Coccotylus brodiei, C. truncatus and other Phyllophoraceae (Rhodophyta) in Danish waters

Steffen Lundsteen¹ & Ruth Nielsen²

Aarhus University, Institute for Bioscience, Section for Marine Diversity and Experimental Ecology, Frederiksborgvej 399, DK-4000 Roskilde, Denmark.
Natural History Museum of Denmark, Algal Herbarium, Ø. Farimagsgade 2C DK-1353 Copenhagen K, Denmark

Lundsteen, S. & Nielsen, R., 2015: *Coccotylus brodiei*, *C. truncatus* and other Phyllophoraceae (Rhodophyta) in Danish waters. Forum om marin bundfauna og –flora 2: 1-20. Web: http://bios.au.dk/om-instituttet/organisation/marinbiodiversitet/forum-om-marinbundfauna-og-flora/

Specimens of *Coccotylus brodiei* and *C. truncatus* from Danish waters are presented with a reappraisal of how to distinguish them. An identification key for Phyllophoraceae as they occur in Danish waters is included. Specimens previously referred to as *Phyllophora brodiei* f. *concatenata*, *P. brodiei* f. *filiformis*, *P. brodiei* f. *stellata and P. brodiei* f. *ligulata* are considered to belong in *Coccotylus brodiei*.

Introduction

The two red algal species *Coccotylus brodiei* (Turner) Kützing and *C. truncatus* (Pallas) M.J.Wynne & J.N.Heine were recently reported from Danish waters by Køie & Kristiansen (2014) with the Danish names Smal Rødblad and Kile-Rødblad, respectively. Very little information was given about their morphology, how they are told apart and how to distinguish them from other members of the Phyllophoraceae. Therefore, identification and occurrence in Danish waters need further explanation.

The two species were previously considered to represent morphological variation within a single species, e.g., Wynne & Heine (1992, as *Coccotylus truncatus*). However, DNA barcode analyses on Canadian material revealed two distinct genetic species groups (Le Gall & Saunders 2010). The morphology of the one group corresponded to type material of *C. brodiei* with type locality in Scotland and the other to type material of *C. truncatus* with type locality "the Arctic".

They referred to the thesis by Newroth (1970) and accepted to include *Phyllophora brodiei* f. *interrupta* (Greville) Rosenvinge, 1893 in *C. truncatus*.

Plants from Danish waters were dealt with by Rosenvinge (1931) under the name of *Phyllophora brodiaei* (Turner) J. Agardh. He described two main groups of plants with different kinds of growths, one with apical stipitate leaves and the other with continued apical leaf growth close to *P. brodiei* f. *interrupta* (Greville) Rosenvinge. He found frequent intermediates between the two groups and did not distinguish between them as individual taxa. However, the morphology of the two groups, according to his description, closely resembles *C. brodiei* and *C. truncatus* respectively, as described and illustrated by Le Gall & Saunders (2010 figs. 5 and 6). From the Swedish part of the Kattegat, Kylin (1907, 1944) reported both *P. brodiei* f. *typica*, referable to *C*.

brodiei, and from the southern part in deep water, some specimens of *P. brodiei* f. *interrupta* referable to *C. truncatus*.

Rosenvinge (1931) segregated the loose growing forms *P. brodiei* f. *concatenata* Lyngbye, *P. brodiei* f. *filiformis* Rosenvinge and *P. brodiei* f. *stellata* Rosenvinge, the relationships of which need to be clarified. The same concerns P. *brodiei* f. *ligulata* (C.Agardh) Sjöstedt reported from the Swedish west coast by Sjöstedt (1927) and Kylin (1944). In the recent collections of this study, a plant similar to this forma was noticed.

Material

This study comprises all specimens from Denmark referred to *Coccotylus brodiei* or *C. truncatus* present in the Algal Herbarium of the Natural History Museum of Denmark. Included are plants from recent collections obtained by divers. Some specimens have been fixed and stored in 4% formaldehyde in seawater for one to a few months before they were studied and pressed as herbarium specimens, and many have lost some color during the process. The herbarium specimens also shrink during the drying process. Permanent slide preparations of formaldehyde preserved plants are maintained in Karo © (Corn syrup). A few specimens were photographed and not otherwise preserved.

In total, approximately 950 *C. brodiei* specimens and 100 *C. truncatus* specimens from all parts of Danish waters have been studied.

Key for the identification of Phyllophoraceae in Danish waters

- 1a. Without leaves, small globular parasite up to 5 mm in diameter, consisting of thin dense branches, bleached pink, on *Coccotylus brodiei* and *C. truncatus*: *Coccotylus hartzii*, figure 1
- 1b. With leaves, usually on stone or boulders: 2
- 2a. Blade without terete stipe, U-shaped in transverse section, some plants with papillae on surface. Blade repeatedly dichotomously divided, red-purple to almost black: *Mastocarpus stellatus*, figure 2

Cystocarps develop in the surface papillae. In Danish waters male plants and tetrasporophytes have not been observed (Ruth Nielsen 2015, pers. com.).

- -2b. Terete stipe, blade flattened or undulating, without surface papillae, simple or dichotomously divided, color only dark in old parts: 3
- 3a. Small plant, less than 2 cm high, blade oval to band shaped, rarely bifurcate, on a short terete stipe. Plants usually grow gregariously in patches on stone: *Erythrodermis traillii*, figure 3

Isomorph dioecious gametophytes develop reproductive structures on leaflets from the rim of blades. Spermatangia grow in pale patches. Carposporangial leaflets are small and spherical. Blade margin is often serrated prior to development of reproductive structures. Crustose tetrasporophyte.

- 3b. Larger plants, do not grow in small dense patches, blades may be repeatedly dichotomously divided: 4
- 4a. New leaves from flat side of older blades near apex, not from the rim, often broad midrib in lower part of blade, lobes often very narrow ribbonshaped and much crenulated along margin: *Phyllophora crispa*, figure 4.

