
The utilization of freshwater habitats by gill-bearing snails and clams and intertidal marine, brackish, freshwater, and terrestrial habitats by snails with vascularized mantle cavities comprises a geologic history spanning nearly 400 million years. Not until the Late Jurassic and Cretaceous, however, does the record provide evidence of substantial diversification of nonmarine Mollusca. For the purposes of this symposium, this paper briefly reviews the systematics, biochronology, biogeography, and faunal data base of the Mesozoic nonmarine Mollusca of North America. In addition, I wish to commemorate the recent passing of John H. Hanley, by reviewing his contribution to the study of the paleoecology of Mesozoic and Cenozoic nonmarine Mollusca, through both publication and service.

SYSTEMATICS

To a large extent, the generic and suprageneric classification of fossil nonmarine Mollusca is based on anatomical characteristics of living mollusks. This situation poses obvious problems of accurately assigning many fossils, especially where shell morphology is simple and does not reflect anatomical features. Convergent evolution on certain shell forms by unrelated or closely related taxa adapting to similar environmental settings has frequently resulted in the taxonomic reshuffling of species and reidentification of specimens previously assigned. In many cases, the development of reliable species concepts required more rigorous discrimination of intra- and interspecific morphological variability than was historically employed. Currently, most Mesozoic and early Cenozoic nonmarine mollusk families are in need of comprehensive review. Many thousands of known localities and tens of thousands of collected specimens await analysis, and few stratigraphic intervals or geographic areas have received intensive study. The following review is based on a compilation of nominal and unpublished taxa to show the spectrum of taxonomic diversity of Mesozoic nonmarine Mollusca.

Two classes are represented, the Gastropoda and the Bivalvia (= Pelecypoda). The freshwater bivalve record, represented primarily by palaeoheterodont river clams (unionids) and the heterodont finger-nail clams (pisidiids), consist of approximately 140 species organized into 30 genera, 11 tribes and subfamilies, four families, four orders, and three subclasses. The gastropods are taxonomically more diverse, having invaded both the freshwater and terrestrial realms. Combined, these environments are represented by about 230 species organized into 68 genera, 25 families, five orders, and two subclasses. With the inclusion of the small late
Paleozoic nonmarine mollusk fauna and the relatively species-rich Paleocene and Eocene faunas, approximately 670 pre-Oligocene North American taxa are presently recognized and available for study (see Figure 2).

Gastropoda

The classification of higher gastropod taxonomic categories is in a state flux as paleo- and neomalacologists attempt to distinguish between grades of organization, which predate most classification schemes, and clades, which depict monophyletic ancestry based on homologously derived shared characters. The variations of currently employed classifications are illustrated in Table 1.

Table 1. Suprafamilial Classification of Mesozoic Nonmarine Gastropoda

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<tbody>
<tr>
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<td>SBC Pulmonata</td>
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<td>pulmonates not</td>
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</table>

SP = Super, SB = Sub, C = Class, O = ORD = Order, F = Family

The differences between the organizations presented by these classifications are largely the result of the weighting of certain anatomical criteria. The basic similarity between these schemes suggests that the taxonomic categories distinguish reasonably well the intertaxon variability, but, as has been noted by Hubendick (1978), Graham (1985), Haszprunar (1985), and Solem (1985), they do not necessarily represent monophyletic groupings, or incorporate fossil data. For the purposes of review, Haszprunar’s cladistically-based classification will be followed with reference to the others.

Prosobranchs. Prosobranchs (or streptoneurans) display the primary features resulting from the process of torsion. Torsion alters the larval animal's bilaterally symmetrical alimentary and nervous systems, and laterally paired organs, to an arrangement where the mouth and anus are juxtaposed, the nerve cords are crossed resembling a figure-eight, and the position and number of the various visceral organs are changed and/or reduced. The subclass names Prosobranchia and Streptoneura mean forward gill and twisted nerve, respectively, referring to the results of torsion seen in the adult animal. Torsion distinguishes gastropods from members of all other molluscan classes. As with the other mollusks, the mantle secretes the shell, and the radula represents molluscan dentition. Prosobranchs have a distinct head with a single pair of tentacles. The mantle cavity contains the ctenidia (gills). The sexes are usually distinct. Many prosobranchs have an operculum, which is an organic, partially or completely mineralized plate of varying design. The operculum is used to close off the aperture as the animal retracts inside its shell. Unfortunately, the operculum is not frequently preserved in the fossil
record. Prosobranchs evolved in the Early Cambrian and have since inhabited marine, freshwater, and terrestrial settings.

