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STRUCTURE, MORPHOGENESIS OF CALYPTRA AND NOMENCLATURAL IDENTITY OF *TRICHODESMIUM ERYTHRAEUM* EHR. (CYANOBACTERIA) NEWLY RECORDED OFF THE SOUTH-WEST COAST OF BANGLADESH

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Abstract

Trichodesmium erythraeum Ehrenberg 1830 (Cyanobacteria) has been described and newly recorded from three km off the west coast of the St. Martin's Island (SMI), Cox's Bazar, Bangladesh. The Red Sea algal bloom was narrowly elliptical raft-like loose aggregates 20-40 cm long, 4-8 cm wide and 2-3 cm thick. Volume of small and large Sea sawdust were 160×10^{-6} to 960×10^{-6} m^3 consisting of 25-153 millions flat tuft or spindle-like colonies measured 830-1500 µm long and 155-260 µm wide with 13-16 filaments laterally in the median region. Sheath was present around each trichome even covering the tip cell wall the feature has so far not been reported for the *Trichodesmium* spp. Because of most likely sticky nature of the sheath 300-600 µm long filaments of 195-450 formed compact colonies without colonial sheath around. In interior filaments cells were rectangular 7-10 µm long and 6.3-10 µm wide with abundant gas vacuoles, bluish-green red, no diazocyte developed and without calyptra. Cells of peripheral filaments were without gas vacuoles, cytoplasm disorganized, appearing necrotic with glycogen granules, and produced convex to sickle-shaped four-layered calyptra consisting of outermost sheath followed by outer extra thick wall, tip cell wall and inner extra thick wall on the tip cell. Calyptra was also produced on tip cells of tapered filaments. Presence of sheath around each trichome binding all filaments into a colony without colonial sheath described here, and N_2 fixation during day in diazocytes and night times on the periphery described and discussed in literature made the authors to consider *T. erythraeum* Ehr. a distinct taxon under family Microcoleacece.

Introduction

Trichodesmium erythraeum Ehr.a non-heterocystous filamentous colonial Cyanobacterium was first found at Bay of Tor in the Red Sea, west of Saudi Arabia and it was probably the colour produced by blooms gave the "Red Sea" its name by Ehrenberg in 1830 (Hoffman, 1999). It is also called by sea sailors as "Sea-sawdust" (Cook, 1842) or 'Windrows' cells with abundant gas vacuoles (Walsby, 1978) and is one of the open ocean Cyanobacteria (Lee, 2008) of tropical and subtropical regions (Hynes *et al.*, 2012) playing a key role in global carbon and nitrogen budget (about 40% nitrogen supply through N_2 fixation) in oligotrophic oceans (Breitbarth *et al.*, 2007). Along North-eastern Bangladesh coast Islam and Aziz (1975) and Aziz and Islam (1979) studied marine phytoplankton covering summer, monsoon and autumn period in 1973 from 16 locations widely situated between lat. 21º 3′ and 21º 44′ N and long. 91º 36′ and 91º 58′ E, and recorded 23 genera with 64 species of diatoms, 10 genera with 32 species of dinoflagellates and 2 genera with one species each of *Oscillatoria* and *Anabaena* from SMI and Sundarbans by Islam (1976) and a "Red-tide" alga from SMI by Tomascik (1997) but *T. erythraeum* was not recorded. Boonyapiwat *et al.* (2008) recorded *Oscillatoria erythraea* (Ehr.) Geitler 1932 (synonym *T. erythraeum* Ehr.) as

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a dominant phytoplankton in three pelagic zones of the Bay of Bengal (at 16º 45′ N - 18º 45′ N and 88º 0′ E - 90º 45′ E) south-east of Myanmar/west of Thailand and east of South India. Kumar *et al.* (2012) reported occurrence of *T. erythraeum* bloom in the coastal waters of south Andaman (11º 33' 20" N and 92º 42' 52" E). Consideration of *T. erythraeum* Ehr. as *Oscillatoria erythraeum* (Ehr.) Geitler (1932) and its use by Boonyapiwat *et al.* (2008) is questionable specially when *Trichodesmium* exhibited colony formation in association with sheath production and cell differentiation along trichomes (Golubic, 1977), N_2 fixing potential (first reported by Carpenter and Price, 1977) and presence of groups of short strings of golden-yellow cells along central region of trichomes called diazocytes by Bergman and Carpenter in 1991 and later by Fredriksson and Bergman (1997).

