ABSTRACT. A taxonomic and biostratigraphical re-assessment of Subterraniphyllum Elliott (Corallinales, Rhodophyta) is presented. Results from studies of the type collection and of newly collected material from north-eastern Italy and northern Slovenia have shown that this taxon is not a geniculate coralline red alga as originally suggested by Elliott and most subsequent authors. Vegetatively, Subterraniphyllum most closely resembles certain living members of the Corallinales; however, the phenetic and phylogenetic relationships of Subterraniphyllum to other Corallinales cannot be determined with greater certainty. The exclusion of Subterraniphyllum from any group of Corallinaceae with genicula is based on unequivocal evidence that branch formation does not involve the occurrence of genicula. Subterraniphyllum seems to be restricted to the Oligocene. Reports of occurrences in Upper Eocene and Lower Miocene sediments cannot be substantiated. Subterraniphyllum, however, cannot be considered a useful stratigraphical marker until further data on its occurrence in well-dated carbonate sequences are acquired. This study illustrates the problems associated with placing fossil coralline algal specimens into geniculate genera without the preservation of relevant morphological characters. This is especially true in the absence of the careful assessment of fossil material with respect to current taxonomic concepts of geniculate coralline genera, all of which are based on studies of living species. According to the current concepts for geniculate coralline genera, the placing of fossil specimens into geniculate genera without appropriate evidence must be avoided by grouping all potentially geniculate fragments under the informal group 'Geniculate sensu lato'. Furthermore, for all those many fossil specimens where unequivocal evidence is not present, it is possible to utilize ‘form genera’ based on characters that are normally preserved. This leads to creating a consistent, workable system of applying names to most fossil corallines so that they can be reliably used in relation to stratigraphical and palaeoecological studies.

Elliott (1957) established Subterraniphyllum as a genus of geniculate coralline red algae (Corallinales, Rhodophyta) for specimens occurring mainly in Oligocene carbonate deposits in Iraq, Persia (Iran), Oman, and Sicily. Elliott (1957) provided a brief account of the only included and newly described species, S. thomasii (as thomasi), chose a specimen from Iran as holotype, provided nine photographic illustrations of his material, and assigned the genus to the subfamily Corallinoideae within the family Corallinaceae. Elliott (1957, pp. 73–74) also suggested that the species was useful as a biostratigraphical dating tool because it appeared to be restricted to Upper Eocene–Lower Miocene deposits.

Elliott (1957, p. 74) chose the specific epithet to honour A. N. Thomas, who (Thomas 1950, 1952) first noted the occurrence of the species in Asmari Limestone deposits in south-west Iran and who considered the alga to be stratigraphically useful.

Since 1957, Subterraniphyllum thomasii has been treated as a geniculate coralline red alga by most authors (but see Discussion), and it has been recorded from Oligocene deposits in Greece (Johnson 1965, p. 812), Borneo, Indonesia (Johnson 1966, p. 277), Italy (Mastrorilli 1968a, p. 1277; 1968b, p. 388), and Macedonia (Lemoine 1977, p. 34). S. thomasii has also been reported from the Upper Eocene and Oligocene of Crete (Bonneau 1970, p. 1124), from the Upper Eocene of Karpathos, Crete and Rhodes (Aubouin et al. 1976, p. 389), and from Madagascar (Lemoine 1977, p. 36, citing an unpublished thesis of Karche, 1972). An unidentified species of Subterraniphyllum has also been reported from the Oligocene and Lower Miocene of Sicily (Blondeau et al. 1972), and from the Oligocene of Cuba (Beckmann and Beckmann 1966, p. 30), but no further species have been described or formally transferred into the genus.
Subterraniphyllum is also the only genus which has been referred to the Corallinales (subfamily Corallinoideae) that appears to be confined to fossil occurrences (reported from the Upper Eocene, Oligocene and Lower Miocene deposits; there are no known living species. Later, Poignant (1979a, b, 1985) included in this list Metagoniolithon Weber-van Bosse, 1904 and Subterraniphyllum Elliott, 1957. *Archaeoamphipora nomen nudum; Late Devonian; Magathan (1985, p. 176).


<table>
<thead>
<tr>
<th>Genus</th>
<th>Stratigraphical distribution</th>
<th>References</th>
</tr>
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<tbody>
<tr>
<td>Amphiroa Lamouroux, 1812*</td>
<td>Upper Cretaceous-Recent</td>
<td>Beckmann and Beckmann (1966); Lemoine (1939); Conti (1950); Johnson (1961), Poignant (1977, 1979a)</td>
</tr>
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<td>Arthrocardia Decaisne emend. Areschoug, 1852</td>
<td>Upper Cretaceous-Recent</td>
<td>Raineri (1920); Conti (1950); Johnson (1961), Poignant (1977, 1979a)</td>
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<tr>
<td>Calliarthron Manza, 1937</td>
<td>Lower Miocene-Recent</td>
<td>Johnson (1961); Beckmann and Beckmann (1966)</td>
</tr>
<tr>
<td>Corallina Linnaeus, 1758</td>
<td>Upper Cretaceous-Recent</td>
<td>Pfender (1924); Conti (1950); Johnson (1961, 1964); Poignant (1977, 1979a)</td>
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<td>Jania Lamouroux, 1812</td>
<td>Upper Cretaceous-Recent</td>
<td>Lemoine (1927); Conti (1950); Johnson (1961); Poignant (1977, 1979a)</td>
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<tr>
<td>Metagoniolithon Weber-van Bosse, 1904</td>
<td>Upper Paleocene-Recent</td>
<td>Poignant (1977, 1979a, 1985)</td>
</tr>
<tr>
<td>Subterraniphyllum Elliott, 1957</td>
<td>Oligocene</td>
<td>Elliott (1957); Johnson (1965, 1966); Beckmann and Beckmann (1966); Mastrozilli (1968a, b); Poignant (1977, 1979a, 1985)</td>
</tr>
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</table>

Subterraniphyllum is also the only genus which has been referred to the Corallinales (subfamily Corallinoideae) that appears to be confined to fossil occurrences (reported from the Upper Eocene, Oligocene and Lower Miocene deposits; there are no known living species. By contrast, the other six genera of geniculate Corallinales reported from the fossil record (Table 1) occur in various deposits from the Cretaceous onwards, and all six are also represented by species in the Recent.

