original scientific paper
received: 1. 9. 2000

UDC 574.5(267-14)

CALCAREOUS STRUCTURES BUILT BY THE CORALLINE ALGA *PNEOPHYLLUM CONFERVICOLA* (KÜTZING) CHAMBERLAIN (CORALLINALES, RHODOPHYTA) IN A MARINE CAVE IN THE GULF OF OMAN

Jože ŠTIRN
SI-6230 Portorož, Fizine 8

Guido BRESSAN, Lia Angela GHIRARDELLI & Lorenza BABBINI
Dipartimento di Biologia dell'Università degli studi di Trieste, IT-34127 Trieste, Via L. Giorgieri 10
e-mail: ghirardl@univ.trieste.it

ABSTRACT

A peculiar marine ecosystem has been discovered in a karst cave system, popularly named the Tiwi Sinkhole, which is located in the south-western coastal zone of the Gulf of Oman, Indian Ocean. This small, isolated ecosystem comprises a very unusual benthic community occupying the sinkhole's sunlit walls. Its components occur in the form of calcareous layers enveloping the primary bedrock and sometimes forming bulk concretions produced apparently only by one prolific population of a crustose coralline species. The results of microscopical analyses and other taxonomical examinations of numerous typical specimens demonstrate that all the structures are produced just by one species, identified as Pneophyllum confervicola *(Kützing) Chamberlain.*

Key words: bioconstruction, coralline alga, *Pneophyllum confervicola,* marine cave

STRUTTURE CALCAREE COSTRUITE DALL'ALGA CORALLINA *PNEOPHYLLUM CONFERVICOLA* (KÜTZING) CHAMBERLAIN (CORALLINALES, RHODOPHYTA) IN UNA GROTTA MARINA NEL GOLFO DI OMAN

SINTESI

Un peculiare ecosistema marino è stato rinvenuto in un sistema di grotte carsiche, popolarmente chiamato Tiwi Sinkhole, localizzato sulla costa sud-occidentale del Golfo di Oman, nell'Oceano Indiano. Questo piccolo, ecosistema isolato, comprende un'inusuale comunità bentonica che occupa le pareti soleggiate della cavità. Le sue componenti si presentano in forma di strati calcarei ricoprenti il substrato di base e, a volte, in forma di grandi concrezioni, prodotte apparentemente da da una popolazione di un'unica specie corallina crostosa, prolifica. I risultati delle analisi microscopiche e di altre indagini tassonomiche di numerosi esemplari tipici dimostrano che tutte le strutture vengono prodotte da una sola specie, identificata come Pneophyllum confervicola *(Kützing) Chamberlain.*

Parole chiave: biocostruzione, alga corallina, *Pneophyllum confervicola,* grotta marina

INTRODUCTION

Occurring throughout the world's oceans in photic benthic zones of hard bottoms, and often on detrited soft bottoms as well, the many genera and species of the Corallinales are important builders of several types of calcareous concretions and structures. Apart from ubiquitous encrustations enveloping primary rock-substrata, detrited rubble and living sessile organisms (epiphytes), there are quite massive and extensive calcareous structures that many crustose corallines are able to produce. For many coastal ecosystems these structures are of great importance, particularly in the tropical areas. For example, crustose species, belonging mainly to the genera *Porolithon, Lithophyllum* and *Neogoniolithon*, are, in addition to stony corals, the second most important framework builders, framework cementers and infillied elements of all coral reefs to which they contribute up to 35% of carbonate material (Adey, 1998). In temperate and subtropical environments, however, some crustose species built extensive framework structures, which are almost entirely composed of coralline material such as the reef-like formations found in the Mediterranean Sea and the adjacent NE Atlantic: upper-littoral "trottoirs" of *Tenarea tortuosa* (Esper) Lemoine and deep-littoral coralligenous platforms built by a number of species belonging to the genera *Mesophyllum, Lithophyllum, Lithothamnium* etc. (Margalef, 1985).

It is the deep-littoral platform that is remarkably similar, by its structure, to the one evolved in a peculiar marine ecosystem discovered in a karst cave system, popularly named the Tiwi Sinkhole, located in the south-western coastal zone of the Gulf of Oman (Indian Ocean).

This small, isolated ecosystem whose habitats are briefly described below, also comprises a very unusual benthic community, which occupies the sinkhole's sunlit walls. All its macro-components, *i.e.* few non-crustose algae and faunal species, are mainly attached to the secondary hard substrata that occur in the form of calcareous layers enveloping the primary bedrock or forming bulky concretions, produced apparently only by one prolific population of the crustose coralline species this paper is dealing with.

