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ASSESSMENT OF A REEF COMMUNITY FROM LOWER JURASSIC (PLIENSBACHIAN) STRATA IN THE CENTRAL HIGH ATLAS MOUNTAINS OF MOROCCO

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ABSTRACT: **During the Early Jurassic, reefs in the shallow seas of the Atlas Rift experienced substantial changes as they recovered from the end-Triassic mass extinction. Excellent Lower Jurassic reef deposits documenting this change occur in the Central High Atlas region of Morocco, and herein we describe Owl Olistolith, a micro-olistolith found in lower Pliensbachian-aged (∼ 188.7 million years ago) Moroccan strata. The olistolith records the composition of a reef that grew within the Atlas rift zone and represents a snapshot of reef recovery ∼ 10 million years after the end-Triassic mass extinction. Owl Olistolith is derived from a reef that was originally situated on an outer platform within fair weather wave base; it broke loose and was transported to deeper water and deposited amongst marls. Corals and microbialites formed the primary framework of the reef; microproblematica, foraminifera, and other minor components were also present. The reef can be divided into two dominant facies: a microbialite facies that contains no corals (54%–94% microbialites), and a coral-microbialite facies with substantial proportions of both microbialite (23%–50%) and corals (14%–72%). The micro-olistolith contains at least 15 distinct coral types. In this study, seven coral genera were identified, three of which represent taxa that span the Triassic/Jurassic boundary, including *Coryphyllia*, *Stylophyllopsis*, and *Margarosmilia*. These results indicate that, although surviving taxa played a significant role, newly evolved corals were the most important taxa in the reestablishment of reef ecosystems in the Early Jurassic of Morocco.**

INTRODUCTION

The end-Triassic Mass Extinction (∼ 201.3 Ma) was one of the most severe reef collapses of the Phanerozoic (Kiessling et al. 2009). A combination of factors, including the rapid release of carbon dioxide and other volcanic volatiles associated with the Central Atlantic Magmatic Province, led to rapid climate change and the onset of the end-Triassic Mass Extinction (Hautmann 2004; Tanner et al. 2004; Greene et al. 2012; Martindale et al. 2012; Lindström et al. 2017; Petryshyn et al. 2020). Reef building taxa were heavily impacted due to their positioning in lower latitudes, on carbonate substrates, and in shallow water (Kiessling et al. 2007), as well as their sensitivity to decreasing pH and saturation state of the ocean during the end-Triassic event (Greene et al. 2012; Martindale et al. 2012). The severe extinctions of reef builders, such as corals and sponges, led to the virtual elimination of tropical reef ecosystems at the beginning of the Jurassic (Kiessling et al. 2009; Lathuilière and Marchal 2009).

Reef recovery began with Triassic holdover taxa forming small structures alongside newly diversified Jurassic taxa in the Hettangian stage of the Early Jurassic (Kiessling and Aberhan 2007; Kiessling et al. 2009; Stanley et al. 2018; Atkinson 2019). Although recovery of reef biotas began during the Hettangian (Lathuilière and Marchal 2009; Brandolese et al. 2019), reef ecosystems were not fully ecologically recovered until the late Pliensbachian (middle Early Jurassic) (Wilmsen and Neuweiler 2007; Boivin et al. 2018; Dunhill et al. 2018). While many coral species survived the extinction and diversified during the earliest Jurassic, survivors were frequently solitary and did not commonly construct reefs (Leinfelder et al. 1994; Hodges and Stanley 2015; Stanley et al. 2018; Atkinson 2019). Reefs that were constructed during the Hettangian and Sinemurian occurred predominantly in extra-tropical latitudes, indicating a potential zone of increased survival and recovery within the northern Tethys (Popa 1981; Kiessling et al. 2009; Gretz et al. 2013, 2014).

One issue with investigating reef recovery in the Early Jurassic is the paucity of quantitative data on reef structure and composition. Most work on Early Jurassic reefs has focused on documenting faunal presence and broad ecology (e.g., Stanley and McRoberts 1993; Leinfelder et al. 1994; Hylton 1999; Fraser et al. 2004; Kiessling et al. 2009; Gretz et al. 2014; Echevarría et al. 2017; Sadki and Sha 2018; Brame et al. 2019), but has lacked detailed compositional data that would allow better ecological comparisons between reefs. There are notable exceptions that give detailed descriptions of the composition of individual reefs, which are useful when comparing how reefs changed through the Early Jurassic (e.g., Blomeier and Reijmer 1999; Della Porta et al. 2013; Gretz 2014; Mannani 2016; Boivin et al. 2018). Nevertheless, more data are needed to make meaningful comparisons across intervals, which is why this paper focuses on the collection of abundance data as well as microfacies analysis of a reef ecosystem.

As reef building and dwelling fauna diversified throughout the Early Jurassic, reef construction and the importance of certain faunal associations also evolved. Tracking how these reefs changed during an environmentally and ecologically turbulent time can provide insight into

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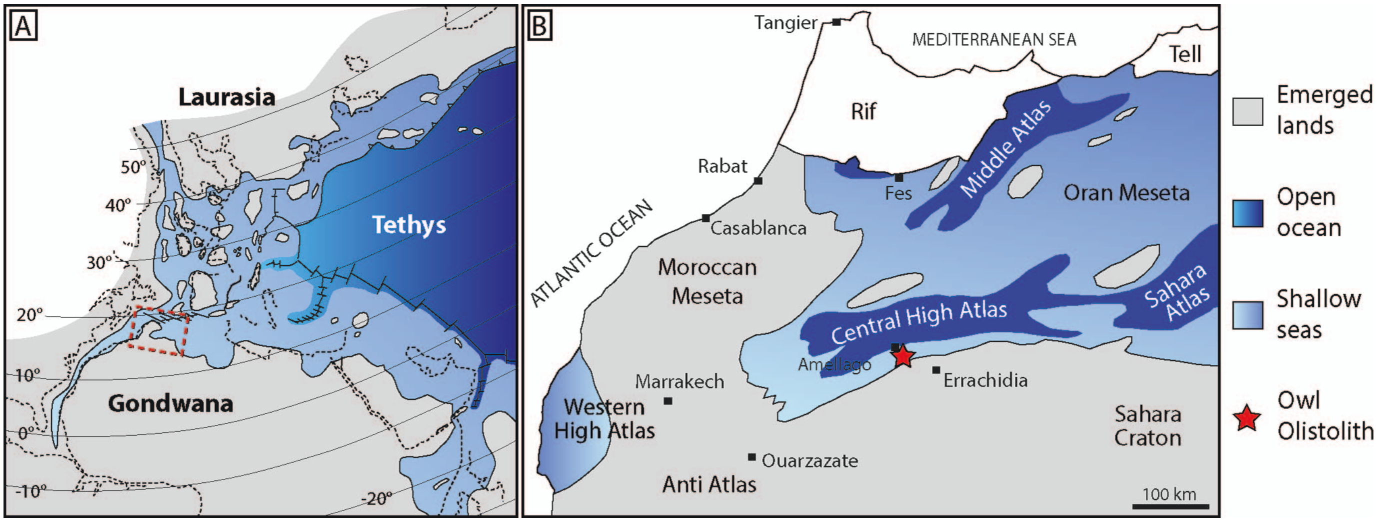


FIG. 1.—A paleogeographic map of the Atlas Rift zone during the Early Jurassic. **A**) The Atlas rift zone formed between Gondwana and Laurasia and was connected with the Tethys Ocean. **B**) Owl Olistolith's position in the Atlas Rift Zone and the location of the modern Central High Atlas. Modified from Bassoulet et al. (1993).

the recovery process. For instance, we know there is a general trend towards higher proportions of scleractinian corals within reefs throughout Morocco's Early Jurassic (Chafiki et al 2001; Sadki and Sha 2018). Recent work documented higher coral diversity during the Pliensbachian Stage than has previously been reported (Melnikova and Roniewicz 2020; Vasseur and Lathuilière 2021), but how environmental changes caused shifts in Pliensbachian reef building regimes is still being assessed. Ongoing work on the Early Jurassic focuses on establishing a clear connection between environmental setting and reef composition. Here, we quantitatively document the faunal components of an olistolith shed from a late Sinemurian—early Pliensbachian reef.

GEOLOGIC SETTING

The Atlas basin in Morocco began rifting during the Late Triassic (Beauchamp et al. 1999), opening new shallow water environments in tropical latitudes near the Tropic of Cancer (Fig. 1) (Elmi 1996; Elmi et al. 1999; Warme 1988). The rift zone would eventually contain diverse ecosystems (Leinfelder et al. 1994; Della Porta et al. 2013; Brame et al. 2019), but recovery from the end-Triassic extinction was slow (Lathuilière and Marchal 2009; Boivin et al. 2018). For the first several million years of the Jurassic, despite the presence of shallow subtidal environments, large scale subtidal carbonate build-ups did not exist (Wilmsen and Neuweiler 2007). Basin-wide, primary production was planktonic, while shallow subtidal areas of the basin were dominated by benthic heterotrophs such as brachiopods, crinoids, and framework-building sponges (Wilmsen and Neuweiler 2007). In the middle Sinemurian, sponge-algal mounds composed of subphotic siliceous sponges and microbial stromatolites formed within storm wave base in subsiding areas of the rift zone (Chafiki et al. 2004).

Sea level rise in the early Sinemurian led to the development of carbonate ramps within the rift zone (Warme 1988; Verwer et al. 2009). Renewed rifting in the late Sinemurian and the early Pliensbachian caused established carbonate ramps to rift apart and become isolated (Blomeier and Reijmer 1999). The isolated areas developed into more complex, high-relief carbonate platforms such as Djbel Bou Dahar (Blomeier and Reijmer 1999; Verwer et al. 2009). By the late Pliensbachian, diverse assemblages and thriving reef ecosystems were established throughout the Atlas rift zone (Leinfelder et al. 1994; Della Porta et al. 2013; Sadki and Sha 2018).