There are three major problems associated with the taxonomy and potential biostratigraphical value of Subterraniphyllum. Firstly, Elliott (1957) concluded that Subterraniphyllum was a geniculate coralline based on the occurrence of ‘incipient bifurcation’. Fully developed genicula were absent from his material,

EXPLANATION OF PLATE 1

Fig. 1. Subterraniphyllum thomasii Elliott, 1957; Elliott’s Collection; Department of Palaeontology at The Natural History Museum, London (UK); ×1. 1A, V34628; holotype and isotypes, Rupelian of Gach Saran, Persia (Iran). 1B, V34629; isotypes, Oligocene of Gach Saran, Persia (Iran). 1C, V34630; paratypes, Oligocene of Falaj, Oman. 1D, V34631; paratypes, Oligocene of Tawi Silaim, Oman.

Figs 2–3. Subterraniphyllum thomasii Elliott, 1957; holotype, sample V34628, Elliott’s Collection; Rupelian of Gach Saran, Persia (Iran). 2, medial longitudinal section of a branch together with Sphaerogypsina globula; ×40. 3, enlarged view of holotype showing the pseudoparenchymatous thallus with monomerous construction; note probable cell fusions (F) and the abrupt transition to much smaller cells near the periphery; ×90.
BASSI et al., Subterraniphyllum
and consequently, assignment of the genus to the subfamily Corallinoideae was presumptive. Moreover, Elliott did not see reproductive structures, especially conceptacles (which occur in all Corallinaceae), and thus placement of Subterraniphyllum in the family Corallinaceae was also presumptive. Secondly, the relationships of Subterraniphyllum to other Corallinales have not been examined in a modern context. Thirdly, the potential biostratigraphical value of Subterraniphyllum (see Elliott 1957, p. 73) has yet to be fully assessed.

These problems became apparent after specimens referable to Subterraniphyllum thomasii were recognised in Oligocene carbonate formations of northern Slovenia and northeastern Italy (Bassi and Nebelsick 1997; Nebelsick and Bassi 1999). The present study was initiated to address the above problems through a re-examination of the original collections upon which Subterraniphyllum was based and through detailed study of the newly collected material.

MATERIAL AND METHODS

Examinations were carried out on Elliott’s original material, currently housed in the Department of Palaeontology, The Natural History Museum (London), on thin sections of Ungaro (1978) coming from the Oligocene Calcareniti di Castelgomberto, outcropping at Lumignano (eastern Colli Berici, Veneto, north-eastern Italy); and on newly collected specimens from the Lower Oligocene Gornji Grad Beds, outcropping near Sv. Anton (Gornji Grad area, northern Slovenia; Bassi and Nebelsick 1997) (Text-fig. 1). In all cases, data were obtained from thin sections using light microscopy. Anatomical and morphological terms are those used by Woelkerling (1988), and Woelkerling et al. (1993). Ungaro’s collection (1978) is deposited at the Museo di Paleontologia of the Dipartimento di Scienze Geologiche e Paleontologiche, University of Ferrara (Italy); thin sections of Gornji Grad Limestones are deposited in the Institute and Museum of Geology and Palaeontology of the University of Tübingen (Germany).

RESULTS

The Elliott collections: typification

Elliott (1957) based the genus Subterraniphyllum and the species S. thomasii on specimens in thin sections on four microscope slides (Pl. 1, fig. 1) now housed in the Department of Palaeontology at The Natural History Museum, London. Two of the slides (V.34628, V.34629) are based on material from Gach Saran, Persia (Iran); the third slide (V.34630) is based on material from Falaj, Oman; and the fourth slide (V. 34631) is based on material from Tawi Silaim, Oman. The whereabouts of the rock samples from
which the thin sections were prepared is unknown. Elliott (1957) also referred material identified by Van Bellen (1956, pl. 2, figs b–c) as *Dendrophyllum cf. gurgurdanensis* from Iraq to *Subterraniphyllum thomasii* and mentioned further material from Sicily. The Van Bellen material has not been found, and there are no specimens in the Elliott collections to substantiate the record from Sicily, although Elliott (1957, p. 74) acknowledged obtaining information from F. E. Eames on the occurrences of the alga.

Elliott (1957, p. 74, pl. 13, fig. 5) designated one of the specimens on slide V.34628 as a holotype and considered certain other specimens (namely those on his pl. 13, figs 2–4, 9) from slides V.34628 and V.34629 to be paratypes. While Elliott’s selection of a holotype is in accord with the International Code of Botanical Nomenclature (ICBN) (Greuter 1994), his designation of paratypes is not. All material on slides V.34628 and V.34629 constitutes part of the same gathering (even though two different slide numbers were used), and thus in accord with ICBN Art. 9.3, all specimens on these two slides (other than the designated holotype) are isotypes (i.e. duplicates of the holotype) rather than paratypes. On the other hand, the specimens on slides V.34630 and V.34631 from Oman constitute true paratypes in the context of ICBN Art. 9.5, where paratype is defined as a specimen cited in the protologue (i.e. the original account) that is neither the holotype nor an isotype. The Van Bellen (1956, pl. 2, figs b–c) specimens from Iraq cited by Elliott (1957, pp. 73–74) also qualify as paratypes, but the status of any material from Sicily is uncertain because Elliott (1957) neither mentioned particular specimens nor published illustrations, and vouchers have not been found.

