

THE ECOLOGY OF THE FRESH-WATER PEARL MUSSEL
MARGARITIFERA MARGARITIFERA (L.)

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ABSTRACT

This paper reviews the ecological literature on the fresh-water clam *Margaritifera margaritifera* (Linnaeus), and presents original observations on a population in the Kettle River near Boys, Stevens Co., Washington. Data are summarized on habitat, substratum and water depth, stream velocity, shell attitude and orientation, turbidity, temperature, desiccation, light, lime, population density, seasonal beha-

avior, associated organisms, reproduction, and duration of life. The value of several shell characteristics in drawing ecological conclusions in ethnomalacological and paleoecological works is discussed. References cited constitute a bibliography of margaritiferid ecology plus a selected number of references on freshwater pearls, pearl fisheries, systematics and paleontology of the Margaritiferidae.

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INTRODUCTION

The preparation of a report on the ethnomalacology of the fresh-water pearl mussel *Margaritifera margaritifera* (Linnaeus) for the University of Oregon Museum of Natural History necessitated a review of the widely scattered ecological literature on this species (Roscoe, 1962). Field observations on a population of *M. margaritifera* in the Kettle River near Boyds, Stevens Co., Washington, were begun by the present authors in September 1962 and continued by the junior author to August 1964. The authors stress the preliminary nature of their field observations. The site is readily accessible and they strongly urge more detailed long-range studies by local residents having time and facilities. The present report, incorporating both literature review and field observations, supplements the previous major ecological reviews of the British malacologists Jackson (1925) and Boycott (1936) and amplifies the meager American literature.

Margaritifera margaritifera has the widest range of any naiad in the world (Simpson, 1914). It is found throughout the Palearctic as far south as Japan. In the Nearctic it extends from Newfoundland to Pennsylvania and New York in the east, to the upper Missouri River area in the central states, and to below the 40th parallel in the west (Walker, 1910; Simpson, 1914; Ingram, 1948; Clarke and Berg, 1963). The zoogeographic significance of *Margaritifera* is discussed by Scharff (1907, 1911) and Beauford (1951).

ECOLOGY OF MARGARITIFERA MARGARITIFERA (L.)

HABITAT. *Margaritifera* is essentially, although not exclusively, a river inhabitant. Boycott (1936) speaks of *M. margaritifera* as living in "a well-defined river habitat, though it is a little difficult to specify the essential qualities Most of its habitats are places in which fishermen would expect to get trout and hope for salmon" Several other authors

also mention trout streams as the most favorable habitats. Lake dwelling populations are recorded from both Europe (Boycott, 1936) and North America (Clarke and Berg, 1957; Clarke and Rick, 1963).

Kettle River, the site of our original field observations, is a typical river habitat of *Margaritifera*. To avoid interruption of the continuity of the ecological account details of the Kettle River habitat are given below, under "Description of Study Area."

SUBSTRATUM AND DEPTH. *Margaritifera margaritifera* is said to be usually found in accumulations of sand behind large stones (Boycott, 1936) and to be generally absent from deep holes and muddy bottoms (Boycott and Bowell, 1898). A preference for "eddies and pools which are rather deep with a steady and lively current and with gravelly and sandy bottoms" is noted by Ortmann (1919). In Europe the species has been recorded from millstreams in the vicinity of artificial stone weirs (Harms, 1907). Exact depth figures cited vary from 1.5 to 5 feet, with a stated preference of about 3 feet (Boycott and Bowell, 1898; Haas, 1908; Harms, 1907; Ortmann, 1919; Jackson, 1925).

In the Kettle River the mussels were noted in September 1962 as mostly confined to one side of the stream just above a sharp bend over an area of about 1500 sq. ft., at depths of from 2 to 4 feet. The bottom material consists of a mixture of boulders and gravel with some sand and slight amounts of silt and clay. At the upstream margin of the bed the mussels tended to occur singly, but farther downstream they were grouped together in clumps of from two to about eight individuals, often in sand behind larger stones and boulders. Just below this bed a deep hole occurs on one side of the stream in which no mussels have been detected to date.

