Colaconema basiramosum sp. nov. (Colaconemataceae, Rhodophyta) from the Sultanate of Oman, northern Arabian Sea

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Abstract – The red algal species *Colaconema basiramosum* (Colaconemataceae, Colaconematales) is newly described from the Sultanate of Oman, the Arabian Peninsula. Its distinctive features include undivided basal cells, suprabasal branching, monoecious gametophytes, and the apparent absence of monosporangia and tetrasporangia.

Arabian Sea / Colaconema / Colaconema basiramosum sp. nov. / Colaconemataceae / Rhodophyceae / Sultanate of Oman / taxonomy

Résumé – Colaconema basiramosum sp. nov. (Colaconemataceae, Rhodophyta) du Sultanat d'Oman, nord de la Mer d'Arabie. L'algue rouge Colaconema basiramosum (Colaconemataceae, Colaconematales) espèce nouvelle du Sultanat d'Oman, Péninsule arabique, est décrite. Elle se distingue par les cellules basales indivises, une ramification subrabasale, des gamétophytes monoïques, et une absence apparente de monosporanges et de tétrasporanges.

Colaconema / Colaconema basiramosmum sp. nov. / Mer d'Arabie / Colaconemataceae / Rhodophyceae / Sultanat d'Oman / taxonomie

INTRODUCTION

The genus *Colaconema* currently contains 32 marine species (Guiry & Guiry, 2007; Afonso-Carrillo *et al.*, 2007) (Table 1). This total includes a number of Pacific North American taxa recently moved into the genus by Gabrielson (in Gabrielson *et al.*, 2004, 2006). The genus was established by Batters (1896) based on the type *C. bonnemaisoniae* Batters, and since that original account the concept of *Colaconema* has undergone multiple circumscriptions (Papenfuss, 1945, 1947; Feldmann, 1962; Stegenga, 1985; Garbary, 1987; Lee & Lee, 1988).

