CERAMIUM DIAPHANUM (LIGHTF.) ROTH, 
ITS VARIETIES AND FORMS AS FOUND 
IN THE NETHERLANDS

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INTRODUCTION

The genus *Ceramium* is one of the most difficult genera of the Algae. The species vary a great deal and, even when the differential characters are carefully chosen, still are connected by transitions. Moreover, there is a strong reticulate relationship within the genus, and henceforth there exists a great diversity of opinion regarding the limits of taxa of various ranks. The author is much indebted to the directors of the "Rijksherbarium" at Leiden, the Botanical Museum at Copenhagen, the "Universitäts Botaniska Museum" at Lund, "Botaniska Museet" at Uppsala, as well as to Dr L. G. Sjöstedt, who have rendered it possible to study a number of types, viz. of Kützing, Kylin, Petersen and Sjöstedt. Unfortunately, there was no possibility of studying the types of *Ceramium diaphanum* (Lightf.) Roth var. *diaphanum*, var. *tenussimum* Roth * and f. *corticatulo-strictum* Kylin. It is to be regretted that Petersen failed to indicate type-specimens. The result is that the type-collections of his taxa are sometimes very extensive.

The author is also much indebted to the directors of the "Rijksherbarium" at Leiden (L.), the "Zoölogisch Station" of the "Nederlandsche Dierkundige Vereeniging" at Den Helder (N.D.V.) and the herbaria of the Universities of Amsterdam (A.) and Utrecht (U.) for putting at his disposal their Netherlands' material of *Ceramium diaphanum* (Lightf.) Roth. It is a great pleasure to the author to express his particular gratitude to Dr Josédhine Th. Koster for her extensive assistance regarding this difficult investigation as well as to Dr R. A. Maas Geesteranus and Dr S. J. van Ooststroom for giving some nomenclatural advice. In the text most literature references are abbreviated; for full titles the bibliography at the end of the paper should be consulted.

* According to the Director of the Staatl. Mus. f. Naturk. u. Vorgesch., Oldenburg, Germany (in a letter to the Rijksherbarium, Leiden, 15 May 1951) the herbarium Roth has been moved from this museum to the Botanical Museum, Berlin, where it was destroyed during the war, 1940–1945.
ON THE DELIMITATION OF CERAMiUM DIAPhANUM (Lightf.) Roth


However, C. cimbricum H. Petersen (Fig. 9), brought to C. strictum (Kütz.) auct. f. stricto-tenuissimum (H. Petersen) by Sjostedt (1928), does not belong to C. diaphanum. C. cimbricum seems to be a good species because of the very slight cortication and the small number of pericentral cells, being 4—5 in the said species and 6-8 in C. diaphanum. Beside the type material the author had at his disposal some specimens, washed ashore near Katwijk (Netherlands) attached to a bunch of cork, 17th November 1950, Lucas 888 (L.). Most probably they originate from the Channel.

Ceramium strictum (Kütz.) Harv. is based on Gongroceras strictum Kütz. The type of this species appears to belong to Ceramium deslongchampsii Chauv., so C. strictum (Kütz.) Harv. is a synonym of Ceramium deslongchampsii Chauv. Moreover Roth (1806) had already previously described a species Ceramium strictum which has been brought to Hutchinsia by Lyngbye. According to De Toni Hutchinsia stricta (Roth) Lyngb. is a synonym of Polysiphonia urceolata (Lightf.) Grev. Since it is impossible to examine the type specimen this question can not be settled. From Roth's description one gets the impression that his C. strictum is not the same species as C. diaphanum.

THE DIFFERENTIAL CHARACTERS

A. The series var. diaphanum (Lightf.) Roth — var. zostericola (Thur.) Feldm. Maz. — var. tenuissimum Roth.

In this series the thickness of the thallus-base decreases gradually from about 250—600 μ in var. diaphanum and about 170—300 μ in var. zostericola to about 100—200 μ in var. tenuissimum and at the same time the height of the corticated zones decreases from about 180—600 μ via about 75—170 μ to about 50—120 μ, whereas the length of the hyaline internodes increases from about 1—4 times via about 1—6 times to 1—10 times the width. The number of lateral ramuli is great in var. diaphanum (except f. modificatum H. Petersen and f. corticatum (Kylin) Kylin), small or none in var. zostericola and var. tenuissimum. The tetrasporangia are not or only slightly projecting in var. diaphanum, faintly so (in rare cases much) in var. zostericola, and considerably so in var. tenuissimum.

