Dissecting *"Lithiotis"* Bivalves: Implications for the Early Jurassic Reef Eclipse

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Following extensive Late Triassic coral-constructed reefs and the aftermath of the Triassic–Jurassic mass extinction, Early Jurassic buildups are rare and constructed primarily by bivalves. The Pliensbachian exhibits a radiation of aberrant pterioid bivalves, the "Lithiotis" bivalves, which include: Lithiotis problematica, Cochlearites loppianus, Gervilleioperna *sp.,* Mytiloperna *sp., and* Lithioperna scutata. *These large bivalves are ubiquitous in shallow, nearshore tropical waters and restricted to the Early Jurassic recovery interval. Field and thin-section observations indicate a strong zonation of "Lithiotis" bivalves in shallow nearshore environments.* Gervilleioperna *and* Mytiloperna *are restricted to tidal-flat and inner-platform facies.* Lithioperna scutata *is found throughout the lagoonal subtidal facies and even in some low-oxygen environments.* Lithiotis *and* Cochlearites *construct buildups in subtidal facies, and both taxa exhibit discordant valves—one valve is converted into a pedestal, the other is an opercular valve. The largest buildups attain lengths over 60 m and thicknesses of 3–5 m. It is proposed that the reef-building bivalves* Lithiotis problematica *and* Cochlearites loppianus *filled the relatively empty ecological niche of reef-building during the Early Jurassic (Lias), only to be replaced by their predecessors, the scleractinian corals, by the Middle Jurassic. The other "Lithiotis" bivalves (*Lithioperna scutata, Mytiloperna, *and* Gervilleioperna *sp.) lived in restricted lagoonal environments with possible fluctuating salinity on Early Jurassic (Liassic) carbonate shelves.* Lithiotis *and* Cochlearites, *in contrast to many oysters, do not orient their commissure planes in a single direction. Instead, these two buildup-constructing genera radiate out from a central bouquet, possi-*

bly maximizing exposure to light rather than current. Due to their growth habit, extensive calcification, presumed oligotrophic environment, and pseudocoloniality, these two genera may have harbored photosymbionts. Severe environmental changes and associated unusual seawater chemistry of the protracted Early Jurassic recovery may have led to suppressed coral-reef growth and the rapid radiation of reef-building bivalves.

INTRODUCTION

Throughout the Phanerozoic, nearshore tropical carbonate environments contain higher biodiversity than

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other marine ecosystems, yet are more vulnerable to global biogeochemical events. Reefs are often the first ecosystems decimated in biotic crises and often the last to return (Droser et al., 1997). One of the most striking effects of the end-Triassic mass extinction was the total loss of reef ecosystems that had flourished, notably in the Northern Calcareous Alps and elsewhere, until the end of the period. The Early Jurassic, or Lias, represents a slow but steady paleogeographic change due to the reconfiguration of the continents with the rifting of Pangaea (Nance and Murphy, 1994). The Early Jurassic is also punctuated by a significant second order extinction—the Pliensbachian–Toarcian extinction event (Aberhan and Fürsich, 1997)—and the shifting and diminishing carbonate-platform space due to rapid sea-level change and associated climatic warming (Hallam and Wignall, 1999). One of the proposed causes of environmental stress at the end-Triassic and Early Jurassic is a rapid rise in CO_2 levels caused by the outpouring of the Central Atlantic Magmatic Province (CAMP) as a result of the rifting of Pangaea (Marzoli et al., 1999). Some paleobotanical evidence and carbon isotopes from oolithic goethites and pedogenic calcite estimate a

2,000–4,000 ppm increase in atmospheric CO_2 levels (Yapp and Poths, 1996; McElwain, et al., 1999). However, others propose only a 250 ppm increase based on carbon isotope paleosol data, approximately double that of pre-Industrial Holocene atmospheric CO_2 (Tanner et al., 2001).

The link between this rapid rise in CO_2 and ecosystem degradation has not been explored in Early Jurassic shallow tropical marine environments. Colonial metazoan reefs are unknown in the Hettangian, but stromatolite reefs have been reported (Stanley, 1988 and 1997; Kiessling et al., 1999; Fig. 1). Sinemurian reefs with Late Triassic coral species are known from volcanic islands in the ancestral Pacific (Stanley and Beauvais, 1994). The number of reefs per million years rose in the Pliensbachian only to drop after the Early Toarcian extinction event. Only by the Bajocian (Middle Jurassic) did reefs constructed by colonial metazoans become reestablished on a global scale (Beauvais, 1984; Fig. 1). The development of reefs may have been complicated due to dramatic sea level change during the Late Triassic and Early Jurassic. At the Triassic–Jurassic transition, sea level dropped to an extreme eustatic low. During the Early Jurassic, sea level slowly rose, progressively flooding shallow-water platforms, which allowed for the return of carbonate buildups. Extensive carbonate buildups occur in this interval, but they are not dominated by coral reefs as in the preceding Late Triassic.

However, Lower Jurassic tropical marine environments are exceptional for the great number of bivalve-construct-
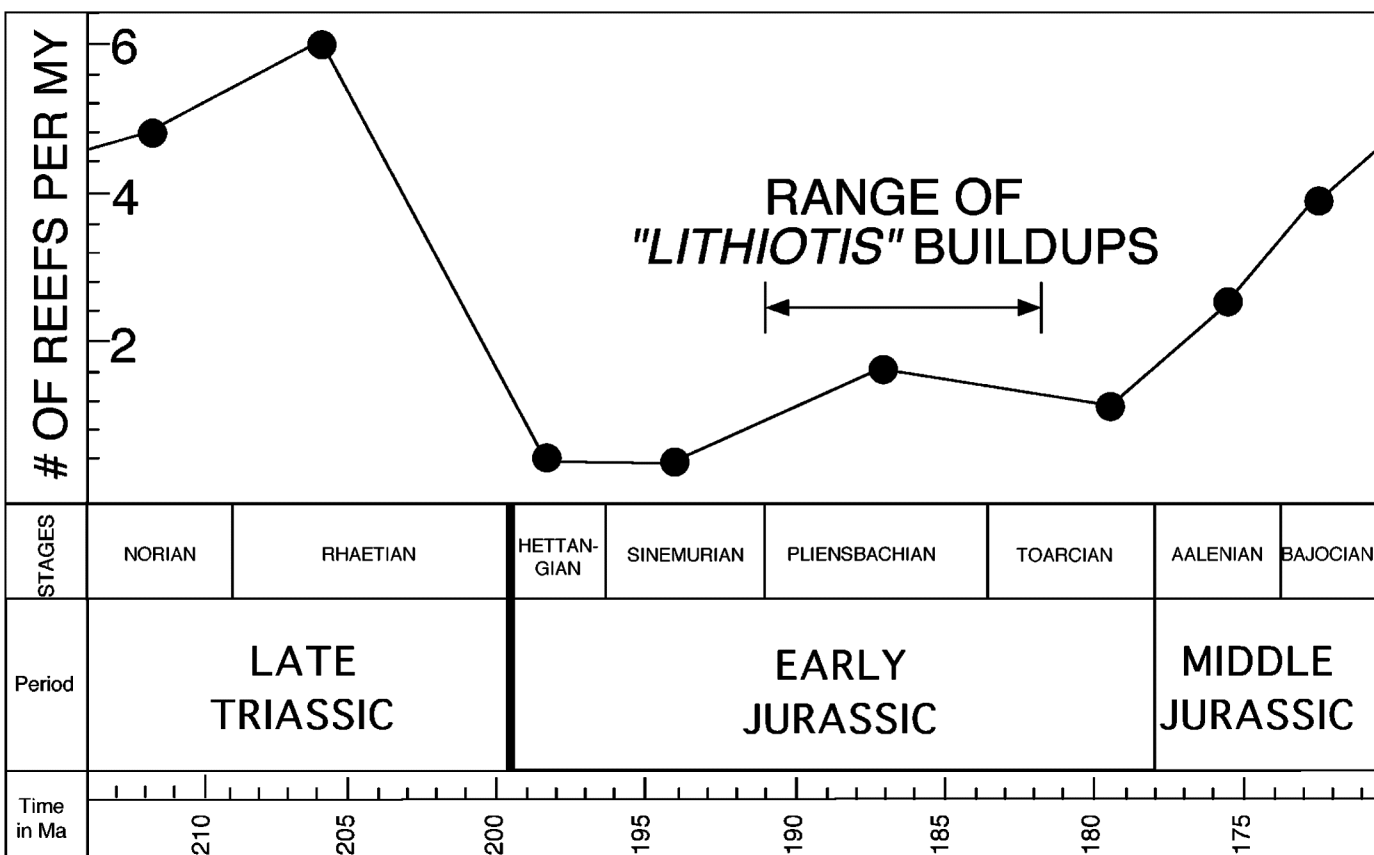
FIGURE 1—The Early Jurassic reef eclipse and range of "*Lithiotis*" facies bivalves. Norian–Rhaetian boundary from Gradstein et al. (1994), Early Jurassic stages after Pálfy et al. (2000). Jurassic reef curve from Flügel and Flügel-Kahler (1992) and Kiessling et al. (1999).

ed buildups (Kiessling et al., 1999; Fig. 2). The term "*Lithiotis*" bivalves refers to five unique bivalves notable for their heavily calcified valves, multivincular ligaments, and dominating presence in Pliensbachian and Lower Toarcian nearshore tropical ecosystems. The "*Lithiotis*" bivalves include: *Lithiotis problematica, Cochlearites loppianus, Gervilleioperna* sp., *Mytiloperna* sp., and *Lithioperna scutata* (Geyer, 1977; Fig. 2). The bivalve *Lithiotis problematica* formed extensive rudist-like buildups, yet not all "*Lithiotis*" facies bivalves constructed bioherms (Broglio Loriga and Neri, 1976). The term "*Lithiotis*" bivalves has been applied haphazardly to all bivalves found in Lower Jurassic shallow carbonate deposits (e.g., Lee, 1983).