Isomorph dioecious gametophytes and tetrasporophyte, reproductive structures occur on flat side of blade. Spermatangia develop in cavities of globular stipitate leaflets about 0.5 mm in diameter, cystocarps are stiptate and rosette-like, 1-2 mm in diameter, tetrasporangia in platelike leaflets horizontally on blade.

Young plants without the characteristic vegetative or reproductive structures can be very similar to *C. truncatus*.

- 4b. Leaves rarely from the flat side of blades and if so not near apex, no basal midrib, leaves or lobes if band shaped neither strikingly narrow nor crenulated along edge: 5
- 5a. Stem usually longer than leaf; leaf broad and fan shaped, more than 90° diverging laterally, repeatedly dichotomously divided with many lobes; young leaf with violet tinge: *Phyllophora pseudoceranoides*, figure 5

Isomorph dioecious gametophytes and tetrasporophyte. Spermatangia in pits of small colorless leaflets from rim of leaves, cystocarps are lemonshaped, stipitate from rim of leaves, tetrasporangia in dark patches on both sides of lower part of blade.

Specimens of *P. pseudoceranoides* and *C. truncatus* can look rather similar, especially in brackish water. The first leaf of *P. pseudoceranoides* can be sessile on the basal disc and resemble *C. truncatus*. Identification must then rely on color difference, best seen in transparent light.

- 5b. Leaf simple or divided into few to several lobes; when broad and fan shaped the stem is short; young leaf red-brown: 6

The plants are usually monoecious with spermatangia in the surface near apical rim of blades and globular carpotetrasporangial outgrowths apically.

- 6a. Branching by stipitate leaves from all parts of plant; often apically; leaf usually almost wedge shaped, simple, bi- or trifurcate or further divided into lobes that are characteristically distinctly pointed; if elongate and with rounded apices, the the sides are asymmetrically wavy: *Coccotylus brodiei*, figures 6-12

Carpotetrasporangial outgrowths up to ca. 2.5 mm in diameter, at or near rim of blade, often on raised portions or on the stipes of new young leaves.

See comment to *Phyllophora pseudoceranoides*.

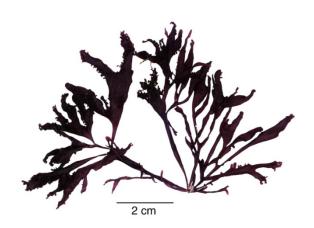
- 6b. Branching only from below of plant; short stem; principal leaves broad fan shaped, repeatedly dichotomously divided; lobes long, sides even or symmetrically curved, apex rounded in the growing season; adventitious leaves, if present, without stipes: *Coccotylus truncatus*, figures 13-15.

Carpotetrasporangial outgrowths ca. 1 mm in diameter near apical blade rim. See comments to *Phyllophora crispa* and *Phyllophora pseudoceranoides*.

References: Dixon & Irvine 1977, Guiry & Garbary 1990, Guiry & West 1983, Le Gall & Saunders 2010, Maggs 1989, Newroth 1971b, Rosenvinge 1931, Tolstoy & Österlund 2003.



Figur 1: *Coccotylus hartzii*, 5 mm in diameter, on same *Coccotylus brodiei* as in figure 6b. Schultz's Grund, Kattegat S., 7.8 m, 23 August 2014.



Figur 2: *Mastocarpus stellatus*. Northern harbour jetty, Frederikshavn, Kattegat N., exposed side, 0.5 m, 6 June 2004.







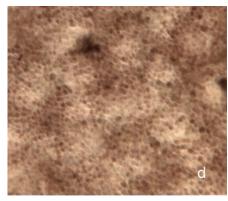


Figure 3: *Erythrodermis tralii*. (a) Plant with carposporangial outgrowths from rim of blade, right side. (b) Plants with divided blade. (c) Several plants in typical gregarious assemblage. (d) Surface of thin cortex layer with medullar cells easily visible below as seen in microscope. Scale bars: (a-c) 5 mm, (d) no scale.

(a) Lønstrup Rødgrund, Skagerrak, 12.7 m, 15 August 2014; (b-c) Per Nilen, Kattegat N., 11 m, 12 August 2014; (d) Kims Top, Kattegat E., 14.5m, 16 August 2012.

