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Paleoenvironmental and paleoclimatic significance of freshwater bivalves in the Upper Jurassic Morrison Formation, Western Interior, USA

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Abstract

Freshwater unionid bivalves are spatially and temporally distributed throughout the Morrison depositional basin, and locally dominate the biomass of many aquatic depositional environments. Two bivalve assemblages are identified. Within-channel assemblages are death assemblages that have been transported and may represent mixed assemblages from multiple communities. These assemblages are predominately disarticulated, in current stable orientations, and composed of higher stream velocity ecophenotypes (medium size, lanceolate form, and very thick shells). The floodplain-pond assemblages are disturbed neighborhood assemblages in the mudstones inhabited during life. The bivalves are predominately articulated, variable in size, and composed of low stream velocity ecophenotypes (large maximum sizes, ovate shell shapes, and thinner shells).

The glochidial parasitic larval stage of unionid bivalves provides an effective means of dispersing species throughout drainage basins. These larvae attach to fish and are carried through the fluvial drainage where the larvae detach and establish new bivalve communities. Preliminary paleobiogeographic analyses are drawn at the genus level because of the need to reevaluate bivalve species of the Morrison. *Unio* spp. and *Vetulonaia* spp. are widespread throughout the Morrison depositional basin, but *Hadrodon* spp. are restricted to the eastern portion of the Colorado Plateau during Salt Wash Member deposition, suggesting that Salt Wash drainage was isolated from other contemporaneous regions of the basin.

Bivalves from five localities in the Morrison Formation were thin-sectioned for growth band analysis. Growth bands of modern unionid bivalves are produced when the valves are forced to close. Closure can produce annual growth bands in response to seasonal variation, such as temperature-induced hibernation, or precipitation-induced aestivation or turbidity. Pseudoannual growth bands form from non-cyclical events such as predation attacks or isolated storm turbidity. *Vetulonaia* sp. from the Tidwell Member, Green River, Utah, and from Tidwell-equivalent beds at Como Bluff, Wyoming, exhibits continuous growth with no annual banding, suggesting that seasonality of climate and discharge did not vary appreciable during the year. *Hadrodon* sp. from the Salt Wash Member in Colorado National Monument, Colorado, exhibits annual banding with subequal light and dark bands indicating seasonal cyclicity. *Vetulonaia* sp. from the Cleveland-Lloyd locality, Utah, exhibits complex banding that indicates a combination of annual and pseudoannual bands. This suggests seasonal cyclicity and intermittent periods of environmental stress (predation, storm-produced turbidity and/or volcanic ash falls). Specimens of *Vetulonaia* sp. from Dinosaur National Monument, Utah, are replaced by chert with faint ghosts of bands that are too poorly preserved for environmental interpretations. Preliminary growth band studies suggest a change from a uniform optimum habitat in the Tidwell Member to strongly developed annual growth banding in the Salt Wash Member, suggesting cyclic annual precipitation, and

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finally to irregular banding produced by a complex interaction of weakly developed annual growth bands and pseudoannual bands in the Brushy Basin Member.

Keywords: Morrison Formation; Bivalve; Mollusc; Ultrastructure; Growth bands

1. Introduction

Freshwater bivalves locally dominate the biomass of meandering fluvial and marginal lacustrine depositional environments. The high density of bivalve resting traces at several localities of the Morrison Formation demonstrates that unionid bivalves were dominant members of these Late Jurassic aquatic communities. Bivalve fossils are geographically and stratigraphically distributed throughout the Morrison depositional basin (Evanoff et al., 1998), again attesting to their important role within the aquatic ecosystems of this Late Jurassic basin (Figs. 1 and 2). Three types of analyses are applied to the bivalve paleofauna in order to interpret aspects of the Morrison Formation paleoecosystems. Paleoecological analysis is used to constrain the biotic and abiotic parameters of the depositional paleoenvironments of the bivalve localities. The paleobiogeographic distributions of unionid bivalve species can be used to identify dispersal pathways, which can be used to infer fluvial drainage patterns within the Morrison depositional basin. Finally, cyclic growth banding patterns are examined as a paleoclimatic signal preserved within Late Jurassic unionid shells. Together these three analyses provide information on the Morrison paleoecosystem at a range of temporal and spatial scales.

2. Paleoecologic analysis and refinement of depositional environment interpretations

A wide range of depositional environments have been recognized in the Morrison depositional basin, including fluvial, lake margin, lacustrine, floodplains, coal swamps, and eolian (Peterson, 1972; Peterson and Turner-Peterson, 1987; other papers in this volume). Fossil molluscs have been reported from many aquatic depositional environments of the Morrison (summarized in Evanoff et al., 1998). Dunagan (1998, 1999) and Dunagan and Turner (this volume) have examined the Morrison lacustrine carbonate fauna and flora from east-central Colorado and parts of the Colorado Plateau. Freshwater bivalve assemblages have been analyzed to identify ecological associations that can be used to refine interpretations of depositional environments. The relationship of an individual species to its environment is constrained by the application of taxonomic uniformitarianism (Dodd and Stanton, 1981) through analogy with modern descendants. This analysis uses the ecologic tolerances of extant descendants as a guide to the paleoecologic tolerances of extinct species, but must be evaluated for shifting ecologic tolerances through geologic time within the taxonomic group.

Unionids are taxonomically conservative, making them excellent tools for paleoecologic interpretations by analogy with their modern counterparts. Assemblages of molluscs and co-occurring taxa such as vertebrates, ostracodes, and trace fossils were taphonomically analyzed to identify ant mixing of fossils from disparate ecologic communities that were brought together before burial. The goal of the taphonomic analysis is to interpret the history of assemblages and to distinguish ecological associations of taxa. Then, the depositional environment can be further constrained by the ecologic associations of molluscs and co-occurring taxa. The specific conditions of the depositional environment are restricted to the range of overlapping tolerances of individual taxa that comprise the association. This approach has generated refined interpretations of the Late Triassic Chinle Formation mollusc assemblages (Good et al., 1986; Parrish and Good, 1986; Good, 1989, 1993a,b; Dubiel et al., 1991), and Paleogene mollusc faunas of the Western Interior (Hanley, 1976; Good, 1986, 1987).