STREAM VELOCITY. In discussing unionids in general Eager (1948) has noted that there is seemingly an upper limit to the stream velocity in which the various river forms can survive. He suggests that this critical limit may be determined

merely by the rate at which the shells are washed away in time of flood, "although such a simple explanation appears unlikely in the case of such a large burrowing species as *M. margaritifera*." A limiting velocity for *Margaritifera* in small brooks in Germany has been noted by Altmöder (1926).

Despite the fact that seemingly identical conditions are found in the Kettle River for a distance of about a mile both above and below the clam bed, no additional live specimens were found in September 1962. At this time the current was fairly rapid although the stream was at low-water stage. Following the high water stage of 1963 a second smaller bed of *M. margaritifera* was observed about 1,000 feet below the original bed, and below the deep hole mentioned above. In the late summer of 1964 clams were observed spread over an extensive area downstream from the site of the original 1962 bed. In this new area the bottom is sandy with a few rocks and the water is deeper and swifter than at the site of the original bed. The fate of mussels washed into the deep hole adjacent to a portion of this new area is unknown. We believe that the specimens in the two additional areas were washed down from the main bed. Observations in 1962 on transplants in the Kettle River revealed that occasionally individuals get caught cross-wise to the current and are rolled some distance downstream. Seemingly such washing action does much less damage to the clams than might be supposed.

SHELL ATTITUDE AND ORIENTATION. *Margaritifera* is a burrowing form. A very early account by Redding (1693) states that they may be found "laying on their sides or set up in the sand like eggs in salt, with the sharp edge downwards, and the opening side turned from the torrent." Generally *Margaritifera* does not bury its shell as deeply as does *Anodonta*, a fact probably correlated with the usually harder substrate in which *Margaritifera* lives, but it has been noted as burrowing nearly two-thirds of its length into sand and gravel (Okada and Koba, 1933), at angles of from 25° to 80°

(Harms, 1907; Haas, 1908; Okada and Koba, 1933).

In the Kettle River population generally only a short part of the anterior end of the shell was imbedded in the substrate, although in places almost one-half of the clam was buried. The angle of repose varied from 0° to 90°, i. e., almost parallel with the substrate to upright. Among 25 specimens transplanted in September 1962 to a section of the stream where they could be observed more readily, some individuals would lie almost parallel to the bottom with much of the shell covered by stones. Occasionally an individual would be found lying on its side for a short period of time. Most of the clams in the bed had the siphons directed upstream, but among the transplants the clams assumed every angle from siphons directed toward the current to siphons directed away from the current. In eddies there is a tendency to orient the siphons toward the current.

TURBIDITY. When the water is muddied *Margaritifera* is said to withdraw the mantle and close the valves (Jackson, 1925) responding in much the same way as to reduced light (q. v.). During high water stages the Kettle River becomes so turbid as to render observations of the clams difficult to impossible. Transplanted individuals responded to muddied water as described by Jackson, but their reaction to continued turbidity is unknown.

TEMPERATURE. *Margaritifera* is apparently quite tolerant of cold temperatures, as indicated by its distribution. It is reported in mountain streams off the Arctic coast of Europe where the summer water temperatures reach only about 13° C. (55.4° F.) (Jackson, 1926). Its proclivity for mountain streams in the Nearctic is well established (Ortmann, 1919; Ingram, 1948). The upper temperature limit is unknown, but since in nature this factor would be closely linked to oxygen content discrimination between the effect of the two factors would be difficult.

Unfortunately no instrumental observations were made on the Kettle River population.

Bare-legged wading in the stream is uncomfortable in early September, and the water is cool even during the warmest summer months. Ice forms over much of the stream during the winter months.