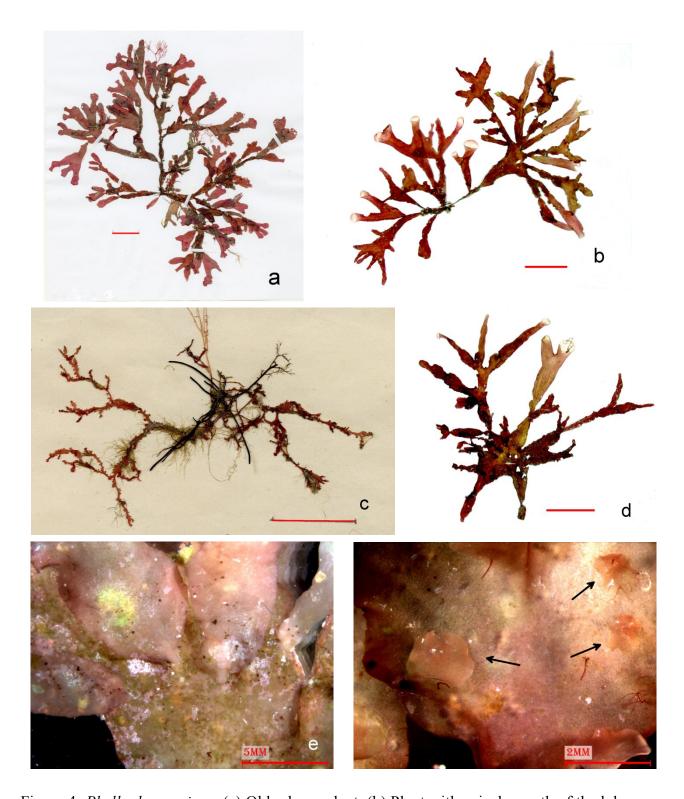


Figure 4: *Phyllophora crispa*. (a) Older large plant. (b) Plant with apical growth of the lobes. (c) Plant with slender crenulated lobes. (d) Old plant with broad star shaped leaf and slender leaves from it. (e) Leaves from flat side of older leaf near apex. (f) Plate-like tetrasporangial outgrowths from blade. Scale bars: (a-d) 2 cm, (e) 5 mm, (f) 2 mm. (a) Herthas Flak, 20 m, Kattegat N., 21 August 1991. (b, d) Kims Top, Kattegat E., 18.3 m, 19 August 2014. (c) Off Fyns Hoved, the Samsø area, 3.5-5.5 m, 8 August 1906, leg. L.K. Rosenvinge. (e-f) Kims Top, 18.3 m, 18 August 2014.

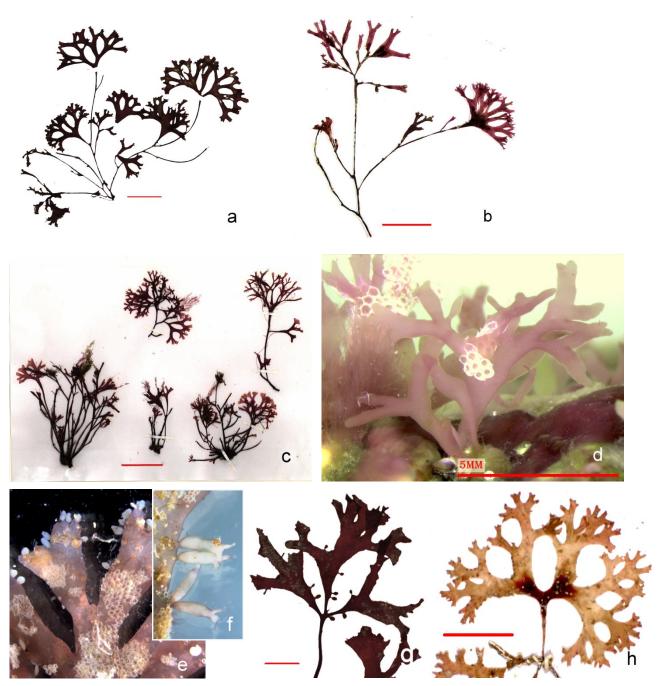


Figure 5: *Phyllophora pseudoceranoides*. (a) The species at its most characteristic. (b) Atypical specimen with few lobes in some leaves. (c) Specimens with continued growth of the blades, more lightly and red than the older parts. (d) Young plants without stem. (e-f) Spermatangial outgrowths from rim of blade. (g) Carposporangial outgrowths from rim of blade. (h) Tetrasporangial dark colored patch at base of leaf. Scale bars (a-c, h) 2 cm, (d) 5 mm, (g) 1 cm, (e-f) no scale.

(a) Off Vejrø, the Samsø area, 15 m, 12 August 1992. (b) Kirkegrund, 8.2 m, the Småland Sea, 8 August 2015. (c) Venegrund, 8 m, the Småland Sea, 26 September 1992. (d) Hatter Barn, 6.3 m, the Samsø area, 20 August 2012. (e) Kims Top, Kattegat E., 18.3 m, 18 August 2014. (f) Tønneberg Banke, Kattegat N., 4.5 m, 13 August 2014. (g) Off Hirsholmene, Kattegat N., drift, 15 January 1975. (h) Kims Top, 22.8 m, 18 August 2014.

Coccotylus brodiei (figs. 6-12)

The repeatedly branched leafy bushes are usually up to 15 cm high, but can reach 33 cm in the Belt Sea. They are red-brown, lightly colored in new parts and darker in older parts.

The cylindrical stem is as a rule relatively long and robust. Branches, in the form of stipitate leaves, spring from all parts of the plants. Branches springing from the leaves usually grow from the rim and most characteristically from the apex but at times also from the flat side of the blade. Leaf growth is arrested at the end of the growing season and new growth resumes as stipitate leaves. Often the stipitate leaves occur in a row. Up to seven generations have been found (fig. 7a). Occasionally the stem or stipes of long branches are merely intermittently flattened. The leaf growth rarely continues without a stipe (fig. 6c inset).

The transition from stipe to blade is gradual with a wedge shaped leaf widening from the stipe (fig. 6), or the basal part can be band shaped (figs. 6c mid, 7f).

The blades are typically dichotomously divided into two lobes attenuated to a pointed apex (figs. 6b-d, 7g). But often three or more lobes are present (figs. 6d-f, 7b, f, g). Elongate lobes (figs. 6e, 7h, 8a, b) also occur, at times with a rounded apex (figs. 6f, 8c). Division of the blade is frequently asymmetric, as especially pronounced in fig. 6e. Undivided blades are at times truncated (fig. 6a bottom right). Undivided elongate oval leaves are common in plants from the deeper parts of the Belt Sea and the Baltic (fig. 7a-e).

Individual plants with leaves of quite variable shape, as in figs. 6c, 7b, g, and 8a, are of frequent occurrence.

Usually the plane of blades and their lobes are wavy while the margins undulate slightly. As the plants are also rather stiff, they are not easy to make flat for pressing, though less so for plants from deep water.

In the young plants, the blade typically is tapering above with a blunt-pointed apex (fig. 9b).

