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Taxonomic identity, ecology and distribution of the calcite-depositing cyanobacterium *Phormidium incrustatum* (Oscillatoriaceae)

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Abstract — The morphology of the common and widely distributed calcite-encrusted cyanobacterium *Phormidium incrustatum* (Näg.) Gomont is redescribed. Numerical analysis indicated that the species was conservative for trichome width and cell length but not for end cell characteristics. *Phormidium incrustatum* colonised travertine (calcium carbonate deposits) in alkaline streamwaters, low in dissolved orthophosphate but high in nitrate-nitrogen. Stream sites were often surrounded by trees, and a bimodal seasonal illumination regime occurred. Biomass, measured as biovolume, was low for this species, averaging 0.28 mm^3 cm^{-2} and resulted from the low illumination regime imposed by calcite deposition and tree shading. No significant correlation was found between the biomass of *Phormidium* and rate of travertine deposition, and the taxonomic value of calcification in this cyanobacterium is questioned. The species has a worldwide distribution currently spanning latitudes 54° N to 30° S. It is common on shaded spring-deposited travertine, and in the encrusted littoral zone of calcareous lakes. In some populated regions, the species has been lost as a result of water pollution or channel modification.

Biomass / Cyanobacteria / distribution / ecology / Oscillatoriaceae / *Phormidium* / stromatolite / taxonomy / travertine / tufa

Résumé — Identité taxinomique, écologie et distribution de *Phormidium incrustatum* (Oscillatoriaceae), cyanobactérie encroûtante. La morphologie de la cyanobactérie encroûtante *Phormidium incrustatum* (Näg.) Gomont, commune et largement répandue, est redécrite. Une analyse numérique montre que l'espèce est homogène en ce qui concerne la largeur des trichomes et la longueur des cellules, mais plus variable pour les caractéristiques des cellules terminales. *P. incrustatum* colonise des tufs calcaires (dépôts de carbonate de calcium) dans des cours d'eau alcalins, pauvres en orthophosphates dissous mais riches en NO_3–N. De nombreux sites en rivières sont ombragés avec un régime d'éclairement saisonnier bimodal. La biomasse, estimée comme biovolume, est faible pour cette espèce, d'environ 0,28 mm^3 cm^{-2} en moyenne; elle résulte de la réduction de l'éclairement due au dépôt de calcite et à l'ombrage des arbres. Aucune corrélation significative n'a pu être mise en évidence entre la biomasse de *Phormidium* et le taux de calcification; ce fait jette un doute sur la valeur taxinomique de la calcification chez cette espèce. *P. incrustatum* a une large distribution mondiale entre les latitudes de 54° N et 30° S. Il apparaît fréquement dans les tufs calcaires de sources ombragées ainsi que dans les zones incrustées littorales de lacs calcaires. Dans certaines régions densément peuplées, l'espèce a disparu à la suite de la pollution de l'eau ou de modifications du lit des cours d'eau.

Biomasse / Cyanobactérie / distribution / écologie / Oscillatoriaceae / *Phormidium* / stromatolite / taxinomie / travertin / tuf

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INTRODUCTION

Among the benthic Oscillatoriaceae (Cyanobacteria), several species are known to become densely encrusted with deposits of calcium carbonate in calcareous streams and rivers. One of these, *Phormidium incrustatum* (Näg.) Gom., is widely distributed in the northern hemisphere. The species was first described as *Hypheothrix incrustata* by Nägeli in Kützing (1849) before the starting point of the group (1892), and transferred to *Phormidium* by Gomont (1892). In the following year it was also transferred to *Lyngbya* by Hansgirg (1893) but was later included under *Phormidium* in the seminal work of Geitler (1932). Subsequently, interest developed in the fossilised Oscillatoriaceae found in ancient travertines, which were often found to be morphologically similar to *P. incrustatum.* These include deposits in the Saar-Nahe Basin dating to the Permian period (Shafer & Stapf, 1978). More recently, Freytet & Plet (1996) and Pitois *et al.* (2001) have described the petrology of modern and ancient deposits formed around *P. incrustatum* in the Paris Basin. Although some attempt to clarify the taxonomy of the calcified *Phormidium* species has been made by Golubic (1973) and Kann (1973), little is known of the ecology of the species apart from some aspects of its biomineralization (Pentecost, 1996). In addition, *Phormidium incrustatum* requires further characterisation in the light of recent taxonomic work in the Oscillatoriales (Anagnostidis & Komárek, 1988; Castenholz, 1992). The aim of this paper is to clarify the species definition and provide additional quantitative morphological and ecological data on a widely-distributed cyanobacterium with a good fossil record (Golubic *et al.,* 1993; Freytet & Plet, 1996).

MATERIALS AND METHODS

Phormidium- travertines were sampled at 13 locations, 10 in the U.K., two in Germany and one in the United States (Tab. 1). Water samples at most sites were analysed for major dissolved constituents (pH, total CO_2, Ca, Mg, SO_4, NO_3–N, soluble reactive PO_4–P), and the calcite saturation quotient Ω calculated (see Pentecost, 1992). Light intensity was measured with a photometer and the relative irradiance in proportion to the unobstructed sky was calculated. Since travertine is deposited in a seasonal pattern, the annual deposition rate could be estimated by measuring couplet distance on vertical sections (Fig. 1) together with their water-holding capacity as described by Pentecost & Viles (1999).

For microscopic examination, small samples of the travertine were decalcified with 5 % ethylene diamine tetraacetic acid (EDTA) at pH 8 and room temperature and squashes observed under the light microscope. For live examination, fresh samples collected during the early summer were placed on 1% agar for a few hours when the *Phormidium* hormogonia moved out, free of mineralisation, onto the agar surface. To estimate *Phormidium* biovolume per unit area, small blocks of travertine were detached with a jeweller's saw and the block dimension recorded under a dissection microscope. The approximate penetration depth of the cyanobacteria into the travertine was recorded by viewing fresh sections under a high power dissection microscope, and the block decalcified with EDTA. The algal mat was gently disintegrated with a hand-held Eppendorf homogenisor. Suspension volume was adjusted to 2 ml then added to an inverted microscope counting chamber so that total trichome length could be determined using the method of Olson (1950). Biovolumes were calculated from total trichome length and mean trichome diameter.