The paleoecological tolerances for Morrison bivalves are drawn from the ecological tolerances of modern unionid bivalves. The tolerances of modern

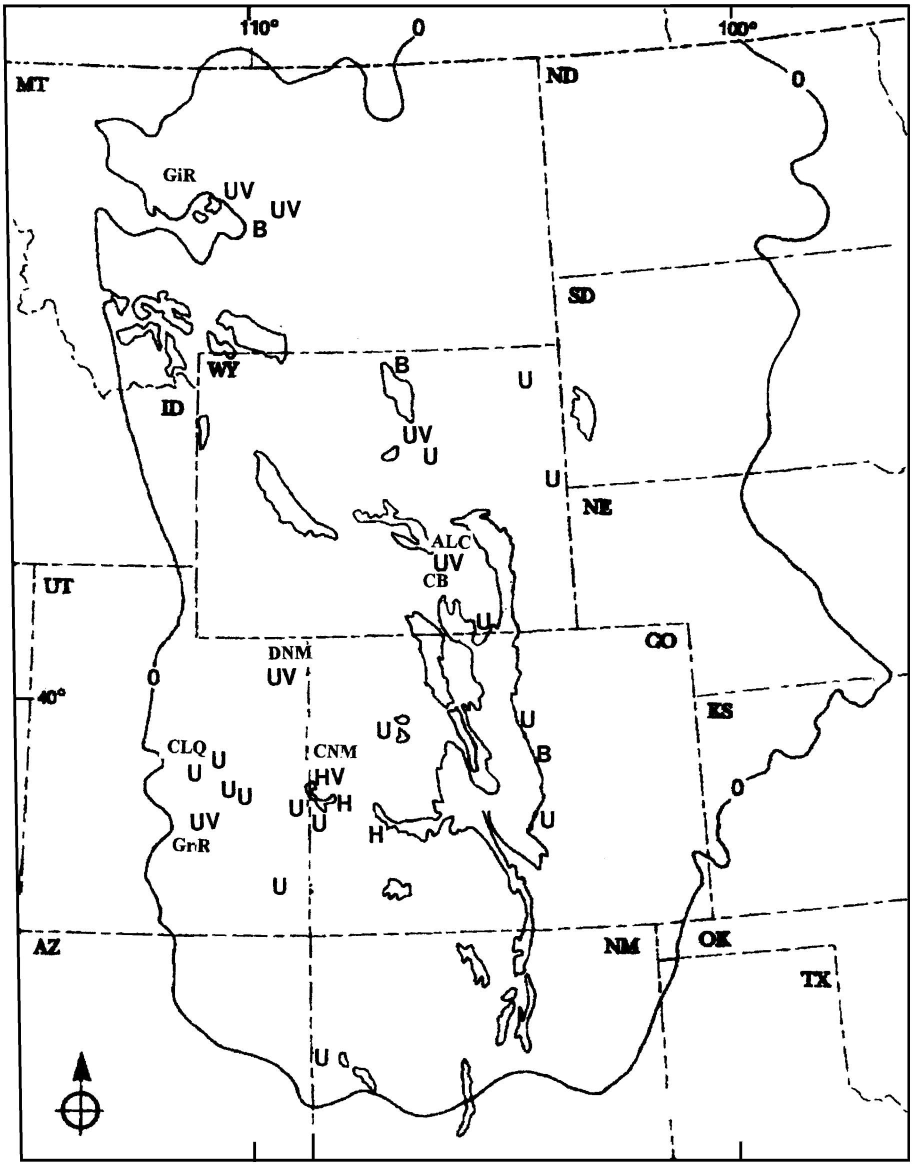

Fig. 1. Distribution of unionid bivalve localities in the Morrison Formation. "H" indicates occurrences of the genus *Hadrodon* (three localities in west central Colorado). "U" indicates occurrences of the genus *Unio*, which is the most widely distributed genus occurring throughout the entire basin. "V" indicates occurrences of the genus *Vetulonaia*, which is also widely distributed. "B" indicates localities where genus identification information was unavailable or indeterminable due to poor preservation. The heavy "0" line represents the edge of the Morrison rocks and the areas enclosed by thin lines represent the edges of modern outcrops of crystalline Precambrian rocks in Laramide uplifts. Specific locality information is available in Evanoff et al. (1998). Bivalve locations reported in this paper are indicated by the following abbreviations: GiR: Gibson Reservoir, Montana; ALC: Alcova, Wyoming; CB: Como Bluff, Wyoming; DNM: Dinosaur National Monument, Utah; CLQ: Cleveland-Lloyd Quarry, Utah; GrR: South of Green River, Utah; CNM: Colorado National Monument, Colorado. Details of each locality are described in Appendix A.