The globular carpotetrasporangial outgrowths are sessile, up to 2.5 mm in diameter, developing at or near the rim of the leaves. They are often apical on raised stipe-like portions of the blade or on the stipes of young leaves (fig. 9a).

Growth place and distribution

The species grows on stone and boulders or is occasionally epiphytic. It has been collected by divers from about 1 m depth (Isefjorden), to 21 m (off Bornholm). By dredging, it has been collected down to 40 m (off Bornholm). It is present in all Danish marine districts.

Literature used for identification

Dixon & Irvine (1977, as *Phyllophora truncata*), Kornmann & Sahling (1978, as *Phyllophora truncata*), Kylin (1944, as *Phyllophora brodiei* f. *typica*), Le Gall & Saunders (2010), Newroth (1971a, as *Phyllophora truncata* f. *brodiei*), Rosenvinge (1931, as *Phyllophora brodiei* in part), Taylor (1957, as *Phyllophora brodiei*), Tolstoy & Österlund (2003, as *Coccotylus truncatus*) and Zinova (1955, as *Phyllophora brodiei*).

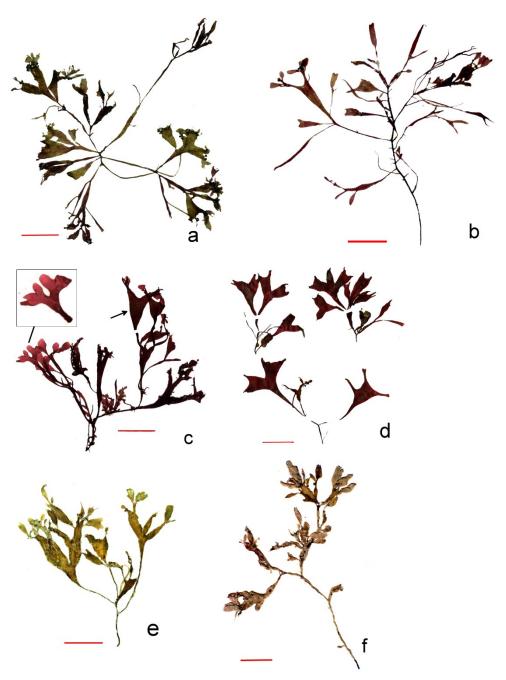


Figure 6: *Coccotylus brodiei* from the Kattegat and the Samsø area. Leaf shapes: (a) Truncate, bottom right. (b-d) With pointed lobes, amid other leaf shapes, bifurcate in b-c, further divided in d. (e) Asymmetric three times divided leaves with elongate pointed lobes. (f) Leaves with rounded lobes. Growth and shapes: (c) Arrow - Stipitate leaf, typical bifurcate with pointed lobes, from apex of older leaf. Inset - dichotomously divided leaf with continued growth and divisions of lobes, with rounded apices. In the middle a band shaped basal part of leaf. Scale bars 2 cm.

(a-b) Schultz's Grund, the Samsø area, 7.8 m, 23 August 2014. (c) North-east of Sjællands Odde, Kattegat S., 9.5 m, 10 March 1997. (d) Off Bramsnæs, Isefjord, 1.5 m, 20 June 1994. (e) Hatter Barn, 8 m, the Samsø area, 20 May 2014. (f) Hatter Barn, 6 m, 22 August 2014.

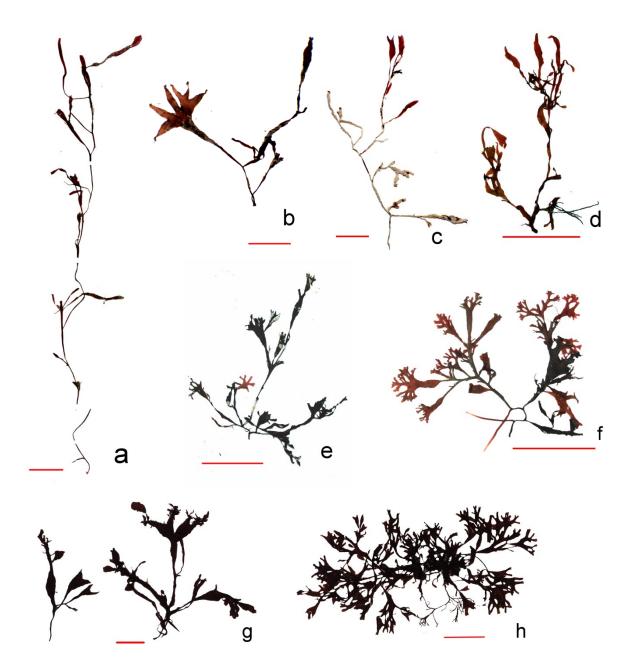


Figure 7: *Coccotylus brodiei*, from the Belt Sea and the Baltic Sea. Leaf shapes: (a-e) Simple elongate oval leaves, often found in the deeper parts of the Belt Sea and the Baltic Sea off Moen, in (a) seven leaves arranged in series in a plant at least seven years of age (Rosenvinge 1931 fig. 499), (b) Plant with prominent star shaped leaf. (f) Leaves repeatedly dichotomously divided as in *Phyllophora pseudoceranoides*, but new leaves from older leaf, in same sample as (e) with one small leaf of same kind. (g-h) Plants collected off Bornholm with various leaf shapes including the typical bifurcate with pointed lobes in (h) with many dichotomously divided leaves. Scale bars 2 cm.

(a) From dredge in the Little Belt, 18-19 m, 17 June 1922, specimen depicted in Rosenvinge, 1931 fig. 499. (b-c) Kirkegrund, the Småland Sea, 8.2 m, 20 August 2014. (d) The Baltic Sea off Moens Klint, 17.4 m, 25 August 2011. (e-f) The Baltic Sea off Moens Klint, 19.4 m, 21 August 2014. (g-h) The Baltic Sea off Hvide Odde, Bornholm, (g) 15 m, (h) 13 m, 17 June 2009.

