

## EARLY JURASSIC BENTHIC FORAMINIFERAL ECOLOGY FROM THE CENTRAL HIGH ATLAS MOUNTAINS, MOROCCO

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**ABSTRACT:** The Central High Atlas Mountains of Morocco have an extensive record of Lower Jurassic deposits from the Tethyan Ocean. In the Amellago region, Ziz Valley, and Dadès Valley several fossilized reef outcrops preserve benthic foraminifera spanning the Pliensbachian and Toarcian stages. This study analyzes benthic foraminiferal assemblage changes across the bi-phased extinctions at the Pliensbachian/Toarcian boundary and the Jenkyns Event (also referred to as the Toarcian Oceanic Anoxic Event). In Pliensbachian samples, assemblages with abundant *Glomospira* sp., *Glomospirella* sp., *Siphovulvulina* sp., *Haurania deserta*, *Placopsilina* sp., *Mesoendothyra* sp., and *Everticyclammina praevirguliana* are observed. Following both the Pliensbachian/Toarcian boundary event and the Jenkyns Event, benthic foraminiferal density, evenness, and species richness decreased, indicating these communities underwent ecologic stress; however, loss of diversity was most substantial between samples that pre-date and post-date the Jenkyns Event. Whereas the Pliensbachian/Toarcian boundary event coincides with the demise of the large benthic foraminifera *Mesoendothyra* sp. and *Everticyclammina praevirguliana*, the Jenkyns Event was detrimental for most clades of benthic foraminifera, including many small, resilient taxa. Based on the evidence provided, we suggest that the Pliensbachian/Toarcian boundary and the Jenkyns Event were distinct events, potentially caused by distinct environmental perturbations.

### INTRODUCTION

The Early Jurassic (201.3–174.1 Ma) is an epoch of origination and proliferation of new benthic taxa following the end-Triassic mass extinction (Bambach et al. 2004; Kiessling et al. 2007). The end-Triassic extinction decimated reef communities and caused the extinction of roughly 41% of marine genera and 12% of marine families (Raup and Sepkoski 1982; Kiessling et al. 2007). Following the end-Triassic extinction, many marine clades began to recover. Scleractinian corals, lithiotid bivalves, and a variety of other benthic fauna dominated Early Jurassic reefs, particularly during the Pliensbachian (Bambach 2006; Brame et al. 2019). These diverse assemblages of the Early Jurassic were decimated by two reef crises: the Pliensbachian/Toarcian boundary event and the Jenkyns Event, also known as the Toarcian Oceanic Anoxic Event (Bambach 2006; Lathuilière and Marchal 2009; Brame et al. 2019; Krencker et al. 2020; Vas-seur et al. 2021).

The degassing of the Karoo-Ferrar (Chon Aike) Large Igneous Province, as early as  $182.779 \pm 0.033$  Ma (Burgess 2014), triggered perturbations of the carbon cycle, leading to warming during the Toarcian, which resulted in faunal turnover (Svensen et al. 2007; Sell et al. 2014). The eruption of the Karoo-Ferrar Igneous Province is often associated with widespread ocean anoxia, but not all sections that recorded the early Toarcian environmental perturbation experienced enhanced anoxia or even dysoxia (e.g., Bodin et al. 2011; Sabatino et al. 2013). Although many have previously used the terms somewhat interchangeably, the Jenkyns Event refers to a variety of early Toarcian environmental perturbations, whereas

the Toarcian Oceanic Anoxic Event refers specifically to ocean anoxia (Reolid et al. 2020). The Pliensbachian/Toarcian boundary event and the Jenkyns Event have been distinguished from one another by their separate carbon isotope signatures (e.g., Hesselbo et al. 2007; Krencker et al. 2020; Kemp et al. 2022; Bodin et al. 2023). Studying assemblages of benthic foraminifera across this interval can provide key insight for distinguishing the two late Early Jurassic reef crises in terms of their environmental perturbations.

Benthic foraminifera were among the clades of marine invertebrates that diversified during the Early Jurassic (Boudagher-Fadel and Bosence 2007; Kaminski et al. 2010). Foraminifera occupy a diverse set of marine environments and have one of the most extensive fossil records of the Phanerozoic, allowing them to be used as proxies for past changes in dissolved oxygen, nutrient input, and ocean acidity (Tappan and Loeblich 1988; Kaiho 1994; Schönfeld 2001; Billups et al. 2020). Following the demise of many clades at the end-Triassic mass extinction, benthic foraminiferal assemblages were dominated by small “competitive” taxa that are typically widespread along carbonate platforms (Fugagnoli 2004; Salazar Ramirez and Herrero 2015; Rita et al. 2016; Boudagher-Fadel 2018). In Early Jurassic shallow-water environments, agglutinated benthic foraminifera were abundant and origination rates were much higher than the Late Triassic (Septfontaine 1988; Reolid et al. 2008, 2019; Kaminski et al. 2010).

During the Early Jurassic, large benthic foraminifera with complex internal structures originated and colonized the southern margin of the Tethys Sea (Bassoullet et al. 1985; Kaminski et al. 2010). Large benthic foraminifera (LBF) are a polyphyletic grouping of multiple families of

epifaunal taxa (organisms that lived on another organism or the substrate). In the modern ocean, LBF are hosts for both prokaryotic and eukaryotic photosymbionts (Hallock 2000; Prazeres et al. 2017), which allow these foraminifera to grow to abnormal sizes that would otherwise be metabolically impractical (Hallock 1981). Due to their photosymbionts, LBF are typically limited to oligotrophic environments, and are often outcompeted by small foraminifera in nutrient-rich environments (Hottinger 1982; Fugagnoli 2004). The presence of photosymbionts within fossilized LBF can only be assumed because their algal symbionts and other micro-symbiotic organisms are not preserved (Prazeres and Renema 2019); however, ancient LBF are hypothesized to have hosted photosymbionts based on the size of their test (the protective skeletal component of a foraminifera) and the occurrence of internal structures that could feasibly host symbionts (Hallock 1981; Lee and Hallock 1987). Although the presence of photosymbionts in extinct LBF is disputed, the ecologic limitations of these taxa are mutually recognized (Hallock 2000). The ecological sensitivity of these taxa means that environmental perturbations, such as those that likely occurred during the Early Jurassic reef crises, cause turnover of LBF.

In this study, Early Jurassic benthic foraminiferal assemblages from the Central High Atlas of Morocco were analyzed to assess the severity of the Pliensbachian/Toarcian extinction and the Jenkyns Event. Due to the ecological limitations of LBF, which prefer an oligotrophic environment, these events are hypothesized to have caused substantial taxonomic shifts in the foraminiferal assemblages. Although LBF dominated shallow water platforms in the Jurassic, species of LBF were often short-lived, either being locally outcompeted for nutrients or dying-off because of reef ecological collapse (Boudagher-Fadel 2018). A more detailed understanding of the extinction and recovery patterns of foraminifera from this expanded sedimentary record in the Moroccan High Atlas provides key information to differentiate the two events, and determine which taxa were most severely impacted at each extinction.

#### GEOLOGICAL SETTING

Tectonic changes and climate directly impacted the success of benthic organisms in the Early Jurassic (Ziegler 1988; Leinfelder 1994). The expansion of the Neotethys Ocean and gradual consumption of the Paleotethys Ocean during the Triassic and Early Jurassic resulted in a multitude of large carbonate platforms developing within the westernmost, relatively shallow portion of the Tethys Ocean called the Tethys Sea (Woodfine et al. 2008; Léonide et al. 2012; Meschede and Warr 2019; Krencker et al. 2020). These carbonate platforms and ramps hosted scattered coral and lithotid-dominated reefs, particularly on the northern margin of Gondwana (Leinfelder 1994; Krencker et al. 2020) (Fig. 1A). The Central High Atlas Mountains of Morocco record mixed carbonate-siliciclastic strata of Pliensbachian and Toarcian age, including numerous reef deposits (e.g., Della Porta et al. 2013; Brame et al. 2019; Vasseur and Lathuilière 2021; Vasseur et al. 2021; Stone et al. 2022). Six localities from the Central High Atlas of Morocco were studied: Owl Olistolith, Ait Athmane (Aganane and Ait Athmane Formations), Gorge Reefs (Choucht Formation), Jebel Toksine (Tafrout Formation), and Aguerd Izegzawne (Tafrout Formation) (Fig. 1B). At these localities, reef bearing units with well-constrained stratigraphic placement were targeted for microfacies analyses of benthic foraminifera. The studied intervals are from four temporal ranges: lower Pliensbachian (*Tragophylloceras ibex* and *Prodactylioceras davoei* ammonite zones), upper Pliensbachian (*Fucinoceras lavinia-num*, *Arietoceras algovianum*, and *Emaciatoceras emaciatum* ammonite zones), lowest Toarcian (*Dactylioceras polymorphum* ammonite Zone, before the onset of the Jenkyns Event), and Toarcian strata deposited following the Jenkyns Event (*Harpoceras serpentinum* and *Hildoceras bifrons* ammonite zones) (Fig. 2). No reef bearing units from the localities of this study were found from strata deposited

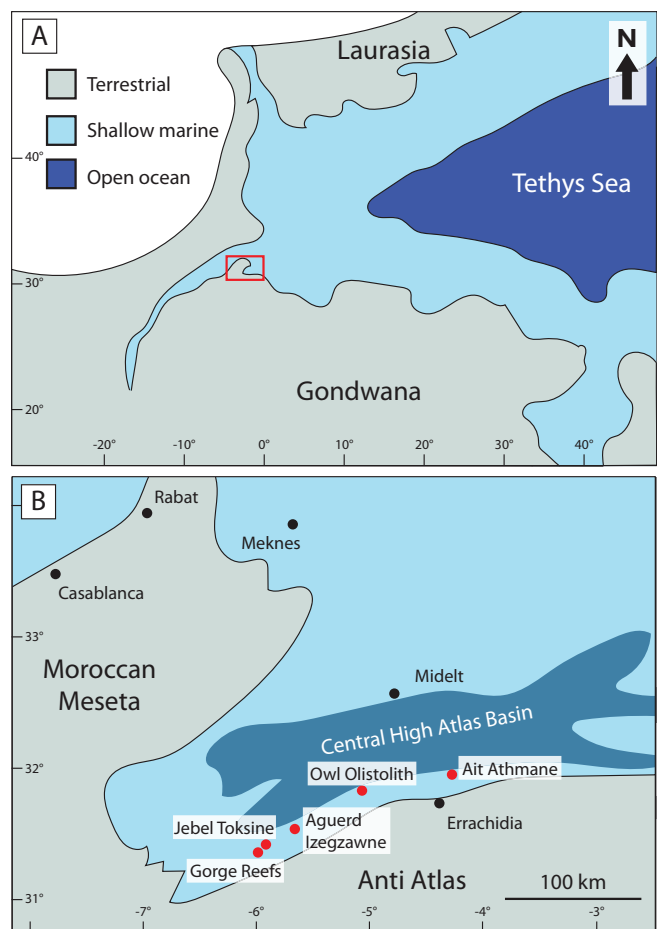


FIG. 1.—Early Jurassic (Toarcian) paleogeographic maps. **A**) Reconstruction of the Tethys Sea during the Toarcian (modified from Bassoullet et al. 1993; Suan et al. 2008a); the red square indicates the approximate area captured in Fig. 1B along the northern Gondwana margin. **B**) Paleogeographic map of the major geological provinces in Morocco and western Algeria (modified from Du Dresnay 1971; and Blomeier and Reijmer 1999) and the locations of the sections discussed in this study.

during the Jenkyns Event, so assessments of the severity of the Jenkyns Event are made by comparing foraminiferal assemblages from before and after the negative carbon isotope excursion.

#### Owl Olistolith

Owl Olistolith is a micro-olistolith in the Amellago region of the Central High Atlas. The olistolith was part of a reef located within an outer platform environment but was redeposited to a deep-water environment, what is now the Aberdouz Formation (Boivin et al. 2019; Stone et al. 2022). The olistolith's lower Pliensbachian age is supported by the biostratigraphic association of both micro and macro-fauna within the reef community. Further, ammonites near the olistolith (*Fucinoceras gr. volubile-pantanelli*, *Reynoceras gr. mellahense-peyrei*, and *Galaticeras aegoceoides*) indicate a transition from the *Tragophylloceras ibex* ammonite Zone to the *Prodactylioceras davoei* ammonite Zone (Boivin et al. 2019). The olistolith is an 8 m by 10 m carbonate boundstone distinct from the surrounding marls of the Aberdouz Fm. (Boivin et al. 2019). Solitary corals, phaceloid coral heads, and microbialites form the primary reefal framework of the olistolith. Owl Olistolith gradually becomes more coral-dominated toward the eastern side, but the original

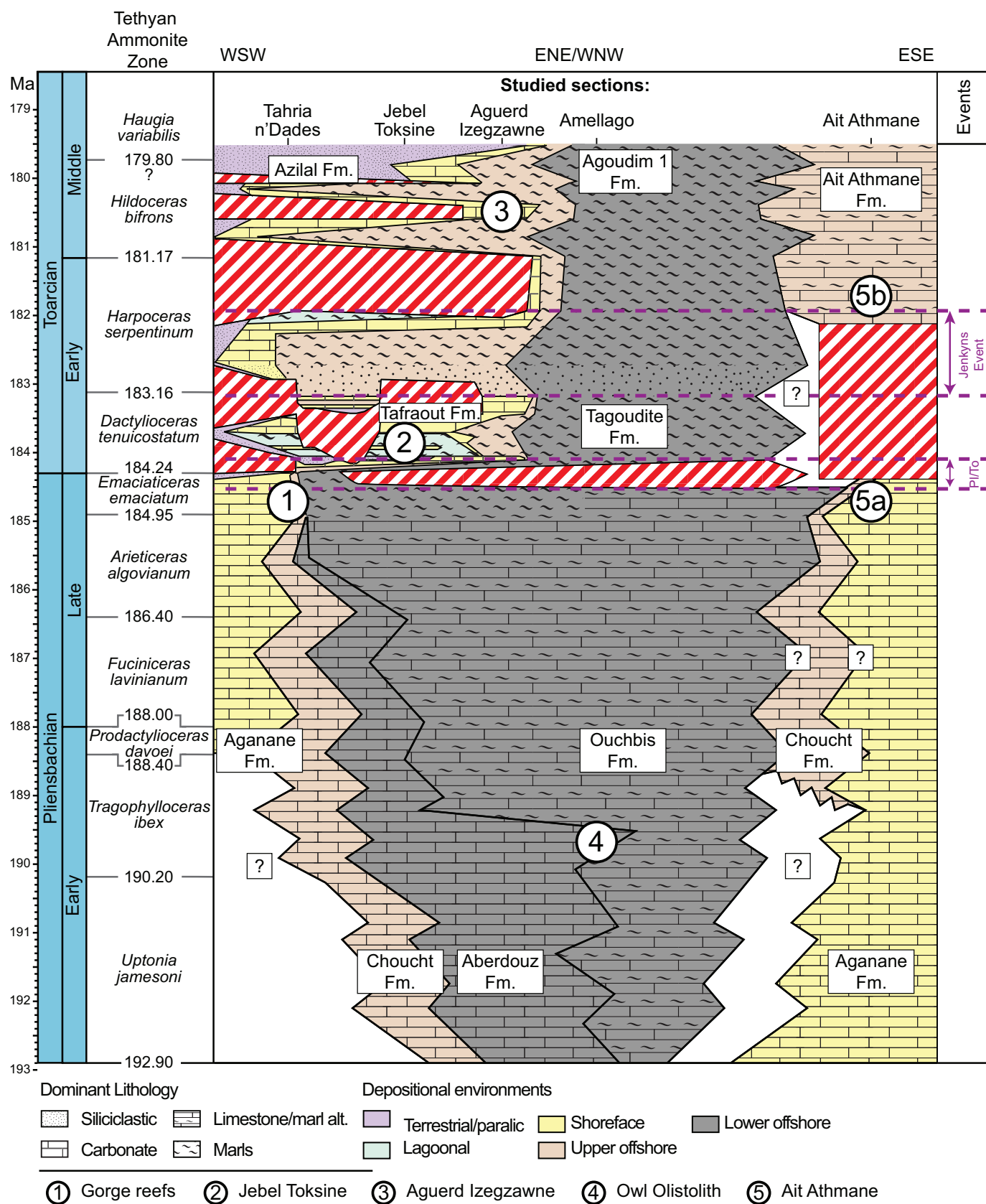


FIG. 2.—Lithostratigraphic chart of the studied sections. Correlation with Tethyan ammonite zones is provided (updated from Krencker et al. 2020). The dominant lithology and depositional environment associated with each section are given, and the approximate placement of each sampling site is indicated by the circled numbers.

