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# Contemporary taxonomic perspectives of fossil Coralline Red Algae: their possible origin and evolution

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## ABSTRACT

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Studies done by various phycologists have brought about remarkable changes in the present-day coralline algal taxonomy. The taxonomy of fossil coralline red algae also has been under the process of continuous revision and modification since 1993. Prior to 1993 it was believed that several diagnostic characters used in recent coralline red algae were unpreservable in fossil forms. Palaeoalgologists have now understood the value of unification of taxonomy, for extant and fossil corallines to accurately interpret the phylogeny, palaeoecology and palaeobiogeography. Phylogenetically, the corallines are very important as they represent a major evolutionary line within the red algae as evidenced by anatomical studies on recent forms as well as various studies on gene sequence analysis. The present contribution deals with the remarkable changes that have taken place since 1993 in the taxonomic aspects of fossil coralline algae and the modern trends of research in this context. Presently, an attempt has been made to establish the possible origin and evolution of coralline red algae.

**Key-words**—Coralline Red Algae, Classification, Taxonomy, Possible Origin, Evolution.

## प्रवाली लाल शैवाल के संदर्भ में समकालीन वर्गीकरणः उनका संभव उद्‌भव एवं विकास

अमित के. घोष एवं सुमन सरकार

## सारांश

विभिन्न शैवाल विज्ञानियों द्वारा किए गए अध्ययन से वर्तमान प्रवाली शैवालीय वर्गिकी में असाधारण परिवर्तन संपादित किया गया है। प्रवाली लाल शैवाल जीवाश्म की वर्गिकी को भी 1993 से सतृत पुनरीक्षण तथा संशोधन की प्रक्रिया के अन्तर्गत किया गया है। 1993 के पूर्व यह विश्वास किया गया था कि आधुनिक प्रवाली लाल शैवाल में प्रयोग कई निदान सूचक लक्षण जीवाश्म रूपों में अपरिरक्षणीय थे। पुराशैलविज्ञानियों ने जातिवृत, पुरापारिस्थितिकी तथा पुराजैवभूगौल की यथार्थ रूप से व्याख्या करने हेतु विद्यमान एवं प्रवाली जीवाश्म के लिए वर्गिकी के एकीकरण के मान को अब समझ लिया गया है। जातिवृतीय रूप से प्रवाली बहुत महत्वपूर्ण हैं जैसे कि वे वर्तमान रूपों पर शारीरिक अध्ययन के साथ-साथ जीन अनुक्रम विश्लेषण के प्रमाणों के रूप में लाल शैवाल में मुख्य विकासीय रेखा निरूपित करते हैं। वर्तमान योगदान असाधारण परिवर्तन में कार्य करता है जिसने प्रणाली जीवाश्म की वर्गिकीय दृष्टि तथा इसके संदर्भ में अनुसंधान की आधुनिक प्रवृतियों में 1993 से स्थान ले लिया है। वर्तमान शोधपत्र में प्रवाली लाल शैवाल के संभव उद्‌भव एवं विकास को स्थापित करने में एक कोशिश की गई है।

**संकेत-शब्द**—प्रवाली लाल शैवाल, वर्गीकरण, वर्गिकी, संभव उद्‌भव, विकास।

## INTRODUCTION

WRAY (1977), Poignant (1984) and several other palaeoalgologists opined that fossil and recent coralline algae have to be classified in different manners and consequently different diagnostic characters were used for the identification of fossil and extant coralline algae. Various diagnostic suprageneric criteria were proposed for extant as well as fossil material which included type and location of conceptacles, character of hypothallium and perithallium (core/primigenous and peripheral/postigenous filaments respectively as per the recent literature) and also the presence or absence and arrangement of heterocysts (trichocytes). Discovery of interfilamental cell-connections (Johansen, 1969) and application of some other diagnostic features like shape of epithallial cells (Adey, 1970), number of epithallial cells (Johansen, 1976) and pattern of cell elongation in recognizing suprageneric taxa (Woelkerling & Irvine, 1986) were employed for the taxonomy of extant coralline algae by the phycologists. However, the post-1993 phase saw prominent work by various workers leading to the view that some key features, e.g. cell-connections, cell-fusions, epithallial cell and meristem characteristics can also be recognized in fossil corallines using light microscopy as well as appropriate SEM techniques (as specified by Braga *et al.*, 1993). In this context the present review summarizes the contributions on morphological/anatomical studies of fossil corallines, present day corallines, their ultrastructural studies as well as gene sequence analysis. Based on these attributes, characteristics of families and subfamilies of the order Corallinales have been discussed in detail. In addition, possible evolutionary lineages of this algal group have been drawn hovering on recent discoveries.