The protologue (Elliott 1957, p. 74) cites both Well no. 10 (under the holotype) and Well no. 6 (in the legend for figs 1–9) as the source of V.34628. The slide (i.e. V.34628) containing the holotype (i.e. Elliott 1957, pl. 13, fig. 5) is labelled as coming from Gach Saran Well no. 6; consequently it is assumed that the citation of Well no. 10 in the protologue is an error. Neither Elliott (1957) nor Thomas (1950, 1952) provided information on Well numbers for the Gach Saran area.

Matters relating to typification may be summarised as follows:

**Genus Subterraniphyllum Elliott, 1957**

*Type species.* *Subterraniphyllum thomasii* Elliott 1957, p. 73. According to the ICBN [Recommendation 60C.1(b)], a second ‘*i*’ is added in the specific epithet as a ‘stem augmentation’.

*Holotype.* Elliott 1957, pl. 13, fig. 5 (on slide V.34628), from Well no. 6, Gach Saran, Persia (Iran). Department of Palaeontology, The Natural History Museum (NHM), London.

*Isotypes.* Specimens on slides NHM V.34628 and NHM V.34629 other than the holotype.

*Paratypes.* Specimens on slides NHM V.34630 (from Falaij, Oman) and NHM V.34631 (from Tawi Silaim, Oman); specimens illustrated by Van Bellen (1956, pl. 2, figs b–c) (repository of specimens uncertain).

*Age of holotype and isotypes.* Rupelian (Early Oligocene), in Asmari Limestone (south-west Iran) (Thomas 1952; Elliott 1957).

The Department of Palaeontology, The Natural History Museum, contains two additional slides (NHM V.56325, NHM V.56326) with material identified by Elliott as *Subterraniphyllum thomasii*. These slides, like NHM V.34631, are based on samples from Tawi Silaim, Oman. They are not mentioned in the protologue (and thus do not qualify as types) and were presented to the Museum by Elliott in 1971.

**The Elliott collections: morphology and anatomy**

The thin sections (V.34628–V.34631) comprising the original material contain fragments of *Subterraniphyllum thomasii* in more or less median longitudinal view, tangential longitudinal view, transverse view, and oblique view. The holotype (Pl. 1, figs 2–3), which looks to be a more or less median longitudinal section, is 1·4 mm long and 0·55 mm in diameter. Other longitudinal fragments vary from
0·72–1·48 mm in length and 0·31–0·55 mm in diameter (number of measurements, 12), while transverse sections measure 0·31–0·78 mm in diameter (number of measurements, 14). No unequivocal branch apices were seen.

At least one fragment in V.34628 (Pl. 2, fig. 1) and in V.34631 (Pl. 2, fig. 2) show obvious points of branching, but in both cases, very little thallus is evident below the point of branching. The onset of another possible point of branching occurs in a fragment in V.34629 (Pl. 2, fig. 3). These fragments show a uniform internal structure with no changes in anatomy or cell arrangement at the points of branching. This means that branch formation in *S. thomasii* does not involve genicula, because genicula always occur at points of branching and genicula always have an anatomy that is different from adjacent parts of a branch (Text-fig. 2; see also Woelkerling 1988, p. 60, figs 43–45, and Bassi 1998, p. 51, pl. 11, fig. 1 for examples).

In longitudinal view (Pl. 1, fig. 3; Pl. 2, figs 2–3), *Subterraniphyllum* fragments appear pseudoparenchymatous with a monomerous construction. In monomerous construction (see Woelkerling 1988, pp. 7–9, fig. 16), there is a single system of filaments in which some contribute to a core that runs more or less parallel to the surface of the thallus and others curve outwards and contribute collectively to a more peripheral region. The relative proportions of filaments in the core and peripheral regions can vary substantially.

In *Subterraniphyllum*, the core region (commonly referred to as the medulla in the older literature; see Woelkerling 1988, p. 17 for a discussion of this term) comprises most of the thallus, and individual core filaments can be traced for a number of cells. Cells are elongate (most commonly 2–3 times longer than broad), and the cells of adjacent filaments are arranged more or less in tiers (i.e. coaxially). Sometimes the tiers appear arched (Pl. 2, fig. 2), but more commonly they are planar except near the periphery, where slight arching can occur (Pl. 1, fig. 3; Pl. 2, fig. 3). Cells in the core region were mostly 90–100 μm long and 30–40 μm in diameter as seen in longitudinal view. Thallus construction similar to that found in *Subterraniphyllum* occurs in some living corallines, including some species of *Mesophyllum* and *Synarthrophyton* (see Woelkerling and Harvey 1993; and Keats and Chamberlain 1994, 1997; Harvey *et al.* 1994; and Keats and Maneveldt 1997a for examples). It also occurs in some fossil species of *Mesophyllum* and *Neogoniolithon* (e.g. Bassi 1998, p. 35, pl. 3, fig. 3; p. 41, pl. 6, fig. 6). Near the periphery, there is an abrupt transition to much smaller cells (Pl. 1, fig. 3; Pl. 3, fig. 2), mostly 10–15 μm long and 10–15 μm in diameter as seen in longitudinal view. This kind of abrupt transition also occurs in some fossil corallines (e.g. Bassi 1998) and in some living corallines, including *Synarthrophyton munimentum* Keats and Maneveldt (Keats and Maneveldt 1997a, p. 460, fig. 32), *S. patena* (Hooker and Harvey, in Harvey 1849) Townsend (May and Woelkerling 1988, p. 59, figs 24–25; Harvey *et al.* 1994, p. 334, figs 9–10), *S. schielianum* Woelkerling and Foster (Woelkerling and Foster 1989, pp. 46–47, figs 12, 15–17), *Mesophyllum lichenoides* (Ellis) Lemoine (Woelkerling and Irvine 1986, p. 386, fig. 16), and *M. incisum* (Foslie) Adey (Woelkerling and Harvey 1992, p. 387, figs 10–11; Keats and Maneveldt 1997b, p. 204, figs 9, 11).

