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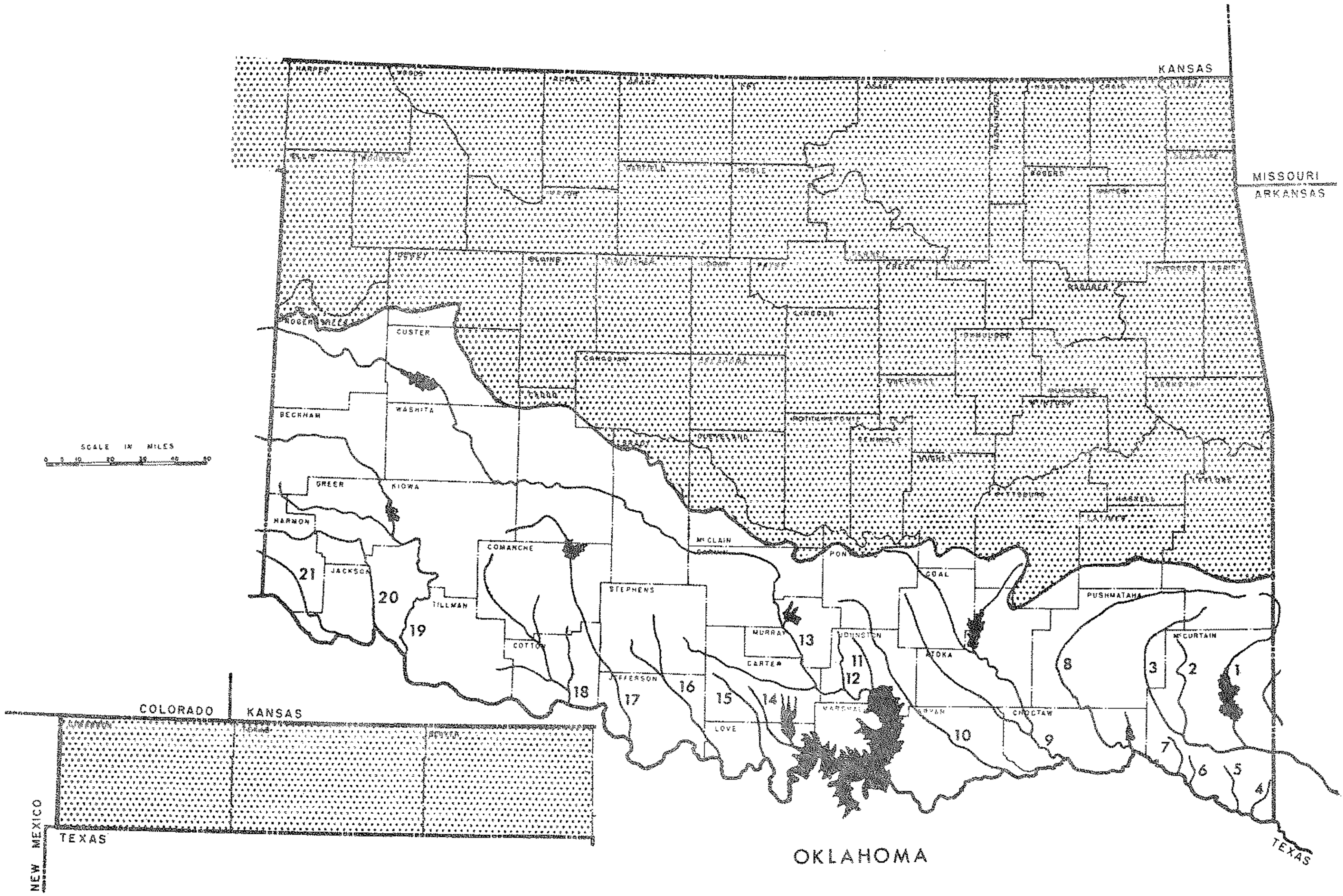

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AN INTRODUCTION TO THE NAIADS OF THE LAKE TEXOMA REGION, OKLAHOMA, WITH NOTES ON THE RED RIVER FAUNA (MOLLUSCA:UNIONIDAE)

Barry Dean Valentine and David Honor Stansbery

Faculty of Zoology, The Ohio State University, Columbus, Ohio 43210

ABSTRACT

The naiad fauna of the Oklahoma tributaries of the Red River is treated, with particular reference to the 17 genera and 24 species of the Lake Texoma region. There are brief discussions of field and laboratory procedures, shell and soft part morphology, subfamilies of Unionidae, a summary review of U. S. genera based on soft anatomy, and a shell key to the 24 species of the region. Genera and species are briefly described, distinguished from similar taxa in the Red River, and discussed in terms of size, range, distribution, nomenclatorial problems, taxonomic problems, and when pertinent, historical changes and ecology.

CONTENTS

FIGURE 1. Oklahoma, showing Red River drainage. Stippled area is Arkansas River drainage. Tributaries are: 1, Mountain Fork R.; 2, Glover Ck.; 3, Little R., 4. Harris Bayou; 5, Norwood Ck.; 6, Waterfall Ck.; 7, Waterhole Ck.; 8, Kiamichi R., 9. Muddy Boggy R.; 10, Blue R.; 11, Pennington Ck.; 12, Mill Ck.; 13, Washita R; 14, Hickory Ck.; 15, Walnut Bayou; 16, Mud Ck.; 17, Beaver Ck.; 18, Cache Ck.; 19, North Fork Red R.; 20, Salt Fork Red R.; 21, Lebos Ck.

INTRODUCTION

Knowledge of the naiads, sometimes called freshwater mussels, or freshwater clams (although strictly speaking they are neither), is used in a broad spectrum of biological activities, and is especially involved in studies of pollution, parasitology, evolution, biogeography, geographic and individual variation, limnology, and invertebrate zoology. Hopefully, these data will contribute something to each, but mainly this study has been written for the beginner. It contains the information needed when interest starts to grow; perhaps, it may whet interest. The naiad specialist will understand that this is only a small platform in the sea of evolutionary, taxonomic, nomenclatorial, and biological uncertainties which beset the study of these animals, and it is most important that the beginner realize this too. We have never seen a group with as many challenging problems. The number and relationships of the families and subfamilies has not been settled. Most of our genera are involved in both taxonomic and nomenclatorial controversies; and even the zoological validity of many current generic and higher level taxa are now under scrutiny or have already been questioned. At the species level, the multitude and magnitude of the problems are staggering. A voluminous old literature, vast lists of synonyms, poor original descriptions, incomplete data on soft parts, extensive individual and geographic variation, difficulty in distinguishing or even suspecting sibling species, and in fact, the usual absence of information on hybridization and gene flow between populations make taxonomy at all levels open to the most divergent points of view.

It is often difficult to establish or substantiate the claims of a careful and respected specialist, and when the specialists disagree, as they often do in the study of naiads, the beginner can become lost in the controversy. We have tried to mention some of the controversial points. In matters of nomenclature we have generally used names that are current and common in the literature except in those cases where the evidence appears clearly to separate correct from incorrect. We fully realize that no specialist in the group will approve all of our choices, and some will approve of very few. However, if he works with care and concern, every specialist faces the same problem.

The senior author is responsible for the planning and execution of the fieldwork in this study, while the junior author has been especially concerned with the taxonomic and nomenclatorial problems raised during the identification of the material collected. We have discussed each of the many problems in detail and in all cases have presented solutions satisfactory to us both.

ACKNOWLEDGEMENTS

We have been fortunate in both the quality and quantity of persons contributing to this study. Valentine's three invertebrate zoology classes at the University of Oklahoma Biological Station (UOBS) bore the brunt of the hard labor, collecting and helping process several thousand specimens. The 1965 class consisted of E. Becky Brownlow, Dana Sue Feining, Dennis E. Deakins, Bette M. Harig, Mary A. Harlow, Robert E. Keen, B. Glen Robinson, Nancy Ann Scott, Jim C. Stribling, and William H. Thies. The 1967 class included J. Larry Renfro, E. Ray Kinser, George R. Biggs, Vance E. Crowe, Mary Louise Glen, Dave L. Kirby, Barry S. Sarber, Dave J. Shetlar, Fred G. Silva, and John E. Trainer. The 1968 class included Cynthia C. Mickel, J. Gilbert Smith, E. Bruce Hart, and James E. Storin. In each case, the first two individuals did most of the work preparing shells for the UOBS collection. Every student made special contributions by extracurricular collecting trips, or assisting in the laboratory, or both, and we are delighted and grateful for their enthusiastic assistance. In 1969 Valentine had the good fortune of having Drs. C. Lavett Smith, Walter R. Suter and W. Frank Wade as field companions, the high quality of the resultant collections is due to their help. The 1969 field work was financed by a National Science Foundation grant-in-aid to Valentine administered by The University Of Oklahoma Biological Station. We are grateful to NSF for this timely assistance, and to Drs. Carl D. Riggs, former Director, and Loren G. Hill, Director of the Biological Station, for their interest, support, and a place to work. Miss Karen Shultz and Miss Kay Davy typed the manuscript, both with characteristic good humor and precision. Finally, Buena Valentine and daughters Susan and Nancy really made it all happen, their interest, encouragement, and understanding made the task much easier, the hours shorter, and the separations easier to bear.

AREA STUDIED

This study originated during the summer of 1965 while Valentine was teaching the invertebrate zoology course at the University of Oklahoma Biological Station at Lake Texoma. Small collections were made in the Lake Texoma area which revealed that the region included the western edge of the Ozark naiad fauna (van der Schalie and van der Schalie, 1950). Our interest increased. In 1967 and 1968 the invertebrate zoology classes made larger collections, especially in the Red River drainage of southern Oklahoma. In 1969, Valentine received a National Science Foundation Grant-in-Aid administered by the Biological Station to fill certain gaps in the data, and spent a month in the area. As over 7,000 specimens accumulated, the number of taxonomic and nomenclatorial problems increased until it became evident that several genera would require detailed revisions before meaningful names could be applied to Oklahoma specimens. We therefore restricted the project to that area which could be treated most completely.

The Lake Texoma region of this paper includes the Oklahoma side of the Red River and especially Lake Texoma (formed by damming the Red River) and its tributaries. Strict application of this definition would exclude the Blue River which enters the Red River east of Lake Texoma, but the Blue is easily accessible from the Lake, it has almost twice as many species of naiads, and by including it, we are able to introduce some of the problems involving the richer fauna of southeastern Oklahoma.

The entire state of Oklahoma is drained by the Red and Arkansas Rivers, both are tributaries of the Mississippi River. The Red River drains roughly the southern third of the state; the Arkansas River drains all the rest, including the western tip. The Red River has most of its major branches on the Oklahoma side; in Texas the first sizeable stream is well west of Lake Texoma. The east to west sequence in Oklahoma starts with the Little River system which forms the principal drainage of McCurtain County, and flows south and then east out of Oklahoma and joins the Red River in Arkansas. This system, in sequence, consists of (the numbers in parentheses coincide with Figure 1) the Rolling Fork (mostly in Arkansas), Mountain Fork River (1), Yanubbee, Yashoo, Lukfata, Boktuklo Creeks, Glover Creek (2), and the Little River (3). Extreme southern McCurtain County has a few small creeks which flow directly into the Red River; chief among these are Harris Bayou (4), Norwood Creek (5), Waterfall Creek (6), and Waterhole Creek (7). Progressively westward, in Choctaw County, are the Kiamichi (8) and Muddy Boggy Rivers (9). The Kiamichi originates on Rich Mountain (on the Oklahoma-Arkansas border) flows in a C-shaped curve westward, southward, and finally southeastward, and borders the Little River system on the north and west. The Muddy Boggy River and all those to the west flow generally to the southeast and more or less parallel each other. In westward succession they are: Muddy Boggy River (9), Blue River (10), Washita River (13), Hickory Creek (14), Walnut Bayou (15), Mud Creek (16), Beaver Creek (17), Cache Creek (18), North Fork Red River (19), Salt Fork Red River (20), and finally Lebos Creek (21) in the extreme southwest corner of the state. Of these, only the Washita River and Hickory Creek drain directly into Lake Texoma. The Washita arm of Lake Texoma receives Pennington Creek (11) just south of the town of Tishomingo. Many other small creeks flow into the Lake; they are mostly intermittent. The Lake was formed by the closure of Denison Dam on the Red River in 1942. It achieved its power pool level of 617 feet above sea level in 1945. Water levels fluctuate considerably; the maximum within one year was in 1957 when high and low water levels were 53 feet apart (L. G. Hill, *personal communication*).

GENERAL PROCEDURE

When feasible, all dead shells were collected, brought back to the laboratory, checked for matching valves, and counted before any were discarded. Live material was obtained by hand groping and by skin diving. Species preserved with soft parts intact were pegged open in the field with twigs or cork stoppers and immediately placed in 70% ethyl alcohol plus a little glycerine. When there was too much material to process in the field, live specimens were kept in open-mesh onion or potato sacks, protected from the heat, and processed that evening. Such sacks are ideal collecting containers. They are strong, light, occupy virtually no storage space, and in use do not fill up with water, or tip over, or float down stream when partly full. They especially allow drainage of excess fluids; this is important when keeping live material, and it helps when a heavy load is carried up a steep river bank after several hours of back-breaking work. As in any collecting container, small or delicate shells should be nested inside larger heavier dead shells for protection, or kept separately.

Before cataloguing, shells were scrubbed with brushes and scouring powder (for the smaller species, Pepsodent tooth brushes outlast all others), allowed to dry and arranged by species in progressive size sequence. University of Oklahoma Biological Station catalogue numbers (UOBS) are prefaced by the year the specimens were catalogued, thus UOBS 67-15 means the fifteenth item catalogued in 1967. All collecting stations, and each visit to a station, receive different numbers, and if more than one species is taken, each species gets a different number. Since most specimens are represented by two valves (which routinely are broken apart before scrubbing) an additional number is used to associate paired shells. Thus 67-15.3 designates the third pair of valves of that species from that locality. Since all specimens of one species are catalogued in decreasing size sequence 67-15.1 designates the largest individual in the series and 67-15.3 is the third largest, etc. When single valves are catalogued this final number is omitted so that a single valve of the same species from the same locality would be UOBS 67-15. In all cases the catalogue lists how many paired and single valves have been catalogued. Ohio State University Museum of Zoology (OSUM) catalogue numbers lack the year prefix, and the suffix numbering for paired valves starts with the smallest individual.

All of the material collected is either in UOBS or OSUM except for the longest series which have been used in part for exchange with students and other museums. Since 1965, there has been an excellent working arrangement whereby a representative set of specimens from each collection site is catalogued in the UOBS collection, and the series, including unidentifiable material goes to OSUM. In exchange, OUBS has received from OSUM a representative collection of the basic naiad fauna of eastern United States; the collection at present contains 40 genera, over 100 species, and is of course not yet complete.

Much information has been culled from the extensive naiad literature and from the collection of the Ohio State University Museum of Zoology; however, the data insofar as they pertain to recent Oklahoma collections are original. Measurements, height/length ratios, and descriptions of color and structure are based on Oklahoma material unless stated otherwise. Length measurements are maximum length, height measurements are maximum height made perpendicular to the line of maximum length and do not include the ligament. The height divided by the length and multiplied by 100 gives a very convenient height index (Stansbery, 1961, p. 14) which expresses the height as a percentage of length.

When using the individual discussions of the Lake Texoma region naiads, it should be remembered that we have listed as synonyms only those names actually reported from Oklahoma; also, we have mentioned in the text every genus known from the state and every species known from Red River drainage in the state.

COLLECTING AND PRINCIPAL COLLECTION SITES

The uncertainties of Oklahoma weather, and the great fluctuation in volume of all of the rivers, make naiad collecting in the state very unpredictable, and at times virtually impossible. Since the more sedentary species survive only in the permanent channel, general collecting for live specimens in a flooded stream bed is hardly worthwhile. Dead shells and occasional live individuals are scattered throughout the bed and lodged in emergent vegetation and on bars, but the main live population will be restricted to the areas that continue to flow when the water level is lowest. This simple fact is the key to obtaining the live material necessary for the serious study of our species. It should also be pointed out that not all naiads are sedentary. Certain thin-shelled species, especially of *Anodonta, Potamilus, Leptodea, Ligumia, Toxolasma*, and *Lampsilis* are more or less famous for their ability to follow the rise and retreat of fluctuating water levels when the substrate is soft enough to permit such movement. These species may be found in mud, sand, or vegetation just a few inches from the water's edge, regardless of the water level, or in deeper water too.

Most collecting is done by hand, feeling blindly along the bottom for the tapering edge and bilateral symmetry that distinguishes naiads. Broken glass, tin cans, and other sharp objects are very common hazards in even the most isolated rivers, so a gentle touch and a good first aid kit are both necessary. Hand collecting requires shallow water, in deeper water, larger specimens can be located with the feet, even wearing sneakers, if the bottom is mud, sand, or fine gravel. By far the most fascinating method of collecting is skin diving or with SCUBA. A simple facemask and snorkel with or without a pair of flippers will open a new world to the collector or observer in the clearer lakes and upland rivers; not just in deeper water, but also in the shallows and riffles where moving water makes aerial observation of the bottom distorted or impossible.

The collector should keep track of dams and thunderstorms upstream, for flash floods can be devastating. One occurred in Glover Creek of the Little River while Dr. Walter Suter and Valentine were collecting naiads. The creek, about 15 to 20 feet wide and up to four feet deep, suddenly began to rise and in fifteen minutes was up at least 6 feet, flowing in a roiling torrent bank to bank, about 200 feet wide, with large uprooted trees sweeping down the channel. In a narrower stream bed, that great a volume would have arrived in a smashing wall of water. They learned later that despite clear skies overhead, a heavy thunderstorm had dumped several inches of rain in the hills upstream.

A few principal collecting sites are referred to repeatedly in the discussions of genera and species. These are discussed briefly below, for they represent the large collections which yielded the most data about the rivers concerned. Many other sites were visited, but are not discussed. In this section, we have simply listed genera and species. For further taxonomic refinements check the discussions of individual taxa.

Lake Texoma. We have no large collections from the lake, but Riggs and Webb (1956) report on a collection of 898 specimens from a previously inundated peanut field just downstream from the mouth of Big Mineral Creek, Grayson County, Texas. None of these specimens are now in the UOBS collection, presumably a set is in the Museum of Zoology, University of Michigan, since material was sent there to verify the identifications. The fauna of the lake is discussed in a separate section of this report.

Washita drainage. Pennington Creek, 2 miles south of Tishomingo, Johnston County. The Washita River, Pennington Creek, and the Washita arm of Lake Texoma all converge south of the town of Tishomingo. It appears that silt deposition is changing the relationships of these three bodies of water so that no two maps agree. Since the principal collection site is south of Tishomingo, just west of the Tishomingo 'airport', some clarification is necessary. The site is a small sluggish, mud-bottomed stream flowing south parallel to the air strip. It is much too restricted to be the main Washita River but it could be part of a braided channel. We feel reasonably certain that the major water source is Pennington Creek, but at least one map shows a connection between the Washita River and Pennington Creek a mile upstream from our site. The collection area bisects portions of Sections 16 and 21 of Township 4S, Range 6E. Nine species have been taken at this site, two others occur in the headwaters. Specimens from the area have been catalogued under the numbers UOBS 67-120 through 124, UOBS 67-165 through 166, and UOBS 67-182. The species represented are *Lasmigona complanata, Anodonta grandis, A. imbecilis, Quadrula quadrula, Uniomerus tetralasmus, Obliquaria reflexa, Truncilla donaciformis, Leptodea fragilis,* and *Potamilus laevissimus.* Upstream collecting adds *Toxolasma parva* and *Lampsilis radiata luteola* to the list.

