

# The Lee Creek Enigma, *McLellania aenigma*, a New Taxon in Fossil Cirrhipedia

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## ABSTRACT

An enigmatic fossil, *McLellania aenigma* Wilson, new subfamily (Balanidae: McLellaniinae), genus, and species, found embedded in the shell of the bivalve *Mercenaria*, occurs in the Pliocene Croatan Formation of Lee Creek, in strata of Yorktown age in North Carolina, Virginia, and Florida, and in the Miocene Choptank Formation of Maryland. The enigmas are calcitic in contrast to the aragonitic shells of *Mercenaria*. The pattern of growth shows that they are produced in the living shell and are not a result of subsequent diagenetic fossilization. Because of characters in common, they are considered to be thoracican cirripeds, probably parasites. A nomenclatorial revision of the principal host-*Mercenaria* species resurrects *Mercenaria corrugata* (Lamarck, 1818).

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## Introduction

An unknown, unidentifiable organism rarely remains an enigma once its habitat is known. Not so in the case of the Lee Creek "curiosities." Specimens of these fossils were first collected as discrete float at Lee Creek and sent to the Smithsonian Institution by Jack McLellan of Texasgulf Inc. They were passed around to paleontologists and finally dismissed by most as not, or probably not, organic. Some of us, however, remained sus-

picious or convinced that they were indeed organic. Later Blake Blackwelder saw a specimen fall from the interior of a shell of a fossil clam, *Mercenaria*, which he was washing. It had been embedded in the shell. Fortunately this shell was not float; it came from a collection made by the author from the Croatan (or upper) shell bed. At this time anyone who would look and hazard an opinion was asked to comment. Despite their interest and amazement, no one could recollect having seen a comparable living or fossil organism. Some, accepting the organic derivation of the specimens, maintained that these fossils were not an entity separate from the *Mercenaria*.

The specimens, eventually dubbed "enigmas," are conical or subconical calcareous bodies composed of alternate light and dark layers; the conical surface has a crystalline appearance, which contributed to the consideration that they might be inorganic. The opposite, subplanar, surface is slightly concave and more or less smooth. The specimens are about evenly divided between "singles" and "multiples," which comprise more than one individual and are described as "aggregates." A certain likeness between the alternate light and dark layers of the enigmas and the bases of some fossil barnacles is apparent. Thus, the possibility that the enigmas were calcitic (like most thoracican cirripeds) rather than aragonitic (like the shell of *Mercenaria* and many other mollusks, both bivalves and gastropods), prompted me to discuss the determination of the mineralogy of the specimens with Zalman Altshuler. Subsequently Cristina Silber made determi-

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nations of five subsamples from different areas of a single specimen (USNM 304379). The results revealed only calcite. The presence of calcite in both cirripeds and the enigmas was interesting and provocative, but it did not rule out the possibility of production by genetically altered mercenarias, pathologic microorganisms infecting the clams, or diagenesis within the *Mercenaria* shells during fossilization. One fact seems contraindicative to genetic production of enigmas. The enigmas are paired in neither of the only two specimens of double-valved "infected" mercenarias. Paratype USNM 305117 has an enigma only in the left valve of the pair. Paratype USNM 305126 has unpaired aggregates in both valves. It would be highly unusual if genetically produced characters in each valve were not mirror images.

At the first opportunity, a search was made for enigmas in specimens of *Mercenaria* from the Croatian Formation at Lee Creek, but none were found. Later, all mercenarias in the Cenozoic systematic collection were searched and in those of Yorktown age many enigmas were found. Further search in related stratigraphic collections turned up still more examples. In all, some forty specimens have been recovered.

All mercenarias in the collection of Recent mollusks in the USNM collections were examined, but no enigmas were found. Although museum specimens of *Mercenaria* are numerous, eventual discovery of living enigmas is not precluded. They should be searched for in large populations of living *Mercenaria* at the southern limits of its range. It is known that Yorktown age beds contain warmer water assemblages than the Recent faunal assemblages in the same latitudes. Jung (1977:846–847) has reported a Pinecrest (Yorktown age) species, *Trigonostoma (Extractrix) hoerlei* Olsson, of Florida, from the Pliocene of Venezuela, which had already been reported in the Yorktown Formation by Campbell et al. (1975:114) from as far north as Chuckatuck, Virginia. The Pinecrest has a large faunal assemblage of decidedly warm water affinities.