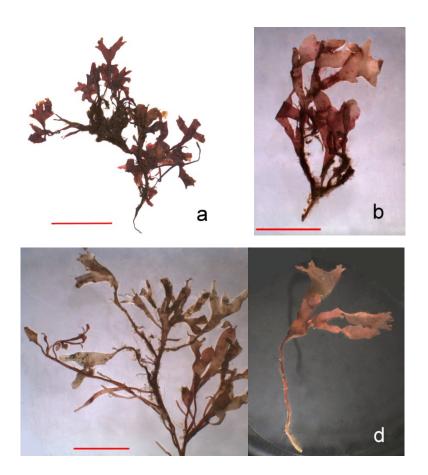


Figure 8: *Coccotylus brodiei* with elongate broad lobes in part dichotomously divided as in *C. truncatus*. Scale bars (a-c) 2 cm, (d) none.

(a) Odense Fjord, 3 m, 12 May 2009. (b-c) Als Sund, the Little Belt, 4.9 m, 9 June 2009. (d) Hatter Barn, the Samsø area, 14.5 m, 8 August 2014.



Figure 9: *Coccotylus brodiei*. (a) Carpotetrasporangial outgrowths, stipitate and with new leaves. (b) Juvenile. Scale bars 5 mm.

(a) Kirkegrund, 8.2 m, the Småland Sea, 20 August 2014. (b) Schultz's Grund, Kattegat S., 4.5 m, 23 August 2014.



Figure 10: *Coccotylus brodiei* f. *concatenata*. (From the same sample as the specimens in figure 8b-c) Scale bar 2 cm. Als Sund, the Little Belt, 4.9 m, 6 June 2009.



Figure 11: *Coccotylus brodiei* similar to f. *stellata*, with small slender apical lobes. Scale bar 2 cm.

Off Sæløen, Isefjorden, 5 m, 31 August 1989.

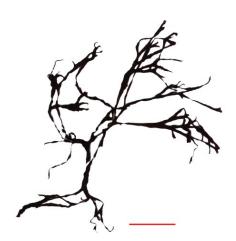


Figure 12: (a) *Coccotytlus brodiei* f. *ligulata*. Scale bar 1 cm. The Baltic Sea off Hvide Odde, Bornholm, 15 m, 17 June 2009.

The loose growing forms

The following descriptions of f. *concatenata*, f. *filiformis* and f. *stellata* are adopted from Rosenvinge (1931), and f. *ligulata* from Sjöstedt (1927) and Kylin (1944).

P. brodiei f. *concatenata* Lyngbye. Slender form, repeatedly branched with asymmetric simple or bifurcate leaves that taper in both ends with a pointed apex from which further stipitate leaf develop (fig. 10). The pointed apex and apical stipitate branches are in accordance with typical *C. brodiei*, and therefore belong in this species. The specimen in fig. 10 was collected by diver, and was probably fixed to the substratum.

P. brodiei f. *filiformis* Rosenvinge. Very thin with gradual transition from the form above with cylindrical shoots 1 mm or less in diameter, flattened intermittently.

P. brodiei f. *stellata* Rosenvinge. Relatively small size characterized by an apical bunch of small shoots which are simple or forked. The larger leaves are simple or bifurcate and elongate, more or less tapering distally (Rosenvinge 1931, figs. 517d, 518). The bifurcate tapering leaves are in agreement with the typical *C. brodiei* and belong in this species. A specimen with the small apical shoots as in f. *stellata* but larger as in the main form is shown in fig. 11.

P. brodiei f. *ligulata* (C.Agardh) Sjöstedt. Plants with repeatedly dichotomous branched leaves with 1-2 mm broad lobes (fig. 12). The form is thought most likely to belong to *C. brodiei* owing to the very brackish conditions of the find off Bornholm where *C. truncatus* seems to be absent. The specimen in fig. 12 is collected by diver and was probably fixed to the substratum.

All four forms are also reported for the Swedish West coast by Kylin (1944), and f. *ligulata* also from the Baltic; f. *concatenata* is also reported for Trondhjemsfjorden, Norway, (Printz, 1926), the USA (Taylor, 1957, as "*catenata*") and for the Russian Arctic (Zinova, 1955).

Coccotylus truncatus (Figs. 13-15)

The plants reach about 10 cm in height with stem and branches bearing an apical leaf. They are red-brown, lighter colored in new parts.

The stem is short (figs. 13-15), shorter than the primary leaves. Branches occur as stipitate leaves basally in the plants. They spring from the stem and more rarely from the rim of lower parts of blades (fig. 13b, c, d). The branching might be repeated. The transition between stem or branches and the leaves are usually abrupt.

Typical overall shape of the older principal blades is broadly fan shaped (fig. 13b, c). In some cases the older part of the leaf is elongate (fig. 13d, g) more or less band shaped or in others broadening (fig. 13e right, f). The blades become repeatedly dichotomously divided into elongate broad lobes and are usually intermittently narrowed. The lobes are symmetrically straight or evenly curved at the sides and have rounded apices in the growing season. Distinctly tapering lobes in the growing season in some leaves (fig. 13d) seem to be an exception. In addition, adventitious leaves occur. They spring especially from the distal part of plants along the blade rims. They have a narrow flattened



Figure 13: *Coccotylus truncatus*. (a) Specimen from the northernmost part of the Kattegat, with broad leaves. (b-c) Specimens from the Samsø area, with several dichotomies. (d) Less developed specimen from same area. (e) The specimens collected during the shallowest dives. (f) From 20 m in the eastern Kattegat. (g) The specimens from the greatest depth as collected by diver. Scale bars 2 cm.

