

LITHIOTIS BIOHERMS IN THE PLIENSCHACHIAN (LOWER JURASSIC) OF NORTH
AMERICA

by

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ABSTRACT

In North America the aberrant pelecypod *Lithiotis* occurs in Upper Pliensbachian strata in Oregon, California and Nevada. The epifaunal, sessile bivalve formed massive, low diversity bioherms in shallow water marginal marine facies, which are most extensive in the Robertson Formation of east central Oregon. *Lithiotis* bioherms of the Robertson Formation comprise three biofacies; (1) a Reef Flank Assemblage; (2) a Death Assemblage and (3) a Life Assemblage. The Reef Flank Assemblage is characterized by *Lithiotis* shelly debris, the gastropod *Nerinea* and terebratulid brachiopods and marks the perimeter of the bioherms. The Death Assemblage is comprised of *Lithiotis* bivalves lying parallel to bedding and the Life Assemblage is made up of *in situ* vertical *Lithiotis*.

Lithiotis is an elongate, stick-like bivalve that reaches over 30 cm in height and is made up of a thick, robust attached valve and a thin, fragile free valve. The free valve articulates with the attached valve by a ridge-and-groove structure on the cardinal face of the attached valve. *Lithiotis* is similar in morphology and occurs in a similar paleoenvironment as the Lower Jurassic bivalve, *Cochlearites* and the Upper Cretaceous oyster, *Konbostrea*. All three bivalves are found in low diversity bioherms that formed in a shallow water, marginal marine environment.

The paleogeographic distribution of *Lithiotis* is widespread. *Lithiotis* occurs in the East Pacific, Circum-Mediterranean region and in the Eastern Tethys Ocean. An endemic center of the bivalves existed during the Pliensbachian in the East Pacific of North America and the Western Tethys Ocean, which indicates that Pliensbachian migration occurred through the Hispanic Corridor. During the Lower Toarcian *Lithiotis* migrated from the endemic center to the East Pacific of South America and to the Eastern

Tethys Ocean. The absence of *Lithiotis* in the Canadian suspect terranes is likely due to collection failure or lack of appropriate shallow water marginal facies. Offshore exploration could well reveal *Lithiotis* in a shallow water marginal marine facies in Wrangellia in the Queen Charlotte Islands area.

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I. INTRODUCTION

A. INTRODUCTORY STATEMENT

Lithiotis GUMBEL (1871) is an epifaunal, sessile bivalve that formed massive bioherms in lower Pliensbachian strata in North America. The bioherms are found in California and Nevada, but are most extensive in the Suplee-Izee area of east central Oregon where they extend over several square km and reach thicknesses of greater than 5.5 m (Figure 1-1). The bioherms are composed almost exclusively of tightly packed *Lithiotis* bivalves forming extremely low diversity communities that contrast with the majority of Phanerozoic reefs. The morphology of the bivalves is also unusual. *Lithiotis* is elongate and stick-like, reaching heights of 30 cm or more, with a width of 4 to 6 cm and an average thickness of 3 cm. The bivalves were prodigious carbonate producers and secreted tremendously large skeletons in proportion to their body size.

In North America *Lithiotis* was first described by Lupper and Packard (1930) as *Plicatostylus gregarius*. *Plicatostylus* has since been recognized as a junior synonym of *Lithiotis* (Loriga and Neri, 1976; Benini and Loriga, 1977; Wiedenmayer, 1980).

The geographic distribution of *Lithiotis* is widespread; it is found in Oregon, California and Nevada in North America (Lupper, 1941; Dickinson and Vigrass, 1965; Taylor, 1977; Hallam, 1983) and in Chile and Peru in South America (Hillebrandt, 1981a). *Lithiotis* is found in southern Europe and Northern Africa throughout the Mediterranean region; in the Middle East and as far east as Timor in Indonesia (Loriga and Neri, 1976; Geyer, 1977).

The purpose and scope of this thesis lies in three areas:

1. the description, structure and ecology of a *Lithiotis* bioherm;

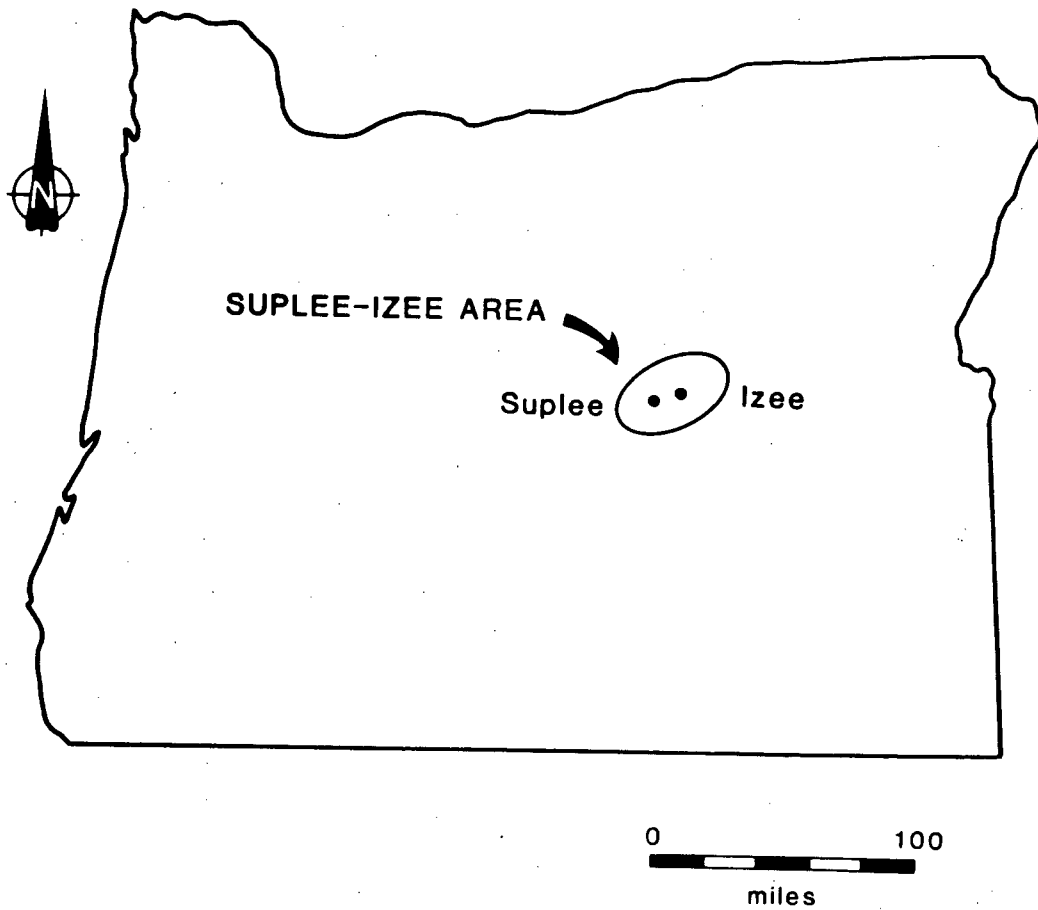


Figure 1-1: Location map of the Suplee Izee area in eastern Oregon.

2. the morphology and taxonomic affinities of *Lithiotis* and
3. the paleobiogeographic implications of the geographic distribution of *Lithiotis*.

The Oregon *Lithiotis* localities were selected for the focus of the study because the bioherms are far more extensive in these areas than in Nevada or California.

B. PREVIOUS WORK

Lithiotis has been briefly mentioned in many papers since it was described (Gumbel, 1871). Boehm wrote several papers comparing *Lithiotis* to the bivalve *Ostrea*, and suggested that *Lithiotis* should be included with the Ostreidae (Boehm, 1892 and 1906). In 1903 Reis published a major paper on *Lithiotis* which he believed was related to the Spondylidae, not the Ostreidae. He proposed a new family, the Lithiotidae, near the family Spondylidae and this classification has remained unchanged since 1903. In 1971, Bosellini and Loriga published the first of a series of papers by Italian authors on the subject of *Lithiotis*. The Italian papers deal with the taxonomy and paleoecology of the bivalve (Cavicchi, Bosellini and Loriga, 1971; Bosellini, 1972; Loriga and Neri, 1976). In 1977 Benini and Loriga published a comprehensive morphological and taxonomic review of *Lithiotis* and a similar bivalve, *Cochlearites* REIS. This review also discussed *Plicatostylus gregarius* from Oregon, and suggested that the two bivalves might be synonymous.

In North America *Plicatostylus* has been briefly described (Lupher and Packard, 1930) and several authors have included the bivalve in regional studies of Oregon, Nevada and California (Muller and Ferguson, 1939; Lupher, 1941; Silberling, 1959; Dickinson and Vigrass, 1965; Stanley, 1971). *Lithiotis*

bioherms in North America have not been studied in any detail from a paleoecological point of view and the taxonomic affinities of the bivalve have not been closely examined. These subjects are of major interest in this thesis, along with the paleobiogeographic implications of the geographic distribution of the bivalve.

C. LOCATION

The Suplee-Izee area is a highly fossiliferous region of mostly Mesozoic marine strata that covers approximately 650 square km in east central Oregon. It is part of the John Day Inlier, an important break in the extensive Tertiary volcanics which cover much of Oregon. The John Day Inlier is located within the Blue Mountains geologic province, which covers northeastern Oregon and westernmost Idaho. The Robertson Formation is part of the lower Jurassic Mowich Group which is exposed throughout the rolling hills of the Suplee-Izee area. The Robertson Formation crops out over an area that extends from 15 km northeast of Suplee along Cow Creek in the north, to 15 km southeast of Suplee (Figure 1-2). Several small exposures of Robertson Formation also occur to the northeast of the Suplee-Izee area, 7 km north of Seneca. The bioherms are most prominent in the northern exposures of the Suplee-Izee area along Cow Creek. The area is easily accessible from Prineville to the west, via Paulina; and from U.S. highway 395 to the east, between Burns and John Day. Numerous ranch roads and logging roads criss-cross the area, making most places accessible by vehicle in dry weather.

Two collecting trips were made to the Suplee-Izee area, in July 1984 and May 1985. The area is in the northwestern corner of the Oregon desert, alongside of the Ochoco and Malheur national forests.

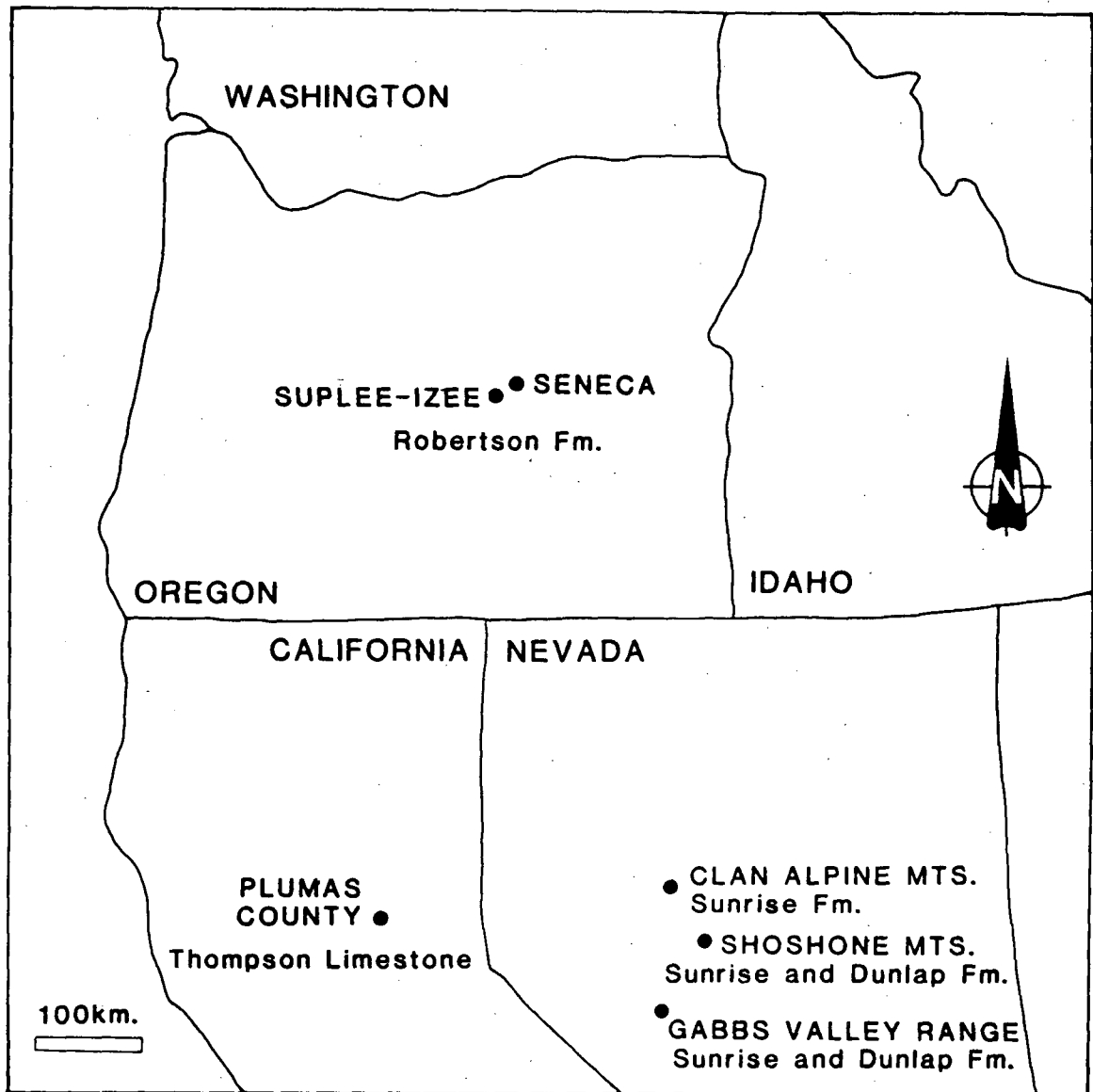


Figure 1-2: Location of stratigraphic units containing *Lithiotis*, in North America.

D. METHODS

The *Lithiotis* bioherms were mapped in the Robertson Formation throughout the Suplee-Izee area. The Funny Butte Quadrangle, N4400-W11930/7.5 Oregon-Grant County map was used as a base map. Seven sections were measured through the Robertson Formation, using the metre stick technique outlined in Compton (1962). Four slabs of reef rock measuring approximately 0.7 m by 0.3 m were collected and later cut into 3 to 6 cm slices in the lab. The slabs were etched in acid and sprayed with a thin coating of acetone. Acetate sheets, 0.3 mm thick, were laid over the slabs and were dried, peeled off and used as negatives for a series of enlarged photographs of the bivalves. SEM photographs were taken of the details of the bivalves, but were not as successful as the acetate peels in displaying morphologic details. The fossils are considerably recrystallized and detail of the shell structure is lost. The slabs were stained with a protein stain, "Ninhydrin" (Triketohydrindene Hydrate) to see if traces of the organic template within the shell could be highlighted, however nothing was revealed by staining. Carbon and oxygen isotope work was attempted on the fossils, which were sent to the University of Ottawa for analysis but the fossils proved to be too recrystallized (written communication Al-Issam). Numerous *Lithiotis* float specimens were collected, thin-sectioned and their morphology extensively examined. Samples from the rock units superjacent and subjacent to the bioherms were collected, thin-sectioned and several were processed with Quaternary-O to check for microfossil content.

II. STRUCTURE

A. STRUCTURE OF THE JOHN DAY INLIER

In the John Day inlier the structurally lowest rock assemblage is the Devonian to Triassic melange strata of the Baker terrane. Ophiolitic components of the terrane imply that the melange is a subduction complex of oceanic materials deformed during plate consumption. Upper Triassic clastics of the Izee terrane locally rest unconformably on the Baker terrane but are largely faulted against it. The upper Triassic clastics are mainly thick turbidites comprised of eroded uplifted melange, volcanoclastics and reworked upper Triassic sediments. Dickinson and Thayer report (1979) that "Structural relations, paleocurrent trends and facies changes suggest both tectonic transport and sediment dispersal to the southeast as the upper Triassic rocks accumulated in a succession of local wedge-shaped basins with actively deforming margins on the west and north." Regional relations suggest that upper Triassic sedimentation occurred in trench-like basins associated with subduction downward to the northwest, perhaps during arc-continent collision. The same style of deformation persisted into the Early Jurassic. Largely volcanoclastic mid-lower to mid-upper Jurassic strata, representing forearc environments, rest unconformably on all older units. Regional relations suggests that the Jurassic sequence was associated with a continental arc related to subduction downward to the southeast along the continental margin.

B. STRUCTURE OF THE SUPLEE-IZEE AREA

The Suplee-Izee area can be divided into four major structural divisions: (Figure 2-1)

1. The Western Paleozoic Upland is a belt of up-faulted Paleozoic rock of the Baker terrane that crops out along the western edge of the Suplee-Izee area.

2. The Pine Creek Downwarp is a synclorium of downfolded Jurassic strata lying east of the Western Paleozoic Upland and flanked on the northeast and southeast by exposures of upper Triassic rock.

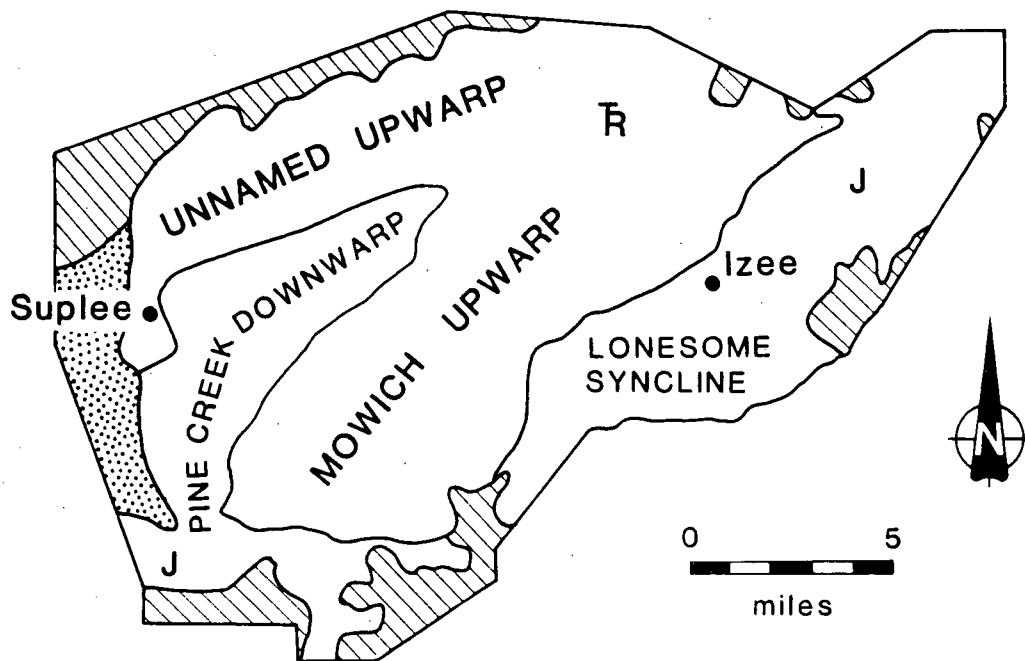
3. The most dominant structural feature of the area is the Mowich upwarp; an anticlinorium cored by upper Triassic rocks and flanked by Jurassic strata. An unnamed companion upwarp of folded Triassic rock lies along the northwest edge of the area.

4. The Lonesome Syncline is a deep structural trough of Jurassic strata lying southeast of the Mowich Upwarp along the southeastern edge of the area.

The Suplee-Izee area can be divided into three major structural units which are divided by the Permo-Triassic unconformity and the Jurassic-Cretaceous Orogeny.

The basal unit is a substrate of indurated and mildly metamorphosed Paleozoic rock representing a little known period of upper Paleozoic marine sedimentation and volcanism. The end of this period is marked by the Permo-Triassic unconformity when orogeny and igneous intrusion halted sedimentation.

The middle structural unit is an upper Triassic to upper Jurassic sequence representing a period of marine sedimentation and volcanism. The upper Triassic strata is an accumulation of clastic detritus eroded from



LEGEND





- | | |
|---|---|
|  | Peripheral plateaus mainly Cenozoic volcanics |
|  | Mainly Jurassic marine |
|  | Mainly Triassic marine |
|  | Western upland mainly Paleozoic |

Figure 2-1: Major structural divisions of the Suplee Izee area. From Dickinson and Vigrass, 1965, p.12.

tectonic highlands and deposited in adjacent tectonic basins. Limited contemporaneous volcanism added to the clastic detritus. During the early Jurassic, sedimentation was interrupted by the Ochoco Orogeny, which resulted in major folding and faulting of the Triassic strata. The Orogeny had terminated before deposition of the lower Jurassic Mowich Group which rests unconformably on all older strata. In the western part of the Suplee-Izee area the Mowich Group rests with marked angular discordance upon the Triassic Begg and Brisbois Formations, which were thrown into tight upright or slightly overturned folds with northerly trends. In some places discordance between the Mowich Group and the underlying strata is as much as 90 degrees. The Triassic strata in the eastern part of the Suplee-Izee area was pushed into open folds, and the discordance between the Mowich Group and the underlying strata is slight. This suggests that the Ochoco Orogeny started earlier and continued longer in the west or that it was much more intense in the west. A crudely parallel set of north to northeast trending reverse faults was activated during the orogeny.

After the Ochoco Orogeny rapid deposition of volcanoclastic debris with subordinate contributions from other sources took place until late early Jurassic or middle Jurassic time. In the middle Jurassic mild warping and local erosion gave rise to angular unconformities. Upwarping of the western part of the Suplee-Izee area was accompanied by removal of the Mowich Group northwest of the axis of the Pine Creek Downwarp. The upwarping established the raised Suplee platform as distinct from the Izee basin to the east. The age of this deformation is not necessarily middle Jurassic. The earlier onset of the Ochoco Orogeny in the west, restriction of the Robertson Formation bioherms to the west, and thinning of the Hyde Formation in the western part of the Suplee-Izee area suggest that the

Suplee platform existed before the middle Jurassic.

The upper structural unit is divided from the Jurassic clastic sequence by the Jurassic Cretaceous Orogeny. This orogeny resulted in intense deformation and diagenetic alteration of Jurassic strata prior to deposition of upper Cretaceous strata. In the Suplee platform area open folds with gentle east or southeasterly trends developed as a result of the deformation. In the Izee basin the thick Jurassic sequence was arched downward into the east trending Lonesome Syncline, a downfold with many thousands of feet of structural relief. The upper Triassic strata folded during the Ochoco Orogeny were refolded and the statistical fold axis changed from a horizontal position with a northerly strike to a vertical position where the original folds were isoclinal, and to a nearly random position where the original folds were open.

Following the Jurassic-Cretaceous Orogeny a period of shallow marine sedimentation and continental volcanism occurred through the Cretaceous and Cenozoic. This period of sedimentation and volcanism was interrupted by intermittent warping, faulting, uplift and erosion.

III. STRATIGRAPHY

A. STRATIGRAPHY AT LITHIOTIS LOCALITIES IN OREGON

Lithiotis occurs in the Robertson Formation in the Suplee-Izee area of east-central Oregon. The Robertson Formation is the basal unit of the Mowich Group which crops out as part of the John Day Inlier. The Inlier is made up of three distinct terranes which are fault bounded and distinguished from one another by their distinctive stratigraphy (Silberling et al., 1984) (Figure 3-1). The Izee terrane (termed the "Mesozoic clastic terrane" by Dickinson (1979)) is made up of clastic sedimentary rocks and subordinate volcanoclastic rocks of late Triassic through middle Jurassic age. The Izee terrane is divided into four main lithologic units; the Vester Formation, the Aldrich Mountains Group, the Jurassic Volcanoclastic sequence and the Lonesome Formation. The Mowich Group is situated at the base of the Jurassic volcanoclastic sequence. The Baker terrane (termed the "Central melange terrane" by Dickinson (1979)) crops out in the northern part of the John Day Inlier. It is made up of a melange belt of disrupted upper Paleozoic oceanic crust and associated deep marine sedimentary strata of late Paleozoic to mid-Triassic age, as well as tectonically admixed blocks representing a wide variety of rock types (Silberling et al., 1984). The Grindstone terrane crops out in the southwest corner of the John Day Inlier. It was characterized as the "Melange terrane of the Grindstone-Twelvemile area" by Dickinson and Thayer (1978) and is a tectonically disrupted assemblage of Devonian to lower Triassic rocks.

