

MALACOLOGY

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CONSUMPTION OF RABDOTUS ALTERNATUS ALTERNATUS
(SAY, 1830) BY THE ABORIGINAL INHABITANTS OF THE
TUCKER ARCHEOLOGICAL SITE, 41NU46, IN SOUTH
TEXAS

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ABSTRACT

Recent discovery of an intact hearth designed for cooking land snails has answered the question of how the Archaic inhabitants of the Corpus Christi, Texas, area prepared Rabdotus alternatus alternatus (Say) for consumption. Confirmation of the use of land snails as a food by the later inhabitants, the Karankawa, is found in sixteenth century literature accounts.

INTRODUCTION

Adult shells of Rabdotus alternatus alternatus (Say, 1830) are characterisitcally found in great concentrations at archeological sites in south Texas. The great numbers of large adult shells has led workers to conclude that these snails formed an important resource in the diet of the prehistoric and historic aborigines of the area (Hester, 1976). The method of preparation of these snails has been the subject of some debate. It has been proposed that the aboriginal inhabitants of south Texas boiled the snails as a means of both cooking them and extracting them from the shells. However, the Archaic people of the area were aceramic and apparently had no containers in which to boil water. Large marine shells (Busycon and Pleuroploca) available in the nearby marine waters were often used as tools and could have served as cooking pots, but no fire-darkened specimens were discovered. Additionally, roasting has been rejected because the shells show no sign of charring, nor is there any sign of mechanical extraction of the animals from the shells. The accounts of Cabeza de Vaca's sojourn have been cited in support of the use of land snails in this way by the Karankawa indians (Hester and Hill,

1975), but again there is no information on the method of preparation of the snails. It also has been argued that Cabeza de Vaca's account does not actually state that the snails were used as a food source by the Karankawa (Clark, 1973, 1975; Hester and Hill, 1975).

Recent archeological excavations at a site in Corpus Christi, Texas, uncovered an undisturbed hearth that apparently was never opened by the aboriginal inhabitants. Analysis of the hearth has allowed the formation of conclusions about the method of preparation of Rabdotus for consumption at this site. A sixteenth century account has been found which confirms that the Karankawa in south Texas ate land snails.

METHODS

The seven-acre site, designated 41NU46 and referred to as the Tucker site (Smith, 1985), is situated along the banks of Oso Creek in the flood plain. It was excavated by members of the Coastal Bend Archeological Society under the supervision of Dr. Herman Smith. Seven features were mapped and excavated carefully in order to reveal their structure. The features included hearths and remnants of wattle-and-daub structures. Carbon dates were obtained for the older layers from charcoal samples analyzed by the Radiocarbon Laboratory at the University of Texas at Austin. Age of the upper layers was determined by analysis of the artifacts collected. Mollusk specimens were obtained by surface collection, sieving or hearth excavation and were deposited in the collections of the Corpus Christi Museum for identification and ecological analysis. Funding was supplied by a grant from Mr. Henry Tucker. Valuable comments on this manuscript were given by Raymond Neck and Herman Smith.

RESULTS

Five species of land snails shells were found during the excavation of 41NU46. These were: Polygyra texasiana texasiana (Moricand), Praticolella berlandieriana (Moricand), Praticolella pachyloma (Menke), Helicina orbiculata (Say), and Rabdotus alternatus alternatus (Say). The specimens were found at all occupation levels of the site. Rabdotus was the most frequently found species, with an estimated density of adult shells of 30-200

per square foot on the surface. None of the Rabdotus shells recovered were of juvenile animals.

An undisturbed hearth was discovered at Feature 7, located within the confines of what has been concluded to be the remains of a wattle-and-daub structure (Smith, 1985). The hearth was lined with baked clay nodules and filled in with layers of charcoal and ash underlying a dense layer of adult Rabdotus shells (Fig. 1). It was sealed by a layer of dirt and ash, and was covered over by compacted soil mixed with daub fragments.

Carbon dates of charcoal removed from several hearths were set at 2800 +/- 70 y.b.p., 2880 +/- 90 y.b.p., and 2750 +/- 320 y.b.p., showing occupancy by people of the Archaic period. Artifacts collected at the site also indicate the presence of the Karankawa after 1200 A.D. (Smith, 1985).