## POTENTIAL TAXONOMIC CHARACTERS IN PRESENT DAY AND FOSSIL CORALLINE ALGAE

Bosence (1991) raised some important questions regarding the preservation of taxonomic characters and relationships between fossil taxa and groups of extant taxa. He emphasized on the significance of reassessment and revision of well known fossil taxa along with detailed measurements and statistical analysis because many of the fossil coralline taxa were suffering from excessive splitting only on the basis of very few characters. According to Bosence (1991) in case of fossil corallines, palaeoalgologists should increase the use of potential taxonomic characters which can be revealed by excessive analysis of thin sections and SEM observations. Later on, Rasser and Piller (1999) applied the neontological taxonomic concepts to coralline algae. Presently, all these potential taxonomic characters are commonly used by the palaeoalgologists (Fig. 1).

Various taxonomic measures proposed for living and fossil algae facilitate their use as effective palaeoenvironmental indicators and at the same time favour the understanding of the evolutionary biology of the group. In most cases, diagnostic features used for separating genera in present-day corallines can be identified in fossil plants except the uncalcified reproductive structures or developmental features that are not preserved in relic material and hence cannot be used for generic identification. Recently, there has been a trend to propose reproductive and developmental features as prevalent diagnostic criteria for modern coralline taxonomy. However, their consistency and systematic significance is still a point of discussion. In cases when diagnostic criteria are not preserved then the ancillary characters recognizable in fossil material or the application of informal generic names with a broader circumscription as compared to the living representatives can be used as the best options for palaeontological taxonomy.

Various diagnostic characters used for the separation of taxa at different taxonomic levels have changed throughout the history of biological and palaeobiological research, with coralline red algae not being an exception. Secondly, till date no general agreement on classification scheme for modern and fossil coralline algae has been formulated and

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Fig. 1—Potential taxonomic characters in Recent and Fossil coralline algae (modified after Bosence, 1991; Rasser & Piller, 1999).

| GENERAL CHARACTERS | OCCURRENCE OF CHARACTERS* | | |
|---|---|---|---|
| | RECENT | FOSSIL | |
| | | *Commonly used* | *Potentially usable* |
| *Growth Form* | | | |
| Encrusting | ◙ | ◙ | ◙ |
| Warty | ◙ | ◙ | ◙ |
| Lumpy | ◙ | ◙ | ◙ |
| Fruticose | ◙ | ◙ | ◙ |
| Layered | ◙ | ◙ | ◙ |
| Foliose | ◙ | ◙ | ◙ |
| Arborescent | ◙ | ◙ | ◙ |
| Articulated | ◙ | ◙ | ◙ |
| Articulated branching | ◙ | □ | □ |
| *Epithallium* | | | |
| Thickness | ◙ | □ | ◙ |
| Cell shape | ◙ | □ | ◙ |
| Meristematic cells | ◙ | □ | ◙ |
| Trichocytes | ◙ | □ | ◙ |
| *Thallus organization* | | | |
| Monomerous | ◙ | ◙ | ◙ |
| Coaxial | ◙ | ◙ | ◙ |
| Non-coaxial | ◙ | ◙ | ◙ |
| Peripheral filaments | ◙ | ◙ | ◙ |
| Core filaments | ◙ | ◙ | ◙ |
| Palisade cells | ◙ | ◙ | ◙ |
| Dimerous | ◙ | ◙ | ◙ |
| Postigenous filaments | ◙ | ◙ | ◙ |
| Primigenous filaments | ◙ | ◙ | ◙ |
| Primary pit connections | ◙ | ◙ | ◙ |
| Secondary pit connections | ◙ | ◙ | ◙ |
| Cell fusions | ◙ | ◙ | ◙ |
| Genicula | ◙ | ◙ | ◙ |
| *Asexual conceptacles* | | | |
| Location | ◙ | ◙ | ◙ |
| Perforations | ◙ | ◙ | ◙ |
| Shape | ◙ | ◙ | ◙ |
| Primordia | ◙ | □ | ◙ |
| Tetraspores | ◙ | □ | ◙ |
| *Sexual conceptacles* | | | |
| Location | ◙ | ◙ | ◙ |
| Shape | ◙ | ◙ | ◙ |
| Spermatangium | ◙ | □ | ◙ |
| Carpogonium | ◙ | □ | ◙ |
| Carpospore | ◙ | □ | ◙ |
| *Biochemical* | | | |
| Staining of sporangial caps | ◙ | □ | □ |
| *Developmental* | | | |
| Spore cell division | ◙ | □ | □ |
| Conceptacle developments | ◙ | □ | ◙ |

