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Evidence for seagrass meadows and their response to paleoenvironmental changes in the early Eocene (Jafnayn Formation, Wadi Bani Khalid, N Oman)

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Abstract

The recognition and understanding of vegetated habitats in the fossil record are of crucial importance in order to investigate paleoecological responses and indirectly infer climate and sea-level changes. However, the low preservation potential of plants and macroalgae hampers a direct identification of these environments in the geological past. Here we present sedimentological and paleontological evidences as tool to identify the presence of different seagrass-vegetated environments in the shallow marine settings of the lower Eocene Jafnayn platform of Oman and their responses to paleoenvironmental changes. The studied lower Eocene deposits consist of well bedded, nodular packstones dominated by encrusting acervulinid and alveolinid foraminifera passing upward to an alternance of packstones with echinoids and quartz grains and grainstones rich in *Orbitolites*, smaller miliolid foraminifera and quartz grains. The presence of seagrass is inferred by the occurrence of encrusting acervulinids and soritid *Orbitolites*, as well as by their test morphologies together with further sedimentological criteria. The clear shift observed in the faunal assemblages and sedimentary features may be related to a major reorganization of the carbonates system passing from a carbonate platform to a ramp-like platform with increased terrigenous sedimentation. Heterotroph tubular acervulinids and oligotroph alveolinids of the carbonate platform were replaced upward by more heterotroph organisms such as large, discoidal *Orbitolites* and smaller miliolids, most likely due to enhanced nutrient levels which would have led to a change of phytal substrate, from cylindrical-leaf dominated grasses into flat-leafed ones.

Keywords: epiphytic foraminifera, seagrasses, paleoenvironment, early Eocene, Oman

1. Introduction

In the photic zone of tropical and temperate carbonate settings, seagrass meadows represent a very influencing environment, playing an important role in the oceanic carbon budget as one of the most productive marine habitats. The high productivity of seagrass habitats and their role as carbonate factories result from the direct calcification of the grasses (Enríquez and Schubert, 2014), from the sediment retention promoted by the plant canopy (Scoffin, 1970; Gacia and Duarte, 2001; Agawin and Duarte, 2002; Mateu-Vicens et al., 2008) and more significantly from the great abundance of calcifying epiphytes, infaunal and epifaunal organisms associated to the grasses (Brasier, 1975; Perry and Beavington-Penney, 2005; Corlett and Jones, 2007; James et al., 2009; Mateu-Vicens et al., 2012; Brandano et al., 2014). Additional important ecological roles of seagrasses include nursery and food source for other marine organisms, sediment stabilization and shoreline defense, and nutrient cycling (e.g. Costanza et al., 1997; Hemminga and Duarte, 2000; Hein et al., 2006; Orth et al., 2006; Vassallo et al., 2013). Moreover, seagrasses are one of the most common habitats in the shallow-water, soft bottoms during the Cenozoic, particularly from the Miocene, a time where many seagrass genera diversified and expanded geographically. Therefore, in order to preserve this valuable ecosystem, numerous studies have focused on understanding the interactions and responses of seagrasses to environmental changes and stressors such as increased light, eutrophication, sedimentation and turbidity, climate change, and water quality. Seagrasses can respond to these changes in different ways such as regulating the physiological activity of the plant, changing the plant morphology, and/or the species composition and biomass (e.g. Duarte, 1991; Short and Neckles, 1999; Gacia et al., 2002; Lirman and Cropper, 2003; Koch et al., 2007, 2013; Ralph et al., 2007; van Katwijk et al., 2011; Jordà et al., 2012; Govers et al., 2014). Furthermore, seagrass-associated organisms, especially of epiphytic foraminifera, are widely used as proxies to characterize specific habitats and to reflect present and past environmental changes such as climate change, sea-level fluctuations, changes in light and nutrient levels and/or substrate type (e.g. Langer, 1993; Wilson, 1998, Fujita and Hallock, 1999; Semeniuk, 2005; Richardson, 2006; Moissette et al., 2007; Brandano et al., 2009; Mateu-Vicens et al., 2010, 2014; Reuter et al., 2011).

Seagrasses have been considered to originate in the Tethys Ocean and their fossil record extends back to the Late Cretaceous (Den Hartog, 1970; van der Ham, 2007). It was only during the early Eocene when this ecosystem became well established and spread throughout the Tethys (Brasier,

1975) and the Western Atlantic-Caribbean (Vélez-Juarbe, 2014). However, the understanding of the functioning of seagrass ecosystems in the geological record is limited, with only few studies focusing on the distribution of seagrasses and their response to environmental changes during the Cenozoic (e.g. Brasier, 1975; Eva, 1980; Domming, 2001; Moissette et al., 2007; Vélez-Juarbe, 2014). This is likely a consequence of the scarcity of fossil remains of seagrasses, due to the low potential of preservation of these plants (Brasier, 1975; Reich et al., 2015 and references therein). Therefore, commonly, the identification of paleo-seagrasses can only be done through the recognition of indirect sedimentological and biological indicators, by comparison with modern seagrass habitats. Common indirect criteria are: specific benthic foraminiferal assemblages, specific composition and growth morphology of crustose coralline red algae, bryozoans, ostracods and mollusks, occurrence of specific taxa of echinoderms, and the presence of unsorted sediments with micritic matrix (for a complete review of these and further indirect indicators of past seagrass habitats the reader is referred to the reviews of Beavington-Penney et al. (2004) and Reich et al. (2015).

Here we provide evidence for the presence of different seagrass environments in the shallow water carbonates of early Eocene age (Jafnayn Formation) in Wadi Bani Khalid (N Oman). To our knowledge, this is the first time that seagrass environments are reported in Oman during the early Eocene. Also, this study documents the capacity of seagrasses and their associated communities to respond to environmental changes such as enhanced runoff, suggesting that seagrasses ecosystems were well evolved and relatively complex already at the early times of the history of the group.