Blue River drainage. Blue River, below Durant Dam, just north of Armstrong, Bryan County. The Blue River is the last stream with good species diversity as one travels westward in Red River drainage. Streams to the west may have abundant individuals of a few species, but in the Lake Texoma region, the Blue has the richest fauna; east of the Blue the rivers have even larger faunas, but the differences are not as great as those between the Blue and the Washita.

Immediately below the spillway of Durant Dam there is a large pool, heavily frequented by fishermen, below this the channel divides around a gravel bar which is reinforced by many emergent plants. This bar is at times loaded with dead shells and the adjacent coarse gravel channels have an abundant live fauna. Our first trip to this site yielded 800 naiads of nineteen species; we have however, been careful to restrict collecting primarily to dead shells to conserve the fauna. Subsequent trips have turned up two more species, both single specimens. Of the 24 species in the Lake Texoma region, only three (*Megalonaias gigantea, Ptychobranchus occidentalis,* and *Ligumia subrostrata* are absent below the dam.

Water levels at this site have fluctuated about two feet between high and low water, however we have never visited the site immediately after a large storm. When large volumes of water are coming over the dam, swift current, high turbidity, and excessive amounts of broken glass make collecting difficult. Samples of most of the species from this site have been catalogued as UOBS 67-125 through 139, and UOBS 68-1 through 18.

Blue River drainage. Blue River, ¼ mile north of Milburn at Oklahoma route 48A bridge, Johnston County. The site is in Section 35, Township 3S, Range 7E. The river has a long stretch of sandy bottom with isolated patches of mud and gravel. Three hundred and forty-eight specimens of naiads, of eight species were taken. Four species were represented by one or two dead shells, the remainder consisted of 244 *Fusconaia* sp., 25 *Quadrula pustulosa,* 47 *Lampsilis radiata,* and 26 *Lampsilis ovata.* Representatives of all eight species have been catalogued as UOBS 67-146 through 153. The live shells were mostly scattered in the deeper parts of the river bed, there was no major area of concentration, however numbers increased with distance downstream from the bridge. Two years later, Valentine revisited the site for about half an hour and again found eight species, however three were different from the previous visit. *Tritogonia verrucosa, Ptychobranchus occidentalis* and *Toxolasma parva* were not found, but *Leptodea fragilis, Villosa* sp., and *Lampsilis anodontoides* were present. As before, one *Ligumia subrostrata* was found, and by far the commonest form was *Fusconaia* sp.

Blue River drainage. Tributary of the Blue River, about ¼ mile east of Oklahoma route 99 on Oklahoma route 7, Johnston County. Section 25, Township 2S, Range 6E. Although Valentine's fieldnotes state that the site is ¾ mile east of Oklahoma route 99, and there is a tributary at that point, we suspect a slip of the pen, and that the actual collection is ¼, not ¾, mile east of Oklahoma route 99 on Oklahoma route 7, at another and smaller branch of the Blue. The site is a small clear creek at most four feet wide, narrowing to one foot when the water pours between large rocks, and with a maximum depth of two feet. It flows through tall grass and weeds and in part is bordered by shrubs and small trees. The bottom varies from rock to sand to fine gravel to mud. After heavy rains the creek overflows into the surrounding vegetation and covers some small gravel bars perhaps 50 yards downstream from Oklahoma route 7. In a short length of this unlikely rivulet, the invertebrate zoology class took 625 naiads, distributed among six species. A set is catalogued as UOBS 67-154 through 159. There were 41 *Anodonta imbecilis,* 7 *Ptychobranchus occidentalis,* 3 *Toxolasma parva,* 370 *Ligumia subrostrata,* 6 *Villosa* sp., and 198 *Lampsilis radiata.* See the discussion of *Ligumia subrostrata* for additional information about this site.

Kiamichi drainage. Kiamichi River, 1 mile south of bridge of Oklahoma route 93, or 9 miles north and east of U.S. route 70, at a spot called 'Spencerville Crossing' by local youths, Choctaw County. When visited first in July 1967, the river was in flood and only a few shell fragments were found. On July 14, 1968 the river was shallow enough to wade across without having to swim; eighteen species and approximately 700 specimens were collected, of which only 61 were alive. Emergent sand bars on the far side of the river were littered with dead shells most of which were badly eroded. Even the best live shells lacked beak sculpture and some were in pitiful shape with holes into the mantle cavity, tattered periostracum, and other signs of extreme erosion. On July 19, 1969 the river was a foot and a half higher than the previous year and the wide, emergent bars were reduced to linear strips. A steamshovel, a bulldozer, and a drag line were all operating in the river just downstream from the bars, dredging material from the channel out onto the banks. It seemed an opportunity to sample the main channel, but most of the shells had been buried under piles of additional gravel, and many of those that were still uncovered were crushed by the heavy equipment. The best collecting was still the emergent bars on the far side, and approximately 450 individuals were selected. All dead shells of the rarer species were collected, but hundreds of *Amblema plicata, Quadrula pustulosa, Actinonaias ligamentina,* and *Potamilus purpuratus* were left behind. Only a few live specimens were found, they were scattered about the sandy bottom.

The nineteen species collected at this site form a very important assemblage, for among them is *Arkansia wheeleri*, the only recent record for the state; also, three additional genera reach their western limits here: *Actinonaias, Plagiola,* and *Obovaria,* as well as the rare species *Leptodea leptodon*. The remaining forms include *Megalonaias, Tritogonia, Quadrula quadrula, Fusconaia, Ptychobranchus, Obliquaria, Truncilla truncata, Leptodea fragilis, Potamilus laevissimus, Lampsilis anodontoides, L. ovata,* and *Villosa* sp., near *lienosa*.

Kiamichi drainage. Gates Creek and Lake Raymond Gary, about 2 miles south of Fort Towson, Choctaw County. Gates Creek enters the Kiamichi River close to the junction of the latter with the Red River. It has been dammed south of Fort Towson to form Lake Raymond Gary. In July, 1968, we found the lake had been drained; the dry bed contained only *Anodonta grandis, A. imbecilis,* and occasional specimens of *Leptodea fragilis, Potamilus laevissimus,* and *Lampsilis radiata*. In June, 1969 the lake was full again; the repopulation of the fauna would make an interesting study. On July 9, 1967, two collections were made in Gates Creek below the dam. One was in the main channel below the concrete spillway. Only eight species were found, all common in eastern United States (*Anodonta grandis, A. imbecilis, Amblema plicata, Quadrula quadrula, Q. pustulosa, Potamilus purpuratus, Lampsilis anodontoides,* and *L. radiata luteola*). The bottom here is mud with extensive patches of emergent plants, just downstream is bedrock, then gravel and mud; of the forty-six specimens found, all but 3 or 4 dead shells were in the first muddy area below the dam. The second collection was from a small slough or sluggish stream east of the main concrete spillway, which issues below the eastern part of the dam into a narrow rocky pool. The bottom is mud and boulders for a short distance, then silt, mud and occasional sand. An astonishing fifteen species and 413 specimens were taken here. The two dominant species, *Quadrula pustulosa* and *Truncilla donaciformis* accounted for 102 and 101 specimens respectively. Most of the *Quadrula* were alive, most of the *Truncilla* were dead with the valves still attached. The list includes all but one of those taken below the main spillway (*Lampsilis anodontoides*), plus *Tritogonia verrucosa, Fusconaia, Obliquaria reflexa, Leptodea leptodon, Potamilus laevissimus, Toxolasma,* and *Lampsilis radiata luteola*. Ten of the species from these two sites are catalogued as UOBS 67-168 through 178, the series are in OSUM:1967: 360 and 361

Little River drainage. Little River, at low bridge 5.2 miles east-northeast of Cloudy, Pushmataha County. We do not yet have a large collection from the Little River proper, as distinct from its major tributaries Glover Creek and Mountain Fork River. The present site is the best to date; 150 shells were found on July 22, 1968 and only 16 more on June 27, 1969. The two collections contain nineteen species, none of which are outstanding. *Amblema plicata* far outnumbers all others. The river flows mostly over large rocks and coarse gravel; almost all shells, even the few live specimens, were found in the shallows or on the shore, especially on a sandy, bush, and tree-covered bar upstream from the bridge, on the west bank. UOBS 68-126 through 143 provides a sample.

Little River drainage. Glover Creek, above Oklahoma routes 3 and 7 bridge, 9 miles west-northwest of Broken Bow, McCurtain County. This excellent spot was recommended by local fishermen, and visited twice in 1969, on June 23 and July 7. The earlier date was interrupted by the flash flood described elsewhere in this paper, the second visit was to assess the effects of the flood and out collecting, and to augment the short series of some of the species. Three quarters of the total collecting effort was by skin diving. Twenty-two species were taken, totalling 470 specimens. Hundreds of live naiads were left *in situ* or thrown back, especially *Amblema plicata, Quadrula pustulosa, Fusconaia* sp., *Obovaria* sp., and *Actinonaias ligamentina*. Live specimens of almost every species were taken, including several that are rare or interesting, especially *Strophitus undulatus, Lasmigona costata, Quadrula cylindrica,* and *Plectomerus dombeyanus*.

During low water, Glover Creek occupies a small fraction of the river bed along the west shore, leaving a broad expanse of coarse gravel exposed. The channel is mostly gravel, and the current is sufficiently swift in the narrow areas to require constant effort if a skin-diver is to maintain his position. The majority of naiads were in the narrow part of the channel quieter water had fewer species snd more widely scattered individuals. When in flood, Glover Creek is full from bank to bank, and the current over the permanent channel is strong enough to sweep a skin-diver downstream despite the most strenuous efforts.

During the first visit, many live naiads were thrown back into the channel; however a flash flood developed before they had time to reestablish their positions in the substrate. On the second visit, a special attempt was made to assess the effects of the flood on these displaced individuals, with inconclusive results. A number of naiads were found not or incompletely buried and could have been either from the first collection or washed in from upstream. Most naiads were normally dug in, with only the algae-covered posterior projecting, and it was impossible to tell if they had dug in recently or years ago. The bottom appeared slightly disturbed in spots, but naiads were still very abundant. Obviously some sort of marking and recognition system must be worked out--perhaps a small triangular file can be used to make semi-permanent notches which could be felt with the fingers without digging up the specimens, or markers could be driven into the substrate next to sedentary species. Thoma, *et al.* (1959) review a number of marking techniques. The whole subject of population structure, species and individual interaction, movement, etc. has received little recent attention.

Little River drainage. Mountain Fork River, at concrete ford (or low water bridge), about 6.5 miles southwest of Smithville, McCurtain County. This lovely spot was first visited on July 8, 1967. The river was sweeping over the low concrete bridge and full from bank to bank. No collecting was attempted. A year later on July 15, 1968, the bridge surface was dry, the water flowing through the large pipes beneath, and extensive gravel bars were present below the bridge. There were hundreds and hundreds of fresh, dead shells on these bars and in the adjacent shallows, including many small fragile specimens, and small numbers of live specimens. Valentine and his invertebrate zoology class picked up 1,541 specimens, mostly clean paired valves, representing 15 species. It was an unforgettable experience. Despite the superabundance of shells, *Lasmigona costata* was represented by one badly eroded pair of valves, *Lampsilis radiata* by one fresh pair, and *Leptodea leptodon* and *Potamilus purpuratus* by two specimens each. From 10 to 558 specimens were taken of each of the other species. Since the commonest species was a member of the *Ligumia-Villosa-Lampsilis* complex of uncertain identity, Valentine returned to the site on July 1, 1969 to obtain live specimens. The river was only slightly higher than before, but only 70 specimens and nine species were found; only two specimens were living, neither one was the uncertain form. The lack of soft parts left many unanswered questions, so he made one final try en route back to Ohio on July 9. Skin-diving for several hours in the very shallow water below the bridge resulted in 129 specimens, representing twelve species; however 60 of the specimens and ten species were taken alive and preserved on the spot; almost two dozen were the unknown species. Included was one specimen of *Ligumia subrostrata*, a genus and species not taken previously, thus raising the number of species found to sixteen. The live specimens were imbedded in the gravel, usually on the downstream side of the larger rocks, or in the occasional small patches of bare sand which were scattered over the strewm bed, these patches were at most four or five inches in maximum diameter and often supported several naiads, of mixed species, per patch. Fourteen of the species from the 1968 collection are catalogued as UOBS 68-78 through 91.

LAKE TEXOMA SPECIES

The naiad fauna of Lake Texoma has not been adequately investigated. Although Riggs and Webb (1956) sampled an area of 60 acres, the lake has 700 miles of shoreline, and covers approximately 93,000 acres.

Isely (1925) collected at four river sites that are now covered by Lake Texoma. Three of these were in the Red River above the mouth of the Washita River, and one was in the lower Washita River. Living species collected at the three Red River sites were *Truncilla donaciformis, Leptodea fragilis, Potamilus laevissimus,* and

Lampsilis anodontoides form *fallaciosa*. Dead shells of *Quadrula quadrula*, *Q. pustulosa*, *Anodonta grandis* form *stewartiana*, and *Lampsilis ovata* were also found. At the lower Washita River site he found living *Quadrula quadrula*, *Q. pustulosa*, *Lasmigona complanata*, *Truncilla donaciformis*, *Leptodea fragilis*, and *Potamilus laevissimus*. Dead shells of *Tritogonia verrucosa*, *Obliquaria reflexa*, *Lampsilis anodontoides* form *fallaciosa*, and *L. ovata* were also found. A collection by Isely from the Washita River upstream from the present limits of Lake Texoma added only *Potamilus purpuratus* and *Toxolasma parva*. The only other species recorded upstream from the present lake site are Isely's records from Cache Creek which add *Uniomerus tetralasmus*, *Anodonta imbecilis*, *Truncilla truncata*, and *Lampsilis anodontoides* form *anodontoides* to the list. Thus there was an original fauna of sixteen species above the site of Denison Dam. The present fauna of Lake Texoma contains eight of these sixteen species. Riggs and Webb (1956) and Sublette (1957) record seven of these: *Anodonta grandis* form *stewartiana* (under the names *grandis* and *corpulenta* respectively), *Anodonta imbecilis*, *Quadrula quadrula*, *Truncilla donaciformis*, *Leptodea fragilis*, *Potamilus laevissimus*, and *Toxolasma parva*. We can add the eighth species, *Lasmigona complanata*, based on specimens in the UOBS collection.

The survival of the remaining eight species has not been investigated, since we have no data from the main channels of the Washita and Red Rivers, and Cache Creek. One collection stop was made in the Washita River at the bridge between Ravia and Russett, in Johnston County, but no naiads were found.

In Lake Texoma, Riggs and Webb (1956) estimated there were 15,647 naiads per acre in the area they sampled immediately downstream from the mouth of Big Mineral Creek, Grayson County, Texas. Of the 898 individuals collected, there were *536 Potamilus laevissimus*, 220 *Quadrula quadrula*, 90 *Truncilla donaciformis*, 31 *Toxolasma parva*, 17 *Anodonta grandis* form *stewartiana*, and 2 each of *A. imbecilis* and *Leptodea fragilis*. We have, incidentally taken the liberty of changing the nomenclature of two of these species to conform with the present study. Riggs and Webb, and Henry van der Schalie who verified their determinations used the names *Anodonta grandis* form *stewartiana*, and *Leptodea laevissima* rather than *Potamilus laevissimus*. Discussion of these changes can be found under the appropriate species.

LITERATURE

We have tried to solve the problem of introducing the voluminous naiad literature by including the principal references to Oklahoma and adjacent states, and supplementing them with a few important regional, taxonomic, and biological studies not directly concerned with the southwest. It is important to realize that the list contains only a handful of references. For those who wish to pursue this further, the main starting point is the *Zoological Record*, Section 9, on Mollusca. A number of journals are conspicuously important for the study of naiads, the most important is *Nautilus*. Other major sources are the *Annual Reports of the American Malacological Union*, *Sterkiana*, *Malacologia*, and *Occasional Papers on Mollusks* (of Harvard University). Journals of more general content noted for important papers about naiads are: *American Midland Naturalist*, *Occasional Papers* (also the *Miscellaneous Publications*) of the *Museum of Zoology, University of Michigan*, and the publications of the United States Bureau of Fisheries.

A number of particularly important works could be cross-indexed under almost any heading, they constitute the basic library. In alphabetical order they are: Conrad (1834, 1835-1838), Lea (1828-1874), Ortmann (1911, 1912, 1919), Rafinesque (1820, 1831), Say (1817, 1830-1834), and Simpson (1900, 1914). Haas (1969) should probably be included in this list, however we have not had time to translate any of the German text. The first paper by Simpson (1900) contains a 63 page World bibliography covering the period before the turn of the century. Most of the literature references in the present paper are dated after 1900. As a rapid index, we present a breakdown by subject. Papers about shell and soft anatomy are cited in the pertinent morphology discussions.

OKLAHOMA: Baker (1909), Branson (1966a, 1966b, 1967, 1969), Call (1885), Ferriss (1906), Frierson (1927, 1928), Isely (1911, 1914, 1925), Marshall (1895), Ortmann (1919), Riggs and Webb (1956), Sublette (1957).

TEXAS: Murray and Roy (1968), Singley (1893), Strecker (1931), Vaughan (1893), Walker (1915).

LOUISIANA: Branson (1966b), Frierson (1900), Vanatta (1910), Vaughan (1893).

ARKANSAS: Call (1895), La Rocque (1962), Meek and Clark (1912), Ortmann (1919), Ortmann and Walker (1912), Wheeler (1914, 1918).

OTHER STATES: Baker (1922, 1927, Illinois) (1928, Wisconsin), Heard and Burch (1966, Michigan), Call (1900, Indiana), Clarke and Berg (1959, Central New York), Clench and Turner (1956, Gulf Coastal Alabama, Georgia, and Florida), Goodrich and van der Schalie (1944, Indiana), Johnson (1970, Atlantic Slope from James River system, Virginia to Altamaha River system, Georgia), La Rocque (1967, Ohio), Murray and Leonard (1962, Kansas), Ortmann (1911, 1919, Pennsylvania), (1918, upper Tennessee River), Scammon (1906, Kansas), Utterback (1915, 1916, 1917, Missouri), van der Schalie (1938, 1970, southeastern Michigan), van der Schalie and van der Schalie (1950, Mississippi River north of St. Louis, Missouri), Starrett (1971, Illinois River in Illinois).

LARGER REGIONS: Clench (1959, U.S. genera), Frierson (1927, North and Central American classification and checklist), Haas (1969, World classification, genera and species), Heard (1968, southeastern U. S. genera), La Rocque (1953, Canadian catalogue), Lea (1828-1874, World genera and species), McMichael and Hisock (1958, Australian Region), Parodiz and Bonetto (1963, South American), Pennak (1953, U.S. genera), Preston (1915, India and Burma), Simpson (1900, World synopsis), (1914, World classification, genera and species), Walker (1918, U. S. genera).