* ◙ = Yes, □ = No.

| Character | Corallinaceae | Sporolithaceae | Hapalidiaceae |
|---|---|---|---|
| Arrangement of spores within tetrasporangia | Zonate | Cruciate | Zonate |
| Tetra/bisporangia producing apical plugs | No | Yes | Yes |
| Tetra/bisporangia produced beneath multiporate plates | No | No | Yes |
| Tetra/bisporangia borne within conceptacles or calcified compartments | Conceptacles | Calcified compartments | Conceptacles |

Fig. 2—Diagnostic characteristics of the three families of Corallinales based on the reproductive organs (after Harvey *et al.*, 2003).

| **Subfamily** | **Genicula** | **No. of pores in sporangial conceptacles** | **Predominant interfilamental cell connections** | **Sporangial plugs** |
|---|---|---|---|---|
| Amphiroideae | present | uniporate | Secondary pits | absent |
| Corallinoideae | present | uniporate | Cell fusions | absent |
| Metagoniolithoideae | present | uniporate | Cell fusions | absent |
| Choreonematoideae | absent | uniporate | Absent | present |
| Lithophylloideae | absent | uniporate | Secondary pits | absent |
| Mastophoroideae | absent | uniporate | Cell fusions | absent |
| Melobesioideae | absent | multiporate | Cell fusions | present |

Fig. 3—Key characters of subfamilies of the Corallinaceae according to Woelkerling (1988).

modifications are being continuously made by the workers pertaining to unification of taxonomic analysis.

The monographic work of Woelkerling (1988) was for a long time considered as the most complete and comprehensive study of generic and suprageneric taxonomy of the Corallinales. Key features for delimiting subfamilies, and most of the characteristic features used by Woelkerling (1988) at generic level, can be observed in fossil plants too with appropriate microscopic techniques like SEM (Braga *et al.*, 1993). However, after this work, the circumscription of some living genera previously delimited by vegetative features recognizable in fossil examples has been modified. Characters with poor or no preservation potential, such as features of spermatangia, have been categorized as diagnostic (Penrose, 1992; Chamberlain & Keats, 1994; Woelkerling, 1996a, b, c), making the identification process very difficult or rather nearly impossible for the fossil specimens.

## DIFFERENT CLASSIFICATION SCHEMES PROPOSED FOR THE ORDER CORALLINALES

The Order Corallinales includes three families, viz. Corallinaceae, Sporolithaceae and Hapalidiaceae (Fig. 2) following a recent contribution by Harvey *et al.* (2003) on 18S rDNA phylogeny and recognition of Hapalidiaceae as a distinct family of Corallinales.

| **Corallinaceae** | **Genicula** | **Number of pores sporangial conceptacles** | **Predominant interfilamental cell connections** | **Sporangial plugs** | **Fossils** |
|---|---|---|---|---|---|
| Corallinoideae | Present | Uniporate | Cell fusions | Absent | Common |
| Metagoniolithoideae | Present | Uniporate | Cell fusions | Absent | Unknown |
| Austrolithoideae | Absent | Multiporate | Absent | Present | Unknown |
| Choreonematoideae | Absent | Uniporate | Absent | Present | Unknown |
| Lithophylloideae | Present/Absent | Uniporate | Secondary pits | Absent | Common |
| Mastophoroideae | Absent | Uniporate | Cell fusions | Absent | Common |
| Melobesioideae | Absent | Multiporate | Cell fusions | Present | Common |
| **Sporolithaceae** | Absent | Spores cruciately arranged in calcified compartments (sori) | Cell fusions | Apical plugs present | Common |

Fig. 4—Key characters of subfamilies of the Corallinaceae and Sporolithaceae (Modified after Woelkerling, 1988; Verheij, 1993; Harvey & Woelkerling, 1995; Bailey, 1999; Braga, 2003).