Table. 1. Site descriptions and ecological/environmental measurements

Site No.	*Location*	*Latitude/ Long.*	*Month sampled for water analysis*	*Water temp.°C*	*Water pH*	*Total CO_2 mM*	*Ca mM*	*Mg mM*	*SO_4 mM*	*Saturation quotient*	*NO_3^--N µM*	*PO_4^--P µM*	*Lyngbya biovolume mm^3 cm^{-2}*	*Travertine deposition rate mm a^{-1}*
1	Cherwell, U.K.	51.56N 1.32W	4.92	5.6	8.24	3.29	2.99	0.08	0.043	7.3	550	1.3	0.03	2.0
2	Nash Brook, U.K.	51.24N 3.32W	9.92	12.3	8.16	5.38	3.19	0.14	0.37	2.5	550	9.0	0.19	2.5
3	Harrietsham, U.K.	51.17N 0.39E	3.93	14.2	8.28	5.08	3.13	0.009	0.37	16.0	540	1.6	0.35	1.5
4	Menai Bridge, U.K.	53.14N 4.10W	mean 1973	9.8	8.44	3.61	1.13	0.79	0.35	3.9	47	0.3	0.03	0.7
5	Plaxtol, U.K.	51.16N 0.17E	5.96	11.8	7.96	5.69	3.57	0.14	0.69	1.5	980	–	0.26	1.5
6	Porthkerry, U.K.	51.24N 3.32W	4.91	11.3	7.75	5.89	3.47	–	–	5.6	490	3.9	0.02	2.3
7	Priory Mill, U.K.	51.56N 1.32W	3.92	8.6	7.70	5.19	3.08	0.02	0.24	2.6	600	2.1	0.18	2.6
8	Shelsley Walsh, U.K.	52.18N 2.28W	9.91	10.2	8.00	4.83	1.79	1.05	–	3.2	–	–	0.50	3.2
9	Waterfall Beck, U.K.	54.05N 2.08W	mean 1989	10.9	8.28	2.29	1.24	0.04	0.09	3.6	42	0.5	0.70	3.7
10	West Malling, U.K.	51.17N 0.30W	7.96	20.4	8.29	4.35	2.65	0.16	0.79	15.0	1000	–	0.25	2.6
11	Dusselbach, Germany	49.30N 9.25E	9.92	9.1	8.1	6.05	2.19	0.75	0.07	7.0	–	–	0.18	7.0
12	Fleinsbrunnen-bach, Germany	48.30N 9.25E	8.92	14.3	8.10	4.12	2.27	0.06	0.02	7.1	–	–	0.47	2.1
13	Prices Falls, Ok. U.S.A.	34.27N 97.12W	1.88	12.1	8.33	2.42	5.21	0.56	0.01	19.0	–	–	0.51	2.4
mean	–	–	–	11.6	8.07	4.48	2.76	0.34	0.28	8.7	530	2.7	0.28	2.23
range				5.6-20.4	7.8-8.3	2.3-6.1	1.1-5.2	0.08-1.1	0.01-0.8	1.5-19	40-1000	0.5-9.0	0.02-0.7	0.7-7.0