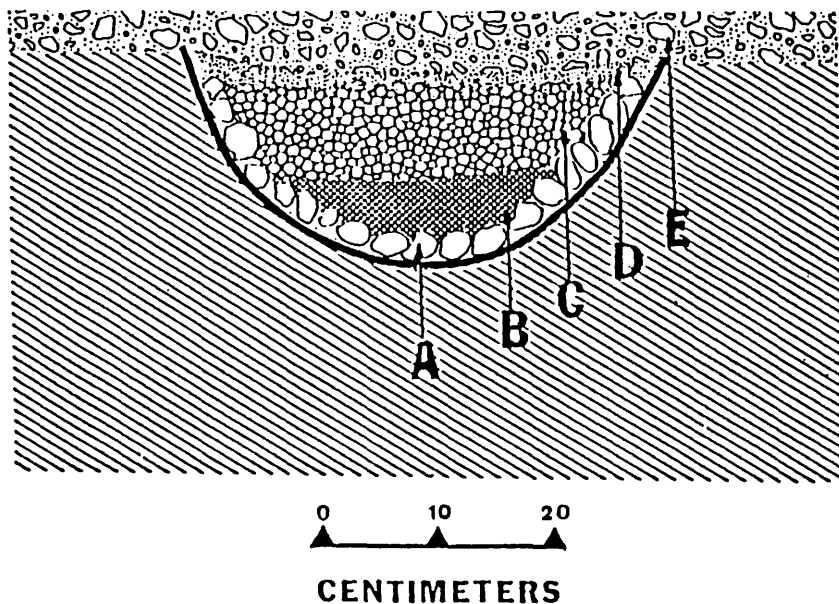


Figure 1 - Profile of "snail hearth" from site 41NU46. A: lining of burned clay nodules; B: charcoal and ash; C: Rabdotus shells; D: compacted soil with daub fragments. Hearth is 40 cm in diameter and 21 cm deep (after Smith, 1985).

DISCUSSION

None of the five species of land snails represented throughout the excavations at the Tucker site are unexpected in this locality. The same species are still found living near or at the site today and are typical of the South Texas chaparral environment. All species except for Rabdotus alternatus alternatus (Say) are present in numbers equivalent to those expected as a result of normal population levels. Although the representatives of this snail are intensely colonial, the enormous numbers of adult shells (ranging from 30-200 shells per square foot on the surface, to dense layers of nothing but shells) found throughout all levels of the Tucker site excavations and the paucity of juvenile and immature shells indicate a selective factor operating in shell deposition. Density was especially great inside the undisturbed hearth at Feature 7 (Fig.1). These animals do not represent a naturally occurring colony. The density originally may have been even greater throughout the site but has been reduced by heavy erosion which has washed many shells into Oso Creek.

Neck (1981) reported the presence of this same heavy-shelled form in large numbers at archeological sites in Jackson County, Texas, out of the normal range of this taxon. A lack of non-adult shells was found at the Jackson County sites just as at the Tucker site. Rabdotus alternatus alternatus estivates in the summer months on the prickly pear cactus (Opuntia lindheimeri Engelm.), the fruit of which formed a prime summer source of food for the aborigines of southern Texas (Smith, 1871; Bandelier, 1905; Bishop, 1933; Krieger, 1956; Hedrick and Riley, 1974). The unusual locality and the skewed distribution of adult shells when coupled with the snail's habit of estivating on the cactus during the time that the cactus fruit are ripe caused the author to postulate that this species was gathered as a food source and was transported back to the winter dwelling site to be stored for later consumption. A similar density of shells and lack of immature specimens occurs both at the Tucker site as well as at the Choke Canyon sites (Thoms et al., 1981; Scott, 1982), where tuff rock hearths associated with piles of Rabdotus and freshwater shells were assumed to be used in preparation of the mollusks for consumption (Brown et al., 1982).

Two difficulties with the "snails as food" hypothesis in south Texas specifically have been pointed out by previous authors (Clark,

1973, 1976; Hester and Hill, 1975). The first of these is that there is no evidence of how the snails could have been prepared for consumption as the shells are neither crushed nor charred. Boiling has been suggested but the Archaic people occupying the Tucker site, which has been carbon-dated at approximately 2800 years B.P., were aceramic. They had no flame-proof containers in which to boil foods, although limited cooking could have been done in clay-lined baskets, traces of which were found at the site (Smith, 1985). The second difficulty is that there were no known ethnographic accounts of land snail consumption by the later inhabitants of the Texas coast, who also occupied the Tucker site after 1200 A.D. A further difficulty complicating the analysis of land snails in archeological sites is the burrowing habit of many terrestrial gastropods. Unless circumstances are clearly otherwise, land snail shells in archeological sites could result from natural invasion of the area. However, the density of Rabdotus at Texas Archaic sites (Hester, 1976), and the construction of the "snail hearth" at the Tucker site argue in favor of the intervention of a human agency in the accumulation of shells.

The uncovering of an undisturbed hearth at Feature 7 of the Tucker site apparently overlooked by its builders reveals that Rabdotus was prepared by baking the snails in a manner similar to that used at a New England clam bake (Smith, 1985), where shellfish are steamed between layers of damp vegetation in a dirt-sealed pit. As has long been known by malacologists and collectors wishing to clean gastropod shells, the cooking procedure destroys the effectiveness of the columellar muscle of the snail allowing the meat to be removed readily from the intact shell with fingers or a small, sharp twig or bone fragment. This method leaves the shells uncrushed and unmarked by fire, thereby accounting for the undamaged shells that have been so puzzling.