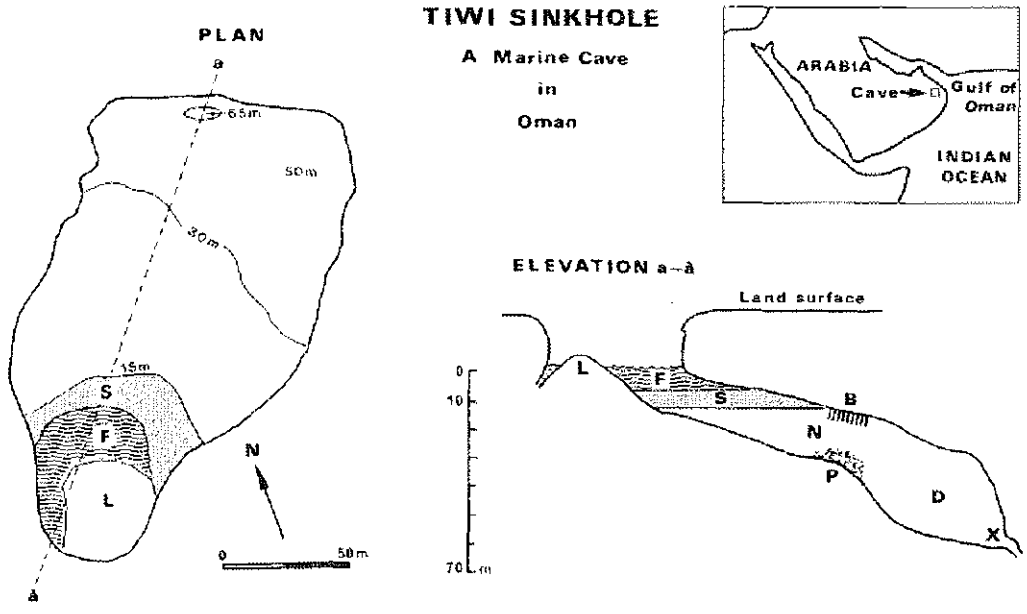


Fig. 1: Diagrammatic topography of the Tiwi Sinkhole cave-system (based on the survey by R. Hill and the Oman Cave Divers; Anon., 1995), also showing characteristic water masses (Štirn, 1996), of which only the "lake's" brackish and oxic layer (F) supports macroalgae and benthic macrofauna, whereas the deep, anoxic and H_2S-bearing layers (S, N and D) are inhabited only by suspended sulphur bacteria (S) and peculiar bacterial macroaggregates (B). Marked with L is the dry land of the rockpile evolved when the roof of the cave have collapsed, P indicates pyrite sediments and X a possible connection to the sea. See also table 1.
Sl. 1: Shematična topografija jamskega sistema ponorja Tiwi (izdelana na osnovi raziskav R. Hilla in omanskih potapljačev; Anon., 1995), ki ponazarja tudi značilne vode mase (Štirn, 1996), med katerimi le "jezerska" brakična in oksična plast (F) zagotavlja razmere za rast makroalg in bentoške makrofavne, medtem ko globoke, anoksične plasti in plasti s H_2S (S, N in D) naseljujejo le suspendirane žveplene bakterije (S) in nenavadni bakterijski makroagregati (B). Črka L označuje del kopnega (gmoto skal), nastalega po zrušitvi stropa jame, P piritne sedimente, X pa možno povezavo z morjem. Glej tudi tabelo 1.

Habitat and Community Description

The Tiwi Sinkhole and the large cave system beneath developed in tertiary limestones, along the fissure in a Pleistocene marine terrace, which is now some 20-25 m above the sea level. The sinkhole is the only known entrance into the cave, and is located inland, nearly 900 m from the sea shore of the south-western Gulf of Oman between Muscat and the village of Tiwi, its geographical position being roughly 23°01' N and 59°06' E. This vertical (15-25 m deep) and to the surface open shaft is actually the upper part of a large and at least 64 m deep cave whose roof apparently collapsed (Figs. 1, 2). Consequently, almost half of the sinkhole's bottom surface is dry land (a rockpile of rubble and boulders), whereas the rest is occupied by the "lake" (Figs. 1, 2). This 4-7 m deep water body is actually the surface layer of a large water mass that occupies the main, completely submerged cave below, which obviously has a hydraulic connection with the sea (Fig. 1), for the "lake" shows clear, but for some 90% reduced, tidal oscillations (Tab. 1).