All of the "*Lithiotis*" bivalves appeared during the Early Jurassic and all but one became extinct before the Middle Jurassic (*Mytiloperna* ranges into the Middle Jurassic), thus they represent failed crisis progenitors (sensu Harries et al., 1996). Failed crisis progenitors are unique evolutionary and ecological recovery taxa—in the aftermath of a mass extinction these organisms appear uniquely adapted to the environmental conditions of the recovery
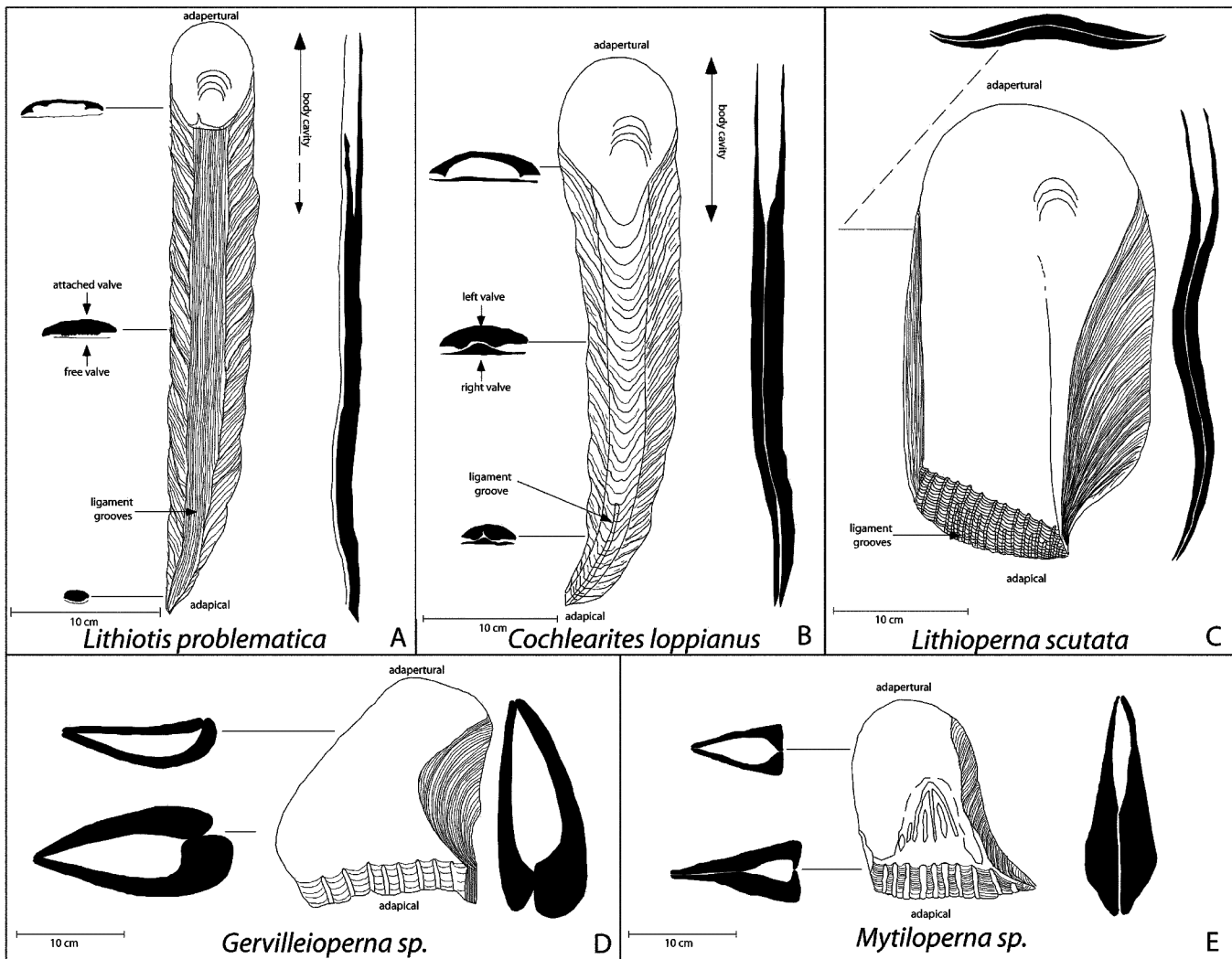
FIGURE 2—Early Jurassic "*Lithiotis*" facies bivalves. (A) *Lithiotis problematica*, right valve; (B) *Cochlearites loppianus*, left valve; (C) *Lithioperna scutata*, right valve; (D) *Gervilleioperna* sp., left valve; (E) *Mytiloperna* sp., right valve.

only to become extinct when normal conditions return. *Lithiotis*, *Cochlearites*, and *Lithioperna* constructed carbonate buildups. Bioherms constructed by *Lithiotis problematica* in particular have been assigned in previous studies to restricted nearshore environments of rapidly fluctuating salinity and temperature, based on the low diversity of the bioherms and morphological similarity to modern oysters (e.g., Bosellini, 1972). This assessment should be questioned. Depleted diversity is to be expected after mass extinctions and does not necessarily indicate restricted nearshore environments (Bottjer, 1998). A non-uniformitarianist view of recovery intervals should be applied as many of the constraints on new niches, organisms, or interactions are relaxed in the interval immediately following a mass extinction.

Reefs and Buildups

The term "reef" is fraught with controversy. The strictest definition of a reef is a "rigid wave-resistant framework constructed by large skeletal organisms" (Ladd, 1944, p. 26). However, to prove conclusively that a buildup could withstand wave action is very difficult in the extensive fossil record of reefs. In particular, because the major framework-building constituents of reefs have changed significantly throughout the Phanerozoic, it is even more difficult to use uniformitarian principles to define ancient reefs. Wood (1999; p. 401) proposed a more encompassing definition of a reef as a "discrete carbonate structure formed by in situ or bound organic components that develops topographic relief on the seafloor." Other terms used to describe carbonate buildups include bioherm and biostrome. The term bioherm designates a lens-shaped structure with some topographical relief constructed by in situ biota, but not necessarily wave-resistant or created by skeletal elements (James and Bourque, 1992). Biostrome is used to denote a tabular body without significant topographic relief and consists of biological elements that are often but not always in life-position (e.g., a death assemblage; adapted from Wood, 1999). For the purpose of this paper, the term carbonate buildup is used in an attempt to refrain from genetic implications associated with biostrome, bioherm, or reef. The term reef or bioherm is used when the criteria of Ladd (1944) have been sufficiently met.

"*Lithiotis*" Facies Bivalves

Lithiotis problematica originally was described as an alga, thought to be related to the modern *Udotea*, by Gümbel (1871). Later, Tausch (1890) and Reis (1903) correctly placed it within the Mollusca. Carter (1990) proposed that the "*Lithiotis*" bivalves should be placed in the Family Isognomidae, which radiated during the Early Jurassic from the Family Bakevilliidae within the Pterioida. *Lithiotis problematica* is a sessile, monomyarian bivalve characterized by its unusual morphology, prismatic aragonite mineralogy, and propensity to aggregate in rudist-like bioherms (Fig. 3A). *Lithiotis problematica* has a spoon-shaped shell, which reaches a height of 30 cm or more, a width of

4–6 cm, and an average thickness of 3 cm (Accorsi Benini and Broglio Loriga, 1982; Fig. 2A). *Lithiotis* has a thick, attached pedestal valve (Fig. 2A) described as the left or right in the literature (e.g., Accorsi Benini and Broglio Lo-
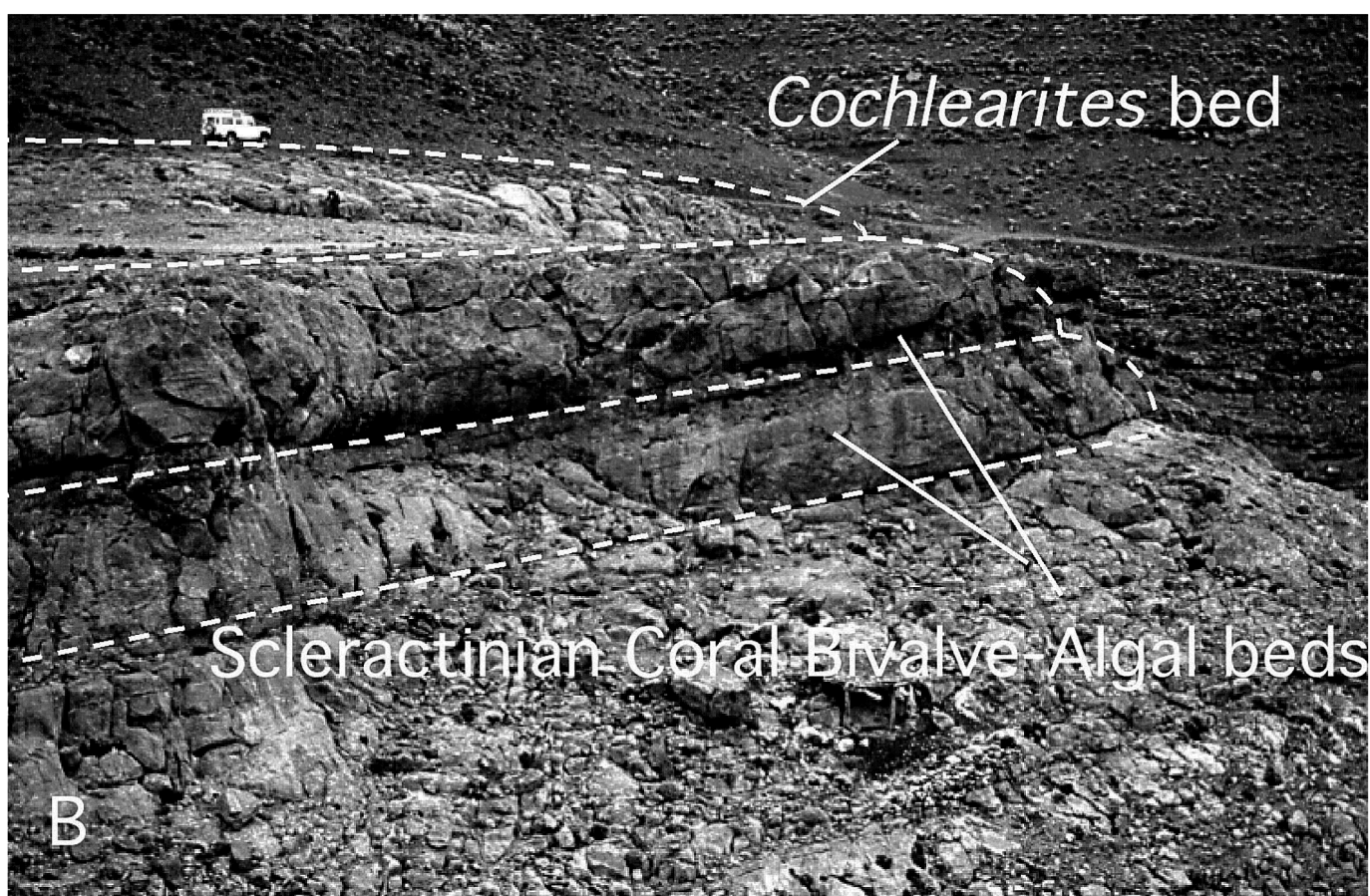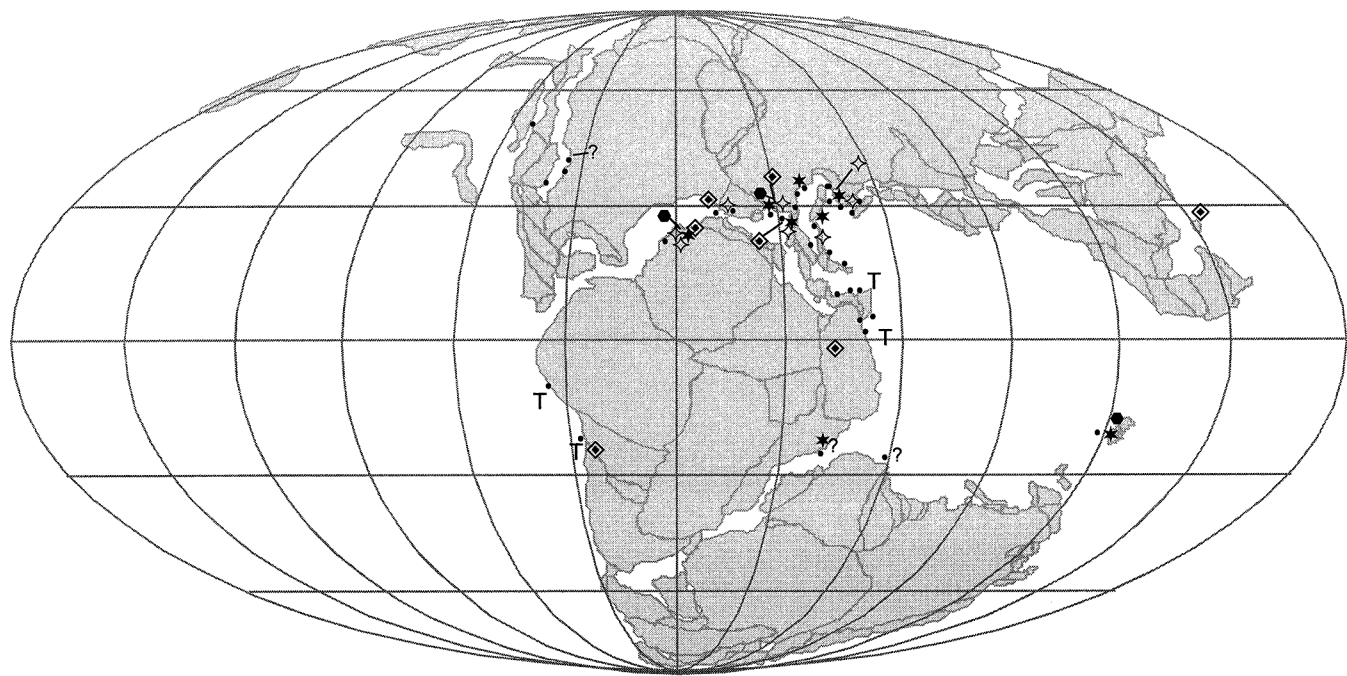