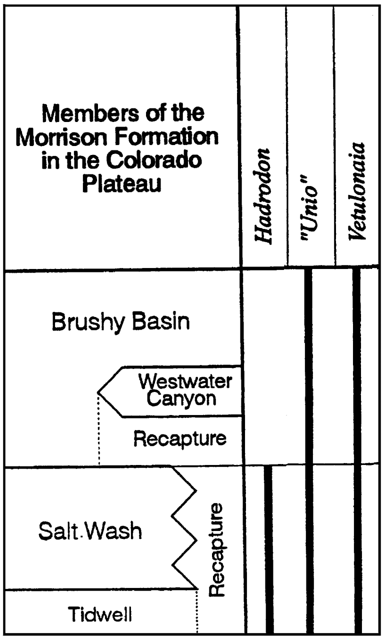

Fig. 2. Distribution of bivalve genera in the members of the Morrison Formation on the Colorado Plateau. The members are arranged in relative stratigraphic position and have no thickness or absolute time significance. Modified from Evanoff et al. (1998).

unionids define habitats where unionids are able to thrive in abundances similar to those observed in Morrison unionid localities. Those tolerances are summarized in Table 1. Unionids are noted for their ecophenotypic plasticity (shell form is modified to adapt to a particular habitat). Shell obesity (measured as shell convexity/length, see Fig. 3a) is positively correlated with increasing energy of the fluvial system and inversely correlated to flow velocity because individuals with less obese shells are able to burrow more quickly and prevent potential entrainment in the flow during fluvial bed scouring). The size of shells (shell length) is positively correlated with energy of the fluvial system and the degree of protection from currents afforded by the benthic habitats of lacustrine systems. Shell height is negatively correlated with flow velocity, with greatest heights of shell developed in large sluggish fluvial systems and protected lacus-

Table 1
Optimal unionid ecological habitat

Abiotic ecological requirements
• Clean water (high turbidity damages gills)
• Well oxygenated water (lentic or wave/current-mixed lotic habitat)
• pH slightly greater than 7
• Lime-rich water
• Shallow water (less than 7 m)
• Perennial aquatic habitat
• At least seasonally warm
• Stable substrate
Biotic ecological requirements
• Abundant plankton (filter feeders)
• Fish (and rarely amphibian) hosts for parasitic glochidial larvae
• Modern unionid predators: raccoons (minor), humans (archeologically speaking)
• Potential Jurassic unionid predators: lungfish (shell-crushing toothplate)

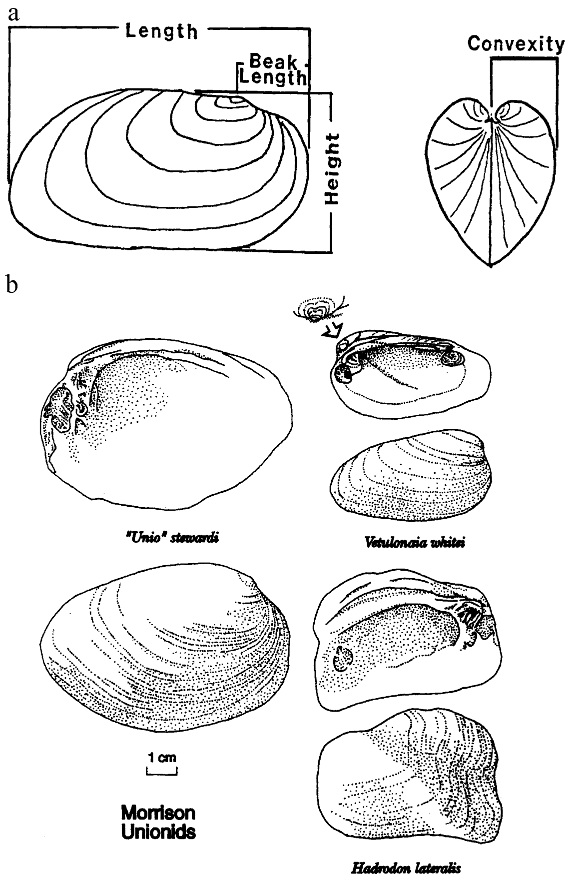

Fig. 3. (a) Morphometric definitions of shell parameters of unionid bivalves. (b) Illustrations of representative species of the unionid genera in the Morrison Formation. The illustrations of *Hadrodon lateralis* and *Unio stewardi* are after Yen (1952; Plate 5, Fig. 2c and d plate 3, Fig. 3d and e). Figure from Evanoff et al. (1998).

trine environments. Shell thickness generally increases as the water velocity of the habitat increases, such that fluvial unionids have thicker shells than lacustrine individuals (Ball, 1922; Eager, 1948; Tevesz and Carter, 1980a; Burkey, 1983). These parameters were used to identify three ecophenotypic subpopulations within species of Chinle unionids: fast velocity fluvial, slow velocity fluvial, and lacustrine (Good, 1993a). Similar analyses have been conducted on the Morrison unionid species. The general shell forms of the three genera that occur in the Morrison Formation are illustrated in Fig. 3.

An analysis of the relationships of the molluscs and other biota of the Morrison aquatic communities (paleosynecological analyses) indicates a relatively short food chain. The lack of significant predators in combination with their "reclusive" infaunal lifestyle has been a successful niche for the Unionidae, as indicated by the high diversity, wide distribution, and abundance of modern unionids. The principal biotic ecological innovation for this success is the glochidial parasitic larvae, which provides a dispersal mechanism for distributing these bivalves upstream. Trophic conditions are of greater significance in controlling modern freshwater bivalve distributions than physical, chemical, or substrate conditions of the niche (Green, 1972). Unionid bivalves are filter feeders, with the filtration rates controlled by both the rate of cilia beating (rate of water transport) and by the angle of cilia beat (affecting gill porosity). Gill sieves are generally fine in bivalves, retaining most material in the 1–200-μm size range. Unionids decrease or cease filtration when particle concentration within the water column is high (turbid), in order to protect the delicate gill structures (Burkey, 1983).

Appendix A summarizes the taphonomic observations and paleoecologic interpretations for each of the eight Morrison bivalve localities analyzed in this study. Two depositional environments of unionid occurrences have been identified: bivalve assemblages preserved within fluvial channels, and bivalve assemblages preserved within floodplain ponds.

3. Bivalve assemblages preserved within channels

Localities 1, 2 (Dinosaur National Monument, Utah; Brushy Basin Member).