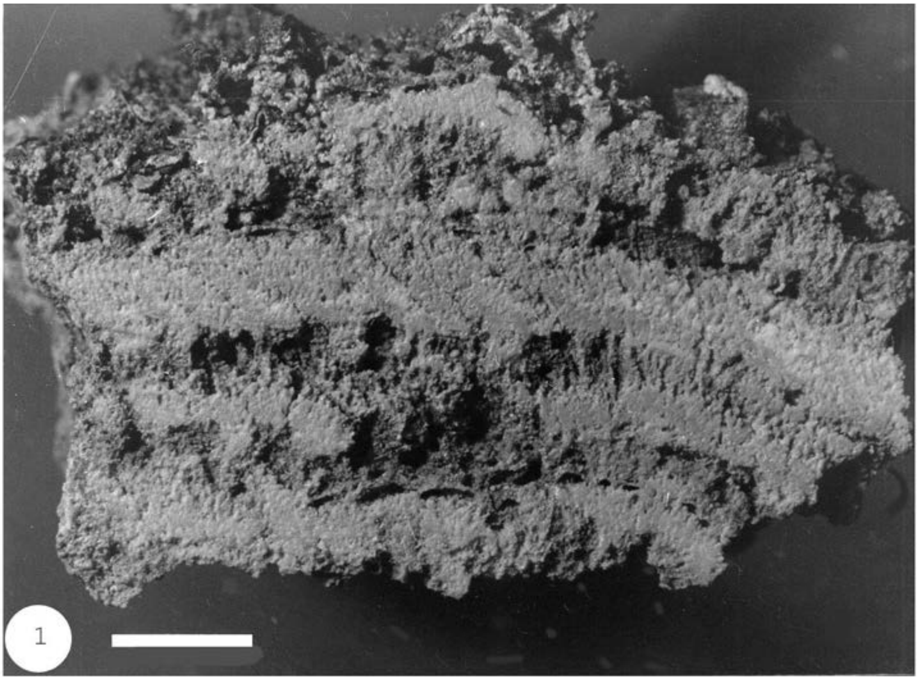


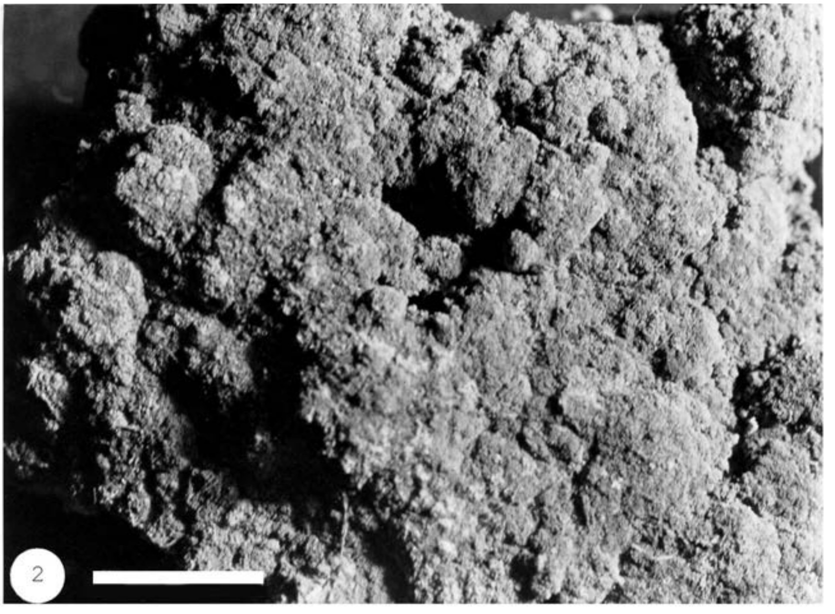
Fig. 1. Vertical section through a travertine sample containing *Phormidium incrustatum* from the Fleinsbrunnenbach, Germany (site 12) showing several seasonal laminae. The thicker, pale laminae are formed during winter and early spring and the darker, more spongy layers are produced in late spring and summer. The series of chironomid tubes in the lower part of the picture (arrow) were formed at the end of spring but do not recur in more recent layers. Travertine surface to top of photograph. Scale = 0.5 cm.

RESULTS AND DISCUSSION

Morphology

Phormidium incrustatum forms characteristic nodular accretions of porous travertine in shallow calcareous streams and lakes. The surface of the travertine becomes colonised by minute, slightly radiating bushes of trichomes growing approximately perpendicular to the surface. Calcium carbonate is soon deposited onto the sheaths, forming a surface of calcareous coalescing nodules resembling a small cauliflower (Fig. 2). Where the water is more turbulent, the surface sometimes consists of a series of larger, regular undulations (Fig. 3).

The trichome apices of the *Phormidium* displayed a range of morphologies (Fig. 4). Most of the apices at site 5 (46 %) displayed an unthickened rounded end (Fig. 4a), while the remainder possessed either a rounded end with slight apical thickening (Fig. 4b, 9 %) or a conical end (Fig. 4c, 18 %). Trichome apices that developed within the sheaths during hormogonium production were invariably hemispherical and unthickened (Fig. 5). A single-factor analysis of variance showed that the mean trichome diameters of these four morphological types were not significantly different (F=0.32, p=0.74).



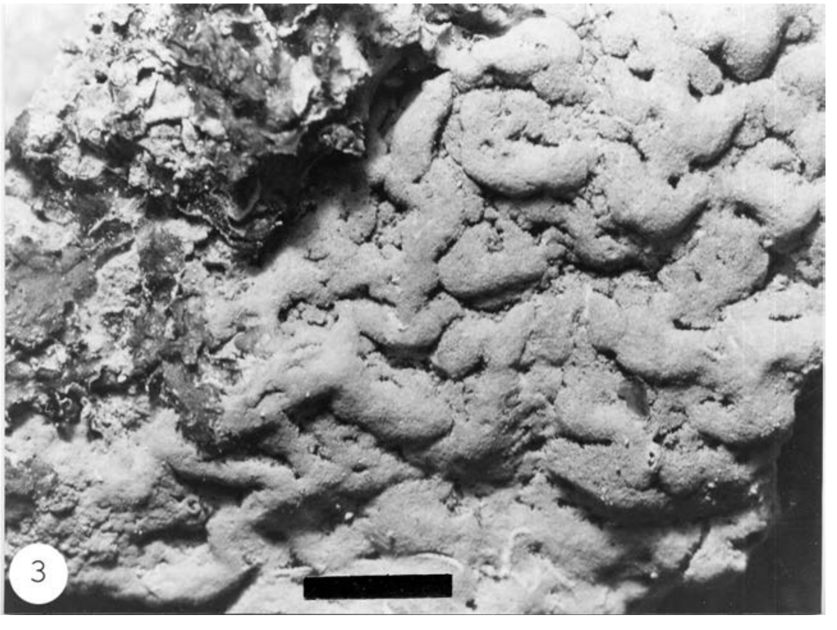


Fig. 2. Surface of a *Phormidium* travertine from Harrietsham, Kent collected in March showing small coalescing colonies combining to form a 'cauliflower crust'. The colonies are heavily calcified. Scale = 1 cm.
Fig. 3. Wavy travertine surface colonised by *P. incrustatum* from Harrietsham, collected in March on a small cascade showing an undulating form reminiscent of rimstone. The travertine surface has a relief of about 4mm and does not exhibit the 'cauliflower' morphology shown in Fig 1b. Scale = 1 cm.

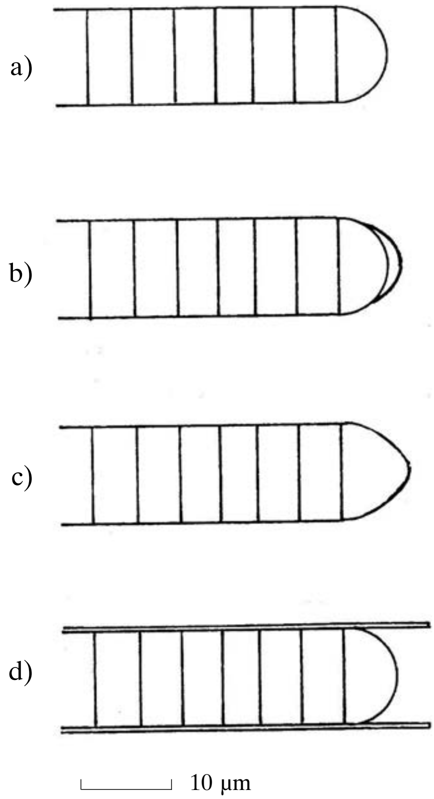


Fig. 4. Illustrations of the types of trichome apices encountered in a large sample of *P. incrustatum* from Plaxtol, Kent. a) simple hemispherical apical cell, most frequently encountered ; b) cell with a thickened cap (calyptra); c) conical apex. Trichomes often break within the sheaths where they take the simple hemispherical form (d).

