

OCCASIONAL PAPERS OF THE MUSEUM OF  
ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

UNIVERSITY OF MICHIGAN PRESS

A TAXONOMIC STUDY OF *QUADRULA QUADRULA*  
(RAFINESQUE)

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*QUADRULA QUADRULA* (Rafinesque) appears to be one of the most variable members of the Unionidae of North America. Its distribution is very wide and includes almost all tributaries of the Mississippi River, some parts of the Great Lakes and their tributaries, the Alabama River system, and various streams of eastern and central Texas. Variants have often been designated as separate species, especially in the southern parts of the range, where a highly variable form occurs. The recognition of such forms as species has resulted in confusion of their proper position and has not contributed to clarification of the unionid nomenclature. The present study was undertaken as an attempt to determine the relationships of the various forms and the validity of the names with which they have been blessed.

The material consisted entirely of shells in the collection of the Museum of Zoology, University of Michigan, which contains the most complete series of *Q. quadrula* that has been assembled. All areas of the range are represented, and all known forms are present. Specimens have been identified by various authorities, including Walker and Ortmann. A complete series of soft parts was not available, and it is doubtful

that studies of such a series would be of value with regard to such closely related forms. Percentage of obesity—the relationship of shell breadth to shell length—was computed for each specimen of every form and was judged to be of little value, since all forms exhibited practically identical ranges in this respect. For this reason, tables showing obesity measurements have been omitted. The most typical shell form is shown in Figure 1, and variations of this character are treated

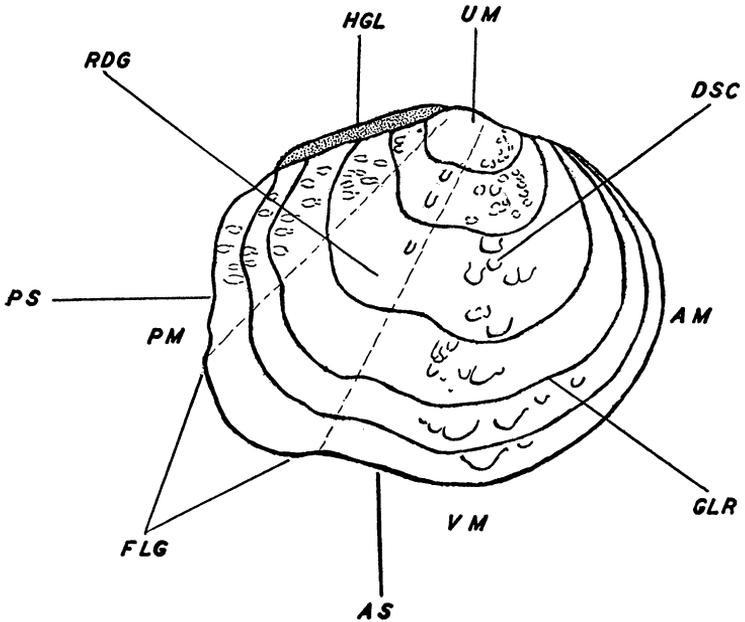


FIG. 1. Typical shell of *Q. quadrata* showing parts referred to in text. *AM*, anterior margin; *AS*, anterior sinus; *DSC*, disk; *FLG*, flange; *GLR*, growth rest; *HGL*, hinge ligament; *PM*, posterior margin; *PS*, posterior sinus; *RDG*, ridge; *UM*, umbo; *VM*, ventral margin.

as to the respect in which they differ from this form. Thorough examination of the hinge teeth disclosed no special characteristic for any form. Furthermore, beak sculpture was found here to be a very unreliable guide, since much erosion occurs and true sculpture may be easily confused with small tubercles that are often situated upon the umbonal areas.

It is rather difficult to determine just what characters earlier authors considered of greatest value when applied to the forms of *Q. quadrula*, although it is evident that they placed emphasis upon shell form, which may have been instrumental in the recognition of so many species. However, they described no shell form beyond the range of variation of the more typical *Q. quadrula*. They apparently emphasized extreme forms which were perhaps quite distinct from their concept of *Q. quadrula*.