H. Petersen, H. Kylin, L. Kolderup Rosenvinge, L. G. Sjöstedt, T. Levrings and A. C. J. van Goor consider the possession of gland-cells to be a good discriminating feature of the var. tenuissimum Roth. However, they noticed that the number of these cells vary a great deal and may be very small. Mrs. G. Feldmann-Mazoyer (1940) does not consider this feature a good one. She observed gland-cells in young specimens of var. diaphanum. The author saw a fruiting
A specimen of this variety with some scattered gland-cells and therefore agrees with Mrs. Feldmann-Mazoyer. The gland-cells are scarce in adult specimens of var. diaphanum, but they are more frequent in var. zostericola and var. tenuissimum, where their number is sometimes so great that they are situated in two whorls.

Another feature of var. tenuissimum mentioned by Petersen and Kylin is the possession of dentate apices. These are mostly formed by gland-cells, though sometimes by ordinary cells (this may also be the case when gland-cells exist in the same specimen). They are found in var. diaphanum and var. zostericola, and especially in var. tenuissimum, being most frequent where the apices are more or less incurved. In var. zostericola the apices are less often incurved than in the other varieties and consequently they are less often dentate. Dentate apices are to be found in other species as well (e.g. C. deslongchampsi Chauv.).

B. Var. diaphanum and forma medium Sjöstedt; forma modificatum H. Petersen and forma corticatum (Kylin) Kylin; var. zostericola (Thur.) Feldm. Maz. and forma corticatulo-strictum Kylin.

Forma medium, f. corticatum and f. corticatulo-strictum differ from var. diaphanum, f. modificatum and var. zostericola respectively in that the cortex in the basal part of the plants proliferate upwards. This proliferation is mostly rather extensive, sometimes even reaching the next corticated zone (vide Kylin 1909); sometimes it is less extensive. In this way var. diaphanum (and possibly also f. modificatum and var. zostericola) are connected with species entirely corticated in the lower parts of the thallus, such as C. areschougii Kylin and C. fruticulosum (Kütz.) J. Ag. It is remarkable that the Netherlands specimens of var. diaphanum are only about 250–370 μ in diam. at the base, whereas f. medium is about 350–520 μ in diam. at the base. This also makes the author believe that f. medium is intermediate between var. diaphanum and the species entirely corticate at the base.

C. These conjectures result in the following scheme:

\[ \text{? Ceramium areschougii Kylin} \]
\[ \text{Ceramium diaphanum (Lightf.) Roth} \]
\[ \text{var. diaphanum} \]
\[ \text{f. corticatum (Kylin) Kylin} \]
\[ \text{var. diaphanum} \]
\[ \text{f. corticatulo-strictum Kylin} \]
\[ \text{var. diaphanum} \]
\[ \text{f. modificatum H. Petersen} \]
\[ \text{var. diaphanum} \]
\[ \text{var. zostericola (Thur.) Feldm. Maz.} \]
\[ \text{var. diaphanum} \]
\[ \text{var. tenuissimum Roth} \]

1 Roth (Cat. Bot. Fasc. 2, 1800, p. 183) described a Ceramium fruticulosum. Judging from the description it is not the same species as Ceramium fruticulosum (Kütz.) J. Ag., so the latter epithet is invalidated. At present the author is not in the position to carry out an investigation as to this point.

2 Ceramium deslongchampsi Chauv., which is related to Ceramium diaphanum (Lightf.) Roth, probably shows a similar series of forms as the last named species. In Ceramium deslongchampsi also the number of lateral ramuli varies from none to numerous, and the development of the cortication varies as well. Material has been
found with proliferous cortication. It seems to be reasonable to regard these specimens as belonging to a separate form, of which the description is given below.

*Ceramium deslongchampsii* Chauv. f. *semi-ascendens* J. Lucas, nov. forma (Fig. 5) — articulorum inferiorum cellulis corticis ascendentibus, sed genicula superiorea confrina non attingentibus.

Type specimen: Den Helder, harbour, 12-4-1950, Swennen and Lucas 281 (L). This form has also been found on the sea dike at Den Helder, 2-9-1948, Swennen 16 (L).
THE SPECIES, ITS VARIETIES AND FORMS

*Ceramium diaphanum* (Lightf.) Roth., Cat. Bot. Fasc. 3, 1806, p. 154. Thallus partly corticated. Corticated zones sometimes proliferating, never entirely covering the internodes. Number of articulations between two main ramifications mostly between 5 and 14, sometimes, especially at the apices much more numerous (e.g. *C. vertebrale* H. Petersen). Pericentral cells mostly 7, covered by 1–4 corticating layers. In young specimens gland-cells among the corticating cells, which afterwards may disappear. Thallus pink, red or more or less brownish, sometimes slightly purplish, but different from the colour in *C. deslongchampsii* Chauv. from which *C. diaphanum* also differs in being more flaccid. Thallus at the base about 100–650 µ in diameter.