In all samples the trichomes of *P. incrustatum* averaged 4-6 µm in diameter and were enclosed by a thin, firm sheath. The range of variation in diameter for the West Malling, Kent sample (Tab. 1, site 10) was small, the coefficient of variation (V) being close to 6 (Fig. 6a). Cell length was more variable (V approximately 33), being dependent upon the growth stage of the cell (Fig. 6b) but the cells were usually discoid and averaged about one third as long as wide. At the surface of the encrusted colonies the sheaths became indistinct, and those of the developing hormogonia were too thin to observe in the light microscope. Healthy, blue-green trichomes were normally only observed in the upper 1mm of the travertine, and below this, the empty sheaths persisted up to 1 cm or more into the deposit.

Measurements of the hormogonia released onto agar by a fresh sample from site 5 indicated an approximate log-normal distribution of their length with an average of 60 µm and a high coefficient of variation (Figs. 5, 7). The hormogonia were motile with a mean average linear translation of 0.52 µm s^{-1}(n=10).

Trichome diameter is considered a good taxonomic character at the species level (Jaag, 1934; Fjerdingstad, 1971) and this is given support by the pres-

Fig. 5. Hormogonia of *P. incrustatum* from an enrichment culture of West Malling material. Minute granules within the cells are mainly cyanophycin. Several adjacent necridia can be seen in the small hormogonium (arrow). Scale = 10 µm.

ent study. The coefficient of variation for trichome diameter is low and comparable with measurements obtained within the genus *Oscillatoria* (Golubic & Schwabe, 1965; Fjerdingstad, 1971).

Taxonomy of *Phormidium incrustatum*

In her taxonomic revision of the carbonate-depositing *Phormidium*, Kann (1973) reduced the number of species from nine to two, *P. incrustatum* and *P. calcareum* Kütz. Both species have trichomes of similar width, *P. calcareum* being distinguished by the presence of an apical thickening (calyptra). This investigation has shown that apparently mature (i.e. non hormogonial) forms with and without a calyptra occur closely associated in the same sample, and it is likely that they represent variants of the same species. When a clean sample of soft limestone was left at one of the sites of two years, a form indistinguishable from *P. incrustatum* was found to have penetrated the underlying rock to about 100 µm depth, clearly demonstrating endolithic behaviour. The evidence suggests that this species is not exclusively associated with calcium carbonate deposition and further characterisation using pure isolates and molecular analysis is required.

Ecological considerations

Water chemical data for the 13 sites are shown in Table 1. In most cases these represent spot samples, but at two sites (4 and 9) detailed measurements

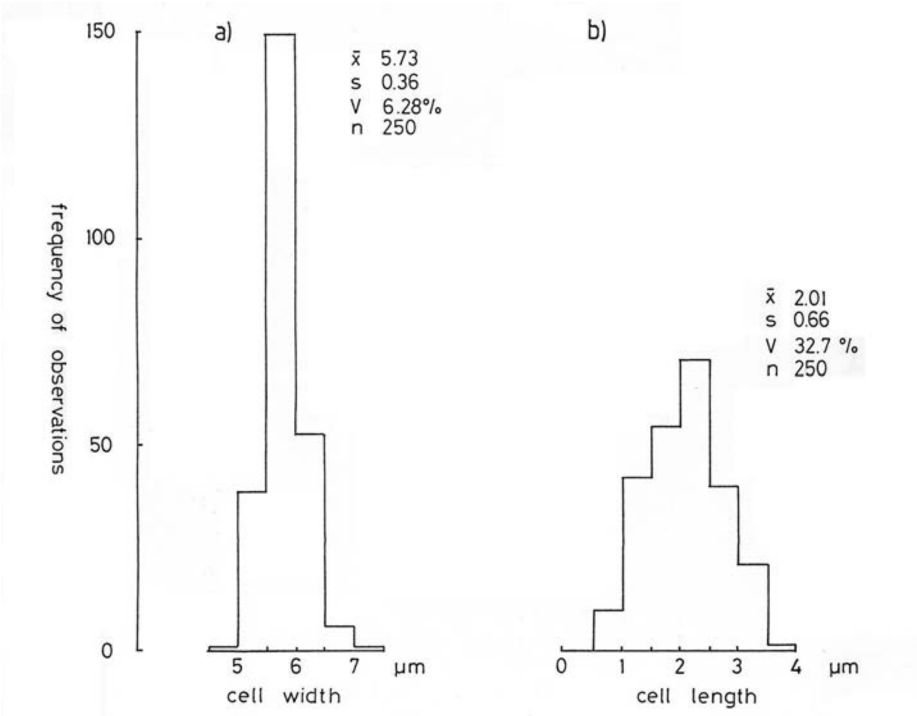


Fig. 6. Frequency histograms and statistics for a sample of *P. incrustatum* from West Malling, Kent. a) Cell width in 0.5 µm classes. b) Cell length in 0.5 µm classes.