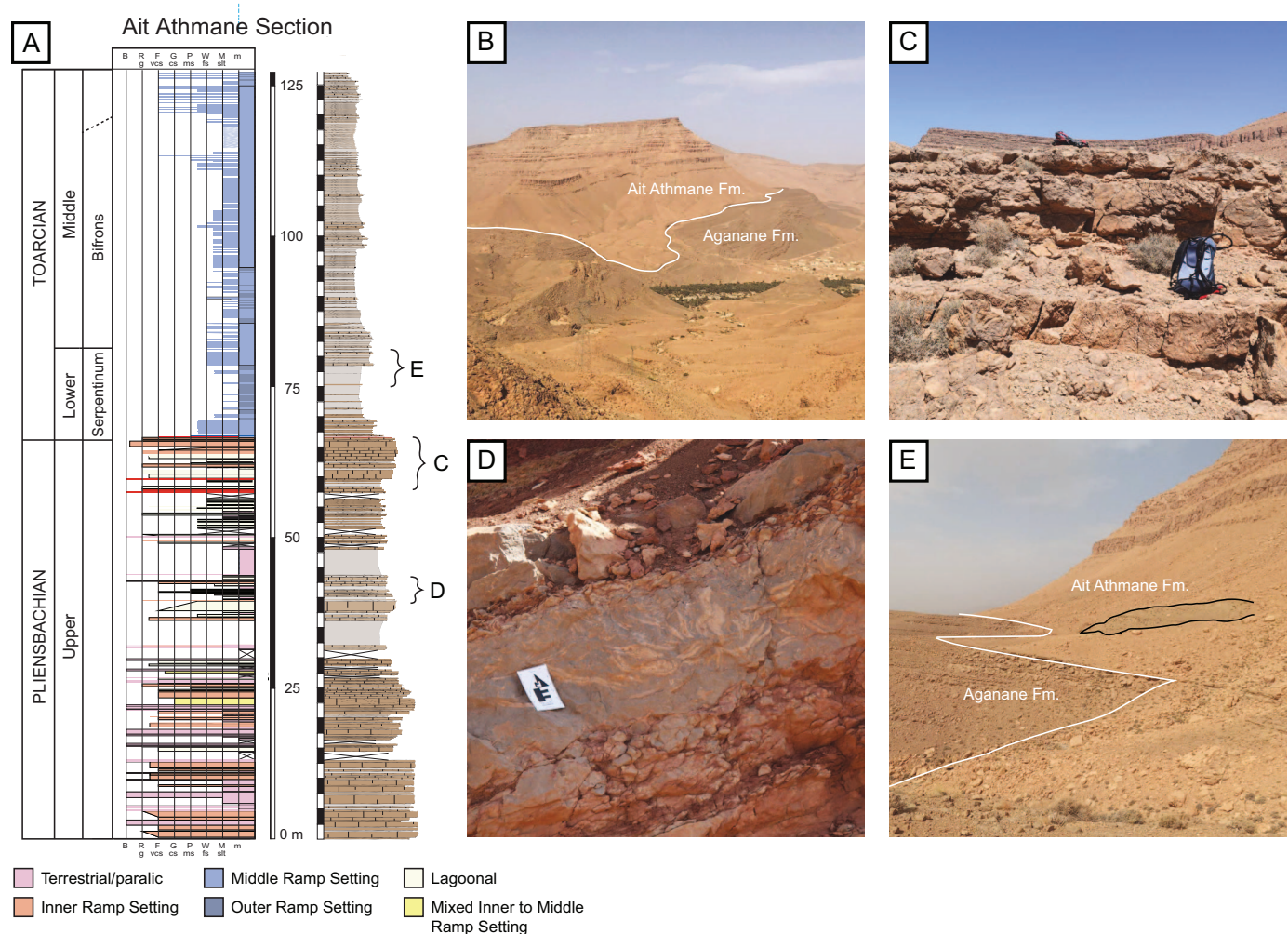


FIG. 3.—Ait Athmane section stratigraphic column and outcrops. **A)** Stratigraphic column of the Ait Athmane section modified from Krencker et al. (2014) with intervals of sampled reefal material indicated. **B)** Ait Athmane section outcropping outside of Errachidia, showing the Aganane Fm. overlain by the Ait Athmane Fm. **C)** Beds of the northern-most Aganane Fm. site. The lower bed is a *Lithioperla* sp./gastropod floatstone that thins laterally between sites. The upper bed contains lithiotids and coral fragments; backpacks for scale. **D)** Lithiotid bioherm or “bouquet” at a site along a roadcut within the Aganane Fm. A thin paleosol forms a recessive layer atop this bed, indicating subaerial exposure. **E)** Site within the Ait Athmane Fm. with the reefal outcrop outlined in black to distinguish it from the underlying scree slope.

orientation of the olistolith is unknown, so temporal relationships cannot be established for the change in coral or foraminiferal assemblages (Stone et al. 2022). Additionally, Owl Olistolith samples include isolated occurrences of the microproblematica *Lithocodium aggregatum*, *Thaumatoporella parvovesiculifera*, and *Baccanella floriformis*.

#### *Ait Athmane (Aganane Formation)*

In the Ziz Valley north of the city of Errachidia, the Ait Athmane section preserves upper Pliensbachian strata from the Aganane Fm. and middle to upper Toarcian strata from the Ait Athmane Fm. (Fig. 3A). The unconformity between the formations is easily identifiable by the stark contrast in color and cementation since the Aganane Fm. outcrops as a rust-colored, cliff-forming unit while the Ait Athmane Fm. is a lighter colored, slope-forming unit (Fig. 3B, 3E). The depositional environment of the Aganane Fm. has been interpreted as a shallow lagoon, due to the photozoan marine limestones and lagoonal marls shoaling to subaerial exposure horizons with paleosols (Wilmsen and Neuweiler 2008; Krencker et al. 2014; Brame et al. 2019). Lithiotid

bioherms are often found in close association with corals throughout the Aganane Fm. (Fig. 3C, 3D); most framework units were built by lithiotids with some small coral fragments, but small phaceloid coral bioherms are also present (Brame et al. 2019). Notably, there is a 1.35 m thick bed containing large phaceloid coral heads that occurs in close association with *Cochlearites* and *Lithioperla* lithiotid bioherms (Brame et al. 2019).

#### *Gorge Reefs (Choucht Formation)*

The Choucht Fm. is an upper Pliensbachian to lowermost Toarcian formation that outcrops in the Dadès Valley as a cliff-forming unit with frequent shallow marine coral bioherms (Krencker et al. 2020, 2022). The coral reefs that dominate the Choucht Fm. grew in a narrow belt on the middle to outer platform (Krencker et al. 2020). Although the majority of the Choucht Fm., and all material analyzed for this work, was deposited during the upper Pliensbachian, *Emaciatoceras emaciatum* ammonite Zone, the unit extends through the Pliensbachian/Toarcian boundary before the carbonate factory collapsed

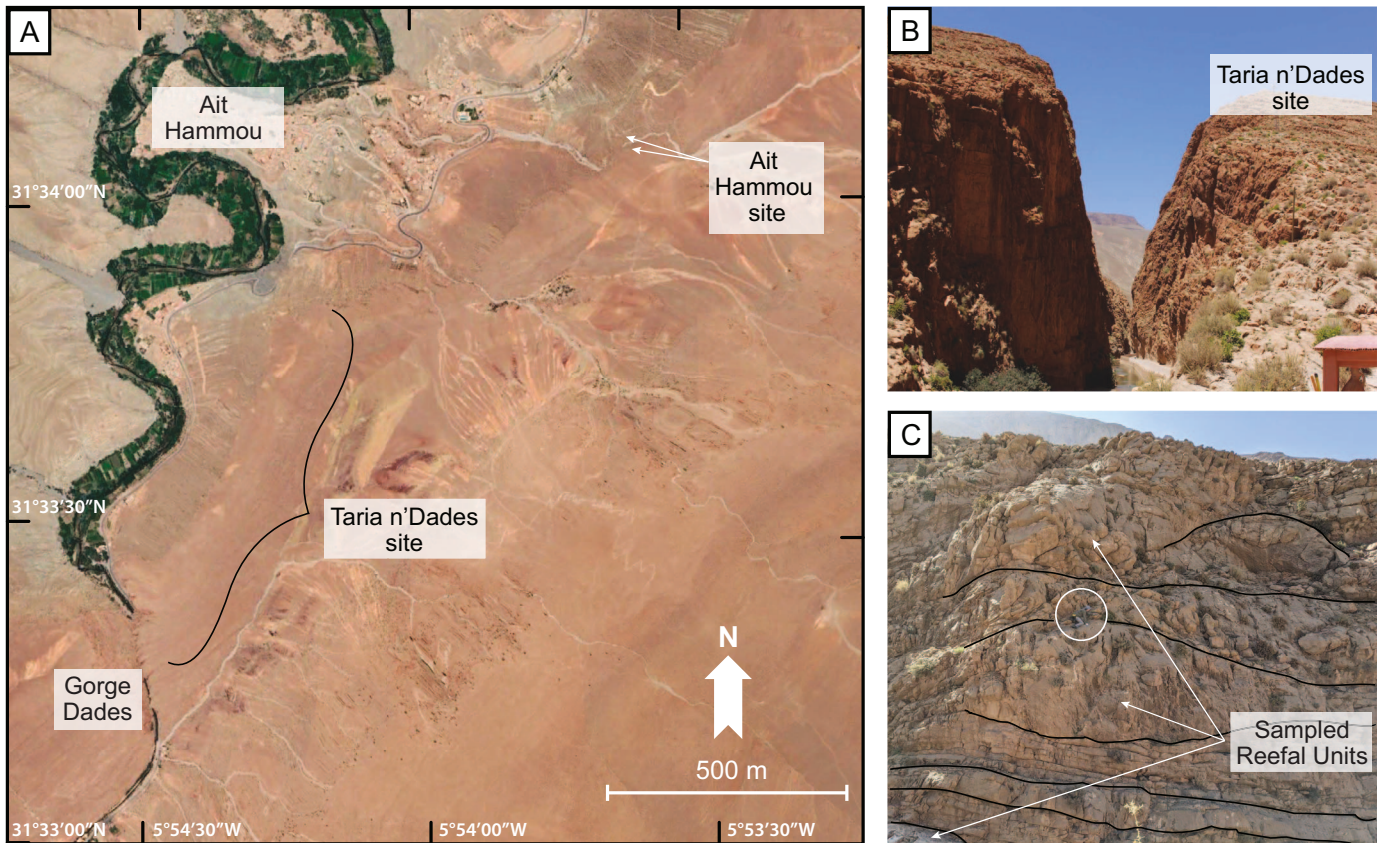


FIG. 4.—Dadès Valley map and outcrops. **A)** Map of the Dadès Valley with the sampled Gorge reef outcrops identified: the Taria n'Dades site and the Ait Hammou site. **B)** The Dadès Gorge with the Taria n'Dades site indicated. **C)** Exposed outcrop from the Ait Hammou site, with alternating reefal and inter-reefal beds outlined and identified, person for scale (circled).

(Krencker et al. 2020; Andrieu et al. 2022). Although evidence suggests the first extinction technically occurs in the lowest Toarcian proceeding the Pliensbachian/Toarcian boundary, this extinction will be referred to as the Pliensbachian/Toarcian boundary event for ease of description (Krencker et al. 2020; Andrieu et al. 2022). The unconformity atop the Choucht Fm. indicates a lack of deposition during the *D. tenuicostatum* ammonite Zone due to an interval of carbonate platform shutdown (Krencker et al. 2020). Interbedded reefal and non-reefal limestones of the Choucht Fm. outcrop in a gorge near Ait Hammou in the Dadès Valley. Throughout, phaceloid coral colonies, bivalves, microbialites, large gastropods, and variable amounts of non-reefal skeletal material are present.

#### *Jebel Toksine Section (Taфраout Formation)*

The Jebel Toksine section in the Dadès Valley contains lower Toarcian deposits of the Tagoudite Fm. and lower to middle Toarcian deposits of the Taфраout Fm. The Tagoudite Fm. is a siliciclastic unit deposited following the first carbonate collapse in the lowest Toarcian (Krencker et al. 2020; Andrieu et al. 2022). High terrigenous input, derived from the erosion of surrounding orogenic belts composed of Triassic and pre-Mesozoic basement rock, is characteristic of Tagoudite Fm. deposits (Brechtbühler et al. 1988; Krencker et al. 2020). The overlying Taфраout Fm. contains abundant oolitic grainstones as well as lithotid biostromes and thin coral reefs that were deposited following the Pliensbachian/Toarcian boundary and before the Jenkyns Event (Brame et al. 2019; Krencker et al. 2020). The presence of wood fragments and *Arbacoid* echinoids infrequently throughout the Taфраout Fm. indicates terrigenous

input in an open marine setting; therefore, the Taфраout Fm. is assigned to an inner to middle carbonate ramp environment (Brame et al. 2019; Krencker et al. 2020). Lithotid bioherms and biostromes found in the Taфраout Fm. are predominantly composed of *Cochlearites*, but also contain *Lithioperla*, other bivalves, and infrequent colonial and solitary corals (Brame et al. 2019).

