A conceptual model for freshwater mussel (family: Unionidae) remain preservation in zooarchaeological assemblages

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ABSTRACT

Expectations for survival of vertebrate remains have been well developed and intensely studied in the zooarchaeological taphonomic literature. Taphonomic studies of shellfish remains focus on marine species and on variables relevant to remains from paleontological contexts (e.g., fossil marine beds). In this paper we develop a conceptual framework from which to derive expectations concerning the preservation of freshwater mussel remains focusing on two parameters, shell microstructure and shell shape. Shell size does not influence survivorship. Our model is validated through application to late Holocene zooarchaeological mussel assemblages from north Texas. Taphonomically robust species are important regarding zooarchaeological and biogeographic interpretations based on mussel paleofaunas, and fragile species are important indicators of whether or not an assemblage is well preserved.

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1. Introduction

Within zooarchaeology the topic of vertebrate taphonomy focuses on numerous variables that generally relate to natural and cultural transformation processes as summarized by Schiffer (1987). A central concern is bone preservation, which has been explored in reference to factors that cause fragmentation (Marean and Spencer, 1991; Marean et al., 1992; Stiner et al., 1995, 2005) and how those factors relate to a variety of causal agents such as, burning (Stiner et al., 1995, 2005), green fracturing by humans for use of within bone nutrients (Bar-Oz and Munro, 2007; Brink, 1997; Morin, 2007; Munro and Bar-Oz, 2005; Outram, 2001; Wolverton et al., 2008), crushing and pulverization for extraction of grease (Munro, 2004; Munro and Bar-Oz, 2005), trampling (Gifford-Gonzalez et al., 1985; Stiner et al., 1995), among a host of other agents (e.g., Marean and Cleghorn, 2003; Nagaoka et al., 2008; Pickering et al., 2003). A separate but related concern is how identifiable bone fragments are, a factor that relates to fragment size, which is a product of fragmentation intensity (Lyman, 1994a; Marean and Cleghorn, 2003; Marean and Kim, 1998; Marshall and Pilgram, 1993; Stiner, 1991). Bone preservation itself, however, is most often modeled conceptually as a factor of bone density, and this has been accomplished in a variety of ways—qualitatively (Brain, 1969) and quantitatively (e.g., Lyman, 1984, 1994b; Lam et al., 1998). Conclusions from these models provide the general consensus that bones and portions of bones that are relatively high in density tend to preserve well. All of these studies are at the intraspecific scale because natural and cultural transformations that affect preservation of vertebrate remains have been most often related to answering questions of carcass exploitation for a variety of analytical purposes (Binford, 1978; Broughton, 1999; Nagaoka, 2005, 2006). Only rarely have preservation models relied on variables other than bone density to make predictions about taphonomic survival of carcass parts (see Darwent and Lyman, 2002 for a study of bone shape and diagenesis; see also Stiner et al., 1995, 2005).

Carcasses of vertebrate prey animals are resource patches that were exploited in a variety of ways related to contingencies of search and pursuit time, handling and processing costs, food value of carcass parts (utility), prey availability, and transport distance to occupation sites (Binford, 1978; Cannon, 2003; Munro, 2004; Nagaoka, 2005, 2006; Wolverton, 2002; Wolverton et al., 2008). The same is not the case among many species of mollusks (Bird et al., 2002; Botkin, 1980). For example, the carcass is not a resource patch in freshwater mussels. Instead, *mussel beds* are resources patches (Jones, 1991), foraging returns per individual prey item (but not necessarily per bed) can be expected to be relatively low. As in vertebrate prey animals, the individual carcass can be conceptualized as two portions, edible and inedible (shell). The shell itself, like bone, may have been exploited for a variety of other purposes (e.g., tools and ornamental adornments). But as prey for food, in marked contrast to many vertebrate prey species, mussels are a closed

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exoskeleton with a *small*, edible package inside. Shells would have been most easily opened through either fragmentation, heating, or steaming (Baker, 1942; Muckle, 1985; Parmalee and Klippel, 1974), and foraging returns and preservation in a taphonomic sense are most important at the *interspecific* scale because this is the scale at which body parts and caloric returns vary most (Bird et al., 2002; Randklev et al., 2009).

This paper focuses on factors that influence preservation of freshwater mussel remains. We adopt a few assumptions; first, analysis of the relative abundance of shellfish remains is meaningful (though by no means exclusively meaningful) at the interspecific scale. That is, changes through time in taxonomic abundance reflect either a change in bed exploitation by humans, change in environmental conditions in streams, and/or the effects of taphonomic processes that mediate preservation and potentially archaeological recovery (Bird et al., 2002; Botkin, 1980). Second, in a particular region in a particular mussel community, it should be possible to predict which species are likely to preserve and which ones are less likely to survive effects of fragmentation and diagenesis based on shell morphology much the same as it is possible to predict which skeletal parts are most likely to survive at the intraspecific scale in the vertebrate carcass. Third, even though shellfish remains tend to be fragmented in archaeological faunal assemblages, only some species exhibit morphology that leads to preservation of fragments that are sufficiently large and diagnostic to identify. We provide a conceptual model that predicts which species should preserve well and which should preserve poorly using two parameters—*density* and *shape* of shells—measured as weight per volume and sphericity respectively. We apply that model to several freshwater mussel (family Unionidae) zooarchaeological assemblages from north Texas.

2. Taphonomy of shellfish

Taphonomic studies of shellfish remains are common, especially in paleontology, and these studies often focus on biostratigraphy, paleoenvironmental reconstruction, biological species conservation, among other topics related to zooarchaeology (e.g., Brett and Baird, 1986; Brown et al., 2005; Cintra-Buenrostro, 2007; Claassen, 1998; Edgar and Samson, 2004; Erlandson and Moss, 2001; Helama and Valovirta, 2007; Kidwell, 1986; Lazo, 2004; Morey and Crothers, 1998; Muckle, 1985; Nielsen and Funder, 2003; Parmalee and Bogan, 1986; Parmalee and Hughes, 1993; Parsons et al., 1997; Peacock, 2000; Peacock and Chapman, 2001; Peacock et al., 2005; Peacock and Mistak, 2008; Rick et al., 2006; Warren, 1975, 1991, 1995). A diverse array of agents and processes can influence taphonomic histories in zooarchaeological shellfish faunas including handling and processing for food, the discard process (e.g., height from which shells are dropped by people), orientation of deposition, disparity in burning among shellfish remains of different species, rate of disarticulation of valves, exposure to trampling, chemical weathering in acidic soils, soil formation processes, rates of deposition, sedimentation and erosion, archaeological recovery methods, modification of shells by predators, and shell shape and microstructure. These factors have been studied in experimental and actualistic settings (Best and Kidwell, 2000a2000b; Hoffmeister et al., 2004; Kidwell, 1986; Muckle, 1985; Oji et al., 2003; Rick et al., 2006; Robins and Stock, 1990). Many of these studies seek to determine taphonomic patterns that can distinguish one taphofacies from another and provide analogs through experiments and actualistic geospatial studies that cover a variety of ecological, depositional, and burial contexts (most often in marine species) (e.g., Best and Kidwell, 2000b; Parsons et al., 1997). For example, a study by Wani (2004) identifies taphonomic processes that cause particular fragmentation patterns in *Nautilus* shells. Taphonomic experiments with *Nautilus*

are then structured into analogs with which to gauge the taphonomic histories of paleontological cephalopod faunas.