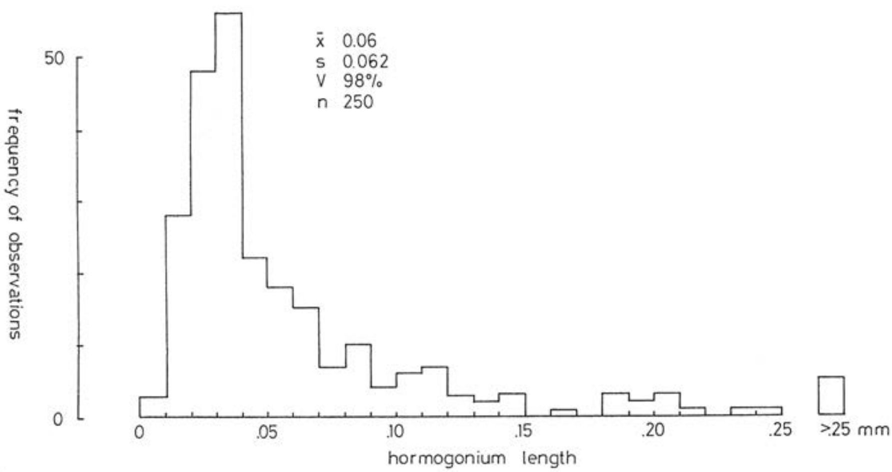


Fig. 7. Frequency histogram for hormogonium length in a sample of *P. incrustatum* from West Malling, Kent in 0.01 mm classes.

were available spanning the whole year. At all sites the water was found to be high in dissolved calcium, carbon dioxide (as bicarbonate) and with a pH exceeding 7.0. They are alkaline calcium bicarbonate type waters typical of those from which travertine is deposited. Measurements of the calcite saturation quotient Ω all exceeded unity, indicating that the waters were thermodynamically unstable and capable of precipitating calcium carbonate. Concentrations of dissolved nutrients varied widely. Nitrate-N ranged from 40-1000 μM (0.5-14 ppm) and reactive orthophosphate 0.5-9.0 μM (0.015-0.28 ppm).

All of the sites investigated were streams rising from limestone springs where levels of calcium and carbon dioxide would be expected to be high. Similar values of these determinands have been reported for some French *Phormidium* travertines by Casanova & Lafont (1985). Soluble orthophoshate levels tend to be low in such waters due to the coprecipitation of phosphate with the calcite, but eutrophication can lead to enrichment, sometimes 'poisoning' the calcite surfaces leading to the demise of deposits (e.g. Edwards & Heywood, 1960). Casanova & Lafont (1985) estimated that orthophosphate levels exceeding 50 μg 1^{-1} inhibited calcium carbonate deposition in *Phormidium* sites, and in an experimental stream channel colonised by *P. incrustatum*, Ladle *et al.* (1976) found 30-50 $\mu 1^{-1}$ PO_4-P in the inflow water. In the present investigation an average concentration of 80 μg 1^{-1} was found in the U.K. These more elevated values probably result from small, possibly periodic inputs of treated sewage into some of the U.K. streams. While soluble orthophosphate levels appear to be consistently low, nitrate-nitrogen levels were found to be much higher, probably the result of groundwater contamination (cf. Ladle *et al.,* 1976). Levels of orthophosphate, exceeding 1 ppm were found by the author in the Cambridgeshire streams that once contained extensive *Phormidium* travertines (Fritsch & Pantin, 1946). However, these streams had also been dredged, so a pollution effect cannot be substantiated. In the United States, Golubic & Fischer (1975) found that acidic industrial effluent had destroyed *Phormidium* travertines in one stream and it is clear that this species and the associated deposits are vulnerable to several kinds of human disturbance.

The travertines were all porous, the void volume ranging from 36-69 %. Travertine deposition rates measured by couplet distances averaged 2.23 mm a^{-1} and ranged from 0.7-7.0 mm a^{-1}. Water temperature ranged from 5.6-20.4° C and the range of variation was site-dependent. At Menai Bridge (site 4) where the deposits formed within five metres of a small spring, the annual temperature range was 7.1-16.0° C, while at Waterfall Beck (site 9) an upland site in the U.K., the annual range 800 m downflow was 6.0-19;7° C.

Irradiance measurements were taken at site 5 over two years. They indicated substantial changes over the season where deposits were shaded by trees. During winter, levels ranged between 80 and 200 μE m^{-2} s^{-1} representing between about 25 and 35 % of the unobstructed sky irradiance. During late spring and summer after leaf break, this value fell to 1-7 % of the unobstructed sky. Using the mean solar irradiance curves in Walsh (1961 p. 34) for lat. 51° N it is possible to estimate the total annual light flux to the surface of the *Phormidium* crusts at site 5. Curve (a) of Fig. 8 shows the calculated annual irradiance for the site, with maximum values during June and July. Curve (b) shows the level of light falling on the *Phormidium* surface, taking account of sky obstruction by banks and trees. It is a bimodal curve with a maximum in late spring just before leaf break and a smaller peak in the autumn after leaf fall. The total annual irradiance at the surface of the crust was estimated as 15 % of that available from the unobstructed sky. Similar values were estimated for the other woodland sites (1-3, 6-8, 10).