Thallus at the base about 250–600 µ in diam., in the Netherlands material only 250–370 µ (mostly about 280 µ) in diam., at the apices about 75–120 µ in diam. Corticated zones usually as high as broad or a little shorter, sometimes longer. Corticating layers (outside the pericentral cells) 3 or 4; corticating cells not arranged in longitudinal series. Cells of the outer layer at the base of the zones about 10–30 µ, mostly 15 µ, in diam., those of the upper part of the zones sometimes slightly smaller. Gland-cells mostly disappearing later on. Internodes 1–4 times as long as broad, ecorticated. Apices often incurved, sometimes dentate. Number of lateral ramuli mostly great. Tetrasporangia immersed in the thallus.

On inquiry, the type specimen could be found neither in the British Museum nor in the Herbarium of the Royal Botanic Gardens at Kew nor in that of the Royal Botanic Garden at Edinburgh. The type specimen of *Hormoceras moniliforme* Kütz. is not present in the "Rijksberbarium" at Leiden. Other specimens, brought to *H. moniliforme* by Kützing, belong to var. *diaphanum*. As to *Gongroceras pellucidum* Kütz., specimens from Triest as well as from Spalato are present in the collection of the "Rijksberbarium". The specimens from Spalato have to be brought to var. *tenuissimum*, those from Triest belong to var. *diaphanum*.

Localities: Monnikendam, 25-7-1905, uncertain whether or not autochthonic there (N.D.V.); Stompe (N.D.V.), the specimen was brought to *C. strictum* Grev. et Harv. by van Goor; Den Helder, harbour, before 1917, on a lighter (N.D.V.); ibid., 15-8-1919, on drifting Zostera (N.D.V.); Den Helder, sea-dike, 27-8-1948, Swennens 83 (L.), washed ashore on a bunch of cork; IJmuiden, 19-12-1949, Mulder 38 (L.), washed ashore on a bunch of cork; Bloemendaal, 13-11-1949, Stock 20 and Hazevoet (L.), washed ashore on cork; Zandvoort-Noordwijk, 26-11-1949, Stock 21 (L.), washed ashore on wood; Noordwijkerhout-Noordwijk, 20-1-1949, Lucas 88 (L.), washed ashore on a bunch of cork; Katwijk, 20-11-1950, Lucas 895 (L.), washed ashore on cork; Scheveningen, Vrijdag Zijnen 2 (L.), washed ashore.

*f. modificatum* H. Petersen, Danske Arter af Slaegten Ceramium

Fig. 6–8. Ceramium diaphanum (Lightf.) Roth var. tenuissimum Roth: 7. with gland-cell and rhizoid originating from hyaline space, 8. with gland-cells and corticating cells arranged in longitudinal series; 9. C. cimbricum H. Petersen, left fig. with more developed cortex; 10. C. diaphanum (Lightf.) Roth f. medium Sjöstedt, nat. size; 11. C. diaphanum (Lightf.) Roth f. modificatum H. Petersen, nat. size.
This form is characterized by the lateral ramuli being absent or nearly so.

The present author has examined both the type material of *f. modificatum* H. Petersen and *f. strictoides* H. Petersen. The two forms differ in the height of the corticate zones, which are about equalling the diameter in *f. modificatum*, being shorter in *f. strictoides*. In the author’s opinion not only the height of the corticated zones is important for separating var. *diaphanum* and var. *zostericola*, but also the reduction of the thallus as a whole, as is described on p. 323. Accordingly *f. strictoides* has to be considered a synonym of *f. modificatum*.


*f. medium* Sjöstedt, Revision of some dubious Swedish Ceramium types, their classification and ecology — Lunds Univ. Arskrift, N.F. Avd. 2. Band 23. Nr. 12, 1928, p. 7 — *Hormoceras cateniforme* Kütz., 1849, p. 675 — *Ceramium diaphanum* (Lightf.) Roth *f. cateniforme* (Kütz.) J. Lucas, 1950, p. 537 — *Fig. 5 and 10.*

This form is characterized by the corticated zones in the lower part of the thallus showing an upward proliferation by means of elongated cells. However, the next corticated zone is not reached. There is no proliferation in the lowermost corticated zones. The degree of the proliferation is variable, both regarding the density of the cells and the length of the internode that is covered. Sometimes the layer of elongated cells is covered by a second one. When the corticated zone shows proliferation, the outer layer of the zone is mostly looser, especially in the upper part of the zone, and the cells of this layer are more or less elongated.