The Central High Atlas Mountains of Morocco (Fig. 2) contain an expanded record of carbonate deposition through the Jurassic. The well-exposed Aberdouz Formation near Amellago, Morocco (Fig. 3) contains micro-olistoliths of Pliensbachian reef material containing corals and other reef builders, such as lithiotids (Boivin et al. 2019). One of these is Owl Olistolith, a reef block which detached from a nearby carbonate platform to the south during the early Pliensbachian (Boivin et al. 2019) and was redeposited within hemipelagic marls, calciturbidites, and slump deposits (Carte géologique du Maroc 1997). The ammonites *Fuciniceras* gr. *volubile-pantanelli*, *Reynesoceras* gr. *mellahense-peyrei*, and *Galaticeras aegoceoides*, present within nearby deposits, confirm deposition within the Carixian (early Pliensbachian) (Boivin et al. 2019).

MATERIALS AND METHODS

Owl Olistolith (Fig. 4) is located within the Amellago region of the Central High Atlas Mountains in Morocco (Fig. 3) (Boivin et al. 2019). The olistolith material is distinct from the surrounding marls in relief and composition: a singular block stands eight meters above the surrounding strata and is composed of carbonate boundstones. Nineteen fist-sized hand samples with vertical, but not horizontal, orientations recorded were collected from all sides of the micro-olistolith to ensure complete community representation (Fig. 5); samples are now curated in the Non-Vertebrate Paleontology Lab at the University of Texas at Austin (see Online Supplemental File data for specimen numbers). The genera and species of corals and foraminifera were identified when possible, and each taxon's temporal range determined. Taxa which existed prior to the end-Triassic extinction were classified as survivor taxa, and those that originated in the Jurassic were classified as newly diversified taxa.

From the 19 hand samples, 24 (50 × 75 mm) thin sections were made. The thin sections were scanned using a Zeiss Axio M2m Imager petrographic microscope to create digital thin sections at 2.5× magnification. The digital slides were loaded into JMicrovision software and point counted using a random grid with 250 points per slide. Grains were broadly categorized into 13 groups: corals, microbialites, green algae, red algae, bivalves, gastropods, brachiopods, foraminifera, intraclasts, microproblematica, echinoderm fragments, and two generations of cement (early or isopachous cement and blocky cement). The percent composition of each grain type was then calculated.

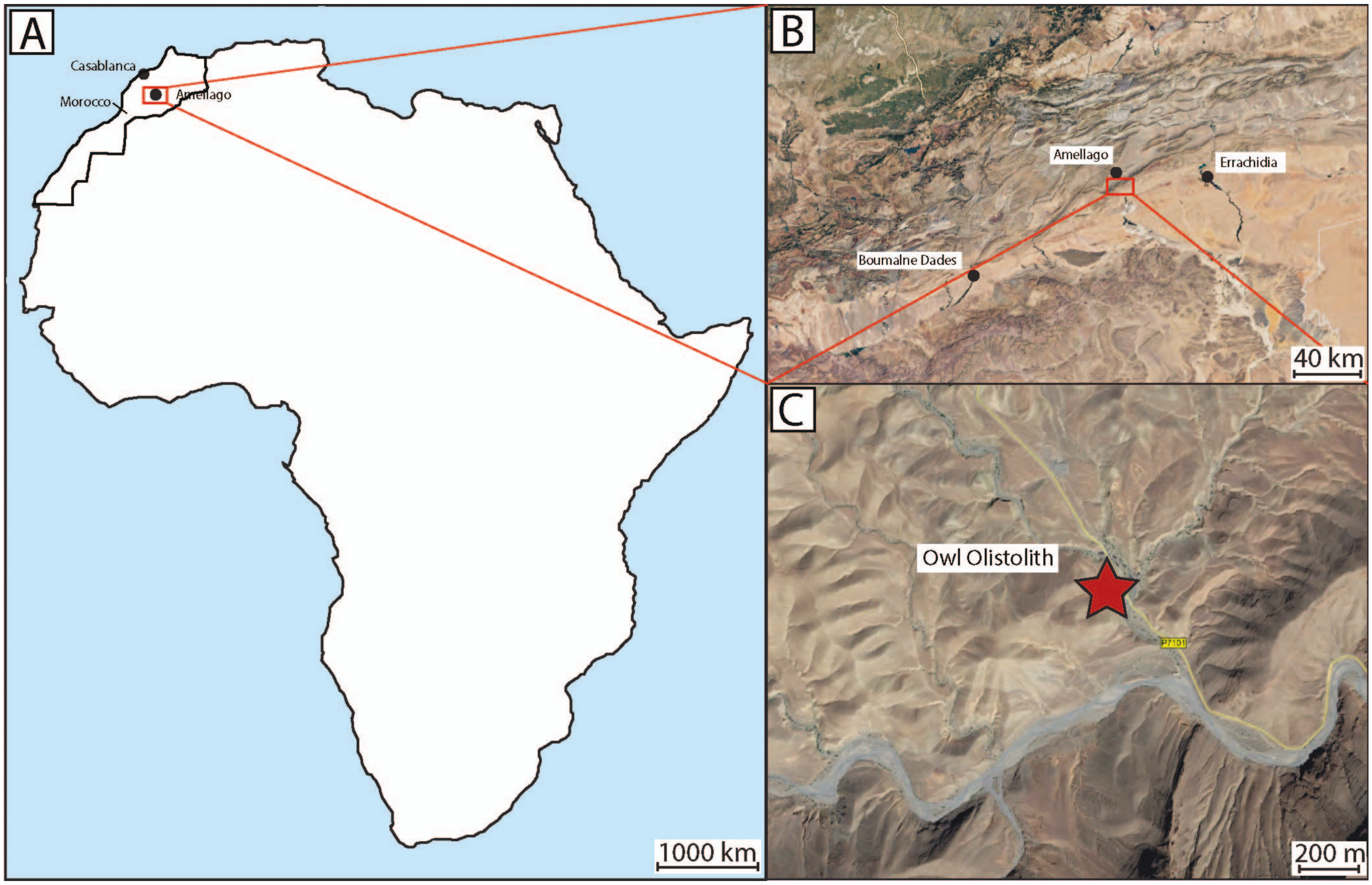


FIG. 2.—The position of Owl Olistolith within Modern-day Morocco, Africa. **A**) A map of Africa highlighting the location of Morocco. **B**) Satellite view of Morocco on the Northwest edge of Africa. Note the proximity of Owl Olistolith and the inset box to Amellago. **C**) The location of Owl Olistolith (N31.93348°W 5.00198°) near Amellago, Morocco, in the Central High Atlas Mountains.

A hierarchical cluster analysis was used to assess the constituents of the block and identify distinct facies across samples. The percent composition for each component was determined using point count data and the similarity between samples was determined with a similarity profile permutation test (SIMPROF) and a cluster analysis using Primer statistical software (v. 7) and methods from Somerfield and Clarke (2013), and Bonuso et al. (2020). The relative abundance data was standardized by squaring it and then a Bray-Curtis similarity test was used to determine which facies were significantly different (5%) and to group the samples into those facies.

RESULTS

Owl Olistolith has an overall composition of ~ 19% corals and ~ 60% microbialites, classifying it a coral-microbial reef. The block is identified as a micro-olistolith (*sensu* Abbate et al. 1970) based on its position within pelagic marls and its size (~ 640 m^3: 8 m high, by 10 m deep, by 8 m wide). It is composed of reefal bindstone containing microbialites and corals, which grew and cemented in place before detaching from the carbonate platform during the late Sinemurian or early Pliensbachian. The most abundant biota of the olistolith are microbialites and corals, which built the framework of the reef. In outcrop, the density of corals varies across the block, with rare corals on the west face of the block grading into more coral-dense areas to the east. Microbialites are a substantial component of all thin sections, consistently binding reefal constituents and filling the gaps between corals. The texture of these microbialites varies from structured stromatolitic domes to micrite with a clotted texture (Fig. 6). Corals, cements, and intraclasts make up the next largest components of the reef, whereas sponges, microproblematica, foraminifera, and assorted skeletal fragments are minor biotic components (Fig. 7, Table 1). Additionally, there are rare examples of macro-borings, and although they are not represented in our sampling, there were rare occurrences of large lithiotid and lithiotid-associated bivalves, such as *Lithioperna*, *Cochlearites*, and *Opisoma*, in this and similar olistoliths in the region (Boivin 2019).

Based on qualitative thin section analysis, samples are classified as microbial bindstones (GO-1, 7A, 13, 15, 16B, 17B, 19), coral-microbial bindstones (GO-7B, 12, 14, 16A, 18), and sponge-coral-microbial bindstones (GO-17A) following Embry and Klovan's (1971) modification of the Dunham (1962) Carbonate classification scheme. These facies seen in thin sections correlate with the west-east change observed in outcrop. Hierarchical cluster analysis identified three facies at a significance level of 5% (Fig. 8), the two dominant microfacies throughout the block are facies A, where microbialites make up ~ 52% to 94% of the point counted sample (microbial bindstones), and facies B, where corals make up ~ 14% to 72% and microbialites make up ~ 23% to 50% of the sample (coral-microbial bindstones). Facies C is only represented by sample GO-17A, which contains 10% sponge material by volume in addition to ~ 78% microbialites and 2% corals. Although some sponges were observed in the field, samples GO-17 and GO-16 are the only hand samples which contain sponge material.