LIFE HISTORY: Allen (1914, 1921, food and feeding), Arey (1921, glochidia), Chamberlain (1931, annual growth), Churchill and Lewis (1924, food and feeding), Clark and Stein (1921, glochidia in plankton), Coker *et al.* (1921, glochidia and propagation), Coker and Surber (1911, metamorphosis of *Potamilus laevissimus),* Conner (1907, 1909, gravid periods), Grier (1922, growth rate), Heard (1967, hermaphroditism in *Anodonta),* Howard (1914a, nonparasitic glochidia) (1914b, 1922, propagation), Isely (1911, juvenile ecology and presence of a byssus) (1914, growth and migration), Jones (1926, anatomy and histology of *Tritogonia),* Lefevre and Curtis (1910, 1912, gill structure, glochidial biology and propagation) (1911, non-parasitic glochidia), Matteson (1948, *Elliptio complanatus)* (1955, temperature, current, silting, migration), Stansbery (1961, age determination), Stein (1968, *Amblema plicata),* Sterki (1898, 1903, marsupial structure), Surber (1912, 1915, glochidial identification) (1913, glochidial hosts), Tepe (1943, hermaphroditism in *Toxolasma, =Carunculina),* Thoma *et al.* (1959, marking techniques for recapture studies), Tucker (1927, 1928, glochidia and juveniles of *Anodonta),* Utterback (1916 gravid periods), van der Schalie (1966, hermaphroditism review), van der Schalie and Locke (1941, hermaphroditism in *Anodonta grandis),* van der Schalie and van der Schalie (1963, *Actinonaias ellipsiformis).*

GENERAL MORPHOLOGY OF NAIADS

SHELL. Since one or both valves are the most commonly available parts for identification, they have traditionally played the major role in the taxonomic literature of the world. Although it was long recognized that shells exhibit intense geographic, environmental, and genetic variation, as well as convergence, divergence, and parallelism, they are used anyway because they are convenient and available. It is therefore important to remember that many species with similar environmental requirements will have similar shells regardless of the actual relationship of the forms involved. Thin-shelled, smooth, and inflated species tend to inhabit lakes, pools, and sluggish water with soft, muddy bottoms; thicker shelled, smooth species that are less inflated tend to inhabit flowing water and gravel bottoms; heavy-shelled species with massive hinge lines and teeth, prominent surface sculpture and compressed bodies are often associated with riffles and water of high oxygen content. Needless to say, all such habitats overlap or intergrade, but the pattern is still evident. This means that the shell of a widespread species collected in the lower, deeper part of a river will be very different from the same species collected in the headwaters. This also means that two species from the same habitat may look more alike than do the upstream and downstream populations of one species. The taxonomic implications are obvious. Although shell variation correlates rather well with environmental factors, see Ball (1922), Brown *et al.* (1938), Eagar (1948), Grier (1920b, 1920c, 1920d 1920e 1922), Grier and Mueller (1926), Ortmann (1920), and van der Schalie (1936b, 1941), the last author points out that in at least one case, river specimens reared in a lake retained the river morphology, implying the genetic consistency of the features involved.

The basic details of the molluscan shell can be found in any general or invertebrate zoology text or encyclopedia. A few comments will suffice. The hinge line and ligament are dorsal; the umbone (which bears the beak at its very tip, and is the oldest part of the shell) is anteriorly placed; the hinge teeth (if present) include the more anterior tooth-like cardinals (often called pseudocardinals), and the more posterior tongue and groove laterals. Hinge teeth can be variously abnormal, or even reversed so that each valve has the teeth which normally occur in the opposite valve, see Geiser (1915) and especially van der Schalie (1936a) for additional data. Muscle scars include anterior adductor, retractor, and protractor, the first two often contiguous, the last slightly separated; the posterior adductor and retractor, the latter usually much smaller, more anterior and attached at the base of the lateral teeth; the pallial line, paralleling the shell margin and connecting the big adductor muscle scars; and a variable group of small scars in the cavity of the umbone. The internal surface, the nacre, can be uniformly colored or variable; colored nacres often fade in dead shells or lose iridescence. In some genera (*Toxolasma* for example) it is important to distinguish between iridescent and pigmentary colors, both can appear blue (or some other color) but are very different in origin. Externally the shell is variously sculptured or smooth; almost all species have a special sculpture on the first portions of the shell formed after metamorphosis, this is the 'beak sculpture', it is present in almost all species even when the rest of the shell is smooth. See Marshall (1890) for a discussion of beak sculpture; Marshall's plate is reproduced in Clarke and Berg (1959). Since the beaks are the oldest portion of the adult shell, they are often eroded and destroyed by chemicals in the water. There is often a ridge extending obliquely downward and backward from the umbonal region to the posterior end of the valve, this is the posterior ridge, which delimits the posterior slope from the rest of the valve. In some species the posterior slope is greatly extended dorsally above the lateral teeth, such a growth is a wing, and the valve is then said to be alate. The surface of the valve is marked with concentric lines of growth, each indicating a period of active shell deposition. During winter, or other adverse periods, a much more pronounced line is formed in the shell these are called growth rests and in many species they serve as an index to the age of the individual. (See Stansbery (1961) and Chamberlain (1931) for a discussion of how to age shells.

Sexual dimorphism occurs in the shells of about half of the species in the Lake Texoma region (primarily *Tritogonia* and most of the Lampsilinae). It is discussed in the pertinent species accounts, and by many authors, especially Grier (1920a).

SOFT PARTS. The main basis for the classification of naiads, down to and including genera, is the soft anatomy. By far the best introduction to this subject is by Ortmann (1911). He followed this landmark study with along paper the next year (1912) and then a remarkable series of studies (1913-16, 1919, 1921, 1923, 1923-24). The above list includes only papers about more than one United States species, many other papers, in the pages of the journal *Nautilus* discuss individual species and the faunas of other regions. Some other authors who contributed to or supplemented Ortmann's studies are Lea (1834-74), Sterki (1898, 1903) Simpson (1900, 1914), and Reardon (1929).

Mantle modifications. Within the subfamily Lampsilinae there is a complex of genera which is separated from other lampsilines by the presence of a specialized area on the inner margin of the mantle anterior and ventral to the branchial (incurrent) opening. Within this complex, the genera are distinguished by the detailed morphology of this specialized area. The genera are *Glebula, Ligumia, Medionidus, Villosa, Conradilla, Toxolasma, Lampsilis*, and *Dysnomia*, several of which occur in Oklahoma. The specialization takes the form of a row of papillae, or a ribbon-like flap, or modified combinations of the two, along a line paralleling the shell margin. In some, the outgrowths occupy a small field close to the branchial opening, in others, they extend half way or more towards the anterior end of the animal. There are still some major problems involved with the use of these structures. First, their development is sexually dimorphic, being better developed in females than in males. In some males, their presence is barely indicated by a ridge of wavy tissue, or by a streak of dark pigment in the correct area. Second, the existing descriptions are often drawn from one or very few specimens, from a single locality, and in varying states of preservation. Preserved material is always variously contracted and quite different (sometimes radically) in appearance and color from living specimens. Third, many species are still not studied, so the limits of variation of their genera are not understood. Fourth, it is possible to discover species which do not fit the existing alternatives, or which are sufficiently variable to combine features of several taxa. Such a creature is the common *Villosa*-complex species in the Mountain Fork and Little Rivers.

Marsupial gills. In naiads there are four flap-like gills, two on either side of the main visceral mass. A gill results from the fusion of many gill filaments which, in more primitive bivalves, lie side by side in anterior-posterior sequence. Since each filament has two parallel sections, an outer one nearer to the shell and an inner one nearer to the visceral mass, the union of all the outer sections forms one gill surface and the union of the inner sections forms the other. These two surfaces are called lamellae, and in unionids they are held together by vertical interlamellar septa; the resulting elongate compartments within each gill are the water tubes. In female naiads some or all of the water tubes are utilized as brood chambers for holding eggs and glochidia during early development; the tubes involved usually become swollen, and that portion of the gill is then referred to as a marsupium. The marsupial area is often recognizable whether it is charged or not for its water tubes are typically more numerous and often there are extra septa, thus, female gills that are or will be marsupial usually have more crowded septa. In addition, marsupial gills will, in histological cross-section usually show septa with a characteristic greater thickness, and especially, a folded or wrinkled epithelium, rather than smooth. Marsupial water tubes are sometimes called ovisacs, and within them, the eggs are often imbedded in an elongate, mucoid mass of varying colors and consistencies called a 'placenta' or 'conglutinate.'

Gravid female unionids with eggs or glochidia in the marsupia aid greatly in the separation of several confusingly similar genera. In fact, some generic identifications are at best guesses until such females are available. This is particularly true in the subfamily Ambleminae where five genera sometimes defy separation based on shell characters alone. In *Fusconaia* all four gills are utilized as marsupia, and the contained ova are variously pigmented, often red. In *Plethobasus* and *Lexingtonia* the ova are red, but only the outer gills are marsupial. In *Pleurobema* and *Cyclonaias* the outer gills are marsupial, but the ova are white. Occasionally *Pleurobema* has eggs in the inner gills too (Ortmann, 1919, p. 70, 71).

Because variation in shape, sculpture, and hinge tooth structure occurs in all three subfamilies, the arrangement of genera into subfamily groups is based primarily on gill structure, marsupial arrangement, and glochidial type. In the subfamily Anodontinae, virtually the entire outer gill is involved in the marsupium, and each water tube, when charged, becomes subdivided by secondary septa into three parallel vertical chambers. The largest (central) chamber is the actual egg-containing part of the water tube. The inner gill is not marsupial.

In the subfamily Ambleminae (=Unioninae in part of many authors) the water tubes do not become subdivided, and either all four gills are marsupial, or only the outer pair is marsupial. Not all specimens of a species are consistent in this character, however, so series of gravid females are highly desirable. Ortmann (1915, p. 106-108) clearly states that only the median half of the outer gill is marsupial in *Lastena (= Hemistena) lata* Raf.; this appears to be the one consistent exception in the subfamily.

In the subfamily Lampsilinae, the water tubes are not subdivided. In thirteen of the genera the marsupia are restricted to the posterior part of the outer gills. In this condition, the marsupium can occupy up to 2/3 or more of the total gill leaving just the anterior 1/3 or less unmodified, or be progressively reduced until only a few water tubes at or close to the posterior end are involved. In the remaining five genera, other arrangements are found, as outlined in the key. Throughout this subfamily, glochidia are released through holes which develop along the ventral margin of the marsupium. In the Anodontinae and Ambleminae, glochidia pass dorsad into the suprabranchial chambers and then out the excurrent opening.

The various features of the soft anatomy involved in the classification of the families, subfamilies, and genera are summarized in the key which follows. The data are taken mostly from the many papers by Ortmann cited earlier; since he customarily worked with very small series, considerably more variation is to be expected. It seems certain that exceptions and refinements will accumulate, and result in concomitant changes in our generic limits. In fact, although the various statements sound quite definite, they are to be interpreted as patterns not rigid rules. When more than one genus keys out in a couplet, the genera are normally distinguished by shell characters.

SUMMARY KEY TO UNITED STATES GENERA OF UNIONACEA, BASED ON SOFT ANATOMY

1. Inner margins of mantle fused between branchial (inhalent) and anal (exhalent) openings; inner gills continuous with palpi; marsupia restricted to inner gills. 2
   Inner margins of mantle in contact but not fused between branchial and anal openings; inner gills not continuous with palpi; marsupia involving all four gills or only the outer pair. . 3

2. Gills with incomplete septa and water tubes; larva a glochidium, enclosed by a bivalved shell; South America and Australasia. . . Family Hyriidae
   Gills with complete septa and water tubes; larva a lasidium, the shell univalve, not completely enclosing the larva; Africa, South America, possibly Asia. . . .Family Mutelidae . . . . and Family Mycetopodidae
3. Branchial and anal chambers incompletely separated by the attachment of outermost gill lamellae to inner surface of mantle; gills without water tubes, the lamellae with scattered, incomplete, diagonal connections; marsupia involving all four gills; glochidia very small, less than 0.05 mm high, semi-circular, with small irregular ventral teeth; Holarctic, possibly Asia. Family Margaritiferidae (=Margaritanidae) . . . 4
   Branchial and anal chambers almost completely separated by the extensive attachment of outermost gill lamella to inner surface of mantle; gills with most septa and water tubes extending the complete dorsoventral height of the gill; marsupia involving all four gills or only the outer pair; glochidia larger, more than 0.05 mm high,

variously shaped, but usually without a row of teeth on the ventral margin; Holarctic, Africa. . . . . .Family Unionidae . 5

4. Each gill with the lamellae connected by isolated, irregularly scattered thread-like strands of tissue . . . . MARGARITIFERA
Each gill with the lamellae connected by thread-like strands of tissue in oblique series which tend diagonally across the gill filaments from posterodorsal to anteroventral. . . . . CUMBERLANDIA

5. Gravid females (absent in non-gravid females and males) with each water tube of the outer gills divided into three vertical, parallel compartments, a very small outer (lateral) and inner (mesal) space and a much larger median one; eggs contained only in the large median space which is closed dorsally, not opening into the suprabranchial chamber; glochidia subovate or subtriangular with a pair of ventral hooks, usually in the epidermis of fish scales or fins. . . . Subfamily Anodontinae . . 6
Gravid females with each water tube of the outer gills not secondarily divided into three compartments, and opening dorsally into the suprabranchial chamber; glochidia rounded, with a short hinge line, without hooks, or ax-head shaped with two pairs of ventral hooks, usually on fish gills. 9

6. Gravid females with the median egg-bearing compartment of each water tube with the egg mass subdivided into smaller masses. . . . STROPHITUS

Gravid females with the median egg-bearing compartment of each water tube with continuous egg masses, not subdivided. 7

7. The two excurrent apertures ('anal' and 'supra-anal' of naiad literature) each no longer than the space between them. LASMIGONA, ARCIDENS, ARKANSIA, ...ALASMIDONTA, ANODONTOIDES
The two excurrent apertures widely separated, the space between them longer than the length of either opening. 8

8. Marsupium normally swollen, surface with vertical lines. . . . ANODONTA
Marsupium enormously thickened, surface wrinkled and granular. SIMPSONICONCHA

9. Females usually with all four gills with marsupial structure. . . . . Subfamily Ambleminae, in part 10
Females with only the outer gills involved in the marsupium. 14

10. Gills with septa often interrupted or perforated, especially dorsally. . . . . GONIDEA
Gills with septa complete, imperforate. 11

11. Eggs whitish, in each water tube forming an elongate - lanceolate mass ('placenta'). 12
Eggs red or black respectively changing to pink or blue as development proceeds, in each water tube forming a somewhat elongate-cylindrical mass. . . . . QUINCUNCINA, FUSCONAIA

12. Dorsal excurrent opening as long as anal and branchial openings combined; egg masses brown. . . . MEGALONAIAS
Dorsal excurrent opening shorter than anal and branchial openings combined; or excurrent opening single; egg masses white. 13

13. Sexually dimorphic, females with anal opening longer and more posterior than in males. . . . . . TRITOGONIA
Not sexually dimorphic. . . . . AMBLEMA, PLECTOMERUS, QUADRULA
NOTE: The genus *Elliptoideus* may key out in the second half of couplet 13, but the only published feature of its soft anatomy is the statement that all four gills are marsupial.

14. Gravid females with all or much of the outer gill marsupial, not folded, moderately swollen, and thin edged, the swelling not distending the gill below its normal margin. Subfamily Ambleminae, in part. 15
Gravid females with marsupium swollen, thick, distended beyond normal gill margin, and if developed anteriorly, may hang in a series of pleat-like folds. . Subfamily Lampsilinae. .19

15. Excurrent aperture not divided. . . . . CYCLONAIAS
Excurrent aperture divided into two openings by partial fusion of mantle edges (resulting in the 'anal' and 'supra-anal' openings of naiad literature). 16

16. Younger specimens with mantle extending through holes in the shell into hollow spines which become solid at maturity. . . . . CANTHYRIA
Mantle never extending through holes in the shell. 17

17. Eggs white. 18
Eggs cream, pink, orange, or red (depending on species and stage of development). PLETHOBASUS, LEXINGTONIA

18. Marsupium occupying most of the outer gill. . . . CYRTONAIAS, PLEUROBEMA, ELLIPTIO, UNIOMERUS.
Marsupium occupying middle half of outer gill. LASTENA (=HEMISTENA)

19. Gravid females with marsupium involving only the ventral ¾ of the outer gill, and usually hanging in a series of wavy folds; more than half to almost all of the gill length involved; gill distended only slightly beyond its normal margin. 20
Gravid females with marsupium involving water tubes which are charged for most or all of their length, not involving the anterior end of the gill, and not folded (however, there often are folds separating the marsupium from the nonmarsupial gill); charged part of gill clearly distended beyond its normal margin. 21
20. Gravid females with marsupium extending for most of the gill length, with five to twenty wavy folds. PTYCHOBRANCHUS
Gravid females with marsupium restricted to the median or post-median part of the gill, with fewer than five wavy folds. DROMUS (=CONCHODROMUS)

21. Gravid females with marsupium occupying less than ten water tubes near the center of the outer gill, these water tubes paralleling each other and curving posteriorly. 22
Gravid females with marsupium extensive, occupying nearly all, or the central and posterior, or just the posterior part of the outer gill, these water tubes varying in number, but forming a spreading, fan like pattern. 23

22. Gravid females with slightly post-median marsupium, the charged water tubes slightly curved. . OBLIQUARIA
Gravid females with marsupium median or slightly ante-median, the charged water tubes very elongate and spirally coiled. . . . . CYPROGENIA

23. Mantle just anteroventral to branchial opening with a submarginal flap, large single papilla (caruncle), or row of papillae, these less developed in males and very small in *Glebula* of both sexes. 27
Mantle just anteroventral to branchial opening wrinkled or unadorned, without a long submarginal flap or papillae. 24

24. Glochidia ligulate (ax-head shaped), usually with two spines on each valve at the ventral corners. POTAMILUS
Glochidia rounded or oval except the hinge which is flatter, without spines. 25

25. Glochidia with valves gaping open anteriorly and posteriorly. PLAGIOLA
Glochidia with valves capable of closing all around the margin. . . . 26

26. Glochidia small, less than 0.1 mm. high. . . . . TRUNCILLA, LEPTODEA
Glochidia larger, more than 0.1 mm. high. . . . . .OBOVARIA, ACTINONAIAS

27. Marsupium occupying most of the outer gill, except for the anterior and posterior ends. . . . . . GLEBULA
Marsupium more restricted, occupying the posterior part of the gill. 28

28. Mantle with one or more submarginal papillae immediately anteroventral to the branchial opening. 29
Mantle without papillae immediately anteroventral to the branchial opening, instead with a narrow, submarginal, ribbon-like flap attached along its long axis and paralleling the mantle edge. . . . . .LAMPSILIS

29. Mantle with a submarginal cluster or one very large papilla antero-ventral to the branchial opening. TOXOLASMA
Mantle with a submarginal row of papillae antero-ventral to the branchial opening. 30

30. Mantle with submarginal row of papillae interrupted in the center and connected by a thin raised ridge. . . . . CONRADILLA
Mantle with papillae in continuous series not interrupted. 31

31. Mantle with 1 - 3 long papillae, separated from branchial opening by a row of much smaller papillae, or the latter absent. . . . . MEDIONIDUS
Mantle with papillae of equal length, or evenly graduated, or of mixed lengths. 32

32. Mantle papillae of mixed sizes and lengths, or largest papillae anterior. . . . . VILLOSA
Mantle papillae of subequal size, shape, and separation, or largest papillae posterior. 33

33. Female mantle with row of papillae paralleling the mantle edge. LIGUMIA
Female mantle with row of papillae sharply diverging from the outer mantle edge. DYSNOMIA (=EPIOBLASMA?)