Taphonomic analysis has been conducted on the bivalve assemblage of the Dinosaur Quarry sandstone bed (Localities 1 and 2). The bivalves represent a death assemblage of disarticulated unionid shells (Good and Kozlowski, 1995). The shells occur in current stable orientations (Fig. 4), occasionally with imbricated stacking, in troughs of mid-channel bars within the thalweg of the channel. The shells are well sorted by size; however, fragmentation and abrasion are minor. These features indicate a transported assemblage but one that has not been transported very far from the original life habitat of the bivalves (probably less than a few kilometers). The shell ecophenotype indicates that the unionids inhabited a small, higher velocity fluvial system. The abundance of the specimens suggests that a nearby upstream optimum habitat for unionid bivalves provided shells from the dead and decayed members of the population. Only a few articulated specimens have been found, and they are generally not in life position, suggesting they were transported, buried, and unable to reestablish life functions. The predominantly disarticulated valves require days to weeks of post-death decay of the ligament to disjoin the valves, suggesting that the fauna represents a transported death assemblage. The shells are replaced by silica. Insect trace-fossil marks on the dinosaur bones in the quarry bed at Dinosaur National Monument and elsewhere indicate subaerial exposure of the bones (Hasiotis et al., 1999), which occurred in the thalweg of the same fluvial channels as the bivalves. The optimum habitat for

Fig. 4. An unionid assemblage preserved in dipping beds on south side of Split Mountain anticline, approximately 1 km east of the Dinosaur National Monument quarry building, Utah.

unionids requires perennial aquatic habitats, suggesting a possible conflict in the paleoenvironmental interpretations. The nearby upstream perennial habitat required for the abundant bivalves contrasts with the evidence for the subaerial exposure of the streambed required to account for the exposure of the bones to boring by beetles (Hasiotis, this volume). A possible explanation for the death assemblage, which includes bivalves and dinosaurs, is that the stream that deposited the quarry sandstone bed went dry during a severe drought such as that reported for the Marsh-Felch Quarry by Evanoff and Carpenter (1998). The bivalves represent individuals of approximately 5–10 years of age by comparison to comparable-sized, similar morphotypes from the Chinle Formation that exhibit annual growth bands. This indicates development of a large unionid colony within a perennial, fast flowing stream. Dead shells from this colony were transported downstream as part of the bedload, and became part of the deposit when the fluvial system dried up.

4. Bivalve assemblages preserved within floodplain ponds

Localities 3 (Cleveland-Lloyd Quarry, Utah, Brushy Basin Member), 4 (Green River Utah, Tidwell Member), 5 (Como Bluff, Wyoming, Tidwell Member equivalent), 6 (Alcova, Wyoming, Brushy Basin Member equivalent), and 8 (Colorado National Monument, Colorado, Salt Wash Member).

This assemblage is preserved in two forms: (1) as fossil shells within mudstones and (2) in the base of sandstone beds as resting trace fossil casts that fill bivalve shell molds in the top of the underlying mudstone beds. These fossil shell assemblages are well preserved and occur in a dark-greenish-gray to gray massive mudstone. The functional morphology of these bivalves indicates lentic aquatic conditions as evidenced by their thin-shelled, large and obese shell form (Fig. 3). These faunas are interpreted as disturbed neighborhood assemblages meaning that they are preserved in sediments that they inhabited during life, but are out of life position. Biostratinomic features that indicate a disturbed neighborhood assemblage are the wide range of specimen sizes, excellent preservation (due to lack of transport), and high proportion of articulated specimens. All of these features suggest that this bivalve assemblage is an ecological association.

The Cleveland-Lloyd and Alcova bivalves inhabited the mudstone facies of a floodplain pond but are preserved as remarkable resting traces at the base of sandstone beds (Figs. 5 and 6). The bivalves resting traces are interpreted to represent a single contemporaneous community of bivalves. The bivalves were entrained and removed during the initial stage of a crevasse splay flooding event, leaving molds in the mud pond floor (indentions). A later stage of the crevasse splay flood event deposited sandstone into the molds, forming the resting traces. The bivalve localities (Locality 6) at Alcova, Wyoming, include six stacked beds of bivalve resting traces indicating re-

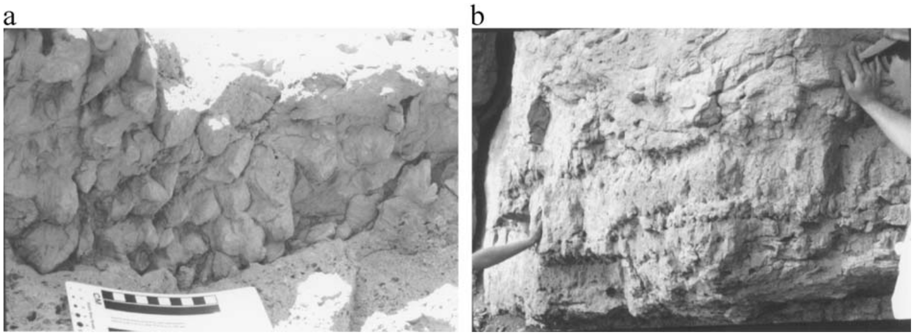

Fig. 5. (a) Bottom surface of a sandstone bed covered by resting traces of unionid bivalves and demonstrating the high density of bivalves in a floodplain pond at Alcova, Wyoming. (b) Outcrop view of the Alcova unionid trace fossil locality showing three stacked horizons of unionid resting traces. (a) Was taken just beneath the hand at the left side of this photo.

Fig. 6. Unionid resting traces preserved on the bottom of an overturned large float block at the Cleveland-Lloyd Quarry, Utah.

peated crevasse splay avulsions into the pond. These remarkable localities provide evidence of the high abundance and concentration of the bivalve individuals in the floodplain pond communities.

Bivalve fragments occur in the floodplain pond carbonate (lacustrine limestones) facies. However, these specimens are too fragmented to be used in this study. See Dunagan (1998, 1999) and Dunagan and Turner (this volume) and this volume for more information on the biota of the lacustrine limestones.