It is critical to note that despite the value of actualistic and experimental studies, particularly those designed for consideration of paleontological contexts, deposition in terrestrial archaeological deposits is much different than accumulation and fossilization in beds. Fossil bed formation is a function of community organization, exposure of shell remains during oscillating episodes of population recruitment, contact with other shells, not to mention a host of sedimentary and water chemistry factors (Best and Kidwell, 2000a,b; Kidwell, 1986). In contrast, as predators humans enhance the probability of shell disarticulation and fragmentation, and remains are potentially buried in shell midden contexts of variable composition (e.g., containing other forms of artifact debris and trash). What can be gleaned from actualistic and experimental studies is a host of parameters that influence shell survival through time whether in marine, freshwater, or terrestrial-archaeological contexts precisely because the starting point of any taphonomic history is an intact shell.

What aspects of shell morphology—at some scale, to some degree—mediate all aspects of shell fragmentation? A study by Zuschin and Stanton (2001) focuses on the properties that affect fragmentation in three marine species; they found that shell thickness at the highest point of the shell (the umbo) is the best predictor of compressive shell strength. Zuschin and Stanton (2001) also link resistance to fragmentation to shell microstructure; some species have less robust lamellar microstructure and fracture more easily than do others (see also Best and Kidwell, 2000b). In addition, the presence of drillholes caused by predators and parasites increases susceptibility to fragmentation during a shell's taphonomic history (e.g., Hoffmeister et al., 2004). Zushin and Stanton's study also emphasizes shell properties that relate to fragmentation caused by sediment compaction; of particular importance is that number of points of contact among shells in beds increases rates of fragmentation. The primary goal of Zushin and Stanton's (2001) study is similar to ours, to determine what macroscale properties of shells are most important in fragmentation and preservation. However, their study does not incorporate zooarchaeological data, focuses on only three species, and does not consider freshwater mussels. Our study builds on theirs by also examining shell shape and density as predictors of preservation in paleozoological contexts. In their study and in ours shell preservation does not relate to common measures of shell size, such as length. What is absent from previous studies is a conceptual model that enables close evaluation of shell preservation related to morphology at the interspecific scale analogous to the photon-densitometry and computer tomography models for the vertebrate skeleton at the intraspecific scale (Lam et al., 1998; Lyman, 1994b).

3. A bivalve shell preservation model

Microstructural strength and shape are often cited as physical characteristics of shells that mediate preservation in a variety of settings (see above). Thickness is the single size measure that appears to relate to preservation. It is important to note that our interest is not in whether or not complete shells preserve, however, but that diagnostic features of shells preserve, such as external morphology, pseudocardinal and lateral teeth, and/or the umbo. Related to the anatomy of these features, it is not thickness that matters most, but thickness relative to shell length and height. Together these variables represent shape, and progressively higher thickness relative to length reflects a compression in shell shape toward an increase in sphericity. No shell is perfectly spherical, but because the index of sphericity we use relies on measurements of length, thickness, and height, the higher an average sphericity index value for a species, the more round in areal-shape the shell is

and the greater is thickness near the umbo compared to length and height, which represent horizontal extensions of the shell. As a result, one can predict that those shell shapes that are rectangular at low thickness are more rod-like and are more likely to be fragmented (see Darwent and Lyman, 2002 for a similar characterization of ungulate tarsals). Those species with shells that are round and relatively thick compared to their length and height are less rod-like and more spherical; physically these attributes are resistant to fragmentation.

Fragmentation is also affected by shell density, which in this model is a proxy for structural strength. However, the relationship between density and fragmentation is mediated by shell shape. For example, smaller species tend to have thinner shells and may even be low density, but if their shape is spherical compared to other species (even some that are higher in shell density), their shape provides a stronger shell that is resistant to fragmentation. As a result, species with relatively spherical, high-density shells are the most likely to survive, species with low density and low sphericity are the least likely to preserve, species with low density and high sphericity can be predicted to preserve moderately well, and species with high density but low sphericity are only expected to survive at low to moderate levels (Fig. 1A). Density has an effect on preservation that can be enhanced or compromised by shell shape.

Fig. 1A represents our conceptual model by dividing a Cartesian plot into 4 quadrants. These quadrants are not discrete categories; rather, they are portions of sphericity and density continua that are used in this paper for heuristic purposes. The quadrants are labeled numerically in rank order of their relationship to shell preservation. For example, Quadrant 1 reflects high sphericity and density, thus good preservation. Transects across these quadrants move along the continua of sphericity and density such that as one moves from left to right density increases, modeling its effect on shell survival. Along the vertical axis, sphericity increases, modeling its effect on shell preservation. To more strongly communicate that our model relies on the continuous variables of sphericity and density and that each variable influences preservation in distinct ways, we illustrate our model in Fig. 1B topographically. As one moves toward the upper right corner of the graph, probability of shell preservation increases. However, the rate of topographic increase is initially higher for sphericity than for density communicating that a species with a low density but comparatively spherical shell is more likely to survive than a species with similar density but lower sphericity. In order to validate this model, we measured shell density and sphericity for a variety of unionid species native to north Texas and examined zooarchaeological assemblages to assess taxonomic abundance.