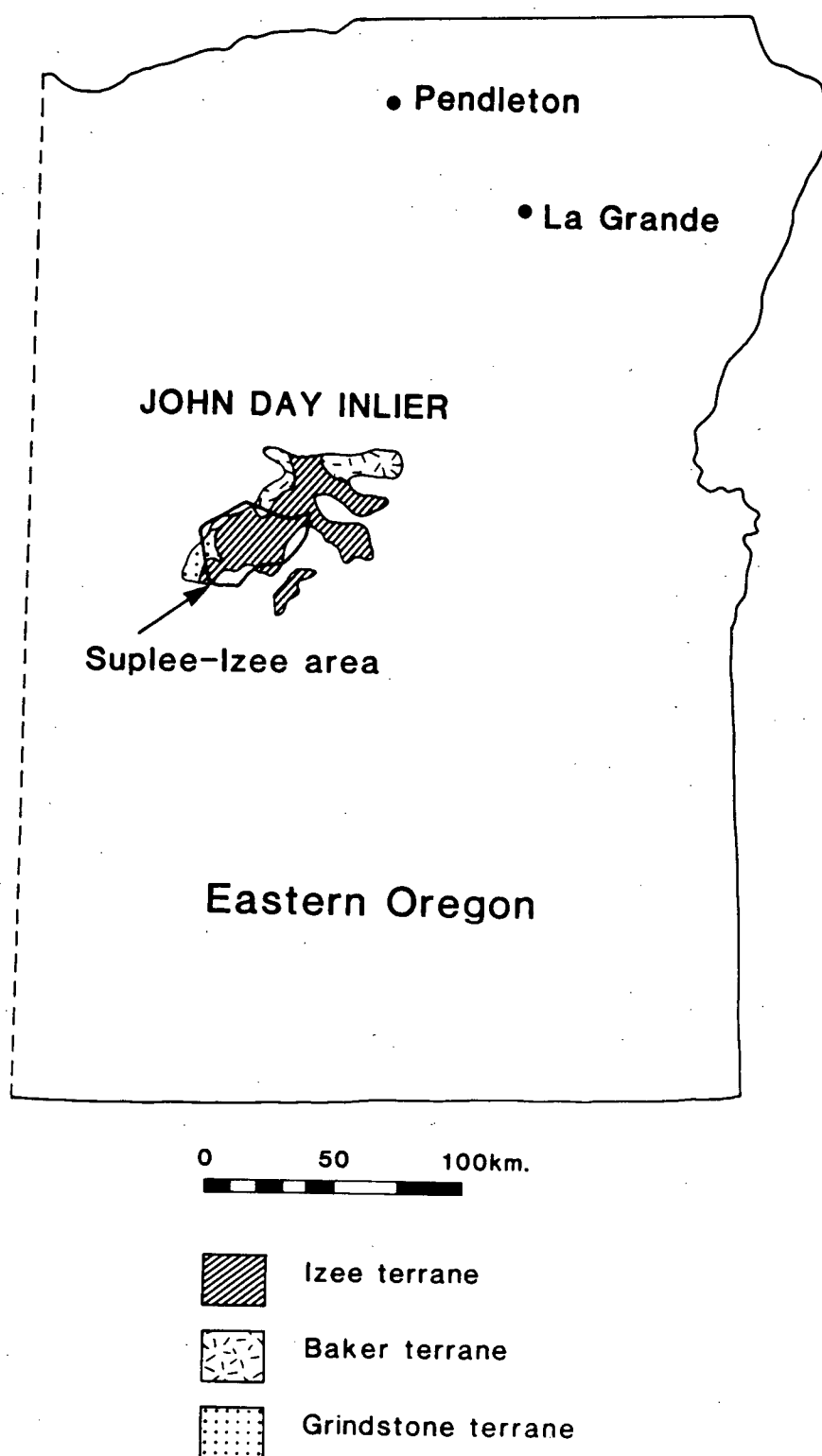


Figure 3-1: Terranes of the John Day Inlier. (adapted from Silberling, et al., 1984)

B. STRATIGRAPHY OF THE SUPLEE-IZEE AREA

The Mowich Group rests with angular unconformity on the older Paleozoic to Triassic rocks of the John Day Inlier whose lithology is reflected locally in the Robertson Formation. Paleozoic rocks crop out in gently rolling uplands west and southwest of Suplee (Figure 2-2). Tightly folded upper Triassic rocks lie with angular unconformity on Paleozoic rocks and underlie approximately 100 square km of the Suplee-Izee area. The Triassic rocks are up to 400 m thick and are divided into the Begg and Brisbois Members of the Vester Formation (Dickinson and Vigrass, 1965). In the northeast part of the area the Begg and Brisbois Members are faulted against the Keller Creek Shale, a poorly exposed, sporadically fossiliferous unit tentatively dated as upper Triassic to lower Pliensbachian (Smith, 1981), which is also unconformably overlain by the Mowich Group. The angular unconformity between the Mowich Group and older rocks marks a period of widespread diastrophism, the Ochoco Orogeny, which created an erosional surface of low relief. The Mowich Group was deposited over this erosional surface in a sea transgressing from east to west in this area.

The Mowich Group has been divided into the Robertson, Suplee, Nicely and Hyde Formations (Lupher 1941, Dickinson and Vigrass, 1965) (Figure 3-2). It crops out in a thin, nearly continuous belt of exposures for a distance of 40 km along the southwesterly plunging nose and southeast flank of the Mowich Upwarp and in discontinuous patches along the northwest flank of the upwarp (Figure 2-2). It is absent northwest of the axis of the Pine Creek Downwarp. The Mowich Group was progressively overlapped by the transgressive lower and middle Jurassic Snowshoe Formation. The contact between the two units is an angular unconformity in the western part of the area and conformable in the east.

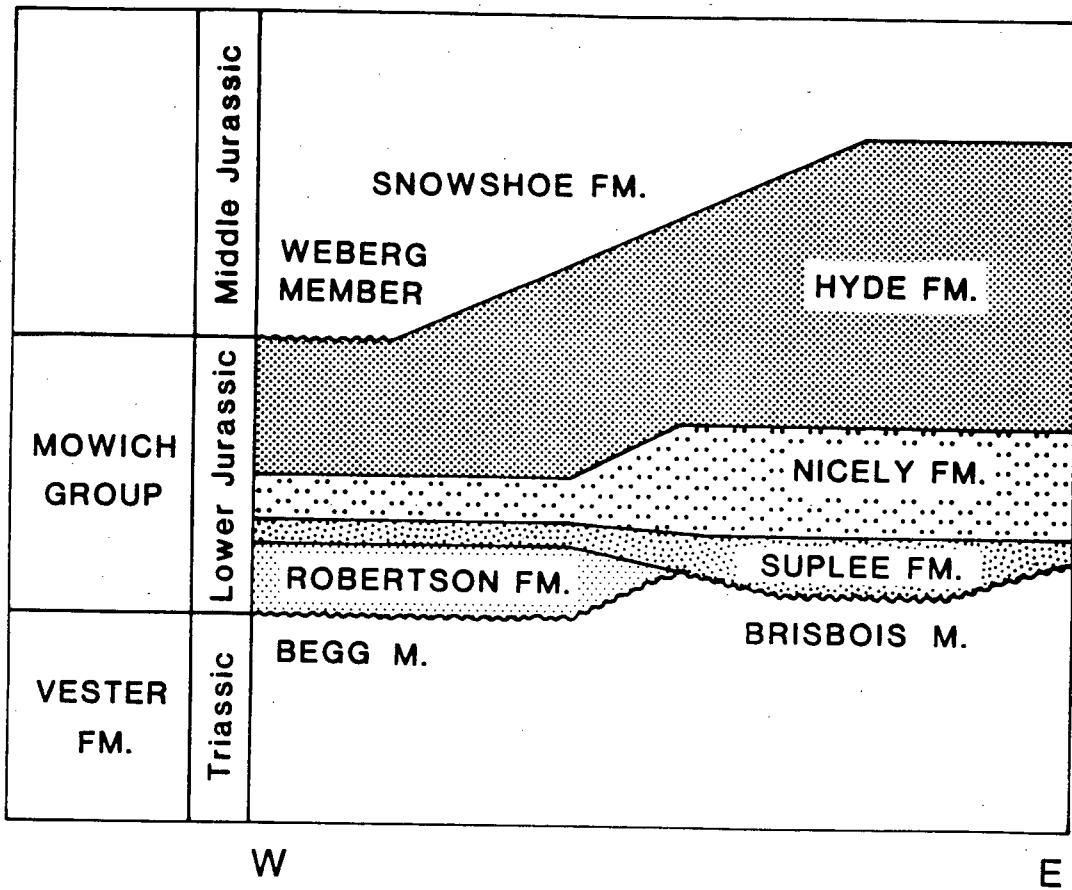


Figure 3-2: Stratigraphic relations of the Mowich Group in the Suplee Ize area. (adapted from Dickinson and Vigrass, 1965)

a. Stratigraphy of the Mowich Group

The Mowich Group which unconformably overlies older Mesozoic units in the Suplee-Izee area has been divided into the Robertson, Suplee, Nicely and Hyde Formations. (Figure 3-2)

b. ROBERTSON FORMATION

The Robertson Formation is the basal unit of the Mowich Group in the western part of the Suplee-Izee area. East of Pyramid Point and the South Fork of the John Day River the Robertson Formation is absent and the Suplee Formation is the basal unit of the group. The Robertson Formation reaches a maximum thickness of approximately 100 m between Swamp Creek and Pine Creek northeast of Suplee and thins rapidly to the east. Sections of the Robertson Formation were measured at the Type Section, located 13 km southeast of Suplee on Robertson Ridge; at Swamp Creek Ranch; and in the northern exposures in the Pine Creek area (Figure 3-3). The locations of these sections are indicated in Figure 3-4. The Robertson Formation includes three rock types; basal polymictic conglomerate, green and brown volcanic sandstone and grey limestone.

c. CONGLOMERATE

A basal conglomerate is found in the southern exposures of the Robertson Formation where the Triassic Begg Member underlies the formation. The Begg Member contains chert-pebble conglomerates which have been reworked and incorporated into the Robertson Formation. In northern exposures of the Robertson Formation the finer grained Brisbois Member underlies the formation and the basal conglomerate is absent. The Robertson conglomerate can be

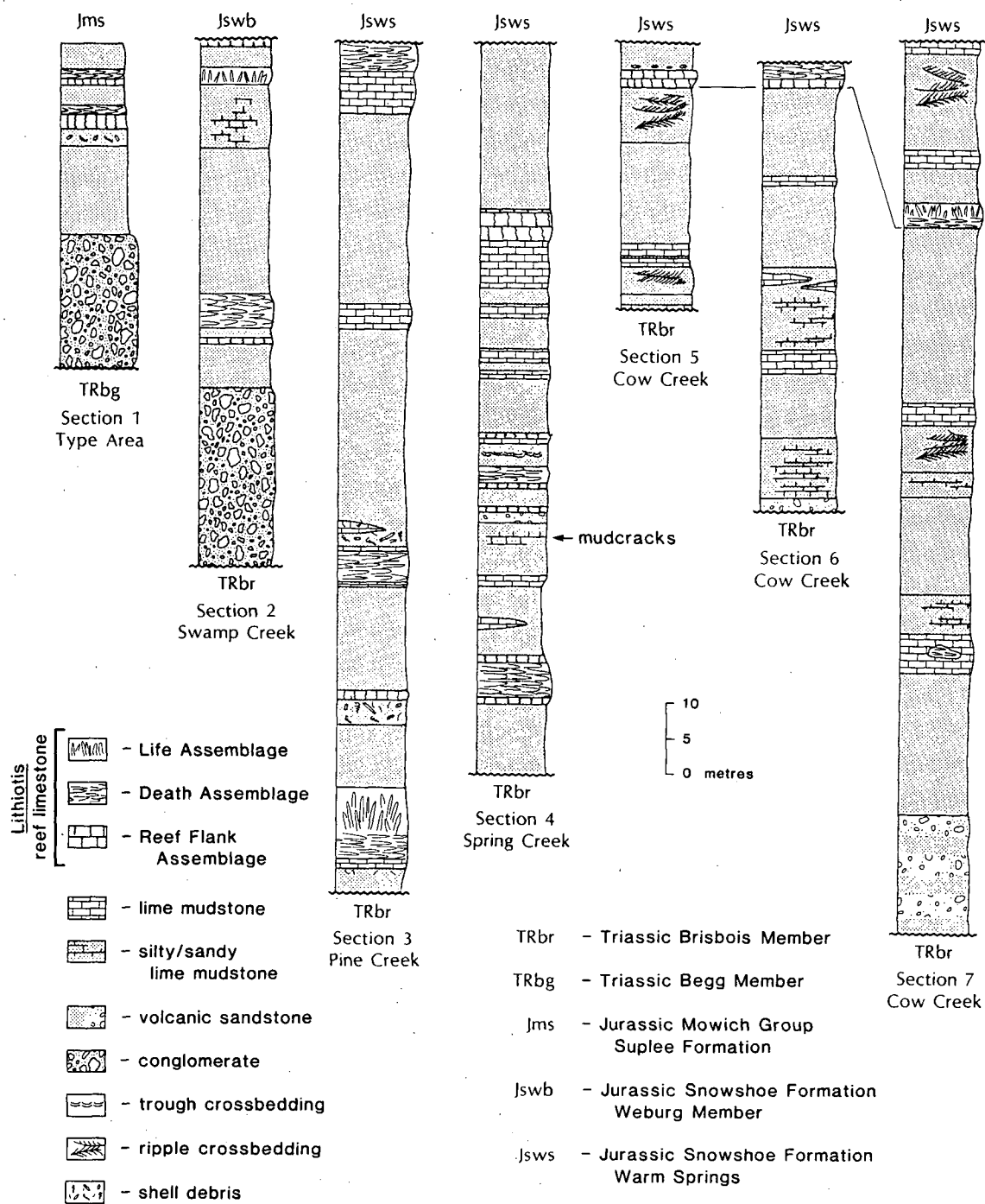


Figure 3-3: Measured sections of the Robertson Formation, locations on Fig. 3-4.

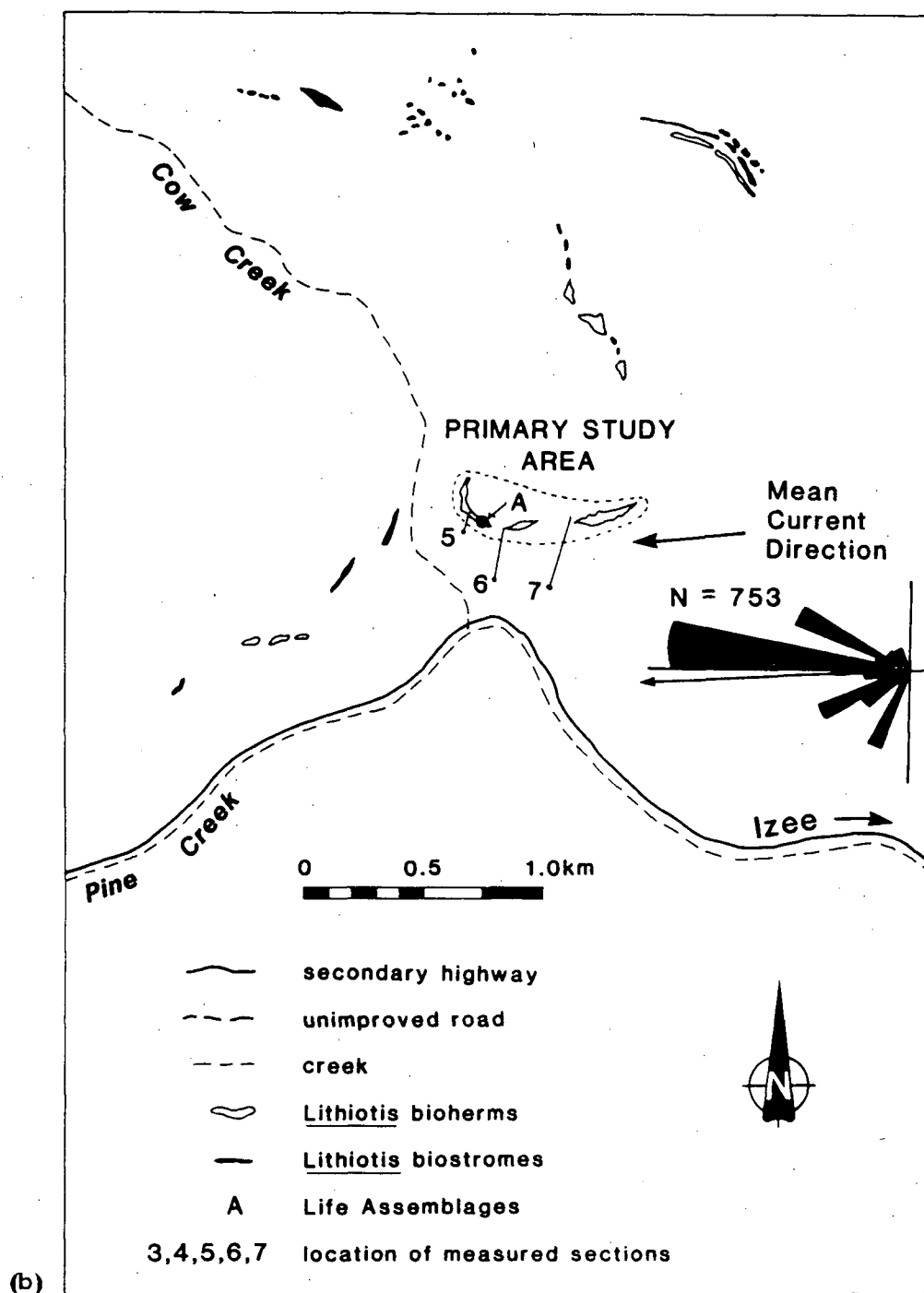
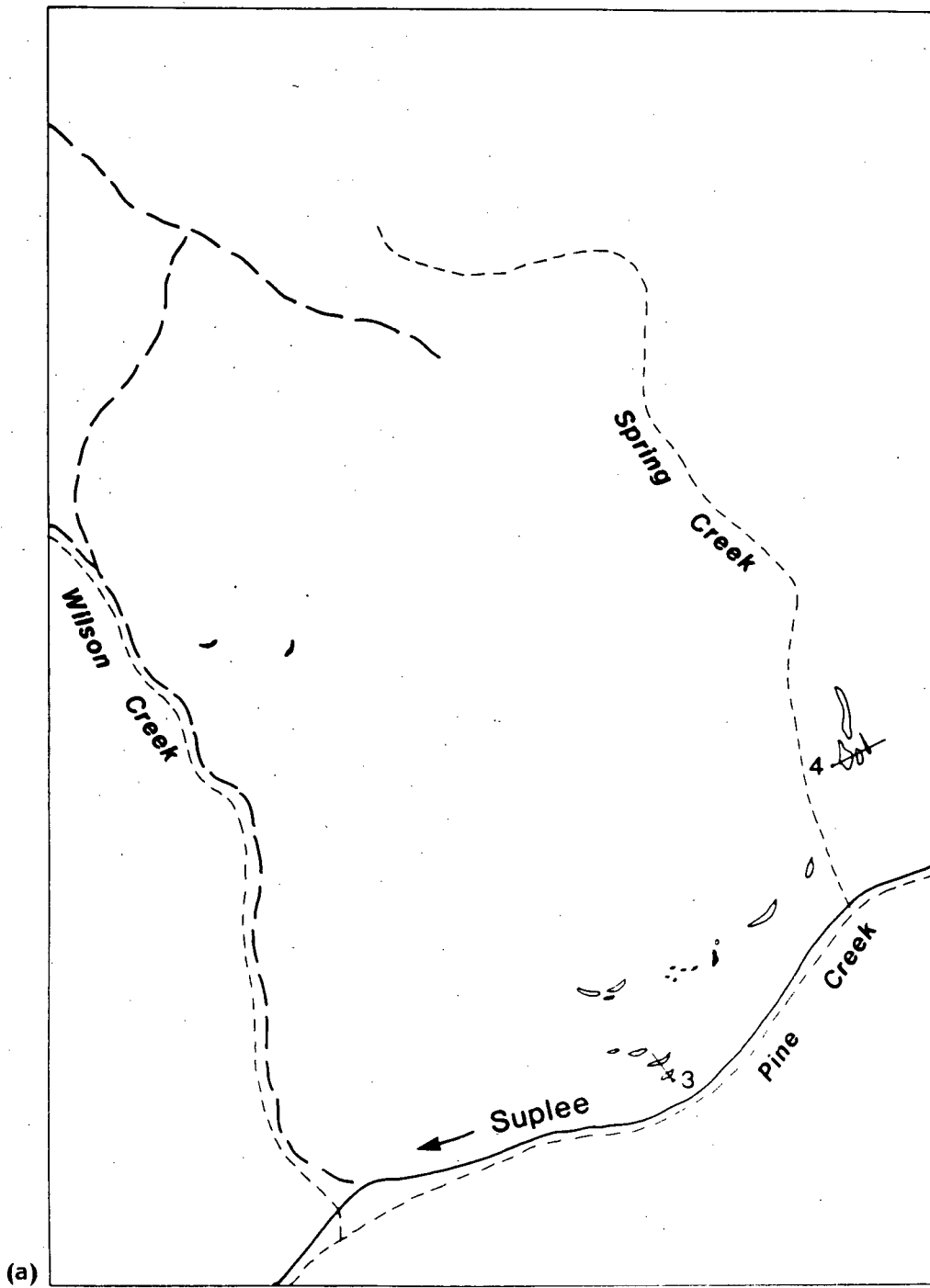


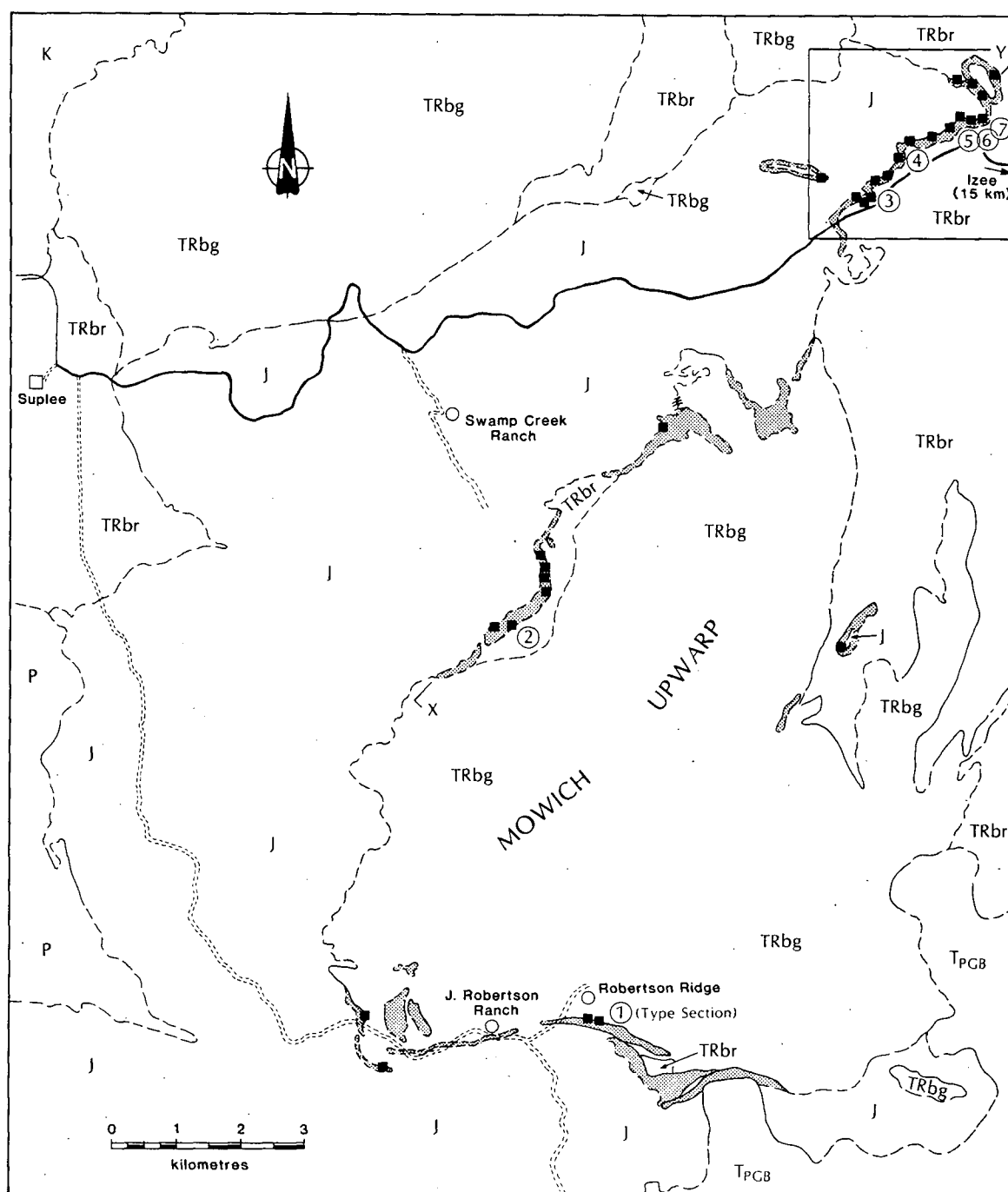
Figure 3-4, (a) and (b): *Lithiotis* bioherms and biostromes in the Robertson Formation from Wilson Creek to Cow Creek. Current data collected from the primary study area at Cow Creek.



distinguished from the underlying Triassic Begg Member Conglomerate by the angular unconformity dividing the two formations and the more rounded clasts and better defined internal bedding in the Robertson Formation. The conglomerate is a massive, resistant sandy pebble conglomerate which locally shows bedding and contains layers of cobbles and rare boulders; it accounts for approximately 40% of the formation in the type area, 35% in the central Swamp Creek area and is absent in the northern exposures (Figure 3-5).

d. SANDSTONE

The dominant lithology of the Robertson Formation is a volcanic sandstone which accounts for 45% to 65% of the formation. The sandstones are massive, locally cross-laminated, well sorted volcanic arenites. They are composed dominantly of subangular to subrounded grains of plagioclase, originally glassy volcanic rock fragments of hyalopilitic or pilotaxitic texture and minor augite. Less than 5% of the detrital grains are quartz, calcite, felsite and chert. The sandstones range from fine sand to granule sand. The most common sandstones are green, medium grained, cemented by chlorite and celadonite and commonly show cross-bedding (Figure 3-6 (A)). In the northern areas thin beds of spotted green sandstones are the result of diagenetic alteration (Dickinson and Vigrass, 1965). Silty calcarenites are commonly grey and weather brown. Those with iron-bearing phyllosilicate cement are green.



