Exceptionally well-preserved *Permocalculus* cf. *tenellus* (Pia) (Gymnocodiaceae) from Upper Permian Khuff Formation limestones, Saudi Arabia

G. W. Hughes1,2

1 Applied Microfacies Limited, Tan Y Gaer, Llanbedr DC, LL15 1UT, UK
2 The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Correspondence: hughesmicropal@gmail.com

Abstract: An exceptionally well-preserved specimen of the articulated rhodophyte *Permocalculus*, compared with *P. tenellus sensu* Elliott, 1955, is described from fine-grained Upper Permian limestones of the Khuff Formation of Saudi Arabia. Longitudinal medullary and sheaf-like cortical filaments extend through the uniserial series of elongate-globular, concave- and convex-terminating, interlocking segments for which they are interpreted to have functioned in articulation. The filaments tend to splay and branch laterally into the cortex where they terminate at the pores. At the terminal aperture, the filaments extend as bifurcating and possibly trifurcating branches and may serve as the origin of a new segment. Numerous elongate-globular branches, up to five in each row and intimately involved with the filaments, are developed in the outer medulla and are considered to represent reproductive sporangia. The specimen is considered to have occupied predominantly low-energy, normal to slightly elevated salinity, shallow conditions within the subtidal regime of a lagoon.

Keywords: *Permocalculus*, sporangia, Upper Permian, Khuff Formation, Saudi Arabia, shallow marine, palaeoecology

Received 2 February 2016; revised 13 June 2016; accepted 27 July 2016

During quantitative analysis of thin sections prepared from core plugs taken from carbonate cores of the Khuff C Reservoir of the Khuff Formation, Saudi Arabia, an exceptionally well-preserved specimen of a calcareous alga, 10.5 mm in length, was observed in an otherwise abiotic mudstone (Fig. 1). Unlike most calcareous algal microfossils where only the skeletal parts of the thallus are either preserved as calcite or as moulds after aragonite dissolution, this specimen displayed exceptionally well-preserved features of the complex internal structure (Figs 2–4). These microstructures are preserved as organic linings and infills. The specimen displays internal bundles of filaments and oval bodies that are interpreted to represent the reproductive organs, termed sporangia. Their presence within the thallus significantly supports assignment to the Gymnocodiaceae, unlike the external reproductive structures of the Dasycladaceae. When microphotographs of the specimen were displayed at the 8th International Symposium on Fossil Algae, Granada, Spain, in 2003, the calcareous algal experts were keen for the specimen to be published as it displayed features never previously preserved with such detail. One low-power photomicrograph was illustrated in a review of Permian to Cretaceous calcareous algae of Saudi Arabia (Hughes 2005a, pl. 1, fig. 9). The sample containing the specimen was collected from an approximate depth of 12 500 ft (3810 m) in a producing hydrocarbon field of eastern Saudi Arabia by Saudi Aramco, as part of a gas field development programme in the Khuff Reservoir.

Micropalaeontological analysis is confined to thin-section studies because the Khuff carbonates are too well-cemented to permit disaggregation and microfossil extraction. Microfossils are of variable abundance and diversity, and include benthonic foraminifera, calcareous algae, ostracods, brachiopod and small mollusc fragments. Other microorganisms, of questionable affinity, include *Aevolsaccus* Elliott, 1958,* Tubiphytes* Maslov, 1956 and *Pseudovermiporella* Elliott, 1958. The figured material, thin-section and original rock samples, are housed in the Core Laboratory of Saudi Aramco, Dhahran, Saudi Arabia.

Geological background

The Khuff Formation (Steinke & Brankamp 1952; Steineke et al. 1958; Powers 1968; Insalaco et al. 2006; Hughes 2008; Maurier et al. 2009) represents the product of one major, but complex, marine depositional cycle that transgressed over the Arabian Platform during the Capitanian/Midian Stage of the middle Permian (Vaslet et al. 2005). Predominantly shallow carbonate deposition, with interbedded siliciclastics and evaporites, continued until the Scythian/Induan Stage of the Early Triassic and the formation contains microfossil and isotopic evidence for the Permo-Triassic extinction. Four members have been mapped in the outcrop (Le Nindre et al. 1990) and include, in ascending stratigraphical order, the Huqayl, Duhaysan, Midhnab and Khartam. In the subsurface of Saudi Arabia, a reservoir classification scheme has been established that consists of the Khuff D, C, B and A units based on four major repeated carbonate evaporite cycles, of which the evaporite forms the seal for the underlying carbonate reservoir (Hughes 2008) (Table 1). The calcareous alga here discussed was collected from the Khuff C carbonate, equivalent to the Duhaysan and Midhnab members (Vaslet et al. 2005) according to Gaillot & Vachard (2007, Fig. 4) and dated as the Wuchiapingian Stage of the Upper Permian.