4. Limitations of the model

The model is limited to consider suites of species on a community by community basis because the sphericity and density gradients are ordinal scale (see below). Inclusion of a new, separate species in the model shifts the others species' values along the gradient continua. This limitation, however, is pragmatic in that distinctive communities should be considered on a case by case basis. That is, shell morphology can be expected to be habitat dependent and varies spatially (Ortmann, 1920). This constraint of the model is analogous to evaluation of density of skeletal parts in vertebrate skeletons; it is considered highly appropriate to independently measure density for species with distinctive skeletal morphologies (see Lyman, 1994b for multiple examples). Further, it is at the scale of the skeleton that differential destruction of bone occurs and is analyzed; it is at the community scale that shell morphology varies and at which differential destruction should be measured. Our model, however, does not preclude cross-community comparison of absolute sphericity and density values for
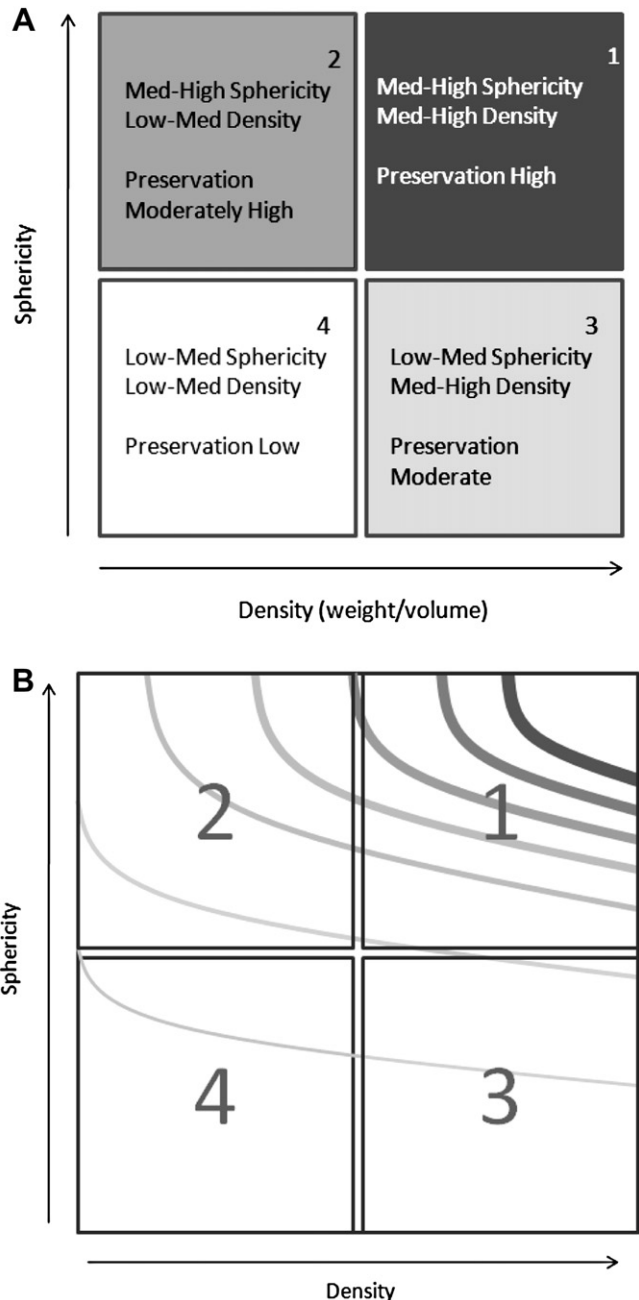

Fig. 1. A) A conceptual model for predicting preservation relative to sphericity and density using quadrants as heuristic devices to explain each continuous variable and how it relates to preservation. B) The same conceptual model as portrayed above, but communicated topographically, which clarifies that sphericity and density vary as continua. Probability of preservation of remains of a species increases upward and right on the graph.

species; thus, a new species can be assessed and compared to previously examined ones in that fashion. It is only the ordinal-scale gradient model that must adjusted by community (see below). The only way to make the ordinal scale model universal would be to define communities at the continental or greater scale and include all species that are represented, an ambitious goal at a minimum.

Another limitation of this model is that it is explicitly designed for consideration of vulnerability of whole shells to fragmentation. Although the model is constrained in this fashion, the logic applies to fragments as well; rod-shaped, columnar fragments are more

likely to fracture again than are robust, relatively spherical fragments (Darwent and Lyman, 2002). In addition, spherical shell shape tends to associate with robust umbo and tooth morphology. At issue is simply identifiability of shells. The most identifiable specimens are whole ones, and an ability to identify fragments declines with fragment size (Lyman, 1994a). Further, species with fragile shells tend to lose diagnostic features, such as umbo ornamentation and tooth morphology, during fragmentation. In the example below we examine fragmented specimens from archaeological sites; those from species with spherical, dense shells tend to preserve more commonly than fragments from species with less robust whole-shell morphology.

5. Materials and methods

Modern freshwater mussel species from the upper Brazos and Trinity River drainages of central and north Texas (Fig. 2) were selected for sphericity and density analysis. Modern samples are reference collection specimens from north central Texas curated in the Joseph Britton Freshwater Mussel Collection, located in the Elm Fork Natural Heritage Museum, Denton Texas. Samples of shells from nineteen species are examined in this study (Table 1). Among these species, it is important to note that *Potamilus ohiensis* is considered a recent introduction into north central Texas (Howells, 1994), however this species was included as a surrogate for *Potamilus amphichaenus*, which was not examined due to small sample size.

To examine the effects of shape and density on unionid preservation, sphericity and density measurements from modern individuals from species representing the entire north Texas mussel community were taken and related to taxonomic frequency data for species represented in six zooarchaeological samples from the upper Brazos and Trinity River drainages (Fig. 2). The upper Brazos River drainage samples are from two sites located on Hackberry Creek a small tributary of the Brazos River (41HI105 and 41HI115). Both sites date to roughly 2300 to 1100 BP based on uncorrected radiocarbon dates using soil humates and mussel shell (Brown et al., 1987). The upper Trinity River samples are from the Clear Fork (41TR205 and 41TR170) and West Fork (41TR114) of the Trinity River and from Denton Creek (41DL8), a tributary of the Elm Fork of the Trinity River. All four sites date to roughly 2500 to 600 BP based on radiocarbon dates of ash deposits (Lintz et al., 2008) and association with temporally diagnostic artifacts (Ferring unpublished data). Freshwater mussels from the late Holocene assemblages on the Clear Fork and West Forks of the Trinity River, Denton Creek, and Hackberry Creek were identified using field guides (Howells et al., 1996; Parmalee and Bogan, 1998) and modern reference specimens.