Lithiotis bed

A

Cochlearites bed

Scleractinian Coral Bivalve Algal beds

B

FIGURE 3—Bivalve-constructed buildups of the Early Jurassic. (A) A *Lithiotis problematica* buildup near Suplee-Izee, Oregon. (B) Assemsouk, an Early Jurassic reef from the Eastern High Atlas; a *Cochlearites loppianus* buildup is located at the top meter of the outcrop, indicated by dashed lines.

riga, 1977 and Chinzei, 1982, respectively). The other valve, referred to as the opercular valve, is of subequal length, flat, and very thin (only 1–2 mm thick; Chinzei, 1982). Because these forms are grossly elongated along the dorso-ventral axis, the terms ventral and dorsal are of little utility. Therefore, the terms adapertural and adapical from other molluscan classes are employed for ventral and dorsal, respectively. A small body cavity space was located at the most adapertural portion of the shell. *Cochlearites loppianus*, also a bioherm-builder, is of a similar morphology but the opercular valve is thicker than that of *Lithiotis problematica* (Fig. 2B).

Lithioperna scutata, ironically the most common bivalve of the "*Lithiotis*" facies, is most often 15–20 cm long, but some specimens can reach 70 cm (Debeljak and Buser, 1997; Fig. 2C). The valves are subequal, with flattened to concave-convex massive shells that are rounded at the adapertural margin (Broglio Loriga and Posenato, 1996). In many *Lithioperna* specimens, the ligament grooves are slightly oblique to the anterior margin (Accorsi Benini, 1979). *Gervilleioperna* sp. is roughly equivalved, with a vertically elongated cuneiform body, massive shells, a narrow prominent umbo, a long posterior wing, and a prosogyrous beak (Cox et al., 1969; Fig. 2D). *Mytiloperna* is an

- *Lithiotis problematica*
- ∗ *Cochlearites loppianus*
- ✧ *Lithioperna scutata*
- ◈ *Mytiloperna* sp.
- ● *Gervilleioperna* sp.

FIGURE 4—Distribution of the "*Lithiotis*" facies bivalves; all sites are Pliensbachian in age except those denoted by a "T" (Toarcian). Unconfirmed occurrences are denoted by a "?". Compiled from Broglio Loriga and Neri (1976), Lee (1983), Nauss and Smith (1988), and Rey et al., (1990). Base map of the Early Jurassic from Schettino and Scotese (2001).

equivalved, mytiloform bivalve with a massive shell and a ridge running from the subterminal beak to the adapical margin (Cox et al., 1969; Fig. 2E). The shell microstructure of the five genera is similar: an outer layer of calcitic prisms with middle and inner nacreous layers (Accorsi Benini and Broglio Loriga, 1982; Broglio Loriga and Posenato, 1996). *Lithiotis*, *Lithioperna*, *Gervilleioperna*, and *Mytiloperna* all have a multivincular ligament. *Cochlearites* has a narrow-groove, simple ligament structure, which may be a secondary derivation (Chinzei, 1982).

The objectives of this paper are: (1) to clarify the term "*Lithiotis*" bivalves by establishing the ecological zonation of the five bivalves and their constructional morphology; (2) detail the growth habit and arrangements of clustering species; and (3) reevaluate paleoenvironmental data in a non-uniformitarian context. The paper closes with a discussion on linking high atmospheric CO_2 and intervals of bivalve-constructed buildups.

STUDY SITES AND METHODS

"*Lithiotis*" facies bivalves are common in Lower Jurassic

nearshore tropical deposits (Fig. 4). Three regions, Western North America, Italy, and Morocco were compared (Fig. 5). Western North American sites are located in the Robertson Formation near Suplee-Izee, Oregon, the Dunlap Formation in the Garfield Hills, Nevada, and the Thompson Limestone at Mt. Jura, California (Figs. 5A and 6; see Appendix for locality information).

Well-developed buildups and carbonate platforms in the Lower Jurassic are much reduced in size and displaced in position relative to the large Upper Triassic carbonate platforms (Cocozza and Gandin, 1990; Cobianchi and Picotti, 2001). The Moroccan and northern Italian sites are the few carbonate platforms of Pliensbachian and Lower Toarcian age. Northern Italian sites are located in the Calcari Grigi Formation on the South Trento carbonate platform, north of Verona in the Monte Lessini district (Zempolich, 1993; Figs. 5B and 6; Appendix). The two Moroccan field sites are located in the Central and Eastern High Atlas Mountains (Figs. 5C and 6; Appendix). Table 1 is a summary of the number of samples from representative facies from each site.

Each site was described based on: (1) buildup structure (lithofacies, stratal geometry); (2) buildup composition (types of fossils, diversity, abundance, and facies); and (3) intensity of bioerosion and encrustation. To assess the buildup structure, four stratigraphic profiles were completed for every site: two at the buildup margins and two in the interior. Along the profiles, bedding thickness, dip of the stratal planes, and the geometry of the buildups
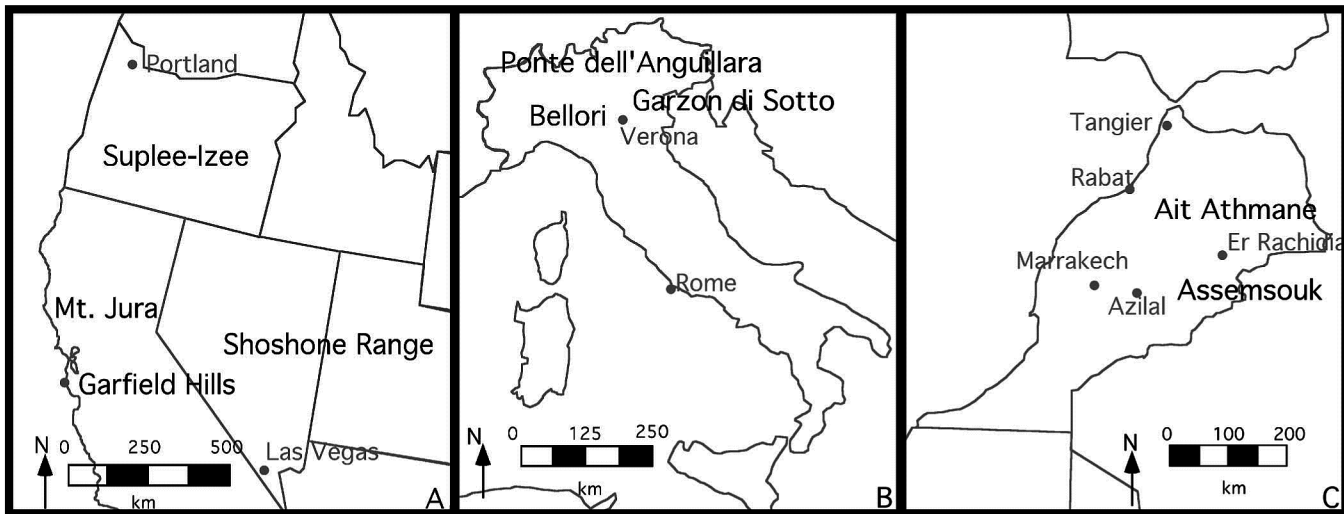
FIGURE 5—Location of field sites, marked by ● on maps. Specific locality information given in Appendix. (A) Western United States. (B) Northern Italy. (C) Central and High Eastern Atlas Mountains, Morocco.

FIGURE 6—Stratigraphy of field sites. The range of the "*Lithiotis*" facies bivalves is shaded gray; hatched areas represent depositional hiatuses.

TABLE 1—Summary of number of samples from field sites and representative facies.

	Western United States			Monte Lessini, Italy			Central & High Atlas, Morocco	
Facies	Suplee-Izee, OR	Garfield Hills, NV	Mt. Jura, CA	Ponte dell'Anguilla	Bellori	Garzon di Sotto	Ait Athmane	Assemsouk
Non-buildup	10	4	3	9	4	4	1	
Buildup	13	5	3				2	4
Flank	3				4			2
Nerineid	3		2				2	
Total	29	9	8	9	8	4	5	6

were measured. Samples for slabbing, acetate peels, and thin-sectioning for detailed analyses of sediment fabric were collected to determine representative lithofacies horizons. On well-exposed bedding planes or reef blocks containing gregarious assemblages of *Lithioperna*, *Lithiotis*, or *Cochlearites*, the orientation of the valves relative to paleocurrent was recorded with a compass on a scale of 0–180°, since it is difficult to determine which valve is right or left in bedding planes. These orientation values were analyzed for significance when compared to an established paleocurrent value by a modified Rayleigh test (Durand and Greenwood, 1958).