Support for the use of Rabdotus as a food resource by the Karankawa can be found in the history of the Indies written by Gonzalo Fernández de Oviedo y Valdés, a contemporary of Alvar Nuñez Cabeza de Vaca in the sixteenth century. Four men survived the ill-fated expedition of Pánfilo de Narváez, among them Cabeza de Vaca and Andres Dorantes de Carranza. The survivors gradually made their way from the "Isla Mal-Hado" on the Texas coast to European civilization in Mexico over a period of six years. During

the sojourn in Texas, Dorantes was separated from Cabeza de Vaca in the spring of 1529. Dorantes lived alone with the local Indians until 1534 when the survivors were reunited at the "River of Nuts". The separate account of Dorantes' adventures was utilized in part by Cabeza de Vaca in the preparation of his narrative but was recorded fully only in the Real Audiencia of Santo Domingo, since lost, and in Oviedo's Historia (Davenport, 1923). Bishop's (1933) use of Oviedo's work in his biography of Cabeza de Vaca confused authors seeking ethnographic evidence to support aboriginal consumption of Rabdotus. The passage cited by Hester and Hill (1975) is not from Cabeza de Vaca's Relación (Smith, 1871) as assumed by Clark (1976). It is found instead in Oviedo's record of Dorantes' story. In this account it states:

"Y éste es el mejor tiempo del año para aquella gente, porque aunque no comen otra cosa sino tunas é algunos caracoles que rebuscan, de que se hartan de día é de noche, están contentos en essa saçon, y en todo el otro tiempo del año se finan de hambre." (Oviedo, 1547, reprinted in Hedrick and Riley, 1974:128).

This translates as:

"And this is the best time of the year for those people, because even though they eat nothing else but prickly pear fruit and some snails that they search for, with which they gorge themselves day and night, they are happy in this season, and in all the rest of the year they die of hunger."

An earlier passage establishes the time of year as August, when the snails are most likely to be found on the cactus, and the identity of the people as the Indians of southern Texas.

The implications of this passage are that the snails were viewed as a boon by the Indians, who were drawn into the distributional range of Rabdotus alternatus alternatus by the ripening of the cactus fruit. Since almost all fish otoliths collected at the Tucker site showed winter death and none summer death (Smith, 1985) it may be that the snail/cactus combination was a more desirable food than fish when the combination was available.

CONCLUSION

With the ethnographic evidence supplied by Dorantes' account and with the evidence of the snail hearth from the Tucker site it can be accepted that both the Archaic and Prehistoric peoples of the Corpus Christi area ate Rabdotus alternatus alternatus. The method of preparation of the snails by the Archaic inhabitants was by baking or steaming the animals in closed hearths. The contemporary sixteenth century account of Dorantes confirms that the Karankawa also ate snails, although the method of preparation is still unknown. The vast numbers of shells found at sites such as the Tucker site show the importance of this snail as a food resource.

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THE MESOCONCH: A RECORD OF JUVENILE LIFE IN
UNIONIDAE

by Arthur H. Clarke

SUMMARY

In the St. Francis River, Arkansas, specimens of Proptera capax (Green) first emerge from below the substrate surface in September, presumably in response to sexual maturation. The shell of this previously hypobenthic juvenile, here termed the mesoconch, is distinctive and is preserved as a discrete structure even in the adult. Mesoconchs are also apparent in some other lampsilines and in some anodontines and they appear to provide evidence about the nature and the duration of the hypobenthic stage in these species. Other aspects of juvenile behavior, including the adaptive value of beak sculpturing, and the possible crucial importance of mussel beds as nurse areas for juvenile mussels, are also discussed.

INTRODUCTION

Malacologists have frequently observed that young juvenile freshwater mussels (Unionidae) are difficult to find but few data exist about which size classes comprise this apparently rare group or where they are actually located. Isely (1911:77-80) reported that he had found small (2.9-22.5 mm long) specimens of several species in Oklahoma attached each by a byssus to small pebbles or to shells in areas of fairly rapid current and

Baker (1928:15) stated that juvenile mussels often burrow deeply into the bottoms of streams. Neves and Widlak (1986) have corroborated and extended these observations and have shown that young juveniles of some species in southwestern Virginia bury into stream substrates, some as deeply as two feet.

In 1984 and 1985 ECOSEARCH, Inc. carried out a distributional and ecological study (1) of the endangered mussel Proptera capax (Green) in part of the west branch of the St. Francis River in Arkansas. All live specimens of P. capax were measured and carefully replaced in the river. Surprisingly, analysis of these measurements and of other data led to conclusions about juvenile mussels (Clarke, 1986(b)), conclusions which appear to be potentially useful in unionid management and conservation programs.

ACKNOWLEDGEMENTS. - I wish to thank my wife Judith, Dr. Mark J. Imlay, Mr. Steven Moyer, Mr. Donald Martin and Mr. Randolph Clark for valuable assistance in the field; Dr. Kenneth J. Boss and Mr. Richard I. Johnson for access to the fine unionid collection at the Museum of Comparative Zoology; Dr. Richard J. Neves for providing unpublished information about his work on juvenile mussels, Ms. Jane E. Deisler for reviewing the manuscript, and Mrs. Frances Trevino of Corpus Christi State University for typing the manuscript. The field research was supported by a contract (No. DACW 66-84-M-1666-R) between the Department of the Army, Corps of Engineers (Memphis District) and ECOSEARCH, Inc.. I am grateful to the Corps of Engineers for that support, and to Corpus Christi State University for generous cooperation and use of the facilities.

