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Reprinted from
Davis, J.R. (Editor). 1982. *Proceedings of the
Symposium on Recent Benthological Investigations
in Texas and Adjacent States*. Aquatic
Sciences Section, Texas Academy of Science,
Austin, Texas.

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ABSTRACT. The ecological factors which influence the geographical distribution of freshwater clams in Texas are reviewed in relation to a map of clam biogeographical subprovinces. The Interior Basin, i.e. Mississippi River system, is the major source of Texas species with limited input from piedmont and coastal areas of adjacent Mexico. Central Texas contains several endemic species. Peripheral species occur in southeastern Texas and the Rio Grande drainage.

Zoogeography involves the study of the past and present geographical distributions of various animal groups with an ultimate goal of understanding the processes which produced observed patterns. The present distributional patterns exhibited by any group are the result of past and present ecological conditions as well as historical factors which affect dispersal opportunities. The purpose of this communication is to analyze the present distribution of freshwater mussels (family Unionidae) in Texas. Only ecological factors will be discussed in the present analysis. Historical factors have certainly affected the distribution of freshwater clams, but analysis of these factors will be presented at a later time.

Knowledge of the life cycle of a group of organisms is essential to an understanding of observed distributional patterns. These mussels may be either monoecious or dioecious. In either case sperm are liberated into the water and are taken into the female clams via the incurrent siphon. Fertilization occurs within the mantle cavity; resultant zygotes are brooded on the gills. Upon attainment of sufficient maturity the larval form, known as the glochidium, is expelled into the water. In most species this form then attaches to a fish. Attachment may occur on the gills, fins or general body surface. At this point the glochidium is a parasitic organism, obtaining all nourishment from the bloodstream of its host. When this stage has matured, it drops off the fish and begins the benthic portion of its life cycle. The familiar clam stage of the life cycle filters plankton and organic matter from the water. Growth generally occurs for three or more years before initiation of reproduction. For a thorough review of unionid bionomics see Fuller (1974).

ECOLOGICAL FACTORS. A number of ecological factors are known to affect the distribution of freshwater mussels. These factors can be grouped into hydrological, substrate and biotic factors.

The quantity and quality of water affect the unionid fauna which can survive in a particular body of water. Water depth and current velocities are extremely important. Carunculina texasensis may be found in water less than 10 cm in depth while other species require a depth of 5 m or more. Few unionids are found in the deeper portions of rivers and lakes. C. texasensis and Unio merus tetralasmus are both typical of still waters; the latter species can even survive lengthy dessication periods (Strecker, 1908; Van der Schalie, 1940). Leptodea laevis, however, requires moving water and is difficult to maintain in quiet aquaria while Megalonoaias gigantea requires 8 to 20 feet of water (pers. observ.).

Water chemistry has profound effects on unionid species (Fuller, 1974). A moderate to substantial amount of calcium is required for the shell of all species. Acidic waters tend to etch the older portions of clam shell, requiring repair when the hole penetrates the inner layer of the shell. Range of pH values normally tolerated is at least 5.6-8.3 (Morrison, 1932). Decreasing pH values requires adaptation to lower dissolved calcium levels but higher dissolved carbon dioxide and metals (Wurtz, 1962; Fuller, 1974:242-243). Recently, Imlay (1973) has hypothesized that potassium level is a significant limiting factor; waters with potassium levels over 7 ppm contain few clams.

Substrate can also be an important ecological factor. Existence of relative proportions of mud, sand or gravel at any particular locality is largely a function of water depth and current but is also affected by upstream geological formations. Variation exists among species of freshwater clams in their ability to properly reorient themselves following transport during periodic floods with concomitant increase in water velocities (Imlay, 1972). Some species are essentially unable to locomote from the place of initial settling; other forms move about readily in soft sediments.

The major biotic factor which affects freshwater clam distribution is the fish fauna which functions as potential hosts for the glochidial stage of the life cycle. Certain species of clams appear to be able to infest a wide variety of fish species while other clams are restricted to several suitable hosts (Fuller, 1974). A few species omit the glochidial stage; these species can exist independent of the fish fauna (except as potential prey of fish).

DISPERSAL METHODS. Freshwater clams classically exhibit low vagility; however, a variety of dispersal methods exist for these animals. Downstream movement may occur during floods but survival of such dispersants is probably unlikely. Some upstream movement by individual clams occurs but is incredibly slow. More rapid

intra-stream movements occur during the glochidial stage when dispersing fish may carry glochidia (=potential young clams) to new areas of a stream or lake.