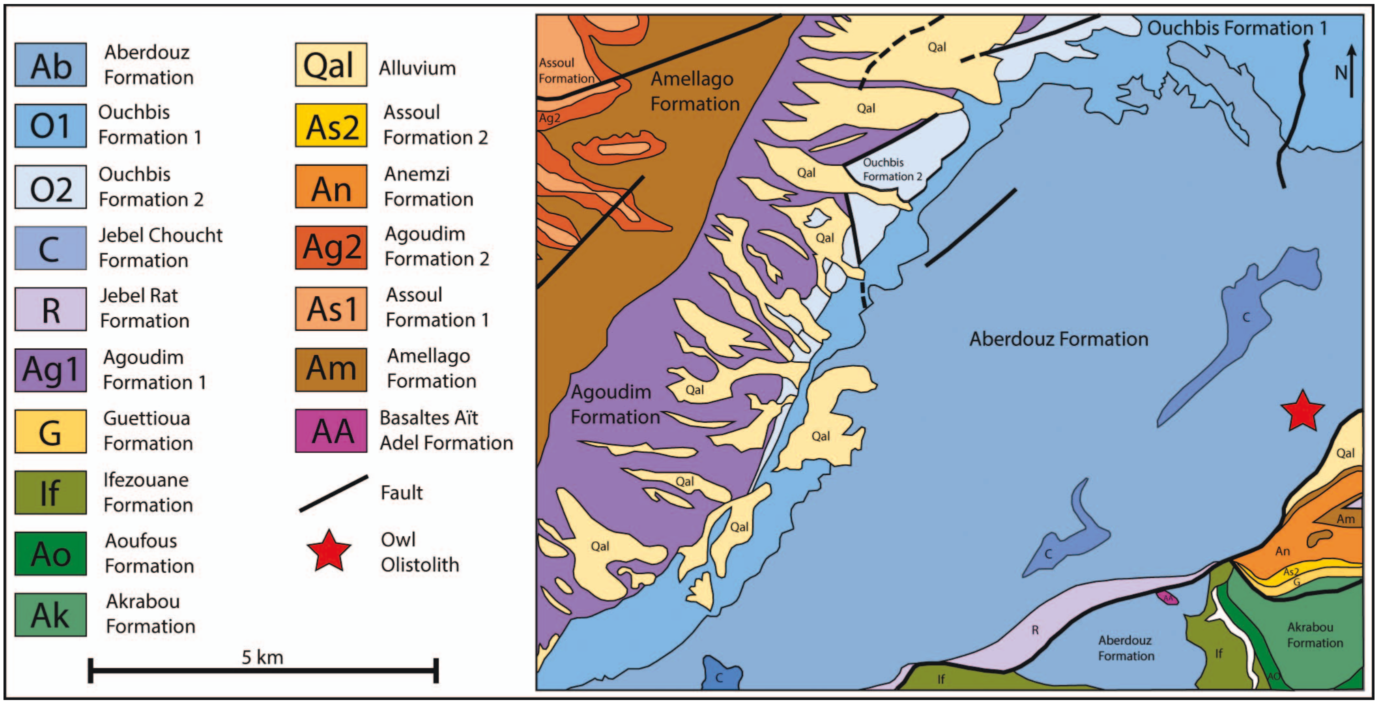


FIG. 3.—A geologic map of the Amellago area of Morocco, in the Central High Atlas Mountains (modified from Carte géologique du Maroc 1997). Owl Olistolith was deposited in the basinal Aberdouz Formation after detaching from a carbonate platform to the south of its current location.

In the olistolith's current position, the coral-microbialite facies is found on the east side of the block, and the microbialite facies on the west side (Fig. 5). The west side of the block has a paucity of corals; although sparse, mostly solitary corals were observed in this part of the outcrop (Boivin 2019; Table 2), but the point-counted data presented here recorded zero coral occurrences. The framework of the western portion of the olistolith is almost entirely microbial, although it contains a similar proportion of minor constituents as the east side. Previously collected samples from the western edge of the block include five species of corals not found in this study (Table 2), but still confirm the trend of increasing coral density to the east (Boivin 2019) (Fig. 9).

Phaceloid, solitary, and cerioid corals constitute the primary framework builders within the coral-microbialite facies. Twelve unique corals were identified in the samples for this study, seven of which could be identified to the genus level (Fig. 9). Phaceloid corals include *Thecactinastraea fasciculata* Beauvais, 1986 (GO-14) and several indeterminable genera (GO-7B, 8, 9, 11). Solitary corals include *Coryphyllia capillaria* Vasseur and Lathuilère 2021 (GO-12), *Stylophyllopsis* sp. (GO-18), *Proleptophyllia* sp. (GO-18), and a member of the *Archaeosmiliidae* family, either *Archaeosmiliopsis* sp. or *Icaunhelia* sp. (GO-4). The cerioid coral is identified as *Hispaniastraea murciana* Turnšek et al., 1975 (GO-16, 17B) and the subdendroid coral as *Margarosmilia* cf. *gemminata* Beauvais, 1986 (GO-10A, 10B).

Previous collections include eight additional species (Boivin 2019; Table 2), consisting of the phaceloid coral *Araiophyllum triasicum* Cuif, 1975, solitary corals *Coryphyllia regularis* Cuif, 1975 and *Neorylstonia pseudocolumellata* Beauvais, 1986, cerioid corals *Chondrocoenia plana* Duncan, 1867 and *Lepidophyllia (Heterastraea) microcalix* Boivin 2019, and thamnasterioid corals *Eocomoseris*? cf. *minima* Melnikova et al., 1993, *Parastraeomorpha minuscula* Roniewicz, 1989, and *Periseris elegantula* d'Orbigny, 1850 (Boivin 2019).

Foraminifera are minor components of the overall composition of Owl Olistolith (less than 2%); however, many taxa are still identifiable and provide useful information for determining the depositional environment and age. Six genera of foraminifera could be identified, although only one to the species level (Fig. 10): *Glomospira* sp., *Glomospirella* sp., *Siphovalvulina* sp., *Mesoendothyra* sp., *Everticyclammina praevirguliana* Fuganoli 2000 and the encrusting *Placopsilina* sp.

Three species of microproblematica were also observed: *Lithocodium aggregatum* Elliott, 1956, *Thaumatoporella parvovesiculifera* (Raineri, 1922), and *Baccanella floriformis* Pantic, 1971. *Lithocodium aggregatum* and *Thaumatoporella parvovesiculifera*, much like the foraminifera, are generally suspended in the microbialites as minor biotic allochems (< 2% of microfacies composition). The microproblematica *Baccanella floriformis*, however, comprises about 26% of sample GO-9, forming a distinct horizon between coral and microbialites, showing that it potentially was a framework building organism under some circumstances.

Small skeletal fragments from gastropods, echinoids, brachiopods, and bivalves are distributed throughout the microbialites. The fragments are typically only 1–2 mm, but in one example from GO-18, the only sample collected that was not attached to the main block, a gastropod measuring 5.5 cm across was observed. These fragments are minor components of the overall reef, composing less than 2% of the volume. The borings present, potentially made by *Gastrochaenolites*, predominantly cut through corals and were bored while the block was still attached to the platform, as they are filled with primary micrite (Fig. 9C). Although rare, the green alga *Palaeodasycladus mediterraneus* Pia, 1927 was identified in samples GO-7B and GO-18.

The microbialite and coral structure of Owl Olistolith, as well as sediment and intraclasts within the reef, is cemented by isopachous early marine cement and blocky calcite, which has preserved the original orientation of the block. Several samples contained geopetal sediment (GO-5, 6,10A, 11, 16B, 18), which indicate the original up direction, with the exception of sample GO-5, which shows two differing orientations of geopetal sediment (Fig. 11). Within GO-5, a shell, originally cemented within the block, dissolved sometime after the olistolith settled in the basin; that void was filled with a secondary blocky calcite and crystal silt, which indicates the new orientation of the block. Differing orientations

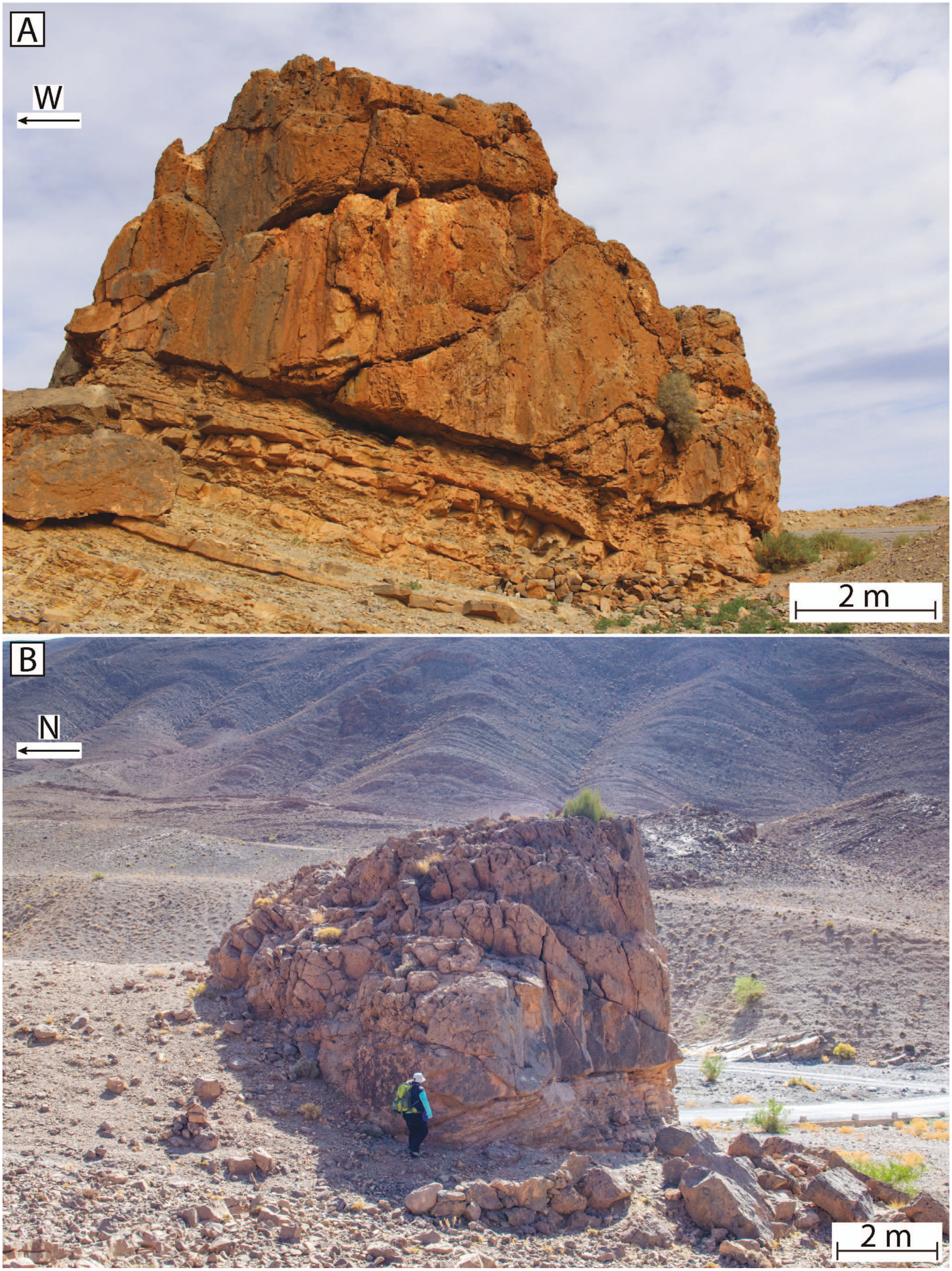


FIG. 4.—Owl Olistolith, a micro-olistolith outcropping in the Aberdouz Formation near Amellago, Morocco. Approximately 8 m × 10 m × 8 m, the block is a small piece of a larger reefal carbonate platform that grew during the Early Jurassic. **A**) The south side of the Olistolith. **B**) The west side of the Olistolith.