(1) Also frequently cited as Potamilus capax (Green).

MATERIALS AND METHODS

Field work under this contract was necessarily done during periods of low water, i.e. principally from September 16 through 26, 1984, and August 8 through 14, 1985. Some sampling was also done from June 18 to 20, 1985, but it was terminated prematurely because of rain and high water. The precise area under study will not be delineated here because P. capax is endangered and it should not be disturbed.

Population location and size estimates were made principally by means of river runs with a canoe. 93 sites, located at intervals of about 1 km, were systematically studied. At each site, where possible, an area of 1000 square meters, extending from bank to bank, was measured off and each such area was repeatedly traversed by 2 to 5 collectors, using face masks and snorkels or viewing boxes and bare feet, until no more mussels could be found. All specimens of P. capax were measured to the nearest cm and carefully replaced in the substrate as close to their original locations as possible. Specimens of all other mussels were tabulated by species and, except for a few specimens needed for other studies, were also replaced in the river. Substrate characteristics, current speed, water depth, and other ecological attributes were also observed and recorded on standard data sheets and all of this information was later filed in a computer storage and retrieval system at Corpus Christi State University.

RESULTS

The number of living specimens in each of 13 size classes seen in the three survey periods are shown in Table 1. Mean length measurements calculated from these data and their standard

deviations are: June, 10.44 ± 1.89 cm; August, 10.04 ± 1.70 cm; and September, 9.16 ± 2.25 cm. The percentage of specimens in each size class in the August and September surveys are shown in Figure 1. (The June specimen total was considered too low for valid comparison by percentages with the August and September totals).

Table 1. Number of Living P. capax in Length Classes

Class (cm)	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
June					1	2	4		6	4			1	18
Aug					2	9	19	21	10	9	6			76
Sep	1	5	4	2	8	24	27	21	13	9	7	1	1	123

Although the mean values of the June, August and September surveys have broadly overlapping standard deviations and are therefore statistically not significantly different, the distribution of specimens within size classes are not the same. The most conspicuous anomaly involves specimens 3 to 6 cm long: these were present in the September survey but were entirely absent in the August and June surveys. Further, the young specimens seen in the September survey were jewel-like, totally unblemished, and in perfect condition.

As mentioned above, the scarcity of juveniles in our survey is a quite typical result of most mussel surveys and there is no reason to believe that P. capax is not reproducing and healthy in the west branch of the St. Francis River. The visible substrates in the areas occupied by most of the adult P. capax were comprised partly or wholly of sand and there were no gravel- or pebble-bottom