#### *Ait Athmane (Ait Athmane Formation)*

The majority of the Ait Athmane Fm. was deposited during the middle and late Toarcian (Krencker et al. 2020); however, coral patch reef deposits are found within the lower Toarcian, corresponding to the uppermost *H. serpentinum* ammonite Zone in the interval after the Jenkyns event (Fig. 3E). Based on storm-related gutters and gutter casts preserved in alternating marl/limestone sequences and the presence of open-marine fossils, the depositional environment has been interpreted as a middle platform setting (Krencker et al. 2020). Additionally, high siliciclastic input is inferred for this system given the amount of muddy matrix present. The small (decameter-scale) coral patch reef is composed of framework-building phaceloid, cerioid, and meandroid coral colonies, and no lithotids are present.

#### *Aguerd Izegzawne Section (Taфраout Formation)*

The Aguerd Izegzawne section, formerly referred to as “Ouguerd Zegzawne” (e.g., Krencker et al. 2015, 2019, 2020), records a more distal setting than the Jebel Toksine and the Gorge reef sites. Here, the Taфраout Fm. represents an outer platform setting with alternating limestone and marl sequences (Krencker et al. 2015, 2020). There are several beds with

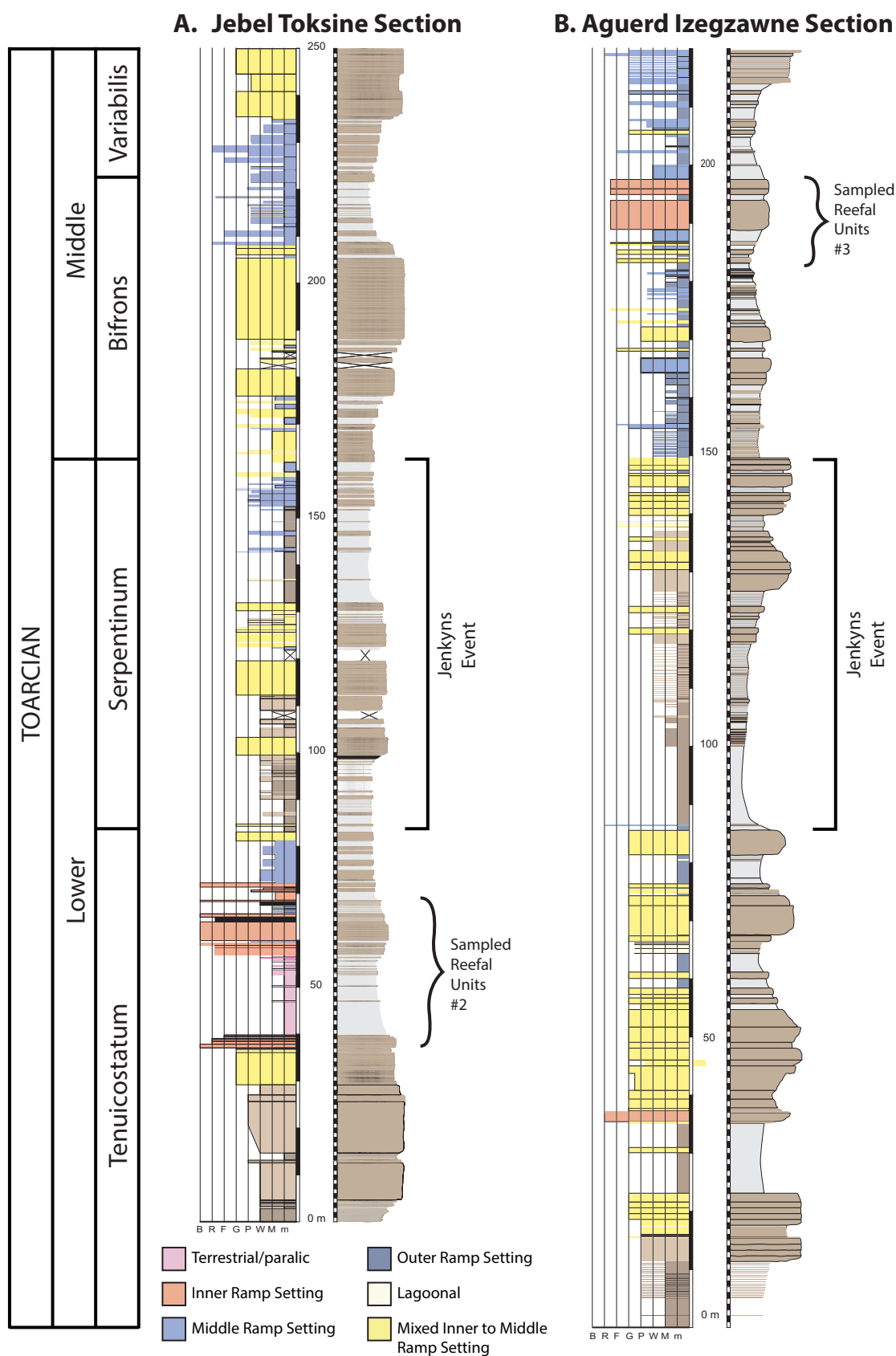


FIG. 5.—Lithostratigraphic columns modified from Krencker et al. (2020, 2022). **A.** Jebel Toksine section. **B.** Aguerd Izegzawne section. Correlation with the Tethyan ammonite zones is provided. The stratigraphic horizons sampled, as well as the Jenkyns Event, are labeled on the right-hand side of each column.



FIG. 6.—Jebel Toksine outcrop. Outcrops of reefal units from the northern site of the Jebel Toksine section with deposits from during the Jenkyns Event indicated.

coral-dominated bioherms observed in the *H. bifrons* and *H. variabilis* ammonite zones of the middle Toarcian (Krencker et al. 2015, 2020). The studied reef deposits are found in strata that represents the recovery of the carbonate factory following the Jenkyns Event and outcrop as cliff-forming patch reefs; the lower patch reef contains reef-building ceroid and phaceloid corals, whereas the upper patch reef's main framework builders are large phaceloid coral heads.

#### MATERIAL AND METHODS

Samples were collected from the six Moroccan sites in 2016, 2017, 2018, and 2021. The facies, lithology, and biotic components of the sections were logged and hand samples from coral, lithotid, or microbial-dominated reefal outcrops were collected for microfacies analysis. Sampling horizons were correlated to stratigraphic columns (Krencker et al. 2014, 2015, 2020) as well as unpublished logged sections, which provided

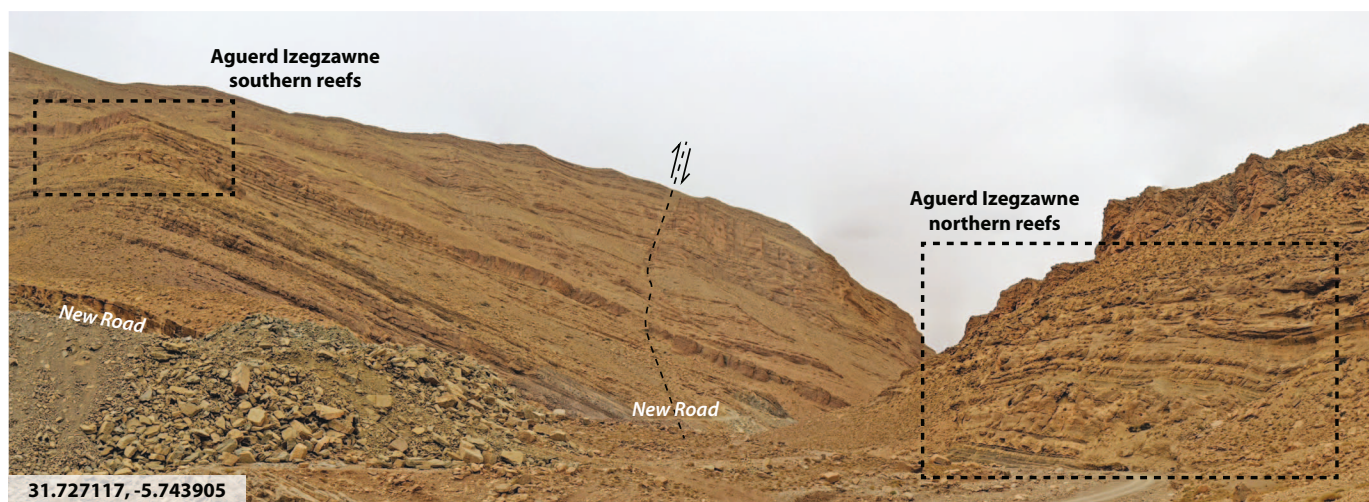


FIG. 7.—The Aguerd Izegzawne outcrop. Annotation denotes the southern (left) and northern (right) reef sites, as well as a fault that offsets the two sites.

TABLE 1.—Number and percent of species from each locality. Total identified specimens (left column) and percent of each species (right column) are given for each of the six localities of this study. The number of thin sections and surface area analyzed are indicated for each locality. Additionally, the average number of foraminifera observed per thin section from each locality and the normalized abundance of all foraminifera are given.

| Time Period                              | Pliensbachian  |     |             |     |                       |     | Toarcian        |     |                |      |                |     |
|------------------------------------------|----------------|-----|-------------|-----|-----------------------|-----|-----------------|-----|----------------|------|----------------|-----|
|                                          | Owl Olistolith |     | Ait Athmane |     | Dadès Valley          |     | Jebel Toksine   |     | Ait Athmane    |      | Aguerd         |     |
| Locality                                 | ?              |     | Aganane     |     | Choucht               |     | Tafraoute       |     | Ait Athmane    |      | Izegzawne      |     |
| Formation                                |                |     |             |     |                       |     |                 |     |                |      |                |     |
| Depositional Environment                 | Outer platform |     | Lagoon      |     | Middle/Outer platform |     | Lower shoreface |     | Outer platform |      | Outer platform |     |
| <i>Glomospira</i> sp.                    | 35             | 43% | 49          | 16% | 12                    | 14% | 9               | 4%  | 0              | 0%   | 1              | 17% |
| <i>Glomospirella</i> sp.                 | 4              | 5%  | 21          | 7%  | 10                    | 12% | 2               | 1%  | 0              | 0%   | 0              | 0%  |
| <i>Siphovulvulina</i> sp.                | 24             | 29% | 54          | 18% | 28                    | 33% | 34              | 14% | 0              | 0%   | 1              | 17% |
| <i>Siphovulvulina colomi</i>             | 5              | 6%  | 15          | 5%  | 6                     | 7%  | 10              | 4%  | 0              | 0%   | 0              | 0%  |
| <i>Siphovulvulina gibraltarensis</i>     | 5              | 6%  | 5           | 2%  | 3                     | 3%  | 11              | 5%  | 0              | 0%   | 0              | 0%  |
| <i>Haurania deserta</i>                  | 0              | 0%  | 117         | 38% | 5                     | 6%  | 162             | 68% | 0              | 0%   | 0              | 0%  |
| <i>Placopsilina</i> sp.                  | 2              | 2%  | 0           | 0%  | 6                     | 7%  | 0               | 0%  | 0              | 0%   | 2              | 33% |
| <i>Mesoendothyra</i> sp.                 | 5              | 6%  | 1           | 0%  | 2                     | 2%  | 0               | 0%  | 0              | 0%   | 0              | 0%  |
| <i>Everticyclammina praevirguliana</i>   | 2              | 2%  | 16          | 5%  | 1                     | 1%  | 0               | 0%  | 0              | 0%   | 0              | 0%  |
| <i>Ophthalmidium</i> sp.                 | 0              | 0%  | 14          | 5%  | 12                    | 14% | 7               | 3%  | 0              | 0%   | 1              | 17% |
| <i>Nodosaria</i> sp.                     | 0              | 0%  | 3           | 1%  | 1                     | 1%  | 3               | 1%  | 3              | 100% | 1              | 17% |
| <i>Planisepta compressa</i>              | 0              | 0%  | 13          | 4%  | 0                     | 0%  | 0               | 0%  | 0              | 0%   | 0              | 0%  |
| Total recorded foraminifera              | 82             |     | 308         |     | 86                    |     | 238             |     | 3              |      | 6              |     |
| Number of thin sections                  | 25             |     | 39          |     | 50                    |     | 40              |     | 33             |      | 37             |     |
| Surface area analyzed (mm <sup>2</sup> ) | 45,086         |     | 89,004      |     | 73,887                |     | 83,385          |     | 76,776         |      | 41,615         |     |
| Normalized abundance                     | 1.82E-03       |     | 3.46E-03    |     | 1.16E-03              |     | 2.85E-03        |     | 3.91E-05       |      | 1.20E-04       |     |

well constrained age and facies correlations. All hand samples were cut to either small (27 × 46 mm) or large (50 × 75 mm) thin sections and analyzed with a Zeiss Imager.M2m petrographic microscope to identify and quantify the microfaunal assemblage.

### Sample Sites

A total of 224 thin sections were used for the purposes of this study; however, upon analysis of the samples only 113 thin sections contain benthic foraminifera (Appendix 1). Sampling from each locality is given as follows:

**Owl Olistolith.**—Thin sections from this olistolith, also described in Stone et al. (2022), were assessed to provide a baseline of taxonomic diversity in the lower Pliensbachian. Of the 25 samples collected across the Owl Olistolith 16 have benthic foraminifera and are used in our analyses. Samples were collected from both the eastern, coral-dominated side and the side of the olistolith with infrequent coral material. See Stone et al. (2022) for a detailed site analysis.

**Ait Athmane (Aganane Formation).**—This study targeted lithotid and coral bioherms in the upper 40 meters of the Aganane Fm. A total of 39 samples were analyzed from bioherm and biostrome associated beds, 33 of which have benthic foraminiferal material. Four lithotid-dominated units were sampled from several outcrops: one site outcropping within the *Arietoceras algovianum* ammonite Zone and three sites from beds of comparable stratigraphic horizons assigned to the *Emaciatoceras emaciatum* ammonite Zone, or the uppermost Pliensbachian. The four units were sampled in regular transects of approximately 10 m.