The main objectives of this paper are to: (i) describe in detail and interpret the facies and depositional conditions of lower Eocene deposits in the Wadi Bani Khalid section, (ii) document and critically revise the variety of indirect indicators (sedimentological and paleontological) of the presence of ancient seagrass-dominated settings, (iii) characterize the epiphytic foraminifera associated to the seagrasses, and (iv) unravel the responses of the seagrasses and associated communities to environmental changes related to the influx of terrigenous.

2. Setting

2.1 Regional Geological setting

The study section is located in the Wadi Bani Khalid, 36 km west of the city of Sur, in the south-eastern end of the Oman Mountains (Fig. 1A). From the Paleocene to the early Miocene, up to 2 km of, predominantly, platform carbonates accumulated in the Oman Mountains (paleolatitude 10°N) after the transgressive Maastrichtian deposits (i.e. fluvialites, shallow marine clastics and shallow shelf carbonates) that followed the obduction of the Semail Ophiolites (Nolan et al., 1990; Racey, 1995). This thick Cenozoic interval represents the most complete succession of Paleogene depositional sequences in the Middle East. Particularly, the Sur region comprises one of the most complete succession with shallow-marine deposits, represented by the Jafnayn, Rusayl and Seeb Formations (defined by Nolan et al., 1990), accumulated in the western part, the so-called Tiwi Platform. Part of these Paleogene shallow-marine facies are well exposed in Wadi Bani Khalid, a narrow valley located 140 km W of the city of Sur in the southern most part of the Tiwi Platform (Fig. 1A). The Bani Khalid succession begins with the transgressive shallow shelf carbonates (~ 100m) of the late Paleocene to lower Eocene Jafnayn Formation, which is divided into two units separated by a depositional hiatus (Nolan et al., 1990; Racey, 1995; Haynes et al., 2010) (Fig. 1B). Due to the mixed stratigraphic nomenclature for the early Eocene (Ypresian vs. Ilerdian-Cuisian) used in the previous studies, here to avoid confusion, and since the stratigraphic discussion is beyond the scope of the paper, we will report the ages as stated by the cited authors in their papers. The lower unit of Jafnayn Formation, dated as late Paleocene (Thanetian), consists of marls and marly limestones interpreted as having formed in shallow, low-energy (lagoonal) shelf environments. The upper unit, which is the object of this study, is assigned to the mid early Eocene (Ypresian) and consists of limestones deposited in shallow, higher-energy (open marine shoal) environments (Nolan et al., 1990; Racey, 1995). More recently, Dill et al. (2007) have interpreted the upper most part of the Jafnayn Formation as subtidal to intertidal environments influenced episodically by storms. The carbonates of the Jafnayn Formation are overlain by the lower Eocene to middle Eocene littoral to inshore deposits (associated with mangroves) of the regressive Rusayl Formation (~ 70 m) (Nolan et al., 1990; Racey, 1995; Dill et al., 2007). Although the contact between the Rusayl Formation and its underlying Jafnayn Formation appears conformable, it may represent a disconformity (Nolan et al., 1990; Racey, 1995). The Rusayl Formation is overlain by the transgressive open marine middle Eocene Seeb Formation (Fig. 1B). Sequence stratigraphy analysis of the platform margin deposits in the Sur region by Razin et al. (2001) have interpreted two depositional sequences in the upper part of the carbonate platform of the Jafnayn Formation: sequence 3b (S3b), Ilerdian in age, and sequence 4 (S4), Cuisian in age, separated by a sequence boundary related to a major relative sea level drop. The overlying Rusayl Formation corresponds to the sequence 5a (S5a), which is Lutetian in age, and represents a mixed carbonate-siliciclastic platform (Fig. 3).

2.2 Biostratigraphy

Various stratigraphic studies have assigned the upper unit of the Jafnayn Formation at the type locality (Wady Rusayl, Batinah coast, central Oman Mountains) to the early Eocene (Nolan et al., 1990 and references therein). Racey (1995) and Racey et al. (2001, 2005) have reported the presence of abundant *Alveolina* including *A.muscatensis, A. rusaylensis, and A. rotundata*, and

Lockhartia hunti, Rotalia trochidiformis, Sakesaria cotteri, Opertorbitolites sp. aff., *Orbitolites* sp., *Heterostegina ruida, Nummulites globulus* and miliolids in the upper unit of the Jafnayn Formation assigning an early Eocene (late Ypresian) age to these deposits. White (1994) performed a detailed biostratigraphic subdivision of the Oman Mountains, based on local Alveolina biozones and ascribed the upper unit of the Jafnayn Formation to its zone 5 / ?base of zone 6 (early Eocene, Ypresian, in age). These local zones are equivalent to the calcareous nannoplankton zones NP 12 and NP 13 of Martini (1971) and Berggren et al. (1995) and the shallow benthic zones SBZ 10 and SB Z11 of Serra-Kiel et al. (1998). The local zone 5 is defined by the abundance of notably flosculinized spherical *Alveolina (A. muscatensis*, *A. rusalyensis, A. bronneri, A. dainellii,* and *A. parva).* According to Hottinger (1960) and Hottinger and Drobne (1988), flosculinized alveolinids appear close to the base of the Ilerdian. Additionally, the local zone 5 contains non-flosculinized alveolinids (*Alveolina* sp. aff., *A. rotundata*, *A. oblonga*), and the rotaliid *S. cotteri*. However, White (1994) remarks that none of the characteristic species of the Alveolina local zone 5 are present at Bani Khalid, and the age equivalence is based on the foraminiferal content of the beds above and below. Recently, Özcan et al. (2015) based on the presence of orthophragminids, alveolinids and associated foraminifera (among those: *Nemkovella stockari*, *S. cotteri*, *Glomalveolina lepidula*, *A. bronneri*, *A. muscatensis*, *Alveolina fornasinii*, *Alveolina leupoldi*, *Opertorbitolites* sp., *Lockhartia* sp., *Orbitolites* sp.), has re-assigned the deposits of the upper unit of the Jafnayn Formation to the early Eocene (middle to late Ilerdian), assignable also to the SBZ 7 to 10.