Nonmarine prosobranchs include freshwater and terrestrial taxa in the Order Archaeogastropoda (raised to a subclass by Runnegar, 1985) and freshwater taxa in the Order Caenogastropoda (nonmarine Mesogastropoda). Nonmarine archaeogastropods are limited to a few families in the Suborder Neritopsina, which includes marine, freshwater, and terrestrial species (Knight et al., 1960). This taxon was raised to ordinal rank (see Burch, 1982) in recognition of its distinct evolutionary history. The nonmarine caenogastropods, representing, in general, a derived condition from the more primitive archaeogastropods, were subdivided by Haszprunar (1985) into the suborders Architaenioglossa and Neotaenioglossa, encompassing "old and new" taenioglossids (= mesogastropods) that share a similar type of radula (see Knight et al., 1960). The architaenioglossans include the Cyclophoridae, Ampullaridae, and Valvatae, whose species comprise about one-quarter of the total Mesozoic nonmarine gastropod fauna (see Figure 2). The neotaenioglossans include the Rissooae, Cerithiaceae, and Littorinaceae. All three superfamilies contain many marine taxa, along with varying numbers of nonmarine species. The nonmarine rissoocean Hydrobiidae and cerithiacean Plueroceridae comprise about 30 percent of the Mesozoic nonmarine gastropod record and continue to be a diverse element, along with the architaenioglossan Viviparidae, into the Paleocene and Eocene of North America. Haszprunar (1985) suggested that the ancestry of the Heterobranchia (including the Pulmonata) is derived from the marine neotaenioglossans.

Pulmonates. Pulmonate gastropods have altered the torted anatomical arrangement of the prosobranchs through the process of detorsion producing a euthyneurous condition (Subclass Euthyneura, see Table 1). Detorsion effectively results in the uncrossing of the visceral nerve cords and the loss of true gills. In pulmonates, the mantle cavity is vascularized and functions, in part, as a lung (Pulmonata). Thus, they respire with atmospheric oxygen, whether inhabiting intertidal marine, brackish, freshwater, or terrestrial environments. Pulmonates are hermaphroditic and do not have an operculum. An epiphram (a thin film of mucous) is secreted by some terrestrial taxa to inhibit dessication.

Mesozoic pulmonates are classified, depending upon approach, into three groups: the Archaeopulmonata, Branchiopulmonata (Basommatophora, s.s. of Solem, 1985), and Stylommatophora (see Table 1). The archaeo- and branchiopulmonates comprise the traditional use of Basommatophora (s.l.). These taxa are the aquatic pulmonates, and, as a group, are distinguished from other pulmonates by the position of the eyes near the base of a single pair of tentacles (see discussion by Hubendick, 1978). The basommatophorans are represented by a wide variety of shell shapes, ranging from patelliform to nearly planispiral to high-spired conic. The archaeopulmonates represent the traditionally accepted ancestral stock for the Pulmonata, although the branchiopulmonates and stylommatophorans, in particular, have a substantially older fossil record (see Solem and Yochelson, 1979, and Solem, 1985). Constituent taxa inhabit marine, brackish, freshwater, and limited terrestrial environments. The Mesozoic nonmarine record includes taxa assigned to the ellobiaceous Otiniidae and Ellobiidae, which comprise less than one-tenth of the gastropod fauna. The branchiopulmonates include the familiar Lymnaeidae, Planorbidae, and Physidae, common to the North American Holocene. The taxonomy of living species, including superfamily, familial, and generic groupings, is a subject of considerable discussion, posing significant classification uncertainties for the paleontologist. The branchiopulmonates comprise about 17 percent of the Mesozoic nonmarine gastropod record, and inhabit a variety of freshwater habitats usually associated with lacustrine environments.