Sphericity is estimated for right valves of modern reference specimens following Darwent and Lyman (2002; see Lyman, 1994b) and is defined as $[(bc/a^2)^{0.33}]$ where a is the average maximum length between the anterior and posterior margin of each valve (shell length) for a species, b is the average maximum length between the dorsal and ventral margin of each valve (shell height), and c is
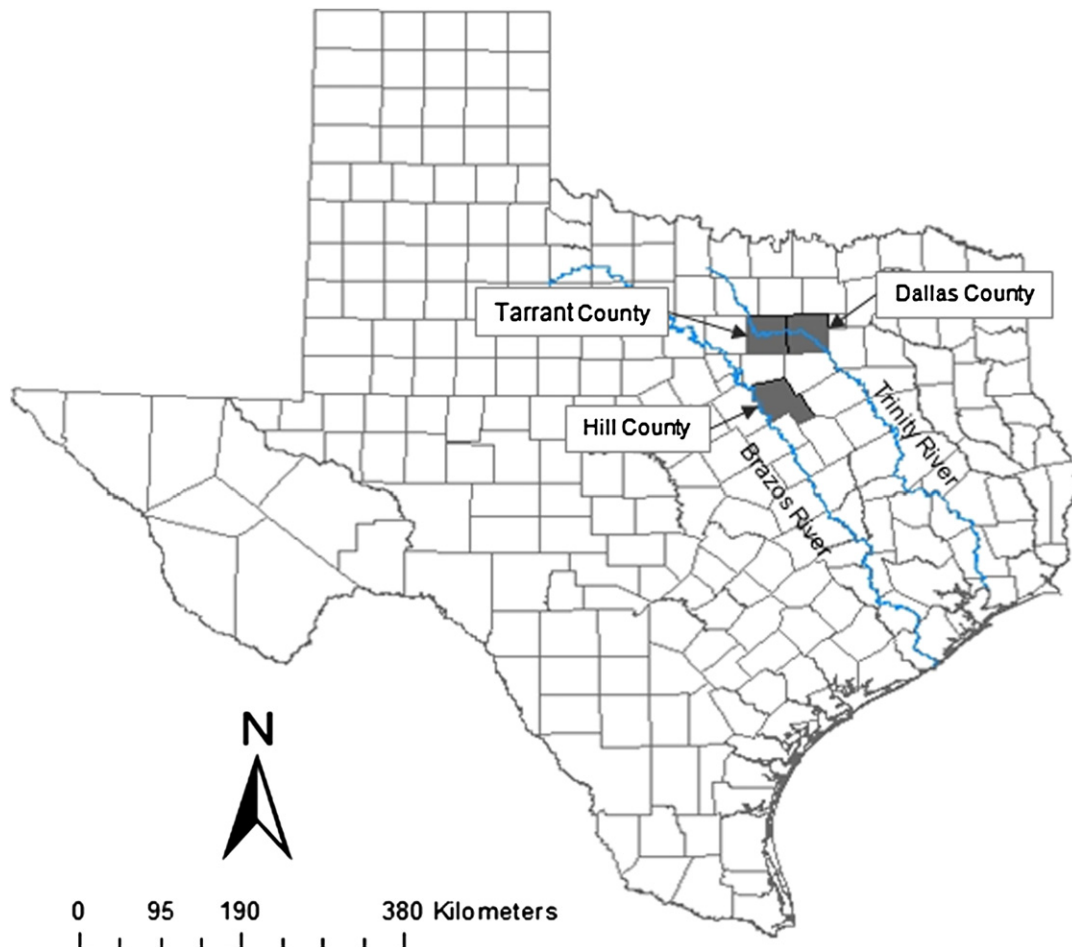

Fig. 2. Map of Texas: shaded counties indicate areas containing archaeological sites; the West (41TR114) and Clear Fork (41TR170 and 41TR205) sites are in Tarrant County, the Denton Creek (41DL8) site is in Dallas County, and samples from Hackberry Creek (41HI105 and 41HI115) are from Hill County.

Table 1
Maximum (shell length), middle (shell height), and minimum (shell breadth) dimensions and shell weight and volume for 19 north Texas mussel species. S = standard deviation.

Species	n	a: Max. (mm) $\overline{x}$ (S)	b: Middle (mm) $\overline{x}$ (S)	c: Min. (mm) $\overline{x}$ (S)	Weight (g) $\overline{x}$ (S)	Volume (mL) $\overline{x}$ (S)
AP *Amblema plicata*	30	93.14 (17.07)	70.99 (13.43)	21.35(6.70)	70.09 (46.31)	32.98 (18.69)
CT *Cyrtonaias tampicoensis*	31	91.30 (28.00)	61.79 (17.48)	20.53 (5.89)	60.57 (62.75)	27.82 (19.88)
LH *Lampsilis hydiana*	30	70.04 (8.98)	41.90 (6.57)	15.82 (4.65)	17.45 (12.51)	14.03 (5.00)
LT *Lampsilis teres*	30	100.59 (17.99)	46.87 (9.32)	17.67 (4.45)	32.21 (21.23)	23.04 (9.23)
LF *Leptodea fragilis*	30	103.64 (13.77)	63.74 (8.59)	17.87 (3.25)	20.50 (10.31)	15.62 (5.65)
MN *Megalonaias nervosa*	18	113.35 (27.57)	80.10 (20.29)	16.98 (3.67)	55.36 (34.30)	33.49 (12.00)
OR *Obliquaria reflexa*	19	52.19 (9.54)	44.51 (8.85)	14.29 (3.87)	23.28 (11.66)	15.47 (6.29)
PD *Plectomerus dombeyanus*	15	89.49 (17.40)	56.95 12.56)	18.22 (4.44)	50.47 (29.23)	28.42 (13.62)
PO *Potamilus ohiensis*	30	105.73 (23.70)	65.24 (16.32)	16.58 (4.52)	23.12 (17.10)	21.22 (6.45)
PP *Potamilus purpuratus*	30	105.72 (19.22)	78.02 (14.26)	21.67 (4.11)	54.16 (34.87)	27.50 (13.97)
PG *Pyganodon grandis*	30	106.79 (20.78)	67.61 (13.52)	24.29 (4.63)	17.36 (11.11)	18.74 (5.68)
QA *Quadrula apiculata*	30	68.69 (8.08)	58.20 (6.26)	18.21 (2.05)	36.48 (12.34)	19.21 (5.47)
QH *Quadrula houstonensis*	30	50.35 (7.54)	42.28 (6.08)	14.61 (2.25)	19.37 (9.53)	15.04 (3.90)
QM *Quadrula mortoni*	30	45.96 (10.86)	41.66 (10.55)	15.66 (4.15)	18.68 (15.02)	14.41 (5.75)
QV *Quadrula verrucosa*	30	119.41 (32.60)	67.42 (16.96)	20.30 (6.24)	95.85 (67.35)	37.08 (19.23)
TX *Toxolasma texasiensis*	30	42.69 (10.11)	24.42 (6.00)	9.54 (2.70)	3.79 (2.54)	10.33 (2.11)
TT *Truncilla truncata*	30	56.18 (11.15)	43.90 (7.06)	14.94 (2.57)	18.30 (8.04)	15.51 (3.35)
UT *Unionmerus tetralasmus*	30	78.07 (12.77)	42.39 (7.32)	12.43 (2.45)	12.35 (7.58)	14.18 (4.11)
UI *Utterbackia imbecillis*	30	64.16 (13.35)	31.34 (7.08)	10.38 (2.77)	1.75 (1.39)	9.66 (0.87)

