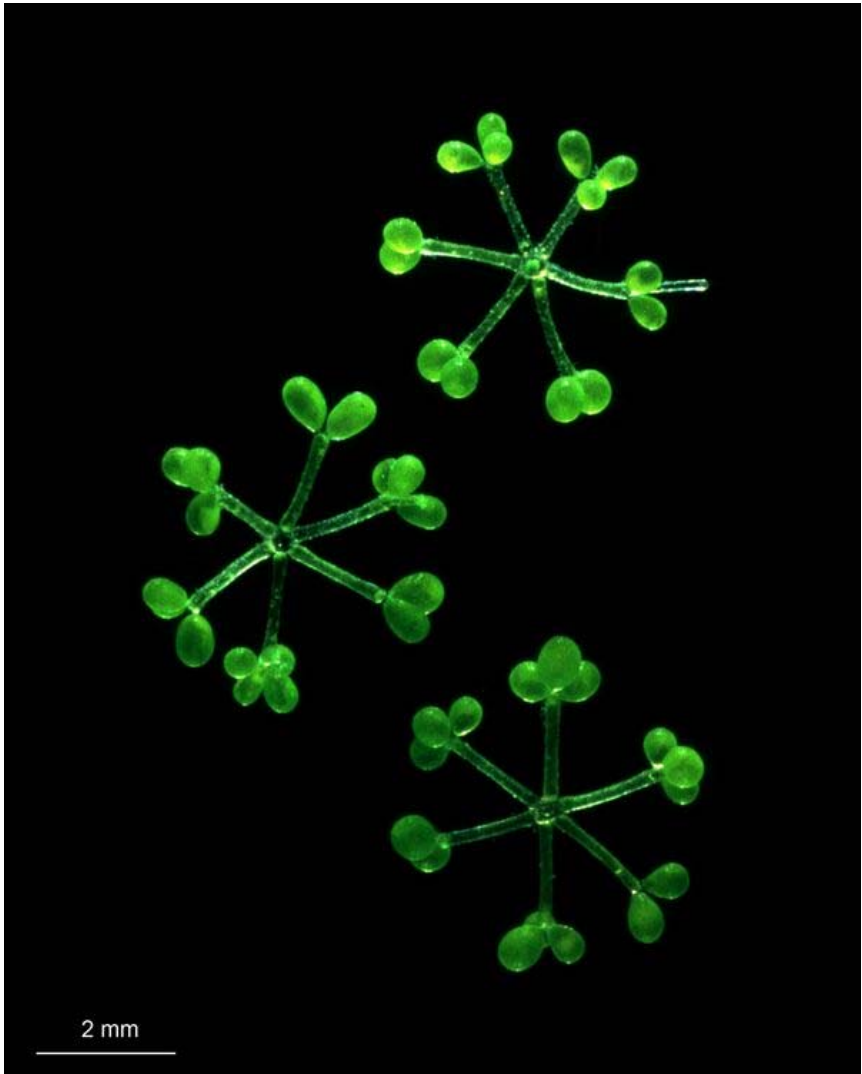
- 289. many germinating zygotes, about 10 days old. *A. acetabulum*
- 290. growing zygote, nucleus visible. *A. acetabulum*
- 291. rhizoid starts to form, nucleus still visible. *A. acetabulum*
- 292. young cell before whorl formation (20 days old). *A. acetabulum*
- 293. young cell before whorl formation. *A. acetabulum*
- 294. growing tip. *A. acetabulum*
- 295. whorl formation stage 1. *A. acetabulum*