After extensively analyzing the genera and subfamilies of extant coralline algae, Woelkerling (1988) proposed a classification scheme (Fig. 3) based on a number of diagnostic features, many of which are observable in fossil specimens with bright field and Scanning Electron Microscopy. Based on these key features, the family Corallinaceae was divided into subfamilies Amphiroideae, Corallinoideae, Metagoniolithoideae, Choreonematoideae, Lithophylloideae, Mastophoroideae and Melobesioideae. The family Sporolithaceae was instituted by Verheij (1993) to separate the genus *Sporolithon* from rest of the corallines. *Sporolithon, Kymalithon* and *Hemiphyllum* represent the fossil record of the family Sporolithaceae but it is mentionable here that till date no fossil record has been reported for the extant genus of this family, *Heydrichia*.

A new subfamily Austrolithoideae (nongeniculate corallines), belonging to Corallinaceae has been erected by Harvey and Woelkerling (1995). Based on 18S rRNA gene sequence analyses, Bailey (1999) recommended the close affinity of the Amphiroideae (geniculate) and the Lithophylloideae (non-geniculate) subfamilies. Ultrastructural studies by Broadwater *et al.* (2000) too support this recommendation that the subfamilies Amphiroideae and Lithophylloideae should be included into one single subfamily -Lithophylloideae.

Based on the contributions of Verheij (1993), Harvey and Woelkerling (1995), and Bailey (1999), a modified scheme (Fig. 4) has been introduced by Braga (2003) in the suprageneric taxonomy system of Woelkerling (1988). In this scheme, three subfamilies of Corallinaceae, viz. Metagoniolithoideae, Austrolithoideae and Choreonematoideae have not been recorded yet in the fossil forms.

Harvey *et al.* (2003) have recently resurrected the family Hapalidiaceae based on the 18S rDNA phylogenetic studies and included the subfamilies Choreonematoideae, Austrolithoideae and Melobesioideae within this family.

The morphological/anatomical scheme of coralline algal taxonomy proposed by Johansen (1981) and Woelkerling (1988) has undergone modifications after the contributions of Bailey and Chapman (1996, 1998), Bailey (1999) and thereafter by Harvey *et al.* (2003) based on rRNA and rDNA phylogenetic studies. In accordance with the latest trends of research on coralline algal taxonomy a modified classification scheme is presented here (Fig. 5) after the contributions of Woelkerling (1988), Verheij (1993), Harvey and Woelkerling (1995), Bailey and Chapman (1996, 1998), Bailey (1999), Braga (2003) and Harvey *et al.* (2003).

## KEY CHARACTERS OF FAMILIES BELONGING TO THE ORDER CORALLINALES

### Sporolithaceae

This family includes those taxa of Corallinales which produce tetrasporangia individually in calcified compartments, and the compartments are grouped into sori. These tetrasporangia produce cruciately arranged spores. Apical plugs are present but they do not develop beneath multiporate plates and an interesting feature is this that the male and female structures are produced in uniporate conceptacles similar to those of other coralline red algae. Phylogenetic studies involving both the sporolithacean genera, i.e. *Sporolithon* and *Heydrichia* have been carried out by Bailey and Chapman (1998), Bailey (1999), and Harvey *et al.* (2002) hovering on 18S rDNA analysis data. These analyses clearly indicate that Sporolithaceae forms a distinct lineage separate from the Corallinaceae and Hapalidiaceae on molecular basis, which is also supported by morphological/anatomical data (Harvey *et al.*, 2002). Although further work using the DNA sequences from additional taxa of Sporolithaceae is required to clarify the phylogenetic relationships within this family, species belonging to the genera *Heydrichia* and *Sporolithon* are clearly different based on morphological/anatomical studies.