3. Methods

The facies variability and stratigraphy of the upper part of the Jafnayn Formation have been analyzed by a detailed composite section, 65-m thick in total, logged at the eastern and western sides of Wadi Bani Khalid (Figs. 2, 3). Rock samples were collected at approximately 1.5-m intervals. A total of 40 thin sections were studied for textural analysis and fossil composition, with special emphasis on encrusting- and large benthic foraminifera (LBF), using optical- and scanning electron microscopy. All the components and matrix were characterized and visually estimated in the thin sections and plotted in cumulative graphs in order to differentiate lithofacies types (Fig. 2). To analyze the sediment composition (quartz-, dolomite- and clay minerals content), a total of 40 samples of powdered bulk rock material were analyzed on a PANalytical Empyrean powder X-ray diffractometer in a Bragg–Brentano geometry. It was equipped with a PIXcel1D detector using Cu K_α radiation (λ = 1.5419 Å) operating at 40 kV and 40 mA. θ/θ scans were run during 23 minutes in a 2θ range of 4-70° with step size of 0.0131° and a sample rotation time of 1s. For the quantitative phase analysis of multicomponent mixtures High score plus (PANalytical) was used; the phase fit was done with Rietveld refinement.

4. Results

4.1 Wadi Bani Khalid Section

Based on sedimentological and stratigraphical data, the 65-m thick section can be subdivided into a lower part (48-meter thick) formed by aggrading, homogeneous carbonate facies and a thinner (17 m-thick) upper part formed by different carbonate facies containing siliciclastic material (Fig. 2). The lower part consists of well-bedded, bioclastic packstones and locally grainstones, dominated by encrusting acervulinid- and alveolinid foraminifera. These deposits are capped by a sharp, erosional surface that marks an abrupt change of facies and of bed colors (Figs. 2, 3B). A level (0.5-m-thick) of reworked material from the underlying strata overlies the erosional surface. Upward the section consists of well-bedded, planar packstones and marly packstones alternating with parallel, well-bedded, occasionally cross-bedded, grainstones. The packstone facies contain abundant echinoids, peloids and quartz grains. The grainstone facies are rich in *Orbitolites* and smaller miliolid foraminifera, peloids, and quartz grains. The age of the section is early Ypresian (early Eocene), by comparison with the faunal assemblage described in the upper unit of the Jafnayn Formation by Özcan et al. (2015). In the studied section the following microfauna has been identified: *S. cotteri, Orbitolites* sp., *Opertorbitolites* sp., *Nummulites* sp., *Lockhartia* cf. *haimei-diversa*, *A.* cf. *leupoldi*, *A.* cf. *bronneri*, *A.* cf. *fornasinii, Alveolina* cf. *canavarii*, *G. lepidula*, and *N*. cf. *stockari* (Fig. 4).

4.2 Lithofacies types

The Bani Khalid succession has been subdivided into three main facies types according to the field observations, sedimentological and textural features, and relative abundance of components. Facies type 1 occurs at the lower part of the section, and Facies types 2 and 3 occur at its uppermost part, above the erosional surface (Figs. 2, 3B).

Facies 1: Acervulinid-alveolinid packstones

Facies 1 occurs in the first 48 meters of the section. It consists of well, horizontally bedded (average 40cm- thick), cliff-forming, nodular foraminiferal limestones (Figs. 2, 5A and B). The bulk of this facies consists of poorly sorted packstones with 10% micrite on average, and locally grainstones, dominated by encrusting acervulinid- (30%) and ~~benthic~~ alveolinid foraminifera (19%) (Figs. 6A and B). Common components are peloids and micritic grains (8%), large rotaliid foraminifera (*Sakesaria* and *Lockhartia*; 7%), and echinoids (5%). Rare constituents are small miliolids (3%), textularids (2%), fragmentary crustose coralline red algae (2%), and intraclasts (2%) and very rare (≤ 1%) are *Orbitolites* sp., *Nummulites* sp., dasycladacean green algae, bivalves and ostracods. The most striking components of this facies are the acervulinid- and the alveolinid foraminifera. The acervulinids occur mainly as encrusting forms whereas free-living forms are rare (Figs. 6B, 7). Taxonomic identification of acervulinids requires observation of juvenile stages. All the specimens whose juvenile stages are well preserved to perform taxonomical studies belong to the genus *Solenomeris,* identified following the criteria of Perrin (1987, 1994). Although juvenile stages of *Acervulina* and *Solenomeris* look similar in several aspects, the height of equatorial chambers seen in axial section decreases towards the periphery of the test in *Solenomeris* while it increases in *Acervulina* (Perrin 1987, 1994). Additional diagnostic criteria provided by Perrin (1994), such as thickness of tangential wall and various morphological features of adult chambers are more difficult to use in practice because this necessitates a prior detailed knowledge about diagenetic alteration undergone by the foraminiferal test (Perrin, 2009). The morphology of the encrusting forms is mostly tubular, and few times hooked (*sensu* Beavington-Penney et al., 2004). The encrusted material is frequently lacking (Fig. 7). Only few specimens encrust on large foraminifera (i.e. alveolinids). The tubular crusts show flat surfaces and a central annular or ellipsoidal hollow ranging from 400 to 700 µm in diameter. In some occasions two hollows adjacent to each other have been observed (Fig. 7B). Fragments of planar crusts of acervulinids, approximately 2-3 mm long, are also present. Some of these crusts show curved margins resembling hooked morphologies although it is sometimes difficult to distinguish between possible hooked forms and fragmented tubular forms (Fig. 7D). The alveolinids show spherical to subspherical forms of approximately 2 mm in length, often flosculinized. Some alveolinids are micritized, fragmented or deformed, indicating some reworking and compaction (Figs. 6A and B).