average maximum length between the interdentum and topmost surface of the shell (shell breadth) (Table 2). Three replicate measurements were taken for each dimension on each shell and were averaged to minimize error. Sphericity values represent a gradient, the higher the value the greater the sphericity of the shell (Darwent and Lyman, 2002). The raw sphericity score for each species is converted to a ten-point community-based ordinal scale (Sphericity Gradient score, SG_i) using Equation (1) where a value of 0 represents the lowest possible sphericity and a value of 10 represents highest possible sphericity (Table 2) (see Bessler et al., 2006).

$$(\text{Sphericity Gradient}) : SG_i = \left[(S_{avgi} - S_{min}) \div (S_{max} - S_{min}) \right] \quad (1)$$

S_{avgi} = mean sphericity for a species, S_{min} = the minimum mean sphericity for a species in the community and S_{max} = the maximum mean sphericity for a species in the community.

Density (g/mL) was measured for right valves of modern specimens using volume displacement. For each valve, dry shell weight

was measured to the nearest 0.1 g using an electronic scale. To measure volume, a single right valve was placed in a graduated cylinder to determine the volume of water needed to fully submerge the valve. In a second graduated cylinder, water was filled to the submerged volume and then poured into the first graduated cylinder containing the right valve; the volume of water left in the second graduated cylinder represented the volume (measured to 0.1 mL) of the shell (Table 3). Density was calculated by dividing valve weight by valve volume; measurements were repeated three times to ensure accurate estimations of valve volume and weight. Raw density scores are converted to a ten-point community-based ordinal scale using Equation (2) where a value of 0 represents the lowest possible density and a value of 10 represents highest possible density for each species (Table 3) (see Bessler et al., 2006).

$$(\text{Density Gradient}) : DG_i = \left[(D_{avgi} - D_{min}) \div (D_{max} - D_{min}) \right] \quad (2)$$

Table 2
Descriptive sphericity statistics, sphericity gradient scores, and shell length variability for 19 mussel species from north Texas. CV = coefficient of variation, SG_i = sphericity gradient score.

Species	Sphericity				Shell Length (mm)
	n	$\overline{x}$ (S)	CV		CV
Amblema plicata	30	0.56 (0.05)	0.08	5.19	0.18
Cyrtonaias tampicoensis	31	0.54 (0.02)	0.04	4.42	0.31
Lampsilis hydiana	30	0.51 (0.04)	0.08	3.31	0.13
Lampsilis teres	30	0.44 (0.02)	0.05	0.19	0.18
Leptodea fragilis	30	0.48 (0.02)	0.04	1.84	0.13
Megalonaias nervosa	18	0.48 (0.02)	0.03	1.93	0.24
Obliquaria reflexa	19	0.61 (0.04)	0.06	7.46	0.18
Plectomerus dombeyanus	15	0.51 (0.03)	0.05	3.10	0.19
Potamilus ohiensis	30	0.46 (0.02)	0.04	1.21	0.22
Potamilus purpuratus	30	0.54 (0.03)	0.05	4.31	0.18
Pyganodon grandis	30	0.53 (0.02)	0.03	3.95	0.19
Quadrula apiculata	30	0.61 (0.02)	0.03	7.35	0.12
Quadrula houstonensis	30	0.63 (0.02)	0.03	8.01	0.15
Quadrula mortoni	30	0.68 (0.02)	0.03	10.00	0.24
Quadrula verrucosa	30	0.46 (0.03)	0.07	1.26	0.27
Toxolasma texasiensis	30	0.51 (0.03)	0.06	3.02	0.24
Truncilla truncata	30	0.60 (0.03)	0.05	6.81	0.20
Unionmerus tetralasmus	30	0.44 (0.01)	0.03	0.57	0.16
Utterbackia imbecillis	30	0.43 (0.02)	0.05	0.00	0.21

Table 3
Descriptive density statistics, density gradient scores, and shell length variability for 19 mussel species from north Texas. CV = coefficient of variation, DG_i = density gradient score.

Species	Density				Shell Length (mm)
	n	$\overline{x}$ (S)	CV	DG_i	CV
Amblema plicata	30	2.02 (0.32)	0.16	8.07	0.18
Cyrtonaias tampicoensis	31	1.92 (1.09)	0.57	7.63	0.31
Lampsilis hydiana	30	1.13 (0.44)	0.38	4.17	0.13
Lampsilis teres	30	1.27 (0.42)	0.33	4.78	0.18
Leptodea fragilis	30	1.29 (0.39)	0.30	4.87	0.13
Megalonaias nervosa	18	1.52 (0.69)	0.46	5.88	0.24
Obliquaria reflexa	19	1.45 (0.24)	0.16	5.57	0.18
Plectomerus dombeyanus	15	1.68 (0.34)	0.20	6.58	0.19
Potamilus ohiensis	30	0.98 (0.56)	0.57	3.51	0.22
Potamilus purpuratus	30	1.86 (0.38)	0.20	7.37	0.18
Pyganodon grandis	30	0.85 (0.35)	0.41	2.94	0.19
Quadrula apiculata	30	1.90 (0.28)	0.15	7.54	0.12
Quadrula houstonensis	30	1.24 (0.38)	0.31	4.65	0.15
Quadrula mortoni	30	1.15 (0.48)	0.42	4.25	0.24
Quadrula verrucosa	30	2.46 (1.27)	0.52	10.00	0.27
Toxolasma texasiensis	30	0.34 (0.20)	0.58	0.70	0.24
Truncilla truncata	30	1.13 (0.30)	0.27	4.17	0.20
Unionmerus tetralasmus	30	0.81 (0.33)	0.40	2.76	0.16
Utterbackia imbecillis	30	0.18 (0.14)	0.78	0.00	0.21

Table 4
Taxonomic list, NISP, and relative abundance of unionid remains from north Texas archeological sites. Denton Creek–41DL8 (DC); West Fork–41TR114 (WF); Clear Fork–41TR170 (CF1); Clear Fork–41TR205 (CF2); Hickory Creek–41H105 (HC1); Hickory Creek–41H115 (HC2). Dashes denote species absence; asterisks indicate exclusion because of small sample size.