### Corallinaceae

This family includes those taxa of Corallinales which produce tetrasporangia in uniporate conceptacles. The tetrasporangia lack apical plugs, and each sporangium contains zonately arranged spores. Male and female reproductive structures are also produced in uniporate

| Family | Subfamily | Genicula | Number of pores in sporangial conceptacles | Predominant interfilamental cell connections | Sporangial plugs | Fossils |
|---|---|---|---|---|---|---|
| **Corallinaceae** | Corallinoideae | Present | Uniporate | Cell fusions | Absent | Common |
|  | Metagoniolithoideae | Present | Uniporate | Cell fusions | Absent | Unknown |
|  | Lithophylloideae | Absent/Present | Uniporate | Secondary pits | Absent | Common |
|  | Mastophoroideae | Absent | Uniporate | Cell fusions | Absent | Common |
| **Hapalidiaceae** | Melobesioideae | Absent | Multiporate | Cell fusions | Present | Common |
|  | Austrolithoideae | Absent | Multiporate | Absent | Present | Unknown |
|  | Choreonematoideae | Absent | Uniporate | Absent | Present | Unknown |
| **Sporolithaceae** | Not yet divided into subfamilies | Absent | Spores cruciately arranged in calcified compartments (sori) | Cell fusions | Apical plugs are quite common | Common |

Fig. 5—Modified classification of Corallinales after the contributions of Woelkerling (1988), Verheij (1993), Harvey & Woelkerling (1995), Bailey & Chapman (1996, 1998), Bailey (1999), Braga (2003) and Harvey *et al.* (2003).

conceptacles. No apical plugs are produced neither do they develop beneath multiporate plates.

The recent concept of the Corallinaceae has brought about significant changes following the contributions of Verheij (1993), Irvine and Chamberlain (1994), Woelkerling (1996a, b, c), Yoshida (1998) and Bailey (1999). This recent concept resulted in the transfer of those taxa to family Hapalidiaceae (including *Choreonema* of the subfamily Choreonematoideae) whose tetrasporangia/bisporangia produce apical plugs and develops beneath multiporate plates (Harvey *et al.,* 2003).

### Hapalidiaceae

Members of this family produce tetrasporangia in multiporate conceptacles. Tetrasporangia possess apical plug, develop beneath multiporate plates and each sporangium contains zonately arranged spores. Male and female reproductive structures are produced in uniporate conceptacles.

Gray (1864) originally established the Hapalidiaceae for a single genus, *Hapalidium* (Kützing, 1843) based on the single species *H. roseolum* Kützing (1843). The family was not recognized by subsequent authors.

Chamberlain (1983) determined that the type of *H. roseolum* was conspecific and a heterotypic synonym of *Melobesia membranacea* (Esper) Lamouroux, the type species of *Melobesia*. Consequently, *Hapalidium* is a heterotypic synonym of *Melobesia.* Nevertheless, as noted by Woelkerling (1988), the family name is legitimate and available for a family that includes the genus *Melobesia.* In the present context of the proposal to place all genera of Corallinales (including *Melobesia*) with the features designated to Hapalidiaceae, the family name Hapalidiaceae becomes the oldest available name for the group.

## KEY CHARACTERS OF SUBFAMILIES

The family Corallinaceae includes four subfamilies:

***Subfamily Corallinoideae*****—**Contiguous vegetative filamental cells are linked by cell fusions, secondary pit-connections are unknown and genicula are composed of a single tier of cells.

Some common genera with high preservation potential as fossils: *Corallina, Jania, Calliarthron, Arthrocardia* and *Subterraniphyllum.*

***Subfamily Metagoniolithoideae*****—**Contiguous vegetative filamental cells are linked by cell fusions, secondary pit-connections are unknown and genicula are composed of untiered multicellular filaments.

No fossil record.

***Subfamily Mastophoroideae*****—**Contiguous vegetative filamental cells linked principally or exclusively by cell fusions, secondary pit-connections are known only in case of one genus i.e., *Metamastophora* and genicula are absent.

Some common genera with high preservation potential as fossils: *Lithoporella, Neogoniolithon, Spongites, Dermatolithon* and *Karpathia.*

***Subfamily Lithophylloideae*****—**Contiguous vegetative filamental cells are linked principally or exclusively by secondary pit-connections, cell fusions are reported for only a single species and genicula, if present, are composed of one or more tiers of cells.

Some common genera with high preservation potential as fossils: *Lithophyllum, Amphiroa* and *Titanoderma.*

The family Hapalidiaceae includes three subfamilies:

***Subfamily Austrolithoideae*****—**Contiguous vegetative filamental cells are not linked by cell fusions or secondary pit-connections, genicula are absent and multiporate plates are composed of cells at maturity.

No fossil record.