Stylommatophora is an order with considerable diversity, as reflected by its numerous families, but is considered to represent a monophyletic clade by Solem (1985) and Haszprunar (1985). Stylommatophorans are terrestrial pulmonates with two
pairs of tentacles. The posterior pair is tipped with eyes. Their subordinal or ordinal classification is based on the form of the excretory system (Hyman, 1967). Solem (1976, 1978, 1985) raised the Stylommatophora to superordinal rank, and the various suborders to orders. The late Paleozoic and Mesozoic nonmarine record in North America includes the Orthurethra and Sigmurethra (see Table 1). The Orthurethra has a questionable Mesozoic record in North America, but diversifies considerably from the Paleocene into Eocene times. The sigmurethrans are relatively well known from the late Cretaceous, with 15 recognized taxa. As with the orthurethrans, there is a marked increase in recorded sigmurethran taxa (about 450 percent) through the Paleocene and Eocene.

**Bivalvia**

The freshwater bivalves of the Mesozoic are almost completely represented by the families Unionidae and Pisidiidae (= Sphaeriidae), with a few additional species known from the Neomiodontidae (Table 2). Together they represent about one-third of the Mesozoic nonmarine Mollusca. These families, like most bivalves are bilaterally symmetrical, with the soft parts enclosed by two lateral valves that are hinged by an elastic ligament. The valves usually articulate on interlocking hinge teeth of different styles (heterodont). The valves have a corresponding bilobed mantle that secretes the shell. Unlike gastropods, bivalves lack a head, radula, and tentacles, and have a highly modified foot. Bivalves are known from the Early Cambrian and occur in marine, brackish, and freshwater environments.

**Unionids.** Freshwater mussels or clams are placed in the Superfamily Unionacea and Order Unionoida of the Subclass Palaeoheterodonta (= Order Schizodonta, in part, of the Subclass Eulamellibranchia). The suprageneric classification of unionids is based primarily on soft anatomy, especially utilizing the structure of the gills in relation to reproduction, and on the larval glochidia (Burch, 1975b; Davis and Fuller, 1981). Considerable variation has existed in the methodology of classification of freshwater clams. As in the gastropods, many organizational schemes were based on features without reference to phylogenetic implications. A recent comprehensive approach, however, by Davis and Fuller (1981) employed a number of characteristics that are believed to produce natural groups. Their classification is used here to order the fossil taxa into tribes and subfamilies (Table 2).

Fossil bivalves preserve morphological features of value in specific and generic assignments. Shell shape is notoriously variable, while dentition and beak sculpture are relatively conservative, which has produced many names that may simply reflect ecophenotypic or biogeographic variation. The problem of accurate, consistent identification is compounded by the incomplete preservation of many nominal taxa. In many cases, in part because of the difficulty of collection, few specimens of a particular taxon are known, prohibiting the recognition of intertaxon variability even at one locality or within a single stratigraphic interval. These problems are not insurmountable and largely reflect the survey approach to the collection and subsequent naming of many taxa in the past.

The present classification of Mesozoic and early Cenozoic freshwater unionids utilizes the beak and umbonal sculpture and shell shape. Russell (1934) first proposed the reclassification of fossil unionids on these features and reassigned many taxa from the Eurasian Unio to extinct genera or to other extant North American genera (see Taylor, 1975). The continued use of Unio in the North American fossil record refers to clams that are unsulptured or are sculptured but have yet to be sufficiently studied to be reassigned or placed in new genera. From their original use in western Canada, the species concepts of Russell's fossil genera and other assignments have expanded through a new generation of pigeon-holing and are in need of comprehensive comparative review.
Unionoids are known throughout the Mesozoic. The number of species reported from the Late Triassic, Late Jurassic, and Early Cretaceous is about that same, collectively comprising about 40 percent of the total Mesozoic bivalve fauna. The Subfamily Hyriinae (Table 2), in the Mesozoic, is known exclusively from the Late Triassic of the southwestern United States and from the Newark Supergroup of Pennsylvania. The Unionidae, including the ill-defined Unio, has been reported from the Late Jurassic and throughout the Cretaceous. The remaining subfamilies are known only from the Cretaceous and include the Ambiliniae, Anodontinae, and Margaritiferinae. Ambiliniae taxa, including Proparreysia and Plesielliptio, are particularly diverse in the Late Cretaceous and comprise over one-third of the recorded bivalve taxa of this epoch. Unionoid faunal composition shifts rather markedly in the Paleocene and Eocene, with the loss of many of the more highly sculptured clams. Generic diversity is also reduced by more than slightly one-third.