In transverse view (Pl. 3, fig. 2), the thallus appears more or less circular in outline, suggesting that the branches are more or less cylindrical. A comparatively narrow peripheral region composed of small cells surrounds the large central core, where cells are much larger in sectional view. This reflects the structure as seen in longitudinal view and is consistent with the structure seen in some living corallines (see references above).

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**EXPLANATION OF PLATE 2**

Figs 1–4. *Subterraniphyllum thomasii* Elliott, 1957; Elliott’s Collection. 1, isotype, V34628; oblique longitudinal section showing a point of branching; ×40. 2, paratype, V34631; longitudinal section at a point of branching; note arched tiers of cells; ×90. 3, isotype, V34629; longitudinal view with slightly arched cells which are connected to one another by cell fusions (F); note possible onset of branching (arrows); arrowheads denote cell fusions in surface view; ×90. 4, isotype, V34629; sublongitudinal section showing possible epithallial cells (arrows); ×230.
BASSI et al., Subterraniiphyllum
Cells resembling epithallial cells occur in several fragments (Pl. 2, fig. 4) but are not well preserved. Outer walls look rounded rather than flattened and flared; the former are characteristic of most genera of living corallines while the latter are characteristic of living species of *Lithothamnion* (e.g. see Woelkerling 1988, p. 176, fig. 192), *Sporolithon* (e.g. see Woelkerling 1988, p. 206, fig. 246), and *Exilicrusta* (Chamberlain 1992, pp. 185–190, figs 7, 12).

Fusions between cells of adjacent filaments occur (Pl. 2, fig. 3; Pl. 3, figs 1–2), but apparently in small numbers, and in some fragments no cell fusions are obvious. Fusions involve the breakdown of part of the common walls between two cells (Pl. 3, figs 1–2), and when viewed from above (Pl. 2, fig. 3, arrowheads), fusions may look like small circular holes in the cell wall. The pattern of cell fusions found in *Subterraniphyllum thomasii* also occurs in various species of *Synarthrophyton* [e.g. *S. magellanicum* (Foslie) Keats and Chamberlain: see Keats and Chamberlain 1997, p. 65, figs 32–33; *S. patena*: see May and Woelkerling 1988, p. 60, figs 27–28; Woelkerling 1988, p. 212, fig. 256; Harvey *et al.* 1994, p. 335, figs 9–11; *S. schielianum*: see Woelkerling and Foster 1989, p. 46, figs 12, 14]. Primary pit-connections were not evident in Elliott’s material of *Subterraniphyllum*, probably owing to lack of preservation. Secondary pit-connections similarly were not evident, and no trichocytes or reproductive structures were found.

The new material

*Calcareniti di Castelgomberto*. This formation crops out along the eastern margin of the Colli Berici (Vicenza, north-eastern Italy; Text-fig. 1) by showing steep morphological slopes with several karst-caves. It overlies the Marne di Priabona (Priabonian, Late Eocene; Ungaro 1969) and is overlain by a red clay horizon followed by siliceous sands and sandstones (Ungaro 1978; ‘Arenarie di S. Urbano’, Early Miocene, in Mietto 1988). The *Calcareniti di Castelgomberto* (Bosellini 1967), characterized by massive or irregularly bedded limestones and marly limestones, range in the Colli Berici from about 80–200 m in thickness. The fossil content is mainly represented by corals, miliolids and coralline red algae. Nummulitids, soritids, molluscs, and echinoids are also present (Geister and Ungaro 1977; Ungaro 1978; Frost 1981). The Eocene-Oligocene boundary in the Colli Berici has been recognized in correspondence to the disappearance of the orthophragminids. The base of the Oligocene is characterized by the occurrence of benthic foraminifera such as *Pararotalia lithothamnica*, *Asterigerina rotula haeringensis*, *Discorbis discoideas*, and *D. kiliani*. This formation has been referred to the Early–Middle Oligocene by the occurrence of the foraminifera *Nummulites fichteli*, *N. vascus*, *Praerhapidionina delicata*, *Spirolina cylindracea*, *Peneroplis glynnjonesi*, and *Asterigerina rotula haeringensis* (Ungaro 1978, pp. 245–246).

*Subterraniphyllum thomasii* occurred in sample nos. 74/10-11 (Pl. 3, fig. 3) belonging to the Lumignano section (Ungaro 1978, fig. 5; Text-fig. 1). More or less transverse and oblique sections were present and were largely concordant with fragments in the original Elliott collections. Cells in the core region measured 60–70 µm long and 40–55 µm in diameter in the oblique sections; these are consistent with what occurs in the type material, although measurements on obliquely oriented cells are somewhat distorted relative to those in longitudinal view. Reproductive structures did not occur.