DESICCATION. *Margaritifera* is said to be very sensitive to desiccation, not frequenting streams subject to drying. The shipment of live specimens is difficult (Boycott, 1921a). In the Kettle River one transplant was observed to remain partially embedded in the substrate (sand-mud-cobble) for a period of three days in September 1962 during which the water gradually lowered until over one-half of the shell was exposed to the atmosphere. The substrate remained moist during this interval. Unfortunately pigs uprooted the specimen before the results of this interesting natural experiment could be learned. Certain physiological mechanisms, such as transfer of calcium salts between shell and blood, may favor desiccation resistance (Prosser and Brown, 1961).

LIGHT. Under a full sun *Margaritifera* is said to emerge and to protrude a portion of the mantle through the partly opened valves; under an overcast sun the mantle is withdrawn and the valves close (Jackson, 1925). A preference for situations where the stream banks are shaded by trees or shrubs is noted by Ortmann (1919).

At the site of the Kettle River population the stream is not shaded by trees or shrubs. Our limited observations of transplants indicate no consistent pattern in regard to response to light. Apparently some locomotion occurs during the late evening, night, or early morning hours.

LIME. The most controversial point in the ecology of *Margaritifera* centers around the chemistry of the waters it inhabits. The absence of this genus from lime-rich regions in Europe has been frequently commented upon. In North America Stearns (1907) raised the question of whether the absence of much of the unionid fauna of the Mississippi Basin from the

Columbia and Pacific Coast regions was due to a smaller proportion of lime in the waters of the latter areas, which would imply a favorable chemical environment in these waters for *Margaritifera*.

In the long list of chemical analyses of waters in which *Margaritifera* has been found, Boycott (1936) shows that the genus occurs in Scotland in waters with a hardness (Ca ppm) of 1 to 79, with the majority running below 30 ppm. Analyses of rivers in the south of England in which these mussels DO NOT occur show hardness of from 70 to 115 ppm. At Cleveland, New York, Clarke and Berg (1959) obtained *Margaritifera* at only one locality, Black Creek, in the softest stream water analyzed in their survey. This locality had a hardness of 46 ppm CaCO₃.

Several workers (Von Hessaling, 1859; McKean, 1882-83; Haas, 1910) have experimentally placed *M. margaritifera* in hard water with no success. However, Boycott (1925) concluded after a series of experiments with waters of varying degrees of hardness that hard water per se is by no means necessarily fatal to *Margaritifera*. He subsequently (Boycott, 1927) recorded its presence in British waters with a calcium content as high as 79 mgs per liter. Haas (1948) has since conceded that this mussel is able, "under conditions not yet known," to exist in water in which considerable lime is present. His views as to the influence of calcium on shell shape are noted later under "Shape."

Boycott (1936) notes that "the case for soft water is up to a point impressive It would almost [be] equally easy to argue that the thing that is requisite and necessary is a quick flowing cool river with clean water and the right kinds of bottom, and that it is as it were a physiological accident that such rivers are nearly always soft (Emphasis ours). Perhaps the solution of this very interesting question may come when someone discovers where the young mussels live after they fall off the [host] fish till they are about 2 inches long — a matter of several years; at present this is quite unknown."

In some experiments on the effect of various salts on freshwater mussels Ellis et al. (1931)

found calcium salts to be less toxic than other groups of salts, and also that there was some difference in tolerance between adult clams and young stages of the same species. The entire matter of calcium metabolism is a physiological problem which bears much further investigation (cf. Prosser and Brown, 1961). The possible relationship between calcium salts and resistance to desiccation in mussels has been noted above (p. 22).