One of the specimens (USNM 305107) (Plate 2: figure 2) from the Yorktown of North Carolina

shows beyond any doubt that the enigmas were produced in the mercenarias during life. The normally expanding growth of the pallial sinus of the *Mercenaria* has overrun an edge of a large enigma. Further consideration of diagenesis as producing the enigmas seemed unnecessary.

Parts of the early noncalcareous (cyprid) stage of Recent barnacles have been found preserved beneath their adherent bases, according to Newman, Zullo, and Withers (1969:217). The chance of their occurring as fossils under the conical basis of an enigma is probably remote. However, a consideration of the amino acids of major higher taxa may also support the conclusion reached here. Each major higher taxon produces its own characteristic amino acids, which may be preserved in fossilized hard parts of organisms. An analysis might determine whether or not the enigmas contain arthropodan amino acids.

No parallel has been inferred between the "cancerous panopes" that occur in the Choptank Miocene of Maryland and enigmas. Some specimens of *Panopea americana* (Conrad) contain conspicuous, dark, amorphous, calcareous masses protruding from under the umbones inside their shells. Cristina Silber (pers. comm.) has determined by X-ray diffraction that the dark amorphous mass is composed of calcite. *Panopea* is one of the bivalves whose shell is aragonitic. A sectioned shell (USNM 305105) shows that the mass was produced during the life of the panope. No explanation of this interesting anomaly has been deduced.

The parallel between certain balanid cirripeds and the enigmas led to a search of the cirriped literature. An illustration (Darwin, 1854, pl. 9) of species of the balanid genus *Acasta* led to specimens of *Acasta cyathus* Darwin in the Smithsonian collection of Recent cirripeds. The basis of *Acasta cyathus* (Plate 1: figure 11) was indeed a homologue of the enigmas. Morphologically they were too much alike to be coincidental. According to Darwin (1854:305), species of *Acasta* not only are embedded in, but are attached to, the fibers of sponges. Thus, the enigmas and the bases of species of *Acasta* are morphologic and functional

equivalents. They are both attached to and embedded in their respective host-organisms: *Acasta* in sponges and *McLellania* in *Mercenaria*.

The enigmas occur in three species of *Mercenaria* from as many geologic horizons. One specimen has been found in *Mercenaria cuneata* (Conrad) from the Choptank Miocene of Maryland and only one in *Mercenaria permagna* (Conrad) from the Croatan Pliocene from Lee Creek, North Carolina. All other specimens are from strata of Yorktown age from Virginia, North Carolina, and Florida. Inasmuch as the search failed to yield additional specimens in Croatan mercenarias, it is assumed that the numerous float specimens at Lee Creek came from the more or less leached beds of the Yorktown Formation; the enigmas being calcitic like ecphoras, oysters, pectens, and barnacles commonly found well preserved in these beds. In the Yorktown strata the enigmas occur in *Mercenaria corrugata* (Lamarck) and in its "tridacnoides" variant. Since this species is the principal host of the enigmas and the name *corrugata* is used here in an American study for the first time, it is necessary to explain its resurrection.