Unlike the deep water mass, which is constantly anoxic and whose salinity and temperature values are invariably high (~35 psu; >29°C), the "lake" water is moderately brackish and shows rather important seasonal variations of salinity and temperature values (ranges of 19-25 psu and 22-33°C, respectively with lower values during winter conditions) and is as a rule quite well oxygenated. Therefore, receiving enough solar light for at least sciaphilic algae to grow on its walls, this unusual habitat provides quite specific conditions for the flourishing productivity of the above mentioned corallines (Fig. 3), and the rest of a relatively rich benthic community (Fig. 4) composed mainly of the following macrocomponents:

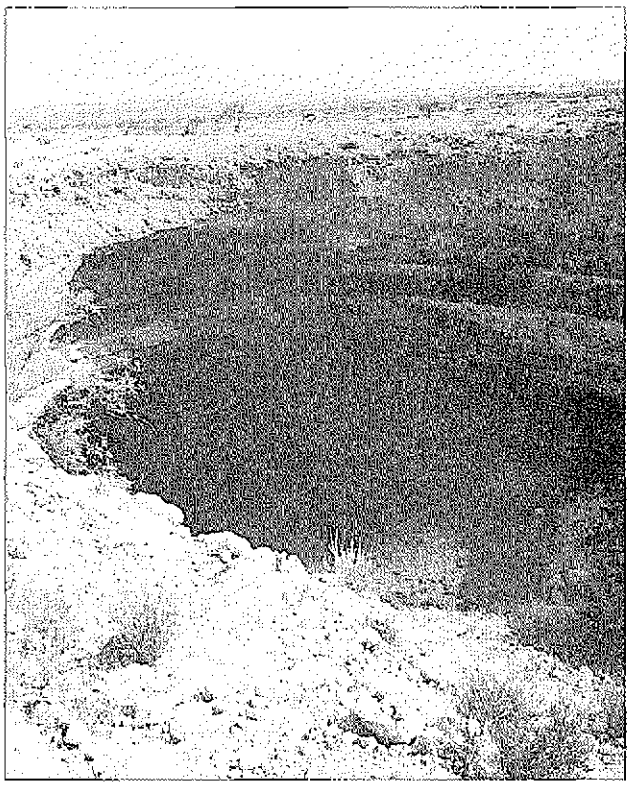


Fig. 2: The Sinkhole photographed from its upper edge showing the "lake" surface and the rockpile of the collapsed roof of the cave. Note at the left horizon, the adjacent coastal sea. (Photo: J. Štirn)
Sl. 2: Ponor Tiwi, fotografiran z njegovega gornjega roba, z "jezersko" površino in gmoto skal zrušenega jamskega stropa. Na levem horizontu je lepo videti dotikajoče se obalno morje. (Foto: J. Štirn)

Tab. 1: Physical and chemical characteristics of habitats in the studied area.
psu = practical salinity unit = approx. ppt; VIS = horizontal UV visibility as estimated by divers; euphotic = for plant growth adequately illuminated habitat; hypoxic = low oxygen environment, arbitrarily <1ml O_2 l^{-1}; H_2S = toxic hydrogen sulphide (rotten-egg-gas); sulphuretum = aquatic community dominated by sulphur bacteria. See figure 1 for explanation.
Tab. 1: Fizikalne in kemične značilnosti habitatov raziskovanega območja.
psu = praktična enota slanosti = pribl. ppt; VIS = horizontalna UV vidljivost po oceni potapljačev; evfotičen = za rast rastlin zadovoljivo osvetljen habitat; hipoksičen = okolje z majhno količino kisika, in sicer <1ml O_2 l^{-1}; H_2S = strupen vodikov sulfid (plin gnilih jajc); sulfuretum = vodna združba s prevladujočimi žveplenimi bakterijami. Glej sliko 1 za pojasnilo.

PARAMETERS	EUPHOTIC/F Depth: 0-7 m	SULPHURETUM/S Depth: 7-17 m	DEPTH/N+D N: 18-24 m D ≥ 25 m
TEMP (°C)	22-33	28-31	29-30
SAL (psu)	19-25	30-31	34-35
OXYGEN (ml l^{-1})	3-6	± 0	0.1-1.5
H_2S (mg l^{-1})	0	~ 180	0
NITRATE-N (mmol l^{-1})	0.1-17	0.1-0.4	0.1-0.5
PHOSPHATE-P (mmol l^{-1})	0.02-0.30	0.10-1.50	0.30-0.60
VIS (m)	1-25	<1	>25