- | | | |
|--|--|--|
| P Paleozoic rocks | J Lower and Middle Jurassic | ■ <i>Lithiotis</i> biostromes and bioherms |
| TRbg Triassic Begg M. | K Upper Cretaceous | ④ Locations of measured sections |
| TRbr Triassic Brisois M. | TPGB Tertiary Picture Gorge Basalt | — paved highway |
| Lower Jurassic Robertson Fm. | | ----- gravel road |

Figure 3-5: Location of *Lithiotis* bioherms and biostromes within the Robertson Formation in the Suplee Ize area. Detail of box (upper right) in Fig. 3-4. Cross-section (X to Y) in Fig. 3-7.

e. LIMESTONE

Lenses of grey limestone constitute less than 5% of the Robertson Formation in the southern exposures and as much as 40% of the formation in the northern exposures. The limestone beds vary from hard light grey unfossiliferous lime mudstone lenses to massive highly indurated rudstone and bafflestone *Lithiotis* biostromes and bioherms. The limestones are interbedded within the sandstones and biostromal and biohermal units are often repeated stratigraphically above one another. Mudcracks have been found between bioherms in the northern areas, indicating a very shallow depositional environment. The *Lithiotis* biostromes and bioherms, discussed in detail in Section 4, are composed of three assemblages: a Reef Flank Assemblage, a Death Assemblage and a Life Assemblage. Calcareous mudstone lenses found within the volcanic sandstone and between the *Lithiotis* bioherms represent inter-reef areas. The pelecypods *Astarte*, *Camptonectes*, *Cardinia*, *Chlamys*, *Coelastarte*, *Gervillia*, *Grammatodon*, *Isocyprina*, *Lima*, *Lucina*, *Modiolus*, *Ostrea*, *Parallelodon*, *Pholadomya*, *P. cf. decemcostata*, *Pinna*, *Pleuromya*, *Trigonia* and *Weyla cf. unca* have been found within these inter-reef limestones (Batten and West, 1976; Dickinson and Vigrass, 1965; Hallam, 1965). Smooth-shelled, recrystallized ostracodes have also been found in the lime mudstones (Figure 3-6 (B)).

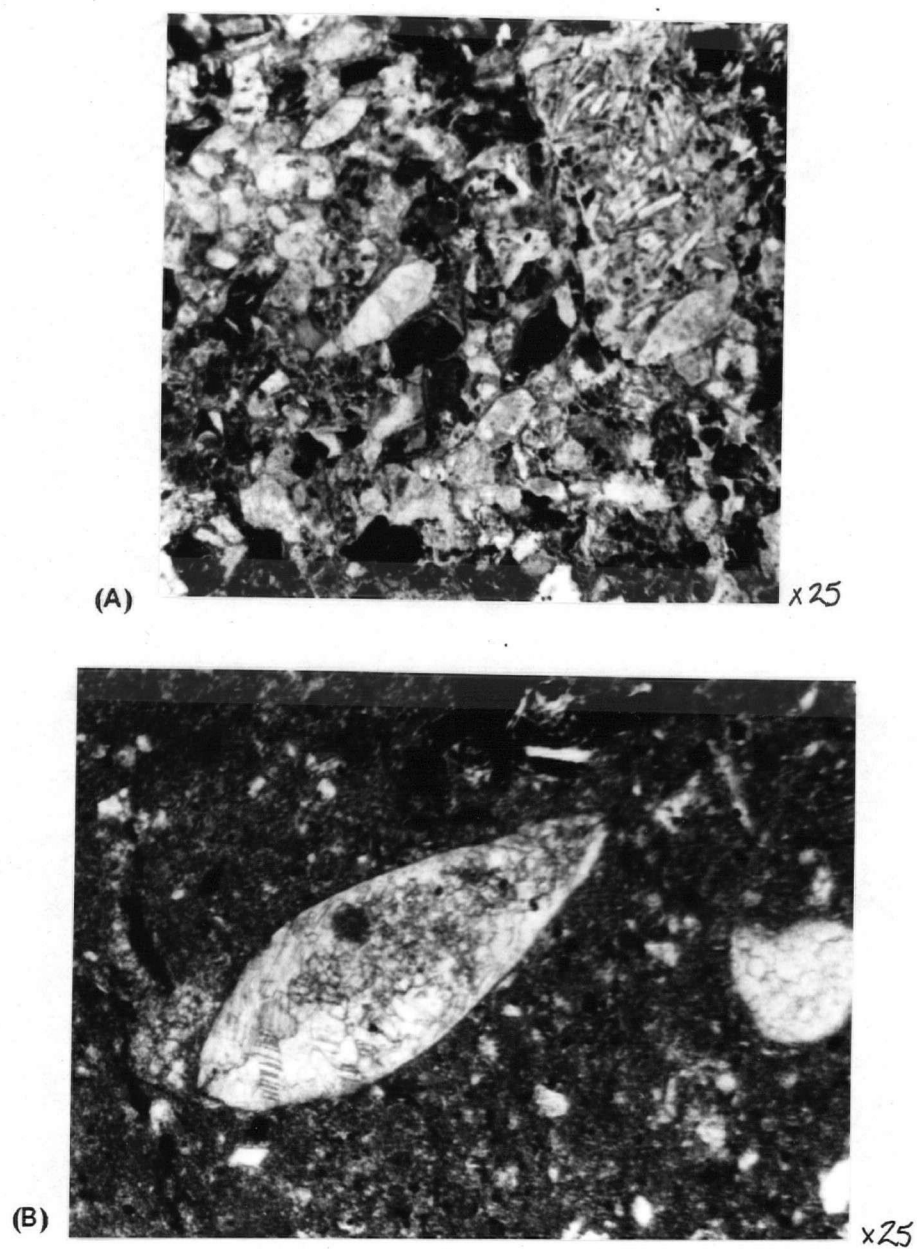


Figure 3-6:

(A) Green, medium grained, volcanic sandstone.

(B) Lime mudstone containing smooth shelled ostracod. Both samples from the Robertson Formation at Cow Creek.

f. AGE OF THE ROBERTSON FORMATION

The Suplee Formation rests conformably on the Robertson Formation in the southwestern part of the Suplee Izee area but in the eastern part of the area is the basal unit of the Mowich Group. Intercalations of green Robertson sandstone occur within the Suplee Formation as far east as the eastern central edge of the Mowich Upwarp (Fig. 3-5), which indicates that the Robertson Formation is in part equivalent to the Suplee Formation (Dickinson and Vigrass, 1965). The formations represent a facies change from very shallow water deposition in a restrictive environment in the west to a nearshore shallow water depositional environment in the east. East of Izee the Suplee Formation rests unconformably on the Keller Creek Shale. The Keller Creek Shale contains basal Pliensbachian ammonites from the Pinnaforme zone (Smith, 1981) and the Suplee Formation contains ammonites from the upper Pliensbachian Carlottense zone (Smith, personal communication). As the Robertson Formation is in part a facies equivalent of the Suplee Formation, the Robertson Formation is likely Upper Pliensbachian in age. The bivalve *Lithotis* is upper Pliensbachian to Toarcian in age, which supports an Upper Pliensbachian age for the Robertson Formation.

g. SUPLEE FORMATION

The Suplee Formation rests conformably on the Robertson Formation in the western part of the Suplee-Izee area but lies with angular unconformity on older Mesozoic rocks in the eastern part of the area. The Suplee Formation consists of up to 23 m of fossiliferous grey calcareous sandstone and sandy limestone. Fossils are abundant; the large pecten *Weyla* is found in nearly every

exposure and the pelecypods *Astarte*, *Camptonectes*, *Pleuromya*, *Trigonia* as well as rhynchonellid brachiopods are common. Other pelecypods in the formation include *Parallelodon*, *Modiolus*, *Pinna*, *Meleagrinella*, *Gervillia*, *Ostrea*, *Coelastarte*, *Lucina*, *Goniomya* and *Homomya*. In one locality *Gryphea* is so numerous that it forms a coquina limestone (Dickinson and Vigrass, 1965). Ammonites are rare in comparison to bivalves but do occur in the upper part of the unit. They have been studied by Imlay (1968) who assigned the assemblage to the Upper Pliensbachian. The fauna of the Suplee Formation contains bivalves which are relatively large, ornate, thick-shelled and characteristic of Taylors' (1982) Assemblage B, from a shallow water nearshore environment.

h. NICELY FORMATION

The Nicely Formation conformably overlies the Suplee Formation. It consists dominantly of black mudstone and shale with subordinate intercalations of calcareous siltstone and sandstone and reaches a maximum thickness of 91 m in the eastern part of the area. Spheroidal concretions up to 30 cm in diameter are abundant in some exposures. Upper Pliensbachian ammonites and the monotid pelecypod *Lupherella boechiformis* (HYATT) are the most common fossils (Imlay, 1968). Rhynchonellid brachiopods occur in sandy beds near the base of the formation and occasional pelecypods are found, including *Entolium*, *Camptonectes*, *Oxytoma*, *Modiolus* and *Pinna* (Dickinson and Vigrass, 1965). The fine grain size of the strata and good collection of ammonites put the Nicely Formation in Taylor's (1982) Composite Assemblage C, which is characteristic of an offshore environment of moderate depth.

i. HYDE FORMATION

The Hyde Formation is the upper unit of the Mowich Group. It rests unconformably on the Nicely Formation and is conformably overlain by the Snowshoe Formation. The Hyde Formation, which reaches a maximum thickness of 365 m, is composed dominantly of thick massive beds of grey marine andesitic tuff and tuffaceous volcanic greywacke which reaches a maximum thickness of 365 m. The Formation is sparsely fossiliferous. Bicostate rynchonellid brachiopods and fragments of late Toarcian ammonites have been found in some locations. The Hyde Formation represents a flood of slightly reworked pyroclastic debris erupted into the sea and distributed by bottom currents.

j. THE MOWICH GROUP IN THE SENECA AREA

A small area of Mowich Group exposures is located to the northeast of the Suplee-Izee area, four miles north of Seneca on the north side of Bear Valley. This locality, described by Lupher (1941), is made up of three small areas of exposures totaling approximately one square km. A 60 m thick sequence of Robertson Formation limestone is present above 18 m of black shale. *Lithotis* bivalves, *Nerinea* gastropods and terebratulid brachiopods are found in some parts of the limestone although much of it is unfossiliferous. A brown calcareous sandstone containing Suplee fauna is located apparently above the Robertson Formation limestone. Black shale tentatively correlated to the Nicely shale is also present.

k. CONCLUSIONS ON STRATIGRAPHY OF THE ROBERTSON FORMATION

Lithiotis bioherms are most extensive on the north side of Pine Creek and in the Swamp Creek area, where the Triassic Brisbois Member underlies the Robertson Formation. In the type area and along the Mowich Upwarp, except for a small area near Swamp Creek, the Begg Member underlies the Robertson Formation and *Lithiotis* appears in biostromes. The occurrence of biostromes and bioherms may be related to the basal conglomerate of the Robertson Formation which is reworked from conglomerates in the Begg Member. It is possible that the basal conglomerates of the Robertson Formation formed a slight barrier on the Mowich Upwarp, which created a more protected shallow water environment, ideal for the proliferation of *Lithiotis*. At Swamp Creek the Robertson Formation rests on a small area of the Brisbois Member and a basal conglomerate derived from the nearby Begg Member is present. This is probably a result of current action and the small area of Brisbois Member exposed (Figure 3-7).

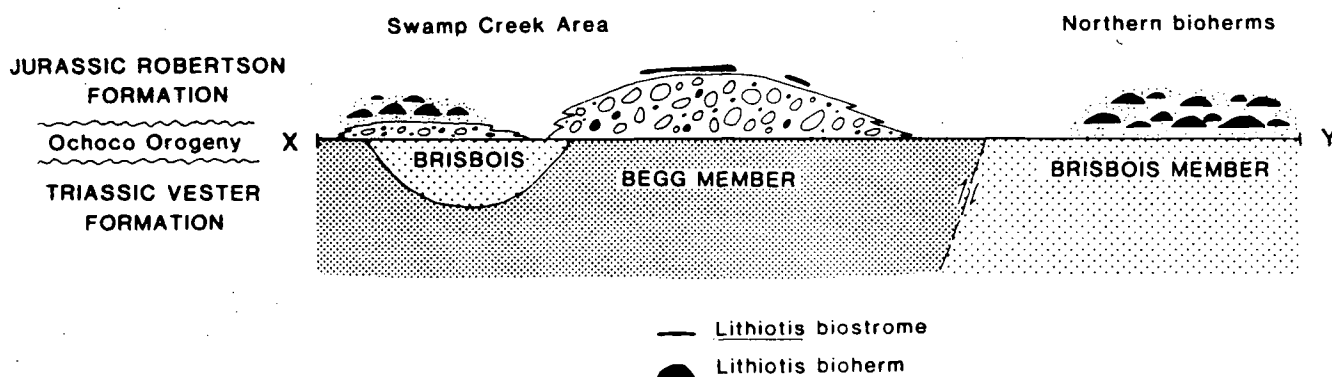


Figure 3-7: Diagrammatic cross-section from X to Y on map, Fig. 3-5.

The bioherms here are not as well developed as in the northern areas,

possibly indicative of a "semi-protected" environment. The biostromes of the type area and along the Mowich Upwarp are possibly representative of pioneering communities becoming established in less than ideal conditions.

The Suplee Formation conformably overlies the Robertson Formation in the type area and in an isolated exposure on the east side of the Mowich Upwarp. Along the western side of the Mowich Upwarp and in the northern area, the Snowshoe Formation, Weburg and Warm Springs Members unconformably overlie the Robertson Formation. This suggests that the sea transgressing the Mowich Upwarp initially covered the southern and eastern sides of the upwarp, and that the northeastern areas were significantly shallower.

C. STRATIGRAPHY AT LITHIOTIS LOCALITIES IN NEVADA

Lithiotis occurs in the Sunrise Formation and Dunlap Formation in west central Nevada, east and southeast of Reno.

a. SUNRISE FORMATION

Lithiotis reefs are developed locally in the Sunrise Formation in the Shoshone Mountains (Silberling, 1959) and rare *ex situ* *Lithiotis* specimens have been found in the Clan Alpine Mountains (Smith, 1981). Both occurrences are in the Mina Peak Member, the uppermost member of the Sunrise Formation (Taylor et al., 1983). The Sunrise Formation contains Hettangian to late Pliensbachian ammonite faunas which are characteristic of the Tethyan Realm (Taylor et al., 1983). The formation consists of 366 to 732 m of marine carbonate rocks and mudstones which are interpreted as shallow shelf deposits (Stanley, 1971).

b. DUNLAP FORMATION

In the Gabbs Valley Range and Shoshone Mountains the Dunlap Formation conformably overlies the Sunrise Formation. *Lithiotis* has been found in the lower part of the Dunlap Formation southwest of the Gabbs Valley Range in the Garfield Hills (Muller and Ferguson, 1939). The Dunlap Formation is sparsely fossiliferous. A Pliensbachian age has been suggested on the basis of a single ammonite specimen, the presence of *Lithiotis* and its general stratigraphic position (Smith, 1981). The Dunlap Formation is made up of clastic sedimentary rocks more than 1,219 m thick which are a heterogeneous mixture of pure quartz sandstone, shallow marine and intertidal carbonates, conglomerates and sandstones, and volcaniclastic sediments derived from local lower Jurassic and Triassic volcanics (Stanley, 1971). The Dunlap Formation is a predominantly terrestrial unit of accumulated alluvial fan and debris flow sandstones (Stanley, 1971).

The Sunrise and Dunlap Formations in the Gabbs Valley Range and Shoshone Mountains are a classic example of a shallowing upwards regressive sequence. *Lithiotis* bioherms were established just prior to regression. The Sunrise Formation in the Clan Alpine Mountains, Westgate District contains a benthonic fauna which suggests that a shallow marine environment was maintained into the Toarcian. (Smith 1981)

D. STRATIGRAPHY AT LITHIOTIS LOCALITIES IN CALIFORNIA

In California *Lithiotis* occurs in the Thompson Limestone at Mount Jura, Plumas County, along with *Nerinea* gastropods and terebratulid brachiopods. The Thompson Limestone is dated as lower Jurassic

(Pliensbachian?) on the basis of the *Lithiotis* fossils. A depositional hiatus from the lower Jurassic through the Toarcian to the lower Bajocian occurs from the Thompson Limestone to the Mormon Sandstone (Batten and Taylor, 1978). Such a hiatus suggests the possibility of a regression at the top of the Thompson Limestone.

E. STRATIGRAPHY AT LITHIOTIS LOCALITIES IN SOUTHERN EUROPE

The classical area of study on *Lithiotis* is in the northern Italian provinces of Viceriza, Trento, Verona and Belluno where *Lithiotis* occurs in the Pliensbachian (Domerian) to lower Toarcian strata of the Calcarei grigi (Grey Limestone). Equivalent occurrences are found in southeastern Spain, the south central Apennines, Yugoslavia, Albania and Greece (Loriga and Neri, 1976; Geyer, 1977).

The Calcarei grigi is a Liassic carbonate unit, which crops out in the western Venetian Pre-Alps and has been subdivided into three members (Bosellini and Loriga, 1971). The lower member is composed of cyclic regressive sequences which include oolitic and laminated algal limestones. The middle member is composed of oolitic calcarenites, commonly with current structures, which are considered to represent a barrier island complex. The upper member, formally named the Member of Rotzo, is composed of a variety of lithologies which can be grouped into five main facies: (1) oolitic and bioclastic calcarenites; (2) micritic limestones with molluscs, brachiopods, foraminifera and algae; (3) micritic and pelletoidal limestones; (4) limestones with *Lithiotis* and coquinas and (5) grey or black marls, sometimes rich in coal. *Lithiotis* bivalves are found in upper Pliensbachian (Domerian) to lowest Toarcian strata.

The oolitic limestones are interpreted as a barrier bar at the edge of a lagoon. *Lithiotis* bioherms are found along the shoaling edges of the lagoon and the traces of coal represent a swampy region beyond the lagoon. A foraminiferal microfauna occurs within the lagoonal deposits and disappears below the *Lithiotis* bioherms, suggesting that they represent restrictive conditions of an extremely shallow marine or estuarine nature.

IV. REEF STRUCTURE AND PALEOECOLOGY

The massive shells of the elongate *Lithiotis* bivalves form thick bioherms and biostromes in restricted marginal marine environments within Tethyan settings. These bioherms are unique in their extremely low diversity and apparent lack of bioerosion, which suggests that the bivalves thrived in a high stress environment.

The purposes of this chapter are fourfold:

1. To describe the geologic setting of the *Lithiotis* reefs in North America and Europe.
2. To describe in detail *Lithiotis* biostromes and bioherms in the Robertson Formation of east central Oregon.
3. To assess and consider the environmental controls on the reefs.
4. To propose a model of the *Lithiotis* reef environment.

A. GEOLOGIC SETTING

a. NORTH AMERICA

OREGON

In east-central Oregon *Lithiotis* reefs are found in the Robertson Formation which was deposited on the Suplee Shelf in a transgressing sea (Dickinson and Vigrass, 1965). The Robertson Formation represents a marginal marine shoaling environment in the lowermost portion of the transgressive Mowich Group.

NEVADA

Lithiotis occurs in the Sunrise and Dunlap Formations in western Nevada. *Lithiotis* reefs are developed locally in the Sunrise Formation in the Shoshone Mountains (Silberling, 1959)

and rare *ex situ* specimens have been found in the Sunrise Formation in the Clan Alpine Mountains (Smith, 1981). Both of these occurrences are in the Mina Peak Member, the uppermost member of the Sunrise Formation (Taylor et al., 1983). *Lithiotis* has also been found in the Dunlap Formation southwest of the Gabbs Valley Range in the Garfield Hills (Muller and Ferguson, 1939) (Fig. 1-2).

In the Gabbs Valley Range and the Shoshone Mountains the Sunrise Formation is conformably overlain by the Dunlap Formation, a dominantly terrestrial unit. The Sunrise and Dunlap formations comprise a shallowing upwards regressive sequence (Taylor et al., 1983).

In the Clan Alpine Mountains the Sunrise Formation is conformably overlain by an unnamed Jurassic Formation (Taylor et al., 1983). Marine deposition continued well into the middle Jurassic within this formation, although a regressive trend can be seen in the shallow water nature of the sediments. Above the *Lithiotis* occurrence are beds containing vertically embedded ammonites interpreted to have been deposited in water less than 10 m deep (Smith, 1981). Above this is a bed of *in situ* *Gryphaea* and *Ostrea* pelecypods, equivalent to a present day oyster bank (Smith, 1981).

CALIFORNIA

Lithiotis occurs in the Thompson Limestone of Plumas County in northern California (Batten and Taylor, 1977). The Thompson Limestone conformably(?) overlies the Hardgrave Sandstone, a shallow water unit containing an abundant pelecypod

fauna including *Pinna*, *Gervillia*, *Entolium*, *Pecten*, *Trigonia* and *Gryphaea* (Diller, 1908). The Bajocian Mormon Sandstone unconformably overlies the Thompson Limestone (Imlay, 1980).

b. SOUTHERN EUROPE

Throughout the circum-Mediterranean region from southern Spain and Morocco to the Southern Alps, the Apennines and Greece, a thick sequence of limestones is developed. The sequence can exceed 1000 m in thickness and ranges from the Triassic to the lower Toarcian. Individual facies provide evidence of supratidal to very shallow subtidal environments (Hallam, 1975). *Lithiotis* has been recorded in Pliensbachian and Toarcian strata throughout this circum-Mediterranean region (see Paleobiogeography, Section 5), but many of the identifications are suspect. Several bivalves including *Perna*, *Gervilleioperna* and *Cochlearites* have commonly been mistaken for *Lithiotis* (Cavicchi, Bosellini and Loriga, 1971). Recent authors use the term *Lithiotis* facies to indicate tentative identification and in this report uncertain identifications are specified.

The classic area of study on *Lithiotis* in the circum-Mediterranean region is in the Southern Alps in Italy where a great deal of detailed work has been done.

ITALY

In the Rotzo region of the Venetian Alps *Lithiotis* is found within the lower Jurassic Calcarei Grigi Formation which is underlain by Triassic cyclic lagoonal and tidal flat deposits of the Dolomia Principale. The Calcarei Grigi are divided into three members. The lower member is composed of cyclic sequences of

dominantly oolitic limestones which are regressive in character. The middle member is composed of oolitic calcarenites with current structures which are considered to represent a barrier island complex (Bosellini and Loriga, 1971). The upper member, the Member of Rotzo comprises five main facies: (1) Oolitic and bioclastic calcarenites; (2) micritic limestones with molluscs, brachiopods, foraminifera and algae; (3) micritic and micritic-pelletoidal limestones with subordinate presence of organisms; (4) limestones with *Lithiotis* bioherms and biostromes; and (5) grey or black marls locally rich in coal (Bosellini and Loriga, 1971). The Member of Rotzo is interpreted as a deposit formed in a lagoon protected from the open sea by the barrier island complex of the middle member (Bosellini and Loriga, 1971).

B. BIOHERMS AND BIOSTROMES

The thick shells of *Lithiotis* bivalves are always found in bioherms or biostromes, which are bedded structures built up by sedentary organisms. Biostromes are flat bedded whereas bioherms are lens or mound shaped carbonate buildups composed of mostly *in situ* skeletal remains (James 1983).

Lithiotis occurrences in the Robertson Formation of the Suplee-Izee area are biostromal in the southern part and biohermal in the northern part of the area. In the southern exposures limestone constitutes about 7% of the formation's thickness in contrast to the northern exposures where limestone constitutes up to 50% of the formation.

1. LITHIOTIS BIOSTROME IN THE TYPE SECTION OF THE ROBERTSON FORMATION

Approximately half of the limestone in the type section of the Robertson Formation is biostromal and the rest is grey calcareous mudstone. A biostrome, typical of the area, on Robertson Ridge has a thickness of 3 m and extends laterally for approximately 30 m before grading into calcarenite and minor calcilutite beds. It is underlain by 16 m of green medium to fine grained andesitic volcanic sandstone and overlain by 10 m of sandstone interbedded with lenses of calcareous mudstone 0.5 to 2 m thick. At the base of the biostrome are large concentrations of the gastropod *Nerinea* and occasional terebratulid brachiopods in a sandy calcarenite matrix. *Lithiotis* shelly debris becomes gradually more abundant upward into the biostrome, and further up into the biostrome numerous *Lithiotis* bivalves lie chaotically arranged, parallel to the bedding plane. The matrix is dominantly sandy calcarenite although some calcilutite is evident. The biostrome thins laterally to calcarenite containing abundant *Nerinea* gastropods and occasional terebratulid brachiopods. The contacts between the sandy calcarenite and grey calcilutite or mudstone are sharp. At the top of the biostrome the calcarenite grades rapidly into andesitic sandstone.

2. LITHIOTIS BIOHERM IN THE ROBERTSON FORMATION AT COW CREEK

The most extensive exposures of *Lithiotis* bioherms in the Robertson Formation are on the north side of Pine Creek from Wilson Creek to Cow Creek 15 km west of Izee (Figure 3-5). The limestones are resistant to weathering and form prominent buff coloured ridges which can be seen on the north side of the Suplee Izee road.

The largest and most completely exposed bioherm is located on the northeast side of Cow Creek (Figure 3-4 (b)). This bioherm extends for more than 190 m along the hillside and reaches a maximum height of 5.5 m. The bioherm is underlain by more than 100 m of massive, fine to coarse grained volcanic sandstones with interbedded lenses of unfossiliferous calcareous mudstone. The sandstone is locally cross-bedded, particularly below the western part of the reef. Approximately 60 m below the centre of the bioherm a portion of reef limestone less than 1 m in diameter is embedded into the volcanic sandstone. In several places small faults offset the reef by 2 to 12 m. Erosion has occurred down dry creeks along the offsets. The eastern side of the bioherm is abruptly truncated at a steep dry wash. The bioherm lenses out into sandstone on the western side. Sandstone with interbedded unfossiliferous calcareous mudstone lenses continues above the western side of the bioherm.