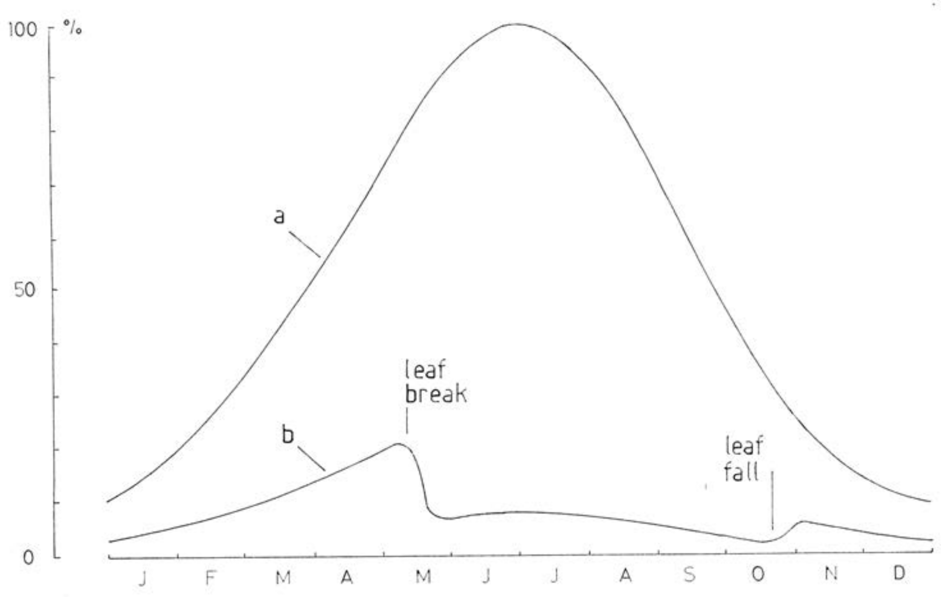


Fig. 8. Mean annual solar irradiance curves for a plane, wetted, horizontal surface at latitude 51°N calculated from Walsh (1961) showing a) relative irradiance at surface exposed to the open, unobstructed sky and b) relative irradiance below the deciduous woodland canopy at the Plaxtol site, U. K. The effects of leaf-break and leaf-fall have a significant impact on the radiation regime.

The environmental investigations have shown that *P. incrustatum* can tolerate a moderate range of temperature, but to date it has not been found colonising thermogene (hot-spring) travertines. Since most collections were taken from streams in wooded areas, incident light will be low during the summer and *P. incrustatum* appears to be adapted to surviving low light intensities. Since the majority of trichomes are covered by a layer of travertine, the average radiation flux reaching the trichomes must be extremely low. The species is also known from carbonate crusts in the littoral zone of lakes. Here, it occurs in depths of 30 cm or more of water where light intensities would be higher during summer than in a broad-leaved woodland. However, a thicker cover of calcite could increase the level of shading, as has been demonstrated in other carbonate-depositing cyanobacteria (Pentecost, 1978).

Biomass of *P. incrustatum* was measured as biovolume and this ranged between 0.02 and 0.7 mm^3 cm^{-2} (Tab. 1). The species was the major algal component of these travertines and the biovolume was correlated with depth of the pigmented (photosynthetic?) layer of the travertine ($P<0.05$). However, there was no significant correlation between the biovolume and the rate of travertine deposition. The biomass estimates are low (0.02-0.7 mm^3 cm^{-2}) when compared with uncalcified cyanobacterial mats (see Pentecost & Whitton, 2000), where it may exceed 4 mm^3 cm^{-2}. These low and variable values probably reflect the low light levels and spatial heterogeneity of the habitat respectively. Similar results were obtained for other cyanobacteria in travertine-depositing sites in northern England (Pentecost, 1991). There was no significant correlation between the biovolume and the rate of travertine deposition, so the study provides no support for a role of photosynthesis in travertine deposition at the sites investigated.

Geographic distribution

The distribution of *P. incrustatum* is shown in Figs 9 and 10. It is found throughout the world and spans latitudes 54° N to 30° S. It occurs in a wide range of precipitation zones (100-2000 mm a^{-1}) with mean summer temperatures ranging from 10-25° C. Most collections have been made from streams but the species has also been reported from the littoral zone of calcareous lakes. Records have been made from fully exposed subtropical wadis (Oman) and from tree-shaded streams and rivers. There have been few records from the tropics, perhaps reflecting the

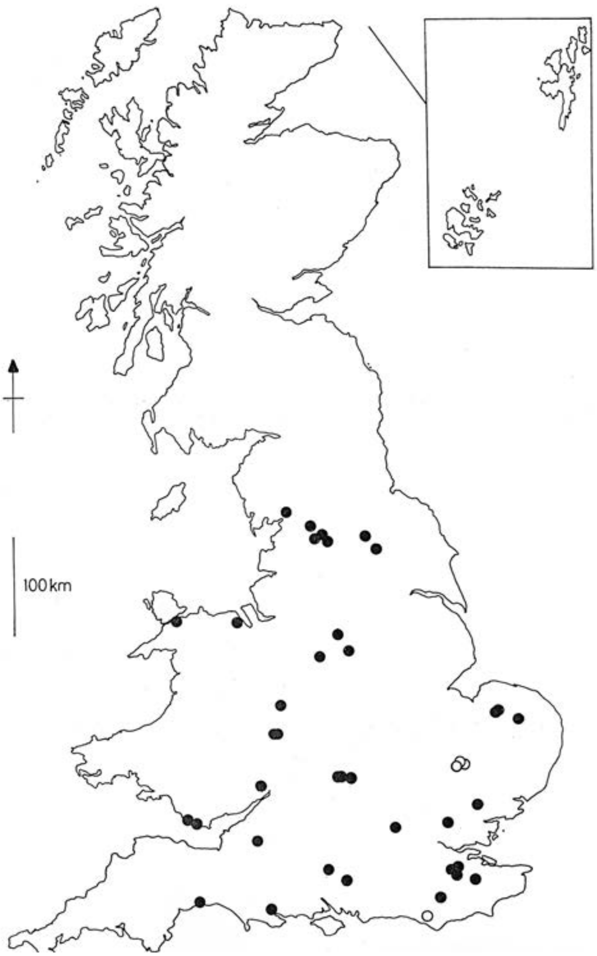


Fig. 9. Distribution of *Phormidium incrustatum* in the British Isles. Sources are Fritsch & Pantin, (1946); Fritsch (1949; 1950); Marker & Casey (1976) and the author's unpublished records. Open circles indicate sites from which the species has disappeared due to human disturbance.