Pisidiids. The finger-nail clams represent a relatively small but important and essentially unstudied component of the freshwater clam fauna. Pisidiids are classified in the Order Veneroida of the Subclass Heterodonta (Table 2). Their shells are small to minute, usually less than 10 mm, but some Late Cretaceous species reach almost 15 mm in length. The shells are thin and fragile, and lateral teeth are present on either side of cardinal teeth. Pisidiid subfamilies are classified on the basis of soft anatomy, but extant genera recognized in the fossil record can be generally distinguished on the basis of shell marginal outline, valve inflation, beak position, and dentition (Burch, 1975a). Pisidiids first occur in the Late Cretaceous, comprising about 15 percent of the bivalve fauna, and continue to diversify into the Palaeogene. They are usually found in lacustrine deposits, claystones of varying size, being associated with minor carbonate deposits or well-sorted siltstones, and may locally represent a significant percentage of the faunule. However, most taxa are known from only a few localities. The number of reported occurrences undoubtedly reflects a collecting bias at known fossil sites, as well as overlooked small localities.

Table 2. Suprageneric Classification of Mesozoic Nonmarine Bivalvia*

<table>
<thead>
<tr>
<th>SBC Palaeoheterodonta</th>
<th>SBC Heterodonta</th>
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<tbody>
<tr>
<td>ORD Unionoida</td>
<td>ORD Veneroida</td>
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<tr>
<td>SPF Unionacea</td>
<td>SPF Corbiculacea</td>
</tr>
<tr>
<td>FAM Unionidae</td>
<td>FAM Pisidiidae</td>
</tr>
<tr>
<td>SBF Ambilininae</td>
<td>SBF Euperinae</td>
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<tr>
<td>SBF Anodontinae</td>
<td>SBF Pisidiinae</td>
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<tr>
<td>SBF Hyriinae</td>
<td>SBF Sphaerinae</td>
</tr>
<tr>
<td>SBF Margaritiferinae</td>
<td>SPF Arcticacea</td>
</tr>
<tr>
<td>SBF Unionidae</td>
<td>FAM Neomiodontida</td>
</tr>
</tbody>
</table>

* after Davis and Fuller, 1981; Newell, 1969; Cox et al., 1969
SP = Super, SB = Sub, C = Class, O = ORD = Order, F = FAM = Family

BIOCHRONOLOGY AND BIOGEOGRAPHY

The North American record of Mesozoic nonmarine Mollusca is documented primarily from the Late Triassic, Late Jurassic, and late Early and Late Cretaceous (Figure 1). Unpublished records and inferences also indicate a record from the Early Jurassic (E. Evanoff and S.C. Good, oral comm., 1987; Harshbarger et al., 1957). This distribution is probably real and reflects the habitats suitable for habitation by freshwater mollusks. Although suitable terrestrial settings probably existed in Upper Triassic and Jurassic deposits, the record does not show terrestrial pulmonates in the Mesozoic until late in the Early Cretaceous. Note,
however, that stylommatophorans are reported from Carboniferous and Permian deposits in North America and Europe (Solem and Yochelson, 1979).

Triassic. Freshwater prosobranchs, unionids, and clams of uncertain affinities have been reported from the Upper Triassic Chinle, Dolores, and Dockum Formations of the Colorado Plateau and eastern New Mexico and adjacent Texas, and from the Newark Supergroup of Pennsylvania and Massachusetts. About 27 taxa are known from these units with one-third occurring in the eastern states. The low familial diversity of the Late Triassic is probably real. The fluvial, lacustrine, floodplain, and upland environments of this time in the southwest were suitable for molluscan taxa as indicated by the other invertebrate, vertebrate, and plant associations (Breed and Breed, 1972; Gottesfeld, 1972; Stewart et al., 1972). The relatively large number of unionids indicate relatively major perennial river systems.