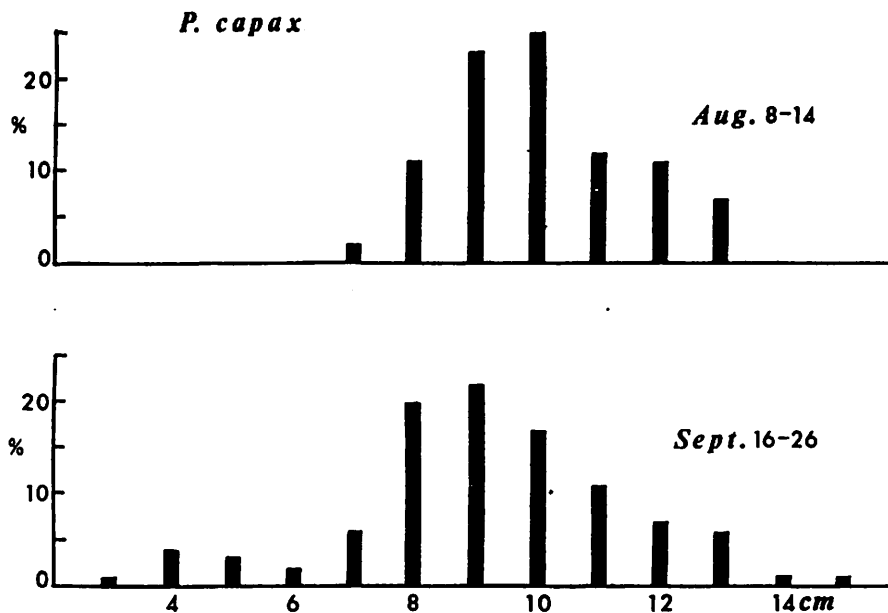


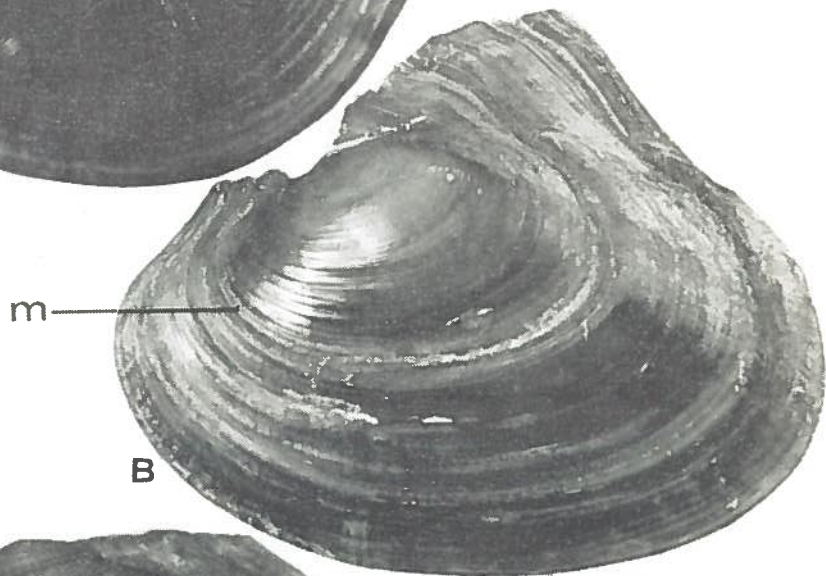
Figure 1. - Percent frequency of Proptera capax within size groups during August and September surveys.

Plate 1. - Unionidae exhibiting a mesoconch. A, Proptera capax, St. Francis River, Arkansas; B, Proptera laevissima (Lea), also from St. Francis River, Arkansas; C, Lampsilis ochracea (Say), Tar River near Tarboro, North Carolina; D, Obovaria olivaria Rafinesque, Ohio River near Mound City, Illinois. All figures x 1.0. m indicates mesoconch annulus in P. capax and probable mesoconch annulus in other species.

PLATE 1



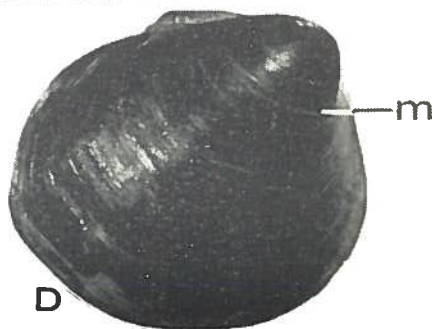
A



B



C



D

PLATE 2



habitats nearby. One must presume, therefore, that burial in sand must be the normal habitus for young P. capax there, but of course controlled and meticulous excavations are desirable to fully corroborate that conclusion. It is most doubtful that burial in mud would permit sufficient circulation of water to permit respiration and feeding to occur.

Additional evidence for probable hypobenthic existence of young is also provided by the beautiful condition of small specimens. No erosion or corrosion could be seen and it seems obvious that such remarkable preservation could only have been achieved if the juveniles were relatively immobile and were completely buried during most of their postlarval lives.

Further consideration of this problem necessitated re-examination of all available material. This consisted of 12 empty specimens (10 shell pairs and 2 single valves) of P. capax retrieved from the west branch of the St. Francis River. During this re-examination it suddenly became apparent that the shiny, characteristic shell formed during the (presumably) hypobenthic juvenile stage was still clearly visible even in those dead-collected, partially worn empty specimens. Even the outer boundary was sharply defined in nearly all of them.

Plate 2. - Unionidae exhibiting a mesoconch. A, Anodonta cataracta Say, x 1.40, Halfway Pond, Plymouth Co., Mass.; B, Lampsilis radiata radiata (Gmelin), x 1.35, Connecticut River, Hartland, Vt.; C, Alasmidonta undulata (Say) x 1.34, also Connecticut River, Hartland, Vt.; D, Lampsilis radiata siligoidea (Barnes), x 1.20, Lake Erie, Monroe, Mich.; E, Ligumia subrostrata (Say), x 1.15, locality unknown. m indicates probable mesoconch annulus.

The little-known term mesoconch (see Cox 1969: 106)⁽²⁾ is applicable for a discrete shell stage which is ontogenetically intermediate between the nepioconch (the area of beak sculpture) and adult shell stages. In Proptera capax the juvenile post-larval shell has two clearly recognizable, sequentially developed parts. The nepioconch comprises that part in which beak sculpturing⁽³⁾ is a dominant feature. The mesoconch is characterized by a smooth, glossy surface; a ground color which in many specimens is in contrast with that of the post-mesoconch; by the presence of one or more annuli which are well-defined but not strongly impressed; and an outer boundary which is marked, in most specimens, by the first broad, strongly impressed, and truly conspicuous annulus, the "mesoconch annulus" (see plates 1,2).

Mesoconch lengths were measured in the 12 available specimens. In ten of the shells the lengths were 4.4, 4.6, 4.5, 5.1, 5.3, 5.4, 5.6, 5.6, 6.0, and 7.2 cm. In one, two conspicuous early annuli were present, one at 2.6 cm (probably from premature emergence) and the other at 6.4 cm. One specimen was too worn to permit mesoconch delineation. All of the measured lengths correspond well with the 3, 4, 5 and 6 cm length classes of newly-emerged juveniles seen in the September survey. Further examination of annuli in our material indicates that the 3 to 6 cm length

- (2) The boundary between the nepioconch and the mesoconch is not defined by an annulus and it could be argued that those terms are therefore not applicable. Nevertheless, real structures are involved and a semantic argument about the applicability of terms should not be allowed to deprecate this fact.
- (3) The term "nepionic sculpturing" may be preferable to "beak sculpturing".

classes correspond approximately with the 2 to 5 year cohorts of P. capax in the St. Francis River, but that conclusion should be verified from better material.