- 296. whorl formation stage 2. *A. acetabulum*
- 297. whorl formation stage 3. *A. acetabulum*
- 298. whorl formation stage 4. *A. acetabulum*
- 299. whorl formation stage 5. *A. acetabulum*
- 300. growth of a new tip after whorl formation. *A. acetabulum*
- 301. growth of a new tip after whorl formation. *A. acetabulum*
- 302. whorl formation stage 1. *A. acetabulum*
- 303. whorl formation stage 2. *A. acetabulum*
- 304. whorl formation stage 3. *A. acetabulum*
- 305. whorl formation stage 4. *A. acetabulum*
- 306. growth of a new tip after whorl formation. *A. acetabulum*
- 307. upper part of a cell with several sets of whorls. *A. caliculus*
- 308. cell with whorls. *A. acetabulum*

309. lower part of a cell with rhizoid. *A. acetabulum*
310. two rhizoids. *A. acetabulum*
311. nucleus of a cell approaching cap formation (nucleus is compressed into the stalk, so it is visible). *A. acetabulum*
312. cell with young cap. *A. kilneri*
313. young cap. *A. crenulata*
314. young cap. *A. schenckii*
315. fully grown cap. *A. acetabulum*
316. several stages of gametangia (cyst) formation in one cap. *A. acetabulum*
317. cap with gametangia. *A. acetabulum*
318. cap with gametangia. *A. acetabulum*
319. cap with gametangia. *A. farlowii*
320. cap with gametangia. *A. peniculus*
321. gametangia-bearing cell. *P. parvula*
322. cap with gametangia. *P. exigua*