From 1865 to 1951, two to three new Late Triassic species were named in about one paper per decade. These publications generally provided little geographic or geologic context for these taxa, which poses difficult problems in evaluating the biostratigraphic potential of the freshwater mollusks of this time. The most recent study of this fauna was presented by Kues (1985) on the Chinle Formation of eastern New Mexico. Kues identified six additional unionid morphotypes from a few closely spaced localities at approximately the same stratigraphic horizon. Similar well-documented records are necessary to upgrade our understanding of the freshwater mollusks of the Late Triassic. Steve Good, of the University of Colorado-Boulder, is presently conducting a review of the unionids from the Late Triassic to Late Jurassic.

Jurassic. The diverse habitats of the Upper Jurassic Morrison Formation supported the primary record of nonmarine Mollusca in the Jurassic of North America. This fauna received some overall taxonomic treatment by Yen (1952), with a more recent general review by Hanley, Evanoff, and Good (1986). In total, 44 taxa from 10, or possibly 11 families have been reported from the Morrison, representing at least a three-fold increase in familial diversity since the Triassic (Figure 3). The fauna is dominated by prosobranchs and unionids, but aquatic pulmonates, including the Lymnaeidae, Planorbidae, Ellobiidae, and Otimidae, make their first significant appearance in North America. A lymnaeid record may also be known from the Lower Jurassic Kayenta Formation (Harshbarger et al., 1957; Imlay, 1980). Nonmarine mollusks are known throughout the geographic extent of the Morrison from the southern part of the Colorado Plateau to central Montana. A generalized nonmarine molluscan biostratigraphy distinguishes upper and lower Morrison in the Colorado Plateau, but does not appear discernible further to the north (Hanley, Evanoff, and Good, 1986). Our present knowledge of the mollusk distribution may, in part, be biased by the greater number of localities known from the lower half of the formation, and by facies control of the animals as evidenced by a homogenization of the stratigraphic distribution in northern exposures. The record of molluscan occurrences is less than adequately known as the ten papers dealing with the Morrison fauna had a primarily taxonomic coverage. Of the nominal taxa, about one-half are known from only one or two localities and over three-quarters are known from three or less. Emmett Evanoff and Steve Good, of the University of Colorado-Boulder, are presently analyzing the structure of the Morrison mollusk record.

Cretaceous. The Cretaceous record of nonmarine Mollusca can be divided into two parts, reflecting primarily an Aptian-Albian and Campanian-Maastrichtian species distribution. The faunas of these intervals are distinctive and separated by the major expansions of the mid-Cretaceous seaway (Haq et al., 1987). The Early Cretaceous record is represented by about 120 taxa, a three-fold increase over the Late Jurassic (Figure 1). The heterodont family Neomiodontidae is first reported in Early Cretaceous deposits, thus recording the initial exploitation of a niche by
small freshwater clams. In addition, the prosobranch Hydrobiidae, Viviparidae, and
Thiaridae are well-documented for the first time in North America, along with the
aquatic pulmonate family Physidae. The Early Cretaceous record also includes the
first Mesozoic occurrence of terrestrial pulmonates including a helminthoglyptid and
a possible achatinellid. The Late Cretaceous fauna contains the first record of the
heterodont bivalve family Pisididae, along with the addition of seven terrestrial
pulmonate families, including representatives of the Camaenidae, Urolopidae,
Subulinaidae, and possibly of the Zonitidae and Helicidae. These taxa make up most of
the four-fold increase in species diversity over the Late Jurassic and doubles the
number of families (Figures 1, 3). As noted by Solem (1985, p. 272), the rise in
importance of pulmonates may have resulted from "the fortuitous appearance of
feathered chariots in the Jurassic...."