Biostratigraphy of the Khuff Formation

Micropalaeontological analysis of field samples and published data from water well SHD-1 (Le Nindre et al. 1990), reappraised by Vachard et al. (2005) and Gaillot & Vachard (2007), have provided comprehensive records of calcareous algae and foraminifera that have been used to date the four members of the Khuff Formation, as recognized in the outcrop belt. Conodont evidence, unfortunately from reworked beds in the lower Midhnab, provides a late Capitanian age, while preliminary Sr isotope determinations suggest a late Capitanian to early Wuchiapingian age (Nicora et al. 2006). The presence of the nautiloid *Titronautalus* gr.
hoernesi Stache from the lower Midhnab (Chirat et al. 2006) supports the Late Permian, Changhsingian, age. The upper Khartam Member is of Triassic (?Induan) age, on the basis of the absence of typical Permian benthonic foraminifera and the presence of Spiorbis phlyctaena Brönniman & Zaninetti and Polarisella hoae (Trifonova). Subsurface micropaleontology has revealed the presence of the Permian–Triassic boundary within carbonates of the B member (Hughes 2005b). Carbon isotope (δ13Ccarb) analysis in Oman (Krystyn et al. 2003) displays a strong negative shift from 4 to 0.4‰ across the Permian–Triassic boundary. Similar shifts have been noted in the Saudi Arabian Khuff, in the lower part of the Khuff B reservoir (Al-Jallal 1995). Plant and palynological biostratigraphy of the Khuff is described by Lemoigne (1981a, b) and Stephenson et al. (2003).

Calcareous algae of the Khuff Formation


Permian calcareous algae of Saudi Arabia are described by Rezak (1959), Manivit et al. (1983), Hughes (2005a, b, 2008), Vaslet et al. (2005), Insalaco et al. (2006), Vachard et al. (2001, 2003, 2005) and Gaillot & Vachard (2007). Calcareous algal diversity in the Upper Permian Khuff carbonates of Saudi Arabia is very low when compared to benthonic foraminifera, and mostly include Permocalculus Elliott, 1955a and Gymnocodium Pia, 1920, belonging to the Family Gymnocodiaceae with Mizia Schubert, 1909 belonging to the Dasyycladaceae. In his description of fossil algae of Iraq, Elliott (1955a) lists a number of Permian algae including Gymnocodium beleropontis, G. nodosum, Permocalculus compressus, P. digitatus, P. forcepinus, P. fragilis, P. plamosus,
*P. solidus* and *P. tenellus*. The systematic assignment of erect calcareous ‘siphonous algae’ to the family of Gymnocodiaceae or Halimedaceae, however, is a matter of some controversy (Riding 1977; Hubmann & Fenninger 1997). As stated above, *Permocalculus* Elliott, 1955a was assigned to the red algae by Elliott (1955a, 1956a), but the suprageneric systematic position of *Permocalculus* to either the red algae (Gymnocodiaceae) or the green algae (Halimedaceae) has been discussed by several authors (Mu & Riding 1983; Roux & Deloffre 1990; Mu 1991; Bucur 1994; Radoičić 2004; Schlagintweit & Sanders 2007). Despite being included in the Phylum Rhodophyta by the Global Biodiversity Information Facility (http://www.gbif.org/species/101000978), there remains

---

**Fig. 3.** Oblique longitudinal thin-section photomicrographs of *Permocalculus* sp. from the Khuff C mudstone. Segments 5 and 4 show medullar filaments, sporangia and polar articulate filament concentrations. Segments 3 and 2 show well-developed sporangia and anastomosing proximal medullar filaments. Segment 6 shows bifurcating and trifurcating filaments emerging from distal aperture. Note the axial longitudinal section of segment 2, with the clearly visible apertural medullar filaments compared to the tangential longitudinal section of segment 5 in which the apertures are not visible.
uncertainty amongst palaeoalgologists whether to consider the genus *Permocalculus* as a calcareous green alga rather than a red alga, or to refer to it simply as a calcareous alga (Schlagintweit 2010). The specimen here described provides significant evidence to support assignment to the Family Gymnocodiacea, and to the genus *Permocalculus*.