In *Oscillatoria princeps* trichomes close to *T. erythraeum* Shukovsky and Halfen (1976) found extensively disrupted thylakoids, cytoplasm displaying general disorganization characteristic of necrotic cells, decrease in width with a corresponding increase in length and decrease in volume of terminal cell with calyptra. The phenomena found in *O. princeps* have not been described so far in *T. erythraeum.* In many tapered cyanobacteria phosphate deficiency results in narrowing of terminal cells forming hair (Livingstone and Whitton, 1983, Aziz *et al.*, 1989).

Aims of the present study are to describe and illustrate the colony structure, morphogenesis of calyptra, identify the newly collected Sea-Sawdust and ascertaining its nomenclatural identity.

Materials and Methods

Occurrence, sampling and water quality determination

Sea-sawdust *T. erythraeum* Ehr. occurred at about 3 km off the west coast of the SMI (NarikelZingira/Narikeldia), Cox’s Bazar, Bangladesh covering water surface of over one square kilometer at around 20° 37' 20″ N and 90° 17' 10″ E, at 9:00 am on 21 February 2017 (Fig. 1A). The bloom was found during return from St. Martin’s Reef situated at about 14 km west of the SMI (visited for collecting living seaweeds for Seaweed Cultivation Project at Cox’s Bazar). Blooms were collected by a bucket and poured in to an empty one liter drinking water bottle as multiple samples. Within half an hour the seawater turned pink and the plankton settled as particles of about one mm long. Formaldehyde was added about an hour later.

The seawater turbidity in the study area as Nephalometric Turbidity Unit (NTU) was measured by Turbidity Meter TU-2016, Taiwan; pH by Hanna Pocket pH meter, conductivity by Combo pH & EC meter, Hanna, Romania; salinity by Refractometer, ATC, China; TDS by TDS meter, China; temperature by Clock/Humidity meter, HTC-2, China; Secchi depth by Secchi disc.

Determination of measurements of Sea-sawdust

The composition of spindle shaped (from top) raft-like floating Sea-sawdust and colonies comprising rafts (Figs 1A-E) were determined as follows: (i) Total volume of a small raft was calculated by multiplying 20 cm long, 4 cm wide and 2 cm thick. Similarly total volume of a large raft was calculated by multiplying 50 cm long, 8 cm wide and 3 cm thick. (ii) The average volume of a colony comprising a raft was calculated by multiplying average values, 1100 µm long, 200 µm wide and 35 µm thick. (iii) The number of colonies constituting a Sea-sawdust was determined by dividing average volume of a raft by the average volume of a colony.

Determining structure of Sea-sawdust

One liter composite bloom samples collected with the seawater contained all the phases of growth, different types of trichomes, calyptrae, associated structures and successive changes of filament characters were photographed (Figs 1B-F, 2A-I) using Nikon Eclipse 50i microscope fitted with Nikon Digital Sight DS-Fi2 Camera at Plant Breeding and Biotechnology Laboratory, Department of Botany, University of Dhaka. Attempt to culture the organism was not made as previous worker(s) failed to culture it after repeated attempts (Baaleh and Brown Jr., 1969).