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- Table 1. The 32 species currently recognized in the genus *Colaconema* Batters (1898) and reference(s) to descriptive accounts of them:
- Colaconema amphiroae (K.M. Drew) P.W. Gabrielson (Drew 1928: 179, as Rhodochorton amphiroae K.M. Drew; Garbary et al. 1983: 10, as Audouinella amphiroae)
- Colaconema asparagopsis Chemin (Dixon & Irvine 1977: 80, as Audouinella asparagopsis (Chemin)
 P.S. Dixon; Abdel Rhaman & Magne 1981: 167, as Acrochaetium asparagopsis (Chemin) Papenf.;
 Jao 1936: 237, as Colaconema americanum C.C. Jao)
- Colaconema attenuatum (Rosenv.) R. Nielsen (Rosenvinge 1909: 106, as Chantransia attenuata Rosenv.)
- Colaconema bonnemaisoniae Batters (Type) (Dixon & Irvine 1977: 82, as Audouinella bonnemaisoniae (Batters) P.S. Dixon; Garbary et al. 1983: 14, as Audouinella bonnemaisoniae; Woelkerling & Womersley 1994: 72, as Audouinella bonnemaisoniae)
- Colaconema caespitosum (J. Agardh) Jackelman, Stegenga & J.J. Bolton (Dixon & Irvine 1977: 84, as Audouinella caespitosa (J. Agardh) P.S. Dixon; Woelkerling & Womersley 1994: 55, as Audouinella caespitosa)
- Colaconema chylocladiae Batters (Dixon & Irvine 1977: 86, as Audouinella chylocladiae (Batters) P.S. Dixon)
 Colaconema coccineum (K.M. Drew) P.W. Gabrielson (Drew 1928: 192, as Rhodochorton coccineum K.M. Drew; Garbary et al. 1983: 16, as Audouinella coccinea (K.M. Drew) Garbary, G.I. Hansen & Scagel)
- Colaconema codicola (Børgesen) Stegenga, J.J. Bolton, & R.J. Anderson (Børgesen 1927: 33, as Acrochaetium codicola Børgesen; Lee 1987: 6, as Audouinella codicola (Børgesen) Garbary)
- Colaconema dasyae (Collins) Stegenga, Mol, Prud'homme & Lokhorst (Collins 1906: 191, as Acrochaetium dasyae Collins; Woelkerling 1973b: 545, as Audouinella dasyae (Collins) Woelk.; Schneider 1983: 7, as Audouinella dasyae)
- Colaconema daviesii (Dillwyn) Stegenga (Stegenga 1985: 314; Woelkerling 1973a: 81, as Audouinella daviesii (Dillwyn) Woelk: Woelkerling 1973b: 550, as Audouinella daviesii; Garbary et al. 1983: 19, as Audouinella daviesii; Schneider 1983: 8, as Audouinella daviesii; Lee 1987, p. 10 as Audouinella daviesii; Stegenga 1985: 317)
- Colaconema desmarestiae (Kylin) P.W. Gabrielson (Kylin 1925: 10, as Acrochaetium desmarestiae Kylin; Garbary et al. 1983: 24, as Audouinella desmarestiae (Kylin) Garbary, G.I. Hansen & Scagel)
- Colaconema endophyticum (Batters) J.T. Harper & G.W. Saunders (Dixon & Irvine 1977: 95 as Audouinella endophytica (Batters) P.S. Dixon; Garbary et al. 1983: 24, as Audouinella endophytica)
- Colaconema erythrophyllum (C.C. Jao) P.W. Gabrielson (Jao, 1937: 112, as Acrochaetium erythrophyllum C.C. Jao; Garbary et al. 1983: 27, as Audouinella erythrophylla (C.C. Jao) Garbary, G.I. Hansen & Scagel)
- Colaconema garbaryi P.W. Gabrielson (Drew 1928: 165, as Rhodochorton simplex K.M. Drew; Garbary et al. 1983, as Audouinella simplex (K.M. Drew) Garbary, G.I. Hansen & Scagel)
- Colaconema gymnogongri (K.M. Drew) P.W. Gabrielson (Drew 1928: 175, as Rhodochorton gymnogongri K.M. Drew)
- Colaconema gynandrum (Rosenv.) R. Nielsen (Rosenvinge 1909: 88, as Chantransia gynandra Rosenv.)
- Colaconema hallandicum (Kylin) Afonso-Carrillo, Sansón, Sangil & Díaz-Villa (Afonso-Carrillo et al., 2007: 121); (Kylin 1906: 123, as Chantransia hallandica Kylin; Hamel 1927: 20, as Acrochaetium hallandicum (Kylin) Hamel; Woelkerling 1973a: 82, as Audouinella hallandica (Kylin) Woelk.)
- Colaconema interpositum (Heydr.) Stegenga, J.J. Bolton & R.J. Anderson (Stegenga et al. 1997: 250)
- Colaconema macounii (Collins) P.W. Gabrielson (Collins 1913: 113; Garbary et al. 1983: 30, as Audouinella macounii (Collins) Garbary, G.I. Hansen & Scagel)
- Colaconema membranaceum (Magnus) Woelk. (Woelkerling 1973b: 566; Dixon & Irvine 1977: 101, as Audouinella membranacea (Magnus) Papenf.; Garbary et al. 1983: 32, as Audouinella membranacea; Lee & Yoshida 1997: 196, as Rhodochorton membranaceum (Magnus) Hauck)
- Colaconema minimum (Collins) Woelk. (Woelkerling 1973b: 572; Rosenvinge 1909: 128, as Chantransia emergens Rosenv.; Dixon & Irvine 1977: 94, as Audouinella emergens (Rosenv.) P.S. Dixon)
- Colaconema monorhizum Stegenga (Stegenga 1985: 320; Stegenga et al. 1997: 252)
- Colaconema ophioglossum (C.W. Schneid.) Afonso-Carr., M. Sansón, & Sangil (Schneider 1983: 13, as Audouinella ophioglossa C.W. Schneid.; Afonso-Carrillo et al. 2003: 109)
- Colaconema pacificum (Kylin) Woelk. (Kylin 1925: 11, as Acrochaetium pacificum Kylin; Garbary et al. 1983: 37, as Audouinella pacifica (Kylin) Garbary)
- Colaconema panduripodium Stegenga, J.J. Bolton & R.J. Anderson (Stegenga et al. 1997: 253)

Table 1. (continued) The 32 species currently recognized in the genus Colaconema Batters (1898) and reference(s) to descriptive accounts of them:

Colaconema pectinatum (Kylin) J.T. Harper & G.W. Saunders (Kylin 1906: 120, as Chantransia pectinata Kylin; Stegenga 1985: 314, as Audouinella pectinata (Kylin) Papenf.)