**Permocalculus systematics**

The specimen here described displays remarkably and unusually well-preserved internal microstructures, especially of the internal filaments and organelles, that have survived biodegradation and other changes associated with diagenesis that are typical of the Khuff. To the author’s knowledge, no similarly well-preserved specimens have been previously photographed or documented. The presence of well-preserved internal reproductive organs in the studied specimen provides clear evidence for assignment to the Gymnocodiacea, following Mu (1991). Riding & Guo (1991, p. 457) conclude that ‘the most likely affinity of the Gymnocodiaceae is with the red algae’ following the initial interpretation of Pia (1937).

The specimen here described is assigned to the Family Gymnocodiacea, of which the candidate Permian genera are *Gymnocodium*, as defined by Pia (1920), and *Permocalculus*, as defined by Elliott (1955a). Differentiation of these genera was made by Elliott (1955a, p. 85), for which he described *Gymnocodium* as hollow calcareous segments, cylindrical, oval or cone-shaped, circular or oval in cross section, rarely bifurcating, the walls perforated by pores which radiate oblique-distally and widen markedly outward; the segment interior may be empty, or may show calcified traces of the plant-fibres that filled it in life, in the form of longitudinal-oblique streaks; sporangia ovoid, in terminal segments. Segments usually smaller than *Permocalculus*, and the perforations usually coarser.

Elliott (1955a, p. 85) defined *Permocalculus* as segments and units of variable form; spherical, ovoid or barrel-shaped segments, or elongate-irregular, finger-like or ‘waxing-and-waning’ units. Calcification varying from very thin to massive or solid; pores small and cortical. Sporangia cortical or medullary. Segments or units usually larger, and the pores finer, than those of *Gymnocodium*.

The studied specimen is, therefore, assigned to the genus *Permocalculus* Elliott, 1955a.

*Permocalculus* consists of a succession of uniserially arranged and articulated perforated calcareous segments. The segments are joined by organic fibres that extend out through a terminal aperture into the succeeding segment and are flexible enough to enable the segments to bend with the current. Within the segments, the central axial region is termed the medulla. From this central zone radiate successions of chambered tubes that are directed to the outer layer, or cortex. These form the reproductive organs termed sporangia, as described by Elliott (1961).

The specimen was first illustrated by Hughes (2005a, pl. 1, fig. 9) and consists of five and a half segments arranged uniserially in a slight curve without any indication of branching (Fig. 1) and with a maximum length of 10.5 mm. The segment profiles vary from squat-cylindrical to elongate cylindrical, and tend to resemble the ‘keg’
shape described for *Permocalculus tenellus* by Elliott (1955a). There is no indication of the ‘waxing and waning’ segment profile. The segments interlock with a distal convex part fitting into the proximal concave part of the succeeding chamber. In the following discussion, the specimen is considered to consist of six segments, and these are numbered consecutively from the oldest to the youngest. The rate of chamber enlargement is low, but this may be a function of the thin section probably cutting obliquely through the specimen (Table 3). These oblique longitudinal sections have provided insights into the three-dimensional arrangements of the internal organelles of the segments. The biometrics of this specimen closely resemble those of *P. tenellus*, but the pores are slightly wider.

Calcification of the red algae typically preserves the outer, cortical, region but the central, or medullary, region is typically poorly calcified and commonly filled with sediment or cement (Flügel 2004). In this specimen, the medullar region is unusually and exceptionally well-preserved owing to carbonization of organelles and filaments arranged along the medullary axis. The outer filaments tend to splay toward the cortex where they ramify and anastomose with each branch terminating at the peripheral cortical pores. These filaments extend along the entire length of each segment, but increase in density at the proximal and distal ends, where they are considered to be involved in articulation of the segments and must, therefore, extend from one segment to the next. Similar medullary filaments have been described from the Gymnocodiaceae by Elliott (1955a), The youngest segment, number 6, displays the free bifurcating, possibly trifurcating, ends, where they are considered to be involved in articulation of the segments. The filaments also develop into components extending from the proximal junction to the peripheral pores. The sporophytes seem to have formed as a necklace-like chain of chambers as the result of expansion or differentiation of a single filament/microtubule.