Results and Discussion

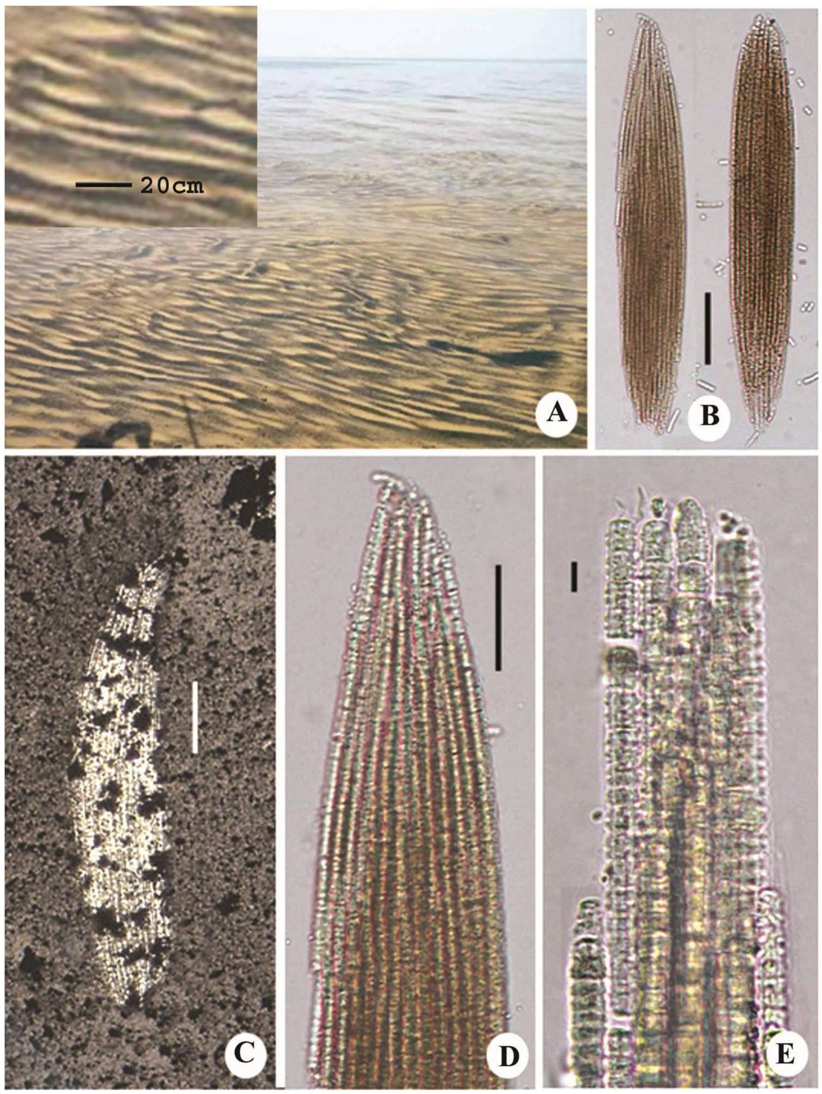
Taxonomic descriptions

Sea-sawdust: Reddish-grey bloom of the Sea-sawdust on examination was found to be *Trichodesmium erythraeum* Ehr. (Figs 1A-F, 2A-I) a member of Division Cyanobacteria, Class Cyanophyceae, Order Oscillatoriales, Family Oscillatoriaceae (Desikachary, 1959; Hynes *et al.*,2012) or Microcoleaceae (Komárek *et al.*, 2014; Wikipedia, 12 Jan. 2020) has been described and illustrated using light microscope for the first time from Bangladesh coast. Sea-sawdust *T. erythraeum* is narrowly elliptical raft-like spectacular floating bodies 20 to 40 cm long, 4 to 8 cm wide and 2 to 3 cm thick (Fig. 1A). Volumes of small and large Sea-sawdust calculated were 160×10^{-6} and 960×10^{-6} m^3, respectively formed of loosely packed 25 to 153 million of flat spindle-shaped (top view) compact colonies (Fig. 1A-D) volume being 6.3×12 cm^3, 830 to 1500 (average 1150) µm long and 155 to 260 (average 200) µm wide with 13-16 filaments in the mid region, total number of filaments per colony was calculated to be 195 to 450 where each trichome is surrounded even the tip cell most likely by a sticky sheath forming a compact colony. Filaments 300 to 600 µm long, cells 27 to 55 in each filament, 7-10 µm long and 6.3 to 10 µm wide (Figs 1B-E). There is no mention of sheath around trichomes of *Trichodesmium.* (Janson *et al.*, 1995; Wikipedia, 2020). The very high density of colonies (25 to 153 million) in Sea-sawdust was compared with samples from tropical and sub-tropical oceans in North Atlantic and Caribbean where Nausch (1996) recorded only 1000 to 55000 colonies each consisting of different number of trichomes having different compactness and colonies were embedded in a muco-polysaccharide layer. Colonies of the present material were without surrounding sheath determined by immerging in Indian-Ink (Fig. 1C). Desikachary (1959) also mentioned absence of the colonial sheath. Golubic (1977) mentioned that *Trichodesmium* exhibited colony formation in association with sheath production.

There are enormous differences on the nature of filaments of peripheral and interior colony. Peripheral part of a colony had almost colourless sometimes with bluish tint trichomes lacking gas vacuoles almost similar in cell dimensions and bound together by mucilage sheath like the interior filaments a few with developing calyptrae on top of primordial hair cell (Fig. 1E). Detached fragmented peripheral filaments were found to have calyptra on very small cells. Baaleh and Brown (1969) found absence of gas vacuoles and destruction of photosynthetic system in *Trichodesmium*by direct sunlight.