Colaconema proskaueri (J.A. West) P.W. Gabrielson (West 1972: 383, as Acrochaetium proskaueri J.A. West)
 Colaconema rhizoideum (K.M. Drew) P.W. Gabrielson (Drew 1928: 182, as Rhodochorton rhizoideum K.M. Drew; Garbary et al. 1983: 49, as Audouinella rhizoidea (K.M. Drew) Garbary)

Colaconema savianum (Menegh.) R. Nielsen (Schneider 1983: 15, as Audouinella saviana (Menegh.) Woelk.; Woelkerling & Womersley 1994: 47, as Audouinella saviana)

Colaconema strictum (Rosenv.) R. Nielsen (Rosenvinge 1909: 108, as Chantransia stricta Rosenv.; Lee & Yoshida 1997: 191, as Acrochaetium strictum (Rosenv.) Hamel)

Colaconema subimmersum (Setch. & N.L. Gardner) P.W. Gabrielson (Lee & Yoshida 1997: 206 as Rhodochorton subimmersum Setch. & N.L. Gardner; Garbary et al. 1983: 56, as Audouinella subimmersa (Setch. & N.L. Gardner) Garbary & Rueness)

Colaconema tetrasporum (Garbary & Rueness) Athanas. (Garbary & Rueness 1980: 17, as Audouinella tetraspora Garbary & Rueness)

Woelkerling (1971) treated *Colaconema* as a "form genus", to include "asexual taxa of uncertain systematic position", and he presented his evidence favoring such a treatment (Woelkerling, 1973). Garbary (1987) proposed a monogeneric circumscription such that all of these acrochaetioid taxa were included in *Audouinella*, the oldest name of the genera in the Acrochaetiaceae *sensu lato* (Bory de Saint-Vincent, 1823). Such a monogeneric circumscription repeats the earlier view of Drew (1928), who included the various acrochaetioids under the single genus *Rhodochorton* of Nägeli (1862). Other authors, such as Lee (1987) and Lee & Yoshida (1997) preferred a taxonomic scheme in which three genera were recognized – *Audouinella*, *Rhodochorton*, and *Acrochaetium* – with *Colaconema* being regarded as congeneric within *Audouinella*.

In the most recent treatment of these genera (Harper & Saunders, 2002, 2003), morphological and molecular differences were used to produce a phylogenetic analysis in which *Colaconema* is separated into its own family (Colaconemataceae) and order (Colaconematales). *Colaconema* includes those taxa in which the vegetative cells have one to several parietal chloroplasts of varying shape, but never stellate. Pyrenoids may or may not be present. Thus, an acrochaetioid plant in which vegetative cells contain a single lobed, parietal chloroplast with a single pyrenoid can be assigned only to *Colaconema* (Harper & Saunders, 2002; Afonso-Carrillo *et al.*, 2007). Thus, a small epiphytic acrochaetioid alga from Oman is described in this paper, and its distinctive features justify its delineation as a new species.

MATERIALS AND METHODS

Specimens of *Nizamuddinia zanardinii* (Schiffner) P.C. Silva were collected from the shallow sublittoral and preserved in 5% Formalin/sea-water. Later, in more closely examining these wet-preserved specimens, small plants of the new *Colaconema* were found as epiphytes on the large brown algal host. From the initial and only "gathering" (Art. 8.2, McNeill *et al.*, 2006) of the new species,

nine microscope slides were prepared of this material, with approximately 10 to 20 (or more) specimens present per slide. Specimens for photomicrography were stained with acid-buffered 1% aniline blue. Photomicrographs were taken using a Carl Zeiss Axioskop 40 microscope (Oberkochen, Germany) equipped with a model 11.2 Spot InSight 2 digital camera (Diagnostic Instruments, Sterling Heights, Michigan, USA). The digital images were composed in Adobe PhotoshopTM 7.0 (Adobe Systems, San Jose, California, USA). Line-drawings were made using a camera-lucida and Zeiss research microscope. GPS coordinates were obtained in the field by using a Garmin eTrex Summit (Garmin International Inc., Olathe, KS 66062, USA). Herbarium abbreviations follow Holmgren *et al.* (1990), and initials for authorities' given names are from Brummitt & Powell (1992).

RESULTS

Colaconema basiramosum sp. nov. M.J. Wynne et C.W. Schneid.

Figs 1-8

Diagnosis: Species novae ab aliis speciebus generis a combinatione characterum cellulas auctas et indivisas basales, ramos singulares suprabasales pseudodichotomas, gametophyta monoecia et manifestas absentias monosprangiorum et tetrasporangiorum includentium differns; maxima similis Acrochaetio kurogio in ubique habitu sed differens ramificationem basalem axium et plastos singulares parietales producenti.