The bioherm is made up of a lens shaped reef core surrounded by flanking sediments partially derived from the reef. The bioherm is composed of three biofacies; (1) a Reef Flank Assemblage, (2) Death Assemblage and (3) Life Assemblage (Figure 4-1). The Life Assemblage and Death Assemblage make up the core of the reef mound and are surrounded by the Reef Flank Assemblage which marks the perimeter of the reef.

a. REEF FLANK ASSEMBLAGE

At the base of the bioherm andesitic sandstone is overlain by calcareous mudstone to floatstone which contains *Lithiotis* shelly debris, *Nerinea* gastropods and terebratulid brachiopods. This fauna marks the perimeter of the reef and is characteristic of the Reef Flank Assemblage. The contact between the underlying sandstone and the mudstone is gradational. The base of the mudstone contains

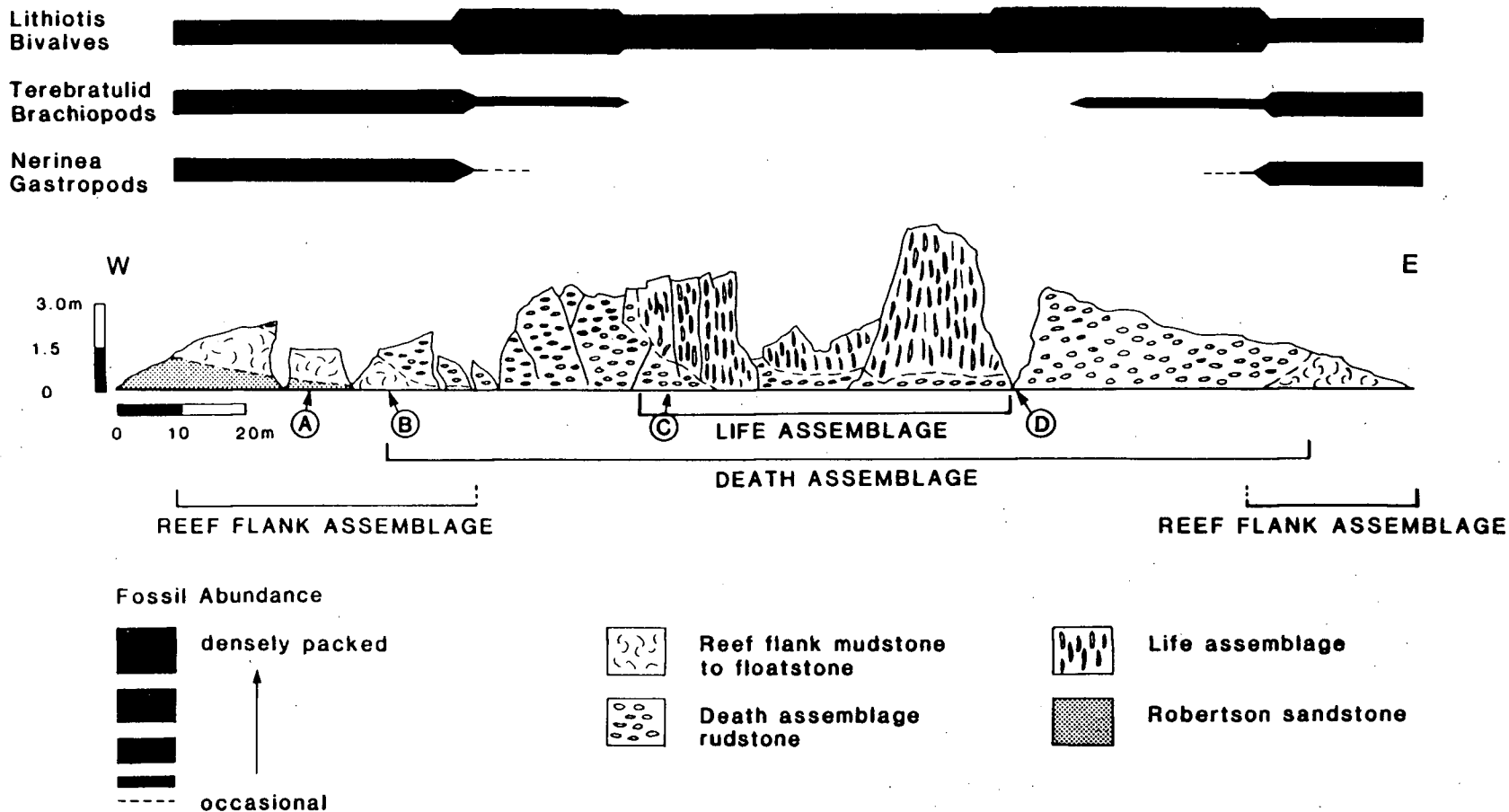


Figure 4-1: *Lithiotis* bioherm from the Robertson Formation, northeast of Cow Creek, in the primary study area (map 3-5). A, B, C and D refer to Figures 4-2, 4-3 and 4-4.

occasional fragments of *Lithiotis* shells in a sandy calcarenite or calcilutite matrix. It grades into a floatstone packed with *Lithiotis* shelly debris, brachiopods and gastropods. The *Nerinea* gastropods are often found in large concentrations in both the calcarenite and calcilutite matrixes (Figure 4-2). The terebratulid brachiopods are most abundant in the calcilutite matrix. The Reef Flank Assemblage lenses out into sandstone on the western edge of the bioherm. The base of the reef is covered near the center of the bioherm, but crops out near the eastern edge before the bioherm is truncated at a steep wash.

b. DEATH ASSEMBLAGE

Above the Reef Flank Assemblage is the Death Assemblage which makes up more than 50% of the bioherm. The Death Assemblage biofacies is characterized by tightly packed *Lithiotis* bivalves lying parallel to the bedding plane. The fauna consists solely of *Lithiotis* bivalves which have fallen over and are either chaotically arranged or are lying parallel to one another. The thick shelled stick-like bivalves are commonly 50 cm long and 8 cm wide and the base and top of the shells are virtually always broken off. The body chamber of the bivalve is small, cone shaped and about 10 to 15 cm long in a 50 cm specimen. Below the body chamber the shell cavity is infilled with calcite which means that the bivalve shells are thick solid tubes of carbonate. *Lithiotis* consists of two extremely unequal valves, the attached valve is robust and solid and the free valve is paper thin in comparison. Within the Death Assemblage the free valve is either wholly or partially separated or broken off the attached valve and only a few remnant pieces remain intact.

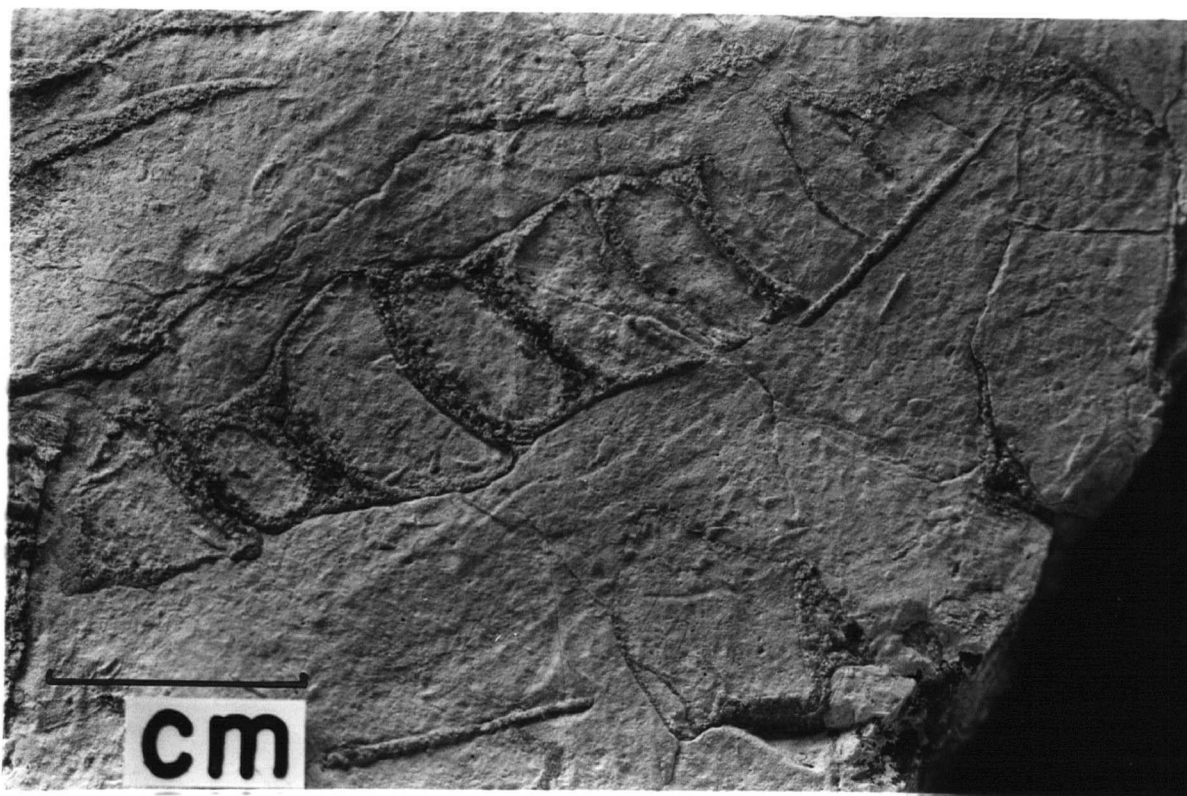
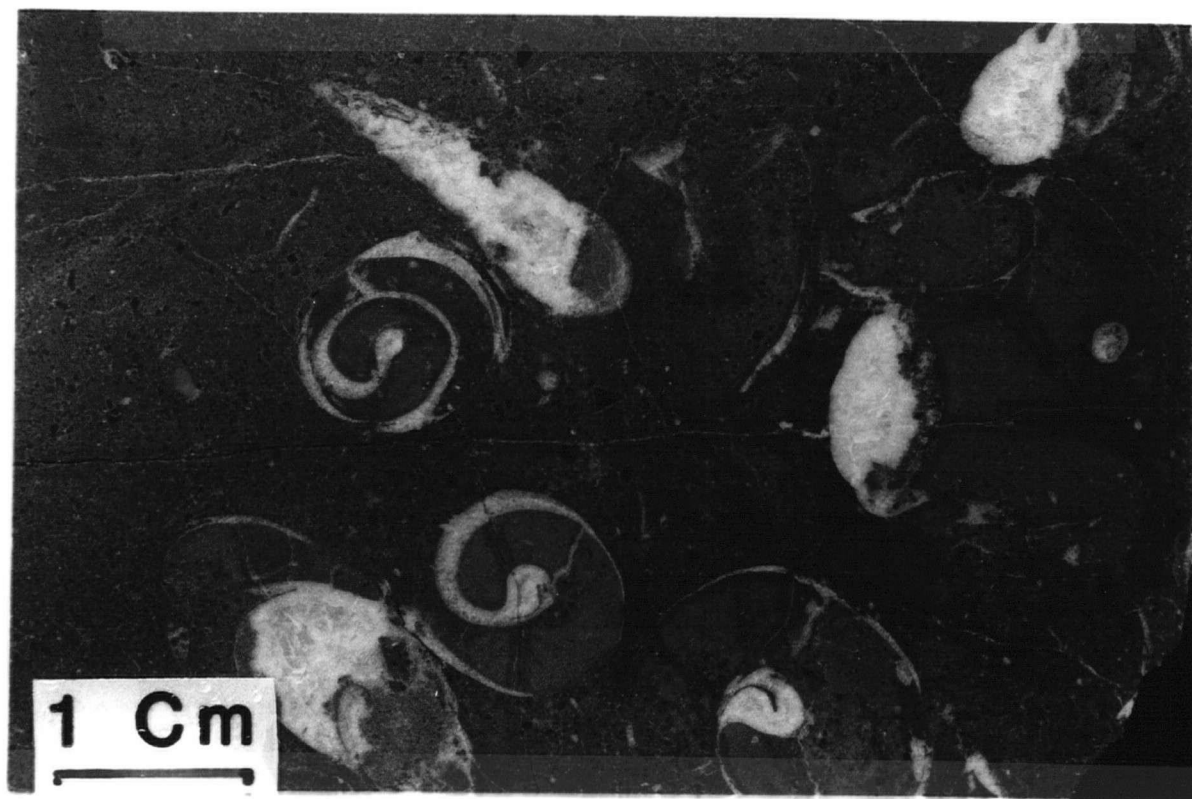


Figure 4-2: The gastropod *Nerinea*, commonly found within the Reef Flank Assemblage. (Locality A on Figure 4-1.)

In the Death Assemblage biofacies occasional fossils show a tendency to curve upwards but for the most part lie parallel to bedding. The bivalves have fallen over from their vertical life position and are either chaotically arranged or are found in large piles lying parallel to one another. The parallel alignment of the bivalves suggests that they were subjected to current action. The Death Assemblage is exposed along a bluff composed of massive, highly indurated limestone (Figure 4-3 (A)). The tightly packed bivalves are exposed in cross-section along the front face of the bioherm and the length of the bivalves are exposed along cracks and fractures. The trend of individual bivalves was measured along their length where good exposures existed and the number of specimens surrounding the bivalve lying parallel to the measured bivalve was counted on the front face of the bioherm. Trends were measured only where the bivalves were clearly exposed. Measurements were taken at 13 localities along the bioherm. The trend of the bivalves was measured within the bedding plane and the orientations were corrected on a stereonet to compensate for the dip of the bed (Pettijohn and Potter, 1977).

The orientation of the stick-like *Lithotis* bivalves specifies a line of movement, not a direction of movement. As the reefs in the Robertson Formation were formed on the shoaling edges of the Suplee-Izee basin it is logical to assume that the direction of movement was towards the shoreline (Fig. 3-4 (b)). The general trend is east-west with a vector mean of 267 degrees. Longshore drift along the edge of the basin is hypothesized as the cause of the fossils alignment.

The tightly packed bivalves of the Death Assemblage (Figure 4-3 (A)) make up a rudstone which is thick, unbedded and highly indurated. The matrix is calcilutite in most areas and occasionally calcarenite. The contact between the Reef Flank Assemblage and the Death Assemblage is abrupt and distinct. The large thick fossils and light buff to grey calcilutite matrix offers a strong contrast to the sandy calcarenite matrix of the Reef Flank and the Death Assemblage fossils are more resistant to erosion and form bluffs that extend over the Reef Flank.

c. LIFE ASSEMBLAGE

The Life Assemblage biofacies is in the centre of the bioherm and accounts for less than 30% of the entire outcrop of the bioherm. The assemblage has an extremely low diversity, the fauna consisting of *Lithiotis* bivalves and rare terebratulid brachiopods. The Life Assemblage appears 150 m from the western edge of the bioherm (Figure 4-3 (B)). Approximately 1.5 m above the base of the bioherm several individual bivalves can be seen bending upwards towards a vertical growth position. The bivalves must have been knocked over by current or wave action and been able to continue growth curving upwards until they resumed their vertical growth position. Presumably the bivalves would only be able to resume growth if they were not buried under numerous other bivalves. The great length of the *Lithiotis* bivalves and the fact that the body chamber is only in the uppermost part of the valves indicates that these bivalves were well adapted to areas of rapid sedimentation. However at the base of the Life Assemblage bivalves that have fallen over to a horizontal position are able to continue growth, twisting back to a vertical position, which



(A)



(B)

Figure 4-3: (A) Tightly packed bivalves of the Death Assemblage, exposed along a bluff of massive, highly indurated limestone. (Locality B on Figure 4-1)

(B) Transition from the Death Assemblage to the Life Assemblage occurs in the center of the photograph. (Locality C on Figure 4-1)

indicates that sedimentation was not rapid enough to bury these individuals before they grew back to a vertical position. The stratigraphic transition from horizontal to vertically positioned bivalves occurs within approximately 30 cm (Figure 4-3 (B), above the hammer). All of the bivalves above are growing *in situ*. The bivalves are closely packed together and are to some extent mutually supporting. Clusters of the bivalves lean on one another near their bases and radiate away from each other as growth continues (Figure 4-4). The bivalves have a tremendous capacity for twisting as they grow. In contrast to recent and fossil oysters which align their planes of commissure parallel to the direction of current flow (Lawrence, 1971), *Lithiotis* bivalves radiate away from each other as though attempting to gain the maximum amount of sunlight. *Konbostrea*, an upper Cretaceous oyster from Japan that closely resembles *Lithiotis* in both morphology and habitat, grows in clusters in which the juvenile shells radiate away from one another and then turn upward to grow parallel as adult (Chinzei, 1986). Although eroded surfaces of the *Lithiotis* bioherms can give the impression of parallel alignment this was not confirmed by cross-sectional views of the bivalves. Elongate Radiolitid rudist bivalves, which are also similar to *Lithiotis* in morphology and habitat, interlock with mutual cementation of neighbouring individuals as they grow upright (Bein, 1976). In some areas the Radiolitid rudists grow in fan-like clusters, morphologically resembling coral heads (Bein, 1976).

The vertical *Lithiotis* bivalves in the Life Assemblage form a bafflestone (Figure 4-4). The matrix is calcareous mudstone which grades into sandy calcarenite in some areas of the reef.

(A)



(B)

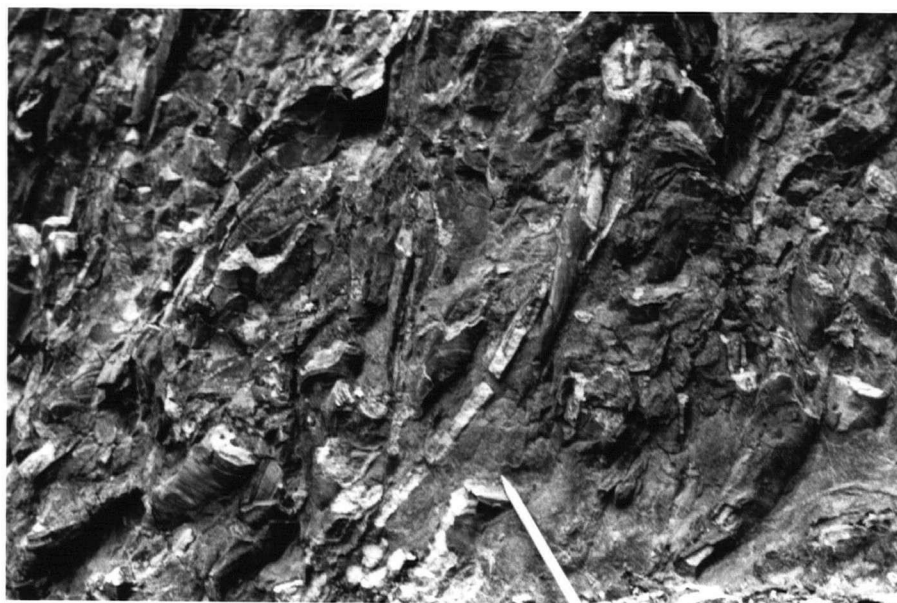


Figure 4-4: (A) and (B) Vertical growth of *Lithiotis* seen in the core of the reef is characteristic of the Life Assemblage. (Locality D on Figure 4-1)

In most areas of the Life Assemblage the matrix is calcareous mudstone and the limestone is massive and highly indurated. The bivalves are grey carbonate and the matrix is grey to buff. There is little contrast between the two and it is difficult to study the reef in detail. In areas where the matrix is sandy calcarenite it is possible to remove large sections of the reef rock. Several pieces of reef approximately 0.5 m long and up to 30 cm across were cut into slabs exposing cross sections through the bivalves. The body chambers of the bivalves are infilled with the calcarenite matrix which is darker than the carbonate shells and protected parts of the valves from recrystallization during diagenesis. In the cross sections infilled body chambers show up at varying levels in each section of reef which indicates that bivalves were growing at different levels. This means that although the bases of the bivalves were possibly anchored in sediment the majority of each valve was not. Most of the matrix sediment was deposited after the bivalves were well established and essentially drowned out sections of the reef.

The Life Assemblage biofacies, like the Death Assemblage biofacies, is more resistant to erosion than the Reef Flank Assemblage or the andesitic sandstone and forms prominent bluffs. These bluffs have been faulted and many large pieces have tumbled downslope from the outcrop. Outcrop ends at the top of the Life Assemblage.

d. COMMUNITY SUCCESSION IN THE ROBERTSON FORMATION *Lithiotis* REEFS

Lithiotis biostromes in the Robertson Formation consist of Reef Flank Assemblages and Death Assemblages but do not include Life Assemblages. The biostromes represent pioneering *Lithiotis* communities

which are analogous to the stabilization stage of community succession described by Walker and Alberstadt (1975). Species diversity is characteristically low, skeletal debris is abundant and the accumulation of *Lithiotis* shells has the effect of stabilizing the substrate. *Lithiotis* bioherms consist of Reef Flank Assemblages and Death Assemblages overlain by Life Assemblages. The Life Assemblage biofacies of the bioherms are analogous to the colonization stage of community succession. Species diversity is still low and a bafflestone is constructed from vertically growing *in situ* clusters of *Lithiotis*. Life Assemblages are found only above Reef Flank Assemblages and Death Assemblages which suggests that the bivalves settle more readily on the shell beds of the Death Assemblage. As *Lithiotis* cements to the substrate the Death Assemblages would provide far more attachment sites than the sand flats surrounding the biostromes.

The controls on reef growth are intrinsic or biologically controlled in terms of attachment sites for the bivalves. Extrinsic controls are more important to reef growth, particularly water depth in the regressive and transgressive sequences common to *Lithiotis* reefs.

C. ENVIRONMENTAL CONTROLS

Lithiotis bivalves lived in an optimum environment for carbonate production that enabled them to secrete massive, thick shells. They flourished in an environment that excluded common bioeroders such as boring algae, sponges and gastropods.

a. PALEOLATITUDE

Lithiotis is characteristic of the early Jurassic Tethys seaway and its continental margins throughout the circum-Mediterranean region. In North and South America *Lithiotis* is assigned to the Tethyan Realm which means that it extended circum-globally beyond the portals of the Tethys seaway at about the same comparatively low paleo-latitudes of the Tethys itself.

In Oregon rare boreal ammonites (*Liparoceras*) have been found with otherwise characteristically Tethyan ammonite faunas in the Mowich Group (Taylor et al., 1984). In Nevada the ammonite fauna of the Sunrise Formation is purely Tethyan (Taylor et al., 1984).

Modern carbonate deposition is concentrated in tropical waters through the equatorial belt and in some areas of warm ocean currents. The low paleo-latitudes of the early Jurassic Tethyan seaway and Tethyan Realm are analogous to present day low latitude tropical environments.

b. PALEOTEMPERATURE

Temperature is one of the most important factors influencing maximum size a pelecypod will attain and all extremely large pelecypods such as *Tridacna gigas* and large species of *Inoceramus* and rudists are found in warm, tropical environments (Nicol, 1964). Present day tropical seas are essentially saturated with regard to CaCO_3 and any process such as increase of temperature which removes CO_2 from normal seawater tending to change bicarbonate to carbonate ions, encourages lime precipitation (Wilson, 1975). The thick shells of *Lithiotis* and low paleo-latitude of the Tethys seaway and Tethyan Realm suggest a warm paleo-temperature similar to present day

tropical seas.

Paleotemperatures can be determined by analysis of oxygen or carbon isotopes in calcium carbonate skeletons as fractionation of isotopes during the precipitation of carbonate is temperature dependent (Dodd and Stanton, 1981). Isotope analysis of paleotemperature can only be done on well preserved fossils as diagenesis alters isotopic concentrations. Isotope analysis of *Lithiotis* bivalves from the Robertson Formation was attempted but the fossils are too recrystallized for reliable results (written communication, Al-aasm, University of Ottawa). Isotope analysis could potentially give an estimation of paleotemperature, indicate extremely high or low salinity and could also indicate the presence of zooxanthellae algae.

c. PALEOBATHYMETRY

Lithiotis bioherms formed in very shallow water, as is indicated by desiccation cracks between *Lithiotis* bioherms in the Robertson Formation. The development of second order cracks and algal laminae directly below the cracks indicates that the mudcracks were caused by subaerial exposure of the sediment surface rather than as a result of synaeresis. In western Nevada the terrestrial deposits in the Dunlap Formation overlying the *Lithiotis* biostromes and the oyster bank found above the *ex situ* *Lithiotis* occurrence in the Clan Alpine Mountains both indicate deposition in shallow water nearshore conditions.

The carbonate mudstone lenses interbedded in the andesitic sandstone of the Robertson Formation, between the *Lithiotis* biostromes and bioherms and extending laterally from the reefs are all similar in lithology. The mudcracks between the *Lithiotis* bioherms are also composed of calcareous mudstone. Carbonate mud can be produced in

several ways. The physical breakdown and abrasion of carbonate skeletons, weakening of skeletal particles by boring micro-organisms and mastication and ingestion by vagrant benthos are dominant processes of lime mud production (Mathews, 1966). The breakdown of lightly calcified green and red algae that disintegrate post-mortem also produces lime mud (Stockman, Ginsburg and Shinn, 1967).

In the Robertson Formation laminations in the sandstone layers directly below the mudcracks found between the *Lithiotis* bioherms indicate that the carbonate mud was deposited by algal mats which were later subaerially exposed. Algal mats are produced by cyanobacteria and are characteristic of shallow water marginal marine waters (Wray, 1977).

Although part of the calcarenite and calcareous mudstone in the *Lithiotis* bioherms is derived from the physical breakdown and abrasion of carbonate skeletons, because of the absence of bioeroders, the shallow nature of the deposits and the evidence of algal deposition in the mudcracks it is probable that the bulk of the mudstone is derived from the breakdown of calcareous algae.