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**EXPLANATION OF PLATE 3**

Figs 1–2. *Subterraniphyllum thomasii* Elliott, 1957; Elliott’s Collection. 1, isotype, V34628; oblique section, with cell fusions involving breakdown of part of the common walls between two cells (arrows); ×90. 2, isotype, V34630; transverse section showing the cell fusions (F); ×90.

Fig. 3. *Subterraniphyllum thomasii* Elliott, 1957; Ungaro’s Collection (1978), Calcareniti di Castelgomberto, Oligocene of Lumignano, Colli Berici, north-eastern Italy; sample 74/10; oblique transverse section; ×90.

Figs 4–5. *Subterraniphyllum thomasii* Elliott, 1957; Gornji Grad Beds, Oligocene of Sv. Anton, Gornji Grad area, northern Slovenia; sample SLO94-044, 4, longitudinal section showing the peripheral cells; ×90. 5, oblique section at a branching point; note the uniform anatomy across the branching point; ×90.
PLATE 3

BASSI et al., Subterraniophyllum
Gornji Grad Beds. The Gornji Grad area (northern Slovenia; Text-fig. 1) represents an important transition zone between the northernmost extension of the Mediterranean Tethys to the south and the developing Paratethys to the north and east. Although the rich fossil content and facies variations of the Gornji Grad Beds are historically well documented (Reuss 1851, 1864; Morlot 1853; Rolle 1857; Stur 1871; Waters 1874; Teller 1885, 1896, 1898), there have been few detailed modern examinations of its fauna, flora as well as microfacies (Hemleben 1964; Barta-Calmus 1973; Drobné et al. 1985; Bricl and Pavcic 1992). The Gornji Grad Beds (formally known as the ‘Oberburger Schichten’, Auctorum) form part of a highly varied transgressive sequence over a Triassic basement. This includes a basal series of terrigenous sediments and conglomerates followed by the Gornji Grad Beds, overlain by marls rich in foraminifera which are capped by thick series of volcanoclastic tuffs. The Gornji Grad Beds themselves consist of both siliciclastics and carbonates of marine origin and transgress above Triassic and Eocene limestones; the basal terrigenous sediments (see above) or conglomerates are of indeterminate age (possibly Eocene). The stratigraphical framework of Gornji Grad is given by Drobné et al. (1985, p. 82) who recognised Nummulites fichteli and N. germanicus as indicating an early Oligocene age. Furthermore, nannoplankton occurring in the marly beds collected just above ‘the reef structures’ (Auctorum; upper part of the Gornji Grad Beds) indicate the NP 23 zone (upper Lower Oligocene; Bricl and Pavcic 1992).

The carbonates consist predominantly of poorly sorted, biogenic rudstones with a wackestone matrix; pack- and grainstones are subordinate. The principal components are represented by coralline red algae together with a moderately diverse coral fauna including both solitary and colonial forms. Large and small benthic foraminifera as well as calcitic shelled bivalves are also common. Subordinate are gastropods, bryozoans, brachiopods, echinoderms, serpulids and green (dasycladacean and halimedacean) algae. Subterraniphyllum thomasii was found only in sample SLO94-044 from ‘Sv. Anton’ section (Text-fig. 1; Pl. 3, figs 4–5). Longitudinal, transverse and oblique fragments were present and were morphologically and anatomically concordant with fragments in the original Elliott collections except that in longitudinal view cells in the core region showed a somewhat greater range in length (65–95 μm) and were somewhat greater in diameter (45–65 μm). In living corallines, such variation in cell size is of no taxonomic consequence (e.g. Woelkerling and Campbell 1992; Woelkerling and Harvey 1993; Wilks and Woelkerling 1994); and Johnson (1966, p. 277) reported similar variation in specimens of Subterraniphyllum thomasii from Borneo, Indonesia. Reproductive structures did not occur.

DISCUSSION

The taxonomic placement of Subterraniphyllum

At least four suggestions on the taxonomic placement of Subterraniphyllum have appeared. Elliott (1957) and most subsequent authors (e.g. Johnson 1965, 1966; Beckmann and Beckmann 1966; Mastorilli 1968a, b) have regarded Subterraniphyllum to be a distinct genus of geniculate coralline red algae and to belong to the Corallinaceae, subfamily Corallinoideae (sensu Lemoine 1939 and Mason 1953). Poignant (1985) similarly considered Subterraniphyllum to have genicula (‘thalles articulés’) but did not indicate family or subfamily placement in his key. Lemoine (1977, pp. 34, 36), by contrast, suggested that the structure of Subterraniphyllum did not resemble that of other genera of Corallinaceae but rather seemed closer to the genera of the red algal order Rhodymeniales. Lemoine, however, did not formally assign Subterraniphyllum to the Rhodymeniales. Thomas (1952, p. 78) thought that it resembled Lithophyllum, while Van Bellen (1956) applied the name Dendrophyllum cf. gurgurdanensis Thomas MS without assigning it to a higher taxonomic group. None of the above suggestions is supported by the evidence obtained during the present study.