THE SUBFAMILIES OF UNIONIDAE

The three long used subfamily names (Unioninae, Anodontinae, and Lampsilinae) are by no means universally accepted as the sole components of the family Unionidae. For example, a bewildering arrangement is proposed by Modell (1942, 1949). The earlier paper has been translated into English by Stansbery and Soehngen (1964). Modell classifies the naiads of the World primarily by tooth structure, beak sculpture, and general shell form and virtually ignores soft parts. In his 1942 paper he partitions our genera into three families and ten subfamilies. The family Unionidae contains *Quadrula* (and its subgenera), *Tritogonia, Quincuncina, Cyclonaias*, and *Megalonaias* in the Quadrulinae; *Lastena* (Modell uses this name for *Anodonta imbecilis* and related species, and *A. suborbiculata* of the American fauna, not for *Lastena* (=*Hemistena*) *lata* Rafinesque, 1820) in the Rectidentinae; and *Anodonta* in the Anodontinae. The family Margaritiferidae contains *Margaritifera* and *Cumberlandia* in the Margaritiferinae; and *Gonidea* in the Pseudodontinae. Our remaining genera are placed in the new family Elliptionidae; *Pleurobema, Lexingtonia, Plethobasus*, and *Fusconaia* are in Pleurobeminae; all our anodontines except *Anodonta* are in Alasmidontinae; *Elliptio, Elliptoideus, Uniomerus*, and *Canthyria* are in Elliptioninae; *Amblema* and *Plectomerus* are in Ambleminae; and all our lampsilines are in Lampsilinae. This arrangement assumes that the various types of glochidia and marsupia have evolved independently in two or more families. This may be possible, but appears to contradict most of the available evidence.

Morrison (1955) suggests that the old family Unionidae contains two families and five subfamilies: family Unionidae, with subfamilies Unioninae, Alasmidontinae and Anodontinae (this family includes what has traditionally been called subfamily Anodontinae as well as some of the Unioninae); and family Amblemidae, with subfamilies Ambleminae and Lampsilinae (the subfamily Ambleminae has traditionally been treated as part of the Unioninae). The explanation for this reclassification is the fact that the European genus *Unio* is not most closely related to the *Amblema-Quadrula-Fusconaia-Elliptio* group of genera despite their long association, but rather if we use glochidial form and marsupial gills, to the *Anodonta-Alasmidonta* group. When *Unio* is placed with its correct relatives, the name Unioninae goes with it, leaving the *Amblema-Quadrula*-etc. complex without a subfamily name. This void was filled with the name Ambleminae. The basis for Morrison's two families rests on the glochidia and gravid female gill structure. In the European *Unio*-complex and the Holarctic *Anodonta-Alasmidonta*-complex the glochidia are shaped essentially like a weakly inflated triangle with the long hinge forming the base; the apex has an incurved spine complex on each valve. The spines are present in fully developed glochidia, but can be absent in earlier stages. Gravid females have marsupial water tubes partitioned into two very small chambers one next to each lamella, and a very large chamber between. Eggs and glochidia occur only in the median chamber. The Palearctic *Unio*-complex has complete hinge teeth, the Nearctic *Alasmidonta*-complex has variously incomplete hinge teeth (especially the laterals), and the Holarctic *Anodonta*-complex has no hinge teeth. In the classification used in this paper they are all called family Unionidae, subfamilies Unioninae and Anodontinae, the latter including both the *Alasmidonta* and *Anodonta*-complexes.

In the strictly Nearctic *Amblema*- and *Lampsilis*-complexes, the glochidia are rounded, elliptical, oval, or ax-head shaped, with short hinge lines, and normally without spines. A few species (particularly those with ax-head glochidia) have two or more pairs of hooks opposite the hinge but even when present they appear to be very different in structure and position from those in the Unionidae and Anodontinae. Gravid females have marsupial water tubes variously swollen or elongated, but not subdivided into three compartments. The *Amblema*-complex and the *Lampsilis*-complex differ markedly in gill structure, in the method of releasing the glochidia, and in breeding habits. In the classification used in this paper they are family Unionidae, subfamilies Ambleminae and Lampsilinae.

LAKE TEXOMA REGION FAUNA

Family Unionidae

Subfamily Anodontinae

LASMIGONA Rafinesque, 1831

This is one of the genera of Anodontinae with developed cardinal teeth and typically an irregular shelf in place of the interlocking lateral teeth found in other subfamilies. Also, the interdentum of the left valve is inrolled, serrate, and projects into a corresponding cavity in the right valve. In the Lake Texoma region these features are immediately diagnostic, but eastern Oklahoma has one, possibly two, rare monotypic genera with essentially similar tooth structure; these are *Arkansia* Ortmann and Walker, 1912, and *Arcidens* Simpson, 1900. *Arkansia wheeleri* Ortmann and Walker, 1912, occurs in the Ouachita River, Arkansas, and in the Kiamichi River in Oklahoma. *Arcidens confragosus* (Say, 1829) has not been recorded from Oklahoma, but since it occurs in Texas, Louisiana, Arkansas, Missouri, Kansas (and farther east), it will probably turn up. Strecker (1931) records *Arcidens* from Red River drainage in Texas, but he does not give the locality. We have searched for it in vain in Oklahoma. These two genera are both much more inflated than the species of *Lasmigona* and in outline look more like odd species of *Quadrula* than like anodontines. *Arcidens* is complexly sculptured with tubercles, zig-zag wrinkles, and oblique ridges, the tubercles tending to form two divergent rows radiating from the umbone, while the wrinkles and ridges vary in their state of development. *Arkansia* has an uneven to smooth shell, the most obvious sculpture is a series of wrinkles on the posterior slope, but even these are sometimes absent. *Lasmigona* includes six or seven compressed species, their flatness distinguishes them from *Arkansia* and *Arcidens*. The genus ranges from the Atlantic Coast to Manitoba to Texas, but is absent from most of the south Atlantic and Gulf Coastal Plain.

Lasmigona complanata (Barnes, 1823).
(White Heel-splitter)
=*Symphynota complanata* of Isely, 1925

This is one of the most distinct species in the Oklahoma fauna. The large, flat, rounded to oval shell, the beautiful white nacre, and the pronounced wing dorsal to the vestigial, non-interlocking lateral 'teeth' all combine to make identification easy. Oklahoma specimens usually are about 110 to 160 mm long; however, Haas (1941) mentions one 216 mm long from the Spoon River, Illinois.

A second species, *Lasmigona costata* (Rafinesque, 1820) occurs in Little River drainage (we have taken it in the Little, Glover, and Mountain Fork Rivers), and also in various eastern tributaries of the Arkansas River. It is much more elongate, and usually has a series of parallel or radiating corrugations on the posterior slope. Occasional specimens have wrinkles over the entire posterior half of the valve, while specimens in The Ohio State University Museum of Zoology from the Ouachita and Caddo Rivers in Arkansas lack all wrinkles so that even the posterior slope is smooth. Similar smooth specimens are mentioned by Ortmann (1919 p. 127) from Randolph County, West Virginia, but such individuals are rare.

The White Heel-splitter occurs widely in Mississippi River drainage, and ranges north around Hudson Bay and northwest into Alberta; it apparently has not been recorded in Texas. In Oklahoma, Isely (1925) records the species from the Washita, lower Blue, and Muddy Boggy Rivers. We have taken it abundantly in the Blue River below Durant Dam but not above, in lower Pennington Creek (Washita drainage), and in Lake Texoma itself.

The two western species of *Lasmigona* appear to replace each other in Oklahoma. *Lasmigona complanata* is more abundant in muddy and silty situations with relatively quiet water (below Durant Dam is a conspicuous exception), while *Lasmigona costata* is more abundant in gravely riffles and high-gradient streams.

ANODONTA Lamarck, 1799

The complete absence of cardinal and lateral teeth, and thin, straight or gently curved hinge line immediately separate this genus from all others in the Lake Texoma region. Immediately to the east there is a confusingly similar genus, *Strophitus* Rafinesque, 1820; the single species in Oklahoma is *S. undulatus* (Say, 1817) [= *S. rugosus* (Swainson, 1822)]. Isely (1925) records *Strophitus* from the Muddy Boggy and Kiamichi Rivers, and we have taken it in the three major branches of the Little River (Little, Glover, and Mountain Fork). *Strophitus* is abundantly distinct in marsupial structure; however, shells are quite similar except that *Strophitus* has simple sometimes posteriorly angulate ridges on the beaks, while in *Anodonta* the ridges are sharply biconvex and angulate, also *Strophitus* has a heavier hinge with a low obtuse swelling which forms a weak angle interrupting the even curve of the hinge line.

The two species of *Anodonta* which occur in Oklahoma are both reported to have hermaphroditic individuals or entire colonies (Heard, 1967; Tucker, 1928; van der Schalie and Locke, 1941; and others cited therein); Oklahoma specimens have not been investigated.

Anodonta is one of the most widespread naiad genera in the world, ranging from Canada to Mexico, Maine to California, and Western Europe to Asia and north Africa. There are two general types (or species groups) in the United States; subgenus *Anodonta* in the restricted sense includes *grandis* and dozens of other names, many of which are surely synonyms; subgenus *Pyganodon* includes *imbecilis* and related species, *suborbiculata*, and the species in Pacific drainage. *Anodonta grandis* and *imbecilis* occur widely in Oklahoma. *Anodonta suborbiculata* probably occurs, as this species has been collected in Louisiana, Arkansas, Kansas, Missouri, Iowa, and farther east. The actual number of Nearctic species in the genus is not established, for no two authors agree; perhaps eight to several dozen is a reasonable range.

Anodonta grandis form *grandis* Say, 1829.
(Floater)
Anodonta grandis form *stewartiana* Lea, 1834. (Slop Bucket)
=*Anodonta corpulenta*, of Isely, 1924

The nomenclature and systematic status of these two forms has not been worked out. They are distinct in some areas, and yet appear to intergrade in others. In general, shells from rivers with appreciable current are referred to *A. grandis* form *grandis*. They are usually smaller, less inflated, and tend to have bluish-white nacre. Shells from lakes, ox-bows, and deep or sluggish rivers tend towards *A.*

grandis form *stewartiana,* being larger (up to 185 mm long), more inflated, and tend to have pink, salmon, or bronze nacre. The differences are not constant, and in Oklahoma (Lake Murray for example) there are large, inflated shells with bluish nacre, and other combinations of the above features. It is possible that man-made lakes that were originally rivers and streams all have *grandis* modified by the change to quiet water, and thus convergent toward *stewartiana,* but this has never been tested, and is further complicated by the possibility of introductions via release of game and bait fish carrying various glochidia.

Juveniles of form *stewartiana,* unfortunately without data, were found among miscellaneous shells left from previous sessions in The University of Oklahoma Biological Station invertebrate zoology laboratory. They are extraordinarily inflated, exceptionally thin, and pale honey-brown. They contrast sharply with juveniles of form *grandis* which are relatively compressed, heavier, and darker greenish-brown. In fact, they suggest genetically different species, not eco-phenotypes, but our material is very meager.

The distribution of this species complex is odd. We have taken *'grandis'* in each of the major eastern rivers (Mountain Fork, Glover, Little, and Kiamichi). There is, at present, no record from the Muddy Boggy, probably due to inadequate collecting. In the Blue River, *'grandis'* is found only below Durant Dam, we have never found it amongst the many hundreds of specimens examined from above this structure. In the Washita River, and its tributary, Pennington Creek, and the Red River, from Lake Texoma westward, most of the specimens appear closer to *'stewartiana'*, as do those from the Coastal Plain in southeastern McCurtain County.

The absence of this complex in the Blue River above the dam suggests that *'stewartiana'* stock may have extended upstream from the Red River as far as the dam and has there converged towards *'grandis.'* Although this hypothesis is reasonable in terms of existing distribution data, the alternate possibility that the Durant Dam population is the isolated remains of once more widespread *'grandis'* stock has not been disproved. Careful morphometric analysis and study of the lower portion of the Blue River may some day help settle the question.

Anodonta imbecilis Say, 1829 (Floater)

This small, and very distinct, fragile species is immediately separable from the *grandis* complex by the flat umbones which normally do not protrude above the hinge line in lateral view. In the *imbecilis*-group the maximum dorso-ventral measurement normally extends from the hinge line to the ventral margin. In the *grandis*-group the maximum dorso-ventral measurement extends from the swollen umbone to the ventral margin. In *Anodonta suborbiculata* Say, 1831, the umbone is flat and not inflated, but the shell is large almost circular in outline, and suggests an excessively fragile saucer; the other eastern species of *Anodonta* are much longer than high. Red River *Anodonta imbecilis* adults are about 45 to 70 mm long The largest seen, from the Scioto River, Ohio, is 105 by 47 mm. In the Blue River series, the largest of 40 specimens is 78 by 38 mm.

The Oklahoma distribution of *A. imbecilis* is incompletely known. We have a single specimen from the Little River, a series from Gates Creek below the dam of Lake Raymond Gary and from the Lake itself (the creek enters the Kiamichi River just above the junction of the latter with the Red River). Isely (1925) records it from both the upper and lower portions of the Kiamichi itself. There are no records from the Muddy Boggy River. In the Blue River the species is rare below Durant Dam, abundant in a small tributary about 12 miles west of Wapanucka, and apparently absent in the main part of the Blue above the dam. The species is recorded in Lake Texomy by Riggs and Webb (1956) and Sublette (1957). In Washita River drainage we have seen specimens from Pennington Creek. Finally, Isely (1925) records it from West Cache Creek in Cotton County.

Subfamily Ambleminae

MEGALONAIAS Utterback, 1915

This genus includes large blackish shells with crowded ridges and nodules on the beaks and a dense pattern of W, M, or irregularly zig-zag ridges on the first few years growth. Later years lack these fine ridges although the posterior half of the shell often has a series of oblique, parallel, undulating corrugations which are smaller and more closely placed on the posterior slope. Most specimens have the same corrugations and diagonal grooves as *Amblema,* and, in fact, the two genera appear quite similar and are combined by some workers. *Amblema* lacks the complicated sculpture of the early years, has a rounded to oval outline, and very large, massive cardinal teeth, while *Megalonaias* is quadrate in outline, especially juveniles, and although attaining a much larger size than *Amblema,* has smaller cardinal teeth. In addition, gravid females of *Megalonaias* have the marsupia forming large purplish pads with rusty brown 'placentae.' Gravid individuals occur in Missouri (Utterback, 1915) from August through the winter to about April.

There appear to be three or more species in the genus in the United States, one widespread, the other two restricted to the Escambia, Apalachicola, and Ochlockonee drainages in Florida and southern Georgia.

Megalonaias gigantea (Barnes, 1823). (Washboard)
= *Quadrula heros*, of Isely, 1925

Large adults have the largest and heaviest (but not thickest) shells in North America, the largest we have seen from west of the Mississippi (from Arkansas) measuring 200 X 155 mm; however, Haas (1941, p. 261) records a gigantic specimen 280 mm long and 203 mm high from the Salt River, Kentucky; this individual is about the size of an 8½ X 11 inch sheet of note paper with the corners rounded off. The few Oklahoma adults are about 130 to 175 mm long. Isely (1925) records the washboard in the Blue, Muddy Boggy, and Kiamichi Rivers, as well as the larger rivers in Arkansas drainage. In southern Oklahoma we have a series from the lower Kiamichi River, have not investigated the Muddy Boggy River, and have looked for it in vain in the Blue River. Since it is said to be a species of deep water it might still occur in the lower Blue River in areas we have not collected. This is, in fact, the only species recorded in the Blue River by Isely which we have not taken. The species occurs widely in the Mississippi drainage from Texas and Missouri east to Alabama and Ohio, and in our experience is much less abundant than *Amblema*.

AMBLEMA Rafinesque, 1820

Among the large, heavy shelled genera of naiads in eastern Oklahoma, this is by far the most common. Three or more oblique ridges cross the shell posterior to the umbone on a line roughly parallel to the line of maximum length. These ridges vary in their number and state of development, and in some populations are more or less continued as smaller corrugations curving dorsally and crossing the posterior slope of the valve. When the latter sre present, they are fewer in number than in *Megalonaias*, nine or less in Oklahoma *Amblema*, fifteen or more in Oklahoma *Megalonaias*, counting only those from the umbone to the posterior end of the lateral teeth. Occasional specimens of *Amblema* lack all ridges, others may have low wrinkles or weak pustules superimposed on the ridges, in some almost the entire valve is covered with wavy ridges; in all such cases a useful feature is the very massive hinge and exceptionally heavy cardinal teeth of adults.

A number of recent authors (for example: Clench and Turner, 1956; Clarke and Berg, 1959; Murray and Leonard, 1962) use the name *Crenodonta* Schluter, 1838 because *Amblema* Rafinesque, 1820 is preoccupied by *Amblema* Rafinesque, 1819. Rafinesque first proposed the name with a single species *(ovalis)* which is unrecognizable. The following year, he used the name in the sense of the present paper. It seems logical to request the International Commission of Zoological Nomenclature to suppress *Amblema* Raf., 1819, and accept the familiar usage of Rafinesque, 1820; this has been done by Clark and Clench (1965), and in anticipation of this decision, and in the interest of stability, we are using *Amblema* Raf., 1820.

A bewildering number of species group names have been applied to populations of *Amblema (plicata, costata, peruviana, undulata, rariplicata, perplicata, quintardi, hippopea*, etc.). We do not know if only one or several species are involved, however it is evident that *Amblema* is a plastic, variable genus. It seems probable that all populations in the vast Mississippi system are variants of *plicata* (Say, 1817) (the oldest name in the genus, described from Lake Erie), while separate Gulf drainage systems have more or less related but isolated populations, some of which may rate species recognition. In assessing these differences, it should be remembered that as in many species of naiads, development of sculpture and shell proportions have been correlated (Ortmann, 1920) with stream size.

Amblema occurs widely in the Mississippi system north to Manitoba, in the Great Lakes and St. Lawrence system, and in Gulf rivers from Alabama to Texas.