To estimate buildup composition, bulk samples of 2.3 kg were taken from stratigraphic intervals less than 1 m in extent; interbuildup facies are represented by single beds and within the various buildup facies (flanks, core, above, and below) by a single sediment type (Table 2). These samples were slabbed at 1-cm thick intervals, and attempts were made to identify organisms to the generic level when possible. Some representative faunal samples were pre-

TABLE 2—Summary of field site descriptions.

pared using acryloid and a mild formic acid bath to remove surrounding matrix to aid in identification. To determine the intensity of bioerosion and encrustation on *"Lithiotis"* facies bivalves, individual specimens were examined from field sites and museum collections at the California Academy of Sciences, Natural History Museum of Los Angeles County, University of Tübingen, the Natural History Museum of Verona, and the University of Ferrara.

RESULTS

Buildup Structure and Lithologic Data

Western North America sites: At Suplee-Izee, the Robertson Formation is typified by volcaniclastic green sandstone with limestone lenses. These lenses are fossiliferous and dominated by *Lithiotis problematica* assemblages. The sediment between the *Lithiotis* valves in these reefs

alternates between gray calcareous muds at the base to sandy limestones at the top of the buildups. The buildups

Site	Location	Age	Depositional Setting	Paleodepth	Buildup Form	Reef-building Fauna	Lithotid bivalves	References
Robertson Formation	Suplee-Izee, OR	Upper Pliensbachian	Volcanic intraarc basin	subtidal to low intertidal	bioherms and biostromes	Lithiotis, spongiomorphs, algae	Lithiotis	Nauss and Smith, 1988 Nauss, 1986
Thompson Formation	Mt. Jura, CA	Upper Pliensbachian	Volcanic intraarc basin	subtidal	biostrome	—	Lithiotis	Batten and Taylor, 1978
Sunrise & Dunlap Formation	Western NV	Pliensbachian-Toarcian	Siliciclastic embayment on craton	subtidal	biostrome	—	Lithiotis	Muller and Ferguson, 1936; Silberling, 1959
Calcari Grigi	Mt. Lessini, Italy	Pliensbachian-Early Toarcian	Carbonate platform lagoon	subtidal to intertidal				
Ait Athmane & Assemsouk	Central High Atlas, Morocco	Pliensbachian-Early Toarcian	Rift basin and carbonate platform	subtidal to supratidal				

bioherms and bio-stromes	*Lithioperna, Lithiotis, Cochlearites*	*Lithiotis, Cochlearites, Lithioperna, Gervilleioperna, Mytiloperna*	Bosellini and Broglio Loriga, 1971
bioherms and bio-stromes	*Cochlearites, Opisoma, Lithioperna,* corals, algae, spongiomorphs	*Cochlearites, Lithioperna, Gervilleioperna, Mytiloperna*	Lee, 1983; Crevello, 1988

TABLE 3—Faunal list. A checkmark indicates taxon is present.

Fauna	Western United States			Monti Lessini, Italy			Central & High Atlas, Morocco	
	Suplee-Izee, OR	Garfield Hills, NV	Mt. Jura, CA	Ponte dell'Anguilla	Bellori	Garzon di Sotto	Ait Athmane	Assemsouk
"*Lithiotis*" Facies								
Lithiotis problematica				√		√		√
Cochclearites cf. *loppianus*								
Lithioperna scutata								
Gervilleioperna								
Mytiloperna								
BIVALVIA								
Astarte				√		√		
Camptonectes				√				
Cardinia				√		√		
Chlamys				√		√		
Coelastarte				√				
Corbis								
Ctenostreon						√		
Entolium						√		
Gervillia				√				
Goniomya						√		
Gramattodon				√				
Gresslya						√		
Isocyprina				√				
Lima				√				
Lucina				√				
Megalodon								
Meleagrinella				√		√		
Modiolus				√		√		

Mytilus			
Opisoma			
Ostrea	√		
Pachyrisma			
Paralleolodon	√		
Pecten juhanus			
Pholadomya	√	√	
Plagiostoma		√	
Pleuromya	√	√	
Trigonia	√	√	
Weyla	√	√	

GASTROPODA

Nerinea	√	√	√
Scurria			

BRACHIOPODA

Rhynchonellids		√	
Terebratulids	√	√	

CNIDARIA

Opelismilia		√	
Phacellostylophyllum	√		
Cerioid corals			

√

√

√

√ √

√ √ √

√ √

√

√

√

√

√?   √?

√   √

√?   √

vary in size from 1–10 m thick, averaging about 6 m thick; the tops of the flank beds are inclined 3–5° (Figs. 3A, 7A). The outlines of these buildups have ragged margins while moving up section, as described for buildups with topographic relief; while others have a lentincular outline consistent with transported death assemblages or biostromes (James and Bourque, 1992). Taphonomically, the biostromal beds consist of highly abraded and broken shells with rounded edges, which, together with biotic evidence below, suggest that the Robertson Formation was deposited in a shallow-water, nearshore environment.

Near the base of the Pliensbachian–Toarcian deposits in the Shoshone Range are transported assemblages of *Lithiotis problematica* (Fig. 7A). The *Lithiotis* valves are completely recrystallized to a white sparry calcite, while the surrounding matrix is a dark gray micritic limestone. In this area, the Dunlap Formation is blue-gray to tan, with mixed siliciclastic and limestone facies. Limestone lenses

are found interspersed with large, lenticular beds of angular bioclasts. Some of the sandier limestone facies are bioturbated, indicated by features similar to *Thalassinoides*. Chert-rich sandstones and conglomerates are found in younger units. Microbial features are found in the siltstone facies above the limestone facies.
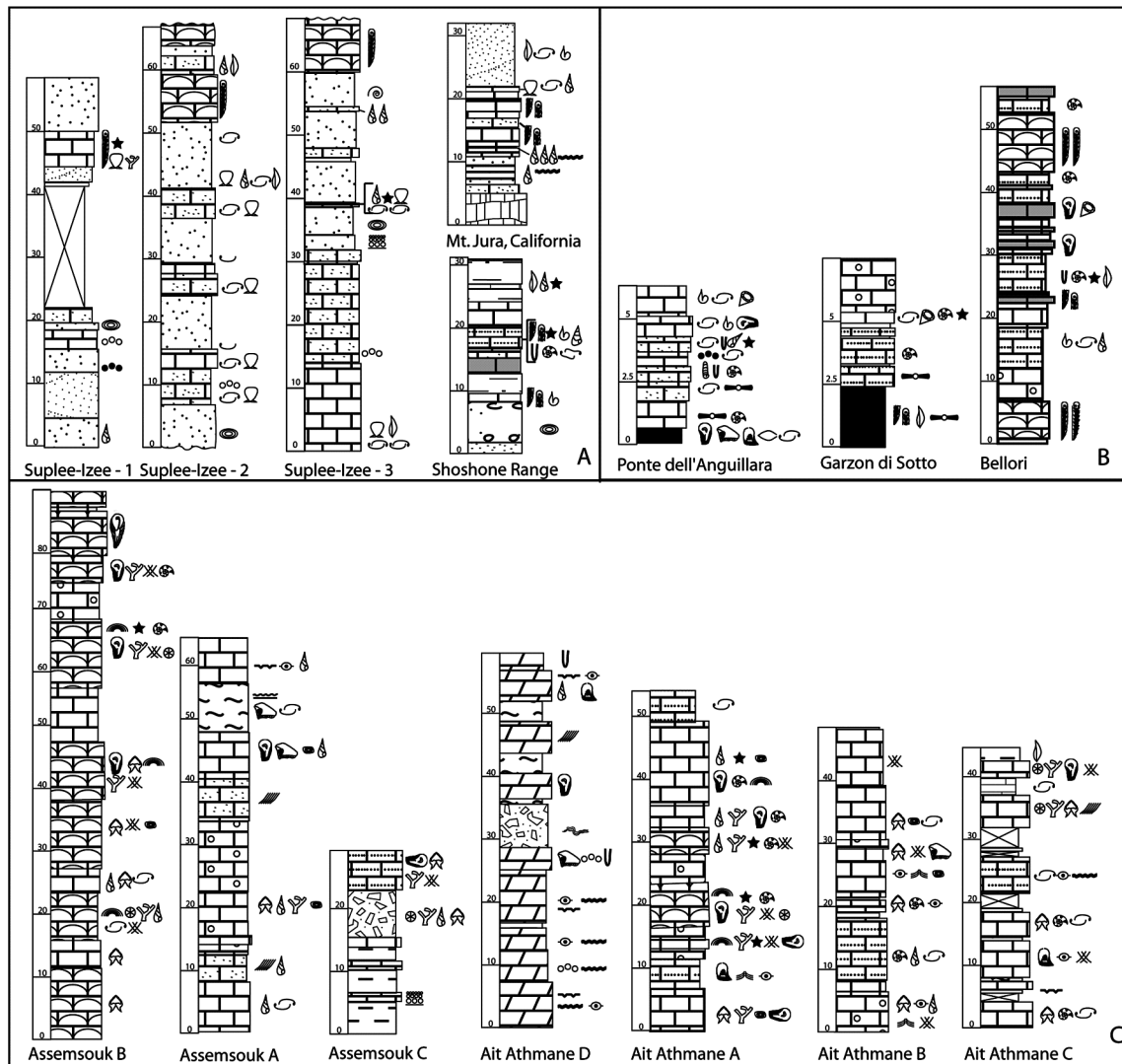
FIGURE 7—Representative stratigraphic columns from the study sites. Locality information for each column in Appendix. (A) Western North American sites. (B) Northern Italian sites. (C) Moroccan sites. (D) Legend of lithologic characters for stratigraphic columns adapted from Corsetti (pers. comm., 2002) and Tucker (1969). Key of symbols for stratigraphic columns adapted from Corsetti (pers. comm., 2002), Tucker (1969), and Swanson (1981).

Unlike other outcrops of the lithiotid bioherms in Western North America, the Mt. Jura locality lacks significant siliciclastic material in the matrix (Fig. 7A). Shells at the site do not appear to be in situ and are broken by physical means. Based on these taphonomic observations, the site represents a nearshore environment with strong wave and current action. The *Nerinea* bed and overlying unit have a feature suggestive of microbially influenced laminae, which are associated with other peritidal carbonate environments.

Northern Italian sites: The Rotzo Member of the Calcari Grigi is comprised mainly of oolitic, peloidal, bioclastic, and intraclastic limestones; marls and clays also are common with occasional lignites (sometimes referred to as brown coals), which have been identified as shallow-water black shales (Boomer et al., 2001). The *"Lithiotis"* facies bivalves are the most distinctive faunal assemblages. At Ponte dell'Anguillara, the lignite at the base of the outcrop has yielded an excellently preserved fossil fauna and flora (Fig. 7B). *Lithioperna*, *Mytiloperna*, and *Gervilleioperna* are common in this unit; however, *Lithioperna* is the only bivalve that appears to be in place. The unit consists of small-sized disarticulated shells and shell fragments, and plant remains (roots, cuticles, and spores), often encrusted with pyrite. Millimeter-scale bioturbation is seen in thin section. At Garzon di Sotto, the base of the outcrop is a lignite facies similar to that found at Ponte dell'Anguillara, however the fossils are a well-preserved death assemblage of *Lithiotis problematica* and brachiopods.