**RESURRECTION OF *Mercenaria corrugata* (LAMARCK).**—Lamarck (1818:558) described two species of fossil bivalves, *Cyprina corrugata* and *Cyprina tridacnoides*, in that order (his Cyprines 4 and 5), both then thought to be from Italy. Under *C. tridacnoides*, Lamarck augmented his description by reference to a figure in Lister (1692, pl. 499: fig. 53). The name is so apt that it might have been possible to recognize the distinctive American fossil, presently known as *Mercenaria tridacnoides*, without the figure. These large heavy shells with conspicuous, broad undulations, otherwise totally unknown in the genus *Mercenaria*, are widely regarded as an "abnormal" or "pathological" form. They occur with the more common *Mercenaria rileyi* (Conrad, 1838), which is always regarded as the "normal" form. These two forms are undoubtedly closely related. Thus, the necessity of using the historically prior name of an "abnormal" variant as the name of the species has resulted occasionally in rather strained circumlocutions in order to avoid just that. Where-

as Gardner's unrealistic arrangement (1943:130–133) is neither nomenclatorially nor genetically defensible, Dall (1903:1310–1311), followed by Palmer (1927:399), had earlier used *tridacnoides* as the specific name.

Favre (1914, pls. 16–19) in his illustrations of the type specimens of Lamarck's fossil invertebrates, figured both *Cyprina corrugata* and *Cyprina tridacnoides*. According to Favre the specimens of both had the original labels of Lamarck. *Cyprina tridacnoides* is represented by a monotype (holotype). The two specimens (syntypes) of *Cyprina corrugata* were recognized by Favre as American fossils and identified as *Venus mortoni* Conrad, 1837 (Favre, 1914, pl. 16: fig. 91) and *Venus rileyi* Conrad, 1838 (Favre, 1914, pl. 17: fig. 92). The specimen identified as *Venus mortoni* has "Cyprine ridée," Lamarck's 1818 vernacular for the species, written on the shell. The other specimen has "Cyprina corrugata" written on it, which shell also has the measurement given in the original description (Lamarck, 1818:558); thus it (Favre, 1914, pl. 17: fig. 92) is the obligatory lectotype of *Cyprina corrugata* Lamarck, here designated. Concomitant with this action, *Cyprina corrugata*, numerically prior, is given absolute priority over *Cyprina tridacnoides* in exercise of my right as first revisor. The name of the species formerly known as *Mercenaria tridacnoides rileyi* then must become *Mercenaria corrugata* (Lamarck). As a convenience the informal term *Mercenaria corrugata* "tridacnoides" is used for the statistically important, striking variant of *Mercenaria corrugata* (Lamarck), which appears to be the most common host of *McLellania aenigma*. This is in conformity with the rule of the code of zoological nomenclature that variations cannot be formally recognized.

One further note on the nomenclature: until the question of the type-species of *Venus* was settled by the International Commission on Zoological Nomenclature (Opinion 195) in 1954, the genus here referred to as *Mercenaria* was more commonly known as *Venus*. It follows that the *Venus corrugata* of Gmelin 1790 has priority over the species in question only so long as the taxa concerned are referred to *Venus*; with the transfer



to *Mercenaria*, the rule of homonymy no longer applies.

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### Systematics

Class CIRRHIPEDIA Rafinesque, 1815

Order THORACICA Darwin, 1854

Suborder BALANOMORPHA Pilsbry, 1916

Family BALANIDAE Leach, 1817

Subfamily MCLELLANIINAE, new subfamily

Solid, calcitic basis, either single or aggregate of anastomosed individuals, embedded in fossil shells of the bivalve *Mercenaria*; embedment results from simultaneous growth of basis and host-*Mercenaria*. Hard parts of capitulum unknown; probably obsolete.

### Genus *McLellania*, new genus

Type-species.—*McLellania aenigma*, new species.

The description of the species serves for both genus and species inasmuch as the genus is monotypic.

### *McLellania aenigma*, new species

PLATE 1: FIGURES 1–9; PLATES 2, 3

DESCRIPTION OF HOLOTYPE.—Small, solid, conical, layered, calcitic basis; in living position, apex down. Upper surface of basis slightly concave, xenomorphic, preserving the contour of the inner surface of the *Mercenaria*, which contains just under its umbo the locus from which the basis came; the basis fitting precisely in the concavity of the locus. Basal surface of a crystalline appearance. Layers rapidly expanding and alternately light and dark. Radial markings of the basal surface formed by minute indentations in the edge of each succeeding layer; markings not expanding in size but new indentations regularly intercalated, producing a uniform appearance from the initiation of the earliest markings to the latest.