Amblema plicata (Say, 1817). (Blue Point, Three-ridge)
=*Quadrula plicata*, of Isely, 1925
=*Quadrula undulata*, of Isely, 1925
=*Crenodonta peruviana*, of Murray and Leonard, 1962

The recognition features of this species are discussed under the genus, and under the related genus *Megalonaias*. Variation is continuous, extensive, and confusing, and the names of the many varieties have often been used incorrectly so that for example *A. plicata* of one author is not necessarily the same as *A. plicata* of another. The name *plicata* (Say, 1817) applies to all populations provided they constitute a single species; in the restricted sense, *plicata* applies to the dwarfed, weakly undulate valves with smooth or almost smooth posterior slopes in Lake Erie; *peruviana* (Lamarck, 1819) is essentially a larger sized *plicata*, and like it, is strongly inflated; with high, full, incurved beaks, and broad weak undulations on the disc and posterior slope, it is characteristic of the largest, deepest, sluggish rivers; *rariplicata* (Lamarck, 1819) is similar except the beaks are lower and it is not so inflated, it is also a slow water form; *perplicata* (Conrad, 1841) is moderately inflated, has low beaks and broad, weak undulations, it is a form of moderate current; *costata* Rafinesque, 1820 is flat, compressed, with low beaks, and strongly corrugated disc and posterior slope, it inhabits the smaller, swifter rivers and the headwaters; *quintardi* (Cragin, 1887) is the extreme swift water form with profuse undulations covering much of the disc, and those on the posterior slope crowded and sometimes branching. Since most populations are variable, it is often impossible to assign them to one of these names. The complex needs careful study.

Larger individuals from Oklahoma range from about 90 to 120 mm long. A specimen from the Muskingum River in Ohio is 155 X 102 mm, and Haas (1941) mentions an Illinois specimen 171.4 mm long. See the generic discussion for the distribution of the species. Some information about the life history is given by Stein (1968, 1970).

TRITOGONIA Agassiz, 1852

Although this is the only member of the Ambleminae with sexually dimorphic shells, not all specimens can be accurately sexed by shell characters alone. Males tend to be shorter and wider, with the posterior margin of the shell obtusely angulate dorsally, then diagonally truncate, and acutely angulate postero-ventrally. Females are longer and more slender, the posterior end drawn out, rounder dorsally and bi-angulate ventrally. Some shells, however, are intermediate. The shells of both sexes usually are densely tuberculate over almost the entire surface, and there is a conspicuous, lumpy, post-umbonal ridge marking the edge of the posterior slope. The periostracum can be dark blackish brown, pale brown, brown with beautiful irregular green markings, or almost solid green; the nacre is white or various shades of pink or purple. The genus is distinguished from almost all other pustulate shells by its elongate form, even in males the height being less than 60% of the length. *Quadrula cylindrica* is even more slender, but it is typically marked with green triangles and has the dorsal and ventral margins of the shell almost straight and parallel; *Tritogonia* has dorsal and ventral margins irregular and not parallel.

There is one confusingly similar genus which occurs in Oklahoma only in Little River drainage (Little River and Glover Creek), *Plectomerus* Conrad, 1853. The single species, *Plectomerus dombeyanus* (Valenciennes, 1827)–[*P. trapezoides* (Lea, 1831), see Walker 1928]–is quite similar to some short stocky males of *Tritogonia* although juveniles are very different. Small individuals of *Tritogonia* are essentially miniatures of the adult, with a broad rounded anterior half and a narrower posterior, when the valves are still attached and widely open they look like a pair of angel's wings with broad shoulders and rounded wing tips; small *Plectomerus* are elongate, spindle shaped, and taper to an acute point posteriorly so that an open pair lacks the 'shoulders' and has pointed 'wing tips.' Adult *Plectomerus* are differently shaped, being less pointed posteriorly, with a very pronounced post-umbonal ridge, and there is often a small scar in the nacre half way from the umbone to the ventral margin and posterior to the anterior adductor and retractor scars. *Tritogonia* lacks this scar, and of course, the distinctive outline of the juvenile shell is visible in the early growth lines.

The genus contains a single widely distributed species which ranges through much of the Mississippi system and the other Gulf drainages from Georgia and Alabama to Texas.

Tritogonia verrucosa (Rafinesque, 1820)
(Buck-horn, Pistol grip)
=*Tritogonia tuberculata* of Isely, 1925

The recognition features of this species are discussed under the genus. This is a variable species but the compressed, tuberculate shell, broadly rounded anterior end, incurved ventral margin, and narrowed posterior end are quite distinctive. White nacre appears to be found almost throughout the range, pink and purple nacred individuals tend to be more common to the south. In the Blue River below Durant Dam, 17 of 64 specimens are various shades of pink. In Gates Creek below Lake Raymond Gary, 10 of 48 are pink, the remainder in these two collections have white nacre; no purple individuals have been seen in Oklahoma, although a few have the pink very intense. Other collections in the state have pink specimens in about the same proportion, but the series are too small to be meaningful.

Most Oklahoma adults range between 100 and 140 mm long; however the species gets considerably larger. The longest seen are from Ohio and measure 180 X 87 mm, and 172 X 92 mm. Haas (1941) cites a specimen 190.5 mm long from the Spoon River, Illinois.

This appears to be one of the most widespread species in Oklahoma, but it is never numerically dominant. We have records from throughout the Blue River, and in the Kiamichi, Little, Glover, and Mountain Fork. In addition, Isely (1925) records it from Cache Creek in western Oklahoma, and the Washita and Muddy Boggy Rivers. We have not seen it from Pennington Creek nor Lake Texoma.

QUADRULA Rafinesque, 1820

The dozen or more species of this widespread genus are almost always externally pustulate or tuberculate, have white nacre, massive and completely formed hinge teeth, and a broad, flat interdentum. There are, however, a number of other pustulate-shelled genera which can be distinguished as follows. Four genera have females typically with all four gills marsupial, as does *Quadrula*. *Tritogonia* Agassiz, 1852, is sexually dimorphic and elongate (height 60% or less than the length) while *Quadrula* is not sexually dimorphic in shell characters and, except for *Q. cylindrica*, is much shorter (height 70% or more than length). *Quincuncina* Ortmann, 1922, restricted to parts of Alabama, Georgia, and Florida, usually has chevron, W or M shaped wrinkles near the umbones (as in many *Quadrula*), but the latter are very flat and non-inflated. *Amblema* Rafinesque, 1820, and *Megalonaias* Utterback, 1915, have three or more oblique ridges on the posterior half of the shell which are independent of the pustule and growth patterns.

All other tuberculate genera have the marsupium restricted to some part, or all of the outer gills. *Obliquaria* Rafinesque, 1820, has a row of knobs from the umbone to the ventral margin, but differs from all of our genera in that the knobs alternate from left to right valves so that no two knobs are opposite each other. *Cyclonaias* Pilsbry, 1922, is very *Quadrula*-like in shell characters, but usually has purple nacre. *Plethobasus* Simpson, 1900, contains both strongly and faintly pustulose species, but the orange soft parts (usually) and yellow to red ova are distinctive. The various anodontine genera can be distinguished by tooth structure, see especially the description of *Lasmigona* and the related genus *Arcidens*. It should be pointed out that *Quadrula cylindrica* (Say, 1817) does not fit the above discussion as well as the other species in the genus; it is even longer and narrower than female *Tritogonia*, it usually has orange and black soft parts (similar in color to *Plethobasus*, but the eggs are white and in all four gills), and a few populations are scarcely pustulate. The species is, however, easy to recognize because of the long, parallel-sided dorsal and ventral margins of the shell, and the ornamentation of small, green triangles.

The genus ranges widely in Mississippi and other west Gulf drainages, and three species (*Q. quadrula*, *Q. pustulosa* and *Q. cylindrica*) have crossed into Lake Erie drainage. These same three species occur in Oklahoma (the first two in the Lake Texoma region), while two others enter eastern Oklahoma but do not extend so far west.

KEY TO THE SPECIES OF QUADRULA IN OKLAHOMA

1. Shell usually ornamented with few to many green triangles, rarely almost the entire shell green. 2
   Shell ornamented with green rays, rounded spots or unmarked. . . . 3
2. Shell elongate-cylindrical or much compressed, much longer than high . . . . . *Quadrula cylindrica* (Say, 1817)
   Shell subquadrate or triangulate only slightly longer than high. . . . . *Quadrula metanevra* (Raf., 1820)
3. Umbone and early growth years densely sculptured; shell usually with a smooth postmedian depression bordered with tubercles. . . . . *Quadrula quadrula* (Raf., 1820)
   Umbone and ewrly growth years not sculptured, or at most one or two small pustules; shell without a smooth postmedian depression. 4
4. Early years growth with a few small pustules, and no green rays; later years with pustules tending to form two diverging rows; posterior end of shell emarginate; interdentum notched. . . . *Quadrula nodulata* (Raf., 1820)
   Early years growth without pustules, and with one or more green rays; later years with pustules random; posterior end of shell rounded; interdentum complete, without a notch. . . . . *Quadrula pustulosa* (Lea, 1831)

Quadrula quadrula (Rafinesque, 1820).
(Maple-leaf)
= *Quadrula forsheyi*, of Isely, 1925
= *Quadrula fragosa*, of Isely, 1925
= *Quadrula lachrymosa*, of Isely, 1925
= *Tritogonia nobilis*, of Isely, 1925

This is a very variable species or perhaps even a complex of sibling species. Adjacent streams often have very different appearing populations, and sometimes a single locality will have a variety of shells. The densely pustulate beaks, interrupted by a smooth post-median depression, constitute the most reliable recognition feature. Since the beaks are often eroded, the fact that the smooth depression continues to the ventral margin of the valve and there forms a concave emargination of the otherwise convex edge is useful. Some shells (for example from Pennington Creek) become smooth after the first few years growth, while others (Gates Creek below Lake Raymond Gary) are pustulose to their outer margins. Such lots appear very different when placed side by side, but most collection sites in southern Oklahoma have material variously intermediate, many are recognizable at sight. Shells vary in size, shape, degree of sculpturing, and also in color. When cleaned, some are solid pale brown, others are lightly to heavily and complexly patterned with green. An attempt to understand the geographic variation of this species was published by Neel (1941); however, more studies are needed. Adult Oklahoma specimens are about 60 to 110 mm long, the two largest specimens seen, from Ohio, are 180 X 87 mm and 172 X 92 mm.

Quadrula quadrula has been taken in every river system in southern Oklahoma from the Arkansas border to Lake Texoma, and Isely (1925) records it also from the Red River to the west, and from Cache Creek. We have taken only one juvenile in the entire Little River drainage, this was in the Little River itself, 5.2 mi NE of Cloudy. None were found in the Mountain Fork River nor in Glover Creek. In the Blue River, above Durant Dam and in Glover Creek in Little River drainage the species is absent although *Quadrula pustulosa* is very abundant. In the Blue River below Durant Dam, *Q. quadrula* is a little more abundant than *Q. pustulosa*. In the Kiamichi River *Q. pustulosa* was the more abundant. In lower Pennington Creek *Q. pustulosa* was absent and *Q. quadrula* was common. The geographic pattern in Oklahoma seems to be one of increasing abundance of *Q. quadrula* in the lower portions of the rivers and on the Coastal Plain, rapid replacement by *Q. pustulosa* above the Fall Line, and only scattered individuals of either species in the high gradient streams and headwaters.

Quadrula pustulosa (Lea, 1831).
(Warty-back, Pimple-back)

If the present conservative taxonomic status is correct, this is one of the most bewilderingly variable species in Oklahoma. The only constant features are the absence of pustules in the first few years, the white nacre, the massive hinge teeth, and at least a trace of one or more green rays on the umbonal region. Individuals can be densely pustuled or entirely smooth (rarely), with the posterior slope pustuled, or costate, or smooth, with the pustules aligned in symmetrical patterns or irregular, with round pustules or linear ones, with round symmetrical outlines or very asymmetrical with the beaks forward and the shell produced ventro-posteriorly to give a triangular outline, and apparently all combinations and intermediate conditions. Someone should carefully study individual and geographic variation in this species, and pay particular attention to the correlation of the various character states with each other and with the environment of the collection site. Perhaps then some pattern might emerge that gives us a better understanding of the species. In this state, adults are about 50 to 70 mm long; a very large specimen from Ohio is 95 X 85 mm.

The distribution of this species is partly discussed under *Quadrula quadrula*. In addition, we have not yet taken it in the Mountain Fork River, and Isely (1925) records it in the Muddy Boggy and Washita Rivers, and in Cache Creek in western Oklahoma.

FUSCONAIA Simpson, 1900

This is one of several rather similar genera, distinguished primarily by soft parts. In *Fusconaia* all four gills are usually used as marsupia, the ova are variously pigmented, and the body ranges from straw colored through orange to red. *Lexingtonia* Ortmann, 1914 (we are aware that the validity of this genus has been questioned), has not been recorded west of the Mississippi River; it also has red ova, but they are carried in the outer gills only. *Plethobasus* Simpson, 1900, occurs rarely in eastern Oklahoma, north of the Arkansas River, it has red ova in the outer gills only, orange body, and a pustulose to very weakly nodulose shell. *Pleurobema* Rafinesque, 1819, has white ova in the outer gills (rarely in the inner gills also), and usually exceptionally asymmetrical, rounded or cornucopia-shaped valves; it is recorded in northeastern Oklahoma by Isely (1925) but we have not taken it in Red River drainage.

Fusconaia includes from one dozen to three dozen species, and is widespread in those rivers and streams draining into the Gulf of Mexico, there is at least one species in the Great Lakes. The two most widespread species-complexes center around *F. flava* (Rafinesque, 1820), usually with orange or red ova, and *F. ebena* (Lea, 1831), usually witn blue or black ova, both occur west of the Mississippi River in Arkansas, however *F. ebena* is not yet known from Oklahoma. The populations of *Fusconaia* in eastern Oklahoma differ from river to river, and sometimes within rivers. Since they have reddish ova, it would be easy to say that all are variants of *F. flava*, but this obscures the essential complexity of the situation. The *flava*-complex needs a detailed study. For example, *Fusconaia* is one of the dominant genera in the Blue River above Durant Dam and in Glover Creek in Little River drainage. These two populations are so different that they suggest distinct species. In Blue River specimens, the valve is relatively small, thin, pale, not inflated, a little asymmetrical, tends to be longer than high, and juvenile and adult shells are similarly shaped. In Glover Creek specimens the shell is large, thick, dark, moderately inflated, becomes very asymmetrical at larger sizes, tends to be higher than long, and juvenile and adult shells are strikingly different in shape, the juveniles being like Blue River shells, but the adults becoming very produced posteriorly, resembling some species of the related genus *Pleurobema*. Between these two populations, in the lower Kiamichi River, *Fusconaia* valves are almost grotesquely thick-shelled, inflated, and have a pronounced posterior ridge preceded by a shallow dorso-ventral depression; they appear similar to the widespread population recognized nomenclatorially as *Fusconaia flava* form *undata* (Barnes, 1823). However, assigning names to all of these various populations would be very premature.

Fusconaia sp., apparently *flava* (Rafinesque, 1820).

= *Quadrula rubiginosa*, of Isely, 1925

The smooth shell, interlocking lateral teeth, broad and flat interdentum, deep umbonal cavity which invades the base of the cardinal teeth, and the broad green ray or rays on the umbonal region, will distinguish this species from all except occasional non-pustulate specimens of *Quadrula pustulosa*. The latter is usually more symmetrical, rounded, heavier, more inflated, and generally less angular, but occasional specimens will be troublesome. The tooth character mentioned in the key (couplet 12) is not perfect, but it works in the majority of cases. Although this species appears exclusively white-nacred in the Blue River, salmon-nacred specimens are known to be scattered throughout the range. Adult specimens of this form are about 50 to 65 mm long above Durant Dam and about 55 to 70 mm long below the dam. The maximum size for *Fusconaia flava* in Ohio is 115 X 75 mm for an elongate individual, and 95 X 75 mm for a higher one.

The Blue River apparently marks the western terminus of the range of this genus in Oklahoma. It has not been taken in Pennington Creek to the west and occurs in all Oklahoma rivers to the east. Peripheral localities for the *F. flava* complex include southern Manitoba, Ontario, New York, West Virginia, Tennessee and Texas.

Isely characterized this species as occasional in the lower Blue River and the dominant species at Durant and Milburn. He gives counts for the Milburn collection where 70 of 148 shells (47%) were *Fusconaia*. Fifty-five years later it was even more abundant as 244 of the total 348 shells (70%) were this species. At Durant, however, there has been a drastic reversal, for the species was the most abundant in Isely's collection, while in 1967, only 19 of 800 (2.4%) were *Fusconaia*. In 1968 the percentage was about 10%, but at least ten other species were more abundant. Since this was a selected, non-random collection, *Fusconaia* was actually much less common than it appeared.

Either the dam at Armstrong, or other unknown factors, have had ill effects on this species. Modern conditions are apparently far less suitable. The great abundance of *Fusconaia* upstream has not been able to maintain the species in its former abundance below the dam.

Fusconaia askewi (Marsh, 1896).

-*Quadrula askewi*, of Strecker, 1931

Recent collections of living specimens in the Sabine River in Texas and Louisiana by parties from the Ohio State University Museum of Zoology were found to have red ova carried in both outer and inner gills, thus requiring the generic combination indicated above. This species complex is poorly known; but seems limited to Gulf drainages.

A single, slightly weathered valve was discovered among the 800 shells collected in the Blue River below Durant Dam in 1967. It is likely that the shell was dropped by one of the many fishermen or children who visit the site, for the species is otherwise unknown in Oklahoma. The Sabine River in Texas (downstream from Lake Tawakoni) where *F. askewi* is known to occur, is only two hours drive from Durant Dam, a distance very compatible with the searching instincts of even a moderately avid fisherman. Strecker (1931) records this species in the Red River drainage in Texas, however actual specimens or localities are not cited. The Red and Sabine Rivers are, of course, parts of different drainage systems.

The species has no outstanding recognition features, except pale pink to salmon colored nacre. The single right valve (OSUM 25790) is 67 mm long and approximately 47 mm high. The point of the beak is 20 mm from the anterior end, measured by dropping a perpendicular line from the beak to the line of maximum length. The valve is about 16 mm wide. Specimens from the Sabine River show the following features. Smaller shells almost egg-shaped in outline and more convex than the other Blue River *Fusconaia*. larger shells (around 85 mm long or more) become very drawn-out and pointed postero-ventrally; periostracum dark brown to pale tan with few to many faint, narrow, darker rays; eroded portions of shell with a pale pinkish or brownish tint, definitely not white; umbone apparently with about three concentric loops which are sharply angulate just anterior to posterior ridge, and weakly sinuate medially; posterior ridge varies from well developed to virtually absent, posterior slope with two almost parallel dark lines or grooves crossing the growth lines; nacre pale pink to salmon colored to white; right cardinal tooth directed above to half way through the anterior adductor muscle scar, the divergence from the hinge line increasing with age; right lateral tooth single, but with a well-developed supernumerary ridge posteriorly, the laterals of both valves not paralleling long axis of shell but directed postero-ventrally; interdentum of right valve impressed, narrow, often with a minute notch, of left valve better developed and entire; anterior retractor muscle scar excavating base of cardinal tooth, especially in right valve; pallial line often becoming weak to vestigial posteriorly.