Previous research on Cretaceous nonmarine mollusks primarily concerns the
introduction of new taxa from local geographic areas or stratigraphic intervals.
About 20 authors in 70 papers have published the primarily pre-1960 record of
Cretaceous nonmarine taxa. Many of these names were introduced by F.B. Meek and
F.V. Hayden, L.S. Russell, and T.-C. Yen. As noted before, few papers have dealt
specifically with the variety of nonmarine environments comprising the Cretaceous
record of North America. An important exception was published by Fürsich and
A soon-to-be published, stratigraphically-organized compilation of primary nonmarine

Figure Explanations:

Figure 1. North American pre-Oligocene Record of Nonmarine Molluscan Taxa.

Geochronology abbreviations: TER = Tertiary, P-E = Paleocene-Eocene; K =
Cretaceous, L = Late, L E = late Early (Aptian-Albian), E E = early Early
(pre-Aptian); JUR = Jurassic, L = Late, E-M = Early and Middle; TRI =
Triassic (subunits as in Jurassic); DEV C PER = Devonian, Carboniferous,
Permian; UND. = undivided. Compiled from primary sources. "Totals"
represent number of species and subspecies in each taxonomic category. 1/
Diagram notes the existence of nonmarine bivalves in the Paleozoic record
but does not express the number of possible North America taxa.

Figure 2. North American pre-Oligocene Record of Nonmarine Gastropod Taxa.

Breakdown of gastropod diversity by orders and subclasses (see Table 1).
Abbreviations - Prosobranchia: ARCHA. = Archaeogastropoda, ARCHI. =
Architaenioglossa, NEO. = Neotaenioglossa; Pulmonata: ARCHA. = Archaeo-
pulmonata, BRAN. = Branchiopulmonata, STYLO. = Stylommatophora; other
abbreviations as per Figure 1.

Figure 3. Worldwide pre-Oligocene Record of Nonmarine Molluscan Families.

Geochronology arranged to be comparable to the North American species
record presented in Figure 1 (see for abbreviations). No families become
extinct, but are not known from every interval. 1/ Figure does not include late Paleozoic bivalve families assigned to the Unionoida.
Compiled from primary sources and from Wenz (1938-44) and Zilch
(1959-60). See also Solem (1976, 1978, 1979) and Solem and Yochelson
(1979). 2/ Figure includes Paleozoic record of non-Unionacean families
assigned to Unionoida (Cox et al., 1969), but are not included in Mesozoic
and Cenozoic tabulations.
### Figure 1

**GEOCHRONOLOGY**

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**NORTH AMERICAN NONMARINE MOLLUSCAN SPECIES**
*(pre-Oligocene)*

- **MOLLUSCA**: Totals: 674
- **GASTROPODA**: 477
- **BIVALVIA**: 197

- Heterodont portion of BIVALVIA record

### Figure 2

**GEOCHRONOLOGY**

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**NONMARINE GASTROPODA**

- **GASTROPODA**: 250, 227, 23, 104, 123, 22, 84, 121
- **PROSOBRANCHIA**: 0, 1, 7
- **PULMONATA**: 0, 50, 100, 150

- Questionable Record
- MesoGastropoda
- Basommatophora

### Figure 3

**GEOCHRONOLOGY**

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**NONMARINE MOLLUSCAN FAMILIES**
*(pre-Oligocene - Worldwide)*

- **MOLLUSCA**: 54
- **GASTROPODA**: 15
- **BIVALVIA**: 3

- Questionable Record
molluscan localities has been completed by Hanley, Kauffman, and Russell. This work represents a significant contribution to the assessment of the biostratigraphic potential of nonmarine Mollusca in the Cretaceous. Their correlation chart will represent a standard for the comparison of new research on the durations of nonmarine taxa. Without question, this compilation only scratches the surface in documenting the Cretaceous record. Many taxa are known from only their type locality. In addition, 50 percent of the known taxa were named prior to the collection of even 10 percent of the presently known localities. As an example, the Kaiparowits Basin of southern Utah includes a nearly continuous Upper Cretaceous section with hundreds of previously unreported nonmarine mollusk localities from coastal floodplain to upland habitats (J.G. Eaton, oral comm., 1987). As noted by Hanley (1977), Cretaceous stages based on ammonite biozones can be recognized by our current limited knowledge of nonmarine molluscan distribution. This resolution will undoubtedly be refined as studies focus on regional and inter-regional biostratigraphy, as evidenced by the molluscan biozonation being established for the Paleocene of the northern Great Plains (Hartman, 1984a, b).