323. opening of cap rays to release gametangia. *A. crenulata*
(in natural habitat)
324. opening of cap rays to release gametangia. *A. caliculus*
325. gametangia. *P. parvula*
326. gametangia. *P. parvula*, left, and *A. acetabulum*, right
327. release of gametes. *A. acetabulum*
328. release of gametes. *P. parvula*
329. release of gametes. *A. acetabulum*
330. release of gametes. *A. acetabulum*
331. several stages of release of gametes. *A. acetabulum*
332. gametes. *A. acetabulum*

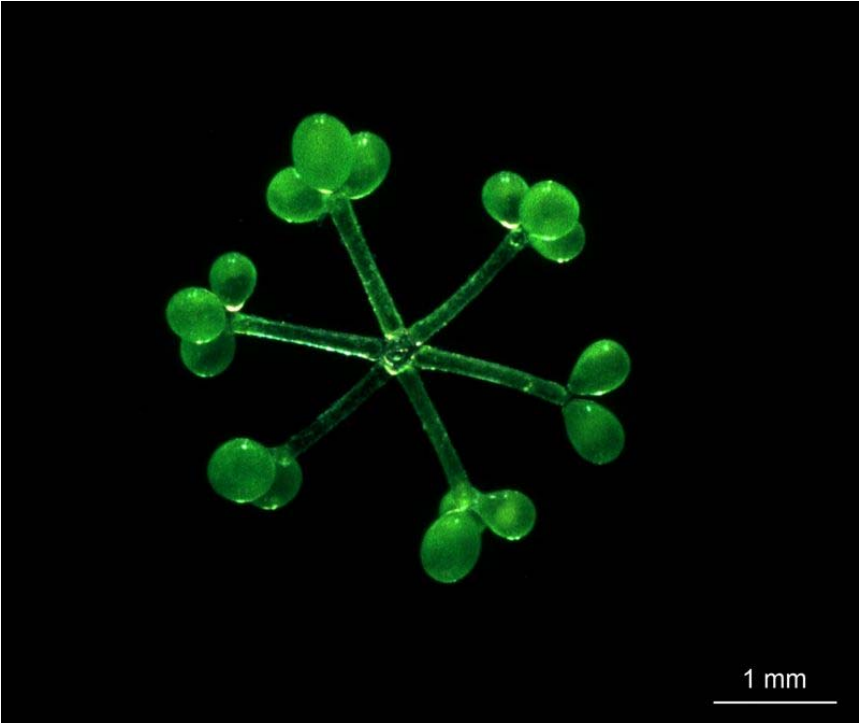
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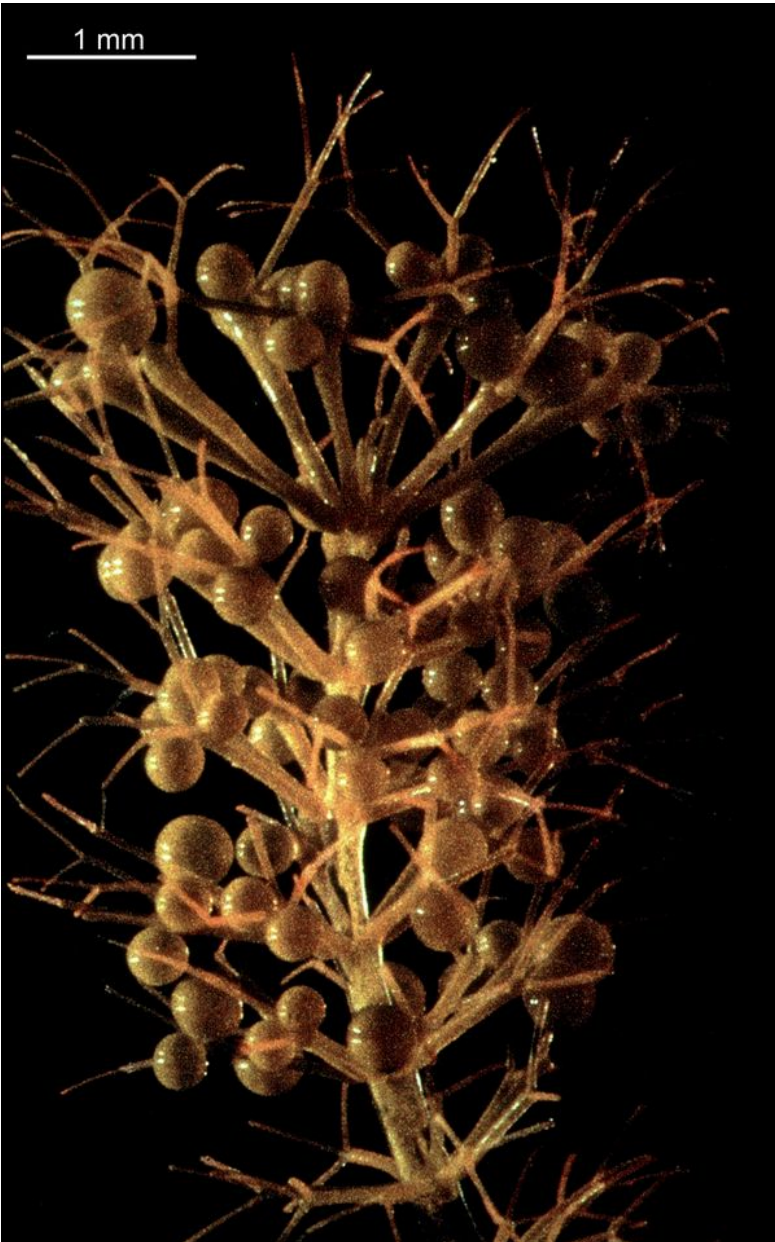
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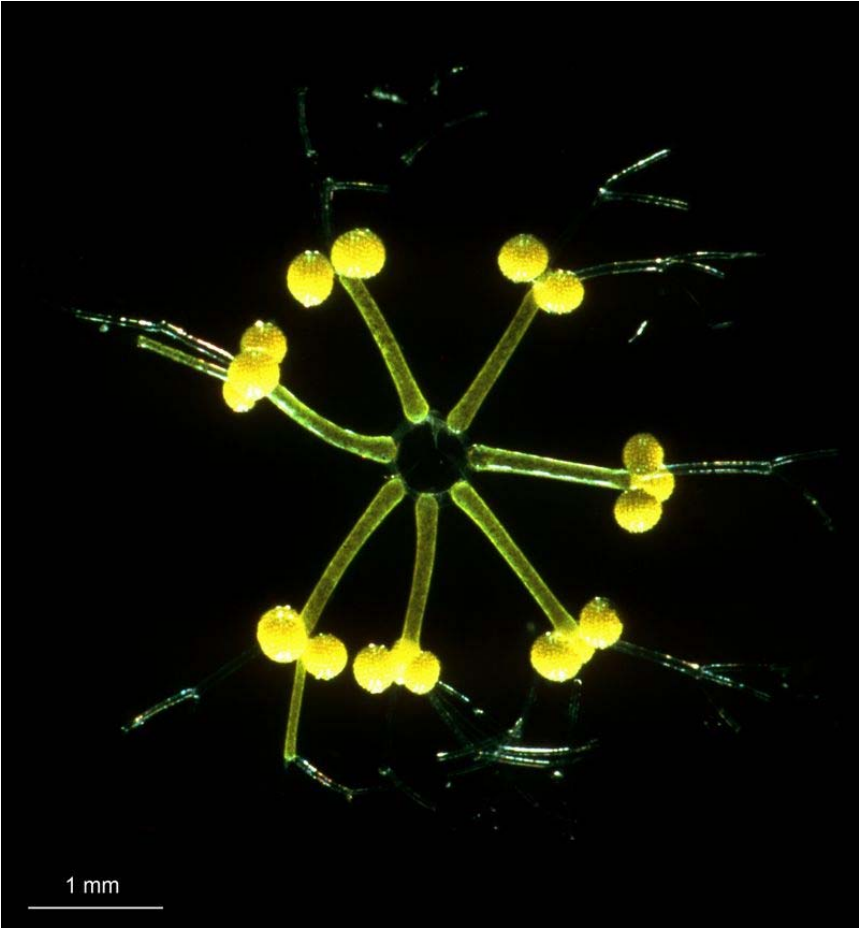
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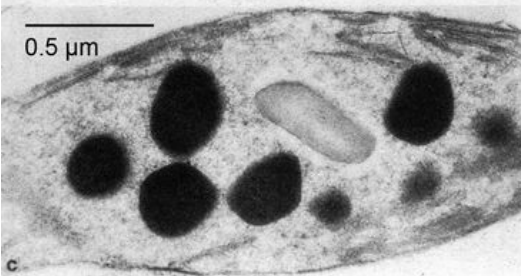
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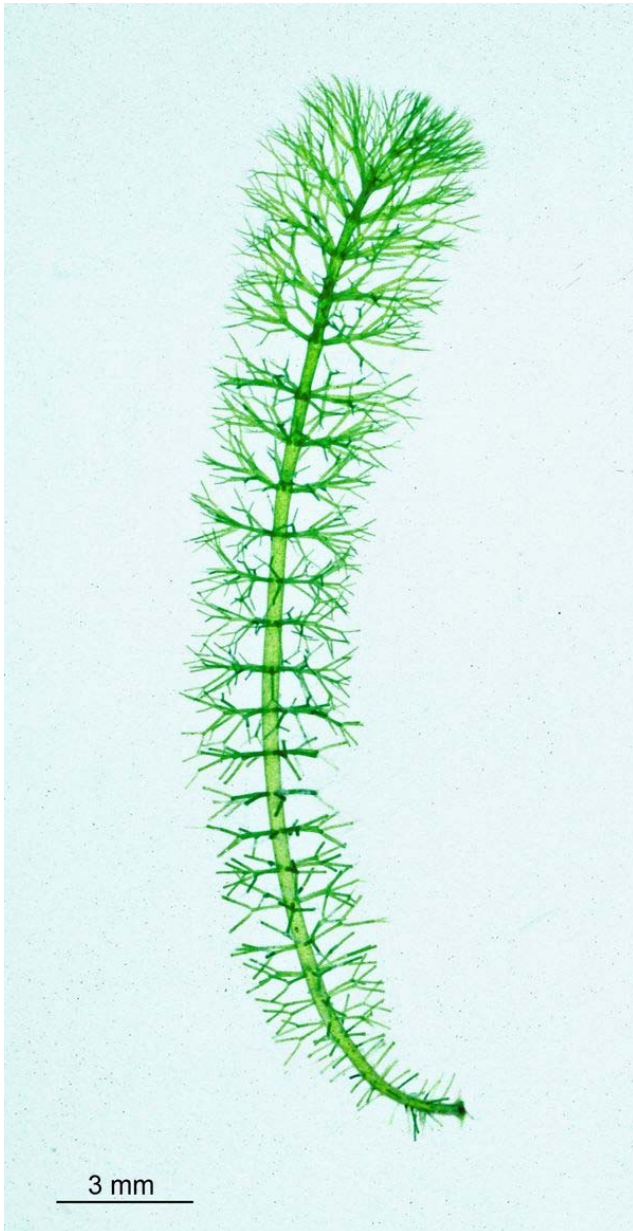