At Bellori, 55 m of the Calcari Grigi is exposed (Fig. 7B). The base of the streambed is a marl and in the upper reaches of the streambed are beds of in situ *Lithiotis problematica*. Above this bioherm unit, an oolitic limestone that lacks fossils is overlain by a silty limestone with small bivalve shells that are disarticulated. A biostrome of *Lithiotis* material is in turn overlain by a silty limestone with large *Thalassinoides*. A series of massive shell beds dominated by *Lithioperna scutata* in the recliner morphology
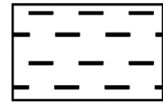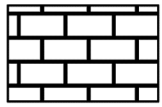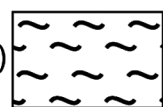
Lithologic Symbols
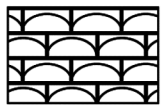
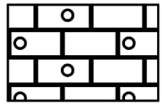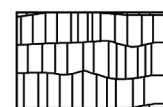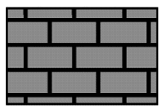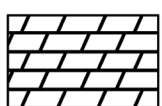| Symbol	Name	Symbol	Name	Symbol	Name
	Buildup		Mudstone		Shale
	Limestone		Lignite (brown coal)		Marl
	Limestone, sandy		Sandstone		Conglomerate
	Limestone, silty		Sandstone, parallel bedding		Breccia
	Limestone, oolitic		Sandstone, cross-bedded		Volcanics
	Limestone, shell bed		Siltstone		Probable disconformity
	Dolostone		Siltstone, interbedded with limestone		
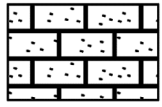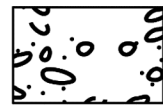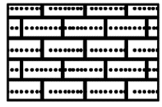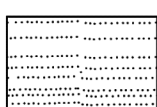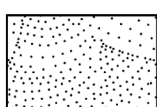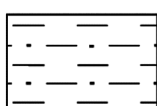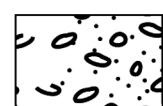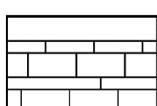
"Lithiotis" facies bivalves

- *Cochlearites*
- *Gervilleioperna*
- *Lithiotis*, broken
- *Mytiloperna*
- *Lithioperna*, broken

microfossils

- *Orbitopsella*
- *Lituosepta*
- other forams
- *Palaeodasycladus*
- other algae
- ostracods

other fossils

- gastropods
- *Opisoma*
- pectinids
- other bivalves
- ammonoids
- brachiopods
- branching corals or spongiomorphs
- domal corals or stromatoporoids
- echinoderms
- undifferntiated fossils
- corals, tabular

sedimentary features

- oncoids
- paleocurrent trend
- nodules
- mudcracks
- bioturbation
- microbial laminae
- cross beds
- collapsed beds
- speroidal weathering
- chert
- graded bedding
- teepee structures
- fenestrae
- ripples

D

FIGURE 7—Continued

(described in the following section) is observed in the upper portion of the section. These beds are similar to the most common *"Lithiotis"* facies (densely packed beds of large, reclining, articulated *Lithioperna*) seen in the Calcari Grigi. Above this unit is a large *Lithiotis* biohermal unit approximately 10 m thick. However, individual bioherm horizons are only 1–1.5 m high, with minor relief. Between the bioherms are occasional incursions of an oolitic facies followed by reestablishment of bioherm construction.

The Rotzo and Massone Members of the Calcari Grigi have been interpreted previously as a lagoonal environment (Rotzo), protected towards the open sea by oolitic bars and shoals forming barrier-island complexes at the margins of the Trento Platform (Massone; Bosellini and Broglio Loriga, 1971; Masetti et al., 1998). Recently the Rotzo Member has been interpreted as a ramp-lagoon environment, protected towards the west by a distal littoral complex (Monte Baldo area) represented by the Massone Member (Masetti et al., 1998). With the exception of the *Lithiotis* beds at Bellori, all other limestone facies studied in the Calcari Grigi appear to have been transported. The *Lithiotis* death assemblage at Garzon di Sotto is associated with open-marine fauna. The shallow-water black shales of Ponte dell'Anguillara have been interpreted as a parautochthonous deposit (Bassi et al., 1999). No shells show evidence of boring or encrustation, signs of abrasion are rare, and broken shells usually exhibit sharp edges.

Moroccan sites: The Central and Eastern High Atlas Mountains are composed almost wholly of Jurassic limestones, marls, and shales. At Assemsouk, a well-exposed, large reef structure is found on the north flank of Jebel Azourki (Fig. 3B; Lee, 1983). The structure, which is 90 m high, 1250 long, and trends east-west parallel to the road, consists of massive beds of pure limestone with four distinct biotic successions: basal *Opisoma* facies, coral-algal bivalve facies, spongiomorph-coral facies, and a *Cochlearites* climax facies (Fig. 7C). The final stage is tightly packed beds of *Cochlearites loppianus* in life position. The

bioherm is approximately 2–7 m high, but it is difficult to discern if this reef stage had significant relief above the seafloor because the reef flanks are not well exposed. In thin section, the *Cochlearites* beds show acicular synsedimentary cements (Lee, 1983). The individual beds exhibit lower, sharp, erosional contacts. Individual valves often are eroded but do not show evidence of significant transport. However, from the acicular synsedimentary cements surrounding the reef fauna, it appears that the reef was subtidal with rare exposures during low tide. The Assemsouk section represents a very shallow subtidal to low-intertidal reef system that was within the photic zone.

At Ait Athmane, the sections are dominated by thick- to massive-bedded limestones with bioclasts of *Opisoma*, *Gervilleioperna*, and *Mytiloperna* that appear to be transported and not in life position (Fig. 7C). Contacts between the beds are well defined. Oncolitic and oolitic lime sands occur interbedded and mixed with bioclasts. Evidence of subaerially exposed environments includes fenestral features, teepee structures, mudcracks, and evaporite breccias. The Ait Athmane sections represent a sequence from outer margin, shoal, inner platform, and restricted lagoon with repeated emergence (Crevello, 1989).

Buildup Composition

Table 3 summarizes the faunal list used for the various sites. Taxonomic assignments used by previous researchers were updated with recent taxonomic revisions where appropriate. For example, previous occurrences of *Lithiotis* in North America prior to Nauss and Smith (1988) were referred to as *Plicatostylus* (Lupher, 1941). North American sites yielded only *Lithiotis problematica* and not the four other "*Lithiotis*" facies bivalves. These sites have a well-developed interreef community of diverse infaunal bivalves and a buildup-flank community (phaceloid spongiomorphs and regular echinoids). The reef core is represented by the monospecific aggregation of *Lithiotis problematica*. Rare, small nerineid gastropods and terebratulid brachiopods occur within the interstices of the lithiotid buildup. In selected sections at the Cow Creek site, this buildup core complex grades laterally into a buildup flank

assemblage typified by regular echinoid debris, including the hollow spines of diademoid urchins, a phaceloid spon-

giomorph, and the bivalve *Weyla* sp. The interbuildup assemblage is similar to the infaunal bivalve facies described by Batten and West (1976) for the Robertson Formation, which is characterized by the bivalves *Modiolus*, *Trigonia*, *Camptonectes*, *Pholadomya*, *Parallelodon*, and *Lucina*. Another facies commonly associated with *Lithiotis problematica* buildups in Western North America is one of densely packed nerineid gastropods, such as that found at Mt. Jura, California.

The faunal composition of the European sites has been the subject of much research, including studies by Broglio Loriga and Neri (1976) and Accorsi Benini and Broglio Loriga (1982) in Italy, and Buser and Debeljak (1994) in Slovenia. The Italian and Moroccan sites contain all five of the *"Lithiotis"* bivalves, and a greater variety of facies can be recognized on the Tethyan carbonate platforms when compared to the accreted terranes of Western North America. Similar associations of buildup-flank fauna are found at the Tethyan sites, including the thick-shelled bivalve *Opisoma menchikoffi*, styllophyllid corals, unidentified cerioid colonial corals, regular echinoid debris, sponges, and the solitary coral *Opelismilia* sp. Aggregations of high-spired gastropods are common at many of the sites. Interreef macrofauna at the Tethyan sites are limited to *Mytilus* sp., *Pecten juhanus*, *Lima* sp., *Pholadomya* sp., and *Ceratomya* sp.

Microfossils and algae are important constituents of the buildup environment. The foraminifera *Orbitopsella praecursor* Gümbel and *Lituosepta recoarensis* Cati, important biostratigraphic markers in the Tethyian realm, are found in both the Italian and Moroccan sites. Other foraminif-

era, including *Mayncina termieri* Hottinger, *Haurania amiji* Henson, *H. deserta* Henson, *Involutina* sp., *Trocholina* sp., and *Frondicularia* sp., are common elements (see Fugagnoli and Loriga Broglio, 1996, for a review). The codiacean algae *Palaeodasycladus mediterraneus* (Pia) and *Thaumatoporella parvovesiculifera* (Raineri) are prevalent in Tethyan facies associated with *Lithiotis* and *Cochlearites*. The rhodophyte *Cayeuxia* sp. is found in association with *Lithioperna scutata*.

In Oregon, the interbuildup area supports a wide array of microfossils including red algae, small miliolid foraminifera, thin-shelled ostracodes, and possibly *Palaeodasycladus* sp. The Cow Creek and Jackass ranch sites are particularly rich in algae.

Intensity of Bioerosion and Encrustation

Entobia (clionid borings) can be seen on individual *Lithiotis* specimens in thin section and on hand samples. The limpet *Scurria* was found in the Assemsouk structure on a *Cochlearites* valve (Lee, 1983) and a shallow ovoid excavation, similar to the resting trace of a limpet, was found on the interior of a transported *Lithiotis*. *Trypanites*-shaped borings without calcareous linings, possibly the result of boring by lithophagid bivalves, were found on a few *Lithiotis* specimens from the northern Italian sites. Several disarticulated lithophagid valves were found in the interbuildup facies of the Robertson Formation in Suplee-Izee. Many of the algae and *Lithiotis problematica* were encrusted by serpulid worms in the Calcari Grigi. Most encrustation occurs on the interiors of disarticulated lithiotid shells and therefore is post-mortem.