Other fewer, heavier, radial indentations beginning at the apex become obsolete or shallow and account for the irregular sinuosity of the overall subcircular outline of the basis. With the apex up, each expanding layer producing a steplike appearance on a microscopic scale.

**DESCRIPTION OF AGGREGATE PARATYPES.**—Almost half of the paratypes are aggregates, specimens made up of two or more anastomosed individuals. Their basal surfaces show the initial areas of the individuals and their subsequent impingement upon each other, but their upper surfaces are so completely anastomosed that they appear to be one individual if seen from above. The aggregate paratypes are all larger than the holotype, and in most specimens the layers expand even more rapidly than in the smaller single individuals. The markings are the same as described for the holotype, but in its larger aspect, an aggregate is more like a topographic model in miniature (Plate 1: figure 7).

**DISCUSSION.**—The definitive description is limited to the holotype, the only specimen once embedded in a *Mercenaria* that has not been forcibly removed. This is the specimen that dropped from the *Mercenaria* during washing (p. 483). It is unique in that the demarcation between the enigma and the host-*Mercenaria* is sharply defined. It is consequently more easily described than paratypes later removed from the mercenarias. These paratypes were firmly embedded in the shells, and none has been removed without difficulty and some damage to the enigma and the *Mercenaria* shell.

The form of the enigma basis is inherently functional; the details and form of the locus in the *Mercenaria* are responsive and the juxtaposition of the *Mclellania* basis with the *Mercenaria* produces xenomorphism in both. The upper surface of the enigma takes the form of the inner surface of the *Mercenaria*, and the shell surrounding the cavity of the locus preserves in minute detail the form and exterior sculpture of the basal surface of the *Mclellania*. Production of this isochronous xenomorphism requires simultaneous growth of both organisms.

Some *Mercenaria* shells contain two enigmas, sometimes two singles, sometimes mixed singles and aggregates, and one contains two aggregates. Some small specimens are so close to each other or to aggregates that they might have become aggregates or parts of other aggregates if growth had continued. A massive aggregate (Plate 2: figure 2) seems to have been formed of several anastomosing aggregates.

The enigmas are found embedded anywhere in the mercenarias above the pallial line, but the preferred position seems to have been in juxtaposition to the anterior adductor muscle of the left valve of the mercenarias (see p. 490). The significance of this preference has not been deduced. One float specimen (USNM 304381) (Plate 1: figure 8) appears to have lived high under the umbo of a *Mercenaria* in space so constricted that it curled back upon itself. The largest paratype (USNM 305107) and most important specimen, other than the holotype, is the massive aggregate which covers 90 percent of a left valve of *Mercenaria* above the pallial line. The normally expanding growth of the pallial sinus of the *Mercenaria* has overrun an edge of the enigma (Plate 2: figure 2). In cross-section (Plate 3) the calcitic layers of the enigma and the aragonitic layers of the *Mercenaria*, superficially, appear to be continuous. However, under magnification a dark layer shows a definite lag and few of the layers are precisely continuous. Both the enigma and the *Mercenaria*, ipso facto, are subject to the same environmental conditions. The lag may indicate that the enigma received its sustenance through the *Mercenaria*.

The enigmas did not fill cavities or depressions in the mercenarias, but they were produced layer by layer at the same rate, probably no more than one layer ahead of the layers of the *Mercenaria* shells. This would be sufficient to prevent the mercenarias from overrunning the enigmas. Some specimens and also a section (Plate 2: figure 2) indicate that the effort to overrun the enigmas may have been more or less constant. In the cross-section, the *Mercenaria* layers are seen to have impinged upon the initial stage of the enigma to

the extent that its width is very much reduced (Plate 3: figure 2). Some enigmas that have been removed from the mercenarias and some of the free-float specimens have white shell that appears to be the aragonitic layers of the mercenarias impinging upon, and caught between, the edges of the layers of the enigmas.