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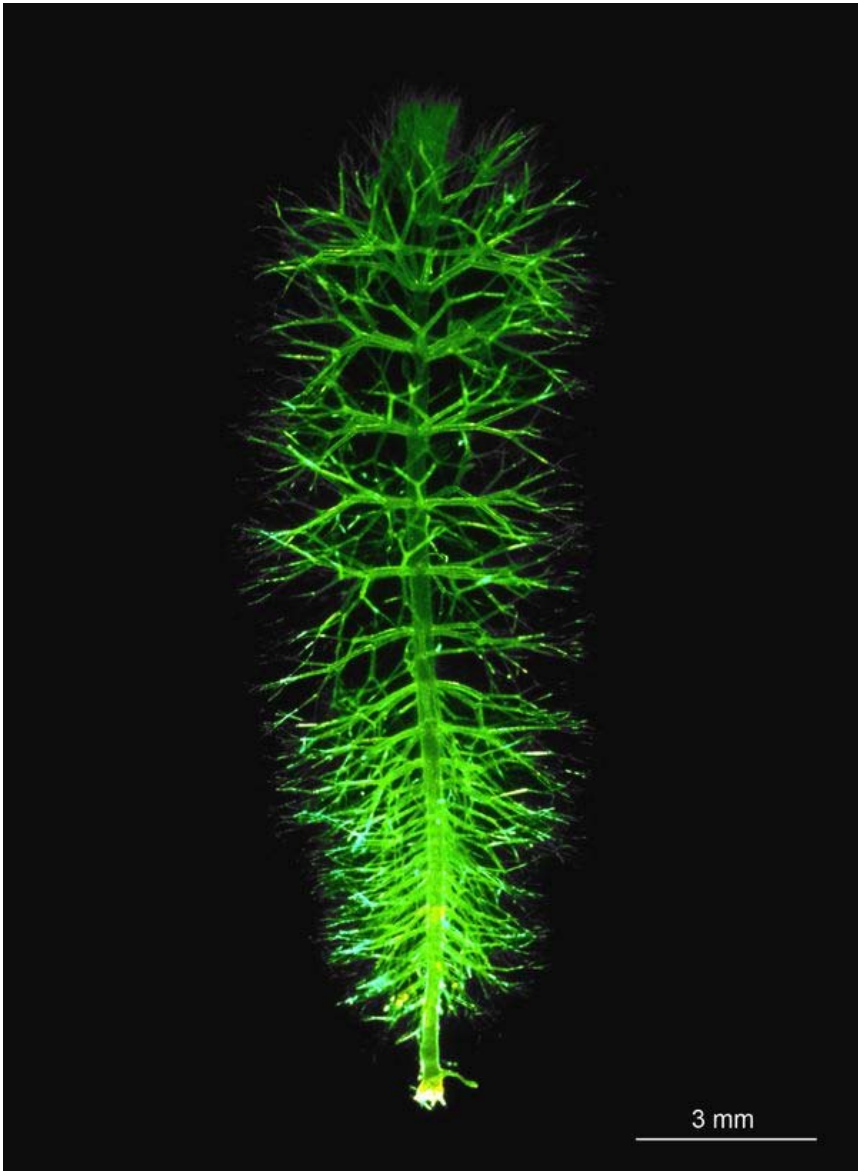
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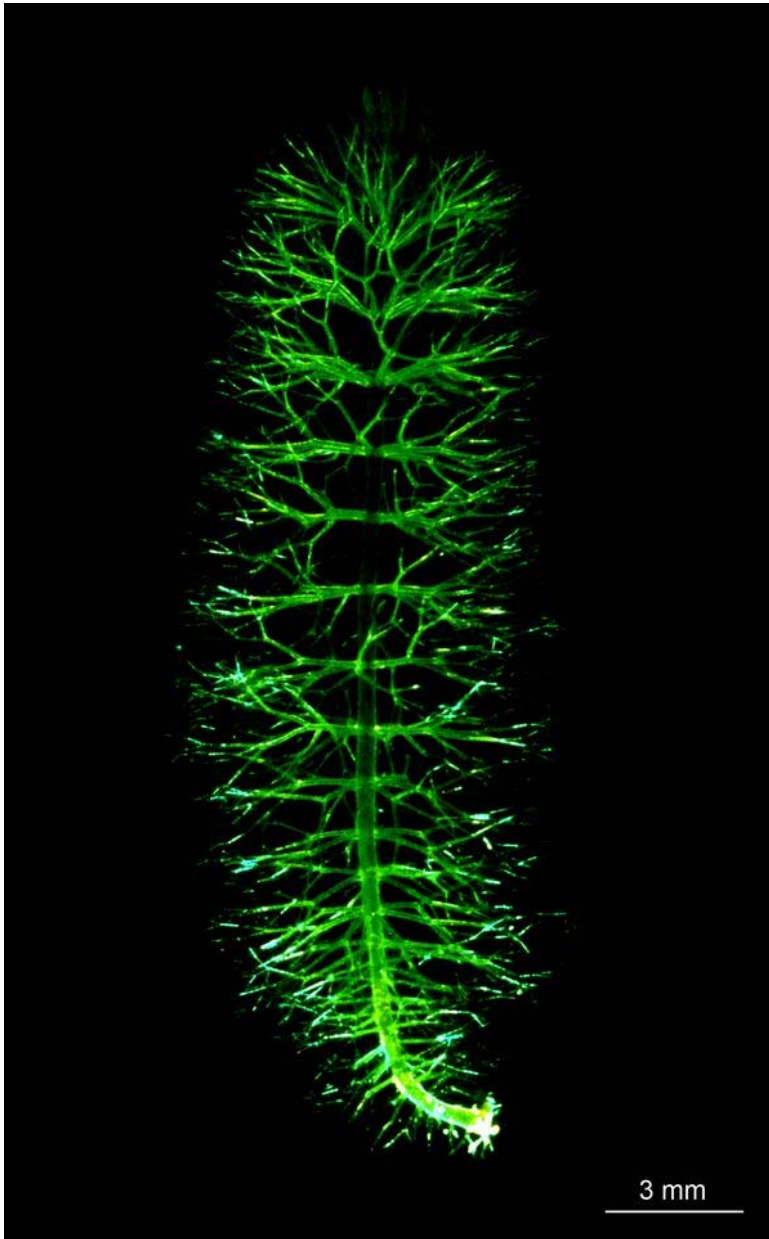
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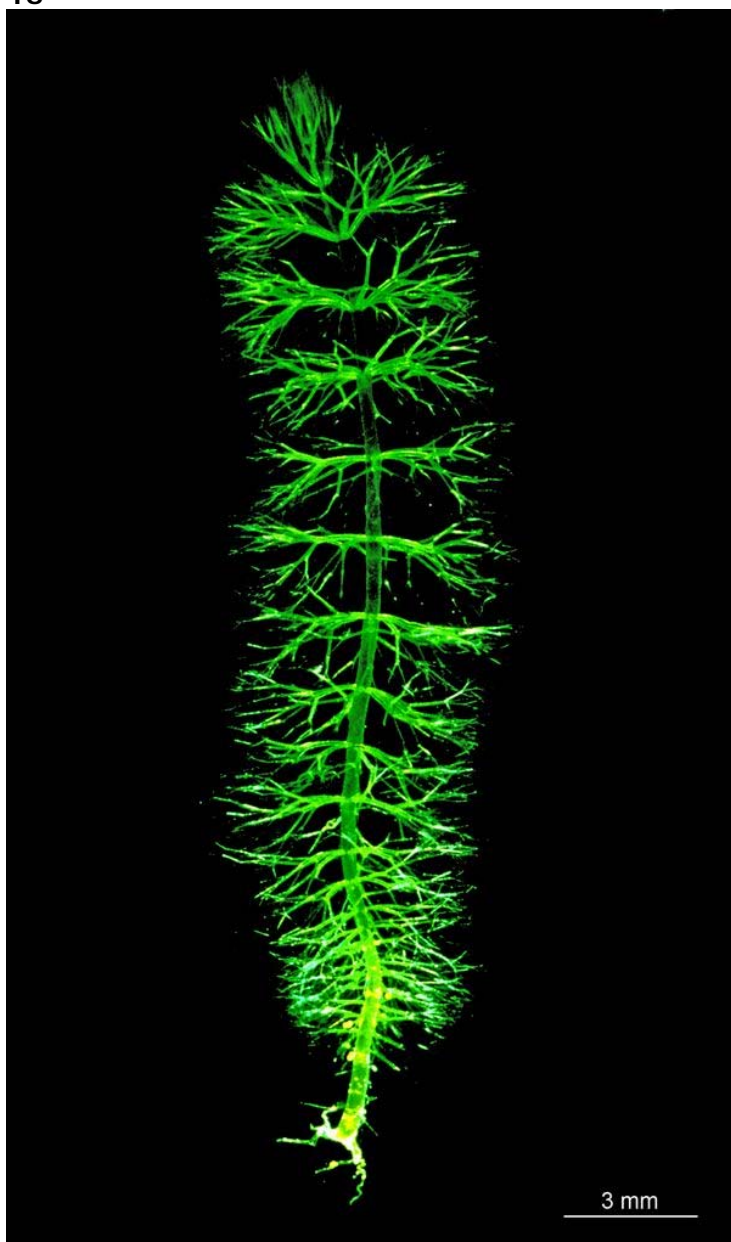
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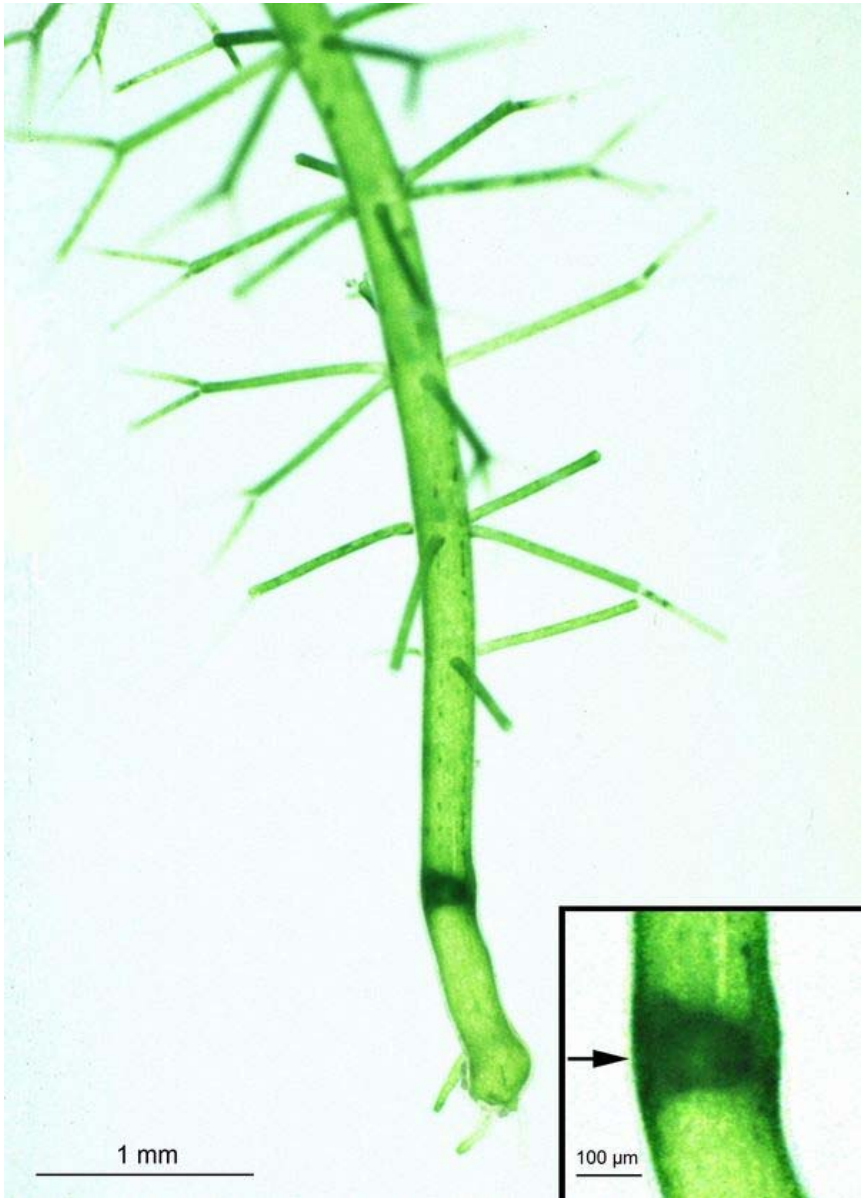
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