Bioerosion is conspicuously absent on the valves of *Gervilleioperna* sp., *Mytiloperna* sp., and *Lithioperna scutata*. The exclusion of bioeroders from estuaries, lagoons, bays, and intertidal zones has been well documented by the modern aquaculture industry (see White and Wilson, 1996, for a review). Similar restrictions may have occurred in intertidal and fresh-water influenced paleoenvironments of the Early Jurassic. Modern coral reefs, particularly reefs in mesotrophic waters, are eroded continuously by a host of bioeroding organisms (Hallock and Schlager,

1986; Wood, 1993). The dearth of bioeroders, encrusters, and other shell-destructive taxa in the Early Jurassic "*Lithiotis*" facies bivalves could be explained by a variety of factors. Harper et al. (1998) attributed lack of evidence for Early Jurassic bioerosion in other Lower Jurassic sites to taphonomy (i.e., poor preservation). However, even at some of the sites where "*Lithiotis*" bivalves are well preserved, bioerosion is rare. A second possibility is that bioeroding organisms were largely eliminated during the preceding mass extinction interval.

Of all the "*Lithiotis*" bivalves, *Lithiotis problematica* would have been most prone to predatory bioerosion. Its thin free valve, only a few millimeters thick, would have left it vulnerable to predatory drilling or shell-crushing. The other four genera have thick valves that would have required significant effort by a predator to penetrate. Although very rare, drilling predators were present in Early Jurassic benthic ecosystems (Harper et al., 1998; Kowalewski et al., 1998). Extraorally feeding asteroids, which are common predators on modern bivalves, have ranges that extend below the Early Jurassic (Gale, 1987). Yet, as discussed below, it is *Lithiotis problematica* that most likely lived in a more open-marine environment. A non-uniformitarian explanation—reductions in the occurrence of predators from the preceding biotic crises—seems likely.

Growth Habit/Arrangement

Many living and fossil organisms (e.g., oysters and barnacles) align their commissures to a current, presumably to maximize filter feeding (Lawrence, 1971). Three of the "*Lithiotis*" facies bivalves (*Lithiotis*, *Cochlearites*, and *Lithioperna*) appear to form aggregations (Fig. 8). The benefits of aggregating behavior are thought to include decreased susceptibility to competitive overgrowth, infestation, predation, or sediment smothering (Jackson, 1983). Conversely, the benefits of aggregation might be limited when compared to availability of suitable substrate for spat to settle (Brown and Swearingen, 1998). Dense populations of colonial or solitary organisms are common despite considerable costs, such as increased competition for food.

Rose diagrams of the orientations of *Lithiotis*, *Cochlearites*, and *Lithioperna* are displayed in Fig. 9. Vector means were computed for these and other groupings and then analyzed for significance by a modified Rayleigh test (Durand and Greenwood, 1958). Using this test, a V′ value of more than 1.645 at the 95% confidence level is needed to reject alignment with a preferred orientation, in this case to a paleocurrent. At Suplee-Izee, Oregon, the orientation of *Lithiotis* shells in a transported death assemblage indicates a paleocurrent direction of 270°. When this value is compared to adjoining in situ *Lithiotis* buildups, a V′ value

FIGURE 8—Photographs of three styles of "*Lithiotis*" bivalve facies aggregations. (A) A *Lithiotis problematica* bouquet at the base of a buildup at Jackass Ranch, Suplee-Izee, Oregon. (B) A bedding plane view of *Cochlearites loppianus* (adapical or dorsal region extends into the readers field of view) at Assemsouk, Jebel Azourki, Morocco. (C) A "fan-like" cross-section arrangement of *Lithioperna scutata* at Ponte dell'Anguillara, Verona, Italy.

of 6.261 was computed (Figs. 8A and 9A). *Cochlearites* from Assemsouk have a V′ value of 1.919 when compared to a paleocurrent of 120° (30° after conversion to 180° scale; Figs. 8B and 9B). In the field, the non-aligned orientation measured above is visible as *Lithiotis* and *Cochlearites* radiate away from each other in "banana-bunch" clusters, morphologically resembling coral heads (Chinzei et al., 1982). This arrangement is in contrast to recent and fossil oysters, which align their planes of commissure parallel to the direction of current flow (Lawrence, 1971). However, *Lithioperna* at Bellori, Italy has a V′ value of 1.421 when compared to a paleocurrent of 5° (95° after conversion to 180° scale; Figs. 8C and 9C). *Lithioperna* exhibits an orientation parallel to the current and therefore may have had a life habit more dependent on filter feeding. Therefore, *Lithioperna* aggregations are comparable to modern oyster reefs. These alignments depend significantly on habitat. For example, channels subjected to consistent tidal currents may produce orientations that do not appear to be aligned with a single current direction. The *Lithiotis* and *Cochlearites* bedding planes do not have scoured beds or other indications of a channel depositional setting. Therefore, *Lithiotis* and *Cochlearites* did not align their planes of commissure parallel to the direction of current flow and may not have had a trophic strategy relying solely on filter feeding.

CONCLUSIONS

Biozonation of *"Lithiotis"* Facies Bivalves

Field and thin-section observations indicate a strong zonation of *"Lithiotis"* facies bivalves in shallow nearshore environments. *Gervilleioperna* and *Mytiloperna* are restricted to intertidal and shallow-subtidal facies. *Lithioperna* is found throughout the lagoonal subtidal facies and even in some low-oxygen environments. *Lithiotis* and *Cochlearites* are found in subtidal facies, constructing buildups. These associations and proposed life habits are discussed below and presented in Fig. 10.

Tidal Flat / Shoal Facies: *Gervilleioperna* sp. and *Mytil-*

operna sp. are associated with the lithofacies found at Ait Athmane, which represent tidal flat and exposed shoal environments (Septfontaine, 1986; Crevello, 1989). Two lithofacies are common: carbonate mudstones and plane-bedded wackestones. The carbonate mudstones are flat-bedded to slightly mounded and locally have fenestral fabrics and desiccation cracks (Crevello, 1989). In thin-section, the mudstones are comprised of peloids and debris from ostracodes, forams, and gastropods. On some bedding surfaces, *Ophiomorpha*-like trace fossils are common. Beds of scattered individuals of *Gervilleioperna* sp. or small clusters of *Mytiloperna* sp. at the Ait Athmane site are capped by an evaporite breccia. In the Trento area of the Calcari Grigi, reports of shallow subtidal associations of *Gervilleioperna* sp. or small clusters of *Mytiloperna* sp. are reported (Monaco and Giannetti, 2002).

In cross-section, *Gervilleioperna* sp. appears as an epifaunal recliner that is thick-shelled and only slightly inequivalved, with the thicker, heavier valve acting as the lower valve, similar to gryphaeid oysters (Fig. 10A). Identification of *Gervilleioperna* sp. in the field is problematic because it lacks many of the distinctive characters that typify other *"Lithiotis"* facies bivalves. Unlike the other *"Lithiotis"* facies bivalves, it does not appear to form gregarious associations.

Three different morphotypes of *Mytiloperna* sp. can be differentiated using the valve discordancy obliquity angle, the angle between the dorsal straight margin, and the more anterior point of the anterior margin (Arkell, 1933;
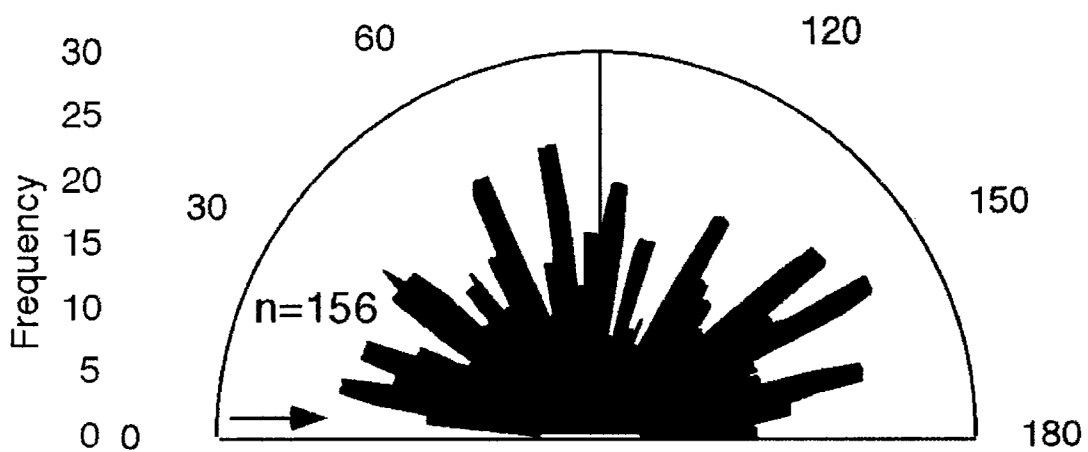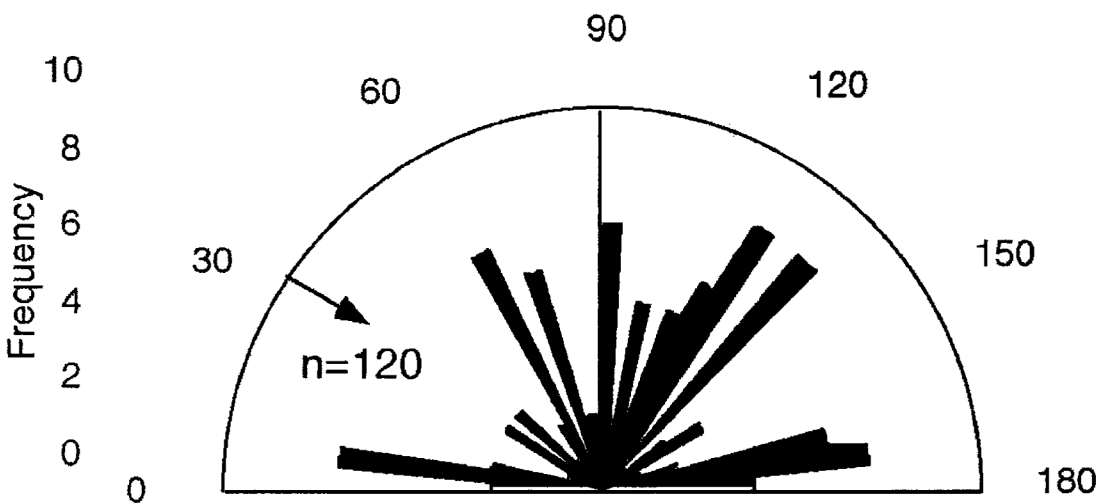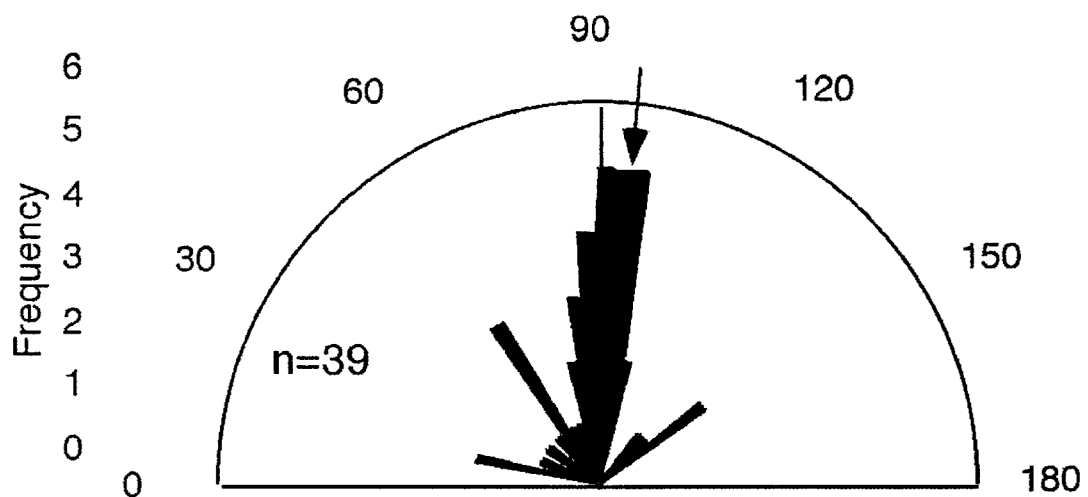
FIGURE 9—Radiation diagrams for the three "*Lithiotis*" facies bivalves found in gregarious arrangements. Arrows denote paleocurrent direction. Results compared with the modified Rayleigh Test created by Durand and Greenwood (1958).