***Subfamily Choreonematoideae*****—**Contiguous vegetative filamental cells are not linked by cell fusions or secondary pit-connections, genicula are absent and multiporate plate is acellular at maturity, composed only of a calcium carbonate matrix.

No fossil record.

***Subfamily Melobesioideae*****—**Contiguous vegetative filamental cells are linked by cell fusions, secondary pit-connections are unknown, genicula are absent and multiporate plate is composed of cells at maturity.

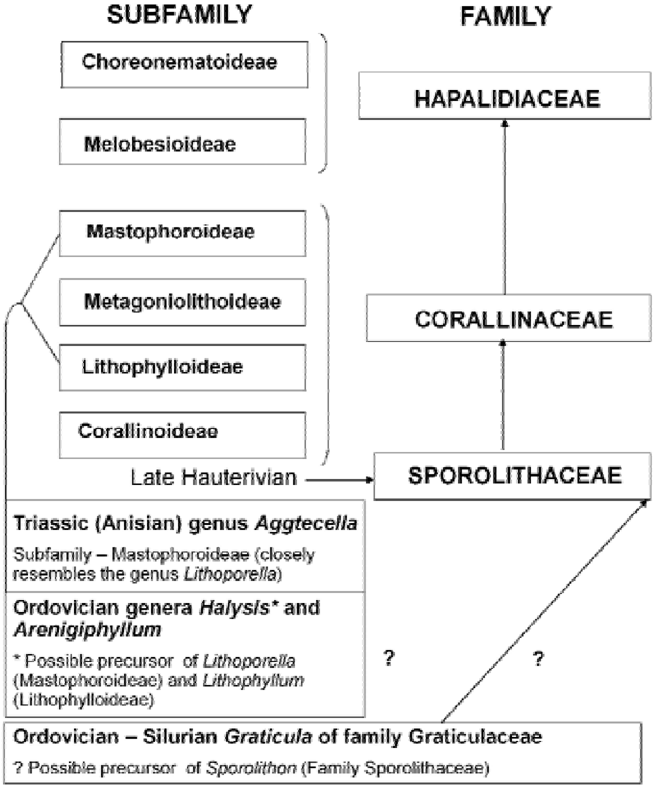

Fig. 6—Possible origin and evolutionary lineage of the Order Corallinaceae (after the contributions of Brooke & Riding, 1998, 2000; Riding *et al.*, 1998; Harvey *et al.*, 2003; Riding & Braga, 2005; Senowbari-Daryan & Velledits, 2007; Tomás *et al.*, 2007).

Some common genera with high preservation potential as fossils: *Mesophyllum, Phymatolithon* and *Lithothamnion.*

## POSSIBLE ORIGIN AND EVOLUTION OF CORALLINALES

Corallinales is presently considered as a separate order of Rhodophyta. Within the red algae the order Corallinales represents a major evolutionary line. During the last few years concepts of families, subfamilies, genera and species of corallines have been changed as a result of extensive new findings on fossil as well as present-day corallines. Corallinales is considered as a monophyletic group that consists of three families, viz. Corallinaceae, Sporolithaceae and Hapalidiaceae. The corallinaceans include both geniculate and non-geniculate forms, whereas sporolithaceans and hapalidiaceans are strictly non-geniculate.

Modern coralline red algae have been significant constituents of benthic fossil assemblages in tropical to polar regions since the Early Cretaceous and the oldest feasible record of corallines is *Sporolithon rude* (Lemoine) Ghosh and Maithy from the Early Cretaceous (Tomás *et al.,* 2007). It is generally believed that corallines diversified during the Cretaceous.

According to some authors corallines appeared in the Late Palaeozoic and were specifically common in the Pennsylvanian epoch. Informally they were designated as ancestral corallines (Maslov, 1956; Endo, 1961; Chuvashov, 1971; Poncet & Morzadec, 1993).