Interstream dispersal is much more limited. Again glochidial dispersal via fish is the most likely occurrence. Such movement may occur when freshwater fish are able to migrate via temporarily-freshened estuaries to an adjacent drainage (Sepkoski and Rex, 1974). Unionids are rather intolerant of high salinities (see Cvancara, 1970). Transport to an adjacent stream system may also occur via stream piracy. Examples of stream piracy will be covered in a future analysis of the historical aspects of the distribution of freshwater clams; for examples outside Texas see Ortmann (1913) and Johnson (1970, 1972).

Another possible method of interstream dispersal involves avian phoresy. Instances of small unionid clams being found in mud attached to the foot of waterfowl have been reported (e.g., Frierson, 1899), but dispersal in this manner must be rare; van der Schalie (1945) rejected this method as a significant dispersal method for unionids. Most examples of clams attached to bird feet involves the smaller fingernail clams of the family Sphaeriidae.

FAUNAL OVERVIEW - NORTH AMERICA. Eastern North America supports the most diverse freshwater mussel fauna known in the world (Burch, 1975). Some rivers in the Tennessee River drainage may contain nearly 60 species. Zoogeographic provinces based on freshwater clams have been delineated by various workers, e.g. Simpson (1895), Henderson (1931), van der Schalie and van der Schalie (1950), and Roback *et al.* (1980) (see fig. 1). Peripheral to the highly diverse Cumberlandian Province lies a number of subdivisions exhibiting less diverse fauna.

FAUNAL OVERVIEW - TEXAS. Previous workers (as mentioned above) have divided Texas into two major provinces. The Mississippian is peripherally located and contains those drainages which function as tributaries to the Mississippi River. Drainages included are the Canadian, Red, Sulfur and Cypress systems. All other Texas streams, from the Sabine to the Rio Grande, empty directly into the Gulf of Mexico and are included in the West Gulf Province. Such a division is meaningful on a large scale but closer examination of the Texas unionid fauna reveals a more complex pattern.

The Texas freshwater mussel fauna contains approximately 50 species. A survey and revision is currently underway; last compilation of Texas unionids was that of Strecker (1931). Lack of precise species number results from a lack of field surveys and from the maddening plasticity of clam shell morphology.

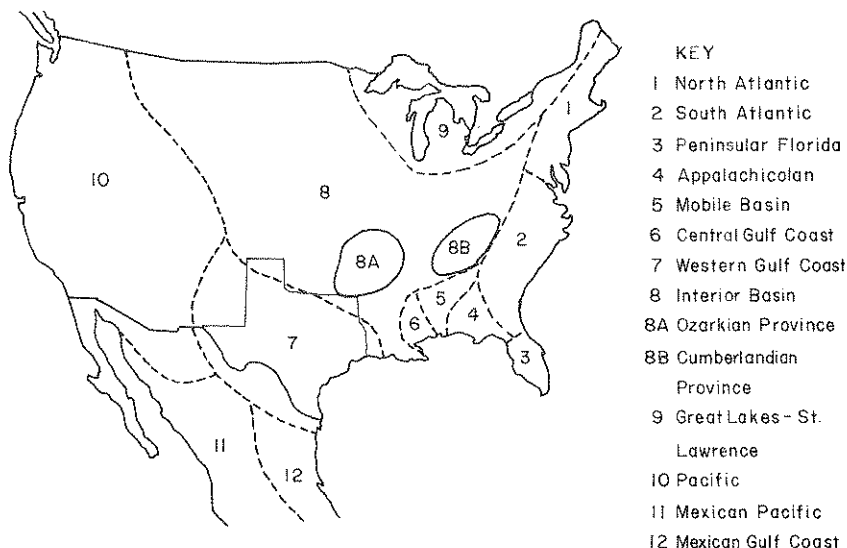


Figure 1. Faunal zones and provinces of freshwater clams of North America after Roback *et al.* (1980).

Variables such as water quality and current velocity may affect the appearance of the shell. Also adding to the nomenclatorial nightmare has been a classical unawareness of genetic variation within a taxon. The habit of christening all variants with a new epithet (to which is attached the name of the descriptor), has severely complicated the taxonomic situation. The fifty-odd valid species which occur in Texas are represented by over 200 specific epithets, most of which have been relegated to various states of synonymy. Analysis of the distribution of the freshwater clams of Texas has allowed the subdivision of the major provinces into several subprovinces (see Figure 2).

The Mississippian Province in Texas is referred to the Texoma Subprovince. It consists of the segment of the Canadian River which transects the Panhandle in addition to the Red River drainage; much of western Oklahoma and Kansas are included in this subprovince. Relatively few species occur in the western areas of this province; only one species is reported from the Texas segment of the Canadian River. Species diversity in the eastern portion of this area is moderately high.