Fig. 10. Global distribution of *Phormidium incrustatum*. Sources: Adolphe & Rofes (1973); Casanova (1994); Casanova & Lafont (1985); Cohn (1864); Desickachary (1959); Freytet & Plet (1991, 1996); Fritsch & Pantin (1946); Fritsch & Rich, 1929; Gardner (1927); Golubic & Fischer (1975); Kann (1978; 1988); Minckley (1963); Pentecost (1985; 1990); Prosperi(1983); Sabater (1989); Scholl & Taft (1964); Starmach (1966); Symoens (1950, 1957); Symoens *et al.* (1951); Symoens & Malaisse (1967); Tiercelin & Vincens (1987); Tilden (1910); Viles & Goudie (1990) and the author's unpublished records.

lack of research on tropical streams. More detailed collecting in the United Kingdom has shown the species to be widely distributed (Fig. 9). It occurs commonly in small calcareous streams with deciduous woodland cover. In areas with a broken canopy, other cyanobacteria often become abundant (e.g. *Schizothrix* spp.) and the travertine may become overgrown with extensive carpets of the moss *Palustriella commutata.* Its absence from Scotland reflects the scarcity of limestone in that region. At most of the sites recorded by Fritsch (1949; 1950) and Fritsch & Pantin (1946) the species no longer occurs either due to channel modification or to water pollution.

CONCLUSIONS

1) Quantitative measurements of trichome and cell dimensions of natural and cultured collections of *Phormidium incrustatum* show that trichome diameter is much less variable than cell length and end cell characters. This has taxonomic implications for the genus *Phormidium* as a whole.

2) Evidence is presented to suggest that the cosmopolitan *P. incrustatum* is not exclusively associated with the deposition of calcium carbonate, so that carbonate deposition may not be a reliable taxonomic character.

3) The species has been observed in calcareous alkaline freshwaters low in dissolved orthophosphate(< 80 μgl^{-1}) subject to low irradiance caused by tree

cover and/or deposits of calcite. The low irradiance results in a low biomass per unit area, which explains the lack of correlation between the rate of calcium carbonate deposition and the amount of *Phormidium* present.

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REFERENCES

ADOLPHE J.-P. & ROFES G., 1973 — Les concrétionnements calcaires de la Levrière. *Bulletin de l' Association francaise, Étude Quaternaire* 35: 79-87.

ANAGNOSTIDIS K. & KOMAREK J., 1988 — Modern approaches to the classification of cyanophytes 3. — Oscillatoriales. *Archiv für Hydrobiologie Supplement* 80: 327-472.

CASANOVA J., 1994 — Stromatolites from the East African Rift: a synopsis. *In* : Bertrand-Sarfati J. & Monty C. L., (Eds) *Phanerozoic Stromatolites II*, Amsterdam, Kluwer, pp. 193-226.

CASANOVA J. & LAFONT R., 1985 — Les cyanophycées encroûtantes du Var (France). *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 22: 2805-2810.

CASTENHOLZ R.W., 1992 — Species usage, concept and evolution in the cyanobacteria (blue green algae). *Journal of Phycology* 28: 737-745.

COHN F., 1864 — Über die Entstehung des Travertin in den Wasserfällen von Tivoli. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 40: 580 610.

DESIKACHARY T.V., 1959 — *Cyanophyta.*, New Delhi, Indian Council of Agricultural Research.

EDWARDS R.W. & HEYWOOD J., 1960 — Effect of a sewage effluent discharge on the deposition of calcium carbonate on shells of the snail *Potamopyrgus jenkinsii* (Smith). *Nature* 186: 492-493.

FJERDINGSTAD E., 1971 — Dimensions and taxonomy of Oscillatoriaceae. 1. *Oscillatoria limosa* Ag. and *O. nitida* Schkorb. emend. *Schweizerische Zeitschrift für Hydrologie* 33: 171-199.

FREYTET P. & PLET A., 1991 — Les formations stromatolitiques (tufs calcaires) récentes de la région de Tournus (Saône et Loire). *Geobios* 24: 123-139.

FREYTET P. & PLET A., 1996 — Modern freshwater microbial carbonates: the *Phormidium* stromatolites (tufa-travertine) of Southeastern Burgundy (Bassin parisien, France). *Facies* 34: 219-234.

FRITSCH F.E., 1949 — The lime-encrusted *Phormidium* community of British streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 10: 141-144.

FRITSCH F.E., 1950 — *Phormidium incrustatum* (Naeg.) Gom. an important member of the lime-incrusting community of flowing water. *Biologisch Jaarboek* 70: 27-39.

FRITSCH F.E. & PANTIN C.F.A., 1946 — Calcareous concretions in a Cambridgeshire stream. *Nature* 157: 397-399.

FRITSCH F.E. & RICH F., 1929 — Contributions to our knowledge of freshwater algae in Africa. *Transactions of the Royal Society of South Africa* 18: 1-92.

GARDNER N.L., 1927 — New Myxophyceae from Porto Rico. *Memoirs of the New York Botanical Garden* 7: 1-144.

GEITLER L., 1932 — *Cyanophyceae*. *In*: Rabenhorst, L. (ed.). Kryptogamen-Flora von Deutschland, Österreich und der Schweiz 14. Leipzig, Akademische Verlagsgesellschaft, 1196 p.

GOLUBIC S., 1973 — The relationship between blue-green algae and carbonate deposits. *In*: Carr N.G. & Whitton B.A. (eds). *The Biology of Blue-green Algae.* Oxford, Blackwell, pp. 434-472.

GOLUBIC S. & FISCHER A.G., 1975 — Ecology of calcareous nodules in Little Conestoga Creek near Lancaster, Pennsylvania. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 19: 2315-23.

GOLUBIC S. & SCHWABE G.H., 1965 — Zur taxonomischen und ökologischen Bedeutung linearer Zellmasse bei den Cyanophyten. *Österreichische Botanische Zeitschrift* 112: 311-330.

GOLUBIC S., VIOLANTE C., FERRERI V. & D'ARGENIO B., 1993 — Algal control and early diagenesis in Quaternary travertine formation (Roccheta a Volturno, central Apennines). *In*: Baratolo F., De Castro P. & Parente M. (eds). *Studies on Fossil Benthic Algae. Bollettino della Societa Palaeontologico Italiana.* Special Volume 1, 231-247.

GOMONT M., 1892 — Monographie des Oscillariées. *Annales des Sciences Naturelles, Botanique,* sér. 7, 16: 91-264.