Fig. 10B). The first form, an orthothetic semi-infaunal re-cliner, has a very low obliquity angle of only 38–40°, a high, narrow body cavity, and a shorter cardinal platform than the other two *Mytiloperna* forms. In addition, the teeth are fewer than in the other forms or completely absent (Fig. 10 B1). The second form has an obliquity angle of 55–60° and is equivalved with a semi-infaunal habit (Broglio Loriga and Posenato, 1996; Fig. 10 B2). The third form has an obliquity angle of about 80°, is strongly in-equivalved, with a wide lunule similar to *Hippochaeta*, and had a pleurothetic habit with the thicker valve below the sediment surface (Fig. 10 B3; Seilacher, 1984). The association of both *Mytiloperna* and *Gervilleioperna* at Ait Athmane with lithologic evidence of subaerial exposure suggests life in intertidal environments.

Lagoonal Subtidal: *Lithioperna scutata* is common at most Moroccan and Italian sites. It occurs in fan-like arrangements at Ponte dell'Anguillara and in solitary arrangements at Ait Athmane, Assemsouk, and Bellori, developing just behind the coral facies at Ait Athmane. Adult specimens of *Lithioperna* exhibit three different morphotypes that are characterized by different behaviors and different environments: (A) spoon-shaped mud stickers with a flat and thin shell forming densely packed fan-like colonies; (B) thick inequivalved, cup-shaped isolated recliners that are concave-convex in cross-section, with a rounded outline; and (C) thin equivalved recliners with an ovoid outline (Fig. 10C; Seilacher, 1984; Broglio Loriga and Posenato, 1996).

The first *Lithioperna* morphotype has an elongated, ovoid outline with a spoon-shaped mudsticker morphotype, and is found in very dense, fan-like arrangements (Fig. 8C). The shells were partially buried in the sediment and grew ventrally or adaperturally with their soft parts at or just above the sediment surface (Seilacher, 1984). While not always visible in bedding-plane arrangements, individual specimens of *Lithioperna* morphotype A aligned their commissures to the current (Fig. 9C) and had a filter-feeding and life habit similar to that of oysters. Debeljak and Buser (1997) proposed that *Lithioperna* shells were byssally fixed to a firm object, similar to other isognomid

bivalves, and that the weight of the heavy shell submerged the posterior portion in sediment, resulting in the anterior region facing upcurrent. *Lithioperna* morphotype A is common at the Ponte dell'Anguillara site in a shallow-water lignitic deposit with significant amounts of terrestrial plant debris between the *Lithioperna* fans. The documented presence of root traces penetrating into the interior of articulated *Lithioperna* shells in life position lends credence to the idea that these organisms occupied a lagoonal habitat, near swamps (Posenato et al., 2000). However, *Lithioperna* morphotype A also is common at Ait Athmane, Morocco, a high-energy carbonate setting along the outer platform margin.

The pleurothetic, cup-shaped recliner morphotypes are characterized by shells with rounded or obliquely ovoid outlines (Figs. 10C2, C3; Broglio Loriga and Posenato, 1996). When compared to the fan-like morphotype, the recliner morphotypes are less elongated. A shorter byssal notch and a smaller central plate give the appearance of a larger body cavity. Shells rested on the convex valve with their commissure roughly parallel to the substrate. Some *Lithioperna* recliners grew in dense arrangements, appearing to have partially overlapped and imbricated with the heavier anterior-dorsal part of the shell partially buried. *Lithioperna* morphotype B has an ovoid outline and is found in deposits (e.g., shell debris, cross-bedded features) interpreted as high-energy inner-platform and restricted-lagoonal facies at Ait Athmane (Fig. 10C2). It may have developed a heavy-weight strategy for bottom stabilization in order to prevent capsizing (Seilacher, 1984). *Lithioperna* morphotype C is a thinner-shelled form and ovoid in outline, with valves up to 10 mm thick and 350 mm high (Fig. 10C3). This morphotype occurs in mud-rich substrates with a minor amount of skeletal debris; therefore, a lightweight strategy or snowshoe function may have developed to prevent sinking into the mud (Seilacher, 1984). This morphotype is common in the back-reef lagoonal environments at the Assemsouk site.

Subtidal Buildup Constructors: Aside from *Lithiotis*- and *Cochlearites*-constructed bioherms, reefs are virtually non-existent during the Pliensbachian and Toarcian (Kiessling et al., 1999). This facies consists of massive lenticular, convex-upward calcareous buildups that interfinger with and grade laterally into thinner beds of *Lithiotis* or *Cochlearites* fragments and in some places an echinoid-
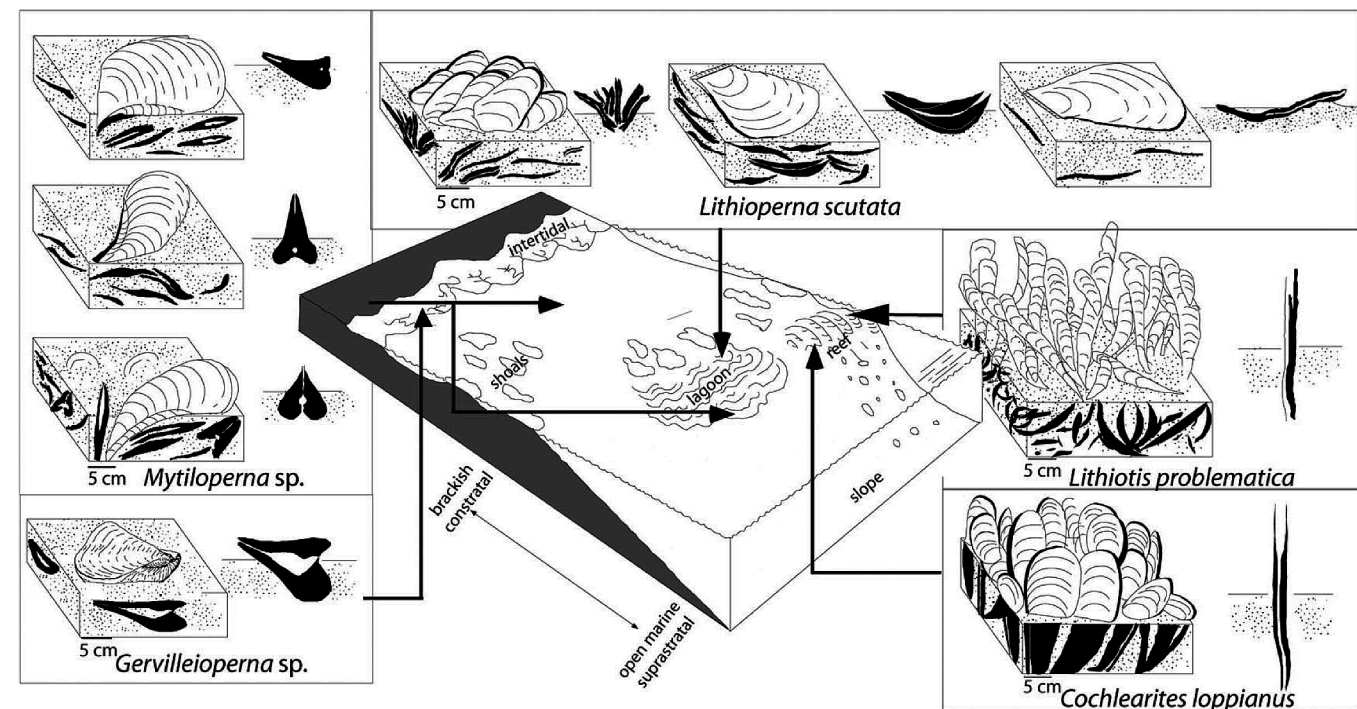
FIGURE 10—Proposed biozonation diagram of "*Lithiotis*" facies bivalves. From the lower left corner in a clockwise direction: (A) *Gervilleioperna*. (B1) *Mytiloperna*, orthothetic semi-infaunal recliner with expanded lunule morphotype; (B2) *Mytiloperna*, orthothetic semi-infaunal equivalved morphotype; (B3) *Mytiloperna*, pleurothetic inequivalved morphotype. (C1) *Lithioperna*, spoon-shaped mudsticker morphotype; (C2) *Lithioperna*, thick cup-shaped morphotype; (C3) *Lithioperna*, thin recliner morphotype. (D) *Lithiotis*, spoon-shaped mudstickers in "banana-bunch" clusters. (E) *Cochlearites*, semi-infaunal spoon-shaped mudstickers. Observations of life habit and mode compiled from Accorsi Benini (1979), Chinzei et al. (1982), Seilacher (1984), Broglio Loriga and Posenato (1996), Debeljak and Buser (1997). Proposed facies relationships are from this study and Broglio Loriga and Neri (1976).

dasycladacean-bivalve flank facies. At the Oregon outcrops, the facies is light to medium gray, massive, cliff forming, and up to 6 m thick (Fig. 3A). Geopetal sediment fills some of the lithiotid shell cavities. Fine- to medium-grained packstone with a matrix of micrite and microspar is found between the buildups. Small cavities within the buildup are filled with carbonate mud and silt; peloids of unknown origin fill the cavities of some fossils like peloidal cement does in many modern reefs (Macintyre, 1977).

Both *Lithiotis* and *Cochlearites* have been described as

upright, spoon-shaped mudstickers. As described earlier, *Lithiotis* are found in vertically oriented "banana-bunch" clusters (Chinzei et al., 1982) with colonies starting on any available hard substrate (rocks or shells; Fig. 10D). Juveniles most likely initially attached themselves with a byssus, and later cemented themselves onto older *Lithiotis* bivalves. In cross section, body chambers are filled with sediment at varying levels. Nauss (1986, p. 72) proposed that "most of the (framework) matrix sediment was deposited after the bivalves were well established." The result was well-cemented buildups that were certainly wave-resistant and rose above the surrounding seafloor (Buser and Debeljak, 1994).