Facies 2: Packstones and marly packstones with echinoids and quartz grains

This facies-type is present in the upper part of the section (48 m above the base). It begins (from 48 to 52m above the base of the section) with well-bedded, parallel-tabular marly packstones to packstones in beds of 5 to 10 cm of average thickness (Figs. 2, 5C). Upwards (from ~57 to 63m of the section), this package pass into 1 to 2 cm-thick beds of marly packstones interbedded with more indurated, 5 to 10 cm-thick beds of packstones with sedimentary structures resembling to hummocky cross-stratification (HCS) (Figs. 2, 5D). Occasionally, normal graded levels characterized by concentrations of oriented shells are observed (Fig. 5E). Facies 2 shows moderate bioturbation, consisting of sub-horizontal and vertical burrows (Fig. 5F). The bulk of Facies 2 consists of moderately sorted, fine-grained packstones, with up to 40% micrite. Main components are echinoids (20%), peloids and micritic grains (10%) and abundant indeterminate bioclasts. Subordinate components are subangular, very fine- to fine quartz grains (6%), small rotaliids (3%) and intraclasts (3%). Very rare components (≤ 1%) are foraminifera of the Orbitolites group (*Orbitolites* and *Opertorbitolites*), bivalves, fragmentary crustose coralline red algae, small miliolids and textularids. Unfortunately, the submilimetric size of most of the bioclasts hinders often their detailed identification at generic or species level (Fig. 6D).

Facies 3: Orbitolites-small miliolid-peloidal grainstones with quartz grains

It occurs intercalated with the marly limestones of Facies 2 in the upper part of the section and comprises tabular beds (60 cm-thick on average), occasionally low-angle planar cross beds, of coarse-grained grainstones (Figs. 2, 5G and H). The grainstone is moderate to well-sorted and is dominated by *Orbitolites* sp. (16%), rarer *Opertorbitolites* sp., small miliolids (10%), peloids and micritic grains (10%), and subrounded quartz grains (10%), ranging from fine to coarse size. Subordinate grains are intraclasts (8%), alveolinids (6%), textularids (5%), rotaliids, mostly LBF, (4%), and echinoids (4%) whereas *Nummulites* sp., bivalves, dasycladacean green algae and fragmentary crustose coralline red algae are very rare (≤ 1%) (Figs. 2, 6E and F). The most striking and most abundant component of the total rock volume is *Orbitolites* sp. This foraminifer shows mainly elongated transversal sections with large, up to 10 mm-long, tests that are often isooriented (Fig. 6F).

5. Discussion

5.1 Facies Interpretation and Depositional Model

Facies analysis carried out in the Bani Khalid section allows us to document the variations in facies, faunal composition, with particular attention to foraminiferal assemblages, and environments of deposition in the lower Eocene (Ypresian) carbonate platform of the upper unit of the Jafnayn Formation in the south-eastern Oman Mountains.

The acervulinid-alveolinid packstones (locally grainstones) likely represent a shallow, inner platform environment (Fig. 8A). The presence of large, symbiont-bearing foraminifera (i.e. abundant alveolinids, rotaliids and very rare *Orbitolites* and *Nummulites*), and dasycladacean green algae are indicative of deposition in the shallow, photic zone. Moreover, the presence of peloids, micritization, and other benthic foraminifera (small miliolids and textularids) is also, suggestive of shallow-water areas. Several lines of evidence suggest the presence of marine vegetation covering this inner platform setting (see section 5.2) and therefore this muddy, grain-supported facies, apparently representing low-energy settings, could result from the trapping and baffling action of seagrasses (e.g. Scoffin, 1970; Mateu-Vicens et al. 2008, 2012). This shallow setting is characterized by an assemblage composed by photozoans (alveolinids, *Nummulites* and green algae) and heterozoans (encrusting acervulinids, echinoderms, small miliolids and rotaliids). In general, large benthic foraminifera (LBF) are considered K-strategists that host endosymbiotic algae and adapt to nutrient-deficient oligotrophic conditions (Hottinger, 1983; Hallock, 1988, Hallock et al., 1991; Langer and Hottinger, 2000). In particular, alveolinids are considered extreme oligotrophs (Lee, 2006; Parente et al., 2008), and thus, their abundance in the inner settings of Wadi Bani Khalid suggests relatively oligotrophic conditions.

The deposition of Facies 2 took place in an open-marine, low-energy environment, supported by the presence of mud-rich sediments, the very rare occurrence of euphotic organisms and the abundant echinoids (Fig. 8B). The presence of quartz grains indicates deposition in a carbonate platform with siliciclastic input and possibly associated nutrient increase (mesotrophic conditions), as suggested by the dominance of heterotrophic organisms (i.e. echinoderms and small rotaliid foraminifera). Occasionally, this setting was influenced by storms as indicated by the presence of HCS and normal graded levels of accumulated shells (Figs. 5D and E).

Facies 3 was deposited in a relatively shallow-water, high-energy shoal environment, above or around the FWWB (Fig. 8B), as indicated by the grain-supported facies, local cross-bedding sedimentary structures, and presence of shallow-water benthic foraminifera (abundant *Orbitolites* and smaller miliolids, rare alveolinids, textularids and rotaliids). The abundance of *Orbitolites* and small miliolid foraminifera, both significant contributors of plant habitats, suggests the presence of marine vegetation standing in the shoals or in their close proximity (see section 5.2). The depositional setting was also influenced by terrigenous input like Facies 2, as indicated by the common presence of quartz grains. The faunal assemblage, dominated by *Orbitolites* (LBF) and heterotroph small miliolid foraminifera, suggests nutrient-enriched waters. Although LBF as a group are regarded as photozoans, it has been demonstrated that present-day soritids of the genus *Peneroplis, Marginopora* and *Sorites*, living relatives of *Orbitolites*, can tolerate higher nutrient levels (Lee, 2006; Parente et al., 2008; James and Bone, 2010). Nevertheless, the presence of few oligotrophs such as alveolinids and green algae suggest not extremely high nutrient levels, but rather oligo-mesotrophic conditions.