However, a coralline like red alga *Craticula gotlandica* (Rothpletz) Brooke and Riding has been recorded by Brooke and Riding (1998) from the mid-Silurian of Gotland, Sweden and the authors established a new family Craticulaceae with *Craticula* as its type genus. Owing to nomenclatural problem, later on, Brooke and Riding (2000) themselves provided a replacement name for the alga *Craticula* as *Graticula* under the family Graticulaceae. They have proposed the family to be placed in the extant class Rhodophyta under the order Corallinales. Brooke and Riding (1998) opined that this coralline-like red alga morphologically resembles the Mesozoic-Cenozoic non-geniculate red alga *Sporolithon* belonging to the family Sporolithaceae. In accordance with Brooke and Riding (1998) recovery of Ordovician-Silurian *Sporolithon*-like alga confirms the long-ranging lineage of the extant sporolithacean coralline algae and the family Graticulaceae has been identified by the authors as an ancestral coralline group (Fig. 6). Another new alga, *Arenigiphyllum crustosum* Riding *et al.*, 1998, belonging to the Lower Ordovician has been described from Llangynog Inlier, Carmarthenshire, Wales. This taxon is characterized by a thin crustose dorsiventral thallus with dimerous construction, consisting of juxtaposed vertical filaments arising from prostrate bases. No evidence of cell fusions, pit-connections or reproductive structures has been deciphered, but in terms of size and thallus structure, *Arenigiphyllum* closely resembles vegetative parts of extant coralline algae. Until the discovery of

*Arenigiphyllum*, *Petrophyton kiaeri* Høeg, from Middle-Upper Ordovician, was considered the oldest known Palaeozoic calcified red algae (Riding, 1994).

Recently, Riding and Braga (2005) reassessed the Ordovician genus *Halysis* Høeg (1932) of uncertain affinity. They have compared *Halysis* with the Mesozoic-Cenozoic thin laminar unistratose coralline red algae. According to Riding and Braga (2005), on certain aspects, *Halysis* is comparable to the mastophoroid non-geniculate coralline form *Lithoporella* (Foslie) Foslie, 1909. Applanate thallus morphology of *Halysis* also resembles the thin laminar species of the genus *Lithophyllum* Philippi. Identification of *Halysis* (Riding & Braga, 2005) as a coralline-like alga establishes the possibility that a variety of corallines were present in the Ordovician (Fig. 6). Recently, *Aggtecella hungarica* Senowbari-Daryan & Velledits has been discovered from the Anisian (Middle Triassic) reefoidal limestones of the Aggtelek-Rudabanya Mountains, N-E Hungary (Senowbari-Daryan & Velledits, 2007). This genus, belonging to the order Corallinales and subfamily Mastophoroideae, has nodular or laterally extended crusts which grow on other organisms, e.g. sponges, "Tubiphytes" etc. and appears dark in transmitted light. The individual layer comprising the cell series of *A. hungarica* possesses similarities to some Cenozoic red algae, e.g. *Lithoporella melobesioides*.

Several coralline species have been reported from the late Jurassic (Lemoine, 1970, 1977; Moussavian, 1991) but doubts still persist on the age of the rocks from where they have been recovered and on the taxonomic circumscriptions of the taxa. Earliest definite Mesozoic report (Arias *et al.*, 1995) of *Sporolithon* is from Hauterivian (123 Ma). It is confirmed (Elliott, 1959; Dragastan, 1971) that the earliest corallinaceans appeared in the Barremian in Iraq and Romania (117 Ma). During the Cretaceous Period the sporolithaceans reached its climax of development owing to the rise of global temperature. Since Palaeocene, diversity of sporolithaceans declined and, corallinacean and hapalidiacean forms became dominant due to the gradual reduction of global temperature as evidenced by $\delta^{18}$O values in benthic foraminifera (Savin, 1977).

A number of phylogenetic studies of Corallinales based on 18S rRNA gene sequences (Bailey & Chapman, 1998), 18S rDNA gene sequences (Bailey & Chapman, 1996; Bailey, 1999; Harvey *et al.*, 2003) have endowed a new perspective on the evolutionary history of this important group of red algae. Further research both on morphological/anatomical and ultrastructural studies both on fossils and recent materials in addition to phylogenetic studies (rRNA and rDNA gene sequence analysis) will throw some more light on the possible evolution and lineages within this algal group, because, till date we don't have sufficient evidences on the Ordovician-Silurian diversity of corallines. Though, coralline-like algal forms have been recorded from the Ordovician- Silurian and Triassic periods (Brooke & Riding, 1998, 2000; Riding *et al.*, 1998; Riding & Braga, 2005, Senowbari-Daryan & Velledits, 2007), molecular data of these forms are not known as they are extinct. However, a probable origin and evolutionary lineage of the Order Corallinales (after Brooke & Riding, 1998; Harvey *et al.*, 2003; Riding & Braga, 2005; Tomás *et al.*, 2007) is presented here (Fig. 6).