Differing from other *Colaconema* species by a combination of characteristics including its enlarged and undivided basal cells, unique suprabasal pseudodichotomous branching, monoecious gametophytes, and the apparent absence of monosporangia and tetrasporangia. Most similar in overall habit to *Acrochaetium kurogii* but differing in having basal branching of axes and single parietal plastids.

Holotype: *leg. Glenn Richards* 19082000-13-44. First cove east of Sadh (17.05755° N, 55.08544° E), east of Mirbat, Dhofar, Sultanate of Oman, 19.ix.2000; epiphytic on *Nizamuddinia zanardinii* (Schiffner) P.C. Silva; monoecious gametophytes. MICH.

Isotypes: BM, L, ON, PC, UC, US, and Herbarium C. W. Schneider.

Etymology: The specific epithet refers to the distinctive pseudodichotomous branching at the base of the plant.

Description: Plants epiphytic, 2-4 mm tall, attached to host by a single large spherical basal cell sunken into the host alga (Fig. 1). Usually, the cell distal to the attachment cell is enlarged, 50-54 μm broad, and the first two cells above the basal cell are collectively 46-50 μm long. Usually, it is the second cell of this main axis, distal to the basal attachment cell, that bears a subservient (secondary and indeterminate) axis (Figs 1, 5). These two axes (main axis and a single secondary axis) later become essentially equivalent axes. Or it may appear that it is the suprabasal cell that bears the secondary axis because there was a subsequent break-down of the pit-plug between the swollen basal cell and the usual first cell (Figs 4, 6). Vegetative cells contain a single encompassing parietal chloroplast bearing a single pyrenoid.

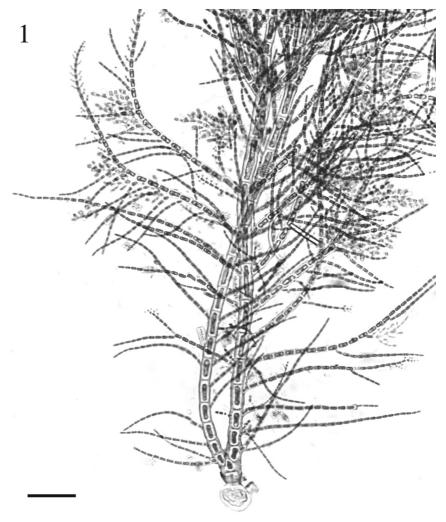
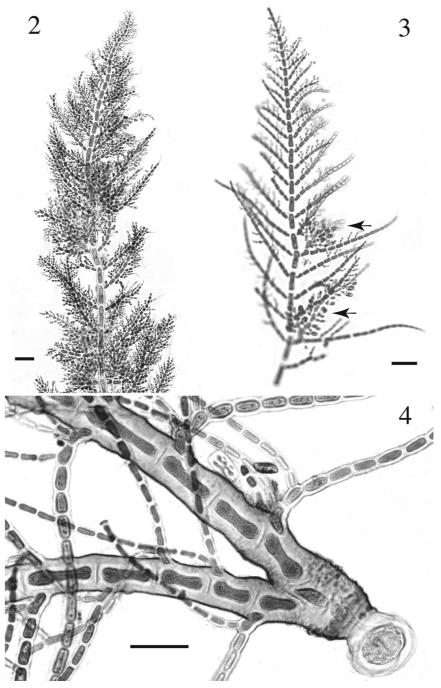
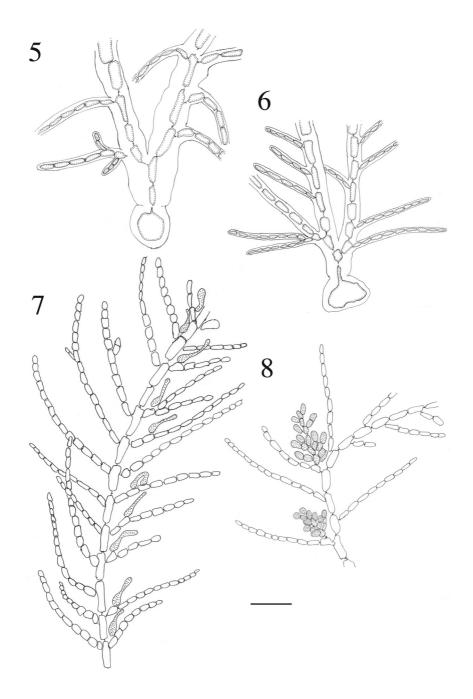


Fig. 1. $Colaconema\ basiramosum$. sp. nov. Habit of proximal portion of plant with pseudodichomously branched axis. Carposporophytes present. Scale bar: $100\ \mu m$.