**MEASUREMENTS.**—The shapes of large specimens of *Mclellannia aenigma* are so ill-defined because of their various locations in the *Mercenaria* that measurements are not particularly meaningful. A few, including the figured aggregate paratype USNM 305107 (Plate 2: figure 2; Plate 3), encompass so much of, or are so spread out over the inner surface of, the shells that even surface measurements are not possible. Measurements of the holotype, the float paratypes, some paratypes that have been removed from their mercenarias, and some surface measurements of a few paratypes still in their mercenarias are given in Table 1.

TABLE 1.—Measurements (mm) of types of *Mclellannia aenigma* (aggregate indicates two or more enigmas occur in one *Mercenaria* and have same catalog number; dash indicates measurement could not be taken because specimens are embedded)

USNM	Greatest diameter	Smallest diameter	Thickness
<b>HOLOTYPE</b>			
304378 (single)	9.5	9.3	3.0
<b>PARATYPE</b>			
304379 (aggregate)	39.2	34.7	8.7
304380 (aggregate)	43.8	29.6	6.6
304381 (aggregate)	26.4	20.4	5.3
304382 (single)	11.8	10.3	2.7
304383 (aggregate)	31.7	23.1	6.4
304384 (aggregate)	43.2	26.6	4.3
304385 (single)	21.8	19.6	5.2
305106 (aggregate)	21.7	16.7	7.0
305108 (single)	13.5	7.9	
305120 (aggregate)	30.7	28.6	5.3
(single)	11.7	10.4	—
305121 (aggregate)	23.7	15.3	
(single)	7.3	6.4	
305122 (aggregate)	50.3	25.3	4.6
305125 (aggregate)	21.3	19.3	~ 3.0

**TYPES AND OCCURRENCES.**—The specimens (primary types) of *Mclellannia aenigma* have been found from Maryland to Florida with by far the greater number in Virginia and North Carolina. The following catalog of the types details the occurrences in the host-*Mercenaria* species and the localities. An “infected” *Mercenaria* and its enigma(s) have been given the same catalog number. USNM 304378 is the holotype; all others are paratypes.

USNM 304378 (single), in left valve of *Mercenaria permagna*: top 1.5 feet (0.46 m) of upper shell bed, north wall, Texasgulf Inc., Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina; Croatan Formation (Plate 1: figures 1–4).

USNM 304379 (aggregate, Plate 1: figures 5–6), 304380 (aggregate, Plate 1: figure 7), 304381 (aggregate, Plate 1: figure 8), 304382 (single, Plate 1: figure 9), 304383 (aggregate), 304384 (aggregate); all float: Texasgulf Inc., Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina; probably Yorktown Formation.

USNM 304385 (single), float: Snell Island fill (USGS 21900), dredged from Tampa Bay, Pinellas County, Florida; occurs with Yorktown assemblage.

USNM 305106 (aggregate), float: Texasgulf Inc., Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina; probably Yorktown Formation.

USNM 305107 (aggregate), in left valve of *Mercenaria corrugata* “tridacnoides”: 15 miles (24.14 km) above Bell’s bridge, Tar River, Edgecombe County, North Carolina; Yorktown Formation (Plate 2: figure 2; Plate 3).

USNM 305108 (single), in right valve of *M. corrugata* “tridacnoides”: 4 miles (6.44 km) northwest of Williamston, Martin County, North Carolina; Yorktown Formation (Plate 2: figure 1).

USNM 305109 (aggregate), 305110 (aggregates), in right valves of *Mercenaria corrugata*:  $\frac{3}{4}$  mile (0.89 km) north of Grimesland, Pitt County, North Carolina; Yorktown Formation.

USNM 305111 (single), in left valve of *M. corrugata* “tridacnoides”: Tar River, right bank of Boyd bridge about one mile (1.61 km) north of Grimesland, Pitt County, North Carolina (USGS 11835); Yorktown Formation.

USNM 305112 (single), in left valve of *M. corrugata*: Shiloh Mills, Edgecombe County, North Carolina; Yorktown Formation.