Species	DC		WF		CF1		CF2		HC1		HC2		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Amblema plicata	33	33.0	6	17.1	65	39.2	37	14.3	315	64.9	613	79.6	1069	58.9
*Arcidens confragosus**	0	0.0	0	0.0	0	0.0	0	0.0	1	0.2	0	0.0	1	0.1
Cyrtonaias tampicoensis	–	–	–	–	–	–	–	–	10	2.1	1	0.1	11	0.6
Lampsilis hydiana	9	9.0	0	0.0	20	12.0	63	24.4	75	15.5	83	10.8	250	13.8
Lampsilis teres	0	0.0	2	5.7	19	11.4	70	27.1	31	6.4	14	1.8	136	7.5
Megalonaias nervosa	–	–	–	–	–	–	–	–	2	0.4	4	0.5	6	0.3
Obliquaria reflexa	2	2.0	0	0.0	0	0.0	0	0.0	–	–	–	–	2	0.1
Plectomerus dombeyanus	13	13.0	1	2.9	16	9.6	20	7.8	–	–	–	–	50	2.8
Potamilus purpuratus	4	4.0	2	5.7	8	4.8	3	1.2	5	1.0	29	3.8	51	2.8
Pyganodon grandis	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.3	2	0.1
Quadrula apiculata	3	3.0	0	0.0	0	0.0	0	0.0	7	1.4	23	3.0	33	1.8
Quadrula houstonensis	–	–	–	–	–	–	–	–	38	7.8	0	0.0	38	2.1
Quadrula mortoni	24	24.0	15	42.9	18	10.8	7	2.7	–	–	–	–	64	3.5
Quadrula verrucosa	0	0.0	7	20.0	17	10.2	40	15.5	0	0.0	1	0.1	65	3.6
Toxolasma texasiensis	3	3.0	0	0.0	0	0.0	14	5.4	1	0.2	0	0.0	18	1.0
Truncilla truncata	6	6.0	2	5.7	3	1.8	4	1.6	–	–	–	–	15	0.8
Uniomerus tetralasmus	3	3.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	3	0.2
Total	100		35		166		258		485		770		1814	

D_{avgi} = mean density for a species, D_{min} = minimum mean density for a species in the community and D_{max} = maximum mean sphericity for a species in the community.

The conversion of sphericity and density to these scales allows clear, direct pairwise comparisons for both variables for species. The density and sphericity gradient scores are used to visualize ordinal scale relationships between each characteristic of shell morphology and proportional abundance in zooarchaeological assemblages from north Texas (see below).

To illustrate the relationship between mean sphericity and mean density among species we conduct an ordination of both variables using non-metric multidimensional scaling (NMDS), which allows us to relate our observations on shell morphology (Fig. 3) to our conceptual model (Fig. 1). NMDS is an ordination technique that scales objects in multidimensional space based on newly derived variables from the original data (references in Quinn

and Keough, 2008); objects that are grouped closer together are more similar (for examined variables) than those farther apart. The NMDS algorithm improves the fit between observed and inter-object distances in a configuration (three-dimensional scaling) by iteratively repositioning the location of objects (in this case characteristics of mussel species) in multidimensional space to maximize the concordance in rank order between observed inter-object distances and those predicted by nonparametric regression. The difference in rank order between observed and predicted inter-object dissimilarity can be used to calculate 'stress' values, which are used to evaluate the configuration of objects in three-dimensional space. Stress values over 0.2 may indicate a spurious configuration (references in Quinn and Keough, 2008). Data were transformed prior to NMDS analysis using the following equation: $y' = y_i/y_{max}$ where y_i is the mean observed value (sphericty or density) for a particular mussel species and y_{max} is the largest mean value for a particular mussel species (references in Legendre and Legendre, 2003). To derive the species matrix of dissimilarities we used Euclidian distance. We chose a three-dimensional model that resulted in a stress value less than 0.1. We used R statistical package (R Development Core Team, http://www.R-project.org) for both the graphs and statistical analyses.

To examine the relationships among sphericity and/or density with zooarchaeological preservation for different species, we construct three-dimensional bivariate scatterplots (lollipop graphs) by applying sphericity and density gradient scores from modern reference specimens to zooarchaeological relative taxonomic abundances for the six assemblages discussed above.

6. Sphericity and density in modern mussels

The multidimensional scaling map portrays interspecies similarity and difference in terms of sphericity and density (Kachigan, 1991). A spanning-tree diagram within the NMDS-plot links species in terms of similarity along both dimensions—sphericity on the vertical axis and density along the horizontal axis (Fig. 3). In order to relate the empirical relationships in sphericity and density in the spanning tree diagram to our expectations about interspecific differences in preservation of mussel remains we have superimposed shaded areas for heuristic purposes that correspond to the conceptual preservation model in Fig. 1.
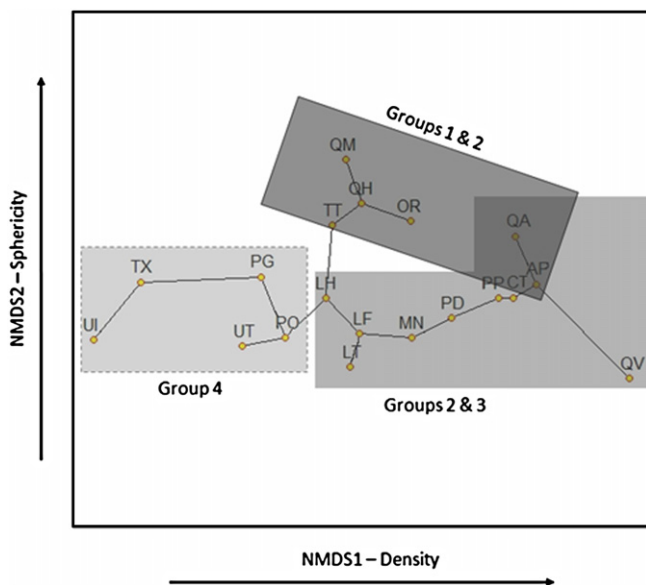

Fig. 3. NMDS spanning tree scaling species to sphericity and density. Shaded boxes coincide with quadrants in Fig. 1A.