*QUADRULA QUADRULA* (RAFINESQUE)

*Obliquaria (Quadrula) quadrula* Rafinesque 1820

*Unio rugosus* Barnes 1823

*Unio lacrymosus* Lea 1828

*Unio asperrimus* Lea 1831

*Unio quadrulus* Rafinesque 1835

*Unio fragosus* Conrad 1836

The most typical shell form is shown in Figure 1. The two sinuses are separated by the posterior ridge, although sinuses and ridge may both become indistinct if the shell is rounded or flattened in this area. The flange may become greatly attenuated in very old individuals, and the slope of the posterior margin may appear less steep, but younger growth-rests show that such shells possessed the more typical outlines earlier in their life history. The beaks are distinct, but usually fail to project above the hinge ligament; the anterior sinus is usually completely smooth, and is typically bounded, front and rear, by a row of large tubercles.<sup>1</sup> The nodules are characteristically tear-shaped, but may project sharply outward. Pustules are nonuniform in size and often become confluent and form costae near the posterior margin; these may end in large tubercles on the ridge, which may be either smooth or costate. The larger tubercles tend to occupy the disk region, and all tubercles vary considerably in size in different shells. The epidermal color may be green, dark brown, or straw yellow; rays seldom occur, and if present are obscured by tubercles. The nacre is pearly white and usually iridescent near the posterior margin.

<sup>1</sup> The terms nodule, pustule, and tubercle are used interchangeably.

A large amount of variation is no exceptional occurrence in any widespread species, and so can hardly be considered unusual in *Q. quadrula*. The designation of variants as species or subspecies merely clogs the literature with superfluous names. Shell form and the size and distribution of tubercles have quite a large range of variation, and the occasional occurrence of extremes of both in one individual offers little support for the recognition of a separate species. Such a form of *Q. quadrula* was described as *Unio fragosus* by Conrad in 1836, and this concept is still retained by some modern authors.

All recognizable forms of *Q. quadrula* have very definite distributions in the southern half of the range, and occur nowhere outside those areas. *Q. fragosa* (?), on the other hand, has a very sporadic distribution in the Mississippi Valley, and the Museum of Zoology collection indicates that very few individuals occur at any given locality, since large lots never contain more than one or two specimens that might be called *fragosa*. As represented in Plate I, Figures 1 and 4, *fragosa* is simply a truncate or rounded form of *Q. quadrula*; the pustulation may be slightly heavier than usual, but such pustules often occur on shells of the more characteristic shape. Figure 4 in Plate I closely resembles Conrad's figure (1836: Pl. 6, Fig. 2) of his type specimen. Figure 1 of Plate I represents a possible intermediate between this form and the more typical *Q. quadrula*; however, the roundness of this form is accentuated by lateral swellings, and the traced outline of Figure 4 differs little from that of a shell of the usual type. This form, *fragosa*, may represent extreme variation, but must be included with the highly variable *Q. quadrula*.

QUADRULA QUADRULA APICULATA (SAY)

- Unio apiculatus* Say 1829
- Unio asper* Lea 1831
- Unio rumpbianus* Lea 1852
- Unio nobilis* Conrad 1854
- Unio blandianus* Lea 1856
- Unio forsheyii* Lea 1859
- Unio speciosus* Lea 1862
- Unio conjugans* B. H. Wright 1899

This form of *Q. quadrula* is distributed from the northeastern tributaries of the Alabama River to central Texas and southward to the Gulf of Mexico. This area also contains *Q. quadrula*, but *Q. apiculata* appears to be the dominant form. It is itself very variable, and some of its extremes have been designated as separate species, probably because the first descriptions were based upon isolated specimens from widespread areas. However, in the present large series, a complete series of intermediates is evident in every instance, which definitely links each extreme with the others and the assemblage of forms of *Q. apiculata* with those of *Q. quadrula*. The two forms *quadrula* and *apiculata* differ only in size and arrangement of tubercles, *apiculata* having small tubercles and a completely pustulate anterior sinus, whereas the first sinus in *quadrula* is smooth or has very few tubercles near its ventral margin. Despite its large amount of variation, *apiculata* never loses the pustules from the anterior sinus, even though other regions of the shell are often quite smooth. Tubercles in this form are generally uniform in size on all parts of the shell. Intergradation between the two forms is clearly shown in Plate I, Figures 2, 3, 5, and 6. Specimens of *quadrula* have often been mistaken for some of the forms of *apiculata*, but such errors were probably caused by assumptions of restricted geographical range that excluded *quadrula* from regions south of the Tennessee River.