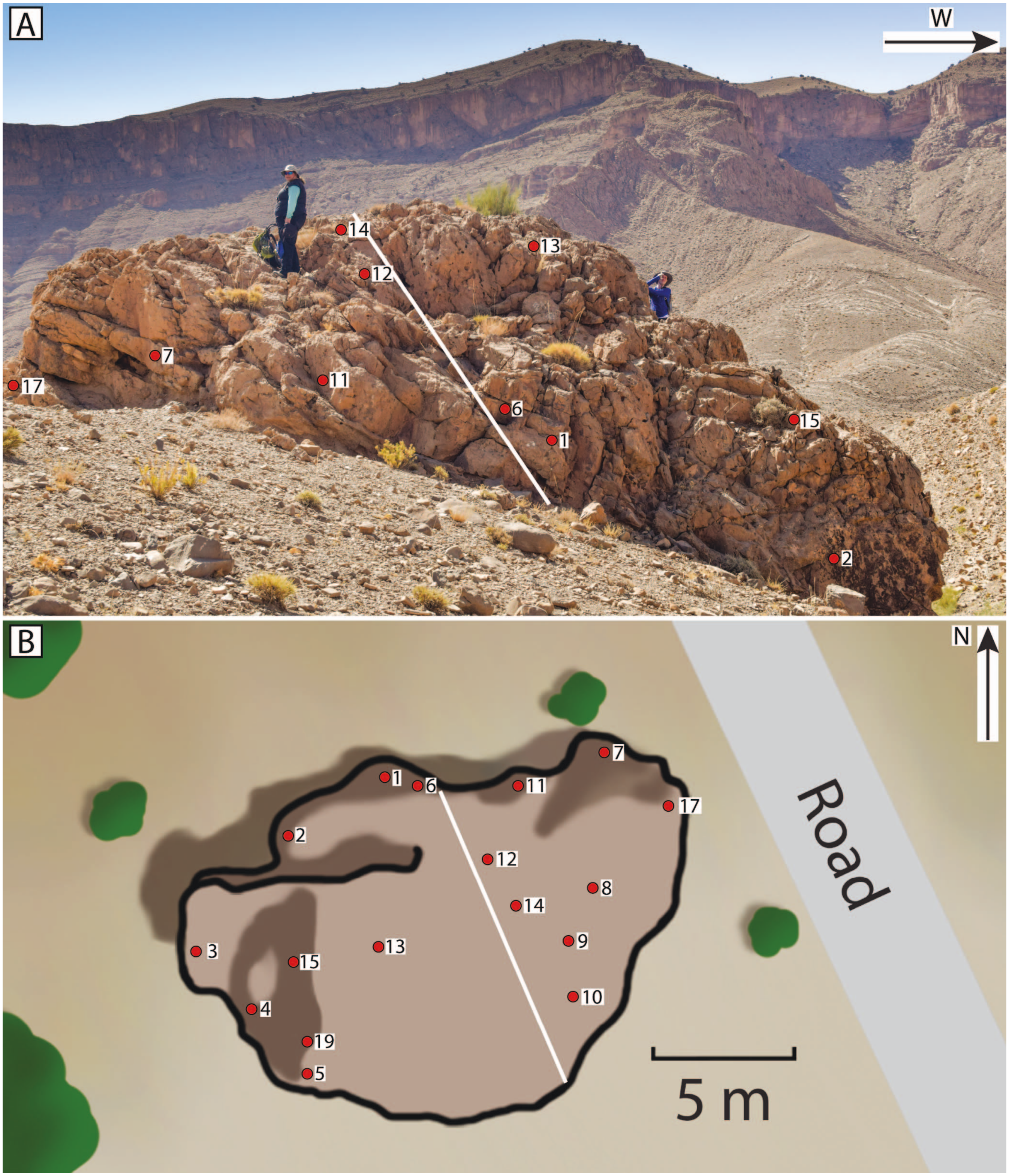


FIG. 5.—The location of collected samples distributed across Owl Olistolith. In outcrop, gradual facies change from east to west can be recognized, grading from predominantly microbialites in the east to a combination of corals and microbialites in the center and west of the olistolith. **A**) Sample locations from the North side of Owl Olistolith. **B**) Sketch of sample locations from above the olistolith. Although corals are present throughout the outcrop, point-counted thin sections from samples to the west of the white line contain no corals, whereas samples to the east contain abundant corals.

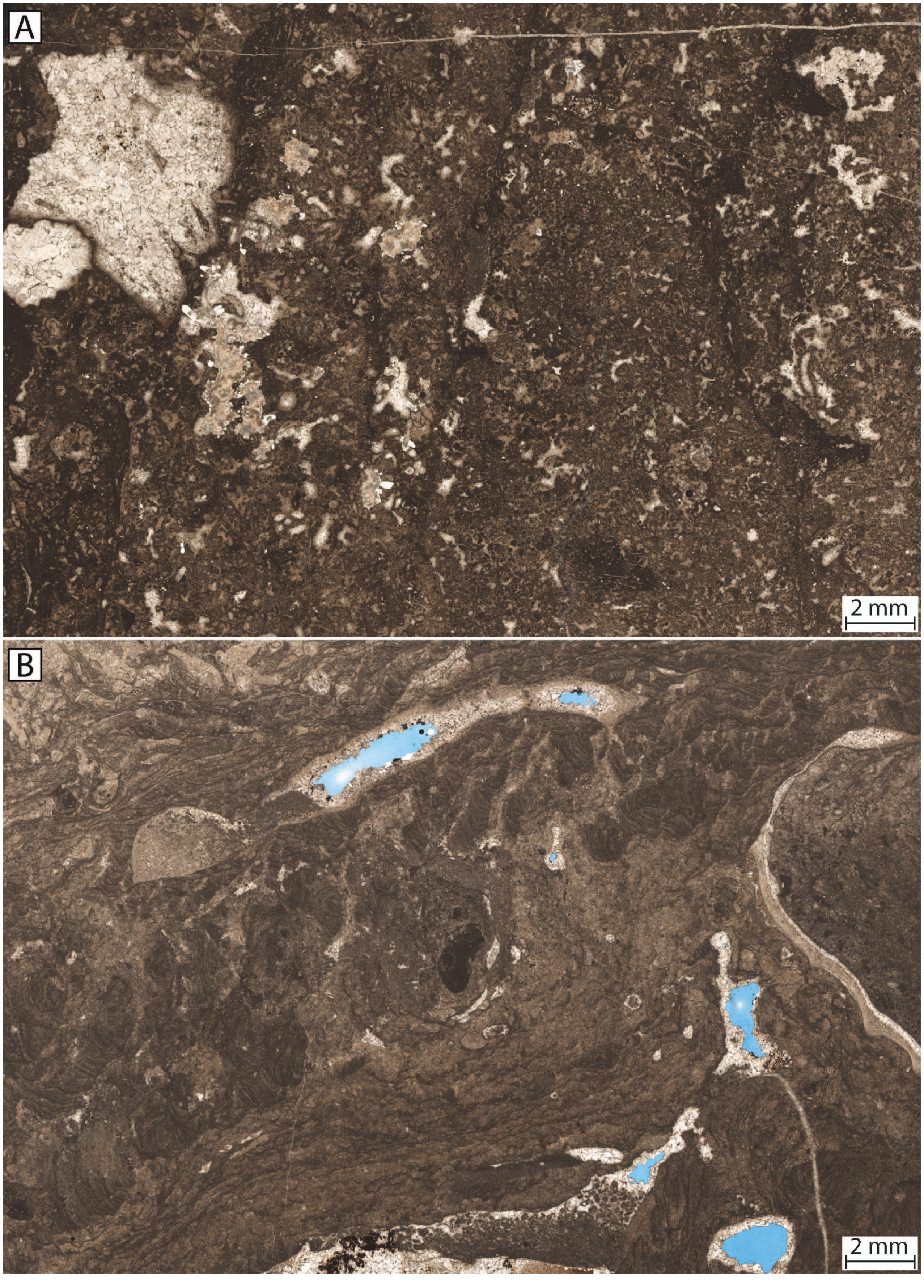


FIG. 6.—Plane polarized photomicrographs of the variations in microbialite texture throughout the olistolith. **A**) The microbialites form a clotted texture in thin section GO-3B. **B**) Stromatolitic domes in thin section GO-5.