USNM 305113 (aggregate), in right valve of *M. corrugata*:  $1\frac{1}{2}$  miles (2.41 km) west of Greenville, Pitt County, North Carolina; Yorktown Formation.

USNM 305114 (two aggregates), in left valve of *M. corrugata*: 3 miles (4.83 km) southwest of Frog Level, Pitt

County, North Carolina; Yorktown Formation.

USNM 305115 (single), in left valve of *M. corrugata*: upper bed, Alum Bluff, Liberty County, Florida; Jackson Bluff Formation.

USNM 305116 (single), in left valve of *M. cuneata*: Choptank River, Caroline County, Maryland; Choptank Formation.

USNM 305117 (single), in left valve of pair of *M. corrugata* "tridacnoides": Bed C, Moore House, York River, York County, Virginia (USGS 24029); Yorktown Formation.

USNM 305118 (single), 305119 (single), in left valves of *M. corrugata* "tridacnoides": Lieutenant Run, Petersburg, Virginia; Yorktown Formation.

USNM 305120 (single and aggregate), in right valve of *Mercenaria* sp.: Sunken Marsh Creek, James River, Surry County, Virginia; Yorktown Formation.

USNM 305121 (single and aggregate), in left valve of *M. corrugata* "tridacnoides": Grove Wharf, Surry County, Virginia (USGS 2452); Yorktown Formation.

USNM 305122 (single and aggregate), in left valve of *M. corrugata* "tridacnoides": Lieutenant Run, Petersburg, Virginia; Yorktown Formation.

USNM 305123 (single and aggregate), in right valve of *M. corrugata*: Suffolk, Nansemond County, Virginia; Yorktown Formation.

USNM 305124 (two singles), in left valve of *M. corrugata* "tridacnoides": 2½ to 3 miles (4.02 to 4.83 km) below Seaboard Railway bridge, Sycamore, Southampton County, Virginia; Yorktown Formation.

USNM 305125 (two singles), in right valve of *M. corrugata*: Sycamore, Southampton County, Virginia; Yorktown Formation.

USNM 305126 (aggregates), in both valves of *Mercenaria* sp.: Yorktown, York County, Virginia; Yorktown Formation.

USNM 305127 (aggregate), in left valve of *M. corrugata*: Yorktown, York County, Virginia; Yorktown Formation.

USNM 305128 (single), in right valve of *Mercenaria* sp.: Yorktown, York County, Virginia; Yorktown Formation.

USNM 305129 (aggregate), in right valve of *M. corrugata*: Yorktown, York County, Virginia; Yorktown Formation.

USNM 305130 (single), in left valve of *M. corrugata* "tridacnoides": Yates cut, unit 3, College of William and Mary campus, Williamsburg, Virginia; Yorktown Formation.

USNM 305131 (single), in left valve of *M. corrugata* "tridacnoides": Golf course, Williamsburg, Virginia; Yorktown Formation.

**GEOLOGIC RANGE.**—The oldest occurrence of *Mclellania aenigma* is the single specimen from the Choptank Formation, Miocene, of Maryland; the youngest is the single specimen from the Croatan

Formation, Pliocene, at Lee Creek. These two occurrences thus span the occurrence of the greater number of specimens from localities that fall in the Yorktown Formation or its equivalents. The age of some of these is based on the presence of the host-*Mercenaria* species *M. corrugata* "tridacnoides" here regarded as indicative of Yorktown age strata. All reports of occurrence of this variant outside these beds are based on single specimens of repaired broken valves. The Yorktown Formation, once the classic late Miocene of the Coastal Plain and based on faunal comparison with the European late Miocene, is regarded currently by micropaleontologists as Pliocene in age. The range then is Neogene; Neogene of the original definition, Miocene-Pliocene, i.e., late Tertiary.

An organism comparable to *Mclellania* may have existed in the Cretaceous. My colleague, Norman F. Sohl of the U.S. Geological Survey, has shown me his manuscript illustration of a depression of unknown origin in a Cretaceous oyster, which is reminiscent of the loci in mercenarias from which enigmas have been removed.