**Gorge Reefs (Choucht Formation).**—Two sites within the *Emaciatoceras emaciatum* ammonite Zone were sampled: one site directly uphill of the “Source du Dadès” Auberge (referred to as the Taria n’Dades site) and a second site along strike near Ait Hammou (Fig. 4A). At the Taria n’Dades site, which is along the eastern cliff of Gorge Dadès (Fig. 4B), 23 thin section samples were collected from coral bioherm material; each sample contained varying amounts of skeletal material, some of which were non reefal. The Ait

Hammou site, which is further northwest along the cliff of the Dadès Gorge, is a 15 m outcrop exposing three reef-bearing beds (Fig. 4C); reefs from the Taria n’Dades site are likely stratigraphically equivalent to the uppermost reefs at the Ait Hammou site. Twenty-seven thin section samples were collected from the Ait Hammou site, with more samples collected from the lowermost and uppermost reef beds due to the inaccessibility of the middle bed. Of the thin sections collected from this locality, 33 contain benthic foraminifera.

**Jebel Toksine (Tafraout Formation).**—The Jebel Toksine section was sampled at three outcrops from two lithotid-dominated units, separated stratigraphically by about 14 m (Figs. 5A, 6). Sampling within the lower lithotid unit occurred along the northern hillslope of Jebel Toksine and along a corresponding roadcut described in Brame et al. (2019) (Fig. 6). The upper lithotid unit was difficult to access at the northern hillslope, so sampling occurred extensively along measured transects at the southern hillslope and along the roadcut. Of the 40 samples collected at Jebel Toksine, 22 thin sections included benthic foraminifera from both the lower and upper lithotid unit.

**Ait Athmane (Ait Athmane Formation).**—Reefal beds in the Ait Athmane Fm. are extremely rare compared to the underlying Aganane Fm. A small patch reef with a dominantly phaceloid coral framework was sampled to analyze foraminiferal assemblages that were recovering from the Jenkyns Event. A total of 33 samples were collected at the reef along 3 m vertical transects from laterally continuous horizons. Of the 33 thin sections made, 28 of the thin sections contain matrix sediments, yet only three thin sections have benthic foraminifera present.

**Aguerd Izegzawne (Tafraout Formation).**—The Aguerd Izegzawne section was sampled from biohermal units occurring above the Jenkyns Event stratigraphic interval (Fig. 5B). Beds within this deposit dip steeply and are crosscut by a dry wash where a new road was constructed, dividing the studied section into a northern and southern side (Fig. 7). Upon analysis of the stratigraphic section, there is uncertainty regarding the placement of the northern site relative to the Jenkyns Event; therefore, foraminiferal

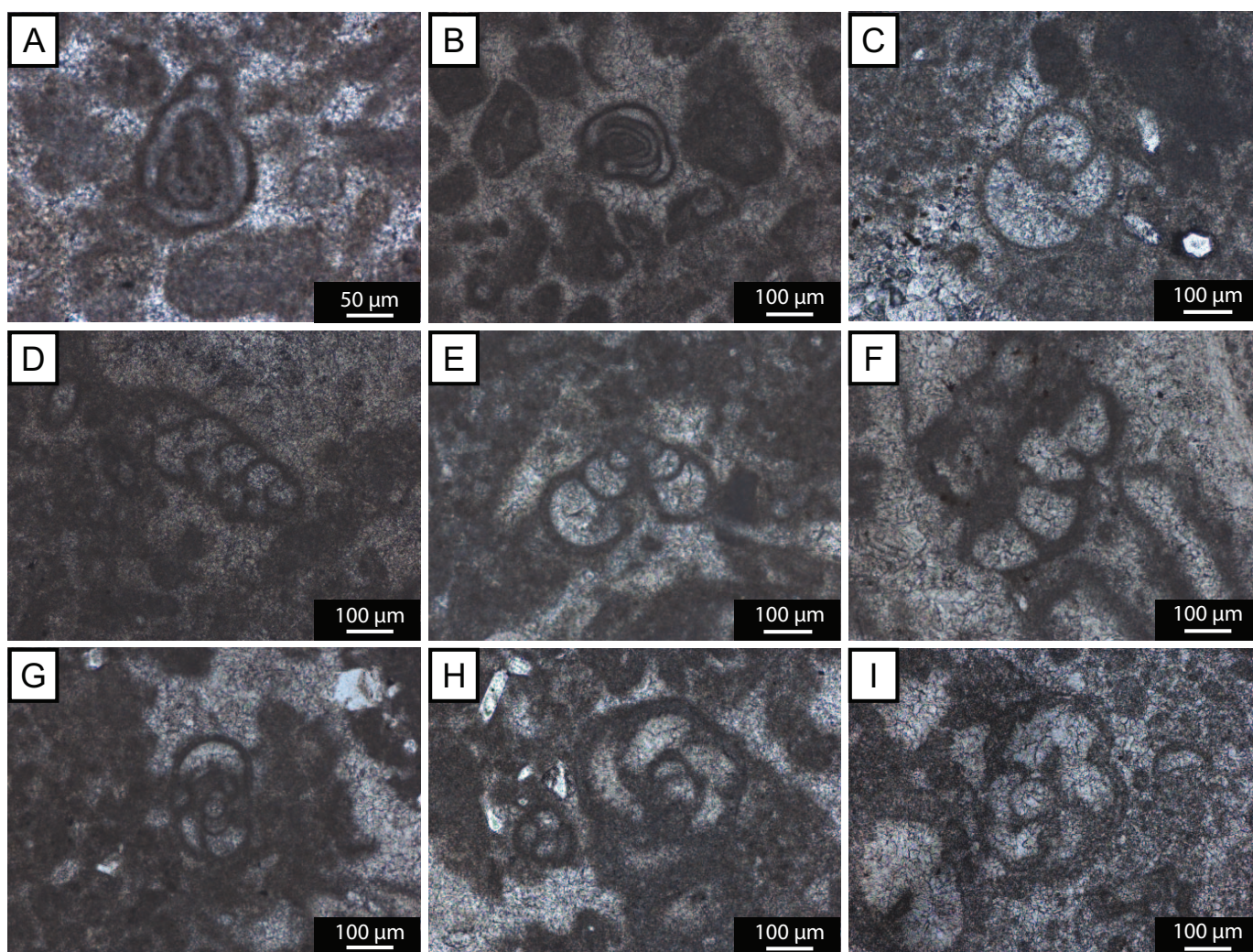


FIG. 8.—Photomicrographs in plane polarized light of benthic foraminifera from Owl Olistolith. **A)** *Glomospira* sp., thin section GO-1 F18. **B)** *Glomospirella* sp., thin section GO-6 F12. **C)** *Siphovalvulina* sp., thin section GO-20 F11. **D)** *Siphovalvulina colomi*, thin section GO-7A F2. **E)** *Siphovalvulina gibraltarensis*, thin section GO-13 F10. **F)** *Placopsilina* sp., thin section GO-7B F5. **G, H)** *Mesoendothyra* sp., thin section GO-19 F16 and thin section GO-1 F40. **I)** *Everticyclammina praevirguliana*, thin section GO-11 F8.

counts were conducted for the northern site, but are not included in the analyses of this study and do not change the overall results of this work (see Online Supplemental File). Most samples were collected in transects of three along the lower, middle, and upper part of each patch reef unit. Of the 21 samples collected from the southern site, only five thin sections contain benthic foraminifera.

#### Data Interpretation

Foraminifera from 113 thin sections were analyzed according to the identification methods of test morphology set forth by Loeblich and Tappan (1964). Once foraminifera were identified (see Systematic Paleontology), rarefaction curves were generated for each locality to ensure a sufficient assessment of diversity had been made (Sanders 1968; Heck et al. 1975). Additionally, the probability of interspecies encounter (or Hurlbert's PIE) is used as a statistical analysis to quantify community evenness, or the comparative abundance of each species to all other species (Hurlbert 1971). Measuring evenness allows for a quantitative assessment of biodiversity, and the disparity between

the number of specimens observed for each taxon is compared between localities.

## RESULTS

### Taxonomic Identifications

The Lower Jurassic reefs yielded a total of 723 specimens assigned to 12 morphogroups of foraminifera. Table 1 provides a comprehensive overview of the number and percent of each foraminifera present at a given locality, as well as the total surface area of thin sections analyzed for each locality (approximately calculated based on the size of the thin section photomicrographs). The species present within each locality, and their relative abundance, are described below.

**Lower Pliensbachian Foraminifera.**—The Owl Olistolith samples contain the following taxa: *Glomospira* sp., *Glomospirella* sp., *Siphovalvulina* sp., *Siphovalvulina colomi*, *Siphovalvulina gibraltarensis*, *Mesoendothyra* sp., *Everticyclammina praevirguliana*, and the encrusting *Placopsilina* sp. (Fig. 8). The two most abundant species are *Glomospira*

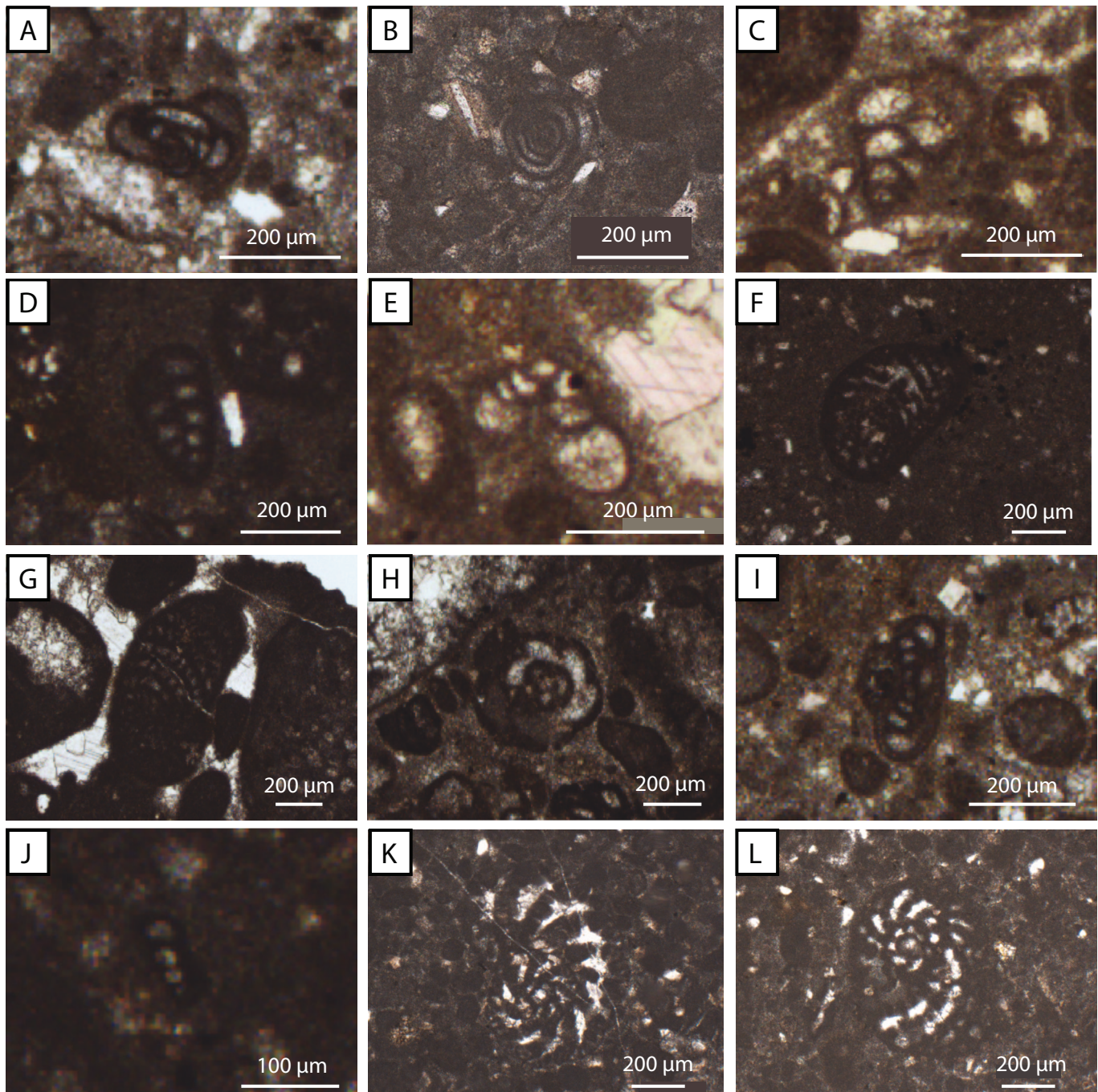


FIG. 9.—Benthic foraminifera of Aganane Fm. shown in plane polarized light. **A)** *Glomospira* sp., thin section AA1N-069 (7). **B)** *Glomospirella* sp., thin section AA1.5R-047 (7). **C)** *Siphovalvulina* sp., thin section AA1M-061 (9). **D)** *Siphovalvulina colomi*, thin section AA1N-070 (19). **E)** *Siphovalvulina gibraltarensis*, thin section AA1M-061 (34). **F, G)** *Haurania deserta*, thin section AA1N-068 (2) and thin section AA1N-070 (9). **H)** *Everticyclammina praevirguliana*, thin section AA1N-069 (6). **I)** *Vidalina* sp., thin section AA1N-069 (16). **J)** *Nodosaria* sp., thin section AA1N-068 (5). **K, L)** *Planisepta compressa*, thin section AA1.5R-047 (12) and thin section MO341\_j.

sp. and *Siphovalvulina* sp., which are 43% and 29% of the total foraminiferal composition, respectively (Table 1). *Glomospira* sp. and *Siphovalvulina* sp. are both small competitive foraminifera typical of a Pliensbachian assemblage (Septfontaine 1985; Fugagnoli 2004). *Mesoendothyra* is a genus of LBF with alveolar continuations along the outer wall, distinct from other genera of the Mesoendothyridae family (Loeblich and Tappan 1987).