In seeking some explanation to account for the demonstrable absence of *Margaritifera* from most high-calcium waters, we are inclined to agree with Boycott (1925, 1927) and Kennard, Salisbury, and Woodward (1925) that search be made for a correlative factor or factors. Correlations do not necessarily prove cause and effect.¹

Before leaving the topic of lime, it should be noted that the excess of carbon dioxide in most waters in which *Margaritifera* lives results in severe erosion of the shells, especially around the beak area. Variation in degree of such erosion from stream to stream has been noted (Jackson, 1925). "Bones" frequently have nothing left but the periostracum, and these "shell skins" have been reported from Holocene deposits in Scotland (Bennie, 1866) and from midden heaps in the Klamath region (Cressman, 1956). No such "skins" were observed by the senior author in the Round Butte archaeological material although most specimens did show extensive erosion. Several "bones" observed in the bed of the Kettle River as well as along its flood plain showed the calcium layers to be more eroded than the periostracum, a situation that would lead to the production of "shell skins."

POPULATION DENSITY. There is little published information on population density in *Margaritifera*. In a half mile of stream at the trout rearing ponds near Truckee, California, Murphy (1942) estimated the number of individuals of *M. margaritifera* over 40 mm. in length at about 20,000. A rough estimate of the Kettle River population indicates a density of a few thousand individuals in an area of about 1500 square feet, while the secondary population established after high-water in 1963 numbered about 60 individuals over an area of about 9 square feet.

SEASONAL BEHAVIOR. A seasonal distribution pattern has been ascribed to *Margaritifera* in stream beds (Jackson, 1925). In the spring the clams are reported to be found in the shallow water near the bank. Here they are said to move about freely, their long curving tracks being very conspicuous on the bottom. These tracks are described as forming a very nearly regular circle, and it is estimated that they travel from 12 to 15 feet each day. Stoppages are said to be clearly visible in the tracks. Later in the year, mid- to late summer, the mussels are reported to be distributed over the entire width of the river (Harms, 1907).

No seasonal pattern of distribution has been detected in the Kettle River population over a two year period. Observation of individual transplants revealed straight and "L" shaped tracks, over stony bottom, but no circular or curving tracks. Stoppages could not always be readily detected in the tracks.

Nothing has been published on winter activities in *Margaritifera*. Ice hampered obser-

^{1/} In the brine shrimp, *Artemia salina*, Gilchrist (1954) has shown that concentration of the haemoglobin in the blood may be correlated with degree of salinity of the water which these organisms inhabit. He points out that this is a false correlation, however, as haemoglobin con-

centration is directly related to O₂, which is inversely related to degree of salinity. Thus salinity is an indirect factor which acts by reducing the amount of O₂ the water can hold, the organism responding by an increase in haemoglobin in the blood.

vations of the Kettle River population, but apparently the clams remain in essentially the same position from fall to spring.

ASSOCIATED INVERTEBRATES. Information on associated species is scant. In Europe *Margaritifera* has been reported as occurring with the clams *Anodonta anatina* and *Unio crassus* (Haas, 1948), while in the upper Weser drainage Boettger (1954) noted insect larvae as common but *Ancylastrum fluviatile* (Müller) the only common mollusk. In New York Clarke and Berg (1959) found *Margaritifera* in association with *Elliptio complanatus* and a few other unspecified clams. The ethnomalacological material collected from near Deschutes River, Oregon, indicates association with crayfish and the snail *Goniobasis* (Roscoe, 1963).

At the Kettle River bed a single specimen of a juvenile *Anodonta*, referable to *A. oregonensis*, was found near the water's edge where the bottom was quite muddy. No snails were observed on or among the clams at this site. Insect larvae were common, and small crayfish were observed.

FISH ASSOCIATES. Freshwater mussels always attest to the presence of fish in streams from which they are collected since these mussels are obligatory parasites on fish during their young (glochidial) stages. According to Morrison (1955) the mantle flaps of the freshwater mussel *Lampsilis* are spotted and resemble small fish. These flaps "pulsate or jerk intermittently like a wounded minnow, to attract fish during the glochidia shedding season." *Margaritifera* does not possess such specialized mantle flaps. More information is needed on the fish hosts of *Margaritifera*. Trout have been observed naturally infected with *Margaritifera* glochidia (Wilson, 1916; Murphy, 1942), and experimental infection has been established in Brown, Rainbow, and Brook trout (Murphy, 1942) and several kinds of minnows (Harms, 1907; Murphy, 1942). Judging from the wide distribution of *Marga-*

ritifera several kinds of fish must be capable of serving as hosts.