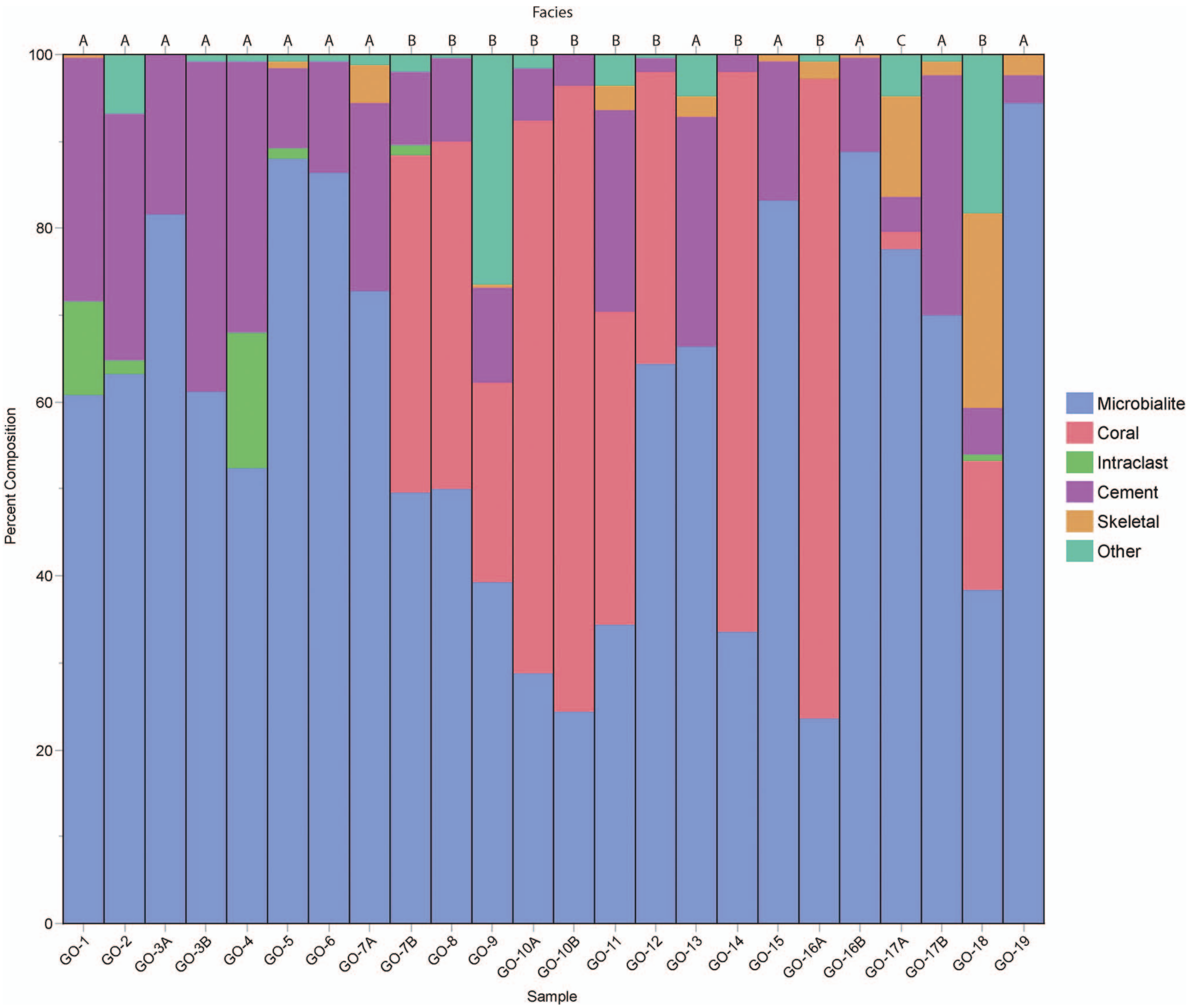


FIG. 7.—Percent composition of reefal components in Owl Olistolith, based on thin section point count data (Table 1). Two main facies exist and are defined by the presence or absence of corals. All samples contain a significant proportion of microbialites, and about half contain a significant proportion of corals. Additionally, there are small amounts of skeletal material from gastropods, bivalves, sponges, foraminifera, echinoderms, algae, and microproblematica throughout the olistolith (denoted here as "other). See Online Supplemental File for raw count data.

within one sample confirm that the block is a micro-olistolith, as it changed position after it broke off the main reef and was transported into the basin below. Any pores not fully cemented at the time of the break, or that experienced dissolution afterwards, allowed sediment to settle and be cemented at this secondary orientation. Because the horizontal orientation of the samples was not recorded, the original growth direction is not known.

Although there are scattered micro-olistoliths within the Amellago region (Boivin et al. 2019), the individual blocks are not part of a larger olistostrome deposit. The Aberdouz Formation contains turbidites and slump deposits, but the mudstones directly beneath Owl Olistolith contain bedding planes (Fig. 4) and the Aberdouz does not contain the large and small-scale heterogeneous material or megabreccias indicative of a larger olistostrome deposit (*sensu* Abbate et al. 1970). Therefore, it is likely Owl Olistolith was deposited here following an Early Jurassic detachment and was not part of a larger submarine landslide or slump.

DISCUSSION

Depositional History and Paleoenvironment

The paleoenvironmental setting and timing in which the Owl Olistolith reef facies grew can be interpreted based on the facies and taxa identified. Compared to the Hettangian–Sinemurian ecosystems, the presence of a more diverse foraminifera community indicates environmental conditions of the western Tethys had stabilized since the conclusion of the end-Triassic extinction (Schmiedl et al. 2000; Fugagnoli 2004; Sevillano et al. 2020). Larger foraminifera, like *E. praevirguliana* and *Mesoendothyra*, are common in oligotrophic carbonate platform environments with consistent

TABLE 1.—*The percent composition of identifiable allochems within Owl Olistolith. Abundance in each sample is shown as a percentage of the 250 points counted on each slide. Raw counts can be found in the Online Supplemental File.*

Sample	Microbialite	Coral	Intraclast	Early cement	Blocky calcite	Gastropod	Bivalve	Brachiopod	Sponge	Foram	Dolomite	Quartz	Annelid	Echinoderm	Pore	Green algae	Red algae	*Bacanella*
GO-1	60.8	0	10.8	25.2	2.8	0	0	0	0	0.4	0	0	0	0	0	0	0	0
GO-2	63.2	0	1.6	15.6	12.8	0	0	0	0	0	4.8	1.6	0.4	0	0	0	0	0
GO-3A	81.6	0	0	9.2	9.2	0	0	0	0	0	0	0	0	0	0	0	0	0
GO-3B	61.2	0	0	27.6	10.4	0	0	0	0	0	0.4	0.4	0	0	0	0	0	0
GO-4	52.4	0	15.6	28.8	2.4	0	0	0	0	0	0.4	0.4	0	0	0	0	0	0
GO-5	88	0	1.2	5.2	4	0	0	0.8	0	0	0	0	0	0	0.8	0	0	0
GO-6	86.4	0	0	11.6	1.2	0	0	0	0	0	0.8	0	0	0	0	0	0	0
GO-7A	72.8	0	0	20.4	1.2	0.8	0.8	2.8	0	0	0	0	1.2	0	0	0	0	0
GO-7B	49.6	38.8	1.2	8	0.4	0	0	0	0	0	0	0	0	0	1.2	0.8	0	0
GO-8	50	40	0	9.6	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0
GO-9	39.3	23	0	7.4	3.5	0	0	0	0	0.4	0	0	0	0	0	0	0	26.4
GO-10A	28.8	63.6	0	5.2	0.8	0	0	0	0	0	0	1.6	0	0	0	0	0	0
GO-10B	24.4	72	0	3.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GO-11	34.4	36	0	22.8	0.4	0	0	0.4	0	0	0.8	0	0	2.4	2.8	0	0	0
GO-12	64.4	33.6	0	0.8	0.8	0	0	0	0	0	0	0	0	0	0.4	0	0	0
GO-13	66.4	0	0	24.8	1.6	1.2	0.4	0.8	0	0	0	0	3.6	0	1.2	0	0	0
GO-14	33.6	64.4	0	1.6	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
GO-15	83.2	0	0	11.6	4.4	0	0	0	0	0.8	0	0	0	0	0	0	0	0
GO-16A	23.6	73.6	0	0	0	0	0	0	2	0	0	0	0	0	0.8	0	0	0
GO-16B	88.8	0	0	10.4	0.4	0	0.4	0	0	0	0	0	0	0	0	0	0	0
GO-17A	77.6	2	0	4	0	0	0.8	0.4	10	0	2.8	0	0	0.4	2	0	0	0
GO-17B	70	0	0	27.2	0.4	0	0	0	0	1.6	0	0	0	0	0.8	0	0	0
GO-18	38.4	14.8	0.8	4.6	0.8	22.4	0	0	0	0	0	12.2	0	0	0	0	6	0
GO-19	94.4	0	0	3.2	0	0	0	0	0	0	0	0	0	2.4	0	0	0	0

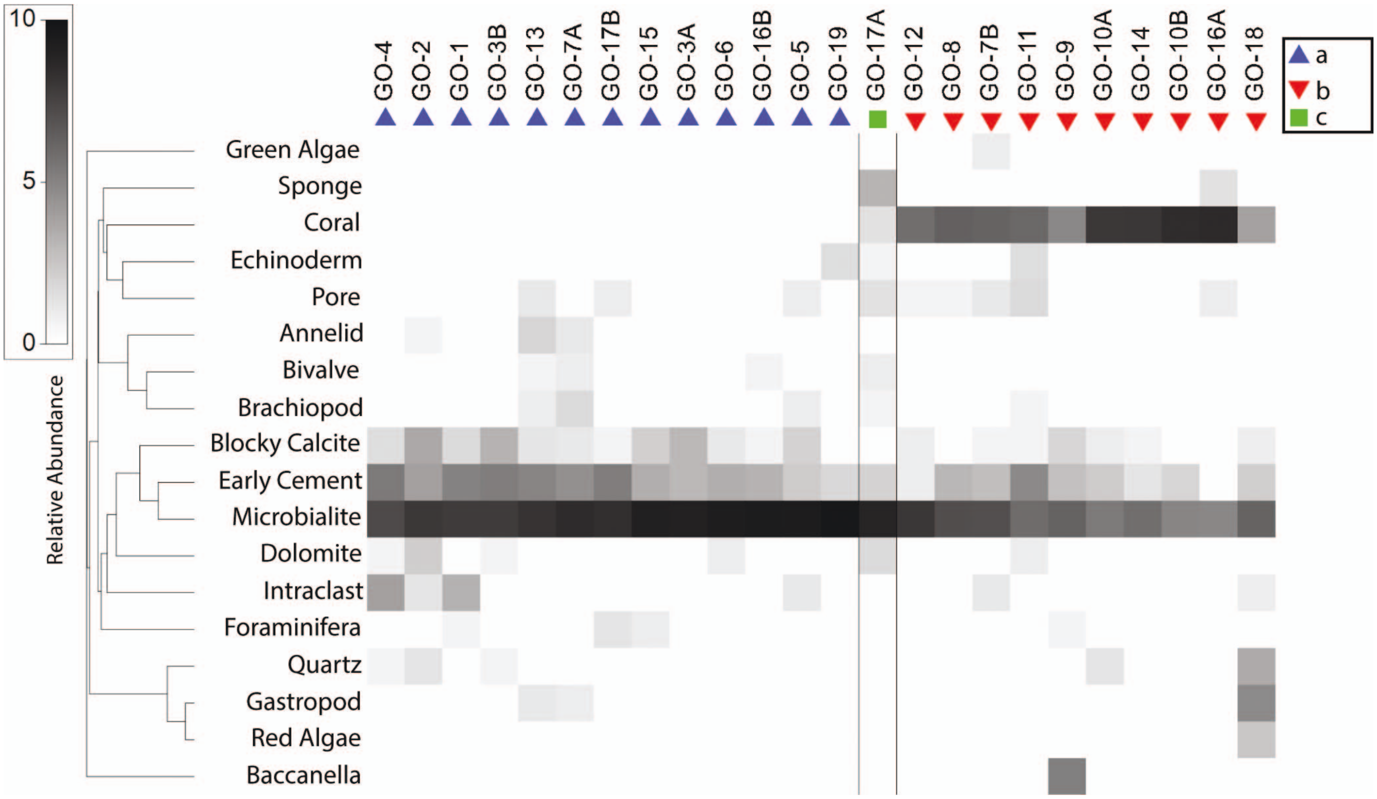


FIG. 8.—Three facies (defined by composition) identified by hierarchical cluster analysis. The relative abundance data was standardized by squaring it and then a Bray-Curtis similarity test was used to determine which facies were significantly different (5%) and to group the samples into those facies.