Our results show that genicula do not occur (i.e. that Subterraniphyllum is not ‘segmented’) because the fragments have a uniform anatomy across points of branching. If genicula were present, there would be an obvious, marked change in anatomy at points of branching (Text-fig. 2; Woelkerling 1988, p. 60, figs 43–45; Bassi 1998, p. 51, pl. 11, fig. 1). Thus, Subterraniphyllum cannot be a segmented (geniculate) coralline as presumed by Elliott (1957, p. 73) and most subsequent authors, and it does not belong to the Corallinaceae, subfamily Corallinoideae or any other group characterized by the presence of genicula.
Thomas’s (1952) suggestion is also untenable. The genus Lithophyllum, and the subfamily Lithophylloideae, to which Lithophyllum belongs, are characterized by the presence of secondary pit-connections and the absence of fusions between cells of adjacent filaments (Woelkerling and Campbell 1992; Woelkerling 1996). Our results show that cells of adjacent filaments of Subterraniphyllum are interconnected by cell fusions, thus ruling out placement in Lithophyllum or the Lithophylloideae. Neither primary nor secondary pit-connections were seen during the present study.

Lemoine (1977) did not provide explicit evidence to support her suggestion that Subterraniphyllum seemed close to the genera of the Rhodymeniales. Anatomically, there is some superficial resemblance between Subterraniphyllum and certain species of Gastroclonium (Champiaceae, Rhodymeniales) [e.g. G. clavatum (Roth) Ardissone, in Bliding 1928, p. 39, fig. 30, as Chylocladia clavata (Roth) Bliding; G. ovatum (Hudson) Papenfuss, in Bliding 1928, p. 24, fig. 15, as Chylocladia ovalis (Husdon) Greville], but in Gastroclonium and other Rhodymeniales, cells of adjacent filaments are linked by secondary pit-connections whereas in Subterraniphyllum cells of adjacent filaments are linked by cell fusions. Thus close affinities with the Rhodymeniales, none of which have cell fusions, seem unlikely.

Van Bellen’s (1956, p. 250) treatment (assigning the fossil to ‘Dendrophyllum cf. gurgurdanensis Thomas MS’) can be dismissed from a botanical taxonomic point of view because the names Dendrophyllum and D. gurgurdanensis appear to be nomina nuda (i.e. names without descriptions or diagnoses). All efforts to find a validly published description or diagnosis have failed, and it is uncertain whether these names originated with Van Bellen, or in unpublished documentation of Thomas to which Van Bellen had access, or from some other source. Names without descriptions or diagnoses have no standing in the context of the International Code of Botanical Nomenclature (Greuter 1994) because they have not been validly published (ICBN, Art. 32.1, 38.1). Moreover, in not indicating any taxonomic affinities for the fossil, Van Bellen (1956) failed to establish a framework upon which any further taxonomic evaluations could be based.

What, then, are the probable taxonomic affinities of Subterraniphyllum? Mastrorilli (1968a, p. 1279,
pl. 102, figs 1–2), who placed the genus in the Corallinaceae, subfamily Corallinoideae, reported a cavity resembling a uniporate conceptacle at the surface of a transverse section of Subterraniphyllum. Poignant (1985) also considered that Subterraniphyllum had uniporate conceptacles, presumably on the basis of the record of Mastrorilli. Unfortunately, it is not clear from the figures of Mastrorilli (1968a) whether the possible uniporate conceptacle was actually produced by Subterraniphyllum or whether instead it belongs to an epiphyte on the surface of Subterraniphyllum. Until unequivocal, independent evidence of conceptacles is found for Subterraniphyllum, this single report needs to be treated with caution.

The absence of reproductive structures in type material of Subterraniphyllum and the uncertainty attending the report of Mastrorilli (1968a) mean that at present we cannot state unequivocally that Subterraniphyllum possesses conceptacles. On vegetative grounds, however, there is nothing to exclude Subterraniphyllum from the Corallinales, and, as noted above, the vegetative anatomy of Subterraniphyllum is similar to that of some other Corallinales, the view of Lemoine (1977) notwithstanding. We suggest, therefore, that Subterraniphyllum be retained in the Corallinales as a genus of uncertain position.

Using the Corallinales classification system employed by Woelkerling (in Womersley 1996) (Table 2) as a framework, the possible affinities of Subterraniphyllum can be somewhat more fully determined. The absence of genicula precludes possible affinities with the subfamilies Amphiroideae, Corallinoideae and Metagoniolithoideae in the family Corallinaceae. All species in these subfamilies possess genicula. The presence in Subterraniphyllum of fusions between cells of adjacent filaments precludes affinities with the Corallinaceae, subfamilies Lithophylloideae, Choreonematoideae and Austrolithoideae, all of which apparently lack cell fusions.

There is no firm evidence at present that would exclude Subterraniphyllum from the Sporolithaceae, or from the Corallinaceae, subfamily Mastophoroideae, or from the Corallinaceae, subfamily Melobesioideae. The possible but poorly preserved epithallial cells observed during the present study appear not to have the flattened and flared cells characteristic of species of Sporolithaceae and of the genera Exilicrusta and Lithothamnion in the subfamily Melobesioideae, but better preserved epithallial cells must be found before any firm conclusions can be reached.

In terms of vegetative anatomy, Subterraniphyllum most closely resembles some living species of Mesophyllum and Synarthrophyton (see references cited above), although species of Mesophyllum and Synarthrophyton generally produce flattened branches rather than cylindrical branches. Amongst living species of corallines, however, differences in cross-sectional shape of branches is not considered to be taxonomically significant at generic level. Both Mesophyllum and Synarthrophyton belong to the Corallinaceae, subfamily Melobesioideae. All Melobesioideae produce tetrasporangia in multiporate conceptacles but produce gametangia within uniporate conceptacles. Thus the report of a uniporate cavity by Mastrorilli (1968a) does not preclude the possibility that Subterraniphyllum belongs to the subfamily Melobesioideae. It is also possible, however, that Subterraniphyllum belongs to the subfamily Mastophoroideae, which is characterized by uniporate tetrasporangial conceptacles. The matter cannot be decided in the absence of further data on reproduction in Subterraniphyllum; consequently, Subterraniphyllum is best treated as a genus of uncertain position within the Corallinales.