HANSGIRG A., 1893 — Beiträge zur Kenntnis der Meeresalgen und Bacterien-Flora der östereichischen-ungarischen Küstenländer. *Sitzungsberichte der Königlichen Böhmischen Gesellschaft der Wissenschaften* 1892: 210-249.

JAAG O., 1934 — Die Zellgrösse als Artmerkmal bei den Blaualgen. *Schweizerische Zeitschrift für Hydrologie* 9: 16-33.

KANN E., 1973 — Bemerkungen zur Systematik und Ökologie einer mit Kalk inkrustierter *Phormidium* Arten. *Schweizerische Zeitschrift für Hydrologie* 35: 141-151.

KANN E., 1978 — Systematik und Ökologie der Algen österreichischer Bergbäche. *Archiv für Hydrobiologie, Supplement* 53 (4), 237 p.

KANN E., 1988 — Zur Autökologie benthischer Cyanophyten in reinen europäischen Seen und Fliessgewässern. *Archiv für Hydrobiologie, Supplement* 80: 473-495.

KÜTZING F.T., 1849 — *Species Algarum.* Leipzig, F. A. Brockhaus.

LADLE M., BAKER J.H., CASEY H. & FARR I.S., 1976 — Preliminary results from a recirculating experimental system : observations of interaction between chalk stream water and inorganic sediment. *In*: Golterman H.L. (ed.). *Interaction between sediments and freshwater.* The Hague, Junk, pp. 252-257.

MARKER A.F.H. & CASEY H., 1976 — The population and production dynamics of benthic algae in an artificial re-circulating hard water stream. *Philosophical Transactions of the Royal Society of London B. Biological Sciences* 298: 265-308.

MINCKLEY W.L., 1963 — The ecology of a spring stream Doe Run, Meade County, Kentucky. *Ecological Monographs* 11: 1-124.

OLSON F.C.W., 1950 — Quantitative estimates of filamentous algae. *Transactions of the American Microscopical Society* 59: 272-279.

PENTECOST A., 1978 — Blue-green algae and freshwater carbonate deposits. *Proceedings of the Royal Society of London B*. 200: 43-61.

PENTECOST A., 1985 — Association of cyanobacteria with tufa deposits: identity, enumeration and nature of the sheath material as revealed by histochemistry. *Geomicrobiology Journal* 4: 285-298.

PENTECOST A., 1990 — The algal flora of traverte: an overview. *In* :Herman, J. S. & Hubbard, D. A. (eds.) *Travertine-marl: spring deposits in Virginia*. Charlottesville, Virginia Division of Mineral Resources Publication 101: 117-128.

PENTECOST A., 1991 — Algal and bryophyte flora of a Yorkshire (U.K.) hill stream: a comparative approach using biovolume estimations. *Archiv für Hydrobiologie* 121: 181-201.

PENTECOST A., 1996 — Significance of the biomineralizing microniche in a *Lyngbya* travertine. *Geomicrobiology Journal* 13: 213-222.

PENTECOST A., & VILES H.A., 1999 — Travertine deposition in a small stream: some hydrological and spatial relationships. *Tübinger Geographische Studien* 11.

PENTECOST A. & WHITTON B.A., 2000 — Limestones. *In*: Whitton, B.A. & Potts M.A. (eds). *The Ecology of Cyanobacteria.* Amsterdam, Kluwer, pp. 257-279.

PITOIS F., JIGOREL A. & BERTRU G., 2001 — Colonization dynamics of an encrusting cyanobacterial mat in a hardwater river (Eaulne, France). *Geomicrobiology Journal* 18: 139-155.

PROSPERI C., 1983 — Curiosa asociacion des dos Cianofitos. *Kurtziana* 16: 149-155.

SABATER S., 1989 — Encrusting algal assemblages in a Mediterranean river basin. *Archiv für Hydrobiologie* 114: 555-574.

SHAFER P. & STAPF K.R.G., 1978 — Permian Saar-Nahe Basin and Recent Lake Constance (Germany), two environments of lacustrine algal carbonates. *Special Publications of the International Association of Sedimentologists* 2: 83-107.

SCHOLL D.W. & TAFT W.H., 1964 — Algae, contributions to the formation of calcareous tufa, Mono Lake, California. *Journal of Sedimentary Petrology* 34: 309-319.

STARMACH K., 1966 — *Cyanophyta-Sinice.* Flora Slodokowodna Polski 2. Warsaw, Panstowe Wydawnictwo Naukowe, 803 p.

SYMOENS J.J., 1950 — Note sur les tufs calcaires de la vallée du Hoyoux. *Lejeunia (Revue de Botanique)* 14: 13-17.

SYMOENS J.J., 1957 — Les eaux douces de l'Ardenne et des régions voisines: les milieux et leur végétation algale. *Bulletin de la Société Royale de Botanique de Belgique* 89: 111-134.

SYMOENS J.J., DUVIGNEAUD P. & VANDEN BERGEN C., 1951 — Aperçu sur la végétation des tufs calcaires de la Belgique. *Bulletin de la Société Royale de Botanique de Belgique* 83: 329-352.

SYMOENS J.J. & MALAISSE F., 1967 — Sur une formation de tuf calcaire observée sur le versant est du plateau des Kundelungu. *Bulletin de l'Académie Royale des Sciences d'Outre Mer* 13: 1148-51.

TIERCELIN J.-J. & VINCENS A., 1987 — Le demi-graben de Baringo-Bogoria, Rift Gregory, Kenya 30,000 ans d'histoire hydrologique et sédimentaire. *Bulletin de Centres de Recherches Exploration-Production Elf-Aquitaine.* 11: 249-540.

TILDEN J., 1910 — *Minnesota Algae I.* Minneapolis, University of Minnesota, 328 p.

VILES H.A. & GOUDIE A.S., 1990 — Reconnaissance studies of the tufa deposits of the Napier Range, N.W. Australia. *Earth Surface Processes and Landforms* 15: 425-443.

WALSH J.W.T., 1961 — *The Science of Daylight.* London, McDonald, 295 p.