**DATA OF UNKNOWN SIGNIFICANCE.**—The hypodigm of *Mclellania aenigma* consists of the holotype and 40 paratypes, eight of which are free-float from the Lee Creek Mine and Florida. These eight specimens, six aggregates and two singles, contribute nothing to the data assembled here. These data are concerned with various aspects of the occurrence of the enigmas in the mercenarias. The other 33 paratypes occur embedded in 26 mercenarias from many localities. Unfortunately, only 2 of the 26 are complete: one (USNM 305126) has an aggregate enigma in each valve; the other (USNM 305117) is "infected" in only one valve, a single enigma in the left valve. Thus, the two complete mercenarias with the three enigmas, two in left valves and one in a right valve, exhibit the skew that is apparent in the remaining 24 "infected" unpaired valves. Of these, 9 are right valves and 15 are left valves. One of the components, 13 enigmas in 10 valves of *Mercenaria corrugata* "tridacnoides" has an even more pronounced skew toward left valves; 9 left



valves (with 12 enigmas) to one right valve (with one enigma). In contrast, the 13 enigmas in 11 valves of the nominate species, *M. corrugata*, are divided thus: 7 enigmas in 6 right valves to 6 in 5 left valves, an unremarkable proportion except in contrast to those in the "tridacnoides" variant. This suggests a relationship between the "tridacnoides" variant and left valves, a relationship which also extends to the enigmas embedded in juxtaposition to the anterior muscle scars of the mercenarias. This is the preferred locus of 13 out of 33 of the enigmas "infecting" the 26 mercenarias. In this case, the 13 enigmas occur in 13 valves, 9 of these valves are the variant and 4 are the nominate *M. corrugata*; 11 of the 13 are left valves and only 2 are right valves. We may be dealing with three interdependent variables: (1) the "tridacnoides" variant, (2) predisposition to left valves and (3) preference for juxtaposition to the anterior adductor muscle. In fact this combination is present in one of the two complete mercenarias. This specimen (USNM 305117), *M. corrugata* "tridacnoides," has an enigma in juxtaposition to the anterior adductor muscle scar of its left valve. It has been assumed that in the "populations" (thanatocoenoses) from which these specimens came that the numbers of right and left valves of these heavy shells are about equal. The equally (or more) important proportion of the variant "tridacnoides" (10 in the present collection) to the nominate species (11 in the collection), however, cannot be assumed. These data, based for the most part on unpaired valves, are interesting, but their significance is elusive, and they may or may not be validated by future collections containing many more complete specimens. Up to now, no mercenarias have been collected for the enigmas; their collection has been fortuitous.

If *Mclellania* eventually is discovered living, its soft anatomy, living habits, and life cycle may help explain these data and give answers to other interesting, and as yet unanswered, questions, such as the nature of the relationship of the individuals that make up the aggregates, how and at what stage the enigma enters the *Merce-*

*naria*, and whether the enigmas have plates at an early stage.

### Discussion of Relationships of *Mclellania*

I have described *Mclellania aenigma* as a balanid cirriped and because of its peculiar or perhaps even unique habitat and evolutionary development, I have erected a subfamily for it. As pointed out, the most convincing evidence is the striking similarity of enigmas and the bases of species of *Acasta* (Family Balanidae); supported by their obvious morphologic and functional equivalence. There is also other, if less striking, evidence. To recapitulate and elaborate:

1. The mode of growth of enigmas and of other balanid barnacle bases is the same, although the final forms are markedly, but superficially, different. Probably in response to their loci, both are irregular in growth and consequently difficult to describe. They are formed of succeeding, expanding layers; in enigmas these are subplanar and in balanids planar to cup-shaped. Each develops characteristically: the enigmas become subconical bodies, and the bases of some species of barnacles become cup-shaped or planar bodies at right angles to the rest of the barnacle shell. In the enigmas, each succeeding layer expands during growth with its edge slightly curved upward to conform to the concave inner surface of its host. In comparison, some balanid bases are ideally described as growing and