All unionids possess a nepioconch (i.e. an area with beak sculpturing) but there are no reports, as far as I am aware, of evidence of a mesoconch. Our unionid reference collection was therefore studied for that purpose. Interestingly, the apparent presence or absence of a mesoconch correlated with subfamily groupings. In the Ambleminae species of the genera Fusconaia, Quadrula, Amblema, Megaloniais, Pleurobema and Elliptio were examined and no clear evidence of a mesoconch was seen. In the Anodontinae species of the genera Alasmidonta, Lasmigona, and Anodonta (but not in Arcidens and questionable in Strophitus) all exhibited a mesoconch. Similarly in the Lampsilinae one or more species of Actinonaias, Cyprogenia, Lampsilis, Leptodea, Obliquaria, Obovaria, Proptera, Ptychobranchus, Truncilla and Villosa were examined and all exhibited a mesoconch.

DISCUSSION AND CONCLUSIONS

Enemies of freshwater mollusks include leeches, insect larvae (e.g. sciomyzid and tabanid Diptera, Odonata, Hemiptera, and Coleoptera), crustacea (ostracods and crayfishes), numerous fishes, turtles, birds and mammals (shrews, muskrats, racoons, and man) (Cook, 1947 and Snyder, 1967). It is therefore more than likely that cryptic behavior in unionid juveniles is an adaptation against predation. The stimuli which elicit varying degrees of burrowing, including deep burrowing, are unknown but they may include predation such as that described by Snyder (1967) for freshwater snails. Many snail species react strongly to small amounts of body fluids released

from a crushed snail of the same species. They exhibit an immediate fright reaction and quickly burrow into the substrate or climb out of the water.

Although Isley (1911) has reported that species of all three unionid subfamilies occur near or at the substrate surface among pebbles (and that the anodontines and lampsilines were byssally attached to pebbles), our data on the presence of distinct mesoconchs in anodontines and lampsilines indicate that their juveniles are often completely buried in sandy (and perhaps other) substrates. Neves and Widlak (1986) have demonstrated, in fact, that young juvenile mussels show similar variations in habitat associations as demonstrated by adults of the same species.

A mesoconch shell stage will be most easily recognizable in the adult shell when (1) the quality of the substrate in which the hypobenthic juvenile is buried is different (4)(5) from that in

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- (4) Clarke (1973) has shown that the ground colors and color patterns in Anodonta and Lampsilis are well correlated with the character of the substrate (sand or mud) in which they occur. The precise reasons for this are unknown. I have also observed that conspicuous changes in ground color may occur in Lampsilis when individuals are moved from one lake to another.
- (5) It is possible that the west branch of the St. Francis River is unusual in this regard, but mesoconchs can be observed in many unionids from various localities. That may indicate that sedimentary changes with depth are of common occurrence.

which the epibenthic juvenile is located and (2) when the disturbance ring formed when the hypobenthic juvenile ascends to the surface becomes superimposed by the winter growth rest. Such conditions would promote contrasting ground colors between the mesoconch and the post-mesoconch and also produce an unusually prominent annulus marking the termination of the mesoconch stage.

Experience also indicates that contrasting ground colors are likely to occur only in species in which normal ground color is pale or of only moderate darkness and not in those which are blackish or dark brown. Since dark periostracal color is a normally-observed feature in amblemines and paler colors are seen in many anodontines and lampsilines, periostracal color contrasts between mesoconch and post-mesoconch stages might be apparent in anodontines and lampsilines but not in amblemines.

Some evidence indicates that the normal emergence of hypobenthic juveniles may be associated with sexual maturation. In Anodontinae and Lampsilinae sperm release and fertilization of ova occurs in the fall and emergence of mesoconch juveniles at that time would probably cause formation of a disturbance ring which would be followed closely by a winter growth rest, i.e. the production of a conspicuous mesoconch annulus. In Ambleminae fertilization normally occurs in the spring or early summer and if late-mesoconch juveniles emerged at that time their disturbance rings would not be superimposed by winter growth rests and would not be conspicuous. Therefore, although our observations indicate the presence of a mesoconch only in anodontines and lampsilines, a comparable shell stage may also occur in amblemines but it may be difficult to distinguish. Neves and Widlak (1986) have shown, in fact, that some juvenile amblemines do occur in the substrate.