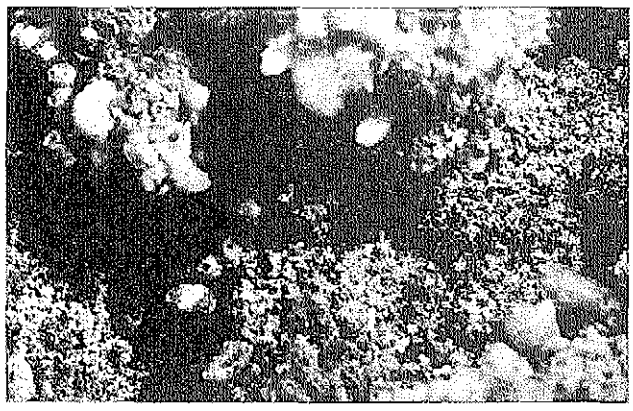


Fig. 3: Crustose envelopes and massive calcareous structures built by the coralline** Pneophyllum confervicola **on the hard bottom of the Sinkhole "lake", here in the dept of 2 m. (UV macrophotograph; by J. Štirn).
Sl. 3: Skorjasti ovoji in masivne apnenčaste strukture, ki jih na trdem dnu - tu v globini 2 m - gradijo koralinske alge** Pneophyllum confervicola. **(UV makrofotografija; J. Štirn)

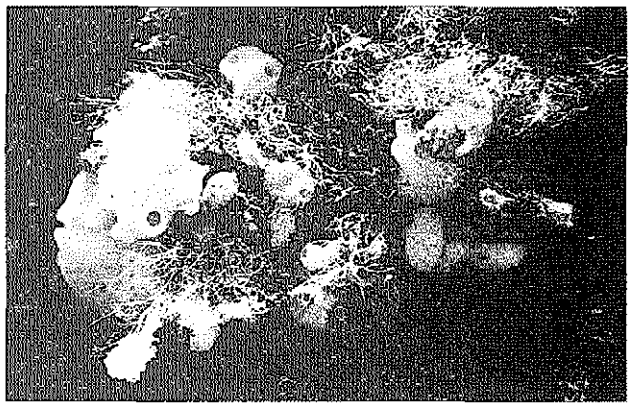


Fig. 4: Benthic community in the Sinkhole "lake" composed here of the bushy red alga** Gelidiella rigidiscula, **purple and yellow sponges** Haliclona **and** Clathrina **spp. and the orange ascidian** Polycarpa colleti. **(UV macrophotograph, approx. surface 1 dm² ; by J. Štirn)
Sl. 4: Bentoška združba v ponornem "jezeru", ki se tu sestoji iz košatih rdečih alg** Gelidiella rigidiscula, **vijoličastih in rumenih spužv** Haliclona **and** Clathrina **spp. in oranžnih kozolnjakov** Polycarpa colleti. **(UV makrofotografija, površina okoli 1 dm² ; J. Štirn)

- non-crustose macroalgae: *Gelidiella rigidiscula* (Feldmann) Feldmann & Hamel, *Valonia aegagropilla* C. Agardh, *Rhizoclonium riparium* (Roth) Kützing ex Harvey and *Cladophora* sp. (Sarà & Bavestrello, 1995; Štirn, 1996)

- sessile filter - feeders: sponges *Haliclona* and *Suberites* spp. and *Tethya omanensis* Sarà & Bavestrello n.sp. (Sarà & Bavestrello, 1995), tubeworm *Leodora knightjonesi* and the ascidian *Polycarpa colleti*;

- grazing snails *Pirenella doriae* Hornung & Mermod and *Planaxis sulcatus* Born, and omnivorous euryhaline fish *Aphanius dispar* Rueppel (Štirn, 1995, 1996).