REPRODUCTION. In Europe *Margaritifera* is reported to breed in mid-summer, July to early August (Harms, 1907). The process may occur as early as the end of May (Schierholz, 1888). In eastern North America breeding is suspected to occur during approximately the same period, June to August (Conner, 1909; Ortmann, 1919). The European *Margaritifera* (Harms, 1907) produce a relatively large quantity of ova in a season. The duration of a single brood is about 16 days in very warm weather, but may extend to about 4 weeks in cold temperature. Unlike *Anodonta*, the ripe *Margaritifera* glochidia are not retained in the gills of the parent over the winter, but are expelled during late July and August within a period of a few days. The mussel is said to frequently change position during the course of expelling its ova.

According to Jackson (1925) the glochidia of *Margaritifera* are extremely small (diameter 0.0475 mm.) as compared to *Anodonta* (0.35 mm.). *Margaritifera* glochidia are without true hooks, possessing six or seven small teeth only and become attached to the gills of the host fish, not to the fins as in *Anodonta*. Within 2-4 hours the glochidia become shut in by a thick cyst. The duration of the parasitic stage on the gills of the host fish depends upon the temperature of the water. It generally occupies about 14 or 15 days, but may be prolonged to 4 or 5 weeks. The larvae then fall to the bottom of the stream and become free-living. Illustrations of the glochidial stages of over 50 species of North American freshwater mussels may be found in Surber (1912, 1915). He does not illustrate *M. margaritifera* glochidia but does include the related *M. monodonta*. Juvenile stages of *M. margaritifera* are discussed and illustrated by Alverdes (1918).

The morphological development of the glochidial and young mussel stages of *Margaritifera* are discussed in detail by Harms (1909). A study of the growth of marked specimens over a two-year period was made by Rubbel (1913).

He failed to detect consistent growth rings, which are rather ill-defined in *Margaritifera*. Growth rate is more rapid in the younger stages, falling regularly from 1 mm./year in shells 60 mm. long to 0.4 mm./year in shells 100 mm. long. As might be expected, growth rate varies from place to place. Altnöder (1926) found that specimens from one locality bearing 20 annuli measured 11.6 mm. in length, while from another they measured 12.4 mm. with 60 annuli. He also found that the size relative to the number of annuli increased in a downstream direction. Saldau (1939) found that the specimens from some rivers had reached 60 mm. in length by 10 years of age and 70 mm. by 13 years, 13 year old specimens from other rivers measured less than 50 mm. Saldau (1939) noted that while growth in *Unio* from the European part of Russia continued in some waters after the eighth year, *M. margaritifera* was growing steadily without any evident falling-off in rate at the thirteenth year.

DURATION OF LIFE. Comfort (1957) notes that it has long been suspected that *M. margaritifera* has by far the longest life-span of any European species. Various inferences and estimates range from 60 to 100 years. Assuming a 60 mm. specimen to be at least 10 years old, Rubbel (1913) concluded that it should take another 20 years to reach 80 mm., and a further 40 years to reach 100 mm. On this basis the natural life-span could not be less than 70-80 years. Comfort (1957) notes that in general, large naiad shells represent a high growth-rate rather than extreme age. The normal maximum age in *Unio* and *Anodonta* is probably not much more than 20-30 years. Comfort (1957) remarks that, if the 100 year estimate of Israel's for *M. margaritifera* is correct, it is the longest-lived invertebrate known. (A similar age has been guesstimated for the giant clam *Tridacna*). Comfort thinks that a life span of this order in the wild would imply an exceedingly low adult mortality. Freshwater mussels are known to be attacked by rodents and birds, and *M. margaritifera* has been fished for many

centuries by man, often in a destructive manner. A direct determination of age-group mortality in marked shells does not seem to have been undertaken, either in fished or unfished waters.