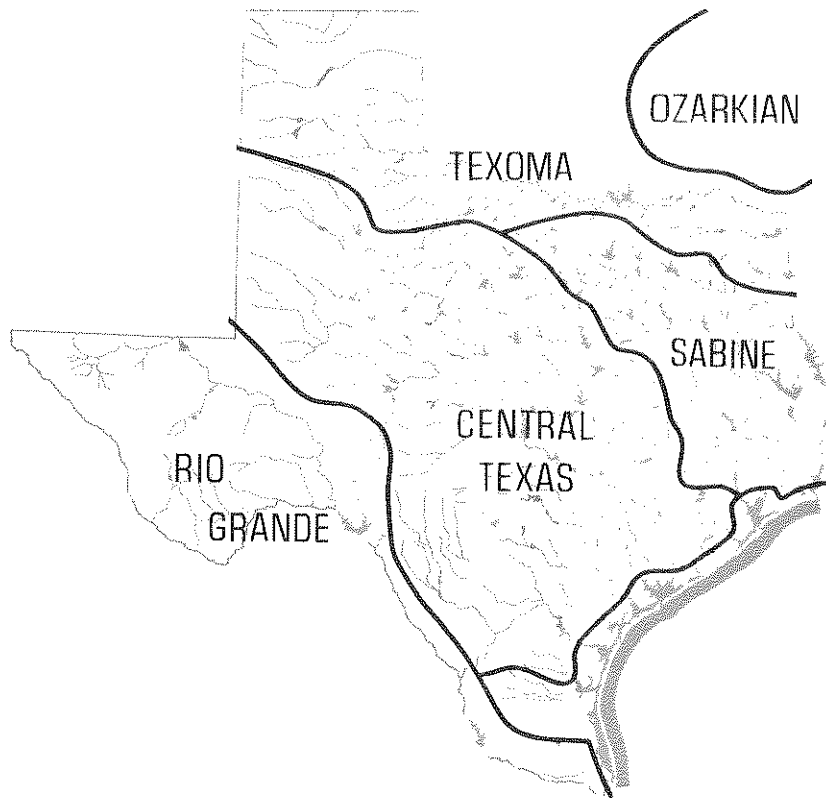


Figure 2. Biogeographical subprovinces of freshwater clams of Texas (no clams native in coastal area as indicated).

The Western Gulf Province includes the vast majority of Texas and has been delineated into three subprovinces. The Sabine Subprovince includes the eastern part of Texas (except for that encompassing the Texoma Subprovince) and adjacent southwestern Louisiana. Texas rivers in this area are the Sabine, Neches, Trinity and San Jacinto. Indicative of the subprovince are Lampsilis satura, Proptera amphichaena and the problematical species in the genera Fusconaia and Pleurobema.

The Central Texas Subprovince consists of the major streams in the area, i.e., Brazos, Colorado, Guadalupe, San Antonio and Nueces plus the shorter coastal plain streams, i.e. San Bernard,

Lavaca, Mission and Aransas rivers. Also included are the creeks feeding into the Baffin Bay system. Species present are wide-ranging Mississippian species, many of which occur southwestward into Mexico. One southern-derived species, Cyrtoneias tampicoensis, occurs throughout this region. This subprovince is characterized by four species which comprise the only endemic freshwater mussel community in Texas. These clams are Quadrula petrina, Quadrula aurea, Lampsilis bracteata and Sphenonaias mitchelli.

The Rio Grande Subprovince in Texas consists of the Rio Grande drainage; its southern extension into Mexico is not clear but does not include the Panuco-Tamesi system of southern Tamaulipas (see Pilsbry, 1909). This province is dominated by the southern-derived C. tampicoensis. Species occurring no further north than the Rio Grande include Popenaias popei, Quadrula couchiana, Disconaias fimbriata and Truncilla cognata. All of these species are rare in Texas and appear to be restricted to the upper portions of the drainage in Texas and Mexico. Few species occur in the New Mexico and Colorado portions of the Rio Grande (Metcalf and Stern, 1976; Brandauer and Wu, 1978).

ECOLOGICAL DETERMINANTS. Each of the subprovinces in Texas can be ecologically characterized in relation to the other subdivisions.

The extreme depauperateness of the freshwater clam fauna of the Texoma Subprovince is due to the extremely low runoff rates in an area characterized by braided, sandy-bedded streams. Tributary streams of the Red in Oklahoma support a number of species typical of the Ozarkian Subprovince. These species are unable to survive in the main streambed of the Red (see Valentine and Stansbery, 1971). That permanent water is the controlling factor is indicated by the increased species diversity of the freshwater clam fauna of Lake Texoma, an impoundment constructed on the Red in the mid-1940's (see White and White, 1977; Neck, 1982-this volume).