Consideration of available evidence strongly indicates that beak sculpturing, the dominant feature of the nepioconch shell, is also adaptive (Clarke, 1986(a)). It is clear that the epibenthic zone is a hazardous environment for tiny thin-shelled mollusks. Every other freshwater molluscan family has evolved physiological or behavioral features, (e.g. mass production of young, viviparity, crypsis of eggs, eggs deposited above the water surface, etc.) which serve as a defense for their most vulnerable life stages and defensive adaptations in freshwater mussels should be expected. In Unionidae two life stages are particularly subject to mortality, the glochidial and the early post-parasitic. Mass production of glochidia has been an effective defense against excessive mortality in the glochidial stage and the development of shell-reinforcing ridges (beak sculpturing) appears to have been the initial defense against excessive predation in the early post-parasitic stage.

Among North American unionids, and except for species which are heavily sculptured as adults (6) and begin development of that sculpture at the nepioconch stage (e.g. Quadrula, Amblema, Megalonaias and Tritogonia), the weakest and least extensive beak sculpturing occurs in heavy-shelled species which develop rather thick shells early-on (i.e. Fusconaia, Pleurobema, Plethobasus, Obovaria, and Plagiola) and the strongest and most extensive beak sculpturing occurs in those species which have very thin shells (i.e. Anodonta, Anodontoides, and Strophitus). This is as would be expected if beak sculpturing functioned as a predator defense for

(6) Some possible functions of adult sculpturing have been discussed in Clarke, 1982.

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thin-shelled, tiny, nepioconch juveniles. Many exceptions occur, e.g. Alasmidonta undulata has very heavy and extensive beak sculpturing although it is only moderately thin-shelled, and the alate genera Proptera and Leptodea are thin-shelled but have weak beak sculpturing. Phylogenetic constraints are also of great significance in the development of beak sculpture. A corrugated shell is stronger than an uncorrugated shell of the same thickness, therefore beak sculpture corrugations must confer selective advantage.

It seems likely that information available from examination of mesoconchs may be useful in conservation and in management programs. One example is: if annulus counts within the mesoconch of an endangered species reveal that the usual age at hypobenthic emergence of that species is, say, four years, complete removal of that species from any particular area will not be achieved until all specimens are collected annually, after each period of emergence, for four years. A second example is: if mesoconch measurements of living specimens in a population demonstrate that hypobenthic emergence occurs principally, say, in the 3 to 5 cm size classes; but no living epibenthic specimens can be found at any time of the year which are smaller than, say, 9 cm; this may be an early indication of reproductive failure.

Finally, it must be mentioned that dense mussel beds in muddy and other inimical habitats may offer the only suitable refuges for young juvenile mussels. Overharvesting of a mussel bed may therefore destroy it as a juvenile nursery area and the bed may therefore disappear. Government regulatory agencies are urged to monitor the health of known mussel beds and of mussel harvesting activities as part of their programs for protecting our mussel resources.

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PRELIMINARY NOTE ON THE ECOLOGY OF THE
EARLY JUVENILE LIFE OF THE UNIONIDÆ.¹

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During the past four years the writer has given considerable time to the field study of the Unionidæ. A number of puzzling questions have arisen as to the relative importance of the various ecological factors that contribute to the environmental complex of these animals. Among the most important of these factors, we may mention bottom conditions, water content, stream volume, stream fluctuations, relation to fish and natural enemies.

In connection with this work, much difficulty was experienced in finding young mussels for study and experimentation. I have collected many specimens from the size of a nickel to a quarter, but mussels under the size of a dime have been rare. A number of experienced field workers have spoken to me of a similar difficulty in finding juvenile specimens.

In order to avoid any misunderstanding, I may state that by "early juvenile life" I mean the period following the time when the mussel completes the parasitic stage and leaves the fish to lead an independent life, until it is about the size of a dime or about fifteen millimeters in length. This would cover, in most species, approximately the first year of independent existence. Other periods may be designated as later juvenile and adult life.

The glochidium stage has received considerable study. Our knowledge of the parasitic period has been recently cleared up and extended by the careful investigations of LeFevre and Curtis.² The later juvenile and adult life has received the attention of hundreds of students. The scattering and meager references in the literature, to the early juvenile stages, give us little information on this important period in the life history of the mussel.

During the past summer, while working on the Red River Mussel

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² "Reproduction and Parasitism in the Unionidæ." George LeFevre and Winter-ton C. Curtis, *Journal of Experimental Zoology*, Vol. IX., No. 1, September, 1910, pp. 79-115.

Survey for the Bureau of Fisheries, I found a fairly good number of species in the early juvenile period of development. The distribution and ecology of these young mussels seem to me to be of special interest. Furthermore, the facts in regard to their habitat seem to clear up some ecological perplexities concerning the adult ecology of the Unionidæ.

Thirty-two specimens are here especially considered, these were attached to rocks and pebbles by a functional byssus. These mussels, representing nine species, were found in three different rivers and in four localities. The situations, however, were similar. Twenty-nine of these specimens weigh less than five decigrams; of this number twelve weigh under one decigram, and ten are under nine millimeters in length.

The thirty-two specimens represent the following species:¹ (1) *Lampsilis luteola*, two; (2) *Lampsilis fallaciosa*, one; (3) *Lampsilis parva*, four; (4) *Lampsilis gracilis*, three; (5) *Plagiola elegans*, one; (6) *Plagiola donaciformis*, sixteen; (7) *Anodonta imbecillis*, two; (8) *Ptychobranthus phaseolus*, two; (9) unnamed species, one.