In summary, and based on the various oblique and near-axial longitudinal sections visible in Figures 1, 3 and 4, the central axis of each segment is considered to consist of medullar filaments. They extend from the aperture at the distal convex end of the previous segment into the aperture at the concave proximal end of the succeeding segment. At the distal aperture of the youngest segment, the filaments extend as branched tufts. These are considered to be essential in both the vascular system of the individual and also as the flexible connective organelle to enable articulation between the individual segments. The filaments also develop into components of the outer, or cortical, region where they bifurcate and terminate at the pores of the segment wall. Although not clearly visible in the specimens, it is highly likely that these filaments are hollow and should be termed microtubules.

Table 1. Khuff lithostratigraphy and reservoir classification scheme of the subsurface of Saudi Arabia

<table>
<thead>
<tr>
<th>Series</th>
<th>Stage</th>
<th>Formation</th>
<th>Member</th>
<th>Reservoir/Seal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower Triassic</td>
<td>Scythian/Induan</td>
<td>Khuff</td>
<td>Khattam</td>
<td>Khuff A evaporite</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Khuff B Evaporate</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Khuff C evaporite</td>
</tr>
<tr>
<td>Upper Permian</td>
<td>Changhsingian</td>
<td>Midhnab</td>
<td></td>
<td>Khuff B evaporite</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wuchiapian</td>
<td>Duhaysan</td>
<td>Khuff C evaporite</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Huquayl</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Diagnostic features of species of *Permocalculus* as defined by Elliott (1955a)

<table>
<thead>
<tr>
<th><em>Permocalculus</em> species</th>
<th>Segment shape</th>
<th>Segment length (mm)</th>
<th>Segment diameter (mm)</th>
<th>Segment wall thickness (mm)</th>
<th>Pore diameter (mm)</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>fragilis</strong></td>
<td>Spherical</td>
<td>1.38 – 2.86</td>
<td>0.13 – 0.26</td>
<td>0.010 – 0.020</td>
<td></td>
<td>Thick-walled; possibly basal part of <em>P. fragilis</em></td>
</tr>
<tr>
<td><strong>digitatus</strong></td>
<td>Finger-like, acuminoid-ovoid</td>
<td>2.08</td>
<td>1.05</td>
<td>0.13</td>
<td>0.020</td>
<td></td>
</tr>
<tr>
<td><strong>solidus</strong></td>
<td>Long, digital</td>
<td>0.91 – 2.86</td>
<td>0.020</td>
<td>Heavily calcified; earlier part of thallus solid</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>tenellus</strong></td>
<td>Keg-shaped</td>
<td>2.0</td>
<td>1.0</td>
<td>0.020 – 0.026</td>
<td>Thick, finely-porous walls; occasionally branching</td>
<td></td>
</tr>
<tr>
<td><strong>compressus</strong></td>
<td>8</td>
<td>2.5</td>
<td>0.05</td>
<td>0.026 – 0.030</td>
<td>Compressed cross-section</td>
<td></td>
</tr>
<tr>
<td><strong>forcepinus</strong></td>
<td>2.86</td>
<td>0.70 – 1.45</td>
<td>0.10</td>
<td>0.020 – 0.025</td>
<td>Distinctive form with open growing tip. Bulging variable diameters, ‘waxing and waning’, thinly calcified</td>
<td></td>
</tr>
<tr>
<td><strong>plumosus</strong></td>
<td>8</td>
<td>2.5</td>
<td>0.05</td>
<td>0.020 – 0.025</td>
<td>Thallus ‘waxing and waning’, thinly calcified</td>
<td></td>
</tr>
</tbody>
</table>

Such organs have been described from *Gymnocodium bellero-phantis* (Rothpletz), with a transverse diameter of 0.29 mm; they represent reproductive organs termed sporangia (Elliott 1955a, 1961). Similar organs have been described by Wray (1977) and from other *Permocalculus* species by Elliott (1961), the Lower Cretaceous *Permocalculus? halimaeformis* described by Bucur (1994, especially pl. 6) and the Upper Cretaceous *Permocalculus gosoviensis* Schlagintweit, 1991 by Schlagintweit (2010). Many of the sporangia in the studied specimen have been replaced by calcite and appear colourless, while others (Figs 3 and 4) have been preserved by carbon and are clearly visible.