UNIOMERUS Conrad, 1853

This is one of the very few thin-shelled genera in the subfamily Ambleminae. In Oklahoma, any smooth, thin-shelled species with most of the outer gills marsupial *and* interlocking lateral teeth, belongs here. Actually, if present, the beak sculpture is distinctive, consisting of a series of concentric arcs which are widely open anteriorly (not attaining the shell margin anterior to the umbone), and which are strongly hooked around the umbone posteriorly. Oklahoma shells average twice as long as high (height 45 to 55% of length), and are usually straw-brown to dark brown externally, with whitish nacre often with pale pink or blue tints. Shells with purple nacre, occurring in some other parts of the range, may or may not be this species. There is very little that is outstanding, and when all else fails, the fact that this genus lacks most of the recognition features of other naiads, is useful. The habitat is quite distinctive for this is often the only species abundant in such temporary situations as roadside ditches, cattle tanks, intermittent ponds and streams, etc. *Uniomerus* is able to withstand extended periods of drought without desiccation by remaining closed in the moist mud of its habitat. Unfortunately, the genus also occurs in streams and lakes in company with a naiad assemblage normal for such situations, and it is particularly on such occasions that identification can be troublesome.

Uniomerus seems to be unsatisfactorily close to the thin-shelled species of *Elliptio* Rafinesque, 1820, of southern and eastern United States, but quite distinct from the heavy-toothed *Elliptio dilatatus* (Rafinesque, 1820), the only species of *Elliptio* which extends into eastern Oklahoma.

There are from two to five currently recognized species of *Uniomerus;* of these *U. obesus* (Lea, 1831) is a coastal species ranging from North Carolina to southern Florida to Texas. The Ohio State University Museum of Zoology also has specimens from Virginia, and an isolated population, perhaps introduced, in central Arkansas; there is a slight chance that it occurs in Oklahoma. It is quite possible that this widespread distribution masks more than one species. A second species is discussed below.

Uniomerus tetralasmus (Say, 1830).

= *Unio tetralasmus*, of Isely, 1925

The recognition features of this species are the same as for the genus. Within the genus, *U. tetralasmus* has the posterior end of the shell almost evenly rounded, while the *U. obesus* complex (based on the Arkansas series) has the posterior end of the shell abruptly narrowed and elongated.

This species ranges from Ohio and Alabama west to Iowa, Colorado, and western Texas. Isely (1925) had specimens from Cache Creek, and two localities on the Texas side of the Red River. Strecker (1931) records it from Harrison, Cooke, Montague, Bowie, Wichita, and Wilbarger Counties, Texas, all in Red River drainage. We found one specimen out of over 1,000 naiads in the Blue River below Durant Dam, and it is also in the Washita River, Pennington Creek, and Rock Creek just to the west of Pennington. County records with no other data are from Jefferson and Marshall Counties, Oklahoma.

Large adult specimens range from about 85 to 115 mm long, while the largest we have seen, from Ohio, is 125 mm long by 63 mm high.

Subfamily LAMPSILINAE

PTYCHOBRANCHUS Simpson, 1900

The very unusual pleated marsupial gills of gravid females are the best feature for recognizing this genus, and in fact, large females have a prominent depression in the nacre running from the umbone obliquely backward and downward marking the position of the marsupium; in some old individuals this is crossed by several smaller depressions marking the individual gill folds. The shells are distinctively compressed, and usually humped so that the dorsal outline is much more arched than the ventral. Ball (1922, p. 111) states '. . . the more swollen forms with a more pronounced hump are to be found in the larger streams, and . . the flatter forms with practically no hump are confined to the smaller rivers.' The cleaned periostracum is straw-yellow with radiating greenish lines or linear rows of spots, the nacre is white or bluish white, the hinge line is arched and massive for the size of the shell, the lateral teeth curve ventrally, the umbonal cavities are exceptionally shallow, and the height is about 48 to 55% of the length. In *Lampsilis radiata luteola* also yellow with greenish lines, the height is proportionately greater, about 53 to 61% of the length, the shells and umbonal cavities are much more inflated, and the teeth and hinge line are thinner and straighter. In *Villosa* sp. (resembling *iris)* in eastern Oklahoma, the shell is as compressed as in *Ptychobranchus*, but more elongate, fragile, and thinner. Both of these genera have the dorsal and ventral outlines of the shell more alike than in *Ptychobranchus*. Another genus and species, *Elliptio dilatata* (Rafinesque, 1820) (=*Unio gibbosus*, of Isely, 1925) has been recorded by Isely from the Kiamichi River and from Arkansas drainage. He mentions (p. 100) that Arkansas drainage specimens have the usual and distinctive purple nacre, but those from the Kiamichi were white nacred. The latter individuals, if in fact they were *Elliptio*, would be difficult to separate from *Ptychobranchus* without soft parts, however *Elliptio* normally has the periostracum dark green to brown to black, and the beak cavities are even shallower than in *Ptychobranchus*. We have no recent records of *Elliptio* from the Red River drainage of Oklahoma. In the field, many dirty specimens of *Ptychobranchus* look like *Elliptio*, and this may be the source of Isely's record.

The genus contains four or five species distributed from the Great Lakes to Georgia, Alabama, Kansas, and Louisiana.

Ptychobranchus occidentalis (Conrad 1836). (Kidney-shell)
= *Ptychobranchus clintonense*, of Isely, 1925
= *Ptychobranchus phaseolus*, of Isely, 1925, not of other authors

Isely (1925) records two species of *Ptychobranchus* from Red River drainage in Oklahoma, *P. occidentalis* -I =*clintonensis* Simpson, 1900 I- and *P. fasciolaris* (Rafinesque, 1820) -I *phaseolus* (Hildreth, 1828) I-, the former from the Blue River at Durant and Milburn, the latter from the Kiamichi River at Tuskahoma. Our collecting has yielded only one species, so the record of *P. fasciolaris* may be an error. *Ptychobranchus occidentalis* is distinguished by the presence of very fine, 'capillary,' green to black lines radiating from the umbonal region, which are continuous or rarely interrupted at a growth rest. These lines may be distributed over the shell or progressively restricted to the posterior slope, they are usually equally spaced but may be in definite groups separated by wider gaps. In contrast, *P. fasciolaris* has the lines in definite groups, and interrupted at several growth rests, or else the lines fuse into broad green interrupted stripes. The difference is primarily one of degree since in Oklahoma most juvenile and occasional adult *P. occidentalis* have interrupted lines, while *P. fasciolaris* occasionally has the groups more dispersed. This is a problem which needs more study.

Ptychobranchus fasciolaris occurs east of the Mississippi River and crosses into Missouri (specimens in OSUM) while *P. occidentalis* is recorded from Louisiana, Arkansas, Oklahoma, Missouri, and Kansas. Some of the records for Kansas (Murray and Leonard, 1962; Branson, 1966a, 1967) are under the name *fasciolaris* but the illustrations and descriptions mention the fine, continuous lines characteristic of *occidentalis*. Call's (1885) record of *P. fasciolaris* (as *Unio phaseolus*) falls in the same category. He says (p. 43) 'The specimens seen from Indian Territory and Kansas are beautifully ornamented with numerous green capillary rays.' Isely's record of *fasciolaris* from the Kiamichi requires investigation. Our collections contain only one dubiously identifiable specimen (UOBS 68-105) from this river; it was catalogued as *occidentalis*. Elsewhere in Red River drainage, *occidentalis* occurs widely in the Little River and its tributaries, and in the Blue River only above Durant Dam. Since well over a thousand specimens of naiads have been collected below Durant Dam, *Ptychobranchus* is now either extremely rare or absent, Isely characterized it as 'common at Durant,' meaning that 5-15 specimens could be collected in thirty minutes. At Milburn, Isely found the species 'occasional' meaning that with extensive collecting, single specimens could be found with some regularity. Our collection from the same site 55 years later resulted in two specimens out of a total of 348 naiads, about the same degree of rarity. The species appears to become more abundant upstream, for at the Oklahoma route 7 bridge (10 miles north of Milburn), 13 of 79 specimens were *Ptychobranchus*. In this latter collection, most adults ranged from 55 to 75 mm long. The largest was 82 mm long by 48 mm high. A large series from the Mountain Fork River, 6 mi S Smithville (over 100 specimens), appears to be somewhat dwarfed; the largest is 70 X 35 mm, and most of the adults are from 45 to 60 mm long. Height/length ratios of Red River system specimens usually fall between 48 and 55%. A specimen from the Ouachita River, Arkansas in OSUM is 107 X 59 mm; the species undoubtedly gets larger.

OBLIQUARIA Rafinesque, 1820

When both valves are present, this is an exceptionally easy genus to recognize, for the single series of widely spaced knobs running from the umbonal beaks to the ventral margin are constructed alternately, first one valve, then the other; most other pustulate or coarsely sculptured taxa form the swollen portions of the two valves simultaneously. Another obvious feature is the great difference in thickness between anterior and posterior portions of a valve. The shell surface, excluding the large knobs, varies from smooth to densely pustulate to wrinkled, and the periostracum can be pale yellow to dark brown, reddish, or green, unmarked, or with green or brown rays of various widths or even radiating rows of small dark spots. Usually even the smoothest shells have some trace of corrugations on the posterior slope. Internally, the pallial line is more distant from the shell margin anteriorly than posteriorly, the nacre is white or occasionally pink or purple, and the hinge teeth are massive for the small size.

This *monotypic* genus ranges from the Great Lakes and Minnesota south to Alabama and Texas. In the south, it is not confined to the Mississippi, but enters several Gulf drainages.

Obliquaria reflexa Rafinesque, 1820.
(Three Horned Warty Back)

Isely (1925) reports this species from the Washita, Blue, Muddy Boggy, Kiamichi, and Little Rivers. Our specimens duplicate all but the Muddy Boggy records. It is evident that this is a downstream, big river species for it is very rare to absent in upland, high-gradient streams. For example, in Washita drainage it was common in sluggish, muddy Pennington Creek. In the Blue River, it is found only below Durant Dam. In the lower Kiamichi it is abundant. In the Little River system all our stations are upland: no specimens were found in the Little River near Cloudy, only 1½ were found in Glover Creek, and in the Mountain Fork River none were found among almost 2,000 naiads collected in northern McCurtain County.

Oklahoma adults range from about 40 to 65 mm long. The largest specimen seen, from the Muskingum River, Ohio, is 84 X 72 mm.

TRUNCILLA Rafinesque, 1820

This genus of small naiads (rarely exceeding three inches long) shares with *Leptodea* the smallest glochidia in the subfamily Lampsilinae. Two of the currently recognized species have glochidia less than 0.1 mm high. The shells are not unique in any one feature, but are generally ovate or elongate, with a posterior ridge, and a strongly developed, pyramidal, cardinal tooth in the right valve which projects deeply into the left. Almost all specimens are rayed, sometimes the lines are entire, sometimes composed of rows of angulate spots, sometimes mixed. The genus *Plagiola* Rafinesque, 1820, with a single species *lineolata* (Rafinesque, 1820) is somewhat similar, but is larger, strongly sexually dimorphic (males very compressed, females smaller, more massive, and inflated), has larger glochidia which gape at each end rather than close perfectly, a broad, flat interdentum, and blunt, massive, cardinal teeth. *Plagiola* is not found west of the Kiamichi River.

Truncilla occurs from Lake Erie to Minnesota, south in the various Gulf rivers from Alabama to Texas. The two common species are variable and widespread, and may camouflage the existence of additional taxa.

Truncilla truncata Rafinesque, 1820
(Deer toe)

= *Plagiola elegans*, of Isely, 1925

The species is larger, relatively shorter and higher than *T. donaciformis*. The height/length index of an adult *T. truncata* varies from 68 to 79%, of *T. donaciformis* from 54 to 67%, overlap probably occurs. The most distinct specimens are the old adults, for most *T. truncata* get progressively higher relative to their length as they age, while *T. donaciformis* usually gets progressively more elongate with the posterior end produced and narrowed. In smaller specimens, *T. truncata* tends to have a sharper posterior ridge and entire rays, while *donaciformis* is less ridged posteriorly, and usually has rays at least in part composed of rows of chevron-shaped or angulate spots. Some specimens are very difficult to identify. In Oklahoma, occasional specimens with pink instead of white nacre are invariably *truncata*, not *donaciformis*. *Truncilla truncata* varies in size at least to 75 X 55 mm, however most Oklahoma adults are in the 45 to 60 mm size range.

The distribution of this species is the same as that of the genus, except that its presence in the Alabama River drainage has been questioned. In Oklahoma, Isely (1925) found it in Cache Creek, and from the Blue to the Little River inclusive. In our collections the species occurs only in the Blue River below Durant Dam, in the Kiamichi River at 'Spencerville Crossing', and Glover Creek in Little River drainage. It is much more common at the first two localities than in Glover Creek, this suggests a large river species.

Truncilla donaciformis (Lea, 1828).
(Faun's Foot)

=*Plagiola donaciformis*, of Isely, 1925

This is a small species which becomes progressively more elongate with age. Its basic recognition features are discussed under *T. truncata*. Its distribution is the same as the genus. Most adults are from 35 to 50 mm long, the largest seen has no locality data, it is 61 X 36 mm.

Within its genus, *T. donaciformis* appears to be the more widespread species. Isely (1925) had it from Cache Creek, Red River (now Lake Texoma), Washita River (one site now in the Lake, one more upstream), and in the Blue, Muddy Boggy, Kiamichi, and Little Rivers. It has been recorded from Lake Texoma by Riggs and Webb (1956) and Sublette (1957). We have collected it washed up on the shores of Lake Texoma, in

Pennington Creek, Blue River below Durant Dam, and Gates Creek in Kiamichi drainage. At the last site it and *Quadrula pustulosa* were by far the most abundant species.

LEPTODEA Rafinesque, 1820

Although the very small rounded glochidium (shared with *Truncilla*) is the best recognition feature, the shells of this genus are fairly easy to distinguish from all others except *Potamilus laevissimus*. In *Leptodea* the shell is very thin and compressed; the periostracum is straw yellow to pale brown, with weak green rays occasional in adults, normal in juveniles, and the posterior slope is contrastingly darker; the nacre varies from white to pink, occasionally with pale purple iridescence; the cardinal teeth are very weakly developed, occasionally unrecognizable or absent, extremely thin and directed through or above the anterior adductor muscle scar; normally, the ends of the valves gape and are incapable of closing tightly. When collecting live specimens a characteristic feature is the length and strength of the foot; for its size and fragile shell, we know of no other Oklahoma genus which anchors itself so firmly in the substrate.

The genus occurs in the Great Lakes, and is widespread in the Trinity, Sabine, Mississippi, Tombigbee and Alabama River systems from Texas to Alabama. The two or three species are capable of relatively rapid movement and are not considered sedentary.

Leptodea fragilis (Rafinesque, 1820).
(Paper-shell)
= *Lampsilis gracilis*, of Isely, 1925

The large, thin, pale brown, sexually dimorphic shells with exceptionally weak pseudocardinal teeth are quite distinctive. In males the greatest height is near the middle of the valve; in females it is posterior to the middle, and the entire posterior end is expanded relative to the male shell. Many specimens, especially younger individuals, have a prominent posterior wing, but the development and incidence of breakage of this structure varies greatly in adults.

The genus contains a second and very rare species which enters southeastern Oklahoma, *Leptodea leptodon* (Rafinesque, 1820). Isely (1925) records it from the Kiamichi River, and we have one or two specimens each from the Kiamichi, from its tributary Gates Creek, from the Little River, and from the Mountain Fork River; additional OSUM specimens are from Missouri, Arkansas, Ohio and Kentucky. The two species of *Leptodea* have different shapes and occasionally different nacre-color; *L. leptodon* is small, elongate, and males are spindle-shaped in lateral outline, the nacre is usually iridescent bluish white grading to pinkish, rarely deep pink to purple, in the umbonal cavity; *L. fragilis* is large, ovate or elliptical, or even triangular when the posterior wing is well developed, and the nacre is uniformly colored, usually pink. The largest specimen of *L. leptodon* seen, from Gates Creek, below Lake Raymond Gary is exceptional, being 98 mm long, it has pale purple nacre; Isely (1925) mentions 40-80 mm for his specimens. *Leptodea fragilis* appears to reach a maximum size of 178 mm (Haas, 1941, Spoon River, Illinois); however most adult specimens from Oklahoma are about 60 to 100 mm long.

Leptodea fragilis has a very wide distribution, occurring from Texas to Alabama in the various Gulf of Mexico drainages, north to Manitoba and New York, and crossing into Atlantic drainage in the St. Lawrence system in the Great Lakes, Vermont, Ontario, and Quebec, and via the Erie Canal into the Hudson River in New York.

As mentioned under the genus, this is an active species. Ortmann (1919, p. 251) says '. . . it is a lively shell, crawling around frequently, and with a speed unusual in other shells.' Utterback (1915, p. 354) says 'No mussel is more active and as it anchors itself so firmly it is often extracted from its bed with great difficulty. The straw-colored and green rayed juveniles are easily located, not so much by color as by their 'tracks' since they are the most active crawlers.' The species occurs widely in southern Oklahoma; Isely (1925) records it from Cache Creek and the Red, Washita, Blue, Muddy Boggy and Kiamichi Rivers. Riggs and Webb (1956) record it from Lake Texoma. We have seen specimens from Lake Texoma, Pennington Creek, Blue River below Durant Dam, Gates Creek, and the Kiamichi River. No specimens have yet been reported from Little River drainage.

POTAMILUS Rafinesque, 1818
(=*Proptera* Rafinesque, 1820)

Large size, pink to purple nacre, and a tendency for the valves to gape anteriorly will separate this genus from all others in the state except *Leptodea*. The definitive ax-head shaped (=ligulate) glochidium of *Potamilus* is the main reason for not combining the two genera, for some *Potamilus laevissimus* shells are easily confused with *Leptodea fragilis*. A number of current workers ignore the glochidia and place *laevissimus* in *Leptodea*, a decision which disregards the one really unique feature of *Potamilus*. It is clear that since *Potamilus* and *Leptodea* are recognized as separate genera based on glochidial characters, the species *laevissimus* belongs in *Potamilus*. If the glochidia are ignored, then all the species of *Potamilus* and *Leptodea* must be combined in one genus. Further details can be found in the discussion of *Leptodea*.

We have recently been informed (Morrison, 1969, and personal communication) that the familiar name *Proptera* is a synonym of *Potamilus* Rafinesque, 1818. It seems likely that future workers will either accept the name *Potamilus* or apply to the International Commission of Zoological Nomenclature for a ruling in favor of *Proptera*. Since we cannot anticipate which alternative will be chosen, we call attention to the problem and use the oldest name.

Potamilus ranges from Hudson Bay drainage to New York, south in Gulf drainages from Alabama to Texas. About six species are currently recognized, four of which occur in Oklahoma, and two enter the Lake Texoma region.

KEY TO THE SPECIES OF *POTAMILUS* IN OKLAHOMA

1\. Cardinal teeth oriented on a line passing through or above the anterior adductor scar; fresh specimens with nacre pale purple to pinkish-white; left valve with posterior cardinal tooth reduced in size or absent. 2

Cardinal teeth oriented on a line beneath or posterior to the anterior adductor scar; fresh specimens with nacre deep purple; left valve with posterior cardinal tooth well developed. . . . 3

2\. Shell greatly inflated; left valve with one large, one small cardinal tooth, right valve with dorsal cardinal very long, low, serrate or jagged. . . . . *Potamilus capax* (Green, 1832)

Shell compressed; left valve with one cardinal tooth, right valve with dorsal cardinal thin, pointed and smooth. . . . *Potamilus laevissimus* (Lea, 1829)

3\. Beak cavities shallow, the majority of small muscle scars visible without tilting the valve. . . . . *Potamilus alatus* (Say, 1817)

Beak cavities deep, the majority of small muscle scars not visible unless the valve is tilted. . . . . *Potamilus purpuratus* (Lamarck, 1819)

Potamilus laevissimus (Lea, 1829). (Paper Shell).