Trichomes: A long growing *Oscillatoria*- like trichome in seawater sample mount on a slide perhaps recently emerged from interior of a colony was over 500 µm long, consisting of uniformly wide (10 µm) cells, up to 8 µm long many were in dividing stage, all cells with compact irregular dark-red gas vacuoles 60-70 % of the cell volume also mentioned in Wikipedia (2020) and glycogen granules as visible cytoplasmic inclusions, appearing blue-green red, apical cell almost rectangular covered by sheath thickened in the central region (Figs 2A-C). The trichomes were without golden yellow cell groups (diazocytes), and neither separation discs (necridia) nor any deeper constrictions in the cross walls to produce hormogonia were found in the present samples. Bergman and Carpenter (1991) demonstrated occurrence of about 15 celled diazocytes confined to a limited number (ca. 10–40 %) of randomly distributed trichomes in the interior of colonies. The diazocyte development was initiated by the degradation of glycogen granules and gas vacuoles (Fredriksson and Bergman, 1997; Sandh *et al.,* 2012) or low carbon nitrogen ratio (Aziz and

Whitton, 1988). Examination of trichomes of interior longitudinally fragmented colony (in the same water mount) revealed over a dozen of compact filaments were individually covered including broken ends by hyaline perhaps sticky mucilage sheath beaded at cross walls (Fig. 2A, arrow and arrowheads, respectively) visible between dissociated trichomes, the feature has not been reported so far.



Figs 1A-E. *Trichodesmium erythraeum* Ehr.: (A) Reddish-gray bundles or "Sea-sawdust" on crystal clear water off the West coast of SMI, inset an enlarged part. (B) Two spindle-like colonies, right hand one more reddish than the left one. (C) A colony mounted in Indian ink showing absence of colonial sheath. (D) Half of a colony enlarged showing compactness of trichomes where almost all longitudinal trichomes are seen in one focus of almost flat spindle shaped structure. (E) A bundle of exterior part of a colony enlarged showing a developing calyptra on the tip of a filament at extreme right and a developed calyptra on the extreme left. Bars: Fig. A =20 cm; Figs B-D = 250 µm; E = 10 µm.

Filaments on the periphery of colonies were almost colourless, cells short, uniform in diameter, highly vacuolated with glycogen granules (Figs 1D-I). Peripheral filaments also form 3-4 celled tapered structure with vacuoles and lighter cytoplasm (Fig. 1E, extreme left). Enrichments in alkaline phosphatase demonstrated efficient organic phosphorus scavenging and utilization by *Trichodesmium* (Dyhrman *et al.*, 2006). Baaleh and Brown Jr. (1969) observed degrading photosynthetic system in filaments of *Trichodesmium* spp. facing direct sunlight, and a very regular array of gas vacuoles in the form of a hollow cylinder shields most of the photosynthetic system. Both types of vacuolated filaments developed calyptra on the top of end cell (Figs 1E, F, H). Transmission Electron Microscopic studies will be done to elucidate details of sheath around trichomes, calyptra formation and other features described here.

Morphogenesis of calyptra in T. erythraeum: Janson *et al.* (1995) showed calyptra formation in the terminal cell where gas vacuoles were disposed at random in the vacuolated cell of *T. erythraeum.* In the present organism calyptra was formed in two types of filaments- (i) on the tip cell of vacuolated uniformly wide filament and (ii) on the tip of smallest cell produced on tapered vacuolated filaments.