The Sabine Subprovince is typified by low-gradient streams over generally soft substrates in an area of relatively high precipitation. Water flows are more dependable than in areas to the west. The Sabine Subprovince follows the area of highest average annual runoff rates in Texas with the exception of the upper and middle portions of the Trinity River (Miller et al., 1963). Water chemistry is typified by acidic waters. The Trinity River is somewhat atypical in this grouping. The upper reaches of the Trinity drain Cretaceous limestones and chalk but these substrates form a small portion of the total area drained. The upper Trinity (above Dallas) does not contain the species typical of this subprovince; however, lack of additional species

indicative of the adjacent Central Texas Subprovince precludes grouping with that subdivision.

The inland portion of the Central Texas Subprovince is drained by high-gradient streams on well-indurated substrates, mostly Cretaceous limestones. Water flow is very erratic varying from severe droughts with almost no flow to catastrophic flooding (Baker, 1975). Water chemistry is typified by high levels of calcium carbonate yielding a moderately hard water. The coastal portion of the Central Texas Subprovince has drainages of low gradient on generally soft substrates. However, water chemistry is greatly influenced by the calcium carbonate-enriched water from upland areas of the Central Texas Subprovince.

The Rio Grande Subprovince is characterized by both high-gradient streambeds on generally hard substrate and low gradient deltaic distributaries on soft substrate. However, the Pecos River contains very alkaline water (gypsum and halite) in an area of unindurated substrates. The dominating portion of this subprovince lies in the area of confluences of the Rio Grande with the Pecos and Devils. The paucity of species native to the Rio Grande Subprovince is probably due to the restricted coastal plain to the south in Tamaulipas as much as the northward increase in seasonality, i.e. the loss of a tropical equable climate. An additional factor is the natural salinity of the Pecos which affects all of the Rio Grande below the confluence of the two streams.

FAUNAL ANALYSIS. The unionid fauna of Texas is seen to be a grouping of approximately 50 species with affinities to the Mississippi drainage to the east and but little influence from the Panuco-Tamesi system to the south. The major factor causing the depauperate nature of this fauna is an apparent mismatch of water supply and niche diversity. Eastern Texas has a supply of water and a nearness to the Mississippi as a faunal source, but the rivers are generally sluggish with acidic waters. The high-gradient streams of central and western Texas exhibit potential niche diversity but have irregular water flow.

Only one area of Texas appears to have been isolated for a sufficient time period to allow evolution of autochthonous forms. *Q. petrina*, *Q. aurea* and *L. bracteaeta* appear to have originated within the Central Texas Subprovince. However, the paucity of published information concerning clam faunas south of the Rio Grande drainage precludes determination of origin of several species occurring no farther north than this stream.

Very few species occur from the Red River to the Rio Grande; two forms that do are *L. teres*, *A. imbecillis* and *M. gigantea*. Taxa of two other genera, *Carunculina* and *Uniomerus*, occur

throughout the state, but species delineation and geographical distribution are still clouded for these forms.

CONTRAST WITH OTHER FAUNAE. Many maps have been drawn to illustrate the distributional patterns exhibited by different faunal groupings in Texas. A synthesis of biogeographic patterns as presented by Blair (1950) was based on terrestrial vertebrates but works very well on certain terrestrial invertebrate groups (Neck, unpub. data.) There are similarities as well as dissimilarities between Blair's map and the clam map presented here. Blair's Austroriparian Biotic Province is very similar to the Sabine Subprovince of this analysis. In a similar manner the more restricted Balconian Biotic Province of Blair is analogous to the Central Texas Subprovince, presented here. This similarity is the result of the dominance of water availability and limestone substrate, respectively, in the two above instances. In other cases, the obvious importance of current drainage patterns in determining clam distributional patterns overrides the terrestrial influences of geological substrate and meteorological parameters. In western Texas, the paucity of permanent water and, concurrently, freshwater mussels, also preclude an increased concordance between these biogeographic patterns.

A greater similarity would be expected between the unionid distributional pattern and another grouping of freshwater organisms, e.g. freshwater fishes. Hubbs (1957) presented an analysis of the freshwater fish distributional patterns in Texas. No map was presented, however; reference was made to an earlier analysis by Knapp (1953). This delineation of faunal relationships was largely drawn along stream divides (although the Navasota River is grouped with the rivers to the east rather than with the Brazos). One would expect a certain similarity with the clam pattern as presented here. However, the major portion of the lower coastal plain is divided quite differently.

ACKNOWLEDGEMENT. I thank T. B. Samsel III for drafting the figures for this publication.

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