The change from homogeneous carbonate facies of the lower part of the section (Facies 1), into alternating packstone and grainstone facies with quartz grains of the upper part (Facies 2 and Facies 3, respectively) is marked by an erosional surface, overlain by reworked underlying sediments. This suggests two temporarily distinct stages in the evolution of the carbonate platform (Fig. 8). The first stage of platform development is characterized by an aggrading, shallow, inner-platform setting (Facies 1) with a relatively dense vegetation cover (Fig. 8A). The second stage of platform development, above the erosional surface, took place in more open-marine conditions, in a carbonate platform with clastic sedimentation that was occasionally influenced by storms (Facies 2), and where high-energy shoals occurred in its shallower settings (Facies 3). The shoals were probably covered by (sparse) marine vegetation or close to seagrasses and fed by the sediment produced in the meadows (Fig. 8B). The aforementioned change of facies and environments of deposition may tentatively be interpreted as a result of a change in the platform profile, from a platform into a ramp-type profile, influenced by storms and clastic input. However, it is worth to mention that this suggested change of platform morphology is difficult to assess based on our limited observations and more comprehensive work (beyond the scope of the present study) is required.

5.2 Evidence for the presence of paleo-seagrasses in Wadi Bani Khalid

Benthic foraminifera assemblages

The use of benthic foraminifera as ecological indicators of recent and ancient environments is well established and has been focus of numerous studies (e.g. Douglas, 1979; Alve, 1995; Hallock, 2000; Langer and Hottinger, 2000; Murray, 2000, 2006; Scheibner et al., 2005; Mateu-Vicens et al., 2008; Bouchet et al., 2012; Reymond et al., 2013; Uthicke et al., 2013; Engel et al., 2015). More specifically, epiphytic foraminifera are considered a good proxy to infer environmental and paleoenvironmental conditions such as phytal substrate, water chemistry, temperature and bathymetry (e.g. Matera and Lee, 1972; Langer, 1993; Langer and Hottinger, 2000; Semeniuk, 2001, 2005; Richardson, 2006; Debenay and Pairy, 2010; Mateu-Vicens et al., 2010, 2014). Recent encrusting acervulinids such as *Acervulina* and *Gypsina* are permanently attached epiphytic foraminifera (i.e. morphotype A of Langer, 1993 and morphotype A* of Mateu-Vicens et al. 2014) in adult stage, and recent discoidal soritids such as *Sorites orbiculus*, although motile, attaches firmly on phytal substrates and is therefore included in the sessile morphotype A of Langer (1993) or in the sessile morphotype SB (symbiont-bearing) of Mateu-Vicens et al. 2014. Also smaller miliolid foraminifera (e.g. *Miliolinella*, *Triloculina*, *Quinqueloculina, Textularia*) can be significantly present in marine vegetated settings, as motile epiphytes (morphotype D of Langer, 1993 and morphotype D* of Mateu-Vicens et al. 2014). All these aforementioned groups are commonly reported as epiphytes living on seagrasses and macroalgae (e.g. Wright and Murray, 1972; Brasier, 1975; Eva, 1980; Reiss and Hottinger, 1984; Langer, 1993; Wilson, 1998, 2008; Fujita and Hallock, 1999; Langer and Hottinger, 2000; Richardson, 2000, 2006; Semeniuk, 2001; Saraswati, 2002; Mateu-Vicens et al., 2010), although they are not restricted to phytal substrates. Wilson (1998) observed that the encrusting acervulinid *Gypsina squamiformis* is the most abundant species living attached to the leaves of present-day seagrasses *Thalassia testudinum* and *Syringodium filiforme* in St. Kitts Island. Also, Langer (1993) noted that *Acervulina* and other permanently attached foraminifera preferably grow on phytal substrates with large, flat leaves (i.e. seagrasses, large algae) and long life-spans, in comparison to small-bladed macroalgae with short life-spans. Moreover, much higher densities of *Sorites sp*. have been observed on seagrass leaves in comparison to most other substrates (e.g. Fujita and Hallock, 1999; Richardson, 2000).

The studied deposits of Bani Khalid show abundant foraminifera that share similarities with the aforementioned communities associated with vegetated environments. Encrusting acervulinid foraminifera of the genus *Solenomeris* are abundant in the inner platform deposits (Facies 1) and soritid foraminifera of the genus *Orbitolites* and smaller miliolids are frequent in the shoal deposits (Facies 3). To our knowledge, this is the first time that the Eocene genus *Solenomeris* has been related to an epiphytic habitat. It has been often associated to reefal and peri-reefal environments, either as reef builder in low-lit settings or as encrusting /binding form on coral reefs (e.g. Perrin, 1992; Plaziat and Perrin, 1992; Scheibner et al., 2007) and to deep infralittoral-circalittoral settings of carbonate ramp (Varrone and d'Atri, 2007). Nevertheless, the morphologically similar acervulinid genus *Gypsina* has been reported as epiphytic form on vegetated substrates from the middle Eocene (i.e. in the Alps, northern Italy: Ungaro, 1996, and in the Apeninnes, central Italy: Tomassetti et al., 2016). The extinct, discoidal-shaped soritid *Orbitolites*, by comparison with its living, close relatives seagrass dwellers *Sorites*, *Marginopora* and *Amphisorus*, has been also interpreted as epiphytes on Eocene vegetated deposits (e.g., Tethys realm: Brasier, 1975 and references therein; N Oman (Seeb Formation): Beavington-Penney et al., 2006; SW Slovenia: Zamagni et al., 2008; central Italy: Tomassetti et al., 2016). In fact, Brasier (1975) used the distribution of *Orbitolites* to reconstruct the distribution of Eocene seagrasses in the Tethyan realm. In the studied Eocene deposits of Wadi Bani Khalid, the presence of hooked-liked and tubular crusts of acervulinids and the assemblage *Orbitolites*-miliolids are therefore highly suggestive indicators of the occurrence of vegetated settings. The abundance of acervulinid foraminifera in the inner platform (Facies 1) may indicate a relatively uniform marine vegetated cover, whereas the dominance of *Orbitolites* and smaller miliolid foraminifera in the high-energy facies (Facies 3) could probably indicate the presence of vegetation in the nearby areas of the shoals or patchy vegetated covers within the shoals.