TABLE 2.—*A comparison between corals found on the east and west side of Owl olistolith by Boivin (2019), this study, and their colony integration type.*

Genus	East	West	Integration
Araiophyllum	x		Phaceloid
Chondrocoenia		x	Cerioid
Coryphyllia	ox	x	Solitary
Eocomoseris	x		Thamnasterioid
Archaeosmilid	o		Solitary
Hispaniastraea	ox		Cerioid
Lepidophyllia	x	x	Cerioid
Margarosmilia	o		Subdendroid
Neorylstonia	x		Solitary
Parastraeomorpha		x	Thamnasterioid
Periseris		x	Thamnasterioid
Proleptophyllia	o	x	Solitary
Stylophyllopsis	o		Solitary
Thecactinastraea	o		Phaceloid

o= This Study x= Boivin (2019)

temperatures and alkalinities (Fugagnoli 2004; Sevillano et al. 2020), so their presence in Owl Olistolith suggests a similar environment.

The presence of photosynthesizing green algae, *Palaeodasycladus mediterraneus*, indicates a shallow water environment within the photic zone, likely on the shelf margin (Moreira et al. 2000; Boudagher-Fadel et al. 2001). The benthic community of *Mesoendothyra* sp. and the encrusting *Placopsilina* foraminifera are also indicative of a shallow water ramp or platform zone (Omaña and González Arreola 2008). Furthermore, *E. praevirguliana* has been found to be restricted to shallow marine platforms (Fugagnoli 2000). These fauna and sedimentological features indicate reef growth above fair-weather wave base in the photic zone, situated on the edge of a carbonate platform.

The microproblematica *Lithocodium aggregatum*—either a filamentous-septate green algae (Schlagintweit et al. 2010) or a lituolid foraminifera (Schmid and Leinfelder 1996)— is almost exclusively found in tropical, shallow-water environments (Leinfelder et al. 1993; Schmid and Leinfelder 1996). *Baccanella floriformis* is a species indicative of shallow, high-energy conditions, and is a common paleoenvironmental indicator for slope/marginal marine systems of Ladinian to Pliensbachian deposits (Rüffer and Zamparelli 1997; Martini et al. 2004). A more recent study supports this assertion, documenting *Baccanella floriformis* within the Djebel Bou Dahar carbonate platform in the High Atlas, Morocco, along the uppermost slope/margin (Della Porta et al. 2013). *Thaumatoporella parvovesiculifera* has been found commonly within *Bacinella irregularis-Lithocodium* microbialite facies, which can range in environment from deep water lagoons to barriers and shoals (Bucur et al. 2005). *Bacinella irregularis* does not occur within our studied sections; however, the *Thaumatoporella-Lithocodium*-microbialite association may indicate the potential for *Bacinella-Lithocodium* microbialite facies within outer parts of the reef from which the olistolith was sourced (Bucur et al. 2005).

Although the large, outer platform reef community grew in warm shallow water, when the micro-olistolith detached from the platform edge, it was transported into the deeper, marl-filled basin of the Aberdouz Formation. Differing geopetal sediment from our samples record at least two different orientations (Fig. 11). In addition to an original, *in situ* geopetal sediment, a second geopetal fill occurs as crystal silt within a shell that was dissolved during diagenesis (Fig. 11). Therefore, the olistolith spent time in at least two distinct orientations during its redeposition.

The foraminifera and green algae found within Owl Olistolith indicate that the reef grew in the Sinemurian to early Pliensbachian. *Everticyclammina praevirguliana* is the oldest Jurassic species of the *Everticyclammina* genus and has a range that stretches from the mid-late Sinemurian to the Pliensbachian (Fugagnoli 2000; BouDagher-Fadel and Bosence 2007). The genus *Mesoendothyra* can be found beginning in the early Sinemurian and throughout the Pliensbachian (Sevillano et al. 2020), and *P. mediterraneus* was present from the Hettangian to the Pliensbachian (Sokač 2001; Sevillano et al. 2020). This age determination is in agreement with the ammonite biostratigraphy from the strata in which the olistolith was deposited, which indicates deposition in the Carixian (early Pliensbachian, ~ 187.7 Ma) (Boivin et al. 2019). The timing of the olistolith break cannot be constrained further. It is possible that the reef grew in the middle to late Sinemurian and then broke off and was redeposited in the early Pliensbachian, or growth and redeposition could have been broadly contemporaneous in the early Pliensbachian.

Importance of Survivor Taxa

The important role of survivor taxa for reef recovery in the wake of the end-Triassic extinction has been discussed previously (Stanley 1988; Roniewicz and Morycowa 1989; Stanley and McRoberts 1993; Leinfelder et al. 1994; Kiessling et al. 2009). Recently, however, it has been suggested that the end-Triassic extinction may not have been as severe for corals as once thought (Vasseur et al. 2021); corals thought to have gone extinct at the end of the Triassic have increasingly been found to have survived well into the Jurassic (Boivin 2019; Vasseur et al. 2021). During the earliest Jurassic (Hettangian-Sinemurian), newly evolved corals were present, but infrequently built reef structures (Beauvais 1984, 1985, 1986; Leinfelder et al. 1994). Once environmental conditions were favorable, surviving taxa began to build reef structures once more, especially within the northern Tethys (Leinfelder et al. 1994; Fugagnoli 2004; Gretz et al. 2014; Sadki and Sha 2018).

The Owl Olistolith coral genera and species (Fig. 9, Table 2) are a mix of surviving Triassic taxa and newly evolved Early Jurassic taxa. The corals C. *capillaria*, *C. regularis*, *Stylophyllopsis*, *A. triasicum*, and *P. minuscula* evolved in the Triassic (Frech 1890; Cuif 1975; Turnšek et al. 1975; Roniewicz 1989; Vasseur and Lathuilière 2021), whereas *Proleptophyllia*, *N. pseudocolumellata*, *M. gemminata*, *H. murciana*, *C. plana*, *E. minima*, *L. microcalix*, and *C. elegantula* all evolved in the Early Jurassic (Beauvais 1986; Melnikova et al. 1993; Vasseur 2019; Vasseur and Lathuilière 2021). The Archaeosmiliid coral is either a branch of the phaceloid *Archaeosmiliopsis* sp., or a solitary *Icaunhelia* sp., but in either case the genera evolved in the Early Jurassic (Melnikova 1975; Beauvais 1986; Melnikova and Roniewicz 2017; Vasseur and Lathuilière 2021), and *Thecactinastraea fasciculata* is known only from the Jurassic (Beauvais 1986). Melnikova and Roniewicz (2017) put the genus *Thecactinastraea* in synonymy with *Phacelophyllia*; which is also the opinion adopted in Brame et al. (2019), but the priority is for *Thecactinastraea* and the first revisors Melnikova and Roniewicz (2017).

The foraminiferan genera found within the olistolith follow a similar trend; *Glomospirella*, *Glomospira*, and *Placopsilina* are long ranging taxa with temporal ranges that extend from as early as the Silurian to as late as the Eocene (Gall 1971; Gazdzicki 1983; Nocchi and Bartolini 1994; Omaña and González Arreola 2008). *Glomospirella*, especially, was previously thought to be heavily decimated by the end-Triassic extinction (Gazdzicki 1983); however, their presence within Owl Olistolith could suggest they were not as severely affected as previously thought.

Although Leinfelder et al. (1994) suggests most Early Jurassic reef taxa are survivors from the Late Triassic, Owl Olistolith clearly includes an important number of newly evolved Jurassic coral and foraminifera taxa. This observation is strengthened when the whole Pliensbachian coral assemblage is considered (Vasseur and Lathuilière 2021); Jurassic taxa overtook surviving Triassic fauna. Together, these results make it clear that during the Pliensbachian, surviving Triassic taxa—which played a significant role in reestablishing Early Jurassic reef ecosystems during the Hettangian—were overtaken by Jurassic taxa as the dominant structural