In the Calcari grigi Formation of the Venetian Pre-Alps in Italy, the Dasyclad alga *Paleodasycladus mediterraneus* (Pia) is found in rare occurrences below *Lithiotis* bioherms and *Thaumatoporella parvovesiculifera* (Raineri) is commonly found between the bioherms (Bossellini and Loriga, 1971). *Thaumatoporella* and rare dasyclads are found in lower Cretaceous strata near Geneva, Switzerland where they are interpreted to be representative of a protected middle infralittoral environment (Conrad, 1975). The Calcari grigi Formation is interpreted as a lagoonal deposit. A similar algal flora might have been present

in the Robertson Formation.

d. TURBIDITY

Turbidity caused by suspended clay and silt particles in water restricts carbonate production by reducing light, thus inhibiting photosynthesis, and discouraging the growth of calcareous algae, and by restricting the growth of benthonic invertebrates by interfering with feeding mechanisms. Cross bedding in the andesitic sandstone of the Robertson Formation and alignment of *Lithiotis* by current action indicates that there was a certain amount of water movement in the environment. The Robertson andesitic sandstone is well sorted and coarse grained which indicates deposition in wave-agitated waters.

e. LIGHT

The elongate stick-like *Lithiotis* bivalve is adapted for raising its body chamber off of the substrate. This adaptation would enable the bivalves to live in areas of rapid sedimentation, however juvenile bivalves are commonly found cemented to the lower and median regions of mature bivalves. This suggests that the elongate form of *Lithiotis* could be a response to competition between the bivalves for light. If *Lithiotis* harbored symbiotic algae, light would be an extremely important environmental parameter.

D. CONCLUSIONS ABOUT THE LITHIOTIS REEF ENVIRONMENT

Modern invertebrates precipitate thicker calcite and aragonite shells in clear, warm waters. Many more calcareous algae thrive there and many reef building corals are restricted to such environments (Wilson, 1975). The thick carbonate skeletons and calcareous mudstones, probably the result of

calcareous algae, and geographic restrictions of *Lithiotis* indicate that the bivalve also lived in a warm, tropical environment.

One of the most striking features of the *Lithiotis* bioherms is the extremely large size of the *Lithiotis* bivalves. The bivalves were able to secrete tremendously large skeletons in proportion to their body size. Algal symbiosis may account for the large size of *Lithiotis* shells. Algal symbiosis promotes calcification in hosts by releasing a great deal of energy to the host. If isotopic anomalies characteristic of algal fractionation were found in *Lithiotis*, the large, thick shells could be attributed to symbiosis. Land et al. (1975) showed that carbon isotopic composition of coral tissue resembles that of algae rather than the surrounding seawater. The fact that the *Lithiotis* bivalves radiate away from each other during growth rather than aligning their commissures with the current suggests that sunlight was important, as it would be if the bivalves harboured symbiotic algae.

The extremely low diversity of *Lithiotis* reefs, along with the absence of bioeroders, is one of their most puzzling features. It indicates that *Lithiotis* was able to thrive in a high stress environment that inhibited other fauna. A similar situation exists in Cretaceous rudist reefs in the Judea Limestone and Talme Yafe Formation of Israel (Bein, 1976). These reefs were constructed almost solely of rudists together with chondrodont pelecypods. The only other fossils present in significant quantity are nerinid gastropods. The setting of these rudist reefs is similar to the *Lithiotis* reefs. They were deposited in shelf, slope and basin environments during transgression and regression events, in shallow water. The rudists grew in a similar fashion to *Lithiotis* bivalves, elongate vertically upright individuals interlock and stability in the reef is achieved through the crowding of the

interlocking fossils rather than attachment to a firm substrate. The major difference in their growth pattern is that individual rudists cement locally to other neighbouring rudists. No evidence of this is seen in *Lithiotis* reefs. Other rudist reefs, such as the Comanche Cretaceous Glen Rose reef in central Texas, contain rudists restricted to the lagoonal environment, away from the shoreline. Caprinid rudist reefs are well developed within the lagoonal facies offshore, and oyster biostromes are developed along the shoreline in an environment that is analogous to that of *Lithiotis* (Perkins, 1974).

The elongate oyster *Konbostrea* found in Cretaceous strata in northern Japan also grows in low diversity communities in a marginal marine environment (Chinzei, 1986). Individual oysters which reach a height of more than 1 m, grow densely crowded together in banks approximately 2 m thick. No other fossils are found within the oyster beds or in stratigraphically adjacent sediments except for traces of boring sponges on the surface of well preserved individuals. These communities have been interpreted as intertidal or brackish water communities (Chinzei, 1986).

Lithiotis grew in extremely shallow water, as indicated by the desiccation cracks between bioherms in the Robertson Formation. Depth zonation of nearshore to offshore invertebrate faunal paleocommunities has been studied in the Suplee-Izee area by Taylor (1982), who proposed a model for shelly invertebrate depth zonation in the Jurassic shallow water marine environment based primarily on the Snowshoe Formation. Four depth related composite assemblages were defined on the basis of unique co-occurrences and relative abundances of taxa. The *Lithiotis* bioherms of the Robertson Formation are part of Composite Assemblage A in Taylors' Western Cordillera Composite Assemblages. Composite Assemblage A

includes faunas from intertidal to very shallow sublittoral high energy environments. Species diversity is characteristically low. Epifaunal taxa are numerically dominant and brachiopods, particularly terebratulids are often the most abundant organisms.

Lithiotis bioherms in the Calcari grigi Formation in the western Venetian Pre-Alps of Italy grew in a lagoon protected from the sea by a barrier island complex (Bossellini and Loriga, 1971). Bivalves common to the *Lithiotis* facies in the Jbel bou Dahar reef complex in the Moroccan High Atlas Mountains formed bioherms in a lagoon protected from the open sea by a barrier reef (Agard and DuDresnay, 1965). Evidence from Oregon, Nevada, Morocco and Italy conclusively limits *Lithiotis* to a very shallow water environment.

Lithiotis bioherms in the Calcari grigi of the Venetian Alps in Italy are interpreted to have grown in the most internal part of a lagoon, bordering on marshes and swamps (Bossellini and Broglio Loriga, 1971). The Calcari grigi Formation has a benthic foraminiferal fauna of species belonging to the Lituolidae, Ataxophragmidae and Ammodiscidae families. The only foraminifera that appears with the *Lithiotis* bioherms is *Glomospira* spp. which can tolerate more stressful marginal marine areas. Smooth thin walled ostracods, *Aeolisaccus*, terebratulid brachiopods and Nerineidae gastropods also occur with the large *Lithiotis* and *Perna* bivalves (Bossellini and Loriga, 1971).

The Cretaceous oyster *Konbostrea* is limited to the innermost part of a basin which opens onto the Pacific, in the Kiji area of Japan. The oyster beds are intercalated in sandstone beds containing coaly matter and conglomerate lenses which are considered to be non-marine or brackish water deposits (Chinzei, 1986).

In the Robertson Formation *Lithiotis* grew in shoaling areas along the edges of the Mowich Upwarp. In some areas current action aligned the bivalves. The current was possibly longshore drift from the Suplee-Izee basin. *Lithiotis* bioherms grew in marginal marine conditions along the edge of the shallow sea. Algal communities grew on sandflats with interspersed pelecypod communities in some areas. A model by Chave, Smith and Roy (1971) shows molluscs growing on a sand flat interspersed amongst calcareous green algae in a sheltered back reef or lagoonal habitat, which is similar to the environment of the Robertson Formation. The extremely marginal marine environment of the *Lithiotis* reefs in the Calcarei grigi formation of Italy suggests that the *Lithiotis* bivalves in the Robertson Formation might also have grown in a similarly restrictive environment which would account for the absence of bioeroders. The *Konbostrea* oyster beds of Japan are another example of bivalves living within a restricted marginal marine environment.

V. PALEOBIOGEOGRAPHY

The global distribution of ancient faunas is an important component in the study of plate tectonics. Paleobiogeography can demonstrate tectonic displacement and place constraints on tectonic reconstructions. The paleobiogeography of *Lithiotis* and assessment of migration routes of the bivalve supports the presence of a rifted seaway, the Hispanic Corridor (Smith, 1983) through the Caribbean and along the North Atlantic preceding the formation of oceanic crust in the early Jurassic.

Ammonite paleobiogeography has been used in the North American Cordillera to demonstrate tectonic displacement and place constraints on tectonic reconstructions (Taylor et al, 1984; Smith and Tipper, 1986). The latitudinal displacements of allochthonous terranes have been estimated using ammonite provinciality along with paleomagnetic data. The presence of *Lithiotis* in the southern terrane, Sonomia and absence of *Lithiotis* in the Canadian terranes, Quesnellia, Wrangellia and Stikinia places constraints on the latitudinal reconstruction of the terranes.

A. GLOBAL DISTRIBUTION OF LITHIOTIS

The geographic distribution of *Lithiotis* is widespread ranging from the western continental margins of North and South America, Southern Europe, Northern Africa, the Middle East and as far east as Timor in Indonesia (Fig. 5-1).

a. EAST PACIFIC

In North America *Lithiotis* occurs in the Robertson Formation in Oregon (Lupher, 1941; Dickinson and Vigrass, 1965; Batten and West, 1976); in the Thompson Limestone in California (Batten and Taylor, 1978); and in the Dunlap Formation (Muller and Ferguson, 1939) and

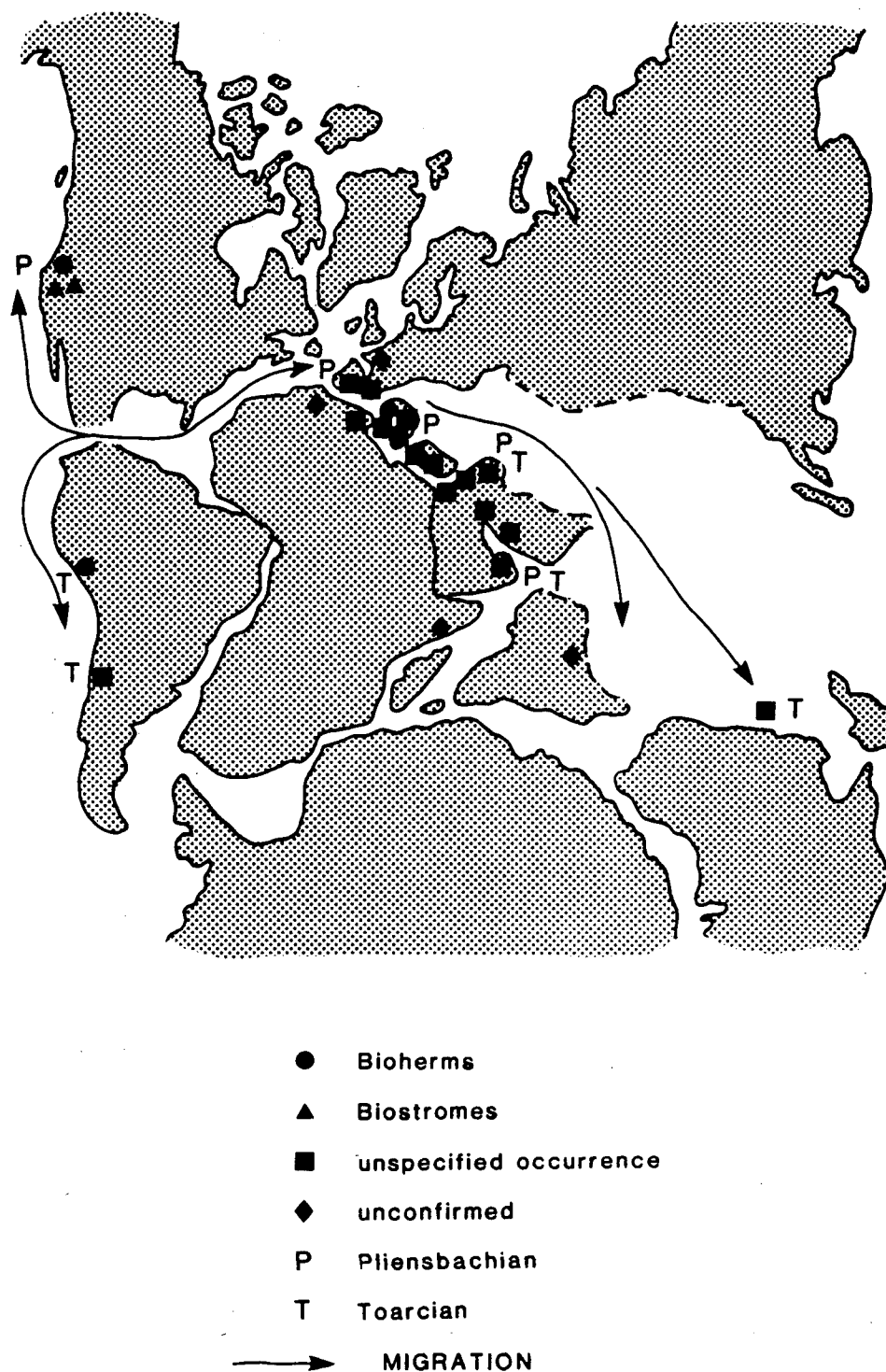


Figure 5-1: Paleogeographic distribution of *Lithiotis* and probable migration routes of the bivalve.

Sunrise Formation (Silberling, 1959; Smith, 1981) in Nevada, 1939) and Sunrise Formation (Silberling 1959, Smith 1981) in Nevada. In all of these areas *Lithiotis* is found in Pliensbachian strata.

Lithiotis has also been reported from the Donovan Formation in eastern Oregon (Lupher, 1941). This report originated from limestone lenses containing abundant irregular dark streaks and spots that resembled sections of *Lithiotis*. Examination and thin section work on samples collected from these lenses has revealed abundant algal laminations and large fragments (up to 10 cm wide and 1 cm thick) of bivalve shells resembling oysters rather than *Lithiotis*.

In South America *Lithiotis* is found in lower Toarcian strata in Peru and Chile (Hillebrandt, 1982).

b. CIRCUM-MEDITERRANEAN REGION

Lithiotis occurs in northern Italy in the Pliensbachian (Domerian) to lower Toarcian strata of the Calcari grigi (Grey Limestone) Formation. (Bosellini and Loriga, 1971; Gohner, 1980). Occurrences of the same age are found in southeastern Spain, the south-central Apennines, Yugoslavia, Albania and Greece (Loriga and Neri, 1976; Geyer, 1977).

There is a possible occurrence of *Lithiotis* in the Sarthe area in northern France (Boehm, 1892). Recent authors have been unable to locate the bioherms and the *Lithiotis* identification has not been verified (Loriga and Neri, 1976).

In Morocco *Lithiotis* has been included in the Pliensbachian fauna from the Atlas Mountains in the Jbel bou Dahar reef complex (Dubar, 1948; Agard and DuDresnay, 1965). Other authors have suggested that large bivalves such as *Perna* have been misidentified as

Lithiotis in this area (Loriga and Neri, 1976; Benini and Loriga, 1977) and plates of the reef fauna include the *Perna*, *Gervilleioperna* and *Opisoma* but no examples of *Lithiotis*.

In Somalia near Mogadiscio a Middle Liassic fauna has been described including *Cochlearites* and *Opisoma* from the *Lithiotis* facies but again *Lithiotis* has not been positively identified (Geyer, 1977).

Lithiotis occurs in Iran, Iraq and Oman in the Middle East. In Iran and Iraq *Lithiotis* occurs in Pliensbachian to lower Toarcian strata and in Oman it occurs in slightly younger strata ranging from uppermost Pliensbachian to upper Toarcian (Benini and Loriga, 1977; Geyer, 1977).

c. EASTERN TETHYAN OCEAN OCCURRENCES

In Indonesia *Lithiotis* is found in Timor in Pliensbachian to Toarcian strata (Krumbeck, 1923).

The *Lithiotis* facies has been mentioned in descriptions of the Kioto Limestone facies in the Himalayas, although identification of *Lithiotis* has not been verified (Geyer, 1977).

d. OTHER OCCURRENCES

Lithiotis has been included in the fauna of Toarcian deposits in Spitzbergen Island, Norway (Wierzbowski, Kulicki and Pugaczewska, 1981). An examination of plates and a cast of the fossil kindly provided by Dr. A. Wierzbowski have shown this to be a misidentification. The small fragment of shell less than 1 cm wide and 1.5 cm long is distinguished by wavy growth lines that could belong to many pelecypod species and is not similar to the growth lines on the outer *Lithiotis* shells.

B. MIGRATION ROUTES OF *LITHIOTIS*

Lithiotis is an endemic Tethyan bivalve and a prodigious carbonate producer presumably restricted to tropical environments. The endemic centre of *Lithiotis* is in the upper Pliensbachian strata of North America and the Western Tethyan Ocean. Since genetic continuity had to have been maintained between the disjunct Pliensbachian populations in the Western Tethys and the East Pacific, migration must have occurred along the central Atlantic Seaway or Hispanic Corridor. There are no *Lithiotis* occurrences in the Pliensbachian of South America (Hillebrandt, 1971 and 1981a) or in the Pliensbachian of Timor (Krumbeck, 1923), although Toarcian occurrences of *Lithiotis* are found in both of these areas. This indicates that migration in the Toarcian spread from the Pliensbachian endemic centre; from North America to South America, and from the Western Tethys to the eastern Tethys. Hillebrandt (1971, 1981a) has suggested that the calcareous sponge *Stylothalamia* used the Hispanic Corridor to migrate from the Tethyan Ocean to the East Pacific during the early Pliensbachian based on occurrences of the sponge in Yugoslavia, Morocco and Peru (Smith and Tipper, 1986). The bivalve *Weyla* also likely migrated along the Hispanic Corridor. *Weyla* is characteristic of the eastern Pacific from the Hettangian to the Toarcian and appears in the western Tethyan Ocean during the early Pliensbachian and in the eastern Tethys during the Toarcian (Damborena and Mancenido, 1978). Migration by a southern route would require its presence first in the eastern Tethyan Ocean. Hallam (1983) made an analysis of lower and middle Jurassic bivalve faunas from North America, South America and Europe. Through the use of Simpson similarity coefficients he showed strong correlations between North American and South American Pliensbachian faunas and between North American and European Toarcian

faunas. He concluded that relatively free migration along the Hispanic Corridor did not occur until the late Toarcian-early Bajocian, but limited intermigration of molluscan faunas must have occurred along a shallow epicontinental seaway during the Pliensbachian. The ammonite genus *Dubariceras* known from the east Pacific by *D. freboldi* and from the western Tethys by *D. dubari* also supports migration through the Hispanic corridor during the Pliensbachian as it has not yet been reported east of Italy and Hungary (Smith and Tipper, 1986).

C. TECTONIC IMPLICATIONS IN NORTH AMERICA

The geographic distribution of European ammonite faunas delineates a Boreal Realm and Tethyan Realm of ammonite provinciality. In the Pliensbachian, the families Amaltheidae and Liparoceratidae form a Boreal endemic center and the families Hildoceratidae and Dactylioceratidae form a Tethyan endemic center (Smith and Tipper, 1986). The two realms are separated by a broad east-west trending boundary which is distinguished by mixed Boreal-Tethyan faunas. The Boreal Realm has a lower diversity fauna than the Tethyan Realm, believed to be the result of greater fluctuations in temperature, salinity, light, climate and food resources. These factors are to some extent latitude controlled and are also the reason for the east-west trending boundary between the realms (Reid, 1973; Hallam, 1972, 1973; Smith and Tipper, 1986). The general worldwide distribution of the Boreal Realm is the northern part of the northern hemisphere and the Tethyan Realm occupies the rest of the globe.

In the Northwest Pacific the boundary trends northwest-southeast as a result of the northward displacement of terranes relative to the North American craton (Taylor et al., 1984; Smith and Tipper, 1986). Suspect

terrane of the Cordillera are recognized by unique stratigraphy; paleomagnetic evidence showing displacements and rotations characteristic to each terrane; major faults on the terrane borders and paleobiogeographic evidence (Coney et al, 1980). The Canadian suspect terranes Wrangellia, Stikinia and Quesnellia and the American suspect terrane Sonomia have yielded a Pliensbachian ammonite fauna that is biogeographically differentiated. The Canadian terranes contain a mixed Boreal and Tethyan fauna in their northern parts and a Tethyan fauna in the south (Figure 5-2 (A)). The American terrane, Sonomia contains a purely Tethyan fauna. Sonomia was accreted to the craton during the Triassic (Speed, 1977) and the Jurassic sediments deposited across Sonomia are in a fixed position relative to the craton and can be considered as cratonal sediments (Smith and Tipper, 1986).

The John Day Inlier has yielded a Tethyan fauna comparable to the Sonomia fauna, but as the inlier is surrounded by Tertiary volcanics it is difficult to determine its tectonic relationship to other terranes. Paleomagnetic data, lithologic discontinuities and structural interpretations indicate that the Canadian terranes have been displaced northwards with a progressive increase in the amount of displacement passing outward from the craton (Taylor et al, 1984). Estimations on the amount of displacement based on paleomagnetic data have varied from 1300 km for late Triassic rocks of Stikinia (Monger and Irving, 1980) and 1300 km or 4900 km for late Triassic Wrangellia, depending on the north or south hemisphere option chosen (Yole and Irving, 1980). Smith and Tipper (1986) have suggested that paleobiogeographic data can help quantify the displacement by determining which side of the paleoequator the paleolatitudes are on based on the "polar bear principle." The Boreal ammonite *Amaltheus* is restricted to the

northern hemisphere, therefore the most southerly occurrences of *Amaltheus* would have been between the Canada-U.S.A. border and Oregon-California border (Fig. 5-2 (B)). The southern limit for displacement of the terranes is similarly limited by the presence of *Lithiotis* in Sonomia and absence of *Lithiotis* in Quesnellia, Wrangellia and Stikinia.

Lithiotis is found in shoaling regions of marginal marine shallow shelf seas in Pliensbachian strata in North America. Pliensbachian occurrences are scattered and poorly exposed in Quesnellia and not fully explored in Stikinia and Wrangellia. *Lithiotis* should occur in the Canadian suspect terranes. Its absence would indicate that the terranes have not been displaced or that *Lithiotis* is not a low latitude indicator. The most likely reason that *Lithiotis* has not been found in the Canadian suspect terranes is collection failure or lack of appropriate shallow marginal marine facies. The most complete Pliensbachian exposures are in Wrangellia on the Queen Charlotte Islands. On the Queen Charlotte Islands the Maude Formation is Pliensbachian to Toarcian in age but is a basinal facies. Offshore exploration could well reveal *Lithiotis* in a shallow water marginal marine facies.

D. CONCLUSIONS

Lithiotis is widespread, occurring in the East Pacific, circum-Mediterranean region and as far east as Timor in Indonesia. *Lithiotis* is found in Pliensbachian strata in North America and the western Tethyan Ocean and elsewhere is found in Toarcian strata. Because it is an endemic Tethyan bivalve migration would have been restricted to low paleolatitudes. *Lithiotis* could have migrated to South America by a southern route around Gondwanaland; between east Africa and India-Antarctica and around the

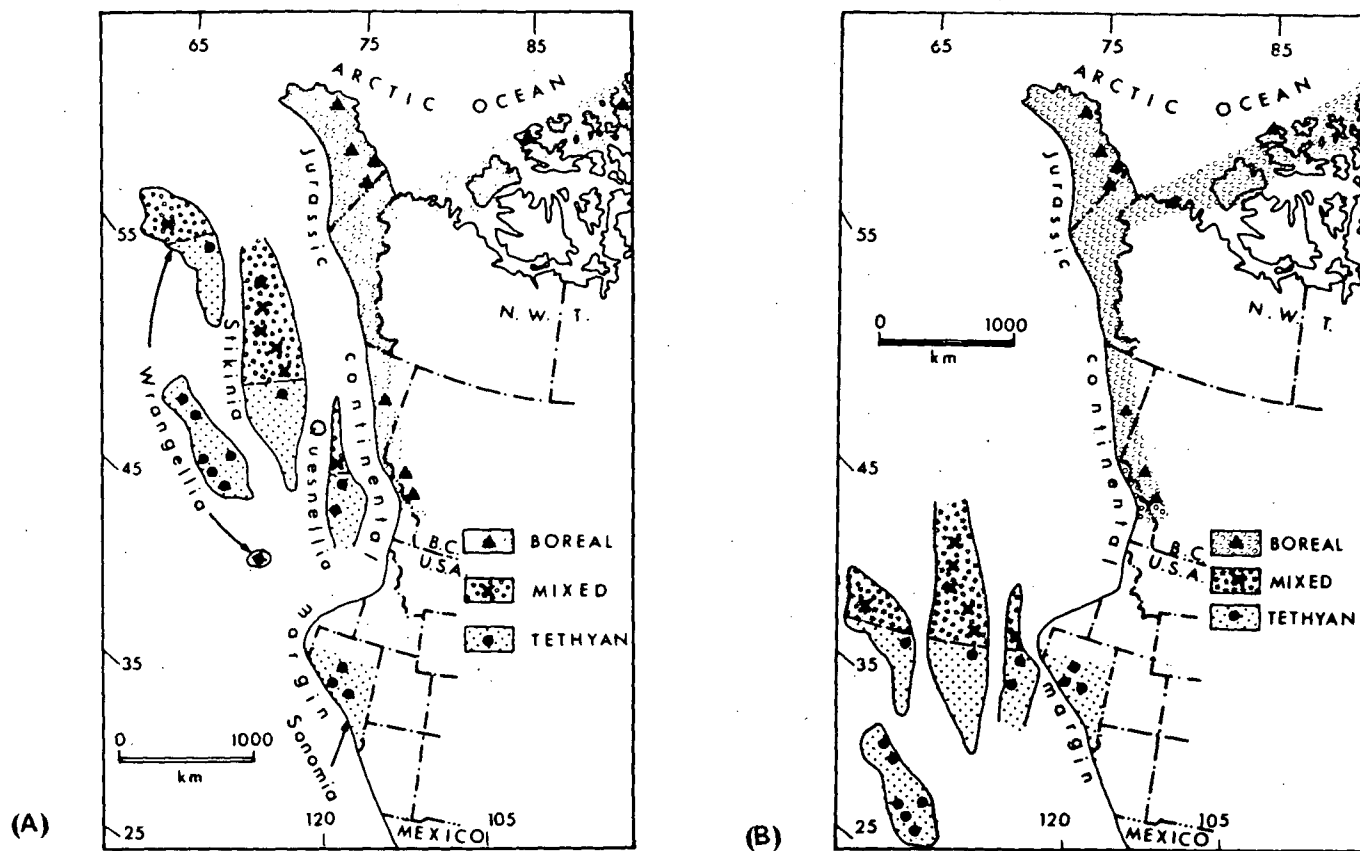


Figure 5-2: (A) North-south biogeographic zonation within the Pliensbachian allochthonous terranes. (B) Latitudinal displacement suggested by biogeographic constraints. From Smith and Tipper, 1986.

southern tip of South America; or via the Hispanic Corridor. The Hispanic Corridor is the most logical route for migration from the western Tethyan Ocean to North America.