PALEOECOLOGICAL CONSIDERATIONS

To what extent can ecological deductions be based on shell features? How reliable are such deductions? These are questions of great importance to the paleoecologist and ethnomalacologist, and it seems some discussion of the shell as a reflection of ecological conditions is merited here.

Size. To a degree at least, size is a reflection of ecological conditions. The largest American specimens of *M. margaritifera* on record, from Pennsylvania, range up to 152 mm. in length and 67 mm. in height (Ortmann, 1911, 1919). The largest European specimen known, from Sweden (specimens deposited in the Zoological Museum, University of Helsingfors) measures 154 mm. in length and 63 mm. in height (Brander, 1956). Haas (1941) gives no data on either American or European members of this species, but does cite an Asian specimen of the subspecies *M. m. dahurica* Middendorff from the Amur River in Eastern Siberia which measured 177 mm. in length and 69 mm. in height.

Shape. To what extent shell shape reflects environmental conditions, and to what extent, it is a factor of age variation is not clear. Two types of shapes have long been distinguished. Linnaeus applied the specific name *margaritifera* to the "kidney-shaped," or arcuate, type (the presumed type specimens from the Linnaean collection are illustrated by Bloomer, 1937). Lamarck later applied the name *elongata* to the non-arcuate type. Several other variants have been given formal taxonomic status by European writers.

As early as 1823 Barnes published figures of both arcuate and non-arcuate types, noting that "The remarkable change in the form of this

species by age as represented in the figures" (his figure 20, indicating a non-arcuate specimen as "young," an arcuate specimen as "old") "might induce an observer to suppose that the shells belonged to different species; but the specimens in our collections of every variety of form, from those that are straight or even slightly rounded on the base, to those that are deeply arcuated, show clearly that all belong to the same species." (*Italics in original*). Recently Clarke and Berg (1959, figs. 57, 58) have illustrated both non-arcuate and arcuate specimens of *M. margaritifera* from New York, designating them as immature and mature respectively.

Simpson (1914) related the difference in shape of *Margaritifera* to an "unfavorable environment," while Haas (1948) has specifically ascribed it to the calcium content of the water. Haas believes that specimens living in streams with low calcium content are larger, longer, wide, thicker, and more arcuate than those living in high calcium waters. Both arcuate and non-arcuate types were present in the Deschutes material, with some non-arcuate individuals as large as some arcuate specimens.

In *M. margaritifera* from several small streams in Germany, Altnöder (1926) found some correlation between obesity and relative height and a negative correlation between relative height and the fall or gradient of the stream. Obese, relatively high forms with rounded lower borders were present where the fall of the stream was least, while in more rapid water the shell became less obese and more elongate with straight and finally "bighted" (arcuate?) or reflected lower borders. The variation in British and Irish *Margaritifera* has been discussed by Bloomer (1927). There has been some additional work on shell morphology of this species by Dyak (1942) which we have not seen. Eager (1948, fig. 5) reproduces a series of illustrations of the shape of *M. margaritifera* shells from streams of various velocities. Apparently no studies have been reported on comparisons of lake and stream populations of the species.

Thickness. Although characteristically thick-

er than *Anodonta*, for its size *Margaritifera* is not excessively thick-shelled. Perhaps this is correlated with its proclivity for lime deficient regions. Other mollusks compensate by building smaller, but normally thick shells in such situations. A few specimens from the Deschutes, Oregon archeology sites exceeded in thickness anything the senior author has observed in this species. The Oregon specimens were strongly reminiscent of descriptions and illustration of *M. auricularia* (Spengler) from the British Pleistocene and Holocene (Kennard, Salisbury and Woodward, 1925; Wenz, 1944; Kerney, 1958). Comparative material of *M. auricularia* has not been available.