The possible relationships of Subterraniphyllum to other fossil genera ascribed at some stage to the Corallinales (see Woelkerling 1988, pp. 44–48 for a listing) awaits further study, including reinvestigations of the original material on which these genera are based.

**Age and stratigraphical distribution of Subterraniphyllum**

Elliott (1957) suggested that Subterraniphyllum could be used as a biostratigraphical marker because it appeared to be restricted to Upper Eocene, Oligocene and Lower Miocene carbonate successions. The reported occurrences of this taxon in the Mediterranean and Paratethys are summarized in Table 3.

The first record is that of Thomas (1952), who found Subterraniphyllum (reported as ‘cf. Lithophyllum’, p. 78) at the bottom of the Asmari Limestones in the Gach Saran area. These beds are set between the Eocene–Oligocene marls with Haplophragmina slingeri Thomas below, and the Oligocene limestones with Praerapydionina delicata Henson above. Moreover, Thomas affirmed that the distinctive species ‘cf. Lithophyllum’ also occurs in the middle part of the Khamir Limestone of Kuh-i-Khamir together with

<table>
<thead>
<tr>
<th>Family/Subfamily</th>
<th>Characters associated with genicula</th>
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<tbody>
<tr>
<td></td>
<td>Occurrence</td>
</tr>
<tr>
<td>Sporolithaceae</td>
<td>absent</td>
</tr>
<tr>
<td>Corallinaceae</td>
<td></td>
</tr>
<tr>
<td>Amphiroideae</td>
<td>absent</td>
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<tr>
<td></td>
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<tr>
<td>Austrolithoideae</td>
<td>absent</td>
</tr>
<tr>
<td>Choreonematoideae</td>
<td>absent</td>
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<tr>
<td>Corallinoideae</td>
<td></td>
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<tr>
<td>Lithophylloideae</td>
<td>absent</td>
</tr>
<tr>
<td>Mastophoroideae</td>
<td>absent</td>
</tr>
<tr>
<td>Melobesioideae</td>
<td>absent</td>
</tr>
<tr>
<td>Metagonio lithoideae</td>
<td>present</td>
</tr>
<tr>
<td>Reference</td>
<td>Locality</td>
</tr>
<tr>
<td>--------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Thomas 1952*</td>
<td>Iran</td>
</tr>
<tr>
<td>Van Bellen 1956**</td>
<td>Kirkuk, Iraq</td>
</tr>
<tr>
<td>Elliott 1957</td>
<td>Iran, Oman</td>
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<tr>
<td>Johnson 1965</td>
<td>Vrakhionia, Greece</td>
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<tr>
<td>Johnson 1966</td>
<td>Borneo</td>
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<tr>
<td>Mastrorilli 1968a,b</td>
<td>NE Ponzone, Piedmont, Italy</td>
</tr>
<tr>
<td>Bonneau 1970</td>
<td>Crete, Greece</td>
</tr>
<tr>
<td>Blondeau et al. 1972</td>
<td>Sicily, Italy</td>
</tr>
<tr>
<td>Aubouin et al. 1976</td>
<td>Karpathos, Greece</td>
</tr>
<tr>
<td>Lemoine 1977</td>
<td>Radovis, Skopje region, Macedonia</td>
</tr>
<tr>
<td>Barbin 1988</td>
<td>Priabona, Italy</td>
</tr>
</tbody>
</table>
Nummulites fichteli (p. 79). This latter is presently considered a marker for the Oligocene shallow benthic biozones 21–22B (Rupelian–Early Chattian; Cahuzac and Poignant 1997).

Afterwards, Elliott (1957) assigned these specimens to Subterraniphyllum thomasii, but did not provide any information on the biostratigraphical setting of the type level. The record of this taxon from the Aquitanian (Early Miocene) of Sicily and Iran reported by Elliott (1957) is not confirmed by any reference nor by successive records. In the Late Eocene–Oligocene of Crete and Karpatos (Greece), Bonneau (1970) and Aubouin et al. (1976) recorded Subterraniphyllum thomasii in flysch deposits, together with larger foraminifera such as nummulitids, orthophragminids, and amphisteginids. This stratigraphical assignment, however, cannot be verified because no species was reported. The stratigraphical setting of Subterraniphyllum ascribed to the Oligocene by Beckmann and Beckmann (1966), Blondeau et al. (1972), and Barbin (1988) seems to be confirmed by the occurrence of biostratigraphical markers such as Nummulites fichteli, Nummulites vascus, Halkyardia maxima, and Lepidocyclina (Eulepidina) undosa (see Butterlin 1981; Cahuzac and Poignant 1997). However, Blondeau et al. (1972) and Barbin (1988) did not illustrate the algal specimens. Other authors referred Subterraniphyllum to the Oligocene on the base of the coralline algal assemblages (Johnson 1965, 1966; Lemoine 1977) or on foraminifera without biostratigraphical meaning (Mastorilli 1968b).

The newly recorded specimens of Subterraniphyllum from northern Slovenia and north-eastern Italy described herein appear to originate from Oligocene rocks. The comparison of the well-documented reports of Subterraniphyllum to biostratigraphically meaningful, large foraminiferal assemblages also suggests that its occurrence in Upper Eocene or Lower Miocene successions cannot be verified. Subterraniphyllum cannot, however, be considered as a useful stratigraphical marker until further data with respect to its occurrence in well-dated carbonate sequences are acquired.