Lithiotis has not yet been found in Canadian suspect terranes, although it should exist in nearshore facies in Pliensbachian strata. Its absence is likely the result of collection failure or absence of suitable shallow water facies.

VI. MORPHOLOGY AND TAXONOMIC AFFINITIES OF *LITHIOTIS*

In this chapter the morphology of *Lithiotis* is described, followed by a discussion on the taxonomic affinities of the bivalve, and the taxonomic classification of *Lithiotis*.

A. MORPHOLOGIC DESCRIPTION OF *LITHIOTIS*

The *Lithiotis* bivalves found in the Robertson Formation are embedded in highly indurated limestone and are extremely difficult to extract. In some areas the limestone matrix varies from calcareous mudstone to calcarenite and it is possible to remove large blocks of the reef limestone. Four such blocks, approximately 1 m by 0.5 m, were cut into 4 to 6 cm slabs, which were polished and acetate peels of the slabs were taken and photographed (Plates 1-3). The morphology of *Lithiotis* was examined from the slabs, from float specimens and within the bioherms. The elongate, stick-like *Lithiotis* bivalves are usually broken at the top and bottom in float specimens and only one crushed specimen was found which included a complete shell cavity. *Lithiotis* is made up of a robust attached valve and an extremely thin free valve. The polished slabs were essential for examining the free valve which is seen only as remnant fragments on float specimens.

The *Lithiotis* bivalves in the Robertson Formation have been recrystallized and details of the internal structure of the bivalves are obscured. The body chamber or shell cavity of the bivalves is infilled with calcarenite which contrasts with the recrystallized carbonate and facilitates examination of the shape of the body chamber. Well preserved *Lithiotis* bivalves have been studied in Northern Italy and information about the internal structure of the bivalves is available from work in these areas. The

morphological descriptions of *Lithiotis* are supplemented with this additional information where appropriate.

1. SHELL OUTLINE

Lithiotis has a dorso-ventrally elongated stick-like shell which reaches a height of 30 cm or more, has a width of 4 to 6 cm and an average thickness of 3 cm. The umbonal region of the shell is round in cross-section in comparison to the upper part of the shell which is elliptical, giving the shell a spoon-like appearance (Figure 6-1 and 6-2). Juvenile shells are cone-shaped and flare rapidly from the umbo, forming an angle greater than 30 (Plate 5). At a height of less than 10 cm the expansion rate drops and the shell margins become sub-parallel.

2. THE ATTACHED VALVE

Lithiotis is made up of a thick, robust attached valve and a thin, fragile free valve. Juveniles are commonly found cemented to adult shells (Plate 4) and likely cemented to cobbles or pelecypod shells in pioneering communities. The umbo is too small to have supported mature bivalves, which were anchored in the sand or mud substrate. The attached valve is characterized by a distinct furrowed plate on the cardinal surface of the valve (Figure 6-1). A plume-like area extends from the margin of the furrowed plate around the outside of the shell (Plate 5 and 7). The plume-like area is made up of individual growth lines which are periodically prominent forming distinct ridges around the outside of the shell. The periodicity of the ridges in *Lithiotis* is very regular and occurs in 1 to 2 cm intervals. The ridges are often subdued resulting in a flat shell surface and small ridges are common. Occasionally thick ridges of up

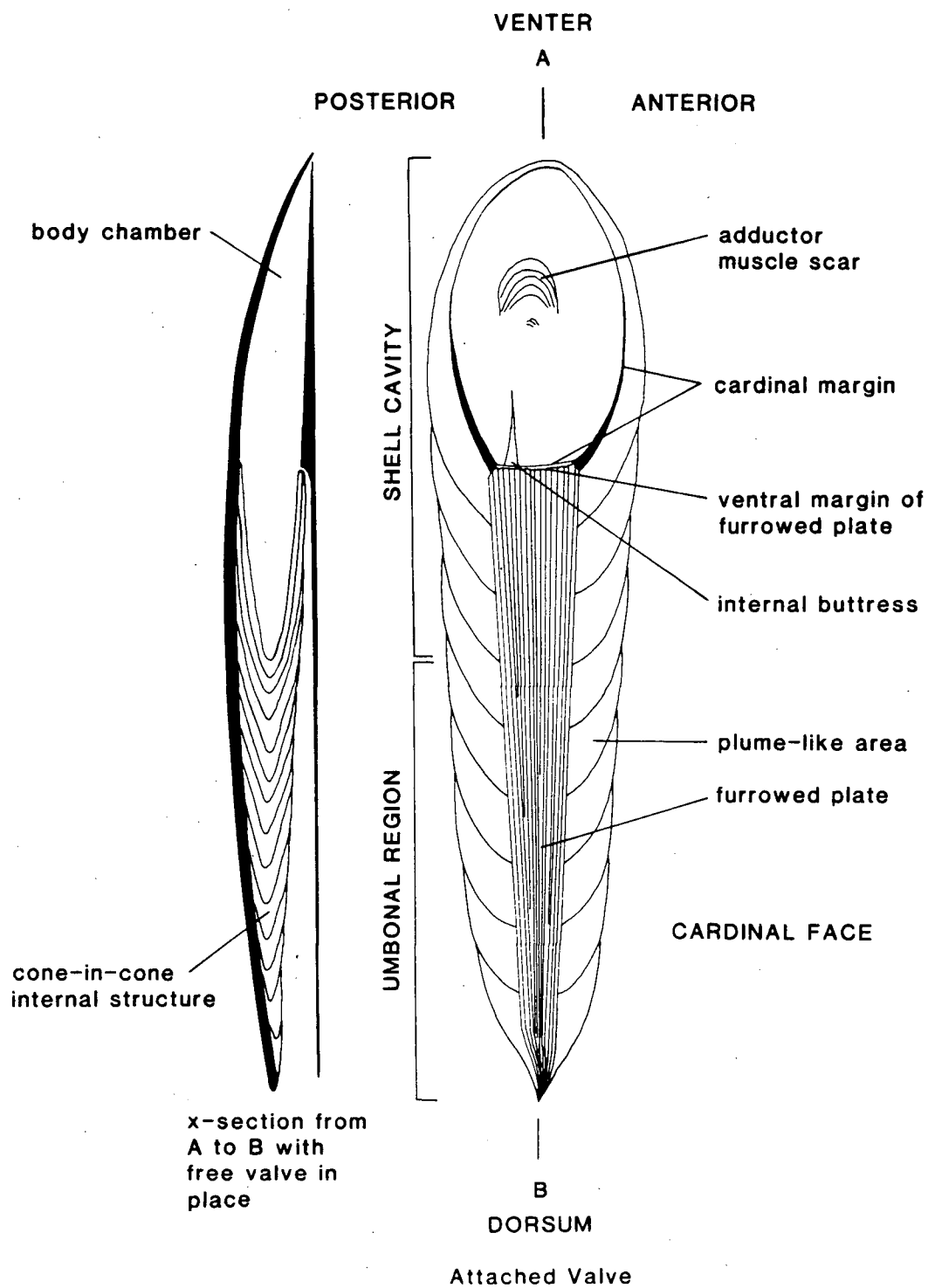


Figure 6-1: Morphology of *Lithiotis*

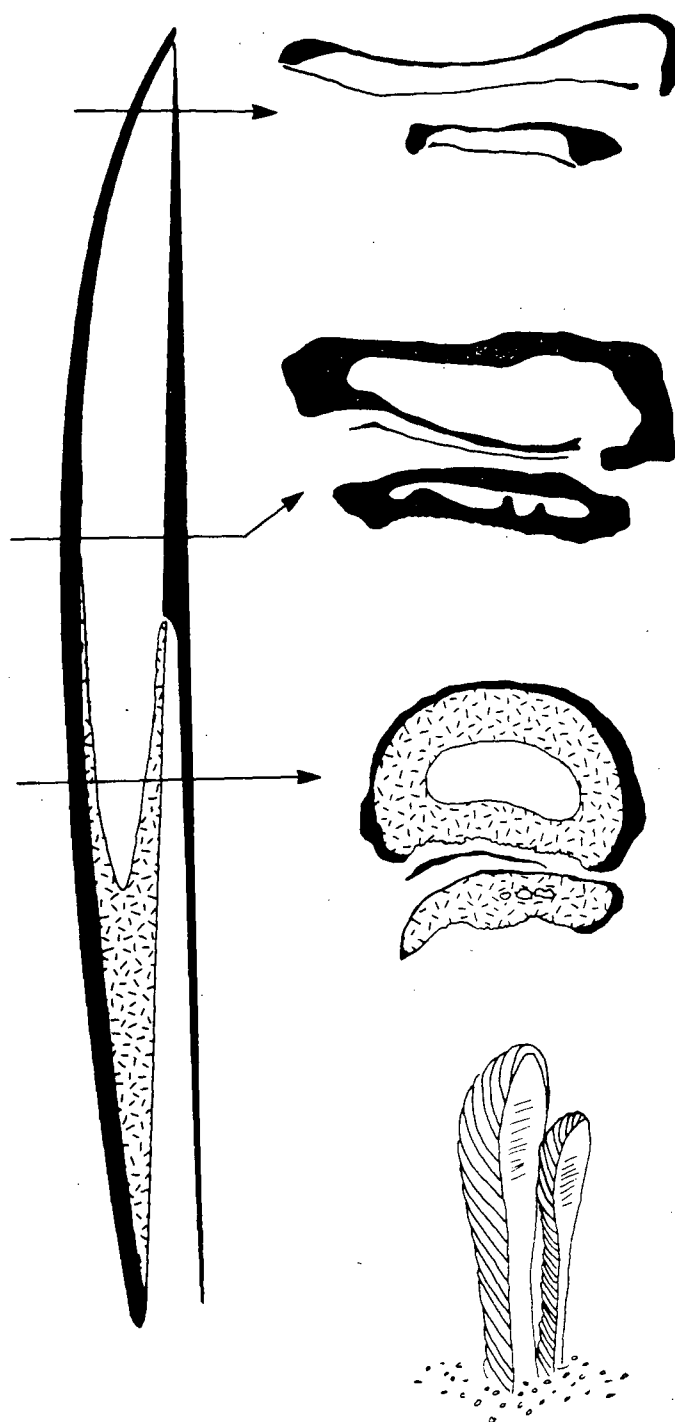


Figure 6-2: Horizontal cross-sectional views of two *Lithiotis* bivalves (right) and their position within the bivalves (left). Specimens EB 1-1 and EB 1-2. Bottom right = sketch of the two bivalves in life position. (X 0.6)

Solid black represents the outer shell. The hatched pattern represents the infilling below the body chamber.

to 1 cm height are developed (Plate 6). In thin shelled specimens the ridges flare out from the edge of the furrowed plate at an angle of 20 to 30 degrees, whereas in the thick, robust shells characteristic of the Swamp Creek area, the ridges flare out at 50 to 70 degrees. The periodicity of the ridges might reflect cyclicity in the growth of the bivalve, however the growth lines were too faint to count. In the Robertson Formation *Lithiotis* bivalves from the Swamp Creek bioherms are distinguished by thick prominent ridges on the outside of the shell. Although ridged shells are also seen in the northern bioherm localities, nowhere else are they as prominent and prevalent. The thick ridged bivalves in the Swamp Creek area are more robust and may reflect adaptation to a higher energy environment. The Robertson Formation in Swamp Creek overlies a small area of Brisbois Member even though the Robertson contains basal conglomerate which is characteristic of reworked Begg Member. There must have been enough current action in this area to accumulate rock from the nearby Begg Member. If the high energy required to transport the conglomerate rock continued through the deposition of the Robertson Formation it could account for the more robust, strongly ridged *Lithiotis* shells. The thick ridges are the only morphological difference seen in the Swamp Creek area bivalves which indicates that the ridges are an effect of environmental conditions and do not represent a different *Lithiotis* species. The periodicity of the plumed-growth lines is reflected in the shell structure of *Lithiotis*.

Specimens from Northern Italy show periodically prominent growth laminae in horizontal cross section (Chinzei, 1982), which are not seen in the Oregon specimens because of recrystallization. The outer shell of the attached valve in the Northern Italian specimens is made up of prismatic and interlayered nacreous aragonite (Chinzei, 1982). *Lithiotis* specimens from

the Robertson Formation have an outer shell of tough, dark grey, prismatic calcite which contrasts with the Italian specimens which have a soft outer shell that is chalky in appearance. This probably reflects differing diagenetic histories.

3. THE FREE VALVE

The free valve of *Lithiotis* is paper-thin in comparison to the attached valve. The attached valve which has an average thickness of 3 cm, whereas the free valve is only 1 to 2 mm thick. The free valve is nearly the same height and width as the attached valve, and covers the furrowed plate and open shell cavity on the cardinal face of the attached valve. Articulation between the free valve and the attached valve is usually difficult to study because the free valve is extremely fragile and is easily eroded. Horizontal cross-sections through *Lithiotis* occasionally show the thin free valve lying against the furrowed plate with less than 1 mm space between the two valves (Figure 6-3).

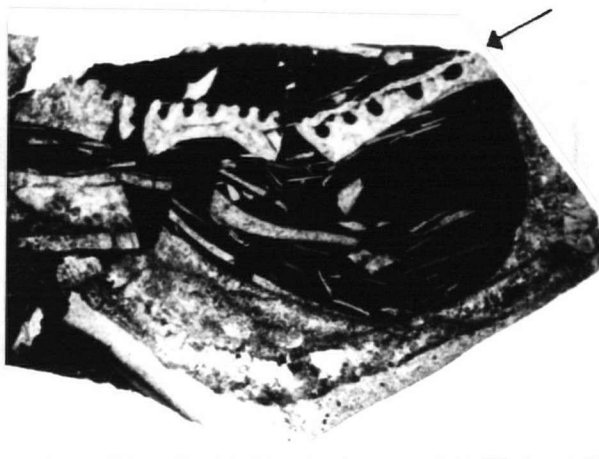


Figure 6-3: Thin section of crushed *Lithiotis* bivalve showing thin free valve lying against furrowed plate. Arrow indicates thin, free valve.

A crescent-shaped adductor muscle scar, 1 to 1.5 cm wide is present on the posterior side of the shell cavity on the attached valve in rare *Lithiotis* specimens from Northern Italy which are completely intact (Benini and Loriga, 1977). The adductor muscle presumably attached to the ventral end of the free valve. Chinzei (1982) has concluded that the free valve bent elastically away from the shell cavity to expose the bivalve soft parts. Several cross-sections from the Robertson Formation bioherms illustrate a more elaborate articulation between the two valves. The furrowed plate of the attached valve is inset approximately 2 mm from the margin of the plume-like areas on the attached valve. The free valve fits snugly into this inset area (Plate 2) and in the center of the furrowed plate what appears in cross-section to be a ball and socket joint connects the free valve to the attached valve (Plate 3, A and B). The furrowed plate is made up of a series of ridge-and-groove structures (Figure 6-7). The ridges have a furrow or open tube in the top of them which articulates with a corresponding round ridge on the free valve. The articulation is preserved only in the center of the furrowed plate; obviously the delicate structures are easily eroded. In all of the cross-sections examined, the free valve is close to the attached valve adjacent to the shell cavity (within 2 mm) and is farther away or absent, adjacent to the umbonal region (approximately 3 mm) (Figure 6-4). The free valve articulated with the attached valve at the ventral margin of the furrowed plate (Figure 6-1 and 6-4) and when open swung away from the shell cavity above the articulation point and toward the furrowed plate below. The free valve is only occasionally present in the umbonal region and was probably broken off in this area while the bivalve was still living. As the bivalve grew the free valve would serve no purpose in the umbonal region but the bivalve would be protected by the

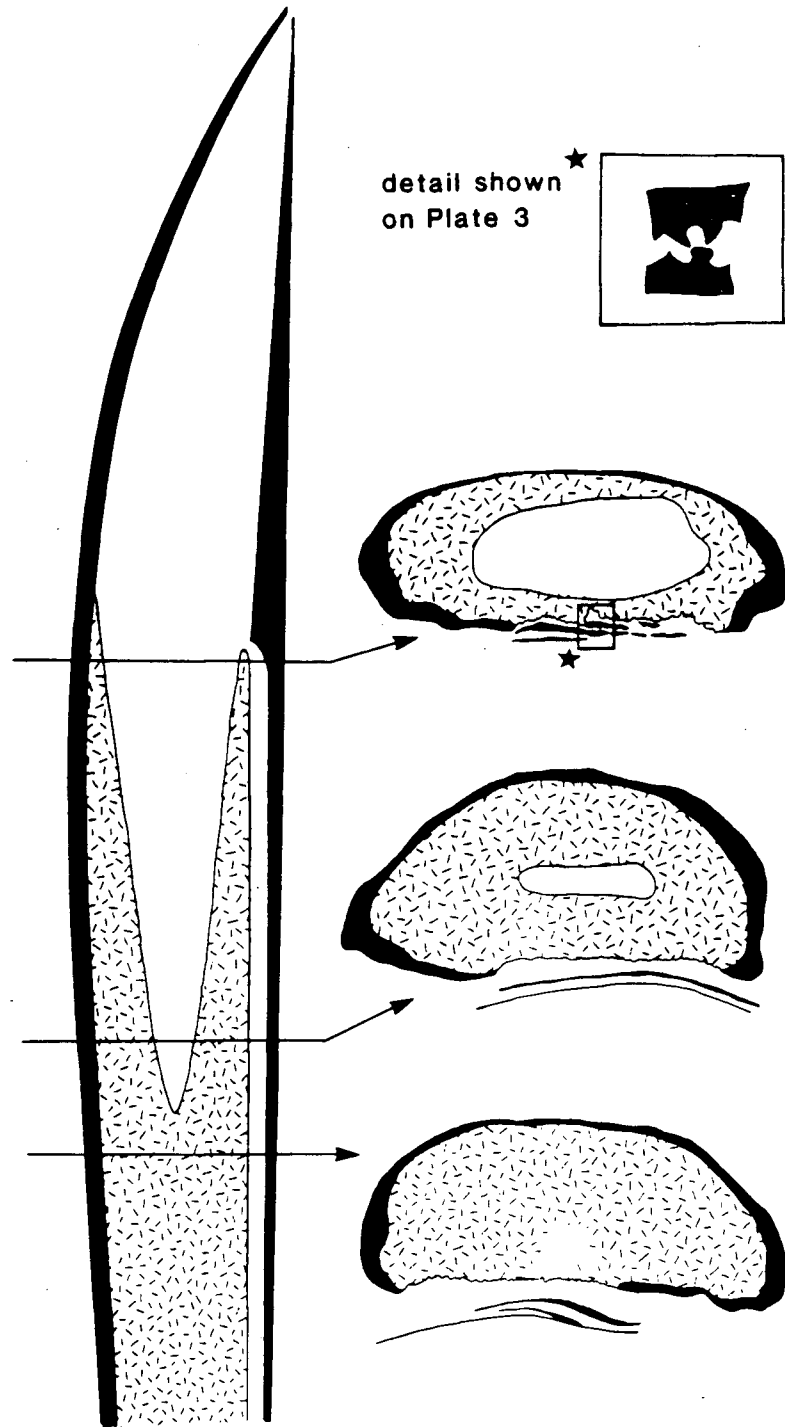


Figure 6-4: Horizontal cross-section of *Lithotis* which illustrates the position of the free valve (right) and the relative positions of the sections within the bivalve (left). (x 0.7) Specimen EB 2-9.

upper part of the free valve. In horizontal cross section the free valve is often split into several layers and fragments of the free valve on float specimens show distinct layers. In the Robertson Formation these layers are recrystallized and the inner shell structure is obscured. The free valve of better preserved *Lithiotis* specimens from Northern Italy is composed of alternating layers of prismatic and nacreous aragonite, interlayered with occasional granular and prismatic layers (Chinzei, 1982).

4. BODY CHAMBER

The body chamber of *Lithiotis* is in the ventral end of the attached valve (Figure 6-1). The body chamber has a circular cross-section near the base of the shell cavity and becomes more compressed ventrally (Figure 6-2). An internal buttress extends from the anterior side of the base of the body chamber to 2 cm past the ventral margin of the furrowed plate on the inside of the shell (Figure 6-1). In many specimens a secondary cone of the body chamber is located on the posterior side of the internal buttress (Figure 6-5). This secondary cone is found in specimens which have not been crowded or compressed by other bivalves, so is clearly not the result of stress on the growing bivalve. The secondary body chamber is not always present and therefore presumably did not serve a vital function or it is possible that it might have served as a brood pouch. Accessory cavities are sometimes present in hippuritid or rudist bivalves and Skelton (1976, p. 98) has suggested that their purpose might have been for incubation of eggs and larvae. A brood pouch is also an ideal site for the transfer of symbiotic algae from parent rudist to larvae (Cowen, 1983). Incubation is known in several oyster species although a few genera are known to be non-incubatory including *Crassostrea* (Stenzel, 1971), which is

closely related to *Konbostrea*, an oyster that closely resembles *Lithiotis*.

As *Lithiotis* grew vertically upwards the body chamber moved upwards and the umbonal region below the shell cavity became more elongate. The space below the body chamber was infilled with carbonate. In specimens from the Robertson Formation the space between the outer shell and below the shell cavity is composed of light grey, blocky calcite. The same space in *Lithiotis* specimens from Northern Italy consists of granular or sometimes prismatic calcite which shows remnant shell structure (Figure 6-5, around the perimeter of the body chambers). The calcite is believed to be recrystallized originally aragonitic shell material, quite similar to altered chalky deposits of oysters such as *Konbostrea* (Chinzei, 1982). Chalky deposits in oyster shells are patches of soft, porous shell material which are considered to be precipitated rapidly to fill and smoothen the irregular inner surface of the shell. An analogous function is assumed for the chalky deposits in *Lithiotis*. Longitudinal sections through *Lithiotis* specimens from Northern Italy exhibit a cone-in-cone internal structure in the infilling area below the body chamber (Benini and Loriga, 1977). A similar cone-in-cone structure can be faintly seen in longitudinal sections of a few *Lithiotis* bivalves from the Robertson Formation.

5. THE FURROWED PLATE

The cardinal face of the attached valve is characterized by the ridge-and-groove structure lying parallel to the long axis of the shell, which Benini and Loriga (1977) named the furrowed plate. The ridge-and-groove structure extends from grooves on either side of the umbo (Chinzei, 1982) to the ventral cardinal margin (Figure 6-1). The grooves form deeper pits at either end of the umbo, which is the only

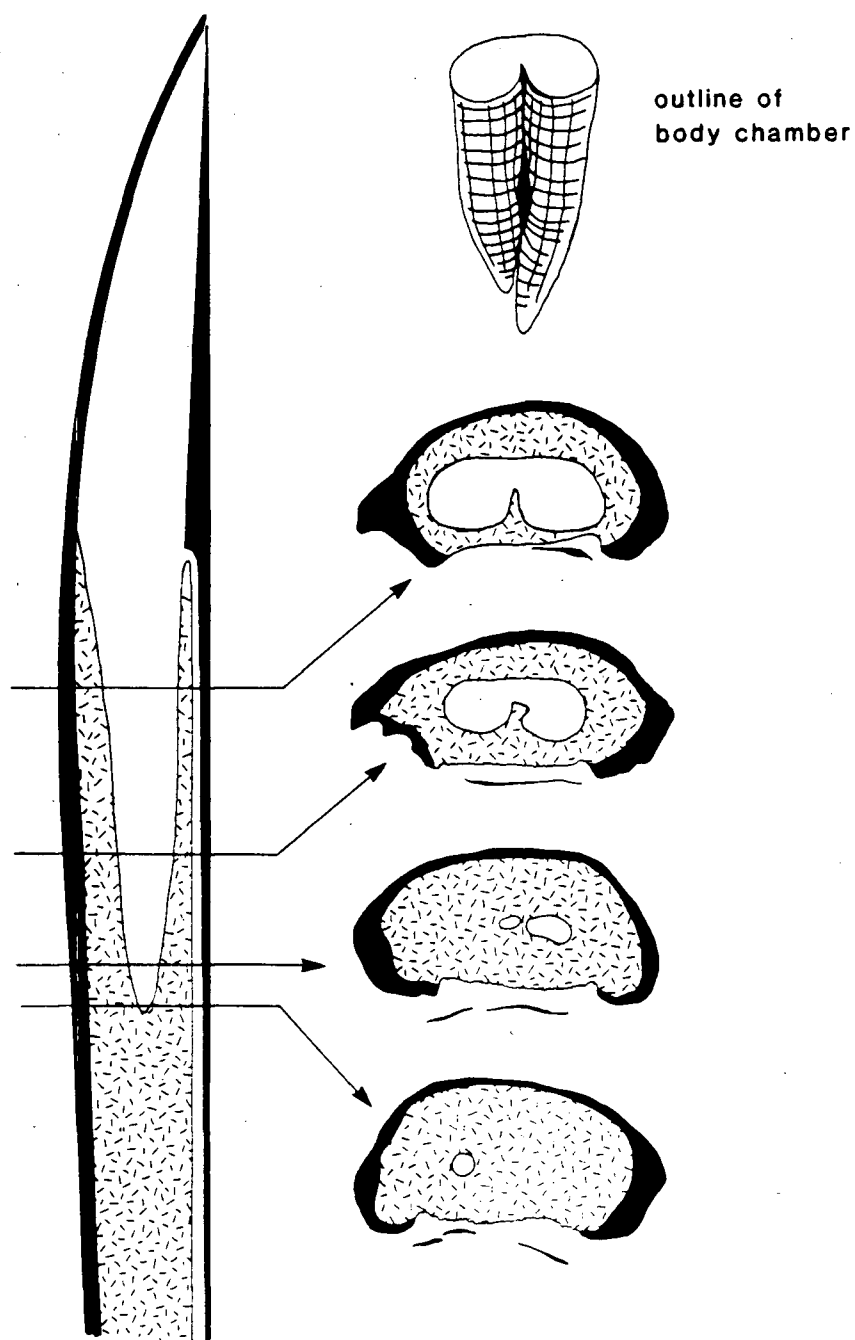


Figure 6-5: Horizontal cross-sectional view of *Lithiotis*, illustrating the shape of the body chamber (right) and the relative position of the sections within the bivalve (left). Specimen EB 2-10. Upper right sketch = shape of the body chamber below the ventral margin of the furrowed plate. (x 0.65)

indication of a possible ligament in *Lithiotis* (Chinzei, 1982). The ridge-and-groove structure consists of a series of ridges which are separated by deep grooves. Each ridge has an open furrow on the top, and can be referred to as an open tube (Figure 6-7). The ridges are up to 1 mm high and 1.5 to 2 mm wide and the grooves are 0.5 to 1 mm wide. The number of ridges varies from less than 5 to more than 20, depending on the width of the furrowed plate. As the furrowed plate gets wider with growth, the ridges branch, thicken and gradually develop a furrow on top, and the former furrow becomes a groove separating two new ridges (Chinzei, 1982).