In the type of this form the proliferation is only slight. In the Dutch material the diameter at the base of the thallus is much larger than in var. *diaphanum*, viz. 350–520 µ (mostly 450 µ). The type specimen of *Hormoceras cateniforme* is even 650 µ in diam. Sometimes the cells of the proliferous layer are not elongated, but more or less angular like the ordinary cells (Lucas 530 and 896). Sometimes it is not in the lower part that the thallus shows proliferation of the corticated zones, but only in the middle parts.

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This form is characterized in that the lateral ramuli are wanting or nearly so and moreover in that the proliferation of the corticated zones in the lower parts is as in f. medium Sjostedt. Kylin himself (1909) regarded Ceramium corticatulum as a form of Ceramium diaphanum (though in his later papers he again considers it a separate species), so the new combination, Ceramium diaphanum (Lightf.) Roth f. corticatulum (Kylin) Sjostedt (1928), was superfluous.

The type specimen measures 350 μ in diameter at the base.

Locality: Wassenaarse Slag-Scheveningen, 30-11-1947, Lucas 289 (L.), washed ashore on Ascophyllum nodosum.

Var. zostericola (Thur.) Feldm. Maz., Recherches sur les Cera-miacées de la Méditerranée occidentale. 1940, p. 314 — Ceramium strictum Harv. var. zostericola Thur., Algues marines de Cherbourg no 123; C. strictum auct. non Roth nec (Kütz.) Harv.; Hormoceras catenula Kütz., 1847, p. 35; ? H. pulchellum Kütz., 1849, p. 676; Ceramium strictum H. Petersen f. vera p.p., 1908, p. 62; C. vertebrata H. Petersen, 1908, p. 63 — Fig. 3.

Thallus at the base about 170-300 μ in diam. (mostly about 230 μ) at the apices about 40–75 μ. Height of the corticated zones less than the width. Corticating layers (outside the pericentral cells) 2 or 3, corticating cells not arranged in longitudinal series. Cells of the outer layer at the base of the corticate zones about 9–25 μ in diam., in the Netherlands specimens mostly 10–12 μ, those of the upper part of the zones often slightly smaller. Gland-cells are often found among the corticating cells, sometimes being arranged in a whorl. Length of the internodes 1–6 times the width, internodes ecorticated. Apices often straight, rarely dentate. Number of lateral ramuli small. Tetrasporangia more or less projecting.

As the ramification in Ceramium diaphanum varies a great deal, it seems useless to separate a form with fasciculate branches from var. zostericola. Both types of ramification have been found in the Netherlands.

Kylin, Sjöstedt and Kolderup Rosenvinge consider the fact that the height of the corticated zones is less than the width a specific character of this variety. However, though this feature is found in very thick specimens (up to about 550 μ), other specimens, measuring only 170 μ in diam. at the base, have corticated zones in which the height equals the width. Therefore this feature does not seem of much value, and the author agrees with Petersen, who separates f. strictoides H. Petersen and C. strictum H. Petersen (non Roth). In his opinion it is the reduction of the thallus as a whole which seems a better criterion for separating this variety.

The type specimen of Hormoceras pulchellum Kütz. is not present in the “Rijksherbarium” at Leiden. A specimen identified by Kützting as this species belongs to var. zostericola. In rare cases the corticated zones are divided into two parts by a horizontal hyaline space.

Localities: Steile Bank, 15-7-1905 (N.D.V.); Den Helder, 3-8-1930, Sobels
(U.), on drifting Zostera; Huisduinen, 9-10-1948, Swennen 10 (L.), washed ashore on Fucus; Noordwijck-Katwijk, 15-11-1949, Lucas 511 (L.), washed ashore on Halidrys siliquosa; Post 85-86, 20-11-1950, Lucas 885 (L.), washed ashore on cork; Scheveningen, 17-9-1941, Creutzberg (L.), washed ashore on Fucus; Kijkduin, 20-11-1949, Lems (L.), washed ashore on a beam.

Of the material, collected by VAN GOOR (1923), only one specimen is left; it originates from Stompe. This specimen, however, belongs to var. diaphanum.