Another important foraminiferal group to consider is represented by the large benthic *Alveolina*, which we found, abundant, associated with the encrusting acervulinids in the inner platform deposits (Facies 1). Some of the tests of the alveolinids show signs of abrasion and breakage, likely evidencing (minor) transport. Although *Alveolina* is not considered to be a seagrass dweller, recent alveolinids have been found living on sandy substrates adjacent to seagrass beds in the Caribbean (Eva, 1980) and in the Gulf of Aqaba (e.g. Hottinger, 1983; Reiss and Hottinger, 1984), where they live in the bared sandy-bottom between individual plants of relatively sparse seagrass or soft-algal meadows that preserve enough space and light. Similarly, Beavington-Penney et al. (2006) interpreted the co-occurrence of *Alveolina* and encrusting foraminifera as epibionts inhabiting sparsely vegetated areas in the middle Eocene Seeb Formation of Oman. We suggest, therefore, that the alveolinids possibly lived within the vegetated areas or immediately adjacent to them.

Specific skeletal growth morphologies

In the study section the (frequent) tubular and (few) hooked growth morphologies identified in the acervulinid (*Solenomeris*) crusts of Facies 1 are indicative of epiphytic adaption (Fig. 7). Also, similar thin hooked coralline red algae are present although scarce (Fig. 7C). Hook, tubular and mushroom-like morphologies are commonly observed in non-geniculate coralline red algae growing around the leaves, leaf margins and stems of present-day seagrasses or macroalgae (Beavington-Penney et al., 2004; Figs. 3 and 10 in Browne et al., 2013) and therefore are considered a reliable indicator of the existence of ancient seagrasses (Beavington-Penney et al., 2004; Mateu-Vicens et al., 2012; Sola et al., 2013; Reich et al., 2015). Nevertheless, adaptive morphologies such as flat, concave-convex and folded-over, have been observed in recent epiphytic foraminifera (e.g. *Planorbulina*, *Gypsina*, *Cyclocibicides, Miniacina, Nubecularia*) growing around different parts of marine plants. Similar functional morphologies have been reported in fossil counterparts from the Eocene of Italy and Spain (Langer, 1993). Ungaro (1996) and Tomassetti et al. (2016) observed semicircular and hooked shaped tests of middle Eocene *Gypsina* species in northern Italy (Alps) and central Italy (Apennines) respectively, and interpreted them as adaptive forms to attaching to the stems (semicircular forms) and to the leaf margins (hooked forms) of marine phytal substrates.

Also, the large, flattened, discoidal tests of *Orbitolites,* abundant in Facies 3 (Fig. 6F) can be considered an adaptation for attachment to vegetation, by comparison with its living homeomorphs *Sorites, Marginopora* and *Amphisorus*, commonly observed growing on present-day seagrasses and algae and particularly, on large, flat leaves of relatively long-lived plants (e.g. Langer, 1993 and references therein; Fujita and Hallock, 1999).

Sedimentological features

Unsorted fine sediments may reflect the baffling effect of plant canopy (Scoffin, 1970), and consequently is a criterion often reported to characterize modern and ancient seagrass environments (Davies, 1970; Pomar, 2001; Brandano et al., 2009; Reuter et al., 2011; Mateu-Vicens et al., 2012), specifically in tropical seas (Reich et al., 2015). In Wadi Bani Khalid the acervulinid-alveolinid packstone (Facies 1) shows unsorted fabrics, with muddy matrix and coarse skeletal particles (Figs. 6A and B). Furthermore, these beds show typically, nodular-like bedding (Fig. 5A), which may result from the physical modification by the rhizomes and roots of seagrasses of the substratum as observed in modern seagrasses (Enos, 1977; Wanless et al., 1995).

5.3 Evidence of change in types of seagrasses in Wadi Bani Khalid

The basic physical requirements controlling seagrass ecosystems are light, nutrient supply, temperature, salinity, substrate and physical exposure. Changes to any or all of these limiting factors may regulate the physiological activity and morphology of seagrasses, and/or change seagrass species composition and biomass (e.g. Duarte, 1991; Short and Neckles, 1999; Gacia et al., 2002; Lirman and Cropper, 2003; Koch et al., 2007, 2013; Ralph et al., 2007; van Katwijk et al., 2011; Jordà et al., 2012; Govers et al., 2014).

The shift from an inner setting in the first carbonate platform stage (Facies 1) into more open marine ramp settings with increased terrigenous input of the second one (Facies 2 and Facies 3), is accompanied by a drastic change in foraminiferal assemblages. We suggest that this shift may be related with changes of type of phytal substrate, which may have been, in turn, triggered by the increased terrigenous runoff. The dominant tubular shape of the encrusting acervulinids of the inner settings (Facies 1) may indicate growth around stems and shoots of phytal substrates, as have been suggested for coralline red algae (Beavington-Penney et al., 2004; Sola et al., 2013) and for Eocene gypsinids (Ungaro, 1996; Tomassetti et al., 2016). Also, in sheltered areas ≤ 40 m depth living specimens of *Acervulina inhaerens* are found attached to the basal part of the stems of the seagrass *Cymodocea* in the Gulf of Aqaba (Murray, 2006, p. 175). Another possibility is to consider that the tubular forms result from attaching to other tube-like surfaces, such as cylindrical leaves, as is the case of the seagrass *Syringodium* (i.e. *Syringodium filiforme* and *Siryngodium isoetifolium*). Wilson (1998) observed the present-day encrusting acervulinid *Gypsina squamiformis* growing preferentially on the cylindrical leaves of *S. filiforme* in comparison to the flat-leafed *Thalassia testudinum* on a seagrass meadow in St. Kitts, Caribbean Sea. *Syringodium* is a common and widely extended seagrass in tropical waters. It has tube-like leafs with widths of approximately 1mm in diameter (e.g. *S. filiforme*: Williams, 1987; Wilson, 1998). *Syringodium* may have only dated back to the Miocene (Brasier, 1975). However the family it belongs to (Cymodoceaceae) has several fossil records from the Eocene (i.e. genus *Cymodocea*: Den Hartog, 1970; Brasier, 1975). Therefore, the abundant tubular forms observed in the studied acervulinids may result possibly from growing on seagrass leaves with cylindrical or tube-like morphologies such as the grass *Syringodium* and/or attached to their stems. The presence of few hooked morphologies of both, acervulinids and coralline algae is commonly indicative of epiphytic growth over the margins of flat leaves of seagrasses (Beavington-Penney et al., 2014), however the scarcity of these forms suggests that flat-leafed plants would have been subordinate and outpaced by the cylindrical-leafed plants or that most of the flat leaves would have been removed from the deposit.