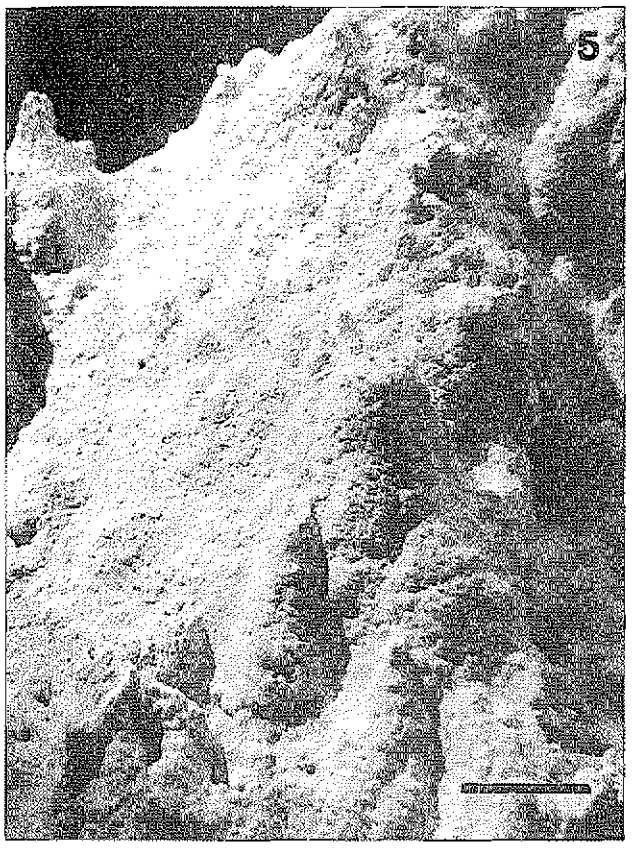
MATERIAL AND METHODS

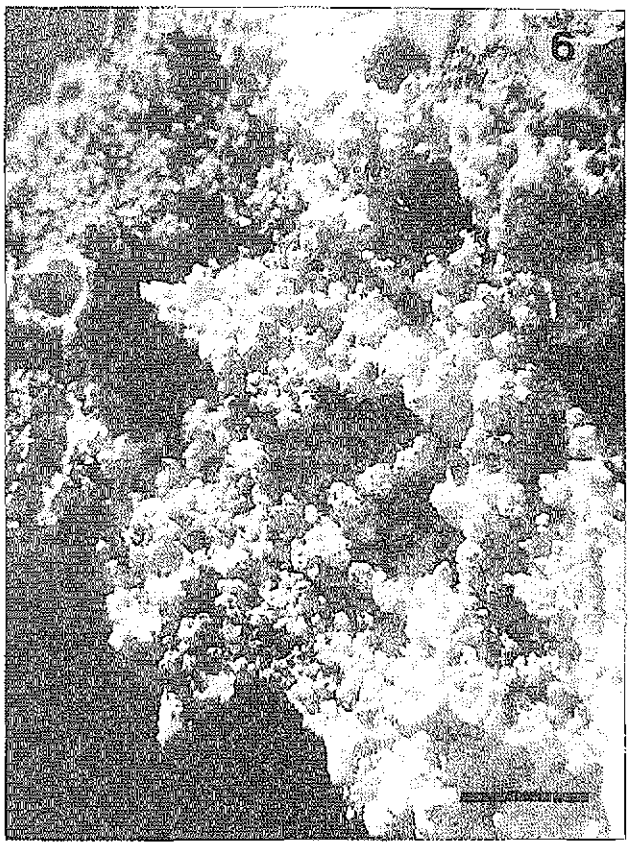
Samples of coralline material needed for this study were collected during 1995-1997 from the walls of the Sinkhole, manually at the surface and by divers at deeper positions down to the depth of 3 m. Some samples were preserved in 2% formaldehyde seawater and other ones as dry samples. For the taxonomic purposes these were morphologically examined in the outer layers as well as deep inside of concretions. Specimens for light microscopy were decalcified in Tellyesniczky solution (acetic acid 5 ml, potassium dichromate 3 g to 100 ml with distilled water) and sectioned by means of microtome, whereas the preparations for SEM were fixed in 4% glutaraldehyde in 0.6 M phosphate buffer, dehydrated in a graded ethanol series, critical point dried and gold-coated. Leica Stereoscan 430i was used for SEM examination. Taxonomic identifications were based upon the following sources: Chamberlain, 1994; Hamel & Lemoine, 1952; Silva *et al.*, 1996 and Suneson, 1943 for coralline algae; Gallardo *et al.*, 1993; Giaccone *et al.*, 1994; Sarà & Bavestrello, 1995 and Štirn, 1996 for non-coralline algae and animals.

RESULTS

Diving observations, supplemented by underwater photography and macroscopic examinations of numerous samples, revealed that crustose corallines cover the entire surface of the upper hard bottom zone of the Sinkhole from the water surface down to the depth of about 3 m. On the north-western walls, which are relatively well illuminated, the corallines produce rather simple but quite thick crusts (4-26 mm), whereas in the shade of deeper sites (2-3 m) they build massive, up to 34 cm thick concretions that occur as two typical varieties: one is bright purple, compact and built in a form similar to the flowstone (Fig. 5), while the other one has a dark red-brown colour, and a porous, travertine-like structure (Fig. 6). This is clearly the result of corallines enveloping and cementing the subfossil and recent aggregates composed of calcareous tubes of the polychaet worm *Leodora knightjonesi*, which are attached directly to the primary rock substrate.

One of these constructions is illustrated on figures 5 and 6. The outer part, faced towards the outside (Fig. 5), shows a compact pink form, while the inner part (Fig. 6), which envelops the aggregates where it is attached, is porous, vermiculate and dark, quite black.





Figs. 5, 6: Macrophotography of the compact (Fig. 5) and the porous (Fig. 6) part of the bioconstruction. Bar 1 cm.

Sl. 5, 6: Makrofotografija kompaktnega (Sl. 5) in poroznega (Sl. 6) dela biokonstrukcije. Merilo 1 cm.