CONCLUDING REMARKS

The taxonomy of living species of coralline red algae (Corallinales) has undergone a marked change since 1960 as a consequence of a number of major studies, many of which are cited in Johansen (1981), Woelkerling (1988), Irvine and Chamberlain (1994), Woelkerling (in Womersley 1996), and Woelkerling and Lamy (1998). The group is now treated as a separate order of Rhodophyta (Silva and Johansen 1986), and is considered to represent a major evolutionary line within the red algae (Bailey and Chapman 1996, p. 364). Concepts of families, subfamilies, genera, and species have changed as a result of extensive new information which has shown that many characters relating to vegetative morphology and anatomy once used to separate taxa vary too much to be taxonomically reliable. New genera have been described, and some genera commonly used in the older literature have been relegated to synonymy. While there still is no consensus on which of several current proposals (e.g. see Cabioch 1972, 1988; Woelkerling, in Womersley 1996; Desikachary et al. 1998; Bailey 1999; older schemes listed by Woelkerling 1988, pp. 54–55) for the classification of Corallinales at family, subfamily and tribe levels best reflects the phylogeny of the group, taxonomic concepts for many species and genera are far different now from what they were in 1960.

These developments have significant implications for the taxonomy of fossil coralline red algae. Many species and genera known only from the fossil record are based on characters that are now known to be of no taxonomic value for delimiting living corallines, and thus by implication are of questionable value for delimiting fossil taxa. This problem has been recognised by a number of people working on fossil corallines (e.g. see Bosence 1991, pp. 103–108; Braga et al. 1993; Iryu and Matsuda 1994, p. 444; Bassi 1995, p. 82; Basso 1995a, p. 576; Braga and Aguirre 1995; Rasser and Piller 1999). There is also an increasing realization (see references above) that most fossil species and genera considered to be coralline red algae require taxonomic reassessment in the context of current knowledge of living corallines, and that re-examination of type collections and/or of material from type localities forms an essential part of the reassessment process, as exemplified by Aguirre and Braga (1998).

Our exclusion of Subterraniphyllum from any group of Corallinaceae with genicula is based on unequivocal evidence that branch formation does not involve the occurrence of genicula. By contrast, the inclusion of most fossil species in various geniculate genera of Corallinales (Table 1) by most authors is
based on the supposition that genicula occur (both at points of branching and within branches), even though they have not been observed. In reality, genicula are unknown for most fossil species placed in geniculate coralline genera, and indeed, genicula, as noted by Lemoine (1939), Johnson (1961), Bosence (1991) and Bassi (1998), are seldom preserved in fossil material.

In the absence of genicula, the placement of most fossil species into geniculate genera has been based mainly on vegetative features observable in fragments presumed to be segments of geniculate branches. This is evident, for example, in keys to genera published by Lemoine (1970) and Poignant (1985) and in many accounts of species placed in geniculate genera (e.g. see Ishijima 1954, pp. 53–75; Johnson 1964, pp. 30–36; Mastrorilli 1968b, pp. 380–388; Lemoine 1970, pp. 192–193). Such placements of fossil species in geniculate genera must be treated with caution, especially in the absence of further assessments of these fossils in relation to current concepts for geniculate coralline genera (e.g. see Johansen 1976; Womersley and Johansen 1996a–c), all of which are based on studies of living species. Bassi (1998, p. 21), recognising the difficulties of placing specimens into geniculate genera without appropriate evidence, chose instead to group all potentially geniculate fragments under the informal group ‘Geniculates sensu lato’. This approach merits further application as it avoids the continued speculative use of names for fossil material.

The absence of critical characters does not mean that identification is impossible, however, as sometimes partial or even full identification can be made from vegetative features that are preserved. For all those many fossil specimens where unequivocal evidence is not present, it is possible to recognise that the specimens cannot be placed with certainty, and to utilise ‘form genera’ to accommodate these specimens based on the characters which are normally preserved. This effort leads to a much better understanding of fossil corallines in terms of which ones can or cannot be unequivocally associated with particular geniculate genera while at the same time creating a consistent, workable system of applying names to most fossil corallines so that they can be reliably used in relation to stratigraphical and palaeoecological studies.

Coralline red algae are more extensively represented in the fossil record than any other group of Rhodophyta, and as a consequence, it is theoretically possible to understand more about the geological and evolutionary history of this group than of any other group of red algae. The extent to which information in the fossil record can contribute to our overall understanding of the Corallinales is dependent on continued interactions between those who work on living corallines and those who work on fossil corallines, and upon striving to interpret the taxonomy of this group using the same classification system for both living and fossil taxa. As taxonomic knowledge of living and fossil taxa improves, it will also be possible to assess more accurately, and place greater confidence in, the stratigraphical value of particular fossil corallines.

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REFERENCES


CHAMBERLAIN, Y. M. 1992. Observations on two melobesioïd crustose coralline red algal species from the British Isles:


— — 1997. The non-geniculate coralline algae Synarthrophyton eckloniae (Foslie) comb. nov. and S. magellanicum (Foslie) comb. nov. (Rhodophyta) in South Africa including a comparison with relevant types. European Journal of Phycology, 32, 55–79.


—— and FOSTER, M. S. 1989. A systematic and ecographic account of Synarthrophyton schielianum sp. nov. (Corallinaceae, Rhodophyta) from the Chatham Islands. Phycologia, 28, 39–60.


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