The subspecies *apiculata* contains three recognizable variants that are treated here as phases. These are *aspera*, *apiculata*, and *rumphiana*, each named according to the specific title it first bore. The *aspera* phase is the basic and most widely distributed form; the others are clearly variants of it. For this reason, it would be desirable to use *aspera* as the subspecies name, but *apiculata* has priority.

In the *aspera* phase the shell is completely covered with small, smooth tubercles that are arranged in rows having a zigzag course along the length of the shell; each row forms an inverted W, the rear arm of which is usually continued into one of the costae near the posterior border. This orderly

arrangement is often disrupted by increase in size of tubercles on the disk and may become indistinct when the nodules are fine and extremely numerous. Shell form usually corresponds to the type shown in Figure 1, but may be considerably shortened, as shown in Plate I, Figure 5. Other examples are shown in Plate I, Figures 8 and 9. Periostracum color varies from yellow to brown, green, or black; rays are uncommon and are usually obscure. This phase evidently occupies the entire range of *apiculata*, although other phases may be more numerous in restricted areas.

The phase *apiculata* represents the form described by Say and is distributed from Louisiana to central Texas. Shell form varies considerably here, ranging from a thick form with distinct sinuses (Pl. I, Fig. 10) to flattened shells with obliterated anterior sinus and high, sharp ridges (Pl. I, Fig. 11). This latter form is the *Unio speciosus* of Lea, 1862. This phase possesses extremely fine pustules, and the epidermal color is usually gray. Arrows in Plate I show the manner of its intergradation with the *aspera* phase.

The *rumphiana* phase (Pl. I, Fig. 12) occurs in the Alabama River system and, though quite distinct, intergrades markedly with the *aspera* phase. The two phases and their intermediates often occur in the same locality (Pl. I, Figs. 5, 9, 12). In *rumphiana* the flange and ridge are devoid of tubercles and stand out distinctly; the pustules are smooth and somewhat flattened, and are usually absent near the anterior shell border. The periostracum is usually straw yellow and quite shiny. The loss of tubercles on the ridge and flange is not confined to this phase, the smooth ridge being occasionally found on specimens from localities other than the Alabama River or its tributaries. However, these individuals lack the distinctive *rumphiana* pustulation, and the pustules are noticeably indistinct on most parts of the shell (Pl. I, Fig. 7, McLennan County, Texas).

When their inability to recognize intergradation in their limited material is considered, it is not remarkable that earlier authors divided *Q. quadrula* into so many separate species. These species were recognized until 1927, when Frierson placed

them as subspecies of *Q. quadrula*. Strecker (1931) supports this concept, though he fails to mention characteristics that enabled him to separate the various subspecies. He was apparently undecided about their relationship in some instances, and questioned the distinctness of some forms, since they seemed to intergrade with others and their juveniles were inseparable.

Say (1829), describing *apiculata*, was aware of its relation to *Q. quadrula* and indicated that on the basis of more extensive collection it could doubtlessly be proven to be a variety of that species. Tuberculation is the only reliable character that may be employed to separate the forms of *Q. quadrula*, and they are definitely shown to intergrade when judged upon this basis. Therefore, there is slight cause for the recognition of more than one subspecies, and the variety *apiculata* may be so recognized only because it retains its most distinctive feature despite a large amount of variation and is the dominant form in the southern portion of the geographical range of *Q. quadrula*. The three phases described above are indicative of the amount of variation that occurs within this form.

The evidence acquired in this study shows *Q. quadrula* to be a very variable, widely distributed species. When examined separately, some of its extreme variants from widely separated areas on the border of the geographical range appear to differ greatly from the usual form, but a complete series of intermediates definitely links all such forms to *Q. quadrula*. Therefore, it appears unnecessary to name more than one subspecies, *apiculata*, the dominant form in the South.

The author is indebted to Calvin Goodrich and Henry van der Schalie for criticism and for use of material, and he wishes to thank Grace Eager for preparation of the plate.