5. Paleobiogeographic distribution of unionid bivalves as evidence of fluvial confluence patterns

The bivalve fauna of the Morrison Formation (Table 2) consists of 17 species (Hanley et al., 1986; Evanoff et al., 1998). See Table 2 for the faunal list of bivalve species of the Morrison Formation. The earliest publications on the Morrison molluscs were published over 100 years ago (White, 1878, 1886, 1905), but research on this fauna has been sporadic and primarily concerned with taxonomies (Logan, 1900; Branson, 1935, 1964; Holt, 1942). The last major publication on Morrison molluscs was by Yen (1952). The taxonomy of all mollusc groups of the Morrison is in need of revision, but despite the problems with the taxonomy, some interesting paleogeographic and paleoenvironmental interpretations can be drawn.

Paleobiogeography of Morrison unionid faunas can be drawn from bivalve distributions and used to interpret histories of drainage interconnections. Unionid bivalves are efficiently dispersed within a drainage basin by the glochidial parasitic larvae that attaches to fish (Kat, 1984). Partial faunas of unionaceans may be transferred between drainage basins during stream capture events in the headland regions (Van der Schalie, 1944). Modern unionid faunas of Atlantic coastal plain rivers indicate "island biogeography" concepts can effectively explain the observed distributions of modern unionid species (Sepkoski and Rex, 1974). Application of such paleobiogeographic analyses to fossil unionid bivalves indicated that no barriers to dispersal existed between the Late Triassic basins of the American Southwest, with through-flowing drainage from the Dockum basin into the Chinle basin (Good, 1992, 1993a). With further work, unionid paleobiogeographic distribution patterns within the Morrison depositional basin may provide evidence of fluvial confluence patterns that functioned as unionid dispersal pathways or of barriers within the basin. More detailed fluvial confluence pattern interpretations for the Morrison depositional basin are not possible until the taxonomy of previous collections are verified and the stratigraphic position of each locality is constrained. At the present time, preliminary paleobiogeographic interpretations of stream confluences can only be drawn on the basis of distributions at the genus level.

Table 2
Bivalve species list for the Morrison Formation

Class Bivalvia
Subclass Lamellibranchia
Order Schizodonta
Family Unionidae
Genus *Hadrodon* Yen
Hadrodon jurassicus Yen
Hadrodon lateralis Yen
Hadrodon trigonus Yen
Genus *Unio* Philippson
Unio baileyi Logan
Unio felchi White
Unio iroides White
Unio knighti Logan
Unio lapilloides White
Unio macropisthus White
Unio mammillaris Yen
Unio nucalis Meek and Hayden
Unio stewardi White
Unio toxonotus White
Genus *Vetulonaia* Branson
Vetulonaia faberi Holt
Vetulonaia mayoworthensis Branson
Vetulonaia whitei Branson

Unio and *Vetulonaia* spp. bivalves are widely distributed geographically and stratigraphically throughout the Morrison depositional basin (Fig. 1). Where present, they are usually abundant. *Hadrodon* spp. are geographically and stratigraphically restricted, occurring only in the Salt Wash Member in the east-central part of the Colorado Plateau region (Fig. 1). *Hadrodon* spp. have also been reported from the underlying Wanakah Formation in the same regions of the Colorado Plateau (Good and Ridgeley, 1989). Summary information of previously published Morrison mollusc occurrences is presented in Evanoff et al. (1998).

6. Unionid growth band evidence for paleoclimate seasonality

Growth bands in freshwater bivalve shells provide evidence for seasonality in molluscan aquatic habitats. Microgrowth increments are produced by changes in the ratio of calcium carbonate to organic matter within the shell. During optimal environmental conditions, bivalves actively pump water from the overlying water column. Respiration is aerobic, and inorganic shell material, calcium carbonate, is deposited. When environmental conditions deteriorate, the valves close, isolating the bivalve from the surrounding environment until conditions improve. Respiration proceeds along anaerobic pathways, and organic-acid waste products accumulate within the closed shells where they are neutralized by the dissolution of calcium carbonate in the shell. This dissolution produces a layer of insoluble organic residue on the inner shell surface. When the bivalve resumes active pumping with the improvement of environmental conditions, deposition of calcium carbonate shell material resumes, preserving the organic layer as a record of the time of shell closure (Lutz and Rhoads, 1980).

Growth banding in freshwater bivalves has been attributed to annual-scale climatic seasonal cycles, called annual bands; and random events, called pseudoannual bands (Coker et al., 1922; Tevesz and Carter, 1980b). Annual bands feature thick, dark-colored, slower growth increments separated by thick, light-colored normal growth increments. Annual bands are produced in temperate climates by hibernation, resulting in sustained valve closure during the winter season (Coker et al., 1922; Negus, 1966). In tropical climates annual growth bands may be produced either by aestivation during dry season loss of habitat due to desiccation of lacustrine or fluvial environments (McMichael, 1952), or by prolonged growth interruptions due to high turbidity during storms typical of monsoonal climate regimes (Tevesz and Carter, 1980a). Pseudoannual bands are relatively thin, incompletely developed around the entire shell perimeter, variable in color and texture, and lack regular spacing or periodicity (Stansberry, 1961; Tevesz and Carter, 1980b). Pseudoannual bands are produced by an event that forces the bivalve to suspend pumping and isolate itself from the overlying water column by closing its valves, such as attempted predation or turbidity produced by isolated storms. Pseudoannual dark increments are much thinner than annual dark increments due to the shorter duration of pseudoannual events. Growth bands are studied by microscopic examination of thin sections of shells or by examination of external shell surfaces.

Bivalves shells from five localities in the Morrison Formation were thin-sectioned for growth band analysis (Fig. 1). Preliminary results of this study were presented in Shultz et al. (1997). Three specimens from each of the localities were thin-sectioned, photographed and analyzed. The following interpretations are drawn from these five localities, but more work is needed to verify the pattern of changing growth banding and possible causal climate change described below.