Segment 4 of the *Permocalculus* specimen (Figs 3 and 4) shows many interesting aspects of the internal microstructure, in which one can see well-preserved ramifying filaments and microtubules extending from the proximal junction to the peripheral pores. The sporophytes seem to have formed as a necklace-like chain of chambers as the result of expansion or differentiation of a single filament/microtubule.
Within the outer part of the medulla and extending into the cortex, the filaments seem to develop swollen sections, up to five in series, representing the reproductive organs here considered to be the sporangia.

**Biofacies and palaeoenvironments**

A moderately shallow-marine palaeoenvironment for *Permocalculus* has been suggested for Upper Permian carbonates of southern Iran (Insalaco *et al.* 2006, fig. 42). They observed a clearly defined onshore-offshore transition of calcareous algae across a carbonate ramp from nearshore *Mizia* to *Permocalculus* to offshore *Gymnocodium*. A similar trend has been recorded by Lai *et al.* (2008), where they observe replacement of the robust forms *Macroporella, Permocalculus solidus* and phylloid algae by the more fragile *Gymnocodium bellerophontis*. This transition is considered to possibly represent hydraulic energy level decrease due to palaeobathymetric variation. This trend was not, however, observed in the Middle–Late Permian of Greece by Vachard *et al.* (2003) where *Permocalculus* and *Mizia* were considered lagoonal genera and *Gymnocodium* to be associated with high-energy shoreline facies.

The *Permocalculus*-bearing sample was collected from mudstones barren of other microfossils. It is considered to represent an episode of highstand progradation of lagoon muds over an ooid shoal flank that is interpreted as the maximum flooding zone of this depositional sequence, the top of which is c. 30 ft below the *Permocalculus* event. The prograding succession overlying the ooid grainstones commenced with lagoon sediments shoreward of the ooid bank, rapidly grading up-section from packstones through wackestones containing brachiopod fragments, ostracods, echinoid fragments and the foraminifera *Geinitzina postcarbonica* Spandel, *Hemigordius schumbergeri* (Howchin), *Protothecosarium rauerae Gerke, Glohiavalunia spp. and Nankiella simplex* (Chen). This microfossils is overlain by the *Permocalculus*-bearing mudstone, which is considered to have been deposited in a low-energy lagoon protected by the ooid grainstone shoal. Absence of other microfossils would tend to suggest adverse conditions, of which elevated salinity could be a factor. The presence of rare specimens of *Agathammina* and *Hemigordius* species of miliolid foraminifera in a sample 5 ft (1.52 m) below the *Permocalculus* sample would tend to support this sequence stratigraphic interpretation (Hughes 2005a, b, 2008). The exceptionally well-preserved organic micro-organisms in the specimen suggest that rapid burial by mud in anoxic conditions that inhibited bacterial degradation.

**Conclusions**

An exceptionally well-preserved specimen of a rhodophyte calcareous alga, identified as a species of *Permocalculus* that bears similarity to *P. tenellus*, has been recorded in a thin section from the Upper Permian Khuff C limestone of Saudi Arabia. Numerous organic filaments are clearly preserved within the calcareous acuminate cylindrical segments. A group of medullar filaments extend through the segment from the proximal to distal aperture from which they protrude from the youngest segment. They are considered to have both vascular and articular-supporting functions. Some medullar filaments extend in a sheaf-like fashion from the central or axial zone into the cortex where they terminate at the surficial pores. It is highly likely that these filaments are hollow and should be termed microtubules. Some of the lateral filaments seem to expand into a series of up to five bulbous structures that are considered to be the reproductive organs and termed sporangia. The preservation of such a delicate specimen is considered to represent deposition in a low-energy lagoon setting. Absence of associated microfossils suggests elevated salinity conditions, and the exceptionally well-preserved internal organic organelles suggest rapid burial in an anoxic setting.

**Acknowledgements and Funding**

The author thanks the Saudi Arabian Ministry of Petroleum and Mineral Resources and the Saudi Arabian Oil Company (Saudi Aramco) for granting permission to publish this paper. Thanks are also due to A. Henderson and Ali Al Ibrahim, of the Saudi Aramco Geological Technical Services Division, for their valuable critique of the first draft of this paper. Bruno Granier and John Marshall are thanked for their helpful reviews.

**Scientific editing by John Marshall**

**References**