On the other hand, the large, discoidal soritid foraminifera *Orbitolites*, characteristic of the shoals deposits (Facies 3), may indicate attachment on a different type (or part) of plant. Living relatives of *Orbitolites*, including the genera *Sorites, Marginopora* and *Amphisorus*, are common epiphytes on plants with long-life spans and large, flat leaves such as *Thalassia* (e.g. mean leaf width of *Thalassia testudinum* ~ 0.9 to 1.3 cm: Zieman et al., 1984; Richardson, 2006), and *Posidonia* (e.g. mean leaf width of *Posidonia oceanica* ~ 0.9 cm, and of *Posidonia australis* ~1.2 cm: Gobert et al., 2006). Furthermore, soritids are also reported as epiphytes on the pioneer, smaller grass *Halodule,* which has flat, narrower leaves (e.g. mean leaf width of *Halodule wrightii* ~ 0.1 cm: Pinckney and Micheli, 1998). Several authors have reported the abundant number of living specimens of *Sorites* and *Marginopora* on the flat blades of *T. testudinum* (Hallock and Peebles, 1993; Fujita and Hallock, 1999; Richardson, 2000, 2006, 2009), on *P. oceanica* (Langer, 1993; Mateu-Vicens et al., 2010) and on *P. australis* (Senemiuk, 2001).

Furthermore, abundant epiphytic assemblages of different species of *Sorites* are observed on *Halodule* blades in the Red Sea (Murray, 2006, p. 75) and in Florida (Moore, 1957; Bathurst, 1975). Also, Debenay and Payri (2010) have reported the presence of *Marginopora vertebralis* on the leaves of *Halodule universis* in New Caledonia. In summary, we suggest that the change of foraminiferal taxa observed in the study section possibly reflects a marked change of the phytal substrate. The cylindrical-leafed plants (e.g. *Syringodium*-like) meadows of the ~~protected~~ inner platform dominated by tubular acervulinids were replaced by grasses with flat (large) leaves (e.g. *Thalassia*-, *Posidonia*-, or *Halodule*-like), hosting discoidal foraminiferal forms such *Orbitolites*.

This suggested change in type of phytal substrate and associated foraminiferal assemblage is coeval with an increase in the input of terrigenous material to the platform (Fig. 2). Terrigenous runoff can influence the shallow water communities in different ways such reduction of light availability (increase in water turbidity and sediment load), changes in water temperature and salinity and increase of nutrient load and levels (e.g. Carannante et al., 1988; Weissert, 1989; Hallock et al., 1993; Dupraz and Strasser, 2002; Mutti and Hallock, 2003). Enhanced sediment load increasing turbidity and reducing light availability are major threatens of seagrasses that respond with changes in plant physiological parameters, species composition and biomass (e.g. Giesen et al., 1990; Terrados et al., 1998; Newell and Koch, 2004; Burkholder et al., 2007; van Katwijk et al., 2011; Hanington et al., 2015). Terrados et al. (1998) related the effects of increased siltation (silt and clay content) and light reduction with changes of seagrass species in SE Asia. The more resistant species to siltation was *Enhalus acoroide,* followed by *Halophila ovalis* and *Cymodocea serrulata.* The less resistant ones were *Halodule uninervis*, *Thalassia hemprichii, Cymodocea rotundata* and *Syringodium isoetifolium*. Also, Hanington et al. (2015)

reported the widespread loss of *S. isoetifolium* after a major flood event. These authors highlight the less resistance of *S. isoetifolium*, respect to other seagrass species such as *Zostera muelleri*, to the low light and low salinity levels associated to flood events.

Moreover, the input of terrigenous may result in increased nutrient contents. Numerous studies have focused on the effects of eutrophication on recent seagrass ecosystems. Eutrophication is believed to be the main responsible of the deterioration of seagrass ecosystems and, if excessive of their disappearance (e.g. Webster and Harris, 2004; Orth et al., 2006; Duarte et al., 2008; Waycott et al., 2009). Nutrient enrichment results in increasing epiphytic loads, which produce shading, overgrow seagrass leaves, and compete for nutrients (e.g. Tomasko and Lapointe, 1991; Bohrer et al., 1995; Duarte, 1995; Cloern, 2001). Moreover, eutrophication causes shifts in plant physiology and morphology, and changes in the composition of seagrass species and their associated communities (e.g. Uku and Björk, 2001; Valentine and Heck, 2001; Hale et al., 2004; Armitage et al., 2005; Richardson, 2006; Burkholder et al., 2007; van Katwijk et al., 2011). Van Katwijk et al. (2011) studied the responses of a pristine seagrass ecosystem in Berau archipelago (Indonesia) to river influence (nutrient and sediment load) and observed that whereas *Halodule uninervis*, *Halophila ovalis* and *Thalassia hemprichii* occur elsewhere (coastal zone, intermediate zone and outer reef zone), *Syringodium isoetifolium* and *Cymodocea rotundata* occur only in the latter two more pristine zones, with diminished river influence. Also, several authors have documented that fertilization in Florida Bay resulted in a change in seagrass species composition from *Thalassia testudinum* to *Halodule wrightii* (Powell et al., 1991; Fourqurean et al., 1995; Frankovich and Fourqurean, 1997), highlighting the capacity of the latter to thrive in nutrient-enriched waters. All these observations would agree with the suggested change of seagrasses taxa in Wadi Bani Khalid. A *Syringodium*-like seagrass association would colonize the meadows covering the inner setting of a pure, probably oligotrophic, carbonate platform whereas seagrasses of the type of *Thalassia* or most likely of *Halodule* would stand on the shoal settings, influenced by terrigenous input and likely increased nutrients.