(i) A calyptra is initiated on the tip of a healthy looking gas vacuolated filament by the thickening of a small portion of its sheath at the centre as an outer extra wall (oew) on parent wall (Figs 2B-C, arrowheads). The thickened oew expanded laterally and downwardly covering the top and sides of the cell, simultaneously slightly thinner cap possibly made of sheath (s) become visible on the top of the oew, and an inner extra wall (iew) developed inside the parent wall (enlarged in Fig. 2E, arrowheads). Janson *et al.* (1995) also described oew and iew development for calyptra formation on the tip cell in *T. contortum* with TEM. It is interesting to mention that a close examination of the Fig. 21 revealed the presence of a double layered thin structure as a sheath equal in length of the hood below (not mentioned or described in the text) while comparing with the light microscopic pictures (Figs 2D-G) of the present sample. All three layers covering the top of bell-shaped vacuolated but glycogen granulated cells extended further down. In the next step (Figs 2F-G, arrows), further thickening and expanding of the extra walls (hood) outer one more than the inner shorter one both producing knob-like thickenings at both ends and the cell wall at this point became constricted. Beyond the knob and constricted wall a loop (Fig. 2G) perhaps by the outer and inner extra walls which further down remain together as double layers inside the sheath, covering the trichome all through, the feature needs to be confirmed by TEM. Finally the tip cell extremely squeezed, covered by sickle-shaped hood, the fully differentiated calyptra (Figs 2H-I, arrows). Thus the calyptras on the tip cell is a four layered- outermost sheath followed by outer extra wall, cell wall and inner extra wall (Figs 2E, G, I).The cells below were surrounded by perhaps extended thick walls and sheath, become healthy with abundant cytoplasm, especially glycogen granules, forming gas vacuoles and started dividing. The light microscopic structures described in calyptra morphogenesis need confirmation by Transmission Electron Microscopy.

(ii) A sickle-shaped calyptra was formed on a small cell at the tip of 3-4 less pigmented gradually tapered vacuolated cells (extreme left Fig. 1E). In an electron micrograph of calyptrate trichome of *O. princeps* Shukovsky and Halfen (1976) observed extensively disrupted terminal cells, cytoplasm displaying general disorganization characteristic of necrotic cells. Detail study was not carried out for filaments in the present material but the pattern appeared to be similar to the cause of development of calyptra described above. However, calyptra formation appeared to be followed by turning the filament into blue-green with some vacuoles still remaining in upper cells, and cells thereafter were without vacuoles and dividing (Fig. 1E). *Trichodesmium* is a prolific phosphorus reducing cyanobacteria that contributes to the turnover of phosphorus in the ocean (Wikipedia 2020).

Why calyptra formed?

Shukovsky and Halfen (1976) observed calyptra formation in extensively disrupted terminal cells of trichomes described above in the *O. princeps*. In the present material trichomes of peripheral part of colonies (under direct sun light) looked almost colourless and without gas vacuoles but with calyptra on small tip cell (Figs 1E, 2D-2F) whereas trichomes of interior part were red with packed gas vacuoles in cells masking blue-green colour and without calyptra (Fig. 2A). Bell and Fu (2005) observed increased cellular concentrations of chlorophyll *a* and phycobiliproteins under low light conditions (reduced O_2 level) in a strain of *Trichodesmium* sp. indicating that the cyanobacteria fix N_2 in the interior colony by diazocytes producing gas vacuoles in cells masking blue-green colour.

A parallelism of hair and calyptra development in cyanobacteria may be drawn where in both cases cells were without gas vacuoles and chlorotic. The presence of calyptra on peripheral trichome tips was due to low nitrogen indicated by absence of gas vacuoles and chlorotic nature of trichomes. Similarly in tapered filaments hair is formed by narrowing of terminal cells under PO_4-P deficiency (Aziz *et al.*, 1989), functions in phosphorus absorption (Sinclair and Whitton, 1977, Livingstone and Whitton, 1983) contributing to the turnover of phosphorus (Wikipedia, 2020). Under phosphate rich environment however, the hair disintegrates (Aziz, 1993). It appears that ATP pool in trichomes was very low limiting chlorophyll, phycobiliprotein and gas vesicle synthesis inducing calyptra differentiation (Figs 1E, 2D-I).