Mesoendothyridae define a simple planispiral clade that occur commonly and persist past the *Orbitopsella* bioseries of the lower Pliensbachian (Septfontaine 2020). Like the genus *Mesoendothyra*, *Everticyclammina* is a genus of LBF species with alveolar walls. *Everticyclammina praevirguliana* is the oldest recorded species of the *Everticyclammina* genus, temporally confined to the mid-Sinemurian to upper Pliensbachian with all other

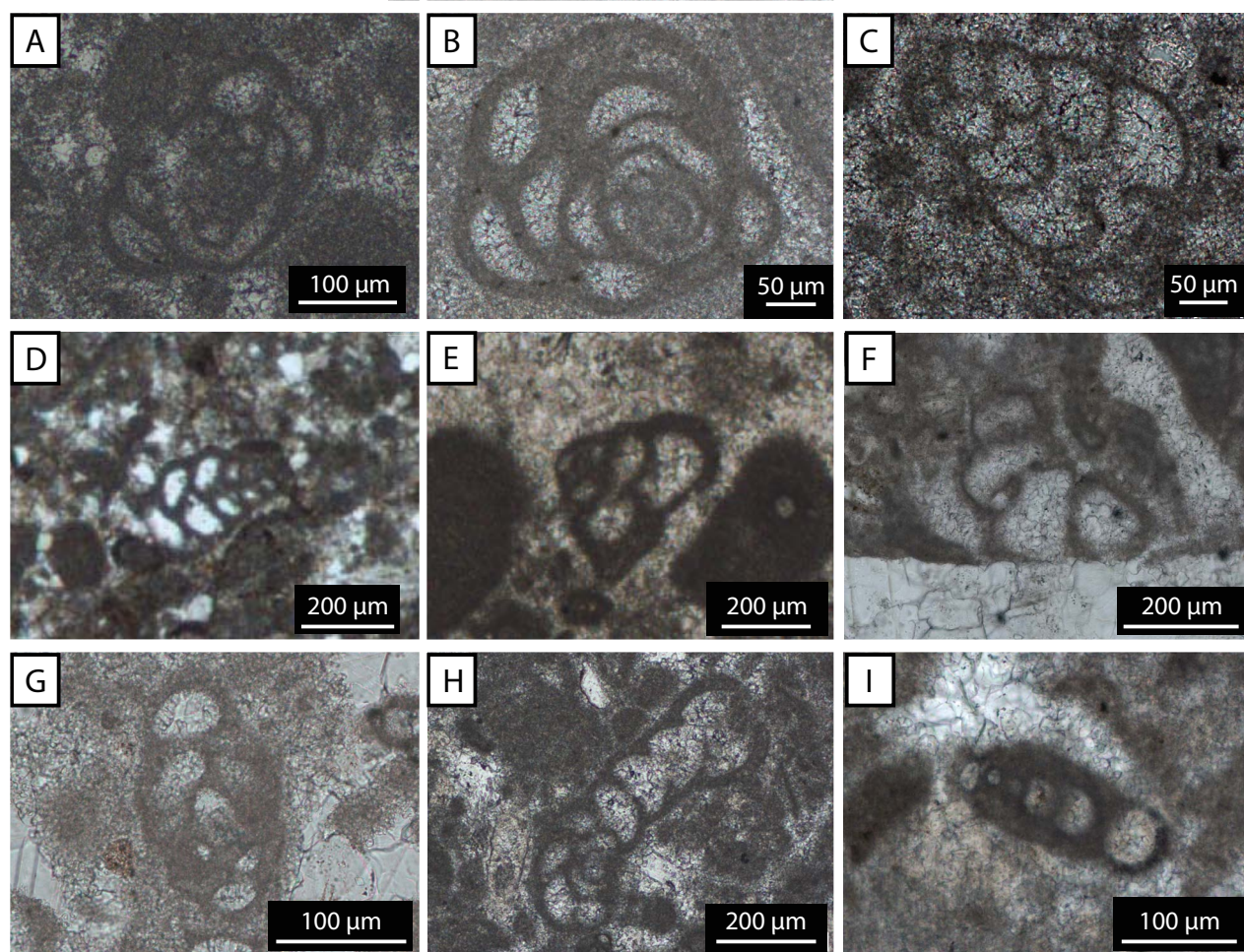


FIG. 10.—Thin sections photomicrographs from Choucht Fm. taken in plane polarized light. **A)** *Glomospira* sp., thin section BR-18-3 (2). **B)** *Glomospirella* sp., thin section BR-18-3 (8). **C)** *Siphovalvulina* sp., thin section BR-18-3 (13). **D)** *Siphovalvulina colomi*, thin section AP-6B-1 (4). **E)** *Siphovalvulina gibraltarensis*, thin section BR-18-3 (4). **F)** *Placopsilina* sp., thin section AP-7 (2). **G)** *Mesoendothyra* sp., thin section AP-3B (3). **H)** *Everticyclammina praevirguliana*, thin section BR-18-3 (14). **I)** *Vidalina* sp., thin section AP-7 (1).

identified species of *Everticyclammina* occurring in the Upper Jurassic (Fugagnoli 2000).

**Upper Pliensbachian Foraminifera.**—Samples from the Choucht Fm. and Aganane Fm. had similar compositions of benthic foraminifera. Both upper Pliensbachian formations contain a similar assemblage of foraminifera to Owl Olistolith (Figs. 9, 10). *Siphovalvulina* sp. and *Glomospira* sp. are the dominant microfauna of the Aganane and Choucht formations, making up 14% or more of the total specimens identified (Table 1). Small foraminifera, like *Siphovalvulina* sp. and *Glomospira* sp., are ubiquitous along Pliensbachian carbonate platforms (Septfontaine 1985, 1988; Boudagher-Fadel et al. 2001; Boudagher-Fadel and Bosence 2007; Jiang et al. 2020; Reolid 2020) (Fig. 11). In contrast, the LBF *Everticyclammina praevirguliana* is rare within the upper Pliensbachian reefs and is more commonly found in samples from the Aganane Fm. than those from the Choucht Fm., with identified specimens making up 5% and 1% of the foraminiferal assemblage, respectively (Table 1, Fig. 11).

Additionally, both the Choucht Fm. and Aganane Fm. include *Vidalina* sp., *Nodosaria* sp., and *Haurania deserta*, which were not observed in Owl Olistolith samples. *Nodosaria* sp. is an elongate, infaunal foraminifera

that has been cited as sensitive to changes in oxygenation (Corliss and Fois 1990; Coccioni and Galeotti 1993; Canales and Henriques 2008; Reolid et al. 2008; Rita et al. 2016). *Haurania deserta* is an abundant species of LBF in the Aganane Fm. (38% of the identified specimens), but it is absent within the Choucht Fm. (Table 1). The Aganane Fm. also includes *Planisepta compressa*, which is a LBF that decreases in abundance and goes extinct before the latest Pliensbachian (Septfontaine 2020).

**Lower Toarcian Foraminifera (pre-Jenkyns Event).**—In the Jebel Toksine section, below the Jenkyns Event, the diversity of LBF is low since specimens of *Mesoendothyra* sp. or *Everticyclammina praevirguliana* are not present and the only LBF recorded is *Haurania deserta* (Fig. 12); however, *H. deserta* are frequent in the Jebel Toksine section (68%). Specimens of *H. deserta* from Jebel Toksine are smaller than those observed in the Aganane Fm., with an average longest diameter of 461 µm and 695 µm, respectively. Apart from *H. deserta*, the most abundant foraminifera within the Jebel Toksine section are *Siphovalvulina* sp. (14%) and *Siphovalvulina gibraltarensis* (5%) (Table 1). Additionally, *Glomospira* sp., *Glomospirella* sp., *Siphovalvulina colomi*, *Vidalina* sp., and *Nodosaria* sp. occur infrequently (4% or less) within Jebel Toksine thin

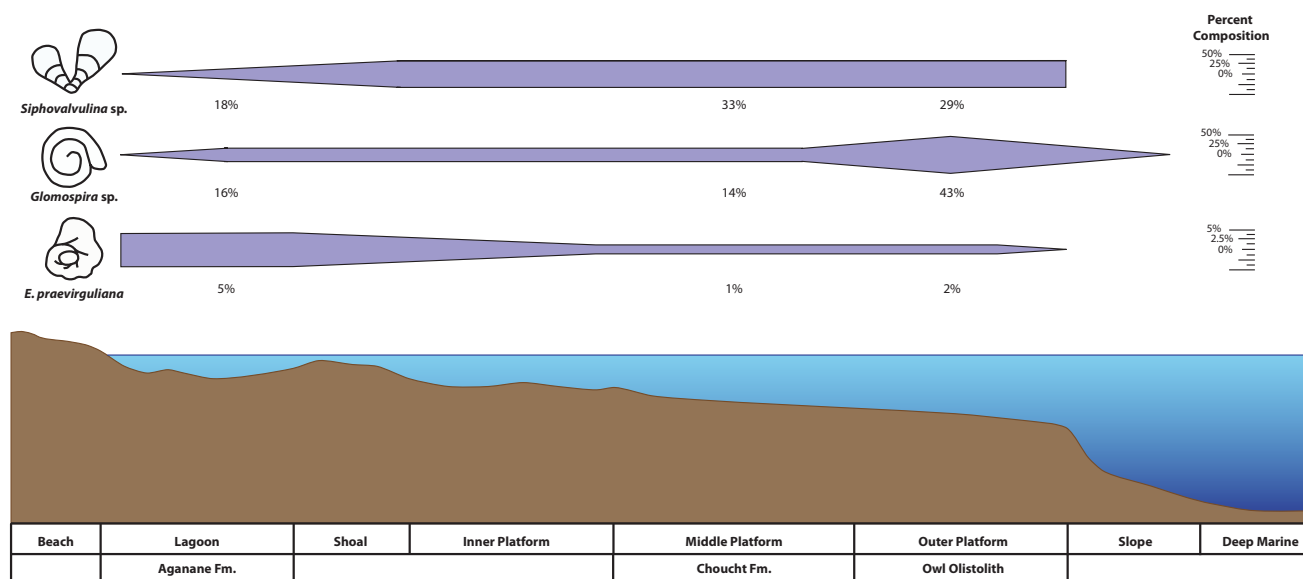


FIG. 11.—Violin plots of abundance along a shallow water platform. The three foraminiferal species, *Glomospira* sp., *Siphovavulina* sp., and *Everticyclammina praevirguliana* are illustrated along the depositional gradients of the Pliensbachian Stage using samples from Owl Olistolith, Choucht Fm., and Aganane Fm.

sections (Table 1). Foraminiferal assemblages from upper and lower lithotid units are relatively similar apart from *Nodosaria* sp. being present only in the upper reefal units.

Overall, thin sections from Jebel Toksine are comparable to the Aganane Fm., which has considerably higher normalized abundance than more distal localities like Owl Olistolith and the Choucht Fm. (Table 1). Species richness, or number of total species recorded for each locality, is lower in the Jebel Toksine reefs (eight recorded species) than the upper Pliensbachian formations (11 recorded species in both the Aganane Fm. and the Choucht Fm.).

#### Lower to Middle Toarcian Foraminifera (post-Jenkyns Event).—

The post-Jenkyns Event reefs sampled from the Aguerd Izegzawne section proliferated in a deeper platform environment than the other Dadès Valley sites discussed (Vasseur et al. 2021) and have a substantially lower abundance of foraminifera than any reef samples from this study that predate the Jenkyns Event (Table 1). Even though phaceloid and ceroid corals appear to have recovered in these reefs, foraminifera are scarce. Only six specimens of foraminifera were observed across all 37 Aguerd Izegzawne thin sections analyzed (about one specimen in every six samples), which is unprecedentedly low compared to the older localities. Of the few specimens identified, only *Glomospira* sp., *Siphovavulina* sp., *Placopsilina* sp., *Vidalina* sp., and *Nodosaria* sp. are present (Fig. 13). No LBF are observed within these samples and both the upper and lower reefal units exhibit a similar paucity of microfauna. *Glomospira* sp., *Vidalina* sp., and *Nodosaria* sp. are small infaunal foraminifera that commonly outcompete LBF following environmental perturbation, which suggests the post-Jenkyns Event assemblage is primarily composed of opportunistic taxa (Hottinger 1982; Septfontaine 1985; Fugagnoli 2004; Arreguin-Rodríguez et al. 2014; Nagy and Naoroz 2018).

Similarly, the Ait Athmane Fm. reef contained a foraminifera-poor assemblage, as only three specimens of *Nodosaria* sp. were observed (Fig. 14). The average abundance of foraminifera per thin section is low in the Ait Athmane Fm. (about one specimen in every 11 samples) compared to the pre-Jenkyns Event localities (multiple specimens per thin section). The number of thin sections analyzed in the Ait Athmane Fm. is comparable to other localities, so the low abundance of foraminifera is not likely a reflection of sampling bias.

#### Ecological Metrics

Rarefaction curves (Fig. 15) reveal that the data from the Owl Olistolith, Aganane Fm., Choucht Fm., and Jebel Toksine sections approach asymptotes, suggesting species richness was thoroughly assessed in these reefs. Bioherms at Aguerd Izegzawne and the Ait Athmane Fm. provide few specimens, and therefore cannot be plotted. Although it is possible we have not assessed the true diversity of these reef ecosystems, the apparent diversity of benthic foraminifera is shown to be lower at Jebel Toksine than the Pliensbachian localities.

Hurlbert's PIE was calculated to assess benthic foraminiferal assemblage evenness. Prior to the end Pliensbachian, all recorded sampling sites have a high evenness, where the Owl Olistolith site has an evenness of 0.73, the Aganane Fm. sites have an evenness of 0.79, and the Choucht Fm. sites have an evenness of 0.84. In contrast, the Toarcian Jebel Toksine sites have a relatively low Hurlbert's PIE value. Comparing the Ait Athmane site (Aganane Fm.) and the Jebel Toksine sites, which share a similarly isolated depositional setting, shows a decrease in evenness from 0.79 to 0.51, indicating shallow-water benthic foraminiferal communities became more stressed between the late Pliensbachian and the early Toarcian. Evenness could not be properly assessed for post-Jenkyns Event reef samples due to the low density of foraminifera.

#### DISCUSSION

##### Foraminiferal Ecology Prior to the Early Jurassic Extinctions

The results of this study suggest that Pliensbachian coral and lithotid reefs of the Tethys Sea hosted a diverse assemblage of foraminifera. Across the three localities studied, the foraminiferal assemblage includes predominantly shallow water, epifaunal taxa. No distinctions were identified when comparing microfaunal assemblages from coral-dominated and lithotid-dominated reefs; rather, the diversity of foraminifera in both reef types from comparable depositional settings were similar. Point counting for Owl Olistolith thin sections conducted in Stone et al. (2022) suggests a rough correlation between a dominance in coral facies and decreasing foraminiferal diversity (see Online Supplemental File).