Cochlearites grew similarly to *Lithiotis*—a vertical life position (Fig. 10E). The orientations of *Cochlearites* in the Assemsouk section barely deviate from upright, without the twisting so common in *Lithiotis* buildups. There is not evidence of cementation or attachment to other clams as in *Lithiotis*. Therefore, it is presumed that *Cochlearites* buildups were not as well cemented or wave resistant as the *Lithiotis* buildups and may have had less topographic relief.

In Oregon, *Lithiotis*-constructed buildups are laterally continuous with a buildup-flank facies bearing a phaceloid spongiomorph as well as spines and plates of regular echinoids, both of which would have been organisms restricted to open-marine or at least normal-salinity conditions. *Lithiotis* probably needed well-oxygenated, clear waters, as it is only found in clean, calcareous facies (Posenato et al., 2000). At Assemsouk, the *Cochlearites* facies caps a well-developed reef containing scleractinian corals (Fig. 3B). While not laterally continuous, it is likely that *Cochlearites* also inhabited more open-marine conditions than the other "*Lithiotis*" facies bivalves.

Photosymbiosis

Lithiotis and *Cochlearites*, in contrast to many oysters, do not orient their commissure planes in a single direction. Instead, these two buildup-constructing genera radiate out from a central bouquet. This arrangement is not the most advantageous for maximizing the filter-feeding, trophic mode of many heterotrophic bivalves. It could be possible that the radiating growth habit exhibited by *Lithiotis* and *Cochlearites* was a result of selection to maximize exposure to light.

The buildup-constructing bivalves *Lithiotis* and *Cochlearites* do exhibit characters proposed by Vogel (1975) for

the recognition of possible fossil bivalve photosymbiosis: growth habit, extensive calcification, presumed oligotrophic environment, and pseudocoloniality, in addition to association with other possible photosymbiotic fauna (e.g., scleractinian corals). Vogel (1975) also suggested thin or transparent valves (windows) that may have let light transmit through the closed valves to photosymbionts, similar to the modern *Fragum* sp. The extremely thin (1–2 mm), free valve of *Lithiotis problematica* may have been thin enough to transmit light to a mantle that harbored photosymbionts.

DISCUSSION

Bivalve-constructed buildups traditionally are placed in two models: oyster reefs and rudist reefs. Oyster reefs are common in restricted-estuarine and lagoonal environments and form relatively monospecific aggregations that commonly are (but not always) aligned with current direction, presumably to maximize passive filter-feeding capacity (Lawrence, 1971). *Lithioperna scutata*, with its fan-like habit and associated restricted-water lithofacies, inhabited a niche similar to that of modern oyster reefs. Rudist-constructed reefs are thought to have inhabited a wide range of habitats on carbonate-platform shelves, with some restricted to lagoonal environments and others

found exclusively in oligotrophic environments associated with modern scleractinian reefs (Perkins, 1974). Elongate radiolitid rudist bivalves, which are similar to *Lithiotis* and *Cochlearites* in morphology and habitat, interlock with mutual cementation of neighboring individuals as they grow upright (Kauffman and Johnson, 1988). These rudist aggregations, when at their climax, could be monospecific (Kauffman and Johnson, 1988), as *Lithiotis* and *Cochlearites* were in the Early Jurassic.

Scott (1995) proposed that the rise of rudists over coral reefs during the Cretaceous was a result of global environmental stress linked to the rapid rise in atmospheric CO_2. The same scenario may be applied to the bivalve-constructed reefs of the Early Jurassic. The appearance of "*Lithiotis*" facies bivalves was delayed by ten million years after the end-Triassic mass extinction at a time when the nearshore tropical carbonate environments were relatively vacant. This niche was then recaptured by scleractinian corals by the Middle Jurassic (Wood, 1999). Beauvais (1984) noted that middle Lias reefs are lower in coral diversity than the Upper Lias and Dogger coral reefs. Stanley and Fautin (2001) suggested that the disappearance or decreased diversity of scleractinian corals is associated with elevated atmospheric CO_2. Three possible global stresses linked to the rapid rise in CO_2 may have inhibited scleractinian coral growth during the Early Jurassic: temperature, inhibition of calcification, and episodic eutrophication of shallow carbonate shelves (McElwain et al., 1999; Cobianchi and Picotti, 2001).

Concomitant with the rise in atmospheric CO_2 was a proposed 3–4°C rise in global sea-surface temperature (SST; McElwain et al., 1999). Modern scleractinian corals have been reported to bleach (i.e., lose their photosymbionts) and experience high rates of mortality when SST exceeds 30°C (Carriquiry et al., 2001). Similarly, some studies of modern bivalves (*Crassostrea virginica*) report a shut-off in shell calcification when water temperatures exceed 28°C and a presumed mortality should such high temperature conditions persist (Surge et al., 2001). Other bivalves, such as *Tridacna maxima*, do not exhibit similar shut-offs when water temperatures exceed those required for coral bleaching (Romanek and Grossman, 1989). Glob-

al SST rise during the Early Jurassic could have caused a similar coral crisis that reduced the number of suitable environments for scleractinian coral growth that might not have similarly affected some bivalves.

Increases in atmospheric CO_2 alter the saturation states of both aragonite and calcite, thereby inhibiting calcification. Studies of modern scleractinian corals show that a 280 ppm increase in atmospheric CO_2 lowers calcification rates by 60% (Langdon et al., 2000). The results are deadly to corals, which experience weaker skeletons, reduced extension rates, and increased susceptibility to erosion (Langdon et al., 2000). No similar modern studies assess the role of CO_2 on bivalve calcification. Because the "*Lithiotis*" facies bivalves have a thin outer prismatic calcite layer, they may not have been as vulnerable to such lower saturation states and thereby were able to utilize the nearshore carbonate niche.

Kauffman and Johnson (1988) proposed that the proliferation of rudists was enhanced by nutrient flooding of shelves by oceanic anoxic events. In the Early Jurassic, deep-water facies (benthos-free, laminated, organic rich limestones and shales) contemporaneous with the "*Lithiotis*" facies bivalves alternate with beds containing high-density, low-diversity faunas, suggestive of opportunistic colonization in dysaerobic conditions (Hallam and Wignall, 1997). A significant extinction at the Pliensbachian–Toarcian transition is associated with a global oceanic anoxic event (Hesselbo et al., 2000). In modern reef environments, increased eutrophication affects the physical environment by decreasing water clarity, increasing the sedimentation rate, and destabilizing oxygen levels and pH (Brasier, 1995). Modern coral-reef workers have noted that nutrients appear to be the controlling factor of reef faunal development by changing phytoplankton and macrofauna distributions, predation, and herbivory, all of which influence the reef community structure (Wood, 1999). However, heterotrophic bivalves tend to thrive in nutrient-rich environments. "*Lithiotis*" facies bivalves, if they were mixotrophs or heterotrophs, may have been less at risk than the scleractinian corals. Presumably, these conditions would have dissipated by the Middle Jurassic when scleractinian corals returned with sponges and microbes to become the dominant reef-builders (Wood, 1999;

Cobianchi and Picotti, 2001).

If the Early Jurassic had a 1000 ppm increase in atmospheric CO_2 as proposed by McElwain et al. (1999), or the minimal value 250 ppm proposed by Tanner et al. (2001), the result of such an increase in CO_2 on scleractinian corals, already diminished by the Triassic–Jurassic mass extinction, would have been devastating. Regardless of which value or the source for the proposed rise in CO_2, it would have had cascading effects on paleotemperature, sea level, carbonate platform development, and organismal calcification. It may be more than coincidence that the two times of global bivalve reef-building, the Early Jurassic (McElwain et al., 1999; Tanner et al., 2001) and the Middle to Late Cretaceous (Johnson et al., 1996; Poulsen et al., 1999), occurred during elevated atmospheric CO_2.

"*Lithiotis*" facies bivalves represent unique recovery taxa within the coral-reef niche. Unlike disaster taxa that expand their distribution after a mass extinction, "*Lithiotis*" facies bivalves were uniquely adapted to the unusual conditions of the Early Jurassic. Whether due to increased atmospheric CO_2, nutrient flux to carbonate shelves, or a combination of both, "*Lithiotis*" facies bivalves thrived and dominated tropical facies only to become extinct when these environmental conditions disappeared as well.

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APPENDIX

STUDY SITES—LOCALITY INFORMATION

Western United States

(1) Oregon localities, Suplee-Izee. Localities include: Cow Creek (Funny Butte 7.5 Minute Quadrangle, SE1/4, SW1/4, sec. 17, T17S, R26E; 44°06.541′N, 119°30.641′W), Swamp Creek (Funny Butte 7.5 Minute Quadrangle, SW1/4, NW1/4, sec. 3, T18S, R26E; 44°02.299′N, 119°35.754′W), Jackass Ranch (Funny Butte 7.5 Minute Quadrangle, SW1/4, NE1/4, sec. 13, T17S, R26E; 44°05.841 N, 119°32.416′W), and Robertson Ridge (Delintment Lake 7.5 Minute Quadrangle, SE1/4, sec. 28, T18S, R27E; 43°58.936′N, 119°37.728′W), described by Lupher (1941), Dickinson and Vigrass (1965), and Nauss and Smith (1988).
(2) Nevada locality, described by Muller and Ferguson (1939), *"Plicatostylus* Basin"* (Garfield Hills 7.5 Minute Quadrangle, center of sec. 8, T7N, R33E; 38°29.725′N, 118°21.534′W).
(3) California locality, described by Batten and Taylor (1978) on the north side of Mt. Jura (Taylorsville 7.5 Minute Quadrangle, SE1/2, SW1/4, sec. 24, T26N, R10W; 40°05.289′N, 120°48.002′W).

Northern Italian Sites

These sites are located north of Verona in the Monti Lessini District, described by Chinzei (1982), R. Zorzin (pers. comm., 2000) and R. Posenato (pers. comm., 2000).

(1) Ponte dell'Anguillara (Bosco Chiesanuova Map Foglio 49 IV, No. 1, 45°29.535′N, 11°01.029′E).
(2) Bellori (Bosco Chiesanuova Map Foglio 49 IV, No. 1, 45°35.360′N, 10°59.298′E).
(3) Garzon di Sotto (Selva di Pregno, Foglio 49, IV, No. 11, 45°35.118′N, 11°08.141′E)

Morocco

These localities are in the Central and Eastern High Atlas Mountains.

(1) Assemsouk. On the north flank of Jebel Azourki (30°43.002′N, 9°04.002′W), described by Lee (1983).
(2) Ait Athmane. Located in Oued Ziz (31°55.914′N, 4°25.464′W), described by Dubar (1948) and Crevello (1989).