6. Conclusions

In this study we describe in detail the well-exposed, early Ypresian upper unit of the Jafnayn Formation in Wadi Bani Khalid, in the south-eastern Oman Mountains, and document for the first time evidence for the presence of seagrass-vegetated environments, as well as their response (together with the associated foraminifera communities) to the environmental changes affecting the area. Two distinct intervals with different facies associations have been recognized suggesting two depositional platform stages: i) inner setting of a carbonate platform, and ii) a carbonate ramp-type platform characterized by open marine conditions with high-energy shoals deposited under the influence of terrigenous sedimentation. Different benthic foraminiferal assemblages characterize the two depositional environments. The inner platform setting includes alveolinids and tubular and hooked crusts of acervulinids (*Solenomeris*), whereas the shoals are dominated by large, flat discoid soritids (*Orbitolites*) and smaller miliolids. These foraminifera and their test morphologies are indicative of epiphytic habitats, and together with sedimentological criteria, strongly suggest the presence of seagrass meadows. However, the drastic shift in facies and foraminiferal assemblages through the section suggests a change in type of phytal substrate, from plants with cylindrical leaves (i.e. *Siringodium*-like), hosting acervulinids, in the lower part of the section, to flat-leafed plants (i.e. *Halodule*- or *Thalassia*-like), hosting *Orbitolites*. This shift is associated with an increase in the input of terrigenous and likely enhanced nutrient levels. The present study provides for the first time evidence for the occurrence of seagrasses in the early Eocene of Oman, providing an exceptional opportunity to investigate seagrass environments at the beginning of the history of the group. Furthermore, it also shows the importance of performing detail sedimentological and micropaleontological analysis in order to infer not only the presence of seagrasses, but also the type and characteristics of the phytal substrate and epiphytal communities, as well as their response to environmental changes.

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Figure Captions

Fig. 1. Geological map and lithostratigraphy of the study area. A) Simplified geological map of the Sur Region (south-eastern Oman Mountains) and location of Wadi Bani Khalid section (modified from Razin et al. 2005). B) Regional chrono- and lithostratigraphy of the eastern part of the Oman Mountains (after Nolan et al. 1990). The study interval (upper part of the Jafnayn Formation) is highlighted in grey.

Fig. 2. Lithostratigraphic section in Wadi Bani Khalid showing sedimentological structures, distribution of facies types, and abundance of the main components and quartz grains (see text for further details).

Fig. 3. Field view of the eastern side of Wadi Bani Khalid showing the two depositional sequences (Ilerdian and Cuisian) interpreted for the upper most part of the Jafnayn Formation and the overlying Rusayl Formation. The two sequences are separated by a sharp, erosional surface marking an abrupt change of facies and of bed colors (dashed line).

Fig. 4. Selected benthic foraminifera from the upper part of Jafnayn Formation in Wadi Bani Khalid section. A) *Alveolina* cf. *leupoldi* (sample BK-0.5). B) *A.* cf. *fornasinii* (BK-4). C) *A.* cf. *bronneri* (BK-17.3). D) *A.* cf. *canavarii* (BK-17.3). E) *Nemkovella stokari* (BK-46). F)

Glomalveolina lepidula (BK-18.2). G) *Lockhartia* cf. *haimei-diversa* (BK-5). H) *Sakesaria cotteri* (BK-18.2). I) *Nummulites* sp. (BK-4). J) *Opertorbitolites* sp. (BK-50.5). K) *Orbitolites* sp. (BK-46). White scale bar= 0.5 mm; black scale bar= 1 mm.

Fig. 5. Field photographs of the upper part of the Jafnayn Formation in the Wadi Bani Khalid section. A-B) Facies 1: well-bedded, cliff-forming, nodular limestones (A) consisting of foraminiferal (encrusting acervulinids and alveolinids) packstones (B). C-D) Facies 2: tabular, thin-bedded (5 to 10 cm thick) marly packstones at the base of the interval of Facies 2 (C) and thin-bedded (few-cm thick) marly packstones interbedded with more indurated, decimeter-scale beds of packstones with hummocky cross-stratification-like structures at the top of the interval of Facies 2 (D). E) Normal-graded bed characterized by concentration of oriented shells in Facies 2. F) (Sub)-vertical burrows occurring in the packstones of Facies 2. G-H) Facies 3: tabular decimentric-scale beds (G) consisting of coarse-grained grainstones (H).

Fig. 6. Microphotographs of the different facies types identified in this study. A-B) Facies 1: poorly-sorted, acervulinid-alveolinid packstones (A), and locally grainstones with tubular-shaped acervulinid crusts (B). C-D) Facies 2: marly packstones with fine quartz, echinoderms and echinoderm spines, peloids, micritic grains and small, undifferentiated fragments of carbonate bioclasts. E-F) Facies 3: *Orbitolites*-small miliolid-peloidal grainstones with fine to coarse quartz. Note the iso-orientation of the grains (F). al= alveolinids; ac= acervulinids; mi= miliolids; ro= rotaliids; ec= echinoderms; sp= echinoderm spines; tx= textularids; q= quartz grains; or= *Orbitolites* sp.; op= *Opertorbitolites* sp.

Fig. 7. Microphotographs of acervulinid foraminifera. A) Adult stage of acervulinid (top) showing a tubular-shaped crust and lacking encrusting material, and free juvenile stage of the

acervulinid *Solenomeris* (bottom) showing the equatorial chambers (eqc) in axial section (arrow). B) Transversal section of two tubular-shaped crusts of acervulinids adjacent to each other. C) Oblique section of a tubular-shaped crust of acervulinid and small, fragile hooked-shaped crusts of coralline red algae (arrows). D) Planar crusts with hooked morphology.

Fig. 8. Inferred depositional model and platform development during the early Eocene for the study area. A) Ilerdian platform stage: shallow, inner setting of a pure carbonate platform covered by relatively dense seagrasses with cylindrical leaves. B) Cuisian platform stage: terrigenous-influenced carbonate platform with a ramp-like geometry characterized by open marine settings and high-energy shoals covered or close to patchy seagrasses with flat leafs and affected by episodic storm action.