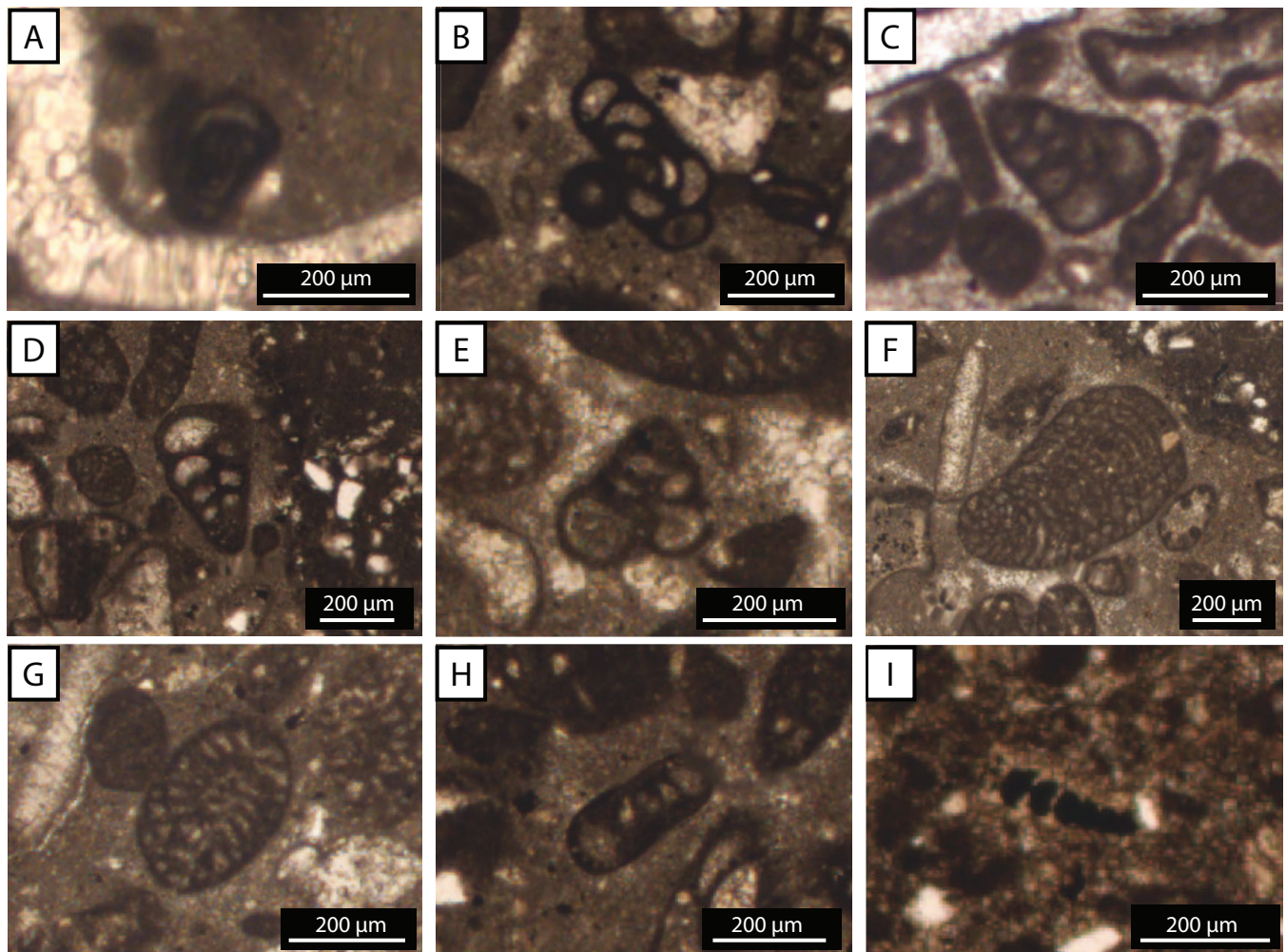


FIG. 12.—Identified benthic foraminifera of Jebel Toksine section, photomicrographs were taken in plane polarized light. **A)** *Glomospira* sp., thin section JTC-M1 (2). **B)** *Glomospirella* sp., thin section JTC-M1 (28). **C)** *Siphovalvulina* sp., thin section JTB 1.4 (6). **D)** *Siphovalvulina colomi*, thin section JTC-M1 (13). **E)** *Siphovalvulina gibraltarensis*, thin section JTC-M1 (7). **F, G)** *Haurania deserta*, thin section JTC-M1 (65) and thin section JTC-M1 (55). **H)** *Vidalina* sp., thin section JTC-M1 (17). **I)** *Nodosaria* sp., thin section JTB 0.8 (6).

Among the most abundant taxa found in Pliensbachian reefs are members of the suborders Textulariina, Ammodiscina, and Orbitolinina, with Miliolina and Nodosariina making up a much smaller component of the total diversity. A dominance of Textulariina and Ammodiscina indicate high-energy conditions in these reef environments (Murray and Alve 1999), and the abundance of LBF (*Everticyclammina praevirguliana*, *Mesoendothyra* sp., *Planisepta compressa*, and *Haurania deserta*) is associated with oligotrophic shallow water carbonate platforms (Hottinger 1982; Omana and Arreola 2008). Therefore, determinations of paleoenvironment based on ecologic constraints of the predominant foraminifera agree with the sedimentological (Krencker et al. 2014, 2015, 2020, 2022) and macrofaunal (Brame et al. 2019; Stone et al. 2022) assessments of the localities.

Although all Pliensbachian reef deposits have similar benthic foraminiferal assemblages, clear distinctions can be made between the Pliensbachian reef communities, which are likely due to differences in depositional environment. We infer that the Aganane Fm. was deposited in more shallow marine setting than the Owl Olistolith and Choucht Fm. based on the occurrence of paleosols and lagoonal marls (Wilmsen and Neuweiler 2008; Krencker et al. 2014; Brame et al. 2019). In the Aganane Fm., LBF compose 47% of the total

foraminiferal abundance, whereas the abundance of these taxa in Owl Olistolith and the Choucht Fm. is only 8% and 9%, respectively. Our results suggest LBF preferentially lived in reefs that grew in lagoonal settings, as these taxa were not as prolific in reefs from middle to outer platform settings; these results are corroborated by evidence of the environmental constraints of LBF in other studies (e.g., Fugagnoli 2000, 2004; Boudagher-Fadel 2018; Septfontaine 2020). Upper Sinemurian and lower Pliensbachian foraminiferal assemblages from Italy reveal comparable results to this study (Fugagnoli 2004), as inner platform assemblages have predominant LBF including *Haurania deserta* and *Everticyclammina praevirguliana*, whereas small taxa such as *Glomospira* sp. are ubiquitous throughout the platform. Further, the sensitivity of LBF is thought to be exemplified during changing climatic conditions, such as those associated with the Early Jurassic reef crises (Hallock 2000; Fugagnoli 2004; Septfontaine 2020).

#### Early Jurassic Foraminiferal Extinction Dynamics

Following the Pliensbachian/Toarcian boundary, reef complexes from the Tethys Sea that had previously hosted a diverse assemblage of

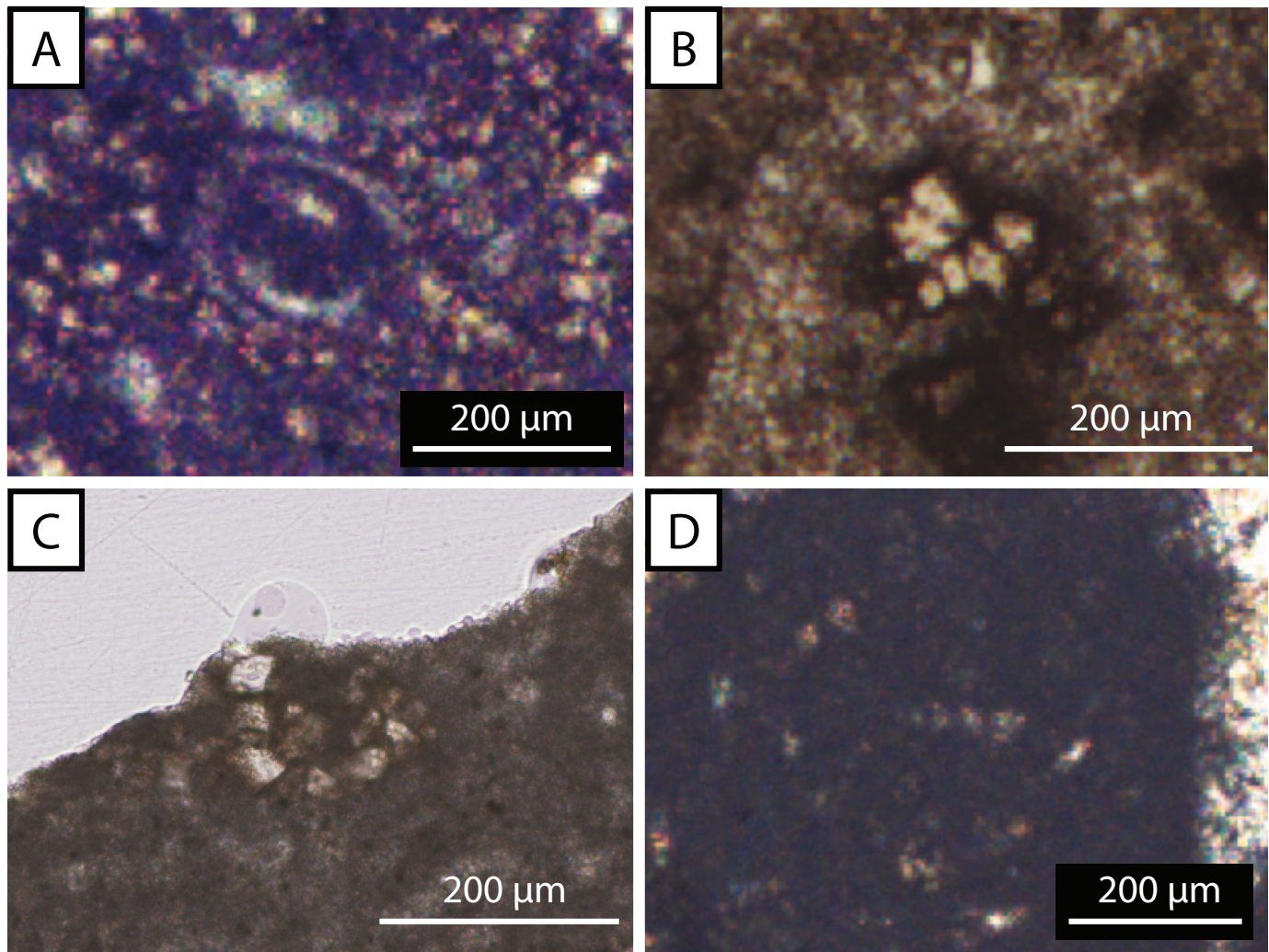


FIG. 13.—Identified taxa of benthic foraminifera from the Aguerd Izegzawne section. **A**) *Glomospira* sp., thin section DV-OZ-UR2 (1). **B**) *Siphovalvulina* sp., thin section OZS-577 (1). **C**) *Placopsilina* sp., thin section DV-OZ-UpperReefFlank (1). **D**) *Nodosaria* sp., thin section DV-OZ-ToarReef1 (1).

foraminifera experienced a decline in species richness. Lower Toarcian bioherms lack many of the LBF observed in Pliensbachian samples (Fig. 16), and the remaining LBF species, *Haurania deserta*, is smaller than the pre-event individuals and thus exhibits the Lilliput effect (Urbanek 1993). Our data supports the conclusion that the Pliensbachian/Toarcian boundary event was particularly severe for LBF (Jiang et al. 2020; Septfontaine 2020). Many authors posit that platform drowning in the Tethyan realm contributed to marine biotic turnover during the late Early Jurassic reef crises (Blomeier and Reijmer 1999; Woodfine et al. 2008; Léonide et al. 2012; Trecalli et al. 2012). Drowning can lead to the demise of benthic biota because organisms with photosymbionts, such as some LBF, rely on high light levels for growth (Schlager 1981, 1999); however, more recent studies suggest the Early Jurassic reef crisis coincides with a sea-level fall and subsequent carbonate factory collapse (Krencker et al. 2020, 2022; Andrieu et al. 2022).

The Pliensbachian/Toarcian carbonate factory collapse in Morocco was likely driven by a catastrophic influx of terrigenous siliciclastic material coincident with a temperature elevation, humidification, increased nutrient levels, and forced regression (Bodin et al. 2010, 2023; Andrieu et al. 2022; Krencker et al. 2022). Influxes in terrigenous sediment to near-shore environments are shown to reduce reefal biologic productivity in

the modern ocean (Freitas et al. 2019; Ranju et al. 2019) and in deep time (e.g., James and Jones 2015). Enhanced terrigenous input likely decimated organisms that could not survive in low light conditions, such as putatively photosymbiotic corals and LBF. The relationship between LBF and light tolerance is well established and considered one of the most important factors driving LBF diversity (Novak and Renema 2018). Additionally, eutrophication at the Pliensbachian/Toarcian boundary could have allowed opportunistic foraminifera to outcompete LBF. Similar studies of LBF from the Central High Atlas (Septfontaine 2020), as well as other regions (e.g., Tibet; Jiang et al. 2020) indicate that eutrophication could have occurred at least within the Tethyan oceanic basin, if not as a globally consistent pattern that caused the demise of many LBF.

The Jenkyns Event is also associated with a carbonate factory shutdown (Dromart et al. 1996; Léonide et al. 2012; Han et al. 2018; Krencker et al. 2020; Jiang et al. 2020) but based on the reef evaluations of foraminifera (this study) and corals (Vasseur et al. 2021) from the Central High Atlas of Morocco, this event had distinct ecological impacts on the Early Jurassic reefs. In contrast to the Pliensbachian/Toarcian boundary event, the Jenkyns Event was catastrophic for all benthic foraminifera; foraminiferal density in this study was substantially depleted across the Jenkyns



FIG. 14.—Image of the benthic foraminifera *Nodosaria* sp. of Ait Athmane Fm., which is the only taxon identified from the Ait Athmane Fm., thin section AA2A-008 (1).

Event. Decreases in specialist taxa like LBF are typical of intervals with intense environmental perturbation (Hallock 1981; Hottinger 1982), but such a substantial decrease in the abundance of nearly all benthic foraminifera implies a severe environmental perturbation at the Jenkyns Event. Ocean acidification at the Jenkyns Event is one possible trigger for ecologic turnover, as the rapid release of atmospheric carbon dioxide is hypothesized to have caused widespread acidification during the Jenkyns Event (Suan et al. 2008b; Hermoso et al. 2009; Trecalli et al. 2012; Krencker et al. 2020; Müller et al. 2020; Ettinger et al. 2021). Considering the relevance of acidification on both reef communities (e.g., Kiesling and Simpson 2011; Greene et al. 2012; Martindale et al. 2012) and extant benthic foraminifera (e.g., Uthicke et al. 2013), an acidification event would explain the severity of the ecologic turnover during the Jenkyns Event. However, no definitive evidence of acidification, such as dissolution, has been reported from the Central High Atlas sections to date.