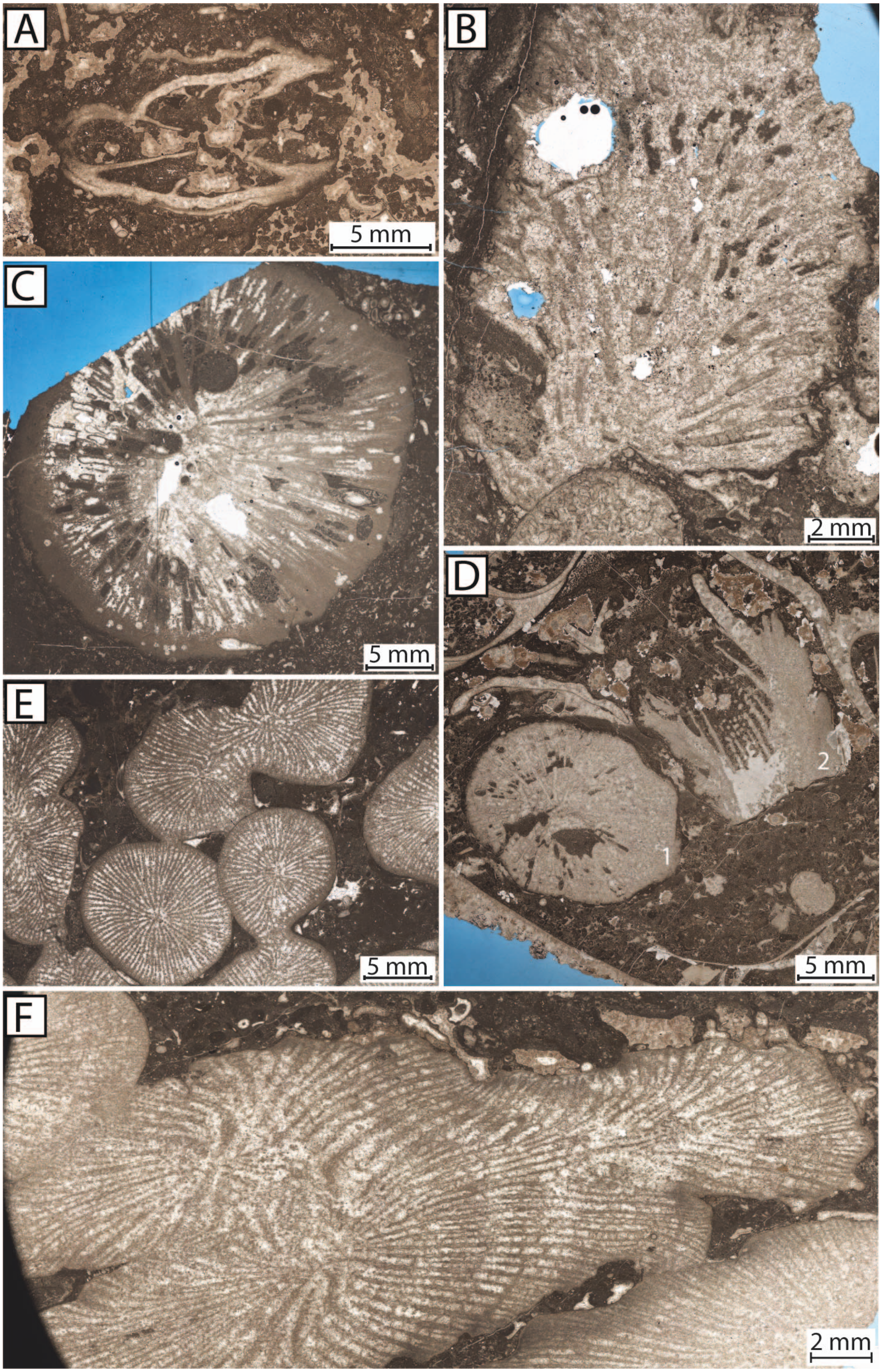
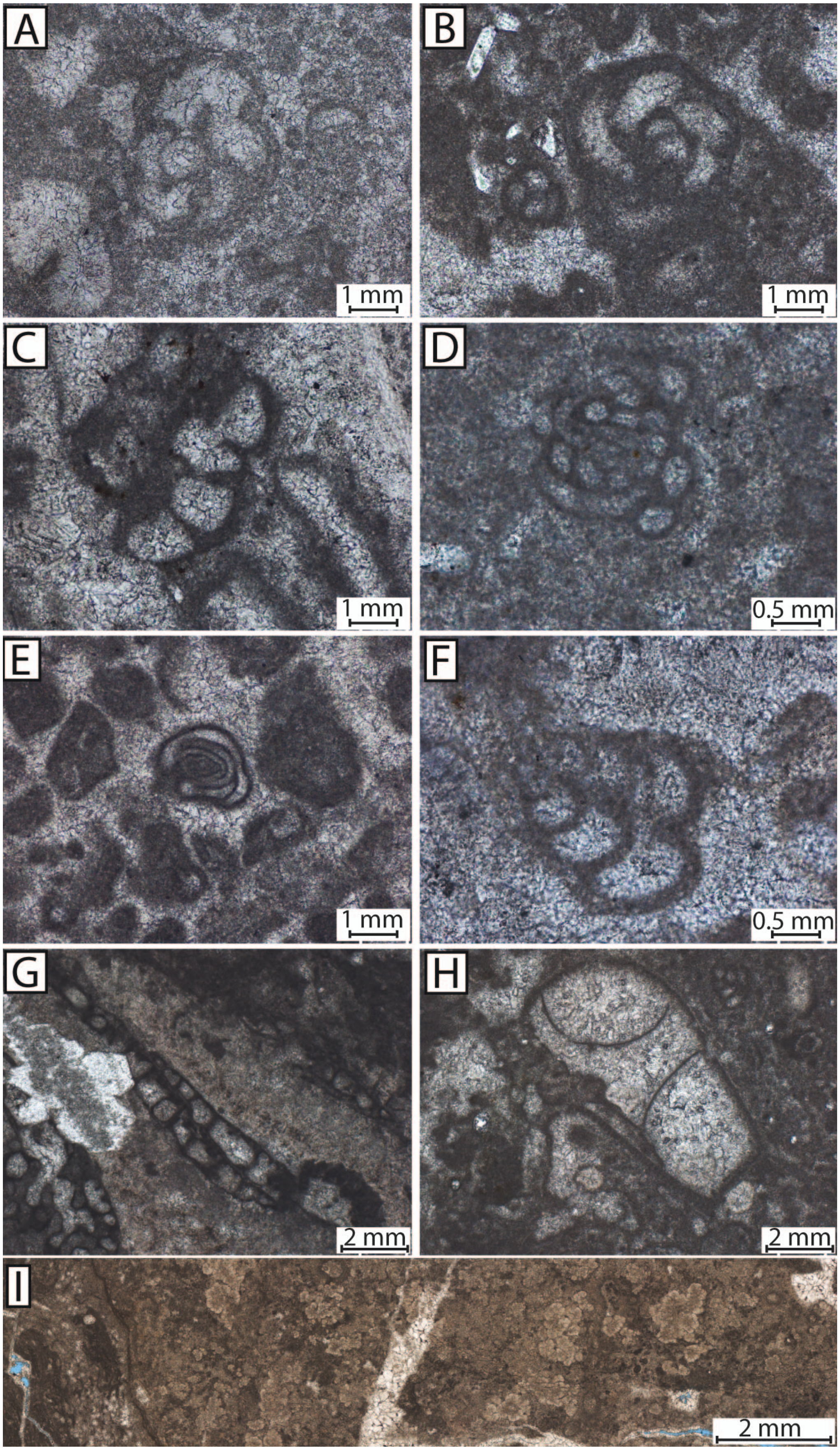


FIG. 9.—Plane polarized photomicrographs of Owl Olistolith corals. **A**) A coral in the Archaeosmiliidae family: *Archaeosmiliopsis*? sp. or *Icaunhelia* sp. (GO-4). **B**) *Hispaniastraea murciana* (GO-16). **C**) *Coryphyllia capillaria* with macro-borings filled with micrite (GO-12). **D**) 1: S*tylophyllopsis*? 2: *Proleptophyllia*? (GO-18). **E**) *Thecactinastraea fasciculata* (GO-14). **F**) *Margarosmilia* cf. *gemminata* (GO-10B).



FIG, 10.—Plane-polarized photomicrographs of Owl Olistolith foraminifera and microproblematica. **A**) *Everticyclammina praevirguliana* (GO-11). **B**) *Mesoendothyra* sp. (GO-1). **C**) *Placopsilina* sp. (GO-7B). **D**) *Glomospira* sp. (GO-1). **E**) *Glomospirella* sp. (GO-6). **F**) *Siphovalvulina* sp. (GO-1). **G**) *Lithocodium aggregatum*. (GO-17A). **H**) *Thaumatoporella parvovesiculifera* (GO-4). **I**) *Baccanella floriformis* (GO-9).