Typically, this encrusting species is forming, in the Sinkhole and elsewhere, small thalli with creeping filaments, which vary from partially (Fig. 7) to entirely unconsolidated forms (Fig. 8). Generally, the thalli are composed of rather small cells (10-16 µm x 20 µm) whose shape, observed in surface view, is squarish and isodiametric (Fig. 8), among them intercalary trichocytes are rare (Fig. 9). There are also epithallial cells for which SEM observations show pits and actual holes where the calcified walls seem to be much thinner (Fig. 8). In section the thalli appear monostromatic and unistratified, except in places were the epithallial cells are visible.

The conceptacles observed by SEM (Fig. 10) in surface view are clearly uniporate, hemispheric and measure 90 µm x 60-70 µm, whereas the light microscopy showed that they are tetra/bisporangial.

Based upon the above-mentioned morphological variability, there were the following two taxonomic forms previously recognised for this species as f. *typica* and f. *lacunosa*, (former f. *minutula*; Chamberlain, 1983). The f. *typica* is a compact form with consolidated filaments (Figs. 8, 11), while the f. *lacunosa* often shows a partially unconsolidated thallus (Fig. 7). The very surface of the Sinkhole's specimens is almost always dominated by the f. *typica*.

DISCUSSION

The results of microscopical analyses (the germination disc with 8 central cells, intercalary trichocytes, uniporate conceptacles) and other taxonomical examinations of numerous typical specimens demonstrate a rather surprising fact that, despite such a great variability, all above structures are produced just by one species only, identified as *Pneophyllum confervicola* (Kützing) Chamberlain (Chamberlain, 1983).

The coralline *P. confervicola* is obviously a very tolerant, euryoecic species, which has a wide geographic distribution from the boreal Atlantic Ocean to the Mediterranean Sea, in the Pacific and the Indian Ocean.

However, in all other records it is reported only as an epiphyte growing on a wide range of macroalgal species (Irvine & Chamberlain, 1994).

The only known exception is the Sinkhole's population whose generations overgrow on previously deposited layers of the same algae, which causes the forma-

Fig. 7: Detail of the bioconstruction with thalli characterised by creeping filaments. Bar 100 µm.
Sl. 7: Detajl biokonstrukcije s steljkami, ki jih označujejo plazeča se vlakna. Merilo 100 µm.

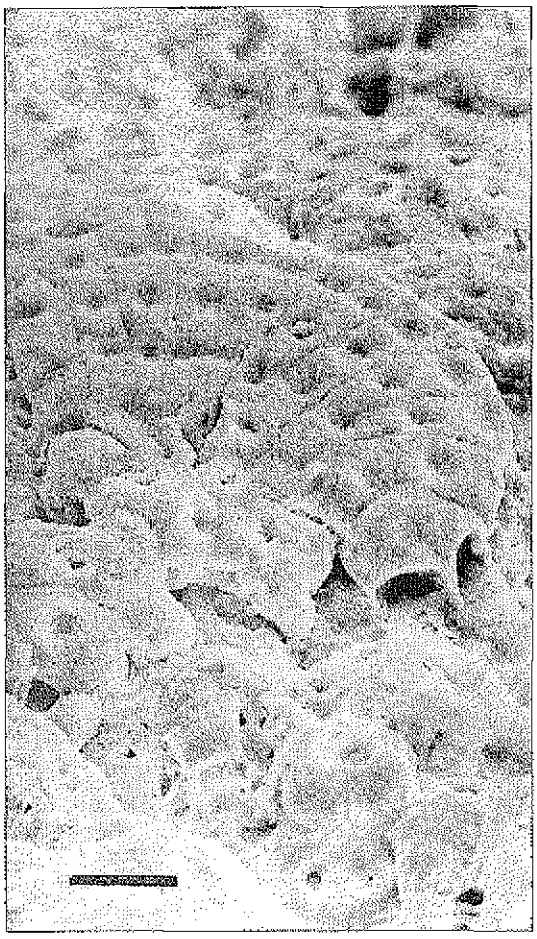


Fig. 8: Young thallus of P. confervicola in which the epithallial cells are clearly visible. Bar 20 µm.
Sl. 8: Mlada steljka koralinske alge P. confervicola z lepo vidnimi epitalialnimi celicami. Merilo 20 µm.