The taxonomic analyses presented here suggests that *Planisepta compressa*, *Everticyclammina praevirguliana*, and *Siphovalvulina* spp., were decimated in the Tethyan realm during the early Toarcian biotic crises (Septfontaine 1984, 1985, 2020; Fugagnoli 2004; Han et al. 2021). The species *Siphovalvulina colomi* and *Siphovalvulina gibraltarensis* are not typically observed in lower Toarcian strata (Boudagher-Fadel et al. 2001; Boudagher-Fadel and Bosence 2007), so the presence of these taxa in the Jebel Toksine section is important for the biostratigraphic context of the lower Toarcian. Although *Mesoendothyra* sp. and *Everticyclammina praevirguliana* are absent in the Toarcian assemblages of this study, the genera *Mesoendothyra* and *Everticyclammina* persist into the Middle Jurassic (Loeblich and Tappan 1987; Banner and Highton 1990; Fugagnoli 2000, 2004; Omana and Arreola 2008), suggesting either an extirpation of these taxa or an extinction of these particular species. Additionally, *Haurania deserta* are inferred to have survived this interval based on isolated occurrences in Bathonian deposits (Athersuch et al. 1992), even though no post-Jenkyns Event specimens of *Haurania deserta* were observed in this study. These results indicate that the loss of many species of foraminifera in the Moroccan sections is considered an extirpation event, rather than a global extinction, which may imply that local conditions were intolerable for these taxa during the Jenkyns Event, but the species survived in refugia.

The extinction, extirpation, and survival patterns of Early Jurassic foraminifera provide useful insight into foraminiferal survival or

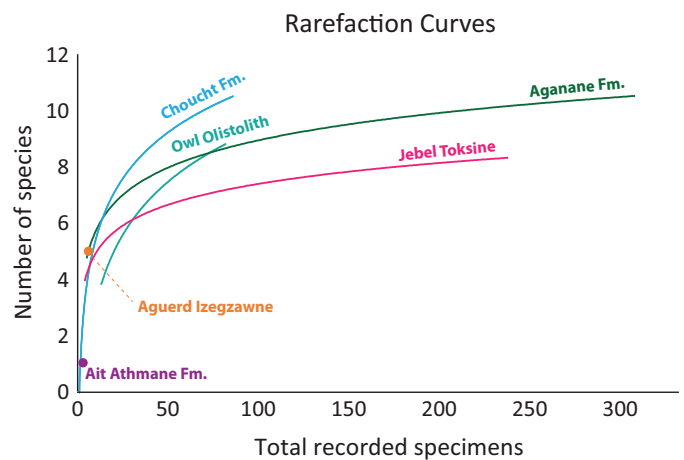


FIG. 15.—Rarefaction plot of each locality. Samples from the Jebel Toksine (pink line) and the Aganane Fm. (green line) have a higher abundance per thin section than any other locality (Choucht Fm. denoted by the blue line and Owl Olistolith by the teal line). Thin sections from the Aguerd Izegzawne section (orange dot) and Ait Athmane Fm. (purple dot) show a significantly low abundance of foraminifera, and therefore cannot be assessed with rarefaction.

decimation. LBF are particularly sensitive to rapid shifts in climate such as the poisoning event brought about during the Pliensbachian/Toarcian boundary. Contrasting benthic foraminiferal assemblages to the Pliensbachian/Toarcian boundary and Jenkyns Event allows us to assert that these events were ecologically distinct from one another. Taxa that do not persist past the Pliensbachian/Toarcian boundary, including *Mesoendothyra* sp., *Everticyclammina praevirguliana*, and *Planisepta compressa*, provide an important biostratigraphic framework for the Central High Atlas of Morocco. Lastly, the patterns of ecologic severity and foraminiferal assemblage shifts observed during the Early Jurassic may help predict future changes in benthic foraminiferal communities resulting from anthropogenic climate change.

## CONCLUSIONS

The foraminiferal communities from the Pliensbachian and Toarcian reef-bearing units in the Central High Atlas of Morocco are assessed in this study. In shallow carbonate platforms of the Pliensbachian, communities of benthic foraminifera thrived, including LBF, such as *Mesoendothyra* sp., *Everticyclammina praevirguliana*, and *Haurania deserta*. Benthic foraminiferal assemblages decrease in species richness across the Pliensbachian/Toarcian boundary extinction and the Jenkyns Event. Reefal samples from the lowermost Toarcian (pre-Jenkyns Event) reveal a foraminiferal assemblage similar to the late Pliensbachian assemblages apart from the diversity of LBF, which decreased across the carbonate crisis just after the stage boundary. The selective extinction of LBF show that these species are ecologically sensitive to the environmental perturbations of the Pliensbachian/Toarcian boundary event, which is consistent with the observed pulse of siliciclastic material and increased nutrient levels. Moreover, measures of evenness indicate several species of small benthic foraminifera outcompete other taxa in Toarcian reefs. In addition to the extinction of lithotids, benthic foraminifera were also decimated during the Jenkyns Event. Although coral bioherms quickly rebounded from the Jenkyns Event, foraminiferal abundance and diversity do not recover within the *H. bifrons* and *H. variabilis* ammonite zones. Very few species are observed in the post-Jenkyns Event study sections, and identified specimens only belong to clades of competitive and infaunal foraminifera. These results suggest that the ecological impacts of the two early Toarcian extinctions are distinct. LBF were clearly more severely impacted by the

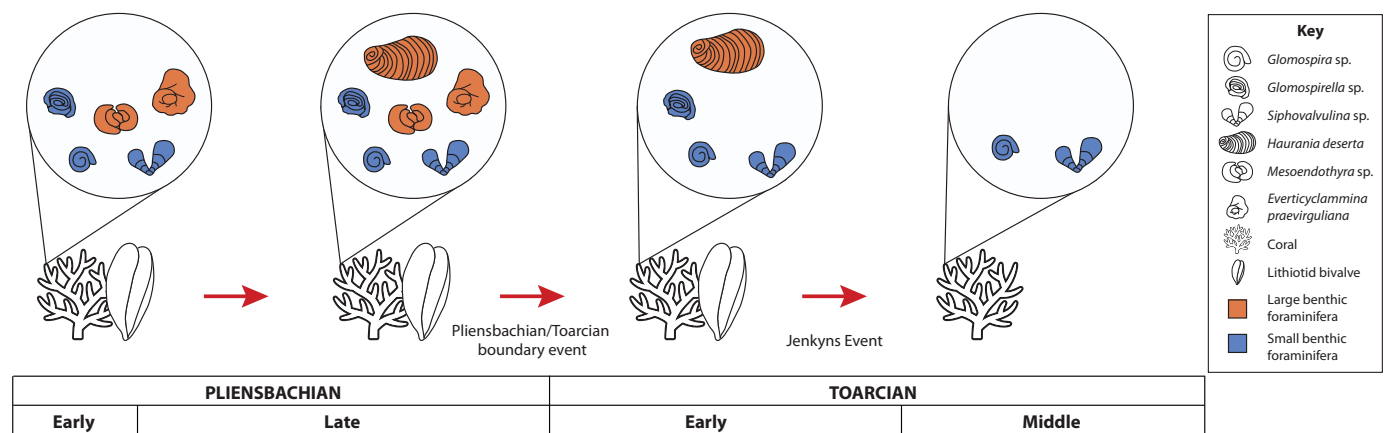


FIG. 16.—Representation of diversity across the Pliensbachian and early to middle Toarcian. The biotic turnover associated with the Pliensbachian/Toarcian boundary decimated the LBF *Mesoendothyra* sp. and *Everticyclammina praevirguliana*. Coral reefs recover locally from the Jenkyns Event by the middle Toarcian, but benthic foraminifera are nearly absent, including only small competitive foraminifera such as *Glomospira* sp. and *Siphovalvulina* sp. Additionally, lithotids were decimated by the Jenkyns Event, leaving coral as the only framework-builders of middle Toarcian reefs.

Pliensbachian/Toarcian event than other foraminifera, but those surviving taxa were decimated substantially by the Jenkyns Event. The assessment of benthic foraminiferal turnover allows for a greater understanding of the Early Jurassic extinction events and their unique environmental stresses on shallow-water platforms.

#### SUPPLEMENTAL MATERIAL

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

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Received 26 July 2023; accepted 6 May 2024.

## APPENDIX 1

## SYSTEMATIC PALEONTOLOGY

Phylum FORAMINIFERA d'Orbigny 1826  
 Suborder AMMODISCINA Mikhalevich 1980  
 Superfamily AMMODISCOIDEA Reuss 1862  
 Family AMMODISCIDAE Reuss 1862  
 Genus GLOMOSPIRA Rzehak 1885

**Diagnosis.**—Finely agglutinated test, forming into planispiral arrangements that are undivided by internal walls. Specimens typically have 3–5 whorls along a singular plane. Equatorial sections typically appear as circular to ovate spirals with irregular whorls, whereas axial sections resemble ovular concentric rings.

**Description.**—Equatorial views can have a longest diameter in section ranging from 131–317  $\mu\text{m}$ . Axial views have a slightly longer diameter than that of the equatorial view, with some specimens greater than 350  $\mu\text{m}$  in length. The average diameter of specimens within the Owl Olistolith thin sections is 212  $\mu\text{m}$ . Test thickness is highly variable, between 4–15  $\mu\text{m}$ , but the average thickness is 7  $\mu\text{m}$ .

**Discussion.**—*Glomospira*, although first appearing within the Middle Triassic, is a genus best represented within the Early Jurassic. The assignment of *Glomospira* to the family Ammodiscidae was made based on similar morphologic features shared with the genus *Ammodiscus*, of which no type specimen was originally described (Loeblich and Tappan 1954). In fact, the original description of the type specimen of *Glomospira* sp. compared its planispiral irregular coil to that of the genus *Ammodiscus* (Rzehak 1885). The genus *Gordiammina* was originally described as part of the family Ammodiscidae as having an agglutinated test that coils streptospirally, but the genus *Gordiammina* has since been synonymized with the genus *Glomospira* (Rumbler 1895).

Phylum FORAMINIFERA d'Orbigny 1826  
 Suborder AMMODISCINA Mikhalevich 1980  
 Superfamily AMMODISCOIDEA Reuss 1862  
 Family AMMODISCIDAE Reuss 1862  
 Genus GLOMOSPIRELLA Plummer 1945

**Diagnosis.**—Agglutinated test with streptospiral coiling, similar in appearance to a ball of twine. Late-stage coiling occurs along a single plane, providing for more ovate morphs in axial section. Whereas the test of *Glomospira* spirals uniformly for 3–5 whorls, the test of *Glomospirella* coils for 6–8 whorls along different planes (Gazdzicki 1983; Loeblich and Tappan 1987).

**Description.**—The longest diameter indicated in equatorial views and axial views ranges from 200–450  $\mu\text{m}$ . The only specimens observed at an axial view are AA1N-069 (13), BR-18-4 (2), BR-18-8 (1), AP-1B (6), and DV-AhmedReef2 (2). *Glomospirella* sp. generally has a greater diameter than *Glomospira* sp., in which the average longest diameter recorded throughout the Owl Olistolith is 249  $\mu\text{m}$ . Specimens observed within the Owl Olistolith samples are anomalously smaller than *Glomospirella* sp. from other sites. No clear patterns in test thickness are observed for these specimens, apart from specimens ranging from 4–13  $\mu\text{m}$ .

**Discussion.**—The genus *Glomospirella* shares a similar temporal range to its sister taxa, *Glomospira*. Additionally, members of both genera are often found in the same benthic assemblage. The type species is *Glomospirella*

*umbilicata*, which was initially assigned to the genus *Glomospira*. The genus *Glomospirella* is characterized by a wide variation of morphotypes dependent upon the specimens' stage of development (Plummer 1945).

Phylum FORAMINIFERA d'Orbigny 1826  
 Suborder TEXTULARIINA Delage and Hérouard 1896  
 Superfamily EGGERELLOIDEA Cushman 1937  
 Family SIPHOVALVULINIDAE Gale et al. 2018  
 Genus SIPHOVALVULINA Septfontaine 1988

**Diagnosis.**—Agglutinated test with triserial chamber arrangement. Specimens are coiled trochospirally with three chambers per whorl, apparent in transversal section as three chambers along separate axes. A central siphon connects each of the apertures and provides for its etymology, but that morphologic feature has since been redefined as an umbilical cavity, because it extends from the umbilical side of the test (Gale et al. 2018). Longitudinal sections of *Siphovalvulina* sp. include two of the three chamber axes with the umbilical cavity shown. Axial sections include chambers along all three axes and do not include the central umbilicus.

**Description.**—Specimens identified as *Siphovalvulina* sp. have their longest diameter in longitudinal view along one of the two chamber axes. The specimens' longest diameter ranges between 140–423  $\mu\text{m}$ , but a few specimens are a morphotype that is longer than 700  $\mu\text{m}$ . The equatorial test width of specimens, measured perpendicular to the longest diameter in longitudinal section, averages 267  $\mu\text{m}$ . Though equatorial test width is often less than the longest diameter, some specimens have greater test width than their longitudinal length. Test thickness ranges between 5–16  $\mu\text{m}$ .

**Discussion.**—*Siphovalvulina* is one of the oldest radiating genera of Lower Jurassic carbonate platforms, with some species originating in the late Hettangian (Velić 2007). Although it was originally defined as a generic name with no description of its morphology, *Siphovalvulina* was redefined as its own monospecific genus, with the type species *S. variabilis* (Loeblich and Tappan 1987; Septfontaine 1988). The genus *Siphovalvulina* was initially designated to the family Pfenderinidae along with the creation of a new subfamily, Pfenderininae, primarily with the justification that Pfenderinidae have a subcameral tunnel and more chambers per whorl than that of the closely related family Verneulinidae (Smout and Sugden 1962; Septfontaine 1988). The genus has since been reassigned to Verneulinidae due in part to the discovery of other siphonal genera within this family (Boudagher-Fadel et al. 2001). The presence of an interiomarginal aperture is a diagnostic feature of this family. *Siphovalvulina* was once more reassigned, because Verneulinidae does not have a canaliculated test; this spurred the creation of the new family Siphovalvulinidae within the superfamily Eggerelloidea (Gale et al. 2018).