The relationship of the species *margaritifera*, *auricularia*, and *durrovensis* has been discussed (Haas and Wenz, 1914; Phillips, 1929; Haas, 1948), but the subject requires further study and re-evaluation. None of the material observed in the Kettle River population exhibited this abnormally thick condition.

Sculpture. This consists of longitudinal ridges, sometimes a little broken. The surface is marked by rude growth lines. Neither the Deschutes nor Kettle River specimens afford anything unusual in this regard.

Periostracum. Sometimes, but incorrectly, called the epidermis, the outer horny covering of the shell is normally thick, blackish or brownish, and somewhat shiny. The Kettle River specimens were normal in this regard.

Nacre. The inner lining of the valves, or nacre which may take up to half of the entire thickness of the shell (Jeffreys, 1862), is shiny in fresh material, and varies in color from whitish to purple. Much of the western United States material has a decided purplish or reddish-purple color, and this was the basis for the nominal subspecies *M. m. falcata* described by Gould from the Columbia River material collected by the Wilkes Expedition. Most naiad specialists are now of the opinion that this is merely a color variation not worthy of even a varietal name. Nacre color tends to fade even in recently col-

lected museum specimens, and is generally absent in fossil and subfossil material. The most extensive discussion of variation in nacre color in naiades is that of Grier (1920) on the Ohio drainage basin fauna.

Specimens of *Margaritifera* from the same locality will often show both colored and white nacre, so that the relation of this feature to ecology is not clear.

Teeth and Muscle Scars. The left valve of *Margaritifera* has two stumpy pseudocardinal teeth; the right valve has one tooth. Lateral teeth are generally absent in adult specimens, although often well developed in juveniles and occasionally occurring in mature individuals. Muscle scars are impressed, the anterior one rough, the posterior one smoother, elliptical. Examination of specimens in the Chicago Natural History Museum collection, the Deschutes material, and the Kettle River population reveals that a considerable amount of variation may occur in the degree of development of the pseudocardinal teeth and muscle scars among comparable sized specimens. The ecological significance of this variation is unknown.

Conclusions. More detailed studies on variation in shell morphology and correlation of these data with ecological conditions are necessary before firm conclusions can be made based on paleontological or ethnomalacological material.

As noted previously, it is an unresolved problem as to how much of the variation in shell morphology of *Margaritifera* is attributable to age and how much to environmental factors. The lack of growth series and of adequate population samples makes most museum collections of little use in such studies.

DESCRIPTION OF THE STUDY AREA

The region in which our original observations were carried out is a part of the Cordilleran complex of the northwestern United States and southwestern Canada (Daly, 1912). The site is in a

stretch of the Kettle River adjacent to the property of Mr. Wallace Redelings in Sec. 20, T. 38 N., R. 37 E. about 1.5 miles west of Barstow, Stevens Co., Washington. It is readily reached via U. S. Highway 395 between Spokane and Laurier. Local inquiry is best made at Barstow.

The Kettle River originates in British Columbia in streams draining the Beaverdell Mountains. After uniting with the West Kettle at Westbridge, the stream flows southward to Rock Creek, turns eastward for a short distance, then makes a large U dipping below the 49th parallel to skirt the Midway Mountains. Near Grand Forks the Kettle is joined by the Granby and again flows eastward to Cascade. Here it turns once more southward through the upper part of the Kettle Valley, past Laurier (nearest U. S. G. S. gaging station to the study site), uniting with the Columbia some 27 miles southward. Between the 49th parallel and Marcus the Kettle River forms the western boundary of Stevens County.

Physiography. The Kettle Valley is generally narrow and deep, with mountains on either side rising rapidly to elevations varying between 4,000 and 5,000 feet. Alluvial terraces from 1/4 to 1 1/4 miles wide border the generally swiftly flowing river. The valley in the region of the study site is open and the stream just below the site describes several marked meanders. The elevation of Kettle River at Laurier is about 1,644 feet; the elevation at its junction with the Columbia is 1,260. Between the 49th parallel and the Columbia the river falls some 384 feet.