= *Lampsilis laevissima*, of Isely, 1925
= *Leptodea laevissima*, of various authors
= *Proptera laevissima*, of various authors

This is a large, fragile, active species, broadly oval in outline, with the umbones more posteriorly placed than the other Oklahoma species of *Potamilus* and *Leptodea*. Some individuals have a conspicuous posterior wing plus a smaller anterior one, but the field recognition feature is the growth pattern and final outline. The photographs in Murray and Leonard (1962, p. 124) are excellent. The greenish-brown to smoky to blackish periostracum is often so thin that parts wear off in nature or during the scrubbing operation leaving grayish lines and patches. Adults range from 100 to 150 mm long.

Although the species has been transferred back and forth between *Potamilus* (= *Proptera*) and *Leptodea*, the ax-head glochidia place it clearly in the former genus. It occurs from Ohio west to Minnesota, south to Arkansas and northern Louisiana, and has been reported from Texas.

Potamilus purpuratus (Lamarck, 1819). (Purple Shell)

= *Lampsilis purpurata*, of Isely, 1925
= *Proptera purpurata*, of various authors

Adults have blackish periostracum, pale to deep purple nacre, the heaviest cardinal teeth in the genus, and pronounced sexual dimorphism. Males are rounded and tapering posteriorly, females are smaller, diagonally truncate, and often grossly inflated posteriorly. Most adults fall in the 100 to 140 mm size range. Occasional specimens or populations are much more thin-shelled than normal, and can then be confused with *P. laevissimus* or *P. alatus*. The growth pattern and especially the position of the umbones is useful in such cases. The shell inflation of this species is somewhat intermediate between *Potamilus alatus* (Say, 1817) and *P. capax* (Green, 1832. *Potamilus alatus* is recorded from Arkansas drainage by Isely (1925); it is much more compressed, has a better developed posterior wing, and shallower beak cavities. *Potamilus capax* is recorded from the Kiamichi River at Roby by Isely (1925); it is the most extremely inflated species of naiad in the state, fragile and thin shelled, pale brown externally, the left valve with the large cardinal tooth directed dorsal to the anterior tip of the valve, the right valve with a characteristically long, low and jagged dorsal cardinal, and nacre tending to be whitish, sometimes pink in the center and pale bluish outside the pallial line. The problem is not to distinguish *P. capax* from the other species of *Potamilus* but from the southwestern populations of the *Lampsilis ovata* complex. The presence of ax-head glochidia in *Potamilus* or of mantle flaps in *Lampsilis* will separate them. The specimen illustrated by Murray and Leonard (1962) as *P. capax* from Kansas, appears to be an old, large female of *Potamilus purpuratus*. We have not yet taken *Potamilus alatus* nor *P. capax* in Oklahoma.

Potamilus purpuratus occurs from western Tennessee, Missouri, and Kansas, south to

Potamilus purpuratus occurs from western Tennessee, Missouri, and Kansas, south to Louisiana and Texas. Isely's specimens (1925) were from Cache Creek and every river from the Washita to the Little. The Washita site is now part of Lake Texoma. Recent specimens are from Blue River below Durant Dam, Kiamichi River and Gates Creek, Little River, Glover Creek, and Mountain Fork River. The species is much more rare at upstream sites, for no more than two per trip were found in the Little River system.

LIGUMIA Swainson, 1840

This is a member of the *Lampsilis-Villosa-Toxolasma* group of genera with specialized structures on the mantle antero-ventral to the branchial opening. In *Ligumia* this area bears a long row of evenly and narrowly spaced papillae, which can be equal-sized or progressively smaller posteriorly, and extent to or beyond the mid-point of the ventral margin. The genus contains three recognized species which vary from black to dark yellowish green with darker rays. As usual in this complex, rays, when present are clearest posteriorly, and often fade out anteriorly.

Ligumia ranges widely, occurring from Manitoba, Hudson Bay drainage, and St. Lawrence drainage south through Gulf drainage systems from Texas to Alabama. Its distribution in the Atlantic Coastal Plain is intermittent from New England to South Carolina.

Ligumia subrostrata (Say, 1831).

=*Lampsilis subrostrata*, of Isely, 1925

Female shells of this species are diagonally truncate posteriorly like those of *Lampsilis* and some species of *Villosa*. Males have the posterior end characteristically pointed with the shell margin dorsal to the point almost straight, and ventral to the point more strongly curved, giving a boat-shaped outline. Occasional old females appear misshapen when they develop a produced posterior tip and a pronounced post-medial ventral swelling.

This is primarily a species of shallow, even intermittent streams and ponds, and is in sharp contrast to *Ligumia recta* (Lamarck, 1819) recorded from Arkansas drainage in Oklahoma by Isely (1925). The latter is a large dark green, brown, or blackish species of the major rivers, recognized by its great length, the height/length ratio varying from about 35 to 45%. See also the discussion under *Villosa*.

Isely's (1925) only records of *subrostrata* from Red River drainage were a small creek and lake on the Texas side. We have found the species progressively more abundant upstream in the Blue River above Durant Dam; in the upper Kiamichi, 0.9 mile south of Big Cedar, Le Flore County; in Glover Creek of Little River drainage; and Lukfata Creek (Little River drainage) about 6 miles south-southwest of Broken Bow, as well as several small streams in Arkansas drainage.

Red River specimens are small compared with individuals from other parts of the range. A large collection of 370 specimens was taken, in one hour, in a tributary of the Blue River ¼ mile east of the junction of Oklahoma routes 99 and 7; the largest male is 71 X 35 mm, the largest female 56 X 32 mm. Most males range from 35 to 65 mm long, while most females are 35 to 53 mm long; male height/length ratios range from 47.6 to 54.5% and average 51.1%, females range from 52.5 to 57%, and average 54.5%. The range of height/length ratios for all Oklahoma material examined is from 45 to 58%. A male from Palarm Creek, Conway County, Arkansas is 90 X 43 mm, larger specimens are to be expected. Valentine's field notes for the large Blue River collections are instructive. 'Heavy rains previous week . . . many *Ligumia* stranded on sand bars by rapidly lowering water level, those still in damp sand or isolated pools mostly alive, those in direct sun or dry sand recently killed, with soft parts still within the shell. Those in the stream were all in shallowest parts, often only one or two inches of water, maximum water depth for *Ligumia* -I *subrostrata* I- about 1 foot! 'The species must really be active for we followed trails in sand all over the place, each terminating in a clam. A few *Lampsilis* -I *radiata luteola* I- on the sand bars, perhaps 10%, while 50% of *Ligumia* on land. *Anodonta imbecilis* in very shallow water, but not caught on land.'

VILLOSA Frierson, 1927

The genus *Villosa* has not previously been recorded from Oklahoma; it therefore was a pleasant surprise to find two species in Red River drainage in the state.

Most of the species of *Villosa* are small, sexually dimorphic lampsilines rarely exceeding 75 mm in length. The genus is best defined by its soft parts. The mantle has a submarginal row of unequal, usually well-separated papillae antero-ventral to the branchial opening (at the same site as the mantle flap of *Lampsilis*). The closely related genus *Ligumia* also has a row of papillae, but in *Ligumia* the papillae are typically equally sized or progressively shorter anteriorly, more crowded, and more numerous, and extend about half way or more toward the anterior end. The differences are slight, for some specimens have slightly irregular papillae and could be assigned on this basis alone to either genus. The shells have few distinguishing features. The beak sculpture of *Villosa* and *Ligumia* is said to be more symmetrically biconvex (double-looped) than *Lampsilis*, but this distinction does not appear to exist in most Oklahoma specimens.

Ligumia recta (Lamarck, 1819) of Arkansas River drainage eastward, and *Lampsilis anodontoides* (Lea, 1831) are more elongate and are easily separated from *Villosa*. *Lampsilis ovata* (Say, 1817) is more robust and less elongate than *Villosa* and can also be easily recognized. The confusion lies with distinguishing elongate specimens of *Villosa* from *Ligumia subrostrata* (Say, 1831) and *Lampsilis radiata luteola* (Lamarck, 1819) when beak sculpture and periostracum are eroded away or discolored, and soft parts are lacking. The latter two species have height/length ratios of 45 to 61%, while those of Oklahoma *Villosa* are 48 to 65%, depending on the species. With practice, most shells can be separated by subtle differences in shape (especially *Ligumia*), but with some *Ligumia-Villosa-Lampsilis* material, only soft parts will settle the matter, and even then a truly objective decision is sometimes impossible.

The dozen or more species of *Villosa* are often listed in the genus or subgenus *Micromya* Agassiz, 1852; however, the latter name was first proposed twelve years earlier for a genus of flies, and is thus not available for use in the Mollusca.

Villosa occurs in St. Lawrence drainage and in the various Coastal Plain rivers from Virginia to Florida to Texas. In the Mississippi system the previous western record appears to be Missouri.

There are two species of *Villosa* in Red River drainage in Oklahoma which we are provisionally referring to *Villosa iris* (Lea, 1829) and *Villosa lienosa* (Conrad, 1834). Neither of these species has precisely the same characters here as found in populations to the east. Each of these two taxa forms widespread complexes which are in very unsatisfactory taxonomic states. Numerous names described from diverse drainage systems are combined under the names *iris* and *lienosa* in spite of rather striking differences. The fact that the Oklahoma populations are on the extreme geographic periphery of these two species complexes makes it even more difficult to assign a name with any great confidence.

Villosa lienosa (Conrad, 1834)

This species ranges westward to the Blue River where it occurs mixed with *Lampsilis radiata luteola* in a ratio of about 1:33. Whereas *Lampsilis*, when scrubbed carefully, is yellowish with green rays, *Villosa lienosa* from the Blue River is all brown and rayless. Dirty or worn *Lampsilis r. luteola* valves are virtually impossible to distinguish from *Villosa*. Males of the two genera have identical outlines. *Lampsilis* females in the Blue River characteristically have the posterior end diagonally truncate so that the line of maximum shell length is much closer to the dorsal than to the ventral margin of the valve. The *Villosa* females from this river are rounded posteriorly, not truncate, so the line of maximum shell length lies almost equidistant between dorsal and ventral margins. Unfortunately, females from eastern Oklahoma are truncate, not rounded, but appear conspecific. They are discussed again below.

Scattered individuals of *Villosa* have been found in the Blue River from below Durant Dam upstream to some of the smaller permanent tributaries. The largest single collection was six specimens taken in the tributary of the Blue River ¼ mile west of the junction of Oklahoma routes 99 and 7. Five of these individuals measure 58 X 33, 53 X 31, 48 X 27, 44 X 26, 43 X 25 mm, and have height/length ratios between 56 and 59%. A male and female, from ten miles north of Tishomingo, measure 47 X 28 mm and 46 X 30 mm respectively; their height/length ratios are 59.5 and 65% respectively.

Ligumia subrostrata also occurs in the Blue River; it has dark rays on a paler ground color, females are diagonally truncate, and males are more elongate.

In eastern Oklahoma, the Kiamichi and Little River systems have populations of *Villosa lienosa* which are dark brown to almost black with very faint rays. Females are strikingly truncate posteriorly and have a prominently swollen posterior ridge. Both sexes are slightly shorter and wider than specimens from the Blue River, the vast majority of males are from 35 to 47 mm long, the largest is 52 X 32 mm; females are from 30 to 43 mm long, and the largest is 53 X 31 mm. Height/length ratios average 63% about six percentage points higher than the Blue River specimens, and range from 56 to 68%. The Little River system also has a species resembling *Villosa iris* (Lea, 1829), which seems to have replaced *Lampsilis r. luteola* in swifter current. This pretty and delicate *Villosa* is yellowish with green rays, and it has sexual dimorphism much less developed than in the other species, females being only a little more inflated, slightly truncate, and less pointed posteriorly than males. Most males are from 35 to 55 mm long and have height/length ratios of 53 to 60%, averaging 56.5%; most females are from 35 to 48 mm long and have height/length ratios of 56 to 63% averaging 59%. The largest individuals of each sex seen (out of over 500 shells) are a male 66 X 36 mm, and a female 51 X 32 mm.

TOXOLASMA, Rafinesque, 1831

(=*CORUNCULINA* Simpson 1898; *CARUNCULINA* of authors)

Included in this genus are the smallest species of naiads in Oklahoma. Most adults range from 20 to 30 mm long, are elongate-oval in outline, and have a 'caruncle' or fleshy projection on the mesial surface of the mantle antero-ventral to the branchial opening, in the same area as the flap of *Lampsilis*, or the more posterior papillae of *Ligumia* or *Villosa*. This structure has been described as wart-like, or consisting of a tight group of papillae, sometimes with a common base; the few gravid females examined from Oklahoma had a blackish wart-like projection which contrasted sharply with the adjacent pale mantle surface. Some populations (species?) in other parts of the range have the projection white not black, and some have a yellow, orange, or red caruncle, or lack it entirely. The periostracum varies from brown or green to black, the palest specimens often have weak rays, the nacre is often iridescent (especially posteriorly) or with a bluish tint, the lateral teeth parallel the ventral edge of the valve or diverge slightly, the beak sculpture is unusually coarse for the size of the shell, consisting of strong, posteriorly rounded ridges which are open anteriorly, and the periostracum of some species often has (in fresh shells) a characteristic satiny luster due to minute ridges between and paralleling the growth lines. As in related lampsilines, when sexual dimorphism is evident, males are slenderer and more tapered posteriorly.

Only one other genus in Oklahoma, *Obovaria* Rafinesque, 1819, has species as small as some *Toxolasma*. *Obovaria castanea* (Lea, 1831) occurs in the Kiamichi and Little River systems, but no farther west. This form is immediately separable from *Toxolasma* because of its round outline (not elongate, the height/length index falls in the high sixties and seventies) and down-curved lateral teeth (not paralleling the ventral margin). Adults of this population range from about 28 to 38 mm long and the largest specimens, all males, range from 40 to 43 mm.

Use of the name *Carunculina* is not justified according to the International Rules of Zoological Nomenclature, for the name *Toxolasma* Rafinesque, 1831, has many years priority (Morrison, 1969). Since the decision to conserve or reject *Carunculina* has not been made by malacologists, the name *Toxolasma* should be used.

Toxolasma parva (Barnes, 1823).

=*Carunculina parva*, of many authors
=*Lampsilis parva*, of Isely, 1925
=*Lampsilis corvunculus*, of Isely, 1925
=*Unio haleianus*, of Call, 1885
=*Unio parvus*, of Call, 1885
=*Unio texasensis*, of Call, 1885

The Oklahoma species of this genus are, perhaps, in even less satisfactory taxonomic condition than the species of *Villosa*. The distribution of at least three species suggests their possible occurrence in Oklahoma.

Toxolasma parva (Barnes, 1823) has been reported from New York to the Dakotas and Alabama to Texas. Isely (1925) reports it from Cache Creek, from a Washita River site now flooded by Lake Texoma, from the lower Blue River, and from the Kiamichi River. Riggs and Webb (1956) report it from Lake Texoma. *Toxolasma texasensis* (Lea, 1857) occurs in Texas, Louisiana, and Arkansas, northeast to Illinois. Call (1885) records it from 'Indian Territory, Red River drainage,' and Strecker (1931) records it in Red River drainage in Cooke and Bowie Counties, Texas. *Toxolasma glans* (Lea, 1831) occurs in Arkansas and Missouri as well as to the north and east. It has not, to our knowledge, been recorded from Oklahoma but may occur.

We have specimens of *Toxolasma* from Lake Texoma, Pennington Creek, Blue River on both sides of Durant Dam, Gates Creek in Kiamichi drainage, Little River, Glover Creek, and Mountain Fork River. The only adequate series on hand are from the Blue and the Mountain Fork Rivers. The Blue River specimens are small, adults range from 20 to 30 mm long, they lack sexual dimorphism, they have a finely ridged and lustrous periostracum, height/length ratios fall in the mid fifties, and they have iridescent nacre with pale blue tints often grading to straw-color in the beak cavities. The Mountain Fork specimens are small, the largest of over 100 individuals is 30 X 17 mm, most are under 25 mm long, they are sexually dimorphic (presumed males are more elongate, and not as high), they have a finely ridged and lustrous periostracum, height/length ratios vary from 53 to 64% with the mean in the high fifties, and the nacre is iridescent pale blue with varying traces of straw-colored beak cavities; they also appear to be *T. parva* but are less inflated than Blue River shells and sexually dimorphic.

Toxolasma parva is locally hermaphroditic (Utterback, 1915, p. 397; Tepe, 1943; van der Schalie, 1966) and thus usually lacks sexual dimorphism, the periostracum has a characteristic silky sheen, the nacre is usually iridescent pale blue; the largest seen, from the Scioto River, Ohio, is 43 X 24 mm. *Toxolasma glans* is sexually dimorphic (females are inflated and diagonally truncate posteriorly), the periostracum is less silky, the nacre is often blue to purple without the iridescence; the largest seen, from the Wabash River, Indiana, is 40 X 24 mm. *Toxolasma texasensis* may be much larger than the preceding two species, the largest male seen, from the Trinity River, Texas, is 62 X 34 mm, while the largest female, from Palarm Creek, Conway County, Arkansas is 55 X 29 mm, adults are usually from 35 to 50 mm long; also there is pronounced sexual dimorphism (as in *glans*), the periostracum is less silky than *parva*, the nacre in some Arkansas and Texas specimens is orange or straw-yellow, in others it is iridescent pale blue, and in others there is extensive orange or yellow within the pallial line and bluish peripherally. Shells of this species can easily be confused with some members of the *Villosa lienosa*-complex; in the absence of soft parts, the posteriorly rounded and anteriorly open beak sculpture of *Toxolasma* contrasts with the biconvex ridges of *Villosa*.

LAMPSILIS Rafinesque, 1820

The distinctive feature of this large and widespread genus is the presence of a submarginal flap paralleling the pallial line on the mesial surface of the mantle just antero-ventral to the branchial opening. The flaps can be protruded from the shell when the living mantle edge is rolled outward around the edge of the valves (see Walsh 1961 or van der Schalie, 1970 for a photograph, and Grier, 1926, for data on temperature responses), but in preserved material the flaps are withdrawn into the shell and greatly contracted. Flap size, shape, and color are variable within a species, and the size is sexually dimorphic, being much larger in females. Of our three species, the flaps are best developed in *L. ovata,* moderately developed in *L. radiata,* and usually least developed in *L. anodontoides;* as a result, a male *L. anodontoides* may have little more than a narrow black ridge on the otherwise pale mantle surface. In gravid females of all three species collected in the Blue River below Durant Dam on June 16, 1969, the mantle flaps are speckled with small gray dots externally, while internally they have two black stripes separated by a pale stripe. The black stripes show various degrees of intensity, and the pale stripe varies from flesh colored to vivid orange. In addition the end of the flap nearest the branchial opening has, on both sides, a variously developed eye-like spot consisting of a rounded black area surrounded by or adjacent to a fleshy to orange colored region.