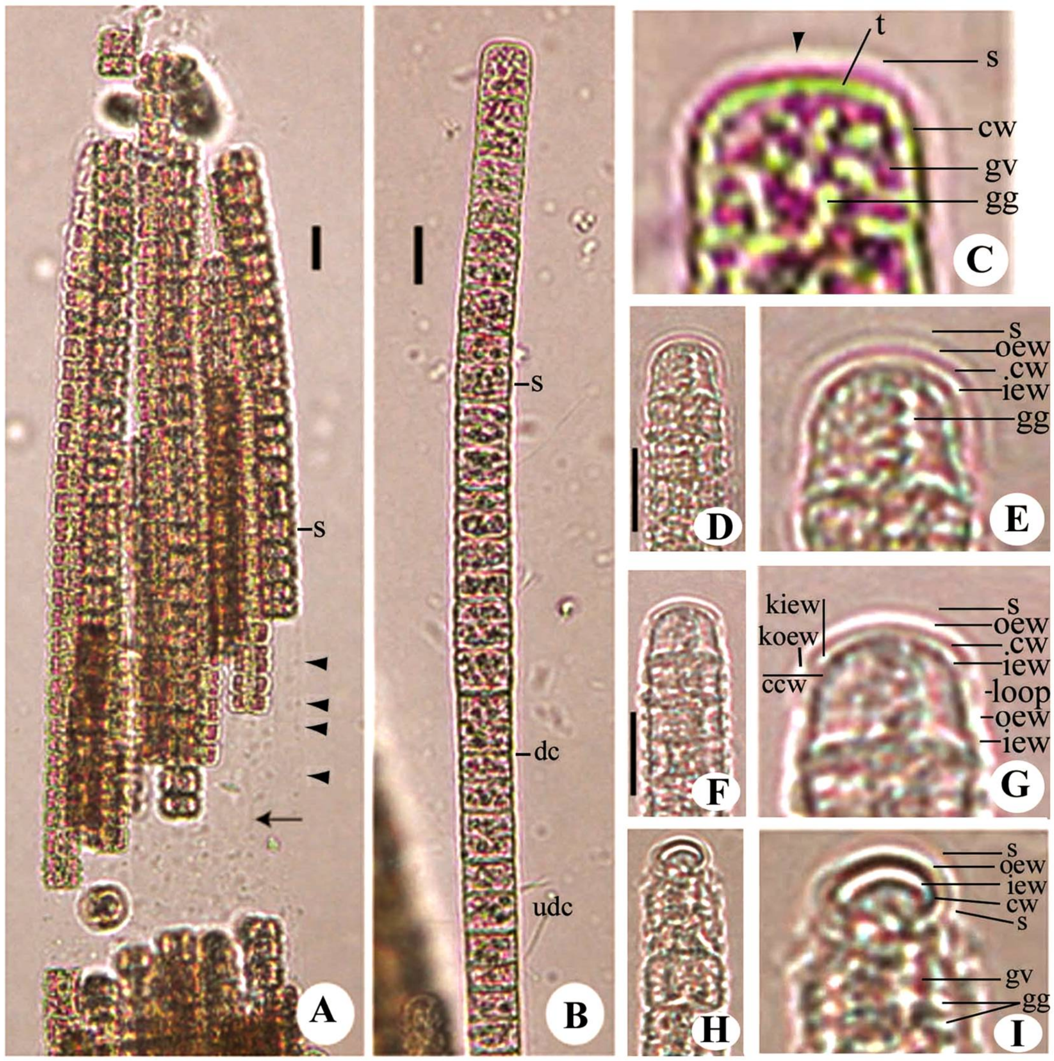
Water Quality and Regional Distribution

The water of the study area off the west coast of the SMI was crystal clear having <1.00 NTU, Secchi depth 5 m, TDS 38.0 mg l^{-1}, salinity 35 ‰, pH 8.0 and temperature 28º C; Water chemistry was not determined due to limited facilities. Breitbarth *et al*. (2007) found optimum temperature range of 24–30° C for growth and nitrogen fixation of *Trichodesmium* that play a key role in global carbon and nitrogen budget (about 40% nitrogen supply) in oligotrophic oceans.

Literature review on the occurrence of coastal (south-east and Sundarbans) and offshore marine plankton revealed a total of 38 genera and 106 species of phytoplankton including *Oscillatoria* and *Anabaena* (Islam and Aziz, 1975; Islam and Aziz, 1977; Aziz and Islam, 1979; Islam and Aziz, 1980; Tomascik, 1997) but *T. erythraeum* was not recorded. Occurrence of *T. erythraeum* in 2017 on the North-east coast off the west coast of SMI, Bangladesh was most likely due to the Cyclone Roanu that hits Bangladesh on 22 May 2016 carrying the Sea sawdust northwardly almost along same longitude from pelagic zone of Bay of Bengal (Boonyapiwat *et al.*, 2008) and south of Andaman (Kumar *et al.*, 2012).The present sampling was carried out from the site about nine months after the cyclone. The assumption is further confirmed by the fact that in 2013 and 2014 the first author studied the seaweed flora of this region and St. Martin's Reef 14 km west of SMI using Naval ship during March and April but did not come across Red Sea bloom off the west coast of SMI. While the organism is commonly regarded as an open ocean cyanobacteria in oligotrophic water (Lee, 2008), Ferguson-Wood (1965) recorded the species extending from shore to Great Barrier Reef.