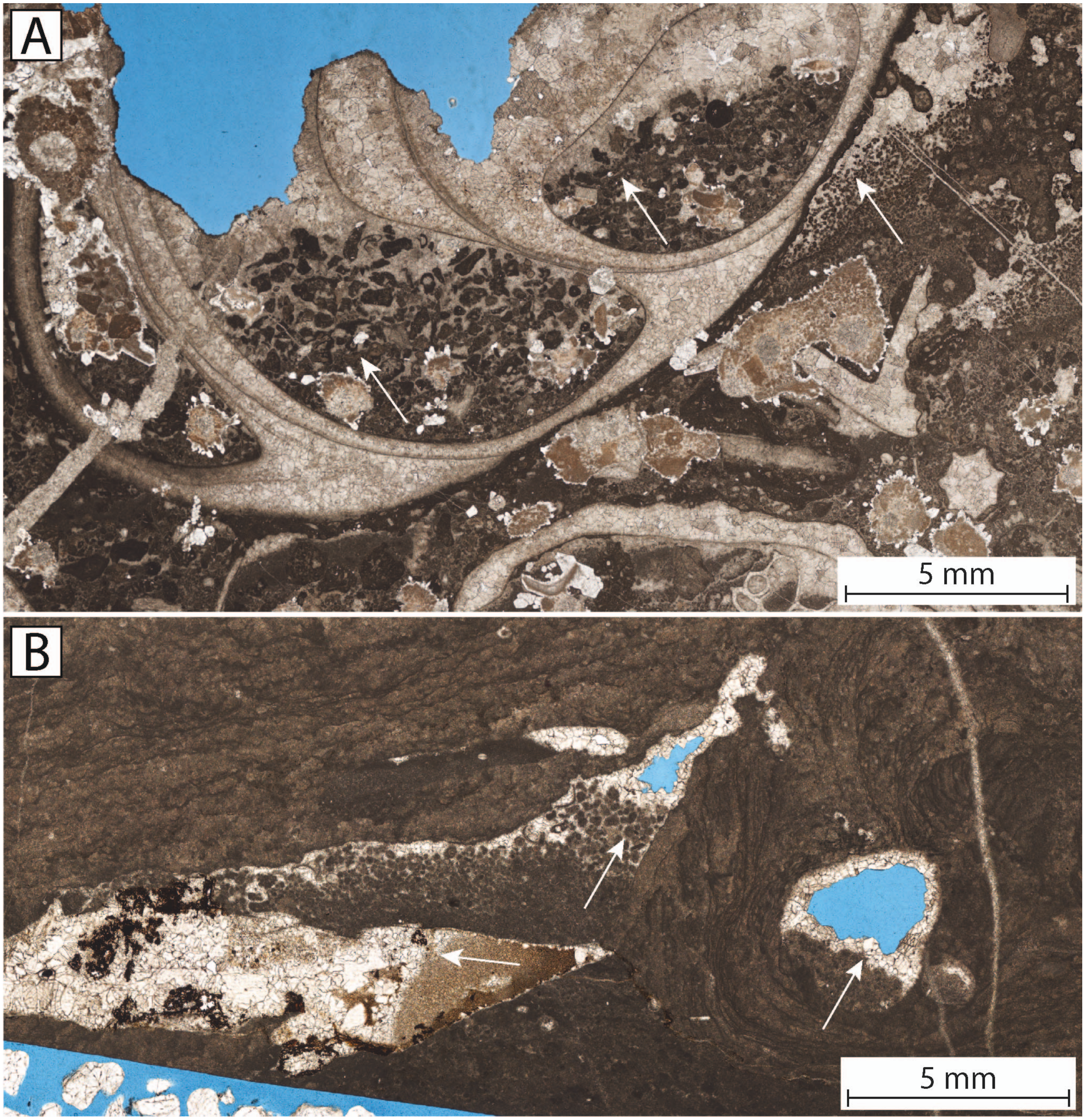


FIG. 11.—Plane polarized photomicrographs of geopetal sediment in Owl Olistolith (up direction noted by arrows). **A**) GO-18, all geopetal sediment is oriented the same direction. **B**) GO-5, geopetal sediment with two different orientations, which confirms that the olistolith is no longer in its original position.

reef components in Morocco (Boivin et al. 2019; Vasseur et al. 2021). The reef represented by Owl Olistolith is an example of a transitional coral community. In the early Pliensbachian, surviving coral taxa played a subordinate role in the construction of coral reefs. This was observed previously in Morocco (Boivin et al. 2019; Vasseur et al. 2021), and is the case for Owl Olistolith, so may be a hallmark of regional recovery.

Assessing the true importance of surviving taxa over newly evolved taxa in the recovery of Moroccan Jurassic reefs will require further quantitative documentation of reef communities as a whole during that time. Although study of the Early Jurassic coral record in Morocco has been limited, recent field campaigns and revisions have created a more comprehensive dataset of Early Jurassic corals and their temporal ranges (Vasseur et al. 2021).

These new data highlight that the recovery of reefs following the end-Triassic was punctuated by a severe two-phase extinction in the Early Jurassic, namely the Pliensbachian/Toarcian boundary and the Toarcian Oceanic Anoxic Event, which was likely comparable in severity to the end-Triassic extinction for corals (Vasseur et al. 2021).

Recovery Dynamics

Globally, reef community recovery from the end-Triassic extinction was slow (Kiessling et al. 2009; Echevarría et al. 2017; Atkinson 2019). Many coral species that survived the extinction and diversified during the earliest Jurassic (Lathuilière and Marchal 2009; Brandolese et al. 2019) were solitary and did not construct reefs (Leinfelder et al. 1994; Gretz et al. 2014; Hodges and Stanley 2015; Stanley et al. 2018; Atkinson 2019). With some exceptions, most reefal bioconstructions were small patch reefs until the Pliensbachian (Kiessling and Aberhan 2007; Kiessling et al. 2009; Gretz et al. 2013; Melnikova and Roniewicz 2017; Boivin et al. 2018). The Early Jurassic also contained structures formed predominantly of lithiotid bivalves (Fraser et al. 2004). These structures were distinctive of the time and were formed by associations between lithiotid and lithiotid-associated bivalves (mainly *Lithioperna*, *Cochlearites*, and *Opisoma)*, corals, and microbialites (Blomeier and Reijmer 1999; Fraser et al. 2004; Wignall et al. 2006; Verwer et al. 2009; Della Porta et al. 2013; Sadki and Sha 2018; Boivin 2019; Brame et al. 2019).

Pliensbachian reefs range from monospecific build-ups of lithiotids or corals to diverse constructions combining lithiotids, corals, sponges, and microbialites, and from small patch reefs to large carbonate platforms (Park 1983; Beauvais 1986; Fraser et al. 2004; Della Porta et al. 2013; Brame et al. 2019). Pliensbachian reefs in the United States and China form extensive, monospecific lithiotid beds (Jiarun and Maoqiao 1998; Fraser et al. 2004), while those in Argentina are built up by corals and contain only smaller, secondary bivalves (Morsch 2001). Spain, Italy, Slovenia, Oman, and Morocco all contain examples of Pliensbachian reefs where there is an interaction between corals and lithiotids (Brame et al. 2019). In Spain and Slovenia, for example, lithiotid beds are capped by diverse coral assemblages (Turnsek 1975; Geyer 1977; Buser and Debeljak 1995). Finally, sites in Morocco show Pliensbachian lithiotids and corals constructing framework together, with lithiotids often constituting the primary framework and corals assuming a secondary role (Turnsek 1975; Park 1983; Beauvais 1986; Leinfelder et al. 2002; Brame et al. 2019; Vasseur et al. 2019).

Owl Olistolith contains only sparse occurrences of lithiotids (Boivin 2019). Although this is potentially not representative of the carbonate platform as a whole, this portion of the reef is classified as a coral-microbialite reef. When compared to only those reefs known to be from the early Pliensbachian, Owl Olistolith, with at least 15 coral genera, does not appear particularly diverse or depauperate of coral taxa. The early Pliensbachian (~ 190 Ma) coral reef located in Murcia, Spain, contains 10 genera and 24 species of corals (Turnšek et al. 1975), while another in Mendoza, Argentina contains only three species from one genus (Morsch 2001). Although the taxonomy of these corals has been reported, the proportions of each as structural builders are lacking, so meaningful comparisons of abundance are not possible.

The platform Owl Olistolith grew on represents the increasing size and diversity of reef structures and carbonate platforms during the early Pliensbachian. The various corals found here are representative of solitary, cerioid, and phaceloid growth forms. The coral abundance (46%) in the coral-microbialite facies of Owl Olistolith is greater than earlier Sinemurian reefs which have had compositional data measured, such as the Le Perthus reef, a coral and oyster-microbialite reef, which showed an average coral composition of about 24% across four transects (Boivin et al. 2018). Owl Olistolith's coral abundance, however, is less than the younger Pliensbachian Djebel Bou Dahar, where corals represent up to 65% of the volume in facies dominated by corals and sponges (Della Porta et al. 2013). This general trend of increasing coral abundance in reefs through the Jurassic aligns with the eventual dominance of corals in the Middle/Late Jurassic (Stanley 1988; Wood 1995). It is important to note, however, that some reefs where composition data has been collected, such as Elmi's reef, break this trend and show that coral dominance in reefs was not a strictly linear process (Kiessling et al. 2009; Gretz 2014).

Owl Olistolith's composition is similar to other early Pliensbachian reefs in Morocco. While lower Pliensbachian Moroccan reefs are known for being dominated by lithiotid bivalves and various corals (Turnsek 1975), lithiotid occurrences are often limited to specific facies of a platform (Della Porta et al. 2013); therefore, low occurrences of lithiotid bivalves here may be a factor of limited platform representation given by a micro-olistolith, and not a mark of their paucity across the whole platform. Diverse coral genera seen within Owl Olistolith and other coral buildups and reef facies described within the Aberdouz, Choucht, Agoudim, and Maftah formations (Beauvais 1986; Vasseur 2019; Vasseur et al. 2021; Vasseur and Lathuilière 2021) confirm that both surviving Triassic corals and newly diversified corals were thriving in the early Pliensbachian of Morocco.

Diversity of reef-building corals, as well as other reefal organisms, would continue to increase throughout the Pliensbachian. In the later Pliensbachian, large platforms were occupied by a diverse grouping of organisms, including echinoderms, brachiopods, microbes, ammonites, sponges, foraminifera, gastropods, and corals (Blomeier and Reijmer 1999; Della Porta et al. 2013). Djbel Bou Dahar developed from a low-relief platform or ramp (Hettangian and Sinemurian) into a high-relief, steep-sided structure through the latest Sinemurian into the Pliensbachian (Merino-Tomé et al. 2012). The platform contains zoned reef areas dominated by (1) siliceous sponges and microbialites; (2) corals, calcareous sponges, and microbialites; (3) microbialites; and (4) lithiotid bivalves (Della Porta et al. 2013). This diversity peaked before the collapse of reefal environments at the end of the Pliensbachian (Beauvais 1984; Vasseur et al. 2021).

CONCLUSION

Owl Olistolith is a Sinemurian–early Pliensbachian micro-olistolith which grew on the edge of a large carbonate platform within shallow waters in the High Atlas Rift Zone. The reef that is recorded in the olistolith was constructed mainly by corals and microbialites; there are three facies, coral-microbialite bindstone, microbialite bindstone, and sponge-coral-microbialite bindstone. The coral-microbialite bindstone and microbialite bindstone grade from one to the other, while the sponge-coral-microbialite bindstone is rare. This study found 12 distinct corals (only seven identifiable genera) within the block; Boivin (2019) identified eight additional species. Of the 15 identified corals, five (C. *capillaria*, *C. regularis*, *Stylophyllopsis*, *A. triasicum*, and *P. minuscula*) are genera which survived the end-Triassic extinction, though some species are Jurassic, and 10 corals (*Thecactinastraea*, *Proleptophyllia*, *N. pseudocolumellata*, *M. gemminata*, *H. murciana*, *C. plana*, *E. minima*, *L. microcalix*, *C. elegantula* and an Archaeosmiliid genus) were newly evolved in the Early Jurassic. Although the olistolith contains a diverse assemblage of corals and foraminifera, it lacks the abundance of lithiotid bivalves commonly seen during the Sinemurian and Pliensbachian, however the studied material might not be representative of the reef ecosystem as a whole. The combined importance of newly evolved coral genera with longer-ranging coral and foraminiferan taxa in reef framework building documented from Owl Olistolith supports the hypothesis that surviving Triassic taxa were still important reef builders during the Pliensbachian while reestablishing reef ecosystems in the Moroccan Early Jurassic.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: https://www.sepm.org/supplemental-materials.

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