Lower cells of these principal axes are 26-30 μm wide and bear distichously arranged opposite branches for some distance. The opposite branches are determinate and in turn bear both opposite and alternate branches (usually short, simple and spine-like). Few-celled third-order branches are again pinnately arranged and present on older plants. Some of the second-order branches continue development in an indeterminate pattern, similar to the main axes. Which branches are so determined seems to be random. The principal axes are mostly straight or just slightly flexuous distally. Usually the final 7-9 cells of any axis or branch are unbranched. The ultimate cell of any branch ends in a conical tip. Cell walls reaching 2.5 μm thickness on main axis, thinning down gradually to 1 μm at the tips.



Figs 2-4. *Colaconema basiramosum* sp. nov. **2.** Habit of distal portion of plant. *Colaconema basiramosum* sp. nov. **3.** Apical region of a plant with both spermatangia and young carposporophytes (indicated by arrows). **4.** Base of plant with typical enlarged basal cell. Scales bars (Figs 2 & 3): $50 \ \mu m$; (Fig. 4): $25 \ \mu m$.



Figs 5-8. *Colaconema basiramosum* sp. nov. **5.** Base of plant with secondary branch originating from second cell distal to basal cell. **6.** Base of plant with secondary branch originating from suprabasal cell. **7.** Young axis bearing sessile carpogonia (stippled) on basal or suprabasal cell of lateral branches. **8.** Young carposporophytes (stippled). Scale bar: $25 \, \mu m$.

Plants are monoecious (Figs 1-3). Spermatangia are budded off the tips and the sides of the cells of distal branches but always in the same plane as the distichously arranged vegetative axes (Fig. 3). Spermatangia are ovoid, about $2 \mu m$ in their longer dimension.

Carpogonia are invariably located on the adaxial side of the basal or suprabasal cells of lateral branches (Fig. 7). They tend to occur in series on just one side of an axis, alternating back and forth. There is only a single sessile carpogonium per basal cell. After budding off, carpogonia are initially ovoid, 8-10 μ m in length. Carpogonia are oriented to extend away from the axis of the thallus. Usually a distal process, or trichogyne, becomes evident, the carpogonium becoming longer (12 μ m) and sometimes even to 21 μ m in its entire length. It is not uncommon to see carpogonia formed on every basal cell of a branch of the same system.

Following presumptive fertilization, a carposporophytic axis grows out from the former carpogonium. The cells of this axis are larger in size than nearby vegetative branch systems, and the initial branch is percurrent, producing lateral branches. From these side branches are produced abundant ovoid carposporangia, about 7-8 μ m in diam. and 14 μ m in length (Fig. 8). When the carpospores are released, the carposporangial walls persist. The most remarkable feature of these carposporophytes is that they have a basal diffuse branching system with a distinct appearance from the vegetative branch system (Figs 1-3). Multiple carposporangia are produced in abundance, most still lying in the same plane as the axis from which they are produced. Monosporangia and tetrasporangia were not observed.

DISCUSSION

Following the proposed taxonomic separation of the genera *Acrochaetium*, *Audouinella*, *Rhodochorton*, and *Colaconema*, a number of species have been transferred into *Colaconema* (Stegenga, 1985; Jackelman *et al.*, 1991; Stegenga *et al.*, 1997; Afonso-Carrillo *et al.*, 2003, 2007; Ateweberhan & Prud'homme van Rein, 2005). Despite its assignment to a different genus, the "acrochaetioid" species that seems most similar morphologically to *Colaconema basiramosum* is *Acrochaetium kurogii* (Y.P. Lee *et* Lindstrom) Y.P. Lee *et* I.K. Lee (Lee & Lindstrom, 1979; Lee & Lee, 1988; Lee & Yoshida, 1997). This species was temporarily transferred to *Chromastrum* (Kuiper, 1983) following the generic circumscription proposed by Papenfuss (1945). The following features are shared by *A. kurogii* and the new *Colaconema* from Oman: a single large basal cell, which lies embedded in the host tissue; erect axes with predominantly opposite branching; and a monoecious condition.