Phylum FORAMINIFERA d'Orbigny 1826  
 Suborder TEXTULARIINA Delage and Hérouard 1896  
 Superfamily EGGERELLOIDEA Cushman 1937  
 Family SIPHOVALVULINIDAE Gale et al. 2018  
 Genus SIPHOVALVULINA Septfontaine 1988

SIPHOVALVULINA COLOMI Boudagher-Fadel et al. 2001

**Diagnosis.**—The species *S. colomi* is distinguished from other members of the *Siphovalvulina* genus by the size of its umbilical cavity and apical angle. *Siphovalvulina colomi* has a narrow umbilical cavity and a set of axes that are nearly parallel, especially in late growth (Boudagher-Fadel et al. 2001).

**Description.**—All referred specimens are identified in longitudinal view. Some specimens of *S. colomi* are greater than 400  $\mu\text{m}$ , but the average longest diameter of specimens is 364  $\mu\text{m}$ . The equatorial test width of *S. colomi* is less than that of specimens of *Siphovalvulina* sp. and *S. gibraltarensis*. Test thickness ranges from 6–15  $\mu\text{m}$ .

**Discussion.**—The species is temporally constrained to the Sinemurian and Pliensbachian, as no literature currently describes *S. colomi* in the Toarcian (Boudagher-Fadel et al. 2001; Boudagher-Fadel and Bosence 2007). The observation of *S. colomi* from lower Toarcian strata in this study indicate the first known occurrence of the species in the Toarcian, thus extending the species temporal range. Nevertheless, this study confirms that *S. colomi* does not persist past the Jenkyns Event.

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder TEXTULARIINA Delage and Héroutard 1896  
Superfamily EGGERELLOIDEA Cushman 1937  
Family SIPHOVALVULINIDAE Gale et al. 2018  
Genus SIPHOVALVULINA Septfontaine 1988

SIPHOVALVULINA GIBALTARENSIS Boudagher-Fadel et al. 2001

**Diagnosis.**—Distinguishing the species from *S. colomi*, *S. gibraltarensis* has a broad umbilicus and a much more broadly flaring test of external angle of spire 90 degrees or more (Boudagher-Fadel et al. 2001).

**Description.**—All referred specimens are identified in longitudinal view. *Siphovalvulina gibraltarensis* has an average equatorial test width of 329  $\mu\text{m}$ , which is greater than that of *S. colomi*. Further, *S. gibraltarensis* has an average equatorial test width greater than the average length of the longitudinal section in the Owl Olistolith samples. Test thickness ranges from 6–15  $\mu\text{m}$ .

**Discussion.**—Like *S. colomi*, *S. gibraltarensis* is only currently described in the Sinemurian and Pliensbachian (Boudagher-Fadel et al. 2001; Boudagher-Fadel and Bosence 2007). This study provides evidence for the occurrence of *S. gibraltarensis* in the *Dactylioceras polymorphum* ammonite Zone of the Central High Atlas Morocco, thus extending the range of the species to the early Toarcian, but not beyond the Jenkyns Event.

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder ORBITOLININA Kaminski 2004  
Superfamily PFENDERINOIDEA Smout and Sugden 1962  
Family HAURANIIDAE Septfontaine 1988  
Genus HAURANIA Henson 1948  
HAURANIA DESERTA Henson 1948

**Diagnosis.**—Agglutinated test, with a dominantly uniserial chamber arrangement. An initial trochospire is apparent in some specimens in longitudinal section. *Haurania deserta* have an apical angle less than 90 degrees and a test that becomes more parallel-sided in late development. The species is elongate along the central axis, with the greatest diameter of some specimens more than 700  $\mu\text{m}$ . Although alveolar walls are lacking, complex structures called hypodermic networks are present. Transversal sections are circular to ovate through one chamber, and the hypodermic network is apparent. Oblique sections are also common, displaying a more ovular view than transversal sections.

**Description.**—*Haurania deserta* specimens of this study are observed only in the Aganane Fm. (late Pliensbachian), Choucht Fm. (late Pliensbachian), and Jebel Toksine (early Toarcian) sites, and have a longest diameter between 283–1114  $\mu\text{m}$  in longitudinal section. Test thickness ranges between 4–14  $\mu\text{m}$ . Test thickness in these specimens is highly variable and does not always coincide with specimen size; two specimens (JTC-M1 (31) and JTC-M1 (47)) of similar size from the same thin section vary in test thickness by five micrometers.

**Discussion.**—*Haurania deserta* was initially assigned to its own family under the superfamily Loftusiacea, which is no longer accepted and synonymized with the superfamily Loftusioidea (Septfontaine 1988; Athersuch et al. 1992). The reassignment of the *Haurania* genus under the family Spirocyclinidae was then proposed (Athersuch et al. 1992). The family Hauraniidae was lastly reassigned under Pfenderinoidea, and the new suborder Orbitolinina belonging to the order Loftusiida (Kaminski 2004). The type specimen was obtained and described by Henson (1948) from a Bathonian bed in Iraq. Earliest recorded occurrences of *Haurania deserta* are from the Sinemurian of the *Orbitopsella* biozone, and the stratigraphically highest recorded *H. deserta* is from lower Bathonian deposits (Athersuch et al. 1992; Fugagnoli 2004). The initial description by Henson (1948) described it as a species of LBF, which is consistent with the observed occurrences of the species in this study.

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder TEXTULARIINA Delage and Héroutard 1896  
Superfamily LITUOLOIDEA de Blainville 1827  
Family PLACOPSILINIDAE Rhumbler 1913  
Genus PLACOPSILINA d'Orbigny 1850

**Diagnosis.**—Agglutinated test forming a uniserial chamber arrangement. The test curves slightly and chambers are semi-rectangular. Septa and chambers often have variable thickness and length, respectively. All specimens identified are in longitudinal section. Alveolar walls are sometimes apparent.

**Description.**—Most specimens observed have three or four chambers of varying dimensions in longitudinal view. The average longest diameter of specimens observed in the Owl Olistolith is 576  $\mu\text{m}$ , though the longest diameter of all specimens range from 275–677  $\mu\text{m}$ .

**Discussion.**—The original description of the genus *Placopsilina*, for which the type species is *P. scorpionis*, compared it to the genus *Webbina* (d'Orbigny 1850). *Placopsilina* is considered as distinct from *Webbina* by having full chambers (d'Orbigny 1850). Although the genera are not taxonomically related, both *Placopsilina* and *Webbina* describe a uniserial taxon with an elongate and sometimes curved test. *Placopsilina* is an encrusting foraminifera that often encrusts the upper surface of coral in clusters (Bosellini and Papazzoni 2003).

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder TEXTULARIINA Delage and Héroutard 1896  
Superfamily LITUOLOIDEA de Blainville 1827  
Family MESOENDOTHYRIDAE Voloshinova in Bykova et al. 1958  
Genus MESOENDOTHYRA Dain in Bykova et al. 1958

**Diagnosis.**—Agglutinated test with a planispiral chamber arrangement. Three to four streptospirally coiled whorls are apparent in axial section, forming thin ovular tests. Chambers are subsequently larger and more concave in late-stage coiling.

**Description.**—The longest diameter of the recorded specimens ranges from 250–369  $\mu\text{m}$ . All referred specimens, apart from GO-1 F40, are in axial view. Specimen GO-1 F40 is shown in equatorial section and has the longest recorded diameter compared to the axial sections. Test thickness ranges from 7–11  $\mu\text{m}$ .

**Discussion.**—*Mesoendothyra* sp. often is used as a biostratigraphic marker for the Lower Jurassic, as its first recorded appearance is from the early Sinemurian, although some species temporally extend into the Early Cretaceous. *Mesoendothyra* is a genus of LBF that are ecologically constrained to shallow marine settings (Loeblich and Tappan 1987; Fugagnoli 2004). Like *Haurania deserta*, species of *Mesoendothyra* species have a subepidermal network, which is hypothesized to be an adaptation to avoid photoinhibition (Fugagnoli 2004). Additionally, *Mesoendothyra* differs from other genera of the family Mesoendothyridae because they have alveolar continuations along the outer wall (Loeblich and Tappan 1987).

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder TEXTULARIINA Delage and Hérouard 1896  
Superfamily LITUOLOIDEA de Blainville 1827  
Family EVERTICYCLAMMINIDAE Septfontaine 1988  
Genus EVERTICYCLAMMINA Redmond 1964

EVERTICYCLAMMINA PRAEVIRGULIANA Fugagnoli 2000

**Diagnosis.**—Agglutinated test, coiled initially planispiral with late-stage uncoiling (Redmond 1964). A single septal aperture extends from the planispiral portion of the test, and becomes terminal in the uniserial, uncoiled chambers. Irregularly spaced alveolar walls in the test are characteristic of *Everticyclammina praevirguliana* (Fugagnoli 2000). *Everticyclammina praevirguliana* has longer alveolar walls than *Everticyclammina virguliana*, differentiating the taxa (Fugagnoli 2000). Axial sections have visible alveolar walls along both sides of the test.

**Description.**—Specimens GO-12 F2 and BR-18-3 (14) are shown in axial view, whereas the rest are equatorial sections. The longest diameter of each specimen ranges from 245–584  $\mu\text{m}$ , and averages 398  $\mu\text{m}$ . Test thickness varies widely between 5–23  $\mu\text{m}$ .

**Discussion.**—The genus *Everticyclammina* was originally assigned to the family Lituolidae, based on *Everticyclammina*'s physical similarities to the sister genus *Pseudocyclammina*; however, these genera have since been reassigned to their own families under the superfamily Lituolacea (Septfontaine 1988). The type specimen of the genus *Everticyclammina* is *Everticyclammina hensoni* (Redmond 1964) and is described as having thinner walls than *Pseudocyclammina* sp. Additionally, the species *Everticyclammina virguliana* and *Everticyclammina kelleri* were reassigned from *Pseudocyclammina* based on the observation of a single, areal aperture distinctive of all members of the genus *Everticyclammina* (Banner and Highton 1990). *Everticyclammina praevirguliana* is the only species of the genus *Everticyclammina* identified within the Early Jurassic, so there is an inferred, yet unobserved, continuation of *Everticyclammina* sp. between the last occurrence of *E. praevirguliana* in the Early Jurassic and other species of *Everticyclammina* in the Late Jurassic (Fugagnoli 2000).

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder MILIOLINA Delage and Hérouard 1896  
Superfamily CORNUSPIROIDEA Schultze 1854  
Family CORNUSPIROIDAE Schultze 1854  
Genus VIDALINA Schlumberger 1900

**Diagnosis.**—Planispiral chamber arrangement with a discoidal, calcareous test. Axial sections show a thin ovular test with 4–5 chambers per whorl. Equatorial sections reveal an elongated elliptical spiral with pointed ends like a marquise diamond. The inner walls in equatorial section have angular protrusions extending to the ends of the ellipse-shaped test. Whorls are semi-regular in thickness.

**Description.**—All specimens, apart from AP-3-2 (2), are observed in axial section. The longest diameter of the observed specimens ranges from 170–360  $\mu\text{m}$ .

**Discussion.**—Although the genus *Vidalina* originated in the Triassic and is common in the Jurassic of the Tethyan realm, *Vidalina* extends to and is most common in the Late Cretaceous.

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder NODOSARIINA Saidova 1981  
Superfamily NODOSARIOIDEA Ehrenberg 1838  
Family NODOSARIIDAE Ehrenberg 1838  
Genus NODOSARIA Lamarck 1812

**Diagnosis.**—Elongate, uniserial chamber arrangement with a calcareous test. There are typically five to seven box-shaped to ovate chambers in each specimen when viewed in longitudinal section. Specimens of *Nodosaria* sp. have a low apical angle and outer test walls that are nearly parallel. Chambers are slightly greater in size in late-stage development and are more angular than globular.

**Description.**—All specimens identified are observed in longitudinal section. The longest diameter of the specimens ranges from 186–308  $\mu\text{m}$ , and those specimens that are longer than 200  $\mu\text{m}$  have more chambers than the smaller specimens. Further, the smallest specimen (AA1N-070 (4)) has only four chambers, whereas the two largest specimens (JTD 1.3 (3) and DV-OZ-ToarReef1 (1)) have seven chambers. Equatorial test width of the observed specimens ranges from 53–118  $\mu\text{m}$  and test thickness is recorded from 9–11  $\mu\text{m}$ .

**Discussion.**—The genus *Nodosaria* first appears in the Late Carboniferous, is described by the type specimen *N. laevigata*, and taxa such as *N. krotovi* proliferate within the Permian (Loeblich and Tappan 1955; Jia et al. 2010). Members of the genus *Nodosaria* have been interpreted as shallow infaunal foraminifera that lived at a depth of less than 5 cm (Olóriz et al. 2006), which would make their incorporation into benthic communities distinct from the other foraminifera observed in this study. *Nodosaria* are considered an anaerobic taxon, indicating an intermediate dissolved oxygen content (Coccioni and Galeotti 1993). Conditions with low oxygenation are thus more advantageous for elongate, infaunal foraminifera such as *Nodosaria* sp. (Coccioni and Galeotti 1993; Kaiho 1994; Schönfeld 2001; Tetard et al. 2021), making their abundance within the middle Toarcian samples of this study substantial for understanding the severity of the Jenkyns Event.

Phylum FORAMINIFERA d'Orbigny 1826  
Suborder TEXTULARIINA Delage and Hérouard 1896  
Superfamily LITUOLOIDEA de Blainville 1827  
Family MESOENDOTHYRIDAE Voloshinova in Bykova et al. 1958  
Genus PLANISEPTA Septfontaine in Kaminski 2000

PLANISEPTA COMPRESSA Hottinger 1967

**Diagnosis.**—Agglutinated foraminifera with a uniserial test and early planispiral coiling. The uniserial portion of the test has up to 12 chambers and the planispiral portion coils two to four times. Additionally, members of the genus *Planisepta* are laterally flattened, especially compared to other related genera such as *Litiosepta* (Septfontaine in Kaminski 2000).

**Description.**—Specimens are identified in axial and equatorial section. The longest diameter of the specimens' ranges from 742–1288  $\mu\text{m}$ , and averages 1080  $\mu\text{m}$  long. Larger specimens typically have more chambers in the uniserial portion of the test than smaller specimens of *P. compressa*. Test thickness ranges between 25–41  $\mu\text{m}$ .

**Discussion.**—The species *Planisepta compressa* is synonymous with the unaccepted *Litiosepta compressa* but was redefined under the genus *Planisepta* by Septfontaine in Kaminski (2000). The genera *Planisepta* and *Litiosepta* differ by size of chambers in the uniserial portion of the test (Septfontaine in Kaminski 2000). *Planisepta compressa*, previously referred to as *Litiosepta compressa*, is the type species of the genus *Planisepta* (Hottinger 1967). *Planisepta compressa* is temporally confined from the Sinemurian to the *Arietoceras algovianum* ammonite Zone (upper Pliensbachian) (Septfontaine 2020).