Geology. The rocks of Stevens County (Weaver, 1920) consist of a thick series of metamorphic and igneous units of indefinite age, some sedimentary deposits of Mesozoic and Tertiary ages, and horizontally bedded Quaternary sediments of glacial and fluvial origin. All of Stevens County has been glaciated and the deposits covering the older formations are largely moraines, presumably of Wisconsinan age.

Climate. Location on the western slope of

the Coeur d'Alene Mountains gives this region a climate with many characteristics of the continental interior and one entirely different from that of western Washington only 150 miles distant. The moderating influences of westerly winds from the Pacific is only slightly felt on account of the high Cascade Range to the west. The climatic data below are from Duyné and Ashton (1915) and Climate and Man, Yearbook of Agriculture, 1941 (1942).

Average annual precipitation at Colville, el. 1635 ft. (nearest meteorological station to the study site) is 16.51 inches. About one-third of this falls during the winter season. Maximum recorded rainfall was 32.83 inches in 1875; minimum rainfall was 8.84 inches in 1873. The average annual snowfall at Colville is about 40 inches. Maximum snowfall was 74.6 inches (no year given); minimum snowfall 23.4 inches in 1901. Snow remains on the ground longer and melts more slowly than in the area to the south.

Average temperature for the coldest month (January) at Colville is 24.6° F., for the warmest month (July), 69.6° F. The highest recorded temperature was 113° F., lowest 32° F., or a range of 145° F. Low temperatures are not as severely felt as would otherwise be the case due to low relative humidity. Even during the warmest months the nights are pleasantly cool. Daily range in temperature, both summer and winter, is much greater than in western Washington. Date of the last killing frost in spring averages May 10, but has occurred as late as August 24 at Colville. The first killing frost averages October 1, but has occurred as early as August 24. Upland areas are free from frost longer than the lowlands due to drainage of cold air into the valleys. The growing season is about 144 days.

There is considerable variation in prevailing wind direction due to topographic irregularities (SW at Colville, but NW at Republic). Tornadoes are unknown and thunderstorms are rare.

Hydrology. The drainage above Laurier is approximately 3,800 square miles. The North Fork is partly regulated by a reservoir at Grand

Forks, British Columbia. There are numerous diversions for domestic use and irrigation. The flow is again regulated slightly by the power plant at Cascade, and below this station there are small diversions for irrigation and domestic use.

Discharge. According to measurements at Laurier, the nearest gaging station to the study site, the average discharge (21 years, 1929-1950) is 2,696 cfs. Monthly figures for the period 1930 to 1960 are available in various U.S. Geological Survey Water Supply Papers. Minimum, maximum and annual figures for this period are summarized below. These show a monthly range between 77 cfs (Jan. 1930) and 18,070 cfs (May 1957) and an annual range between 1250 cfs (1930) and 4112 cfs (1948). May and June are generally the months of maximum discharge, May showing the greatest discharge for 22 of the 31 years during the period 1930-1960, and June showing the greatest discharge for 8 of the years during the same period. The extreme daily maximum during the period 1929-1950 was 35,000 cfs on May 29, 1948.

Chemical composition. No data are available for the study site. Analyses from the nearby Okanogon River (Van Winkle, 1914) from samples collected over the period from March 13, 1910 to January 16, 1911 inclusive show the following means: (parts per million unless otherwise stated)

SiO ₂	14	HCO ₃	81
FE	0.02	NO ₃	0.28
Ca	21	Cl	0.8
Mg	4.6	Dissolved solids	110
Na and K	8.5	Turbidity	25
CO ₃	0.0	Suspended matter	24

Drainage from the Okanogon highlands is over Paleozoic gneisses and schists, with some limestones and granite.

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