Species with highly spherical and moderately dense shells represent a group that is of high interpretive value (group 1; Fig. 3). Members of this group have shell morphologies that are robust and thus that are likely to survive in zooarchaeological assemblages. For nominal-scale biogeographic studies the presence or absence of shells of these species in distinct spatio-temporal settings is meaningful because their absence is less likely to relate to poor preservation than is the absence of a lower sphericity/density species. For taphonomic reasons in studies of subsistence, the proportional abundance of the remains of group 1 species should more reliably reflect prey choice and/or diet breadth, which may relate to foraging efficiency (Botkin, 1980; Broughton, 1994, 1999; Nagaoka, 2001, 2002a Stiner et al., 1999). In addition, subsistence studies that focus on these robust species are more likely to provide reliable data on shifts in freshwater resource patch use (e.g., Nagaoka, 2002a, 2002b) and/or changes (or lack thereof) in environment through time (Byers and Broughton, 2004; Klippel et al., 1978; Wolverton, 2005).

Members of group 2/3 will only provide similarly reliable information in zooarchaeological assemblages that are well preserved. Members of group 4, in contrast, are taphonomically meaningful. The presence and/or abundance of a species that is low in sphericity and/or density in an assemblage indicates that preservation is good or that the species was hyperabundant in the mussel community in the past. Species in group 4 have morphologies that are highly susceptible to fragmentation, decreasing the probability that their identifiable remains will survive in zooarchaeological contexts. In general, for a series of zooarchaeological assemblages in a region (e.g., north Texas) interspecific variability in proportional abundance of the remains of mussel species should correspond to the propensity for the remains of each species to survive taphonomically. Zooarchaeologists simply need to assess the average sphericity and density of species in a community to determine which species are likely to survive.

7. Variability in preservation of mussel remains in north Texas

We depict the proportional abundance of remains of mussel species for six zooarchaeological assemblages from the upper Trinity and upper Brazos rivers in north Texas using three dimensional lollipop graphs with density on the x axis, sphericity on the y axis, and relative abundance on the z axis (data in Table 4). Variability in shell size (length) is much higher within species than is variability in sphericity indicating that size does not account for differences in preservation between species (Table 2). Density is more variable than sphericity, but this may reflect imprecision in the volume displacement measurement technique, which was measured to 0.1 ml in a graduate cylinder compared to size metrics to 0.01 mm by digital caliper. In general, the distribution of abundance in each assemblage matches the expectation that species with spherical/dense shell morphology tend to be high in proportional abundance.

A few important distinctions can be made, however, among the assemblages. In the late Holocene assemblage from the Clear Fork of the upper Trinity River (41TR205), the remains of two species of Lampsilis are high in abundance despite their moderately fragile morphology (Fig. 4A). This probably reflects intense use of mussel beds high in the abundance of these species by late Holocene foragers because only one other fragile species occurs in the assemblage. However, the presence but low abundance of Toxolasma texasiensis, the shells of which are very fragile, suggests better than average preservation at this site. Remains of both species of Lampsilis occur at lower abundance in the other late Holocene assemblage from the Clear Fork (41TR170), but the absence of other species with fragile morphologies indicates that this assemblage is
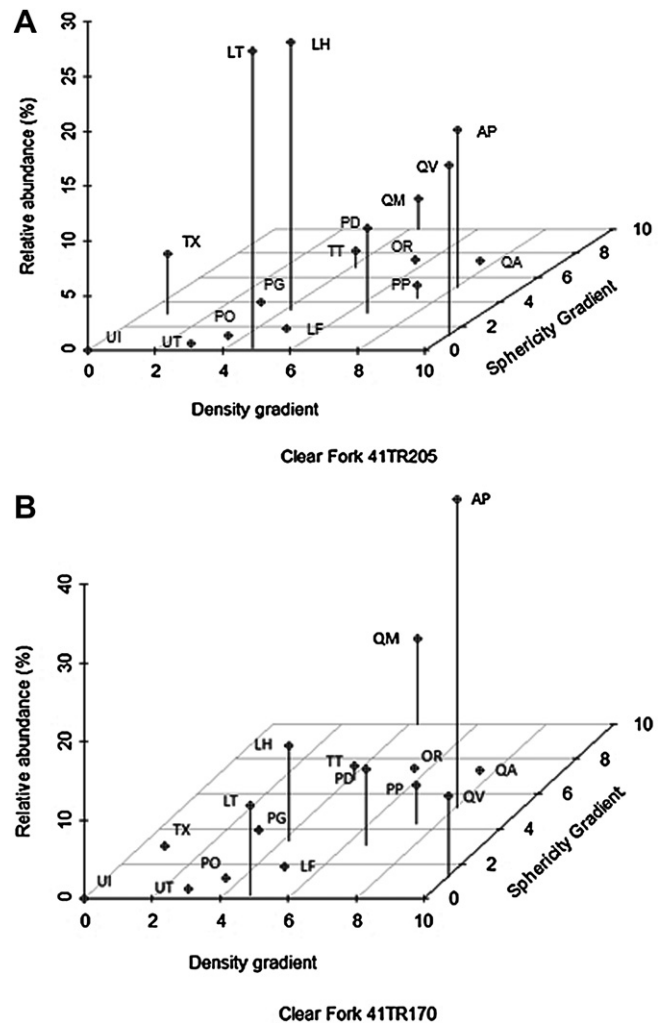

Fig. 4. Three-dimensional lollipop graphs depicting proportional taxonomic abundance of mussel species from two sites on the Clear Fork of the Trinity River. A) Depicts high abundance of two moderately fragile species of Lampsilis at 41TR205 suggesting good preservation of mussel remains at that site compared to B) 41TR170. Abbreviations for species names are in Table 1.

not as well preserved (Fig. 4B). Taken together, evidence from the two assemblages suggests that species of Lampsilis were abundant on the Clear Fork during the late Holocene.

The largest assemblages of shellfish remains reported in this study are from the upper Brazos River drainage (41HI105 and 41HI115). The remains of Amblema plicata dominate these assemblages, which is a species with spherical morphology and dense structure (Figs. 5A & B). That the two species of Lampsilis occur at moderate abundance indicates that this species was common in the upper Brazos as well as in the Clear Fork of the upper Trinity (see above). The same can be said for the assemblage from 41DL8 on Denton Creek in the upper Trinity River drainage. Species abundance in this assemblage declines progressively to the lower left of the lollipop graph (Fig. 5C); however, as in the other assemblages both species of Lampsilis are present and moderately abundant.