(a) Herthas Flak, Kattegat N., 15 m, 5 June 1989. (b) Falske Bolsaks, the Samsø area, 15 m, 13 September 1991. (c) Hatter Barn, the Samsø area, 17.3 m, 22 August 2014. (d) Hatter Barn, 15 m, 20 May 2012. (e) Off Wedellsborg, the Little Belt, 9.2 m, 25 August 988. (f) Store Middelgrund, Kattegat E., 20 m, 4 june 1992. (g) Kims Top, Kattegat E., 24.5 m, 4 February 1996.

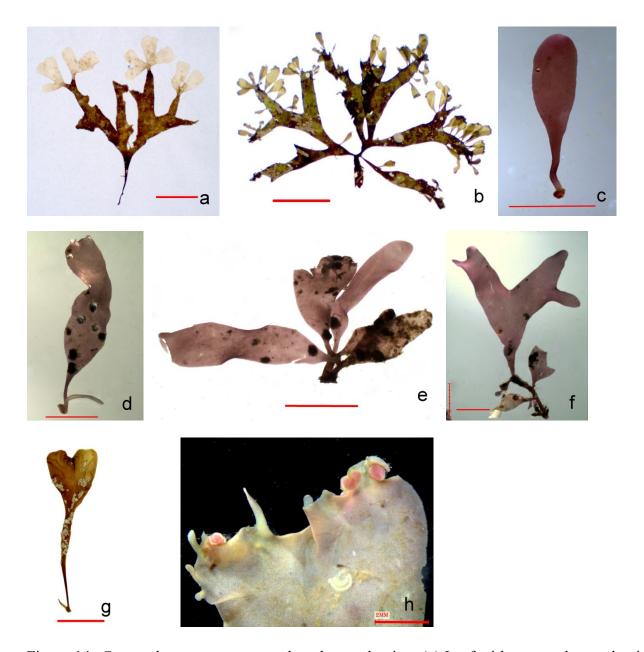


Figure 14: *Coccotylus truncatus*, growth and reproduction. (a) Leaf with resumed growth with new leaves after narrowing of blade. (b) Plant with adventitious new leaves. (c-g) Juveniles or small plants. (g) Young plant with new stem from basal disc. (h) Carpotetrasporangial outgrowths, sessile. Scale bars (a-b) 2 cm, (c-f), 5 mm, (g) 1 cm, (h) 2 mm.

(a) Hatter Barn, the Samsø area, 18.3 m, 19 May 2014. (b) Hatter Barn, 15.9 m, 21 May 2014. (c-f) Store Middelgrund, Kattegat E., 22.5 m, 23 August 2014. (g) Herthas Flak, Kattegat N., 10 m, 14 August 2014. (h) Hatter Barn, 17.3 m, 22 August 2014.





Figure 15: *Coccotylus truncatus* with relatively long stems and stipes, below. Arrow at inset - magnified leaf with curious apical budding. Scale bar 2 cm. Off Vejrø, the Samsø area, 15 m, 1 September 1993.

stipe-like part but not a cylindrical stipe (fig. 14b). This species is easy to flatten for pressing.

The principal yearly development of the leaves is by resumed continued growth (fig. 14a). It is characteristically marked by a narrowing of the leaves during the winter period (fig. 14a). The age of a plant can, therefore, be estimated by counting the number of narrowings in a shoot. In the Danish material, this narrowing is weak in most cases (fig. 13c) or might be missing. When the narrowing is pronounced, the tip of the old blade is almost pointed (fig. 14a right part), rather than rounded as is otherwise usual. The adventitious leaves seem to be especially numerous in old plants, possibly in such where the usual continued leaf growth is arrested (fig. 14b).

The number of narrowings of the leaves in the plant in fig. 13b indicate at least three years of age with the adventitious leaves adding a fourth year. The plant in fig. 13c similarly counted is probably three years old. As these two are the largest specimens found in the collection, it is probable that they are older than usual for the species in Danish waters.

In one season, the dichotomously divided leaf typically seems to produce two dichotomies, with four lobes (fig. 13b). However, numerous closely set lobes are present in specimens from the shallowest finds of the species (fig. 13e top and left).

Some young and less developed plants are shown in fig. 14c, d, and g, one of which has two shoots arising from the basal disc (fig. 14g).

A specimen with relatively long stem and branches is shown in fig. 15. It has curious small apical outgrowths (fig. 15 inset).

The globular carpotetrasporangial outgrowths are about 1 mm in diameter. They are sessile near the rim of the blade, at times several in a row (fig. 14h).

Growth place and distribution

The species grows on stone and boulders. By diver collection it has been recorded from the Northern part of the Kattegat (at Hertas Flak) and into the Belts (off Wedellsborg in the Little Belt and at Broen in the Great Belt), and from depths of 9.2 m in the Little Belt to 27 m in the eastern Kattegat (Kims Top). The species has, been collected by dredging from the western Baltic at about 20 m depth. The only specimen from the Sound was obtained by dredging at 10 m depth (off Vedbæk). Other collections from shallow water are believed to be drift specimens, including one from Aarhus Bay at 5 m depth.

Literature used for identification

Kylin (1944, as *Phyllophora brodiei* f. *interrupta*), Le Gall & Saunders (2010), Newroth (1971a, as *Phyllophora truncata* f. *truncata*), Pedersen (2011), Rosenvinge (1893 and 1898, as *Phyllophora brodiei* f. *interrupta*), Rosenvinge (1931, as *Phyllophora brodiei* in part), Taylor (1957, as *Phyllophora interrupta*) and Zinova (1955, as *Phyllophora interrupta*).

Discussion

Much of the variation in *C. brodiei* illustrated by Le Gall & Saunders (2010, fig. 6) was found in the Danish specimens, if not by exact matches then close, as can be seen by comparing specimens in their fig. 6 with plants in our figs. 6 and 7.