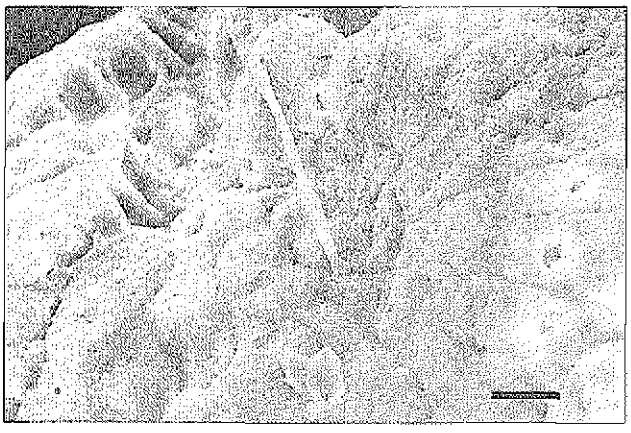


Fig. 9: Detail of the thallus showing an intercalary trichocyte and the monostromatic structure. Bar 10 µm.
Sl. 9: Detajl steljke z vrinjenim trihocitom in monostromatično strukturo. Merilo 10 µm.

tion of massive calcareous structures described above (Figs. 5, 6). From a biological point of view, it seems indeed that it is the overgrowing capacity (Figs. 7, 11) of the thalli of this species on itself that generate the bioconstructions.

The dominance and the richness of *P. confervicola* in these bioconstructions, probably due to a considerable viability of the species, seems to fully accord with what occurs for at least another species of this genus: *Pneophyllum conicum* (Dawson) Keats, Chamberlain & Baba, the only non-geniculate coralline that has been observed to regularly and commonly overgrow and kill corals, especially taxa with small polyps and relatively smooth colonies (Keats *et al.*, 1997).

Also in the case of the bioconcretion of Tiwi, the construction examined seems to have been produced by the overgrowing of a multitude of thalli present under the form of extremely small scales (Figs. 7, 11).

This leads us to believe that the above forms are more likely the ecotypes evolved through a morphic

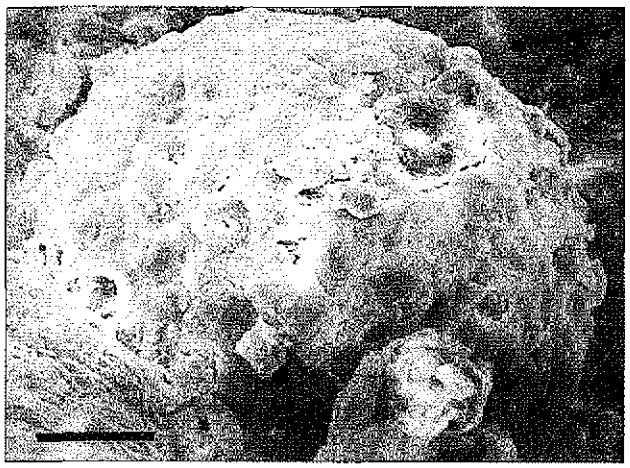


Fig. 10: Uniporate conceptacle. Bar 20 µm.
Sl. 10: Enoporni konceptakel. Merilo 20 µm.

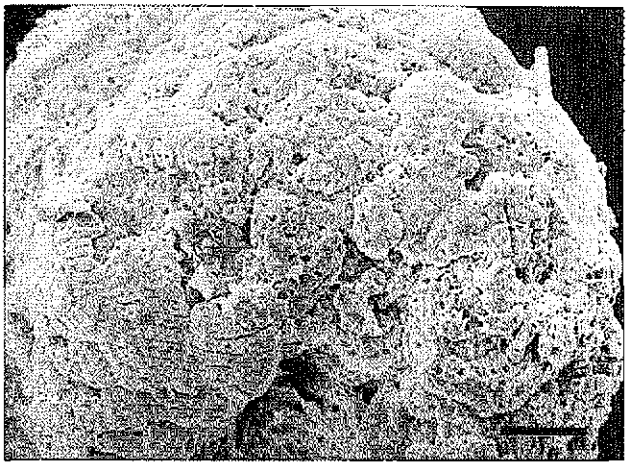


Fig. 11: Overgrowing thalli of** P. confervicola. **Bar 100 µm.
Sl. 11: Razraščajoče se steljke koralinske alge** P. confervicola. **Merilo 100 µm.

process adaptation to small-scale differences in the ranges of environmental factors, among which the illumination intensity probably are the most crucial. Moreover, the total absence of any type of disturbance in such a particular biotope (lack of wind, current and limited tide range) seems to have contributed to the building of these formations. The adaptation ability of this euryoecic species seems justified by the relative structural simplicity of its thallus.

ACKNOWLEDGMENTS

We are very grateful to the Oman Cave Divers, guided by R. Hill, to Miss B. Troian for her assistance during SEM observation, and to Mrs. M. Attilio for the revision of the English text.