In horizontal cross sections of well preserved *Lithiotis* bivalves from Northern Italy, a row of internal tubes is observed behind the ridge-and-groove structure of the furrowed plate (Benini and Loriga, 1977; Chinzei, 1982) (Figure 6-6). Individual tubes are approximately 0.2 to 0.5 mm in diameter and are composed of radially arranged aragonite, or calcite assumed to be recrystallized from aragonite. The tubes are hollow in the center and infilled with sparry calcite. They are continuous from the edge of the cardinal margin to the base of the umbo region. In longitudinal cross section the growth lines are bent at the position of the tube and form a chevron pattern (Figure 6-7).

The function of the ridge-and-groove structures and the internal tubes has to date been unknown. The horizontal cross-sections from *Lithiotis* bioherms in the Robertson Formation bring to light additional information about their purpose. Plate 3 shows that the ridge-and-groove structures articulated the two valves. Articulation was probably active only at the ventral margin of the furrowed plate, suggested by the increasing distance between the attached valve and free valve towards the umbonal

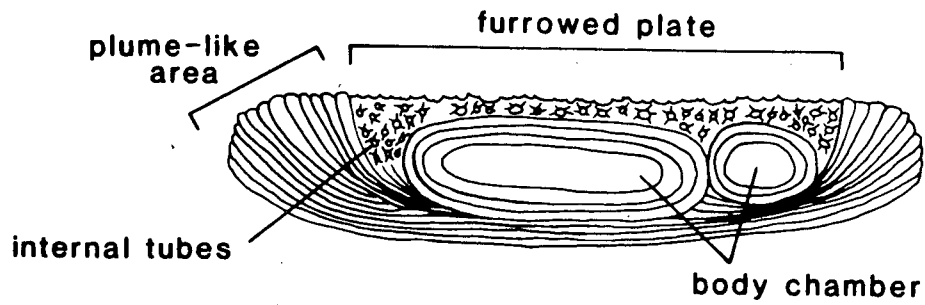


Figure 6-6: Horizontal cross-sectional view of the internal structure of *Lithotis*. Adapted from Benini and Loriga (1977).

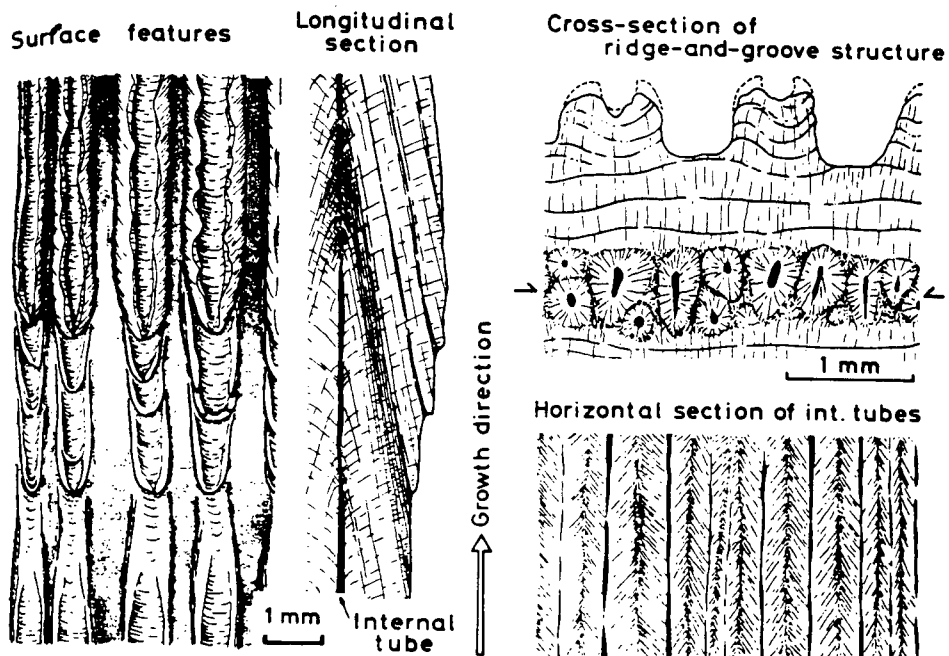


Figure 6-7: Ridge-and-groove structure of the furrowed plate and the internal tubes of *Lithotis*. Arrows in the cross-section (upper right) indicate the position of the horizontal section (lower right). From Chinzei (1982), p.185.

region. It is possible that the internal tubes contained ligaments which fastened to the free valve and aided articulation between the valves.

6. SUMMARY OF *LITHIOTIS* MORPHOLOGY

Lithiotis was a sessile bivalve that grew vertically in low diversity biostromes and bioherms in marginal marine shallow water environments. Juvenile bivalves cemented to hard surfaces, such as shells and probably cobbles, by the attached valve at the umbo. The attachment area is too small to have supported the mature bivalves which were anchored in the sand or mud substrate. The morphology of *Lithiotis* was well adapted for areas with a high rate of sedimentation. Growth lines on the bivalve indicate that accretion of new shell material took place only around the body chamber and that the bivalves grew vertically, keeping the soft parts well above the sediment surface. Upwards growth continued in mature bivalves without significant increase in the body size of the animal. The thin, free valve of *Lithiotis* articulated with the attached valve at the ventral margin of the furrowed plate, a necessary adaptation for living in an environment with a high sedimentation rate. If the two valves articulated at the base of the umbo, sediment particles would become jammed between the two valves.

B. TAXONOMIC AFFINITY OF *LITHIOTIS*

The bivalve *Lithiotis* was almost certainly a suspension feeding animal that trapped food in its gills. Longitudinal cross-sections through the center of *Lithiotis* reveal that the growth lines, which indicate the position of the outer shell, reach only one or two cm beyond the adductor muscle scar (Chinzei, 1982). There is not enough space in the shell cavity for

accommodating gills inside the shell and a fringe of conchiolin rich lamellae probably extended around the ventral margin, comparable to the marginal extensions in living oysters and pteriomorph bivalves (Chinzei, 1982).

Suspension feeding sessile bivalves are rare in areas of rapid sedimentation because attachment sites are scarce and the bivalves are in continuous danger of burial and suffocation by muddy particles clogging their gills. Epifaunal bivalve communities act as baffles, trapping suspended matter between their shells and protecting the trapped particles from subsequent removal by wave action. Sedimentation rates are actually higher within the communities than on barren muddy substrates (Chinzei, 1986). However, such areas are rich in suspended organic material and if the animals can tolerate the environment, food is plentiful. Several sessile bivalves have adapted to shallow water, marginal marine, soft bottom environments and, like *Lithiotis*, all of them have adopted strategies to maintain their body chamber well above the sediment water interface.

Species of the lower Cretaceous oyster, *Crassostrea* and the Miocene oyster, *Saccostrea* have adapted to sessile life on a soft bottom by adopting a "relay type" growth habit (Chinzei, Savazzi and Seilacher, 1982). Although the oyster shells are not markedly elongate, juveniles attach to adult shells of the same species, vertically building up the shell beds in order to remain above the sediment water interface. This strategy is also adopted with *Lithiotis*, juveniles are frequently found attached to the *in situ* mature bivalves.

Elongated species of *Saccostrea* and the rudist bivalves have adopted a "rudist type" morphology which enables the bivalves to live on soft bottoms (Chinzei, Savazzi and Seilacher, 1982). The attached valve is

elongate and the soft body migrates upward in the shell while the void space below is closed off by septa-like thin partitions. The functional ligament follows the upwards growth and the free valve remains small, acting as a lid or operculum. The Caprinid and Radiolitid rudists formed extensive reefs in the early Cretaceous in shallow marine, Tethyan realm environments similar to those inhabited by *Lithiotis*. The rudists grew vertically upright in low diversity communities which tended to be barren of encrusting organisms. In rudist reefs from the Cretaceous, shallow carbonate platform of Israel, echinoids, orbitolinids, fish remains and reptile bones have been found along with the dominant Radiolitid rudists; however, only nerineid gastropods are present in quantity (Scott, 1979). In early Cretaceous coral-algal-rudist reefs from southeastern Arizona, *Exogyra* and *Crassostrea* oysters along with the gastropod *Nerinea*, are common in the near-shore environments and Caprinid-algal reefs are developed within the lagoonal environment, away from the high energy shoaling area (Scott, 1979). The Caprinids are found in fan-like clusters which morphologically resemble coral heads and achieve stability by interlocking, crowding and mutual cementation of the bivalves, rather than attachment to a firm substrate (Bein, 1976).

The Cretaceous oyster, *Konbostrea* has adopted the same growth habit as *Lithiotis* which Chinzei, Savazzi and Seilacher (1982) refer to as the "*Lithiotis* type." *Konbostrea* has a similar dorsoventrally elongated shell that grows vertically upright, with the soft body restricted to the ventral end of the shell. The majority of specimens are 50 to 70 cm high, 4 to 5 cm long, and 2 to 3 cm thick and are found densely packed together (Chinzei, 1986). The space below the body chamber is infilled by porcellaneous carbonate, considered to have originally been very porous, chalky material

(Chinzei, 1986). The attached valve is thick and robust and the outer shell is made of foliated calcite with intervening porcellaneous lenses (Chinzei, 1986). The free valve is extremely thin and composed of calcite. The free valve covers the cardinal area and overlaps the attached valve by approximately 0.5 cm. An adductor muscle is found on the center of the attached valve and a small ligamental area is located adjacent to the umbo. An internal tube is present on the attached valve and is continuous from the body cavity to just behind the ligamental area (Figure 6-7). In some specimens the umbonal cavity is subdivided and there are tubes corresponding to the number of conical spaces. The ligamental area was utilized until the bivalve reached maturity, at which time the elasticity of the free valve is believed to have opened the shell (Chinzei, 1986). *Konbostrea* lived on a muddy bottom in intertidal or brackish water, anchored in the sediment in a vertical position. In Japan, *Konbostrea* oyster beds are found as lenses in sandy mudstone, underlain by sandstone with intercalated coal seams. The only other fossils found within the oyster beds are traces of boring sponges on well preserved shells (Chinzei, 1986).

Lithiotis is similar *Konbostrea* in morphology and environmental habitat, however several differences exist between the two bivalves. Well preserved *Lithiotis* specimens from Northern Italy contain prismatic and nacreous aragonite layers in the outer shell, which indicates that *Lithiotis* originally had an aragonite shell (Benini and Loriga, 1977; Chinzei, 1982). Oyster shells are commonly composed solely of calcite. The adductor muscle scar of *Lithiotis* is located on the posterior side of the shell cavity on the attached valve, which is analogous to the right valve of monomyarian oysters (Chinzei, 1982). Oysters attach to the substrate by their left valve and *Lithiotis* is attached by the right valve. For these

reasons *Lithiotis* has not been classified as an oyster. If the furrowed plate of *Lithiotis* is considered as a hinge plate or tooth structure this also separates *Lithiotis* from the oysters, as the ligament is the sole hinge structure in oysters. It is probable that the internal tube served a similar function in both *Lithiotis* and *Konbostrea*, although the purpose of the tube is not certain.

The bivalve *Cochlearites loppianus* (Tausch, 1890) is often associated with *Lithiotis* in outcrops throughout the Tethyan Ocean, and looks so similar to it that it has often been misidentified as *Lithiotis* in outcrop (Benini and Loriga, 1977). *Cochlearites* differs from *Lithiotis* in having a functional ligament present in its juvenile stages and no furrowed plate. *Cochlearites* is believed to open by the elasticity of its free valve and is attached by the left valve rather than the right (Chinzei, 1982). Like *Lithiotis*, it is composed of aragonite (Chinzei, 1982). *Cochlearites* is found in communities adjacent to *Lithiotis* communities and in the same environment, although the two are not found intermixed (Benini and Loriga, 1977).

PLATE 1: HORIZONTAL CROSS-SECTIONS OF *Lithiotis*

Photographed from acetate peels of slabbed biohermal limestone from the Robertson Formation, northeast of Cow Creek.

- A - Horizontal cross-section through the shell cavity area below the ventral margin of the furrowed plate. The free valve is separated from the attached valve. Specimen EB 1-1, magnification X 2.
- B - Cross-section through the upper shell cavity. The free valve is represented by a thin line and layering can be seen on the right hand side. Specimen EB 1-2, magnification X 4.
- C - Cross section through the umbonal region of *Lithiotis*. The free valve is absent. Specimen EB 2-7, magnification X 4.

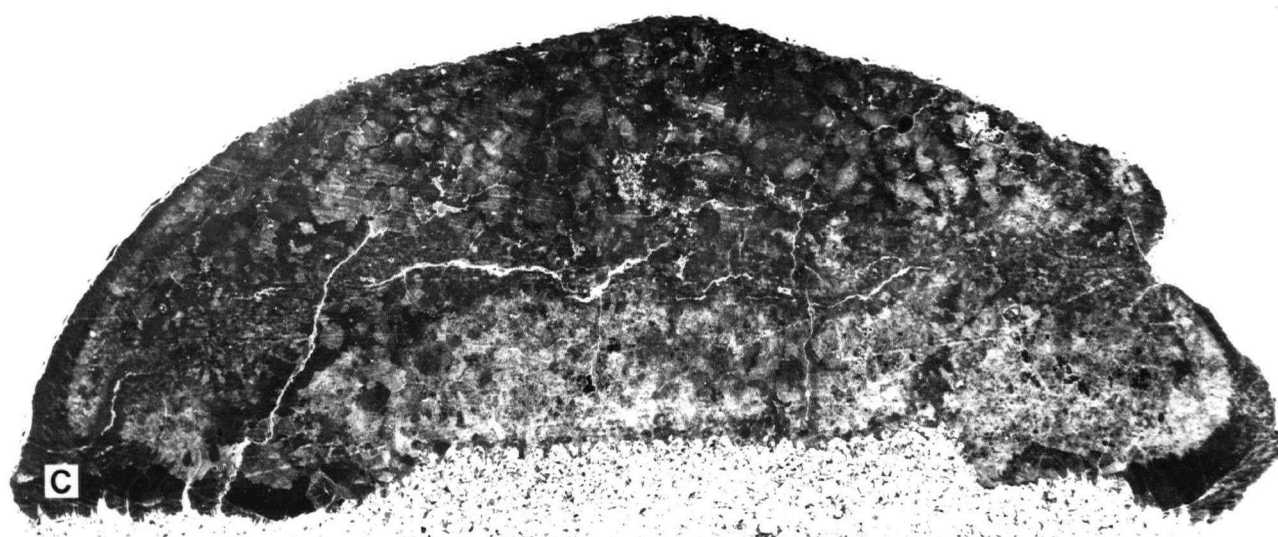


PLATE 2: HORIZONTAL CROSS-SECTIONS OF *Lithiotis*

Photographed from acetate peels of slabbed biohermal limestone from the Robertson Formation, northeast of Cow Creek.

- A1 - Cross-section showing the free valve within the indented furrowed plate area. Specimen EB 2-8, magnification X 1.6.
- A2 - Detail of the free valve showing layering within the valve. The free valve is snug against the attached valve, indicating a longitudinal position directly below the shell cavity. Specimen EB 2-8, magnification X 4.2.
- B - Cross-section of the same specimen as A1, further down in the umbonal region. Specimen EB 2-8, magnification X 1.6.
- C - Cross-section through *Lithiotis*. (Specimen has been crushed and distorted) Specimen EB 3-14, magnification X 3.2.

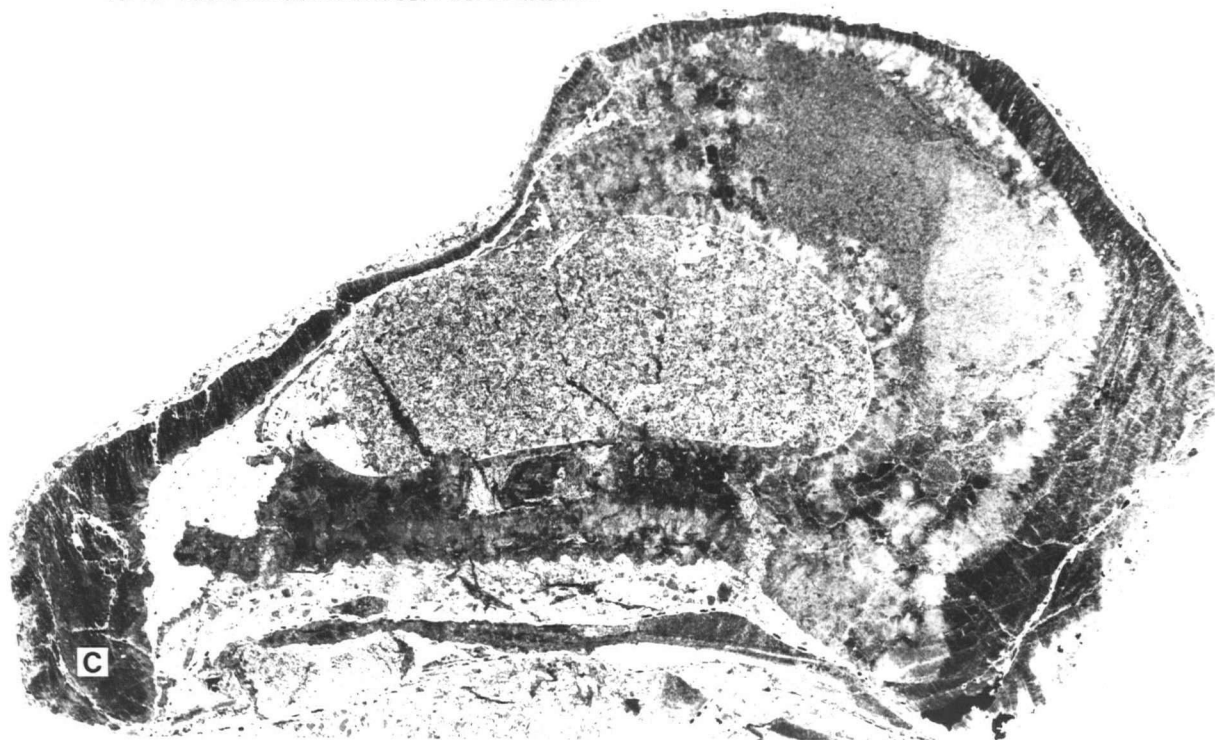
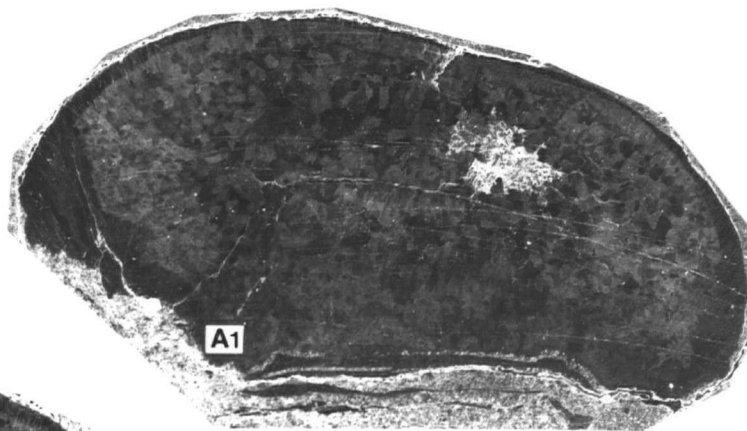


PLATE 3: HORIZONTAL CROSS-SECTIONS OF *Lithiotis*

Photographed from acetate peels of slabbed biohermal limestone from the Robertson Formation, northeast of Cow Creek.

- A1 -** Cross-section through *Lithiotis* near the ventral margin of the furrowed plate. Articulation between the valves is shown in **A2** and figured in **A3**. **A4** is an SEM photograph of the articulating ridge of the attached valve. Specimen EB 2-9, A1 magnification X 1.9, A2 magnification X 5.
- B1 -** Cross-section through *Lithiotis* showing indented furrowed plate area and remnant fragments of the free valve. Specimen EB 1-3, magnification X 2. **B2 -** Detail of remnant fragments of attached valve, magnification X 3.
- C1 -** Cross-section through *Lithiotis* near the ventral margin of the furrowed plate. Specimen EB 1-4, magnification X 2. **C2 -** Detail of the free valve, magnification X 6.

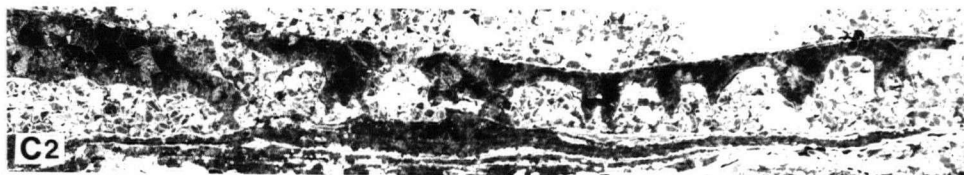
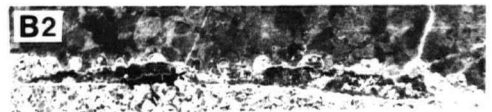
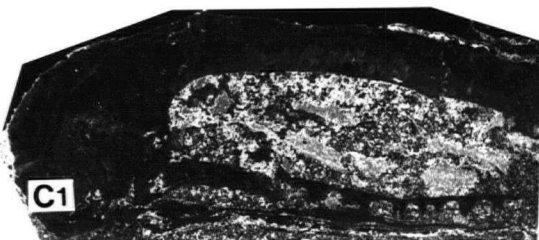
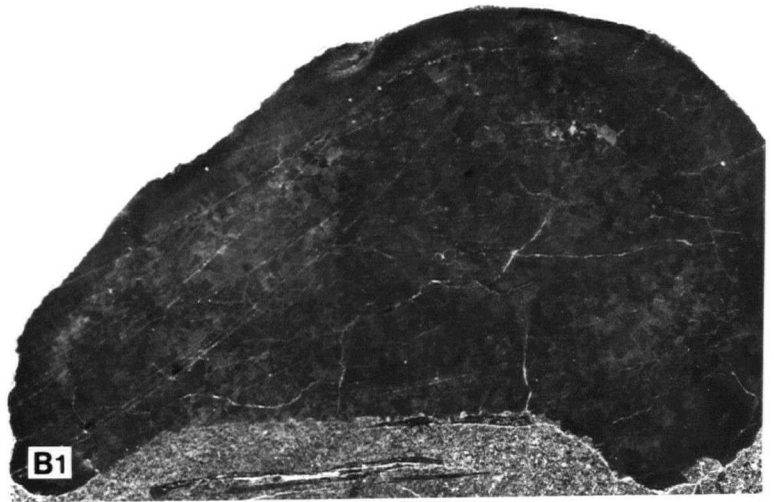
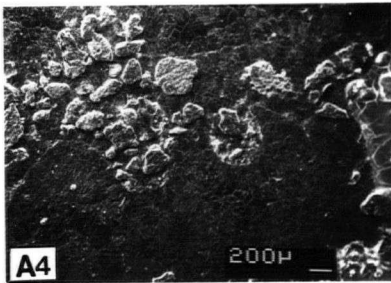
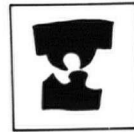
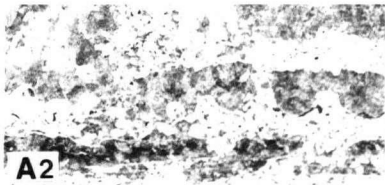


PLATE 4

Top Row:

Lithiotis float specimens from the Swamp Creek area (locality 2, Fig. 3-5) with thick, robust, strongly ribbed shells. Specimens 30-F 1, 2, 3, 4.

Bottom Row:

Lithiotis float specimens from the area north of Pine Creek, with relatively smooth outer shells. Specimens 7-12 1, 2.