Plants of *C. brodiei* in the present investigation, which go beyond what is shown by Le Gall & Saunders (2010) include, in particular, the instances of plants with relatively broad band shaped lobes (fig. 8) and the different forms of *C. brodiei*.

A striking feature of *C. brodiei* to be seen in the present figs. 6 and 7 and that of Le Gall & Saunders (2010 fig. 6) is that the leaf shape varies much from the arguably typical two pronged leaf with pointed lobes, whether by number of lobes or their shape, and often in the individual plant.

Newroth (1971a, as *Phyllophora truncata*) mentions that the leaf rim is often eroded or grazed, leaving, at times, a cylindrical continuation of the stipes. This could explain the narrow breadth of older leaves, which are at times observed in *C. brodiei*, and the intermittent flattening of the stem as reported above for the species.

Most of the examples of *C. truncatus* from Danish waters shown in fig. 13, resemble specimens illustrated by Le Gall & Saunders (2010, fig. 5).

This goes particularly for the shape of leaves in the larger plants, which in both sets of figures are relatively uniformly dichotomously divided with elongated broad lobes and, mostly, rounded apices. Different from the present findings is the specimen with very long stem and the terete proliferations shown by Le Gall & Saunders (2010) in their fig. 5b. Different from their examples are the plants from shallow depth with broad leaves and several closely set lobes (figures 13e top and right) and the plant with adventitious leaves (fig. 15b). Compared to the varied leaf shapes in *C. brodiei*, the relative uniformity in *C. truncatus* is noticeable.

The placement of the spermatangia was not studied here and is not described separately for the two species, neither by Rosenvinge (1929, 1931), Newroth (1971b) nor by Le Gall & Saunders (2010).

Rosenvinges (1931, as *Phyllophora brodiei*) description for each of his two growth forms corresponding to *C. brodiei* and *C. truncatus* is rather detailed. His figures 499, 502 and 516, are obviously *C. brodiei*. The young plants with tapering apices in his figs. 497a, b, e, and g also belong to *C. brodiei* and probably also the other plants in the same figure, including those with several shoots from the basal disc (figs. 497h and 515d). Rosenvinges (1931) figs. 498a – e are examples of plants with dichotomously divided leaves without proliferations. They probably all belong to *C. truncatus*, not least the specimen in fig. 498b with leaf approaching the Arctic f. *interrupta*. Doubtful are perhaps the small reduced plant in fig. 498e and the one in fig. 498a with an almost star shaped leaf in the old portion. The broad fertile leaves in Rosenvinges (1931) fig. 503 belong with much certainty to *C. truncatus*.

Le Gall & Saunders (2010) emphasized that *C. brodiei* and *C. truncatus* can be difficult to distinguish from one another due to their variation.

Thus, as found in the present investigation, *Coccotylus brodiei* may have the elongate apically rounded lobes typical of *C. truncatus*.

Conversely, features more usual for or typical of *C. brodiei* may be found in *C. truncatus*. This concerns a long stem (Le Gall & Saunders 2010 fig. 5b one specimen), apical branches (Newroth, 1971a, *P. brodiei* f. *truncata*) and carpotetrasporangial structures on raised portions of the blade (Lund 1959, as *P. brodiei* f. *interrupta*). These variations from the more typical characteristica of either species call for caution when identifying specimens. Especially the apical branches, considered the main characteristic in *C. brodiei* by Le Gall & Saunders (2010), is considered by Newroth (1971a) to be unusual in *C. truncatus*.

The development of *C. truncatus* elsewhere, indicates that it does not reach its full potential for variation and growth in Danish waters. Some examples are the great difference in broad and narrow parts of the leaf in the Arctic *C. truncatus*, mentioned by Rosenvinge (1931, as *Phyllopora brodiei* f. *interrupta*). The narrowings of the blade also varies there, as explained by Lund (1959), for *Phyllophora brodiei* f. *interrupta* from East Greenland, as he found plants in the upper part of its depth distribution that resembled the specimen from Danish waters illustrated by Rosenvinge (1931, fig. 498b) and those from Throndhjemsfjord, Norway illustrated by Printz (1926, fig. 3). Lund (1959) also mentions a plant with 10 generations of leaf segments and thus probably the same number of years old, compared to four years of age in the oldest specimen in the present material.

A probable reason for less development of *C. truncatus* in Danish waters could be the relatively high temperatures compared to its predominately northern distribution mentioned by Le Gall & Saunders (2010) and possibly the reduced salinities in much of the Danish waters (Sparre, 1984).

Coccotylus brodiei and *C. truncatus* are common in Danish waters, both having been recorded from many localities.

A tally of regional and depth distribution of the two species remains to be done. The impression is that *C. brodiei* grows at shallower depths than *C. truncatus*, with little overlap. An important factor for this is possibly the stratified salinities found in Danish waters with salty water below and more brackish above due to the outflow of brackish water from the Baltic (Sparre, 1984). The shallowest diver collected specimen of *C. truncatus* was from 9.2 m depth in the Little Belt. The species could be expected to occur at shallower depths in northern districts with higher salinity.

Newroth & Taylor (1971, as *Phyllophora truncata* f. *brodiei* and f. *truncata*) examined the material of Edelstein et al. (1969, as *Phyllophora brodiei* and *P. interrupta*) from Halifax County, Canada. They found mixtures of intergrading forms of the two species at intermediate depths. Such intergrading forms between the two species were few in the present study but possibly remain to be detected in greater numbers, especially in the northern districts.

Acknowledgements

Thanks are due to Karsten Dahl, Kim Lundshøj and Michael Bo Rasmussen who made special efforts in collecting *Coccotylus* when diving on the stone reefs during the Danish monitoring cruises in 2013 and 2014. Thanks also to Ole Gorm Norden Andersen for linguistic assistance.