The first of these specimens was secured on August 20, 1910, in the Kiamichi River, near Fort Towson, Oklahoma. While working in a gravel bed, Owen Horne, one of our party, called attention to an unusually small mussel attached to pebbles by a byssal thread. After a search for about two hours we secured eight specimens with byssus, representing four species. These specimens were found in a coarse gravel bed, the pebbles being from one fourth to one inch in diameter. The water was fairly swift, and from one to two feet in depth. The byssus of these specimens was variable in length, sometimes several inches long, and often connecting three or four small pebbles. Sometimes the byssus spread into several branches at the place of attachment. The young mussels were best secured by taking up handfuls of gravel and looking for the thread. The byssus is strong enough to support the mussel in a rapid current, and will sustain the weight of a number of small pebbles, without breaking.

On August 30, 1910, five more specimens were secured in the

¹ Most of the specimens have been examined by F. C. Baker and L. S. Frierson, making sure of the identifications.

Little River, near Garvin, Okla. One of these specimens, found by E. C. Johnston, of our party, was attached by the byssus to the shell of a large *Quadrula pustulosa*. An observation of this kind is described by Kirtland.¹

During the afternoon of August 30, we again investigated a portion of the Kiamichi River, near Roby, Okla. Here we secured fourteen specimens; ten of these I secured in about half an hour, one time bringing up three specimens with a handful of gravel. Here again the environment was typical, fairly swift water, coarse gravel, and rocks.

A search for young mussels was also made in Blue and Boggy rivers, but failed to yield specimens with functional byssus. However, a number of mussels under twelve millimeters were secured, representing *Quadrula pustulosa*, *Quadrula lachrymosa*, *Quadrula coccinea*. In the Washita River, near Davis, Okla., on September 2, we secured the last of our young mussels for the summer. Five specimens were found in swift water about two feet deep. One of these was under three millimeters in length and weighed .005 of a gram.

In the following table I show species, locality, weight in grams, length, height, and breadth in millimeters, of ten of the thirty-two specimens:

Species.	Weight.	Length.	Height.	Breadth.	Locality.
1. <i>L. luteola</i>41	14.5	9.2	5.9	Kiamichi R., Aug. 30, 1910.
2. <i>L. fallaciosa</i>	—	13.5	6	3.4	Kiamichi R., Aug. 20, 1910.
3. <i>L. parva</i>035	7	3.8	2.3	Kiamichi R., Aug. 20, 1910.
4. <i>L. gracilis</i>47	22.5	9.9	4.1	Little R., Aug. 30, 1910.
5. <i>A. imbecillis</i>055	7.1	3.5	1.1	Kiamichi R., Aug. 30, 1910.
6. <i>P. phaseolus</i>15	12.4	5.6	2.7	Little R., Aug. 30, 1910.
7. <i>P. elegans</i>175	9.6	6.9	4.5	Kiamichi R., Aug. 30, 1910.
8. <i>P. donaciformis</i>005	2.9	1.5	1.1	Washita R., Sept. 2, 1910.
9. <i>P. donaciformis</i>01	5.6	3	1.9	Kiamichi R., Aug. 30, 1910.
10. Unnamed sp.014	5	3.3	2.3	Little R., Aug. 30, 1910.

The facts noted above are closely related, not only to the ecology of the juvenile mussel, but also to the ecology of the adult.

1. They indicate the conditions essential for the most successful growth and early development of the Unionidæ. This kind of

¹"Fragments of Natural History," J. P. Kirtland. *American Journal of Science*, Vol. 39, 1840, pp. 166-168.

an environment gives a constant supply of oxygen, and sufficient food; is frequented by suitable fish; is free from shifting sand and silt accumulation. Those mussels that drop from the fish in these favorable situations develop in large numbers, while the less fortunate, that drop in shifting sand and silt, die early.

2. In the study of the ecological factors that are inimical to mussel life, more attention should be given to the consideration of the juvenile habitat. Absence of gravel bars and stony situations may sometimes explain the scarcity of the Unionidæ in certain streams and lakes where frequently water content has been thought the chief unfavorable factor.

3. It is a well known fact that in many streams certain stretches of mud-bottom are found loaded with mussels, while other areas, in the same stream, equally favorable from the standpoint of the habitat of the adult mussels, have only scattering specimens.

This distribution of the adult may be explained by the assumption¹ that the average mussel seldom travels far up or down the stream from the place where it begins successful development. Stretches favorable for juvenile development thus come to be the centers of dispersal in the streams where they occur. As a result, areas of mud-bottom near these favorable habitats, become loaded with mussels by migration.

4. In the study of the life history of the Unionidæ, we may consider the embryonic, the glochidia, the parasitic, the *early juvenile*, and the adult as distinct periods for separate and special study.

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¹This assumption is fairly well established, by experimental study that I have been carrying on for some time, and will be discussed in a later paper.