PLATE 4

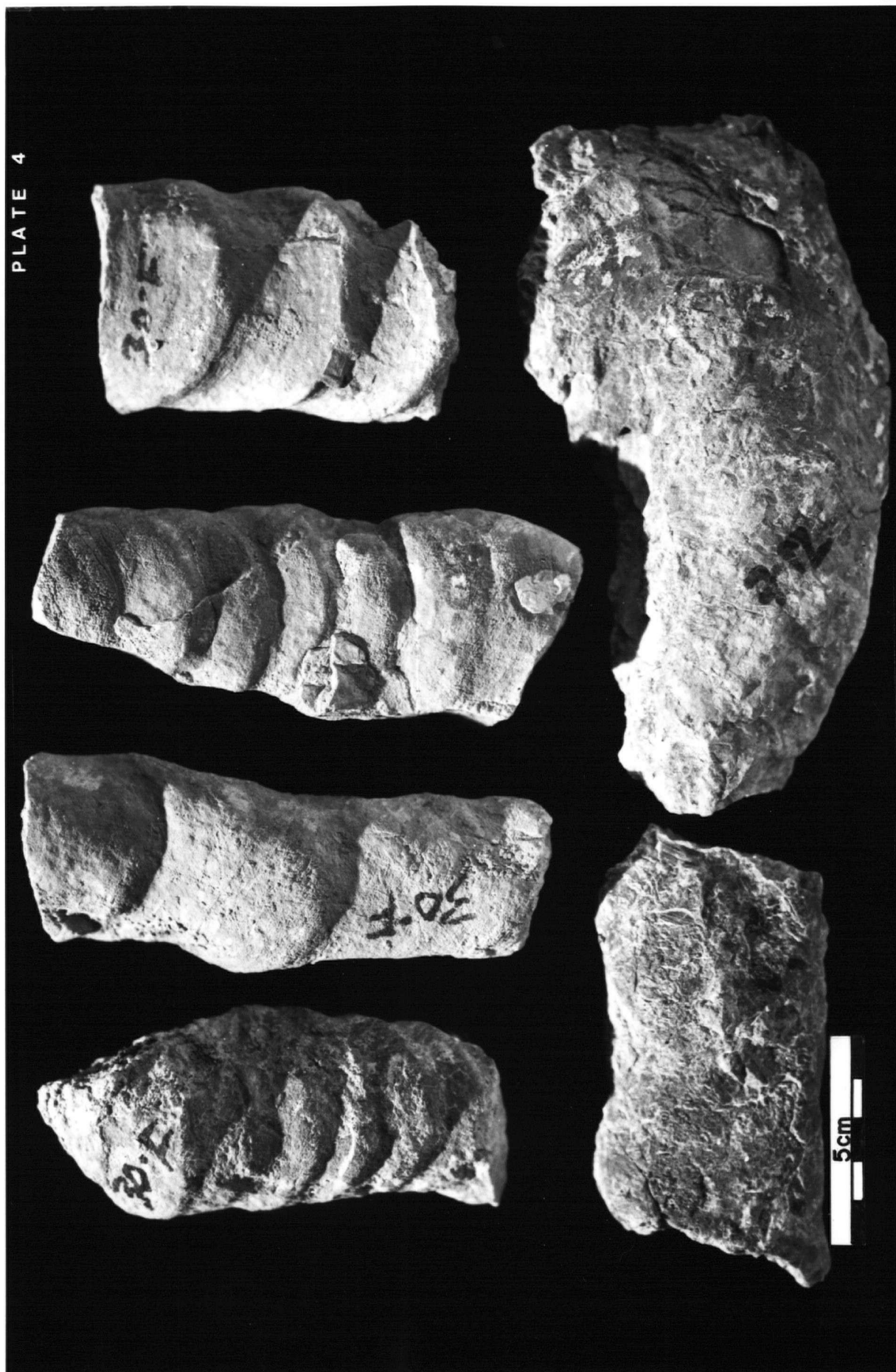


PLATE 5

A1, A2 and A3: *Lithiotis* float specimens from the area north of Pine Creek, exhibiting the furrowed plate and plume-like area on the cardinal face of the bivalve. Specimens F-6, 7, 8.

B1, B2 and B3: Juvenile *Lithiotis* bivalves. **B1** shows the bivalves ability to curve as it grew. **B2** shows a juvenile shell flaring rapidly from the umbo. **B3** shows two juvenile bivalves cemented onto mature bivalve. Specimens F-9, F-10 and 30-F 5.

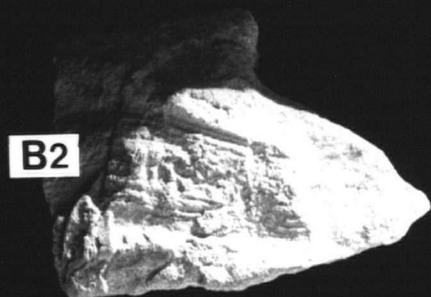
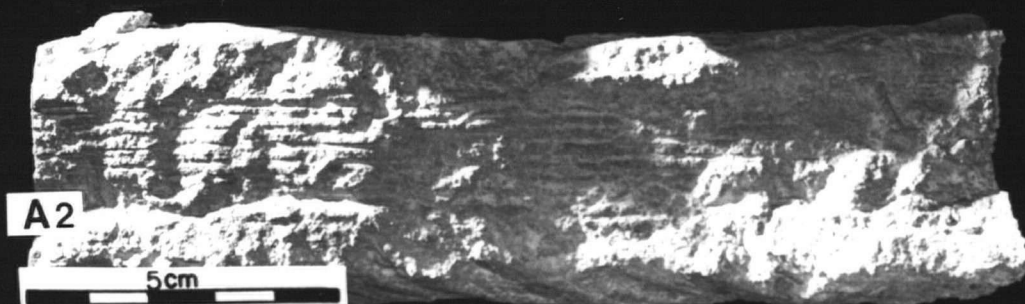
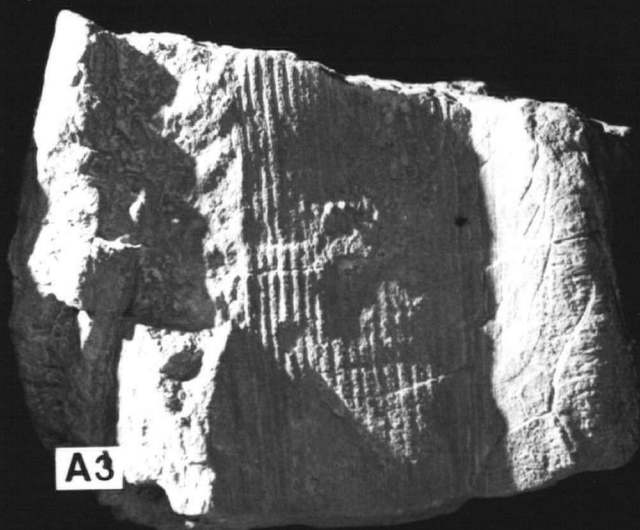


PLATE 6

A1: *Lithotis* bivalve with a strongly ribbed outer shell. Specimen 30-F 6.

A2: *Lithotis* bivalve with a flat outer shell. Specimen F-11.

PLATE 6

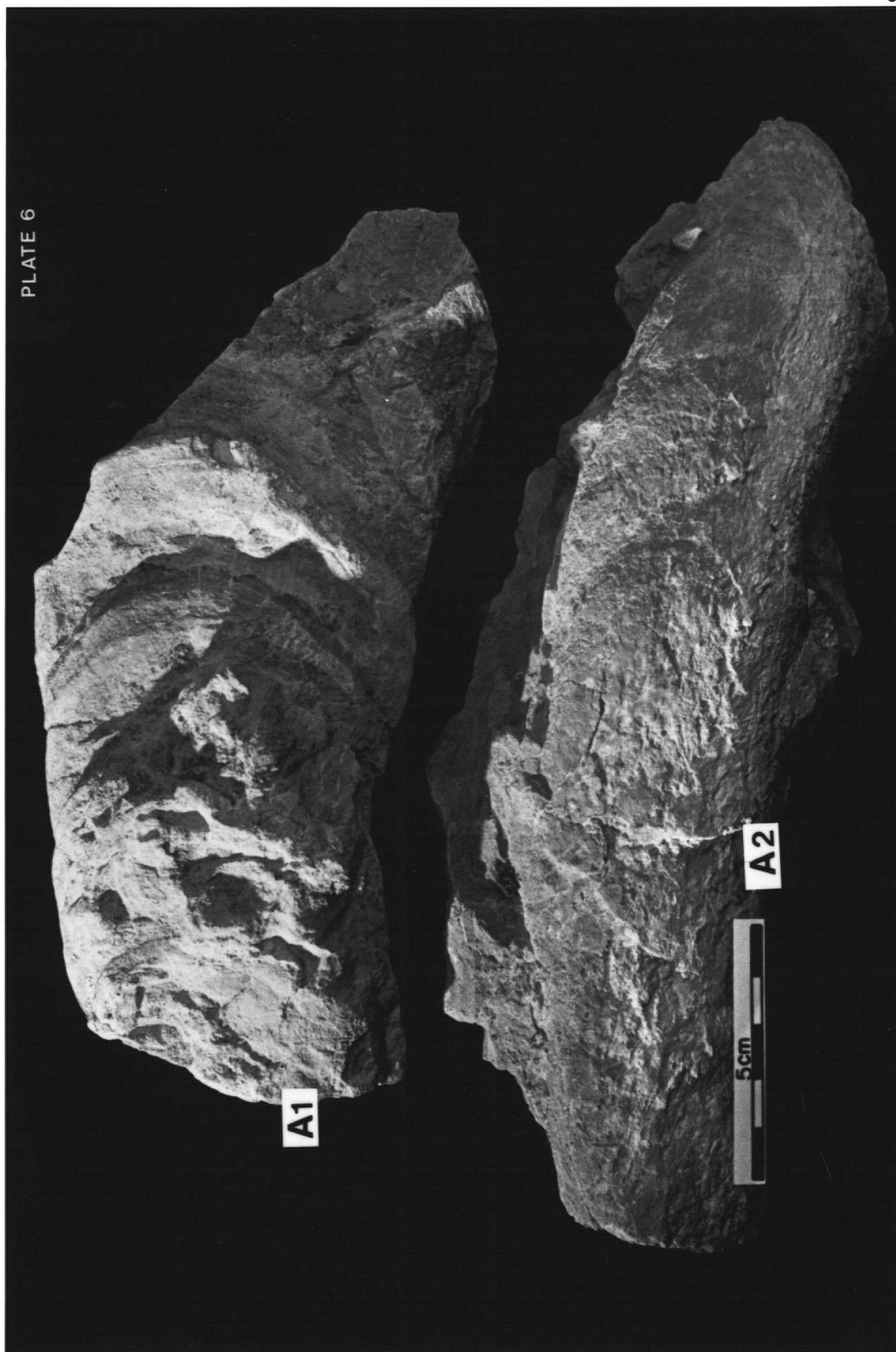


PLATE 7

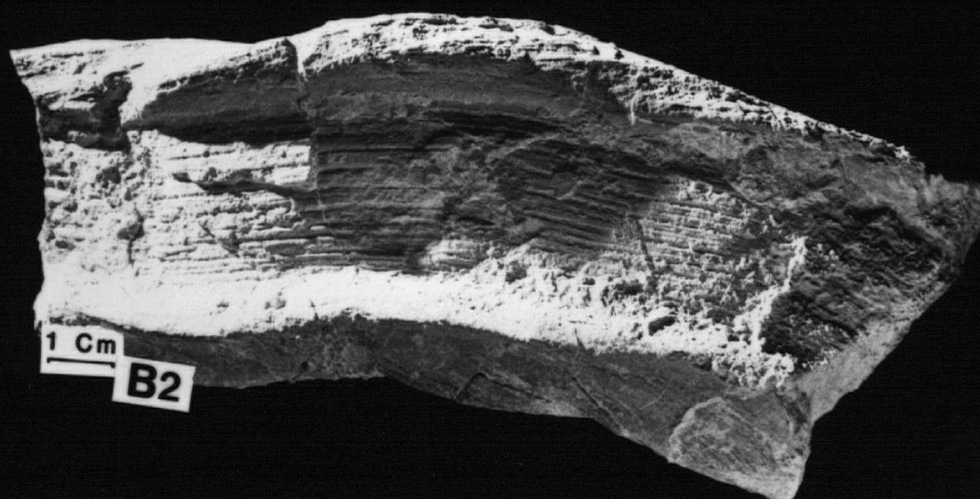
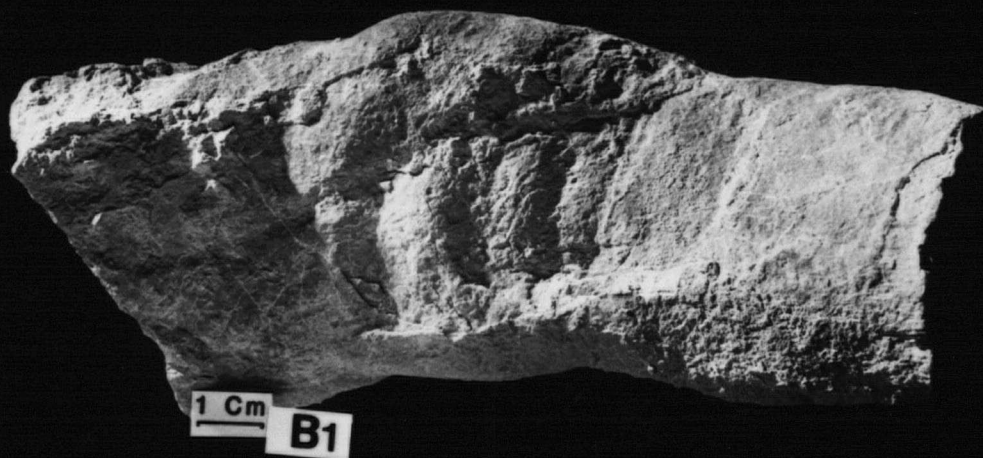
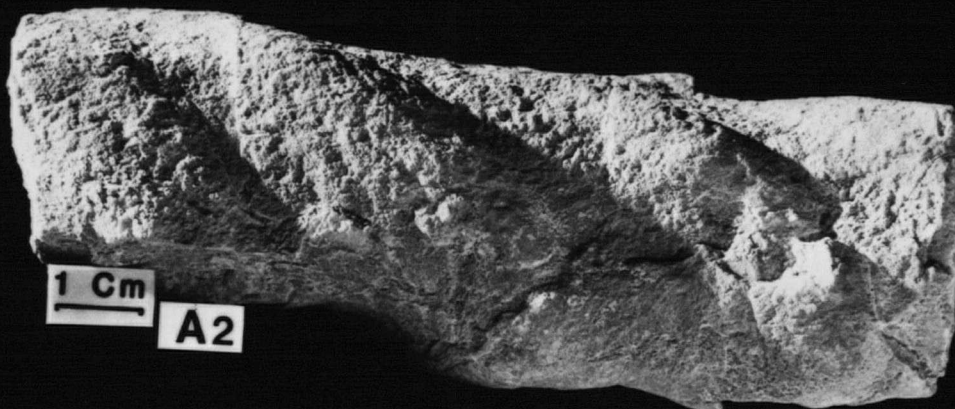
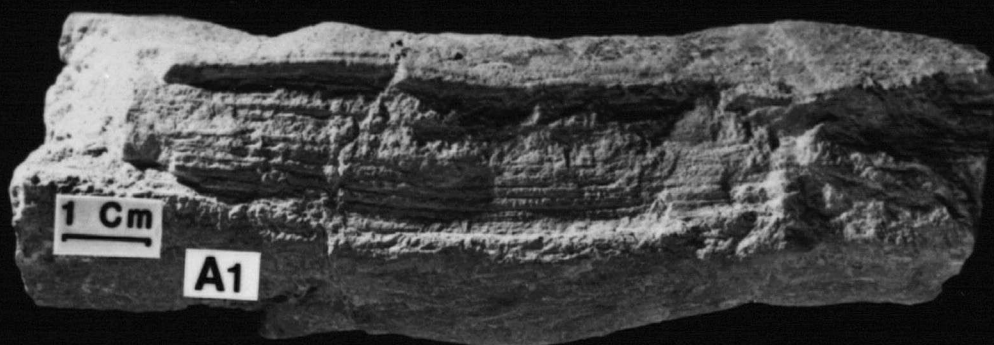
- A1:** Outer surface of *Lithotis* bivalve. Float specimen from the Swamp Creek area, Specimen 30-F 6.
- A2:** Cardinal face of *Lithotis* bivalve. Specimen 30-F 6.
- B1:** Outer surface of *Lithotis* bivalve. Float specimen from the area north of Pine Creek. Specimen F-12.
- B2:** Cardinal face of *Lithotis* bivalve. Note growth lines on plume-like area. Specimen F-12.

PLATE 7



PLATE 8

- A1:** Cardinal face of *Lithotis* bivalve. Float specimen from the Swamp Creek area, Specimen 30-F 7.
- A2:** Outer surface of *Lithotis* bivalve. Specimen 30-F 7.
- B1:** Outer surface of *Lithotis* bivalve. Float specimen from the area north of Pine Creek. Specimen F-14.
- B2:** Cardinal face of *Lithotis* bivalve. Specimen F-14.



VII. TAXONOMY OF LITHIOTIS

Lithiotis is included in the Class Bivalvia, Order Pterioida, Newell, 1965. The articulation of the furrowed plate, position of the adductor muscle scar and the aragonitic composition of the shell separates *Lithiotis* from the oysters. Striking similarities exist between *Lithiotis*, *Cochlearites* and *Konbostrea*. Although there is a wide gap in age between the lower Jurassic *Lithiotis* and *Cochlearites* and the lower Cretaceous *Konbostrea*, the three bivalves have a characteristic "*Lithiotis* type" growth pattern. *Lithiotis* is unique in its hinged furrowed plate and attachment by the right valve. *Cochlearites* and *Konbostrea* are more similar, both having functional ligaments in their juvenile stages and being attached by their left valves. If better preserved *Konbostrea* oysters were found with remnant aragonite within their shells, it would indicate a strong link between *Konbostrea* and *Cochlearites*. Benini and Loriga (1977) established the Suborder Lithiotina for *Lithiotis* and *Cochlearites*, although the two bivalves belong to different families. *Lithiotis* and *Cochlearites* are probably related to the Isognomonidae (Chinzei, 1982) or Bakevelliidae (Seilacher, 1984).

A. SYSTEMATIC DESCRIPTION

Class BIVALVIA Linnaeus, 1758

Order PTERIOIDA Newell, 1965

Suborder LITHIOTINA Benini and Loriga, 1977

Superfamily LITHIOTACEA Benini and Loriga, 1977

Family LITHIOTIDAE Reis, 1903

Genus LITHIOTIS Gumbel, 1871 ammend. Reis, 1903, ammend. Benini and

Loriga, 1977.

SYNONYMS

1930 *Plicatostylus* Lupher and Packard; p. 204, plate 2, fig. 1.

Type Species: *Lithiotis problematica* Gumbel, 1871, p. 48 - 51, fig. 13, 14.

A comprehensive description of the supra-generic taxonomy is included in the work of Benini and Loriga (1977).

LITHIOTIS PROBLEMATICA Gumbel, 1871

Fig. 6-1 - 6-6, tables 1 - 8

1871 *Lithiotis problematica* Gumbel; GUMBEL, p. 41, plate 2, fig. 13, 14.

1879 *Lithiotis problematica* Gumbel; DE ZIGNO, p. 129 - 135,
plate 1, fig. 2, 4, 5, 6.

1890 *Ostrea lithiotis* Gumbel; GUMBEL, p. 67, fig. 1.

1890 *Lithiotis ostreacina* Gumbel; GUMBEL, p. 67, fig. 1.

1890 *Trichites loppianus* Tausch; TAUSCH, p. 18 - 19, fig. 1.

1892 *Ostrea problematica* Gumbel; BOEHM, p. 71 - 73, plate 3, fig. 1 - 3.

1903 *Lithiotis problematica* Gumbel; REIS, plate 6, fig. 17 - 22.

1923 *Lithiotis* aff. *problematica* Krumbeck, p. 80 - 81, plate 176, fig. 9.

1923 *Lithiotis timorensis* Krumbeck, p. 80 - 81, plate 176, fig. 9.

1930 *Plicatostylus gregarius* Lupher and Packard, p. 204, plate 2, fig. 1.

1962 *Lithiotis problematica* Gumbel; DE CASTRO, p. 13 - 14,
plate 10, fig. 1 - 6.

Neotype: Benini and Loriga, 1977; Plate 1, fig. 2, collected by Gumbel,
1870, p. 67, fig. 1.

Type locality: Rotzo (Vicenza), Italy.

Type formation: Calcari grigi (Grey Limestone), Member of Rotzo,

Upper Pliensbachian to Toarcian.

Plastotype: Reis, 1903, plate 6, fig. 8, 9, 11, 14; plate 7, fig. 4, 6, 9a-9e;

Geologische Bundesanstalt, Vienna.

Description: Large; highly inequivalve; with robust, thick attached valve and thin, fragile free valve; dorso-ventrally elongated; circular to elliptical in cross-section, ventrally compressed; umbone very acute, curved in some specimens either to front or rear; prominent furrowed plate on cardinal face extends from umbo to margin of the shell cavity of the attached valve, made up of ridge-and-groove structure which articulates with corresponding ridges on free valve; plume-like areas of growth lines extend from either side of the furrowed plate on attached valve around the outside of the shell, are periodically prominent and can form distinct ridges; monomyarian; commonly with thin internal buttress in each valve passing from lower margin of shell cavity to below posterior margin of adductor muscle scar; ostracum formed of lamellar calcite together with prismatic calcite developed as intercalated layers or as masses of radially disposed crystals surrounding tubular vesicles.

General resemblance to *Cochlearites* and *Konbostrea* but attached by right valve, and lacks median groove for fibrous ligament.

Occurrence: *L. problematica* is reported from Pliensbachian and Toarcian rocks of the western continental margins of North and South America, Southern Europe, North Africa, the Middle East and as far east as Timor in Indonesia.

CONCLUSIONS

Lithiotis is an epifaunal, sessile, aberrant pelecypod found in the Upper Pliensbachian Robertson Formation in east central Oregon. *Lithiotis* bioherms are most extensive in the northeastern part of the Suplee-Izee area, suggesting a "semi-protected" environment in a sea transgressing across the Mowich Upwarp generally from the south and east. The bioherms are made up of three biofacies: (1) a Reef Flank Assemblage; (2) a Death Assemblage and (3) a Life Assemblage. The Life Assemblage represents the core of the reef and is comprised of *in situ* vertical *Lithiotis* bivalves. The Death Assemblage is made up of abundant bivalves lying parallel to bedding and often aligned by current action. The Reef Flank Assemblage is characterized by *Lithiotis* shelly debris, abundant *Nerinea* gastropods and terebratulid brachiopods. The reef diversity is extremely low, indicating that *Lithiotis* thrived in a restrictive environment that inhibited other reef organisms. The Robertson Formation bioherms are interpreted to have been deposited in a shallow water, nearshore, marginal marine, brackish or intertidal environment. *Lithiotis* is also found in Nevada in the Sunrise and Dunalp Formations in similar shallow water, marginal marine environments.

In Southern Europe, *Lithiotis* is found in the Calcari grigi Formation. In Italy the depositional environment of the *Lithiotis* bioherms in the Rotzo area has been interpreted as the shoaling edges of a lagoon, which is protected by a barrier bar. The bioherms are developed in restricted marginal marine conditions, marked by a significant decrease in foraminifera fauna.

Examination of specimens from the Robertson Formation has shown that the free valve of *Lithiotis* was articulated to the attached valve by a series of ridge-and-groove structures on the cardinal face of the attached

valve, at the top of the furrowed plate. The ability of the bivalve to move up in its shell adapted it for living in areas of rapid sedimentation, however as the bivalves were not continually buried with growth, this adaptation may well have been a response to competition for light. *Lithiotis* has a morphology similar to the Lower Jurassic bivalve *Cochlearites* and the Upper Cretaceous oyster, *Konbostrea*. The bivalves have been differentiated on the basis of the placement of the muscle scar in *Lithiotis* and the presence of aragonite in both *Lithiotis* and *Cochlearites*. Given that the muscle scars tend to be central on both bivalves and that aragonite is a relatively unstable mineral, it is reasonable to conclude that *Lithiotis*, *Cochlearites* and *Konbostrea* could be related bivalves.

The environment of *Lithiotis* is similar to that of many Caprinid and Radiolitid rudist reefs. The rudists are found in low diversity bioherms in lagoonal settings. However, rudists tend to thrive within the lagoon itself while oysters are found in the shoaling areas of the lagoons. *Lithiotis* is found in an inshore, marginal marine environment, which has a greater similarity to that of the oysters.

The worldwide paleogeographic distribution of *Lithiotis* reveals that *Lithiotis* migrated from a Pliensbachian endemic center in the East Pacific of North America and the Western Tethys Ocean, to South America and the Eastern Tethys, during the Toarcian. Since genetic continuity had to have been maintained between the disjunct Pliensbachian populations in the Western Tethys and East Pacific, migration must have occurred along the Hispanic Corridor during the Pliensbachian.

The presence of *Lithiotis* in Sonomia and its absence in the Canadian suspect terranes; Wrangellia, Quesnellia and Stikinia, indicates that the terranes have not been displaced or that *Lithiotis* is not a low latitude

indicator. The environmental constraints of *Lithiotis* suggests that the reason for its absence in the suspect terranes is lack of appropriate shallow, marginal marine facies. Offshore exploration in the Queen Charlotte Islands could reveal *Lithiotis* within Wrangellia.

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