The collections of marine algae from Danish waters in the Algal Herbarium of The Natural History Museum of Denmark have been significantly expanded since 1989 with the addition of large collections obtained by divers. The major part originated from collaboration with authorities undertaking the marine monitoring work for the Danish Ministry of the Environment. Samples studied during ongoing work by the Institute of Bioscience, Aarhus University, have also been added to the museum collection. This includes monitoring of Danish stone reefs and the Revfisk project 2014 (33012-13-n-0011), financed by The Ministry of Food and the EU via European fisheries fund (EFF).

Literature

- Dixon, P.S. & Irvine, L.M., 1977: Seaweeds of the British Isles. Volume 1 Rhodophyta Part 1 Introduction, Nemaliales, Gigartinales. British Museum (Natural History), London: 1-252.
- Edelstein, T., Craigie, J.S., McLachlan, J., 1969: Preliminary survey of the sublittoral flora of Halifax County. Journal of the Fisheries Research Board of Canada, 26: 2703-2713.
- Guiry, M.D. & Garbary, D.J., 1990. A preliminary phylogenetic analysis of the Phyllophoraceae, Gigartinaceae and Petrocelidaceae (Rhodophyta) in the North Atlantic and the North Pacific. In: Evolutionary Biogeography of the Marine Algae of the North Atlantic. (Garbary, D.J. & South, G.R. Eds): 265-290. Berlin: Springer-Verlag.

- Guiry, M.D. & J.A. West, 1983: Life history and hybridization studies on *Gigartina stellata* and *Petrocelis cruenta* (Rhodophyta) in the North Atlantic. Journal of Phycology 19: 474-494.
- Kornmann, P. & Sahling, P.-H., 1978: Meeresalgen von Helgoland. Benthische Grün-, Braun- und Rotalgen. Helgoländer wissenschaftliche Meeresuntersuchungen 29: 1-289.
- Kylin, H., 1907: Studien über die Algenflora der schwedischen Westküste: 1-287, Table. 1-7. K.W. Appelbergs Buchdruckerei. Upsala.
- Kylin, H., 1944: Die Rhodophyceen der schwedischen Westküste. Acta Universitatis Lundensis N.F. 40 (2): 1-104.
- Køie, M. & Kristiansen, Aa., 2014: Havets dyr og planter. 2. Udgave: 1-327. Gyldendal A/S.
- Le Gall, L. & Saunders, G.W., 2010: DNA barcoding is a powerful tool to uncover algal diversity: A case study of the Phyllophoraceae (Gigartinales, Rhodophyta) in the Canadian flora. Journal of Phycology 46, 374–389.
- Lund, S.J., 1959: The marine algae of East Greenland. Meddelelser om Grønland 156: 1-247.
- Maggs, C.A., 1989: *Erythrodermis allenii* Batters in the life history of *Phyllophora traillii* Holmes ex Batters (Phyllophoraceae, Rhodophyta). Phycologia 28: 305-317.
- Newroth, P.R., 1971a: Redescriptions of five species of *Phyllophora* and an artificial key to the North Atlantic Phyllophoraceae. British Phycological Journal 6: 225-230.
- Newroth, P.R., 1971b: Studies on the life histories in the Phyllophoracea. I. *Phyllophora truncata* (Rhodophyceaea, Gigartinales). Phycologia, 10(4): 345-354.
- Newroth, P.R. & Taylor, A.R.A., 1971: The nomenclature of the North Atlantic species of *Phyllophora* Greville. Phycologia 10: 93–97.
- Pedersen, P.M., 2011: Grønlands havalger: 1-208. Forlaget Epsilon. DK. Copenhagen.
- Printz, H., 1926: Die Algenvegetation des Trondhjemsfjordes. Norske Videnskaps-Akademi i Oslo. Skrifter. 1. Matematisk-Naturvidenskapelig Klasse. 1926, No. 5: 1-274, Table 1-10; Map. Oslo.
- Rosenvinge, L.K., 1893: Grønlands Havalger. Meddelelser om Grønland 3: 763-981, 2 plates.
- Rosenvinge, L.K., 1898: Deuxième mémoire sur les algues marines du Groenland. Meddelelser om Grønland 20: 3-125.
- Rosenvinge, L.K., 1929: *Phyllophora brodiæi* and *Actinococcus subcutaneus*. Arbejder fra den botaniske Have i København 115: 1-40, 2 plates. Bianco Lunds Bogtrykkeri, København.
- Rosenvinge, L.K., 1931: The Marine algae of Denmark. Contributions to their natural history. Part IV. Rhodophyceae IV. (Gigatinales, Rhodymeniales, Nemastomatales). Det Kongelige Danske Videnskabernes Selskabs Skrifter, 7. Række, 7(4): 491-626, 1 plate.
- Sjöstedt, L.G., 1927: Havsalger från Hallands Väderö och närliggende Skånekyst. Lunds Universitets Årsskrift N. F. Avd. 2. 23 (6): 1-27.

- Sparre, A., 1984: The Climate of Denmark, Summaries of Observations from Light Vessels (IV), Salinity, Means, Extremes and Frequency. Danish Meteorological Institute, Climatological Papers 11: 1-232.
- Taylor, W.R., 1957: Marine algae of the northeastern coast of North America: 1-509. University of Michigan Press, Ann Arbor.
- Tolstoy, A. & Österlund, K., 2003: Alger vid Sveriges Östersjökust en fotoflora: 1-283. ArtDatabanken, SLU, Uppsala.
- Wynne, M.J. & Heine, J.N., 1992: Collections of marine red algae from St. Matthew and St. Lawrence Islands, the Bering Sea. Nova Hedwigia 55: 55-97
- Zinova, A.D., 1955: [Determination book of the red algae of the Northern seas of the U.S.S.R]:1-222. Leningrad and Moscow. (Original in Russian).