Bivalves from the Tidwell Member (Green River, Utah) and the Tidwell Member equivalent (Como Bluff) both exhibited continuous growth with an absence of layering with the shells (Fig. 7a and b). The absence of layering indicates a continuously favorable habitat for filter feeding, suggesting a n environment characterized by uniform temperature, a stable water table and precipitation. Because the Tidwell was deposited in close association with marginal marine deposits of the Windy Hill Member, and also contains some marine beds, a stable water table is to be expected.

Bivalve shells from the Salt Wash Member (Colorado National Monument, Colorado) exhibited strongly developed annual growth bands (Fig. 7c). This indicates strong cyclicity in annual precipitation. Temperature cyclicity can be eliminated from consideration due to the low paleo-latitudinal position of the locality.

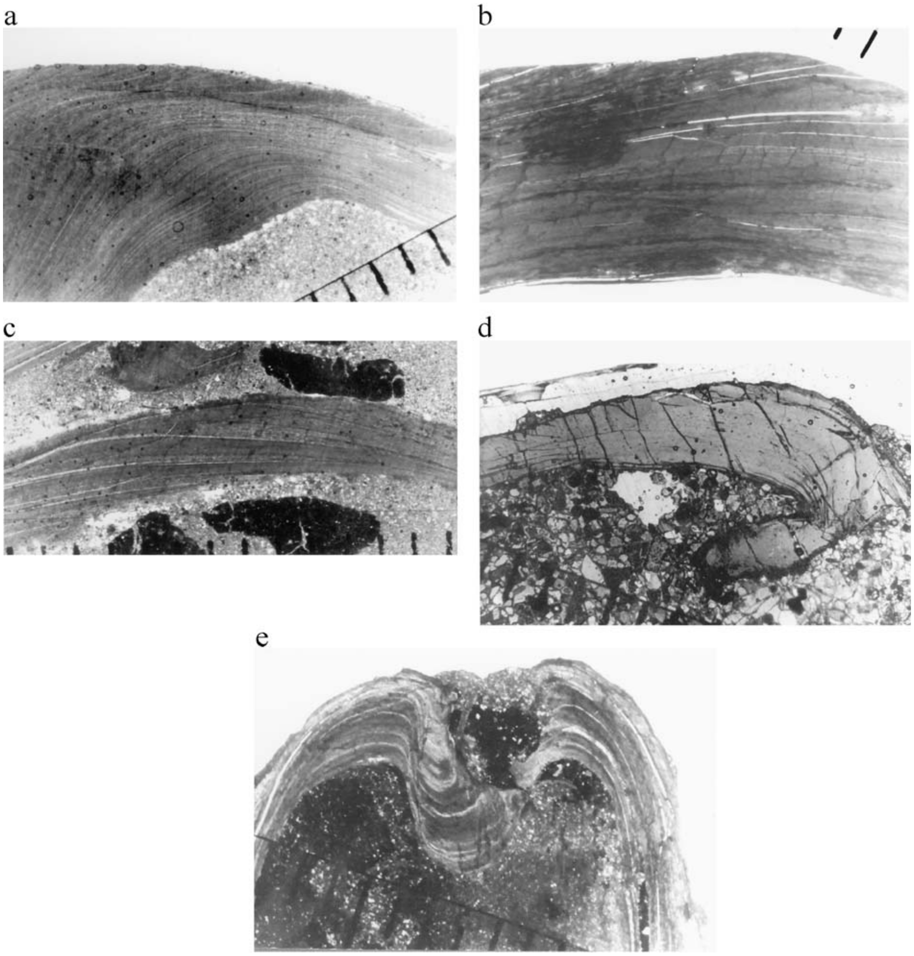

Fig. 7. (a) Thin section of a *Vetulonaia* sp. shell from the Tidwell Member of the Morrison Formation south of Green River, Utah. It exhibits massive ultrastructure indicating the absence of seasonality. Scale bar in 1-mm increments. (b) Thin section of a *Vetulonaia* sp. shell from the Tidwell Member equivalent, Como Bluff, Wyoming. The ultrastructure is massive, indicating the absence of seasonality. Scale bar in 1-mm increments. (c) Thin section of a *Hadrodon* sp. shell from the Salt Wash Member, Colorado National Monument, Colorado, exhibiting annual banding. Scale bar in 1-mm increments. (d) Thin section of a *Vetulonaia* sp. shell from the Brushy Basin Member, Dinosaur National Monument. The shell has been replaced by microcrystalline quartz (chert), but does preserve faint ghosts of ultrastructure. Scale bar in 1-mm increments. (e) Thin section of an articulated *Vetulonaia* sp. shell from the Cleveland-Lloyd Quarry, Utah. This specimen is from the Brushy Basin Member and exhibits complex banding produced by a combination of annual and pseudoannual growth increments. Scale bar in 1-mm increments.

Bivalves from the Brushy Basin Member were examined from Dinosaur National Monument, Utah, and from the Cleveland-Lloyd Quarry, Utah. The Dinosaur National Monument specimens were silicified, and the diagenetic replacement destroyed the ultrastructure (Fig. 7d), which precluded the study of these specimens. The Cleveland-Lloyd Quarry specimens exhibited an irregular banding pattern (Fig. 7e). This pattern indicates a combination of annual and pseudoannual growth bands. The annual bands in the Brushy Basin Member at the Cleveland-Lloyd locality are not as strongly developed as the annual bands of the shells from the Salt Wash Member locality at the Colorado National Monument. This suggests that the annual precipitation cyclicity may have decreased in strength. The pseudoannual banding could be produced by isolated storm events producing increased runoff and turbidity. Another possible cause could be volcanic ashfalls producing periods of higher turbidity. The smectitic composition of the Brushy Basin Member has considerable volcanic ash input into the Morrison depositional basin (Peterson, 1972; Peterson and Turner-Peterson, 1987; Turner and Fishman, 1991).