Shells of our species of *Lampsilis* show no unique feature by which they may be separated from related genera; however, each species complex has shell features which aid in its own identification. On the generic level, shells are usually yellow to pale brown, or dark brown to black with the edge pale; green or brown rays are present or absent; the nacre is white, red, orange, or pink, or has faint blue tints in smaller individuals; the cardinal teeth are usually thin and pointed, or thick and blunt (depending on species, age, and locale), and the lateral teeth parallel or diverge from the ventral margin. All of these features occur in various combinations in *Ligumia* Swainson, 1840, and *Villosa* Frierson, 1927; these two genera, however, typically have a row of papillae in place of the mantle flap.

The species of *Lampsilis* (and related genera) are sexually dimorphic. Males are more compressed, elongate, and taper posteriorly, while females are more inflated, shorter, and the posterior end is diagonally truncate. The genus ranges from Hudson Bay drainage to Florida and Texas, and from the Atlantic coast to the Rocky Mountains. It includes over fifteen species.

KEY TO THE SPECIES OF *LAMPSILIS* IN OKLAHOMA

1. Elongate, length two or more times the height. . . . . *Lampsilis anodontoides*
   Shorter, length less than twice the height. 2
2. Umbone not or weakly inflated; shell outline with dorsal and ventral margins relatively straight, more or less parallel or weakly divergent. . . . . *Lampsilis radiata*
   Umbone inflated; shell outline with dorsal and ventral margins strongly rounded, much too curved to even suggest parallelism. . . . *Lampsilis ovata*

NOTE. Lampsilis rafinesqueana Frierson, 1927 (see also photograph in Frierson, 1928), described from northeastern Oklahoma (Moodys, Cherokee County), has not been included in this key.

Lampsilis anodontoides form *anodontoides* (Lea, 1831). (Yellow Sand Shell)
Lampsilis anodontoides form *fallaciosa* Smith, 1899. (Slough Sand Shell)

The elongate pale yellow to pale brown shells of this complex are very distinctive. The *anodontoides* form is usually larger and unrayed, the *fallaciosa* form is usually smaller and typically marked with radiating green lines. In both, occasional gray or dark brown individuals are found, these are usually weathered shells or very old specimens. The taxonomic status of these two forms is not settled to the satisfaction of all workers. There are reports of intermediate specimens in some parts of the range, and of constant size and color differences in other populations. It is perhaps significant that Isely (1925) records *fallaciosa* from 16 stations in Red River drainage (the most stations for any species), and *anodontoides* from only one-- Cache Creek. In our recent collections we have never taken a living *fallaciosa*, only occasional dubious weathered shells, while *anodontoides* is common. It appears that in the past 58 to 60 years, *anodontoides* has largely replaced *fallaciosa* in southern Oklahoma. Unfortunately, we still do not know if this was the result of gene exchange and submergence of one genotype by another, or due to replacement of a less successful species by a more successful one, or both. It is also possible that Isely's use of these names differs from ours.

The Sand Shells are widely distributed in Gulf drainage rivers from Florida to Mexico, north to Colorado, Minnesota, and Ohio. Different populations vary greatly in size and, on occasion, astonishingly small gravid individuals are found. Larger adults in Oklahoma are about 90 to 130 mm long. The largest individual seen, from Ohio, is 149 X 73 mm; however, Haas (1941) mentions a specimen (as *Lampsilis teres*) from Spoon River, Illinois, 178 mm long. Isely collected sand shells in Cache Creek, the Red River, and all the main tributaries from the Washita River east to the Little River. Our recent collections are from Beaver Creek in Jefferson County, Pennington Creek, Blue River below Durant Dam, Kiamichi River, Little River, and Glover Creek.

Lampsilis radiata luteola (Lamarck, 1819).

(Fat Mucket)

=*Lampsilis hydiana*, of Isely, 1925, not Lea, 1838

=*Lampsilis radiata siliquoidea*, of recent authors

Lampsilis radiata is one of the most widespread and geographically variable species in the family. Morphologically, it is intermediate between *L. anodontoides* and *L. ovata*; in Oklahoma *anodontoides* has the height less than 50% of the length, *radiata* has the height from about 52 to 61% of the length, and *ovata* has the height from about 63 to 76% of the length. It would not be surprising to find occasional specimens of one species with dimensions overlapping those of another. The subspecies *L. r. luteola* (the name change from *siliquoidea* Barnes, 1823, is explained by Wheeler, 1963) is usually straw-yellow to pale brown with green rays which vary from absent to a few dingy lines at the posterior end of the valve, to a very beautiful pattern of wide green stripes over the entire valve. Additional variation is discussed by Gustavson and Tuthill (1964).

There seems to be a tendency for Gulf Coastal Plain specimens west of the Mississippi to be heavier, browner, darker, and with fewer but wider rays than inland material. These are *Lampsilis radiata hydiana* (Lea, 1838), known definitely from Texas, Louisiana, and Arkansas. At present, we have not taken *hydiana* in Oklahoma, but scattered darker specimens from Red River drainage may represent the genetic influence of this form. The situation is occasionally further complicated by a very similar brown species, *Villosa lienosa*, which, however, is usually not rayed in Oklahoma. See the discussion of this genus.

Lampsilis radiata radiata (Gmelin, 1792) occupies Atlantic drainages from the Saint Lawrence to North Carolina. *Lampsilis radiata luteola* intergrades with *radiata* in New York (see Clarke and Berg, 1959, for an analysis) and ranges from the Great Lakes south through most of the Mississippi system and west to Colorado. As in most naiads, the westward distribution is probably not continuous, but broken into isolated populations. In Oklahoma we have not found *luteola* west of Pennington Creek. Isely (1925) records it from the Blue, Muddy Boggy, Kiamichi, and Little Rivers, but our recent collections are curiously spotty. The species is widespread in the Blue River, being dominant in the upper part of the River. To the west, it occurs in the headwaters of Pennington Creek, but we have found no trace of it in the portion of the creek south of Tishomingo. To the east, we have no data for the Muddy Boggy; in the Kiamichi it is not present among the hundreds of shells examined in the lower Kiamichi at 'Spencerville Crossing,' however three fresh single valves were found in the upper Kiamichi, 0.9 mile south of Big Cedar, Le Flore County. In Gates Creek (a tributary of the lower Kiamichi) the species was present in modest numbers (28 of 413 specimens) in the slough below the dam of Lake Raymond Gary. We have no specimens from the Little River as distinct from its tributaries. In Glover Creek it is one of the less common species at our single collection site. In the Mountain Fork River, one fresh specimen out of almost 2,000 may be *luteola*. This individual has the entire shell suffused with pale red unlike anything we have seen in the state; its identity remains uncertain. In the Little and Mountain Fork River sites where typical *luteola* appears to be absent, there is another yellow shell with green rays which is quite abundant. It is a member of the *Villosa iris* complex, and was mentioned earlier. *Ptychobranchus occidentalis* is also present in the same two rivers, it can be distinguished by the very narrow green lines and posteriorly down-curved lateral teeth.

Males from the Blue River average larger than females, most range from 50 to 65 mm long, females from 45 to 60 mm long. Large individuals from the Blue are a male 81 X 42 mm and a female 72 X 44 mm. These are very small compared with some other parts of the range. Ortmann (1919, p. 284) mentions a Pennsylvania specimen 142 X 78 mm.

Lampsilis ovata form *ventricosa* (Barnes, 1823) (Pocketbook)

=*Lampsilis ventricosa*, of Isely, 1925

Lampsilis ovata subspecies. (Pocketbook)

=*Lampsilis ventricosa satura*, of Isely, 1925

This is a big, inflated species with the largest height/length index in the genus; see the discussion under the previous species. Most male and female shells are remarkably different in outline, the males tapered posteriorly, the females truncate and often grotesquely swollen. It should be understood that the degree of sexual dimorphism is geographically variable; some Oklahoma specimens approach the maximum amount of dimorphism.

The shells of *L. ovata* are progressively darker and smaller in eastern Oklahoma. Specimens from the Lake Texoma area are yellowish-brown with variable traces of darker rays, while those from Little River drainage are almost black with brown margins. These dark eastern specimens, as well as others from adjacent states have been called *L. ovata satura* by Isely (1925), however *Lampsilis satura* (Lea, 1852) is a very inflated brown form with paler periphery. Specimens of *satura* from the Sabine River on the Louisiana-Texas border are rayless or nearly so, the left valve has the dorsal cardinal low, elongate, not strongly projecting, and directed above the anterior tip of the valve; in fact if it were not for the mantle flap and the semi-elliptical glochidium these individuals could easily be mistaken for *Potamilus capax*. The blackish *ovata* with pale edges and high projecting cardinals from eastern Oklahoma is not *satura*, rather it appears to be a heavy, dark variant of form *ventricosa*. True *Lampsilis satura* occurs in a few Texas and Louisiana streams which flow directly into the Gulf of Mexico. Additional data on geographic variation in this species complex are presented by Cvancara (1963).

The problem of identifying *Lampsilis ovata* in Oklahoma is complicated by another lampsiline genus *Actinonaias* Fischer and Crosse, 1893. One species, *Actinonaias ligamentina* (Lamarck, 1819) -I = *A. carinata* (Barnes, 1823)I- occurs in Arkansas River drainage and in Red River drainage in the Kiamichi and Little Rivers; one other species *Actinonaias streckeri* (Frierson, 1927) described in the genus *Lampsilis*, occurs in Arkansas River drainage, and yet another form, *Actinonaias pleasi* (Marsh, 1891), may occur. Specimens of *Actinonaias* usually have more massive teeth than *Lampsilis*, are more compressed, and have shells with less sexual dimorphism. Individuals are yellow with green rays, pale straw with green or brown rays, or dark brown to black and rayless. The best way to distinguish the two genera is by the presence of mantle flaps in female *Lampsilis* and their absence in females of *Actinonaias* and all other genera. The presence of flaps becomes even more important when one additional species is considered. *Lampsilis orbiculata* (Hildreth, 1828), or at least members of the *orbiculata*-complex, occur in Arkansas and eastward, but are not yet reported from Oklahoma. They have mantle flaps and are sexually dimorphic but the shell has the thick nacre and heavy teeth reminiscent of *Actinonaias*. Malacologists in Oklahoma should watch for specimens of the *L. orbiculata* complex mixed with collections of *Actinonaias ligamentina*; all specimens with soft parts should be checked carefully.

The *Lampsilis ovata* complex is distributed widely in North America east of the Rocky Mountains. *Lampsilis ovata* form *ventricosa* is the most widespread form, occurring from Hudson Bay and St. Lawrence drainage, to the Mississippi and its many tributaries. According to Ortmann (1919) *Lampsilis ovata* form *ovata* (Say, 1817) is the large river form, confined to the major streams of the Ohio system, primarily the Ohio, Cumberland, and Tennessee Rivers. In these rivers *ovata* is replaced by *ventricosa* in the smaller tributaries. Recent collections reveal that *L. ovata* form *ovata* is either extirpated or replaced by *L. ovata* form *ventricosa* in these large rivers; however, relict populations of form *ovata* survive in some medium-sized streams. In the rest of Mississippi drainage, *ventricosa* occurs alone. This and related problems are currently being studied by several workers.

In southern Oklahoma, Isely (1925) records old weathered shells of *ventricosa* from two sites now covered by Lake Texoma, one in the Red and one in the Washita River, and from the lower Kiamichi. He also had living material from the lower Blue River and from the Blue at Milburn. He records '*ventricosa satura*' from the Muddy Boggy, and the Kiamichi at Tuskahoma. Our records are from the Blue, Kiamichi, Little, Glover and Mountain Fork Rivers. Blue and Kiamichi River specimens are referable to *ventricosa*, while the Little River collections are the extra dark form mentioned above. In the Blue River the species occurs on both sides of Durant Dam, but apparently does not extend north to Connerville. Our most upstream record for *ventricosa* in the Blue is at Oklahoma Route 7 bridge, Johnston County, and the species does not become easy to find until the vicinity of Milburn.

Ortmann (1919, p. 302) mentions a Pennsylvania male 155 X 120 mm, and a female 123 X 88 mm. Oklahoma specimens are considerably smaller but increase in size from east to west; Little River adults from upstream sites are about 65 to 95 mm long, those below Durant Dam are about 95 to 125 mm long. The largest seen are a male from Ohio 160 X 100 mm, a female from Ohio 130

X 89 mm, and a wider female from Missouri 125 X 95 mm.

SHELL KEY TO THE SPECIES OF UNIONIDAE IN THE LAKE TEXOMA REGION

1. Lateral and cardinal teeth absent . 2
   Lateral or cardinal teeth present, sometimes small. 4

2. Umbone not inflated, in side view not projecting above hinge line. . . . . *Anodonta imbecilis*
   Umbone inflated, in side view projecting above hinge line. 3

3. Nacre usually various shades of iridescent pale blue; largest individuals range up to 120 mm long; shell inflated but not grossly; stream form usually in flowing water. . . . .*Anodonta grandis* form *grandis*
   Nacre usually various shades of bronze, pink, or white; largest individuals range up to 185 mm long; shell grossly inflated; lake form usually in sluggish or still water. . . . . *Anodonta grandis* form *corpulenta*

(NOTE. The taxonomic relationship of these two taxa has not been clarified and needs considerable study).

4. Hinge plate with area of lateral teeth not forming an interlocking tongue and groove, but rather flat and shelf-like. . . . . *Lasmigona complanata*
   Hinge plate with lateral teeth typically forming an interlocking tongue and groove, the left valve with the groove, the right with the tongue. 5

5. Shell pustulate, tuberculate, or with raised ridges running obliquely across growth lines and not restricted to posterior slope. 6
   Shell smooth, or if ridged, these paralleling growth lines or restricted to posterior slope. 11

6. Posterior half or more of shell with 2 to many broad parallel ridges, the widest ones fairly straight and running obliquely backward and downward, the narrowest ones (if present) curving up to the dorsal margin of valve. . . 7
   Shell pustulate or tuberculate; at best only one clear cut oblique ridge . 8

7. Umbone and first three or four years growth each with short, irregular zig-zag ridges forming V, W and M patterns which can replace or overlap the larger oblique ridges; usually 15 or more curving ridges reach the dorsal edge of shell along area from umbone to posterior end of lateral teeth. . . . . *Megalonaias gigantea*
   Umbone and first three or four years growth without irregular zig-zag ridges; usually no more than 9 curving ridges reach dorsal edge of shell along area from umbone to posterior edge of lateral teeth. . . . .*Amblema plicata*

8. Umbone and first 2 or 3 years growth with obscure beak sculpture, but without pustules. . . . . . *Quadrula pustulosa*
   Umbone and/or first 2 or 3 years growth with tubercles or pustules. 9

9. Two to four large knobs in a vertical row from umbone to ventral margin, these formed first on one valve then on other so that when valves are together no two knobs are opposite, the knobs of one valve alternating with those of the other valve. . . . . . *Obliquaria reflexa*
   Knobs on shells numerous, not alternating. 10

10. Shell more elongate, height/length ratio 60% or less.. *Tritogonia verrucosa*
    Shell shorter, rounder, height/length ratio 70% or more... *Quadrula quadrula*

11. Interdentum forming a broad flat shelf between cardinal and lateral teeth; umbonal cavity deep and cavernous, invading and hollowing out the base of the cardinal teeth. 12
    Interdentum at best forming a convex ridge between cardinal and lateral teeth; umbonal cavity shallow, not or weakly invading the base of the cardinal teeth 13

12. Longitudinal axis of anterior cardinal tooth (left valve) or socket (right valve) usually passing across center of anterior adductor scar. *Fusconaia flava*
    Longitudinal axis of anterior cardinal tooth (left valve) or socket (right valve) passing along ventral margin or below anterior adductor scar. . . . . *Quadrula pustulosa*

13. Lateral teeth paralleling or diverging posteriorly from longitudinal axis of shell. 19
    Lateral teeth directed towards ventral edge of shell posteriorly, oblique to longitudinal axis of shell. 14

14. Periostracum yellow with a few fine greenish lines, or with green rays, each ray composed of many very fine parallel green lines, these sometimes restricted to the posterior slope. . . . .*Ptychobranchus occidentalis*

Periostracum not rayed, or if so each ray solidly colored, or else each ray mottled, or with a herringbone, or chevron pattern. 15

15. Shell more elongate, height/length ratio 53% or less . . *Uniomerus tetralasmus*

Shell shorter, height/length ratio 54% or more. 16

16. Umbone strongly anterior; highest part of valve (dorsal to ventral margin) well posterior to umbonal swelling; maximum length about 170 mm. 17

Umbone slightly anterior or median; highest part of valve at or barely posterior to umbonal swelling; maximum length about 80 mm. 18

17. Nacre deep purple (can fade to pink or white in dead shells); periostracum almost black, or very dark green; left valve with two strongly projecting, well developed cardinal teeth, right valve with one tall tooth. *Potamilus purpuratus*

Nacre pale purple to pink; periostracum pale to dark brown; both left and right valves with single small thin, barely projecting cardinal teeth. . . . . *Potamilus laevissimus*

18. Shell more elongate, height/length ratio 67% or less. . *Truncilla donaciformis*

Shell shorter, rounder, height/length ratio 68% or more. . *Truncilla truncata*

19. Shell usually with a posterior-dorsal wing; highest part (dorsal to ventral margin) well posterior to umbonal swelling. 20

Shell without a posterior wing; highest part at or adjacent to the umbone. 22

20. Cardinal teeth small, very thin and compressed, almost vestigial, the edges smooth or almost so. 21

Cardinal teeth well developed, or if small, with dorso-ventral depth (pyramidal) or with ragged edges. . . . 22

21. Periostracum yellow to pale brown; nacre usually pale pink. *Leptodea fragilis*

Periostracum greenish to dark brown; nacre usually pale purple. . . . . *Potamilus laevissimus*

22. Nacre purple (in fresh shells) . . . . *Potamilus purpuratus*

Nacre white, iridescent blue, or various other shades, not purple. . . 23

23. Height/length ratio 63% or greater . . . *Lampsilis ventricosa* form *ventricosa*

Height/length ratio 61% or less. . 24

24. Periostracum straw yellow to pale brown, with or without dark rays. . . 25

Periostracum uniform or almost uniform dark brown, rays absent or barely indicated. 28

25. Periostracum dark to pale brown, paler peripherally, with numerous darker rays especially evident around the edges. . . . . *Ligumia subrostrata*

Periostracum entirely straw yellow to pale brown, rays present or absent. 26

26. Height/length ratio 53% or more. . . . . *Lampsilis radiata luteola*

Height/length ratio less than 50%. 27

27. Periostracum not rayed. . . *Lampsilis* . . . . *anodontoides* form *anodontoides*

Periostracum with numerous dark rays. *Lampsilis anodontoides* form *fallaciosa*
NOTE. The taxonomic relationship of these two forms has not been settled.

28. Beak sculpture consisting of a few posteriorly angulate arcs. *Toxolasma parva*

Beak sculpture consisting of many biconvex arcs. *Villosa lienosa*

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