Nomenclatural identity

Presence of *Oscillatoria*-like trichomes in *T. erythraeum* Ehr. 1830 made Geitler (1932) to include the cyanobacterium under *Oscillatoria* (*O. erythraea* (Ehr.) Geitler). Fritsch (1965) also noted lack of sheath around trichomes and exhibit a similarity to *Oscillatoria* only differs in



Figs 2A-I. Detail structure of filaments and morphogenesis of Calyptra in *Trichodesmium erythraeum* Ehr: (A) A bundle of over 15 fragmented filaments from exterior colony enlarged showing individual hyaline sheath around trichomes (arrow) with granular remains (arrowheads) binding the fragments. (B) A long trichome of dividing (dc) and undivided (udc) highly vacuolated cells with surrounding sheath, the flat tip cell developed a thickened portion (arrowhead) at the centre possibly inside the sheath that covered the tip, gas vacuoles etc. (C-I) Morphogenesis of calyptra on tip cell: (C) Terminal flat cell tip forming outer extra wall at the centre (arrowhead); (D-E) Trichome at low and high magnifications, terminal cell become bell-shaped with four layers on the top- outermost sheath on top followed by outer extra wall, cell wall and inner extra wall, all four layers extended downward; (F-G) Trichome at low and high magnifications, bell shaped cell narrowed terminally, outer extra wall of calyptra highly thickened, both the outer and inner extra walls developed terminal knobs at both ends (koew and kiew), cell wall below kiew become constricted (ccw) separating the iew which remain attached with the oew forming loops at both ends of the knob side wall with thick sheath; (H-I) Trichome at low and high magnifications, fully developed calyptra, all the four layers become sickle-shaped on squeezed tip cell, posterior cells with abundant glycogen granules, cells dividing. Bars: 10µm. Abbr.: ccw: constricted cell wall; cw: cell wall; dc: dividing cell; gg: glycogen granules; gv: gas vavuoles; iew: inner extra wall; kiew: knob of inner extra wall; koew: knob of outer extra wall; oew: outer extra wall; s: sheath; t: thylakoids; udc: undivided cell.

aggregation of trichomes in flat bundles. After the nomenclatural change extensive ultra-structural (diazocytes), physiological (N_2 fixation) and biochemical studies *T. erythraeum* accumulated a large amount of information which are:

(i) Colonies spindle-shaped without colonial mucilage (Fig. 1C) consisting of 195-450 compact filaments (Figs 1B-D) where trichomes have individual sheath around covering even the tip cell wall in the present sample (Figs 2B-E) the feature has so far not reported for *T. erythraeum*.

(ii) Bergman and Carpenter (1991) reported N_2 fixation in around 15 golden-yellow cells of same size and shape like vegetative cells containing nitrogenase called diazocyte(s) in 10-40 % trichomes randomly distributed in the interior of colonies.

(iii) There are both temporal and spatial segregation of N_2 fixation and photosynthesis within the photoperiod (Berman-Frank *et al.*, 2001; Fredriksson and Bergman, 1997), the feature first developed in *T. erythraeum* amongst cyanobacteria (Lee, 2008).

The features described above for the present material and N_2 fixation in diazocytes described by others made the authors to consider *T. erythraeum* Ehr. a distinct taxon. Komárek *et al.* (2014) considered it as a valid name based on molecular sequence data.

There is over a dozen of *Trichodesmium* spp. some having overlapping characters. Based on botanical nomenclature, cultures and sequences Hynes *et al.* (2012) documented six species from 21 strains which are *T. contortum* Wille 1904, *T. erythraeum* Ehr. 1830, *T. hildenbrandtii* Gomont1892, *T. radians* Wille 1904, *T. tenue* Wille 1904 and *T. thiebautii* Gomont 1892. Komárek *et al.* (2014) assigned *T. erythraeum* as distinct from the compact clade containing *T. thiebautii*, *T. hildenbrandtii* and *T. tenue* based on the results of molecular taxonomic studies, descriptions and characteristics and created new family Microcoleaceae, Order Oscillatoriales.

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