The shell growth band patterns suggest that changes in the annual precipitation regime occurred over the stratigraphic range of the Morrison Formation. This interpretation is preliminary because it is only based on five localities, and needs to be investigated further. Tidwell Member unionid growth bands indicate uniform precipitation or uniform water table. Salt Wash Member unionids indicate strong seasonality of precipitation. Brushy Basin Member unionid growth bands suggest seasonality of precipitation, but less pronounced seasonal fluctuations than are indicated in the Salt Wash Member. All five localities studied occurred in floodplain pond depositional environments. Unionid shells from localities deposited in channel environments were replaced by silica which obliterated the original ultrastructure, and therefore precluded environmental interpretations.

7. Summary

Study of the widespread and abundant bivalve faunas of the Morrison Formation has provided new paleoecologic and paleoclimatic interpretations that have enhanced understanding of the paleogeography and paleoenvironments of this large depositional basin. Bivalves assemblages are preserved within fluvial channels and in floodplain ponds. The within-channel shell assemblages are transported and potentially ecologically mixed assemblages. The floodplain pond occurrences are disturbed neighborhood assemblages that represent ecological associations of bivalves that lived and died together. The floodplain pond assemblages have resting trace fossil occurrences that attest to the high abundance of bivalves in this habitat.

The unique dispersal mechanism employed by unionacean bivalves permits documentation of paleodrainage confluence patterns, which will enhance understanding of the paleogeography of the Morrison depositional basin. Interpretations can follow after taxonomic reexamination of the Morrison Formation bivalve fauna has been completed. Interpretations thus far are drawn at the genus level and for the Salt Wash Member show that the species of *Hadrodon* indicate a fluvial drainage basin that restricted this genus to the eastern Colorado Plateau region. The wide distribution of unionids throughout the depositional basin of the Morrison Formation indicates that fish must have been an important component of the Morrison ecosystem in order to provide the dispersal mechanism for the unionids (Kirkland, 1998).

This study concludes that a variety of shell ultrastructure patterns is preserved in the Morrison Formation. The absence of annual bands from the Green River and Como Bluff localities, which are in the lower part of the formation, suggests the absence of seasonality in the climate at the time of shell formation. The Cleveland-Lloyd Quarry and Colorado National Monument specimens exhibit growth bands that suggest seasonality during deposition of the Salt Wash and Brushy Basin Members. Preliminary growth band studies suggest a change from a uniform optimum habitat in the Tidwell Member, to strongly developed annual growth banding in the Salt Wash Member, suggesting cyclic annual precipitation, and finally to irregular banding produced by a complex interaction of more weakly developed annual growth bands and complicating pseudoannual bands in the Brushy Basin Member. Psuedoannual growth banding in the Brushy Basin Member could be related to isolated storm runoff turbidity or to increased turbidity from volcanic ashfalls.

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Appendix A

Locality 1	Dinosaur National Monument, Utah, Carnegie Dinosaur Quarry, quarry Sandstone bed, Upper Smectitic part of Brushy Basin Member (Good and Kozlowski, 1995).	
Data	Bivalve (*Vetulonaia* sp.)	
	Condition:	Predominately disarticulated, little abrasion and fragmentation
	Size distribution:	Little variation in the size of shells
	Orientation:	Current stable position (convex up); one articulated specimen occurs in life position
	Density:	Concentrated shell lag in channel bed, in trough areas
	Matrix:	Coarse sand to gravel conglomerate
	Preservation:	Silicified (preserving no internal structure or vague ghosts of shell ultrastructure
	Interpretation: Bivalve shells represent a death assemblage that has been entrained, transported, and deposited in troughs between channel bed bedforms. The hydrodynamic behavior of the shells indicate they constitute the coarsest, least-transportable clast component of the bedload. The minor ragmentation and abrasion suggests the shells have not experienced significant transport. Therefore, this occurrence represents a minimally transported assemblage.	
Locality 2	Dinosaur National Monument, Utah, approximately 1km east of Carnegie Dinosaur Quarry, quarry sandstone bed, Upper smectitic part of Brushy Basin Member (Good and Kozlowski, 1995).	
Data	Bivalve (*Vetulonaia* sp.)	
	Condition:	Predominately disarticulated, little abrasion and fragmentation
	Size distribution:	Little variation in the size of shells
	Orientation:	Current stable position (convex up)
	Density:	Concentrated shell lag in channel bed, in trough areas
	Matrix:	Coarse sand to gravel conglomerate

Appendix A (*continued*)

Data	Preservation:	Silicified (preserving no internal structure or vague ghosts of shell ultrastructure)
	Interpretation: Bivalve shells represent a death assemblage that has been entrained, transported, and deposited in troughs between channel bed bedforms. The hydrodynamic character of the shells indicate they constitute the coarsest, least-transportable clast component of the bedload. The minor fragmentation and abrasion suggests the shells have not experienced significant transport. Therefore, this occurrence represents a minimally transported assemblage.	
Locality 3	Cleveland-Lloyd Quarry, Utah, Upper smectitic part of the Brush Basin Member (Shultz et al., 1997).	
Data	Bivalve resting trace fossils from the base of the sandstone capping the bluff above the quarry site.	
	Condition:	Resting traces of large bivalves
	Size distribution:	Nearly uniform size
	Orientation:	In life position
	Density:	High concentrated, nearly continuous pavement of shell traces
	Matrix:	Medium-grained sandstone, traces preserved as infilled depressions in underlying mudstone.
	Preservation:	No shell material preserved
	Interpretation: This location provides an excellent opportunity to observe the abundance of bivalves within optimum habitat. The bivalves inhabited the muddy substrate of a pond environment.	
Data	Bivalve fossil shells, from site lateral to the bivalve trace fossil bed, outside the Cleveland-Lloyd Park boundary	
	Condition:	Original shell material, subequal articulated and disarticulated, very well preserved
	Size distribution:	Moderate range in size, mostly larger specimens
	Orientation:	Random
	Density:	Moderately concentrated
	Matrix:	Greenish-grey mudstone
	Preservation:	Very well preserved, wall ultrastructure showing complex banding that is a product of annual and pseudoannual banding.