Differs from var. zostericola by the upward proliferation of the nodal cells in the lower parts of the thallus. In the proliferous zone we find elongated cells. According to KYLIN in rare cases the next corticated zone may be reached. The lowermost zones do not show proliferation. The degree of the proliferation is variable as to the density of the cells as well as to the length of the internode that is covered. In the specimens examined the outer layer consists of very few angular cells only, separate or arranged in scattered groups.

KYLIN includes in this form also those specimens of f. corticatum, in which the height of the corticated zone without the proliferous part is less than the width. As stated above this feature seems to be of no special value. The type specimen of f. corticatulo-strictum was not available.

Localities: Zuiderzee at Durgerdam, 4-1882, Weber (L.); Noordwijck-Katwijk, 15-11-1949, Lucas 487 (L.), washed ashore on a bunch of cork.


Thallus at the base about 110–200 μ in diam., mostly 130–140 μ, at the apices about 40–75(–100) μ. Height of the corticate zones mostly less than the width, very variable. Corticating layers (outside the pericentral cells) 1 or 2; corticating cells irregularly arranged or more or less in longitudinal series, especially in the lower part of the zone. Cells of the outer layer at the base of the zones 9–18 μ, (mostly 15 μ) in diam., those of the upper part of the zones mostly smaller. Gland-cells are often found among the corticating cells, sometimes arranged in 1 or 2 whorls. Length of the internodes 1–10 times the diameter, internodes ecorticated. Apices often incurved, dentate or entire. Number of lateral ramuli small. Tetrasporagia strongly projecting, at the outer side of the zones or in whorls.

As stated above neither the presence of gland-cells nor that of dentate apices is a good criterion for this variety. Mrs. G. FELDMANN–MAZOYER, 1940, p. 300 indicates another feature, viz. the arrange-

1 In M. WAERN, Rocky-shore Algae in the Öregrund Archipelago — Acta Phytogeogr. Suec., 30, 1952, p. 207, a paper which appeared after the present one was finished, C. diaphanum (Lightf.) Roth f. corticatulo-strictum Kylin is brought to the synonymy of C. tenuicorne (Kütz.) Waern, together with C. vertebrale H. Petersen.
ment of the corticating cells in longitudinal series. She herself admits that these series are not always distinct. Among the material studied by the author there are some in which the corticating cells are only indistinctly arranged in longitudinal series. One specimen (Lucas 13) shows longitudinal series in the greater part of the corticated zones, whereas in the remaining part the cells are irregularly arranged. Therefore var. *tenuissimum* Roth sensu G. Feldm. Maz. cannot be considered a separate species.

Often a horizontal hyaline space divides the corticated zone into two parts, viz. a narrow lower part and a broader upper one. The corticating cells are arranged more or less in longitudinal series, especially in the lower part. From this space rhizoids may originate, sometimes being arranged in whorls.

**Localities:** Texel, 17-11-1884, Weber-van Bosse (L.); ibid., 7-10-1946, Bloklandter (L.), washed ashore on a bunch of *C. F. H.*; Hoorn, 9-1854, Suringar 148 (L.), on Nemalion; De Balg, 6-1886, Weber-van Bosse (L.); Den Helder, Zuidwal, 9-12-1915, van Goor (N.D.V.); Den Helder, Vangdam, on drifting Zosteria (N.D.V.); Nieuwediep, 7-1887, Weber-van Bosse (L.); IJmuiden, 19-12-1949, Mulder 41 (L.), washed ashore on a bunch of *C. F. H.*; Post 56-63, 21-9-1950, Mulder 65 (L.), washed ashore on *Asph. nodosum*; Zandvoort, 10-1845, Buse (L.), washed ashore on *Chordia filum*; Noordwijkerhout-Noordwijk, 20-9-1948, Lucas 13 (L.), washed ashore on *Chordia filum*; ibid., 24-10-1948, Lucas 537 (L.), washed ashore on *Asph. nodosum*; Noordwijk-Katwijk, 15-11-1949, Lucas 482 (L.), washed ashore on a bunch of *C. F. H.*; ibid., 15-11-1949, Lucas 512 (L.), washed ashore on *Asph. nodosum*; ibid., 15-11-1949, Lucas 513 (L.), washed ashore on *Fucus vesiculosus*; ibid., 15-11-1949, Lucas 514 (L.), washed ashore on *Asph. nodosum*; Katwijk, 29-9-1950, Lucas 818 (L.), washed ashore on *Fucus vesiculosus*.

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