Conversely, there are important differences between these two species. The most important distinction is that there is a single parietal chloroplast with one pyrenoid per cell in *Colaconema basiramosum*, while there is a single stellate axial chloroplast with one pyrenoid per cell in *Acrochaetium kurogii*. The plastid of the new species covers the inner lateral sides of the entire cell membrane. Furthermore, although basal branching occurs in both of these pectinately branched plants, in the new species a single percurrent basal branch is invariably produced from the second cell distal to the intact basal cell. In *A. kurogii*, 4-6 branches are produced directly from the basal cell (Lee & Lindstrom, 1979).

In addition, carpogonia are borne terminally in *A. kurogii*, and a quite simple carposporophyte is produced, usually with only up to three carposporangia produced per carposporophyte. In *C. basiramosum* the most common location for the formation of a carpogonium is on the basal cell of a branch. Typically, a trichogyne is cut off on the adaxial surface of this basal cell, and following presumed fertilization the carposporophyte is developed as a branching system, from which numerous carposporangia are cut off in a relatively loose arrangement. The vegetative portion of the carposporophyte is significant, and the greater dimensions of the vegetative parts of the carposporophyte distinguish them from the gametophytic filaments. Lee & Lindstrom (1979) stressed that the relatively thick and transparent walls (to 5 μ m) of *A. kurogii* are a distinctive feature. In *A. kurogii* the embedded basal cell is larger and lobed, whereas that of the new species remains spherical.

Another species of *Colaconema* that has the features of a unicellular base and a parietal chloroplast is *C. gynandrum* (Rosenv.) R. Nielsen. Rosenvinge (1909, as *Chantransia gynandra*) first depicted this species as having thalli with a nearly globular basal cell giving rise to essentially simple erect filaments and made up of cells with a narrow parietal chloroplast containing an inwardly projecting pyrenoid. Lateral and terminal colorless hairs were produced in abundance. Hamel (1927), who transferred this species to *Acrochaetium*, observed only tetrasporangia in his Atlantic France material, and these sporangia were produced singly and in pairs in sessile positions from the erect filaments. Abdel-Rahman (1985) observed the complete developmental cycle of this species in culture, noting that the tetrasporophytic thalli tend to be more numerous and to be more branched than the gametophytic filaments. Many differences, such as the much smaller size of the thalli, the lack of the distinctive basal branching pattern, the production of colorless hairs, tetrasporangia, and monosporangia, easily separate *C. gynandrum* from *C. basiramosum*.

Similarly, thalli of Colaconema hallandicum (Kylin) Afonso-Carrillo, Sansón, Sangil et Díaz-Villa are attached by a single basal cell, and cells have a parietal chloroplast with a pyrenoid (Woelkerling, 1973a, as Audouinella hallandica). The basal cell of this species elongates into host tissue and has an obvious thickened cell wall unlike the new species (Schneider, 1983, as Audouinella hallandica). Erect thalli of C. hallandicum are moderately branched, lateral branches often extending distally into colorless hairs. Monosporangia are produced in clusters (Kylin, 1906). In his treatment of the "Audouinella complex" of the western Sargasso Sea, Woelkerling (1973a) proposed to treat Acrochaetium dufourii (Collins) Børgesen and A. sargassi Børgesen as conspecife with Audouinella hallandica (Kylin) Woelkerling, asserting that critical comparisons of the three type collections showed the same range of cell dimensions and overall morphological consistency. The distinction of Colaconema hallandicum from C. basiramosum is obvious in regard to the larger cell dimensions, basal cell characteristics and the suprabasal branching of main axes in the new species with distinctive pectinate branching above.

Colaconema panduripodium was described as a new species and as a South African endemic (Stegenga et al., 1997). It was stated to have a single basal cell sunken into the cortical tissue of the host, Desmarestia firma (C. Agardh) Skottsberg, and it was the only species having such a unicellular base of the eight known species of the genus occurring in South Africa. From its unicellular base up to three monosiphonous axes arise, that reach rarely up to 1 mm in height. Lateral branches are short, the branching being mostly secund, and monosporangia are produced adaxially and terminally. Other than having the

enlarged basal cell, this South African species differs significantly from *C. basiramosum*.

The establishment of *Colaconema basiramosum* adds yet another newly described taxon to the benthic marine algal flora of the Sultanate of Oman. In addition to the new Omani taxa listed by Wynne (2004, 2006b) and Schils & Wilson (2006, Table S1), the growing list has been supplemented by the recent papers of Wynne (2005a, 2005b, 2006a) and Wynne & Schneider (2006).

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