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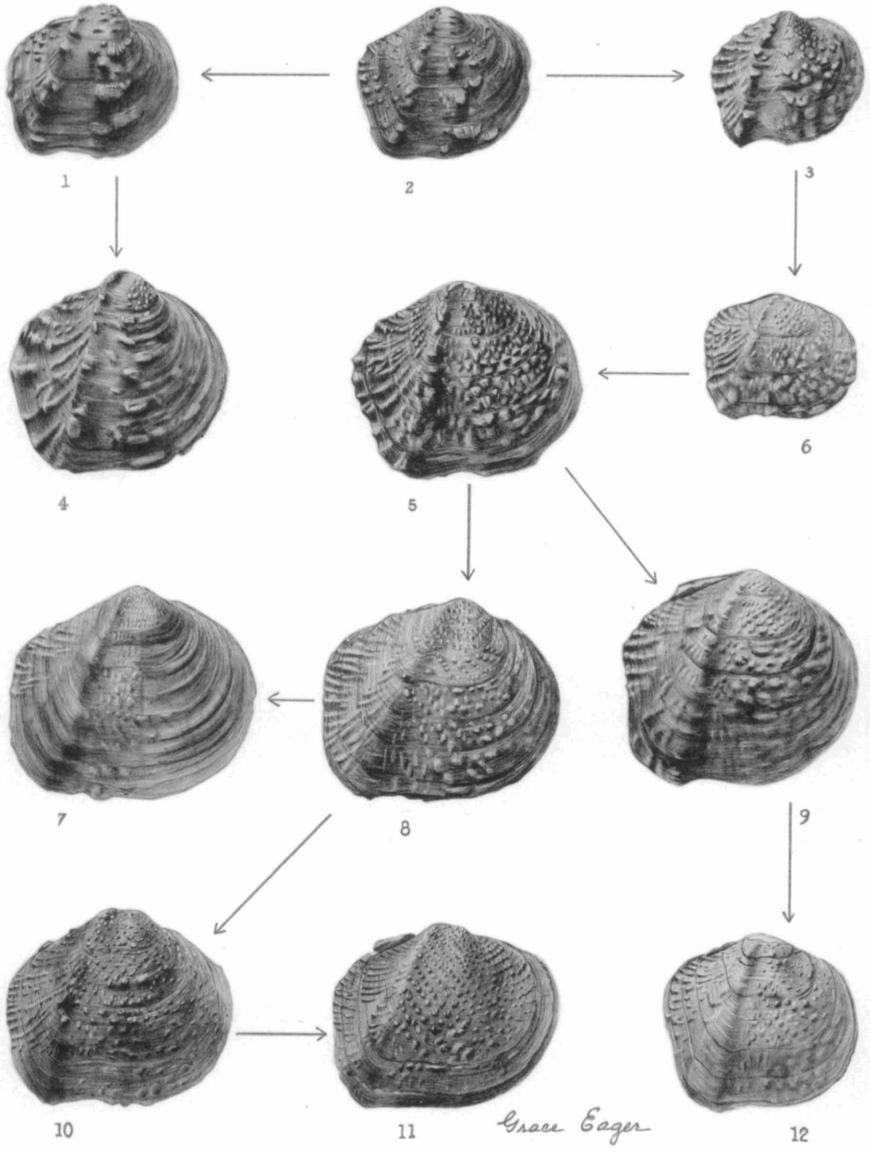
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#### PLATE I

- FIG. 1. *Q. quadrula*.  
 FIG. 2. *Q. quadrula*.  
 FIG. 3. *Q. quadrula*.  
 FIG. 4. *Q. quadrula* (*fragosa*?).  
 FIG. 5. *Q. quadrula apiculata*, *aspera* phase.  
 FIG. 6. *Q. quadrula apiculata*, *aspera* phase.  
 FIG. 7. *Q. quadrula apiculata*, *aspera* phase.  
 FIG. 8. *Q. quadrula apiculata*, *aspera* phase.  
 FIG. 9. *Q. quadrula apiculata*, *aspera* phase.  
 FIG. 10. *Q. quadrula apiculata*, *apiculata* phase.  
 FIG. 11. *Q. quadrula apiculata*, *apiculata* phase.  
 FIG. 12. *Q. quadrula apiculata*, *rumphiana* phase.



Grace Eager