JOHN HANLEY AND PALEOECOLOGY

The major individual effort on the paleoecological study of western interior nonmarine Mollusca has been by John H. Hanley, geologist for the United States Geological Survey. John died unexpectedly last November, and this symposium provides the opportunity to briefly comment on his contribution (see appended Hanley bibliography). John's paleoecologic studies were just beginning to bear fruit. His meticulous devotion to establishing a rigorous foundation for the taphonomic analysis of nonmarine Mollusca began with his dissertation studies on the Eocene Green River and Wasatch Formations of southwestern Wyoming. His latest papers with Romeo Flores, on the Paleocene of the Fort Union Formation of the Powder River Basin, Montana and Wyoming, reflect the potential of his developing methodology.

John considered the taphonomy of nonmarine mollusks of equal importance to sedimentology in the interpretation of depositional processes and in facies analysis. In part, his biofabric studies were the sedimentology of "biological grains." This concept is analogous to the use of fossils in strain analysis in structural geology, where a fossil represents an known previous shape. In sedimentology, the fossil provides a forehand knowledge of the living environment affected by erosional and depositional processes. In addition, the orientation of shells with respect to bedding, their density and dispersion within beds, and their sorting, abrasion, fragmentation, and articulation are all characters that reflect on specific depositional conditions. In the Paleocene of Montana, John was able to differentiate between deposits produced by large and small lakes, and recognize and interpret crevasse splay complexes, along with other fluvial and alluvial plain deposits. A benefit to understanding these processes and environments is the recognition of the control of facies in the distribution of taxa. Such knowledge is fundamental to the construction of meaningful biostratigraphic zonations.

In addition to the above research, John had completed a review of the primary occurrences of the nominal taxa of the Cretaceous, which will be published by the U.S. Geological Survey. At the Fourth North American Paleontological Convention, he presented (with others) an overview of the Late Jurassic Morrison fauna. He was involved in the study of Neogene deposits from the Nebraska Sand Hills and from the Salt Creek Valley area of southeastern Utah. Besides these published works, John devoted much time and effort to the the filing of "fossil reports" on specimens submitted to him through the U.S. Geological Survey and from the academic community. In all, some 170 reports were written between 1973 and 1985, spanning the Jurassic to Recent record, and including coverage of almost every western state, as well as Alaska and a few overseas localities. With his Survey administrative
responsible, this record of assistance to his co-workers and professional associates truly represents a magnificent effort in so short a time.

Besides fossil mollusks, John was actively involved in a teaching program sponsored by the Smithsonian. Young and old alike had the opportunity to see and learn from John and the marvelous collection of fossil vertebrates, invertebrates, and plants he put together with Bob O'Donnell of the U.S. Geological Survey.

Many projects were left unfinished. John completed several field seasons of collecting and study in the early Tertiary of the Bighorn Basin in Wyoming and Montana, leaving behind an unreported record of many new taxa. Also the discovery of Paleocene unionoid glochidia awaits publication. The advantage students of fossil nonmarine mollusks will have in following John's lead, is a well-curated and well-documented record of study in his chosen field.

ACKNOWLEDGMENTS

My thanks go to Bob O'Donnell of the U.S. Geological Survey for permitting my access to the papers of John Hanley to help prepare this review and to put in order his bibliography. Thanks also to Emmett Evanoff and Steve Good of the University of Colorado-Boulder in providing information on the nonmarine molluscan faunas of the Late Triassic and Jurassic. I have appreciated comments made on the manuscript by Craig Schmidt. This research was supported, in part, by the Philip McKenna Foundation and the University of North Dakota Mining and Mineral Resources Research Institute.

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JOHN H. HANLEY BIBLIOGRAPHY


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August 10 - 14, 1987

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