(*continued on next page*)

Appendix A (*continued*)

Locality 3	Interpretation: The locality represents a disturbed neighborhood assemblage (specimens preserved in sediments inhabited during life, but out of life position). This is evidenced by excellent preservation, and relatively high proportion of articulated specimens. The fine grained matrix and morphology of the bivalves indicate pond habitat. The assemblage was preserved by rapid burial by the stream represented by the overlying fluvial sandstone.	
Locality 4	South of Green River, Utah, Tidwell Member, (Shultz et al., 1997).	
Data	Bivalves (*Vetulonaia* sp.)	
	Condition:	Predominately articulated, little fragmentation or abrasion
	Size distribution:	Wide range in size (from juveniles to very large adult specimens)
	Orientation:	Random orientation
	Density:	Highly concentrated over a approximately 6 m lateral distance
	Matrix:	Within greenish-grey mudstone underneath channel sandstone
	Preservation:	Very well preserved ultrastructure, continuous growth indicated by absence of banding within the shell
	Interpretation: The morphology (large obese specimens) of this shell type suggests quiet water pond conditions; an interpretation substantiated by the mudstone matrix. The continuous size gradation, and excellent surface ornament preservation and articulation indicate this was a living community of bivalves, that was preserved due to the rapid influx of sand that buried this ecological association (disturbed neighborhood assemblage). The homogenous ultrastructure suggests an absence of seasonal variability in temperature or precipitation. The abundance of specimens suggests optimum conditions for lime-rich, shallow water (clean, well-oxygenated, pH greater than 7, less than 7 m depth), perennial aquatic habitat, warm, stable substrate, abundant plankton food resources).	
Locality 5	Como Bluff, Wyoming, Tidwell Member equivalent, (Shultz et al., 1997).	
Data	Bivalves (*Vetulonaia* sp.)	
	Condition:	Very well preserved, minor fragmentation and abrasion, disarticulated

Appendix A (*continued*)

Data	Size distribution:	Relatively uniformly large size
	Orientation:	Random
	Density:	Moderate to low density
	Matrix:	Greenish gray mudstone
	Preservation:	Absence of growth bands, indicating continuous, unin terrupted growth
	Interpretation: The morphology of this shell type (large obese specimens) suggests quiet water pond conditions; an interpretation substantiated by the mudstone matrix. The homogenous ultrastructure suggests an absence of seasonal variability in temperature or precipitation.	
Locality 6	Alcova, Wyoming, lower Morrison.	
Data	Bivalve resting trace fossils, occur in the basal 1 m of sandstone as six distinct sandstone beds each with basal bivalve resting trace fossils.	
	Condition:	Trace fossils, no shell material
	Size distribution:	Uniformly of moderate size
	Orientation:	In-life position
	Density:	Very abundant and nearly continuos coverage of channel bed cross section
	Matrix:	Conglomeratic (mostly mud-chip) sandstone, also some petrified wood and dinosaur bone fragments
	Preservation:	Trace fossils
	Interpretation: The bivalves inhabited the floodplain pond that was supplied with water and coarse sediment by periodic crevasse splay floods. The bivalve community developed on the floor of the floodplain pond in the coarse-grained sediment of a previous crevasse splay deposit. The next crevasse splay flooding event entrained and transported the bivalves, leaving indentations in the floodplain pond floor that were filled by material from the later stage of the flood event. The high density of the bivalve community indicates a floodplain pond with optimum bivalve habitat (clean, well-oxygenated water, pH greater than 7, lime-rich, shallow water (less than 7 m depth), perennial aquatic habitat, at least seasonably warm, stable substrate, and abundant plankton food resources).	
Data	Bivalve shell material in sandstone bed about 3 feet above the top of the bivalve resting trace-bearing bed. The 30 cm thick bed was strongly cemented, making collection of samples difficult.	

Appendix A (*continued*)

Data	Condition:	Predominately articulated, many preserved as internal molds, shell material very abraded
	Size distribution:	Medium to large size
	Orientation:	Random
	Density:	Moderately dense
	Matrix:	Medium-grained sandstone, smectitic clay at top
	Preservation:	Poorly preserved, precluding growth band study
	Interpretation: This probably is a crevasse-splay deposit with bivalves representing a transported assemblage.	
Locality 7	Gibson Reservoir, Montana, unknown stratigraphic position.	
Data	Bivalves (too incomplete for identification).	
	Condition:	Well preserved
	Size distribution:	Moderate size
	Orientation:	Random, commissures parallel to bedding plane
	Density:	Very low density
	Matrix:	Greenish fine-grained sandstone, previous collections taken from mudstone units
	Preservation:	Well preserved as impressions, insufficient shell material for ultrastructure study.
	Interpretation: Minimal outcrop and few specimens preclude detailed interpretation. Adult sized individuals indicate adequate habitat, but few specimens suggests it was not an optimal habitat.	
Locality 8	Colorado National Monument, Middle Unit of Salt Wash Member (Shultz et al., 1997).	
Data	Bivalves (*Hadrodon* sp.).	
	Condition:	Very well preserved, predominately articulated, little fragmentation and abrasion
	Size distribution:	Variable sizes represented
	Orientation:	Random orientations
	Density:	Highly concentrated
	Matrix:	Grayish-green mudstone
	Preservation:	Very well preserved, ultrastructure study yielded well developed annual banding
	Interpretation: This assemblage is interpreted as a disturbed neighborhood assemblage, inhabiting a floodplain pond. The climate had well developed annual cyclicity, forcing prolonged annual closure of the bivalves during adverse conditions.	

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