## CONCLUDING REMARKS

A perusal of the foregoing account reveals that the order Corallinales (Rhodophyta) now can be classified into three families, viz. Corallinaceae, Sporolithaceae and Hapalidiaceae based on morphological/anatomical and ultrastructural studies as well as gene sequence analyses.

The family Corallinaceae Lamouroux (1812) emend. Harvey *et al.* (2003), includes those taxa of Corallinales whose tetrasporangia produce zonately arranged spores and their tetrasporangia/bisporangia are borne in uniporate conceptacles but they do not produce apical plugs, tetrasporangia/bisporangia do not develop beneath multiporate plates and are not borne individually within calcified sporangial compartments. Four subfamilies, viz. Corallinoideae, Metagoniolithoideae, Mastophoroideae and Lithophylloideae are included within this family of Corallinales.

The family Sporolithaceae (Verheij, 1993), is restricted to those taxa of the order Corallinales that have tetrasporangia which produce cruciately arranged spores and those tetrasporangia/bisporangia are borne individually in calcified sporangial compartments and produce apical plugs but do not develop beneath multiporate plates and are not produced within conceptacles. Separate subfamilies of the Sporolithaceae have not yet been established.

The taxa of Corallinales included in the family Hapalidiaceae Gray (1864) emend. Harvey *et al.*, (2003) are characterised by tetrasporangia that produce zonately arranged spores and the tetrasporangia/bisporangia are borne in conceptacles, produce apical plugs, develop beneath multiporate plates, but are not borne individually within calcified sporangial compartments. Three subfamilies, viz. Austrolithoideae, Choreonematoideae and Melobesioideae are included within the family Hapalidiaceae.

Two families, viz. Graticulaceae (Brooke & Riding, 2000) and Solenoporaceae (Pia, 1927) known exclusively from the fossil record have been associated with the Corallines. As the genera belonging to these families are known only as fossils, no molecular data are available for these taxa. The genus *Graticula* of Graticulaceae from the Middle Silurian (439-409 Ma) is characterized by sporangial compartments like those of sporolithaceans and the authors placed the new family under Corallinales. Brooke and Riding (1998) commented that future work may demonstrate Graticulaceae as a junior synonym of the Sporolithaceae. However, the confirmed record (Tomás *et al.*, 2007) of *Sporolithon* is from the Early Cretaceous (Early Hauterivian).

Wray (1977) commented that the earliest known representative of the calcareous red algae is Solenoporaceae and the solenopores probably gave rise to the “ancestral corallines” during the middle Palaeozoic. The family Solenoporaceae instituted by Pia (1927) has long been associated with the order Corallinales (Woelkerling, 1988; Brooke & Riding, 1998). However, the systematic position of the family is still uncertain (Aguirre & Barattolo, 2001), because the type species of the genus *Solenopora*, i.e. *S. spongioides* has been created based only on sterile material (Aguirre & Barattolo, 2001). Regarding the placement of the family Solenoporaceae, Woelkerling (1988) opined that it may be put into *incertae sedis*, whereas Aguirre and Barattolo (2001) suggested assigning the family in an *incertae sedis* group of algae. However, the authenticity of *Solenopora* as an alga has been questioned recently and according to Riding (2004), *Solenopora* is a chaetitid sponge, not an alga. The type species of the genus *S. spongioides* consists of tubes with longitudinally flexuous walls, lobate-petaloid cross sections, with septal projections and sporadic cross partitions. These features of internal morphology are not characteristic of calcified red algae (Riding, 2004).

Riding and Braga (2005) reassessed the Ordovician calcareous microfossil *Halysis* Høeg and their reassessment suggests comparison between *Halysis* and Mesozoic-Cenozoic thin laminar unistratose coralline red algae, viz. *Lithoporella* and *Lithophyllum*. The interpretation of Riding and Braga (2005) of *Halysis* as a coralline-like alga strengthen the possibility that a variety of corallines were present in the Ordovician. As a matter of fact, it can be assumed that more than 300 Ma prior to the major diversification of the Coralline Red Algae in the Cretaceous, a variety of coralline-like algal forms appeared.

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