8. The late Holocene biogeography of freshwaters in north Texas

Fig. 6 portrays the average proportional abundance of each species in the late Holocene north Texas mussel community in the
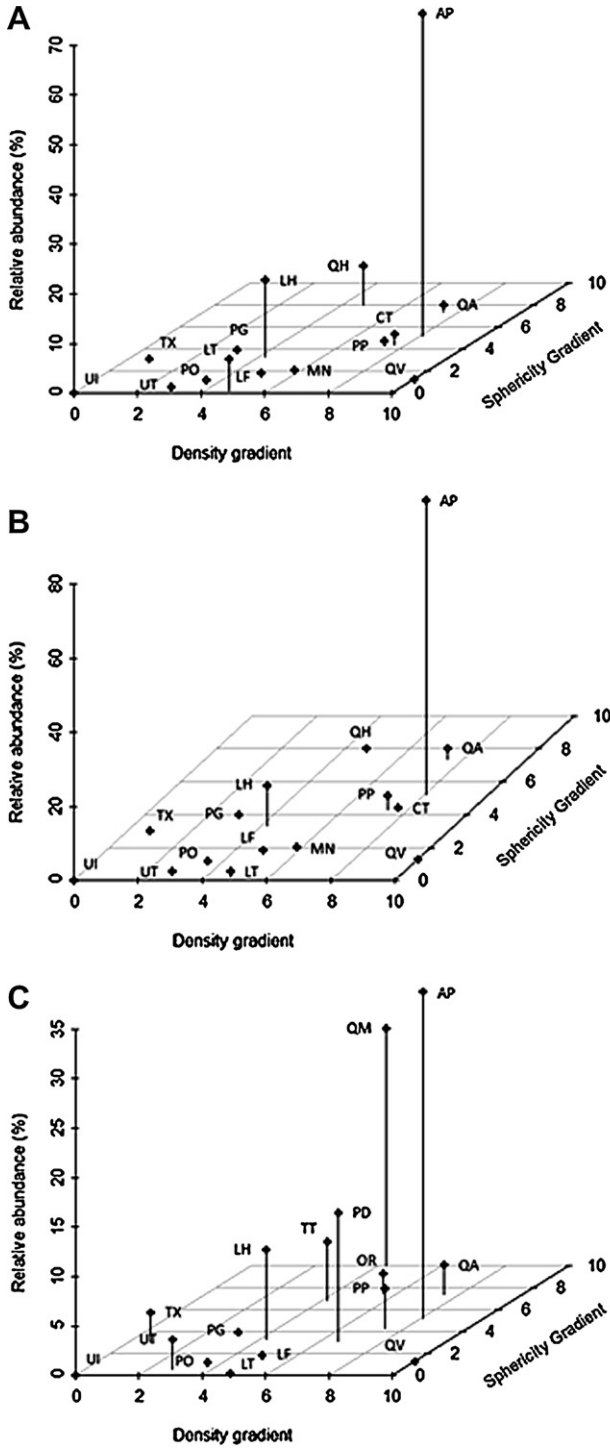
A

B

Fig. 5. Three-dimensional lollipop graphs depicting proportional taxonomic abundances of species at A) 41HI105 and B) 41HI115 on the upper Brazos River and at C) 41DL8 on Denton Creek. Abbreviations for species names are in Table 1.
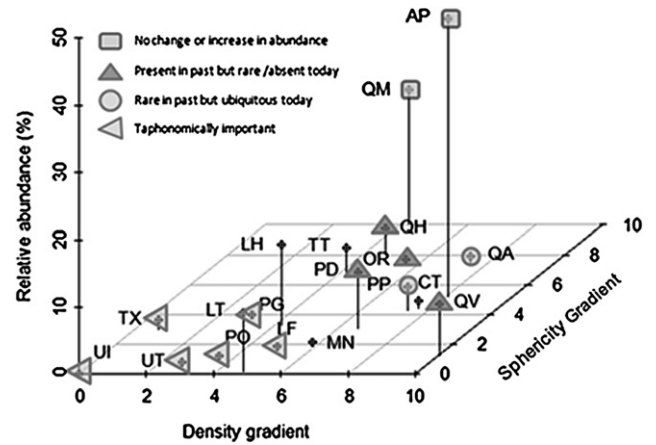

Fig. 6. Three-dimensional lollipop graph portraying the average proportional taxonomic abundance of each species from the six zooarchaeological assemblages. Species are coded using shapes to communicate either their biogeographic/interpretive or taphonomic importance in sites in the region. Abbreviations for species names are in Table 1.

during the late Holocene. We have categorized four species into a third group consisting of species that were "present in the past, but that are rare today," including *Plectomerus dombeyanus*, *Quadrula verrucosa*, *Q. houstonensis*, and *Obliquaria reflexa*. *P. dombeyanus*, for example, does not occur in north Texas today and is thought to have never occurred in the region (Neck, 1990; Randklev et al., in press). The rarity of these species today might relate to a variety of modern human impacts (within the last two hundred years). The upper Trinity River drainage, in particular, is heavily impounded with water retention and flood control reservoirs. In addition, portions of the upper Trinity today are intermittent and fed only by wastewater effluent during the summer months. Although we cannot implicate a causal link between these impacts and the rarity of these species, there is a correlation.

The correlation between rarity of the four aforementioned species and modern human impacts is provocative in light of the fourth group, two species that we have categorized as rare in the late Holocene but common today. *Q. apiculata* and *Potamilus purpuratus* are species that are disturbance tolerant and that thrive in impoundments (Howells et al., 1996). Taken together, the rarity of some species and the commonness of others today portrays a north Texas freshwater mussel community that is tolerant to modern human impacts.

9. Conclusion

It has been known for some time that preservation of shellfish remains relates to shell morphology and structure. We have expanded on previous work to develop and test a taphonomic conceptual model from which to derive expectations about interspecific variability in freshwater mussel shell preservation, which we think also applies to marine shells. It is important that subsistence studies within zooarchaeology that rely on evaluating changes in relative taxonomic abundances incorporate a taphonomic perspective. Shifts in abundance through time may relate to changes in resource patch use, prey choice and diet breadth, environmental change, and/or differential preservation. A taphonomic perspective is also important from a biogeographic perspective. In those rare cases in which species with fragile shells preserve, important paleobiogeographic information is gained. The common condition, however, will be for remains of species with robust shells to preserve; knowing the ecological tolerances and habitat requirements of these

six assemblages. We have categorized several of the species into one of four biogeographic/taphonomic groups. The group to the lower left includes those species that are interpretively important in terms of taphonomy. Remains of these unionid species are fragile, and their presence/abundance reflects good preservation in a zooarchaeological assemblage.

A second group comprises two species (*A. plicata* and *Quadrula mortoni*) that are ubiquitous and abundant in the region today and

species is important for understanding modern and past interactions between humans and the aquatic resources they use and impact.

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