APNENČASTE STRUKTURE, KI JIH GRADIJO KORALINSKE ALGE *PNEOPHYLLUM CONFERVICOLA* (KÜTZING) CHAMBERLAIN (CORALLINALES, RHODOPHYTA) V ENI IZMED MORSKIH JAM V OMANSKEM ZALIVU

Jože ŠTIRN
SI-6230 Portorož, Fizine 8

Guido BRESSAN, Lia Angela GHIRARDELLI & Lorenza BABBINI
Oddelek za biologijo, Univerza v Trstu, IT-34127 Trst, Via L. Giorgieri 10
e-mail: ghirardl@univ.trieste.it

POVZETEK

V jugozahodnem obalnem pasu Omanskega zaliva v Indijskem oceanu je bil v nekem kraškem jamskem sistemu, ki mu domačini pravijo ponor (Tiwi), odkrit prav poseben morski ekosistem. Ta mali, izolirani ekosistem zajema zelo nenavadno bentoško združbo, ki živi na ponorjevih stenah, obsijanih s soncem. Njegove komponente se pojavljajo v obliki apnenčastih plasti, ki obdajajo matični substrat ter tu in tam oblikujejo zrastke, ki jih očitno gradi zelo plodna populacija skorjaste koralinske vrste. Rezultati mikroskopskih analiz in drugih taksonomskih raziskav številnih značilnih osebkov so pokazali, da vse strukture gradi ena sama vrsta, identificirana kot Pneophyllum confervicola *(Kützing) Chamberlain.*

Ključne besede: biokonstrukcija, koralinske alge, *Pneophyllum confervicola*, morska jama

REFERENCES

Adey, H. W. (1998): Coral Reefs: algal structured and mediated ecosystems shallow, turbulent, alkaline waters. J. Phycol., 34, 393-406.

Anon. (1995): Cave diving in Oman. Newsletter of the Oman Diving Federation, 3/2, 10-11

Chamberlain, Y. M. (1983): Studies in the Corallinaceae with Special Reference to *Fosliella* and *Pneophyllum* in the British Isles. Bull. British Museum (Nat. Hist.), 11, 291-463.

Chamberlain, Y. M. (1994): *Pneophyllum coronatum* (Rosanoff) D. Penrose comb. nov., *P. keatsii* sp. nov., *Spongites discoideus* (Foslie) D. Penrose et Woelkerling and *S. impar* (Foslie) Y. Chamberlain comb. nov. (Rhodophyta, Corallinaceae) from South Africa. Phycologia, 33, 141-157.

Gallardo, T., A. Gomez-Garreta, M. A. Ribera, M. Cormaci, G. Furnari, G. Giaccone & C. F. Boudouresque (1993): Check-list of Mediterranean seaweeds. II. Chlorophyceae Wille *s.l.* Bot. Mar., 36, 399-421.

Giaccone, G., G. Alongi, F. Pizzuto & A. Cossu (1994): La vegetazione marina bentonica fotofila del Mediterraneo. II. Infralitorale e circalitorale. Proposte di aggiornamento. Boll. Acc. Gioenia. Sci. Nat. Catania, 27, 111-157.

Hamel, G. & P. Lemoine (1952): Corallinacées de France et d'Afrique du Nord. Arch. Museum Hist. Nat., 7, 17-136.

Irvine, L. M. & Y. M. Chamberlain (1994): Seaweeds of the British Isles. Vol. I. Rhodophyta (Part 2B Corallinales, Hildenbrandiales). The Natural History Museum, London, 276 pp.

Keats, D. W., Y. M. Chamberlain & M. Baba (1997): *Pneophyllum conicum* (Dawson) comb. nov. (Rhodophyta, Corallinaceae), a widespread Indo-Pacific non-geniculate coralline alga that overgrows and kills live coral. Bot. Mar., 40, 263-279.

Margalef, R. (1985): Western Mediterranean. Pergamon Press, Oxford, 363 pp.

Sarà, M. & G. Bavestrello (1995): *Tethya omanensis*, a remarkable new species from an Oman cave (Porifera, Demospongieae). Boll. Zool., 62, 23-27.

Silva, P., P. W. Basson & R. L. Moe (1996): Catalogue of the Benthic Marine Algae of the Indian Ocean. University of California Press, 79, 1156 pp.

Štirn, J. (1995): New marine species discovered in a remarkable Oman coast cave. Bull. Sultan Qaboos Univ., Muscat, 26, 3 pp.

Štirn, J. (1996): Unique ecological features and relict biota of the Tiwi Sinkhole - a marine cave system. Rapp. Sultan Qabos Univ., Muscat, 8 pp.

Suneson, S. (1943): The structure, life-history and taxonomy of the Swedish Corallinaceae. Lunds Universitets Årsskrift N.F. Avd. 2. Bd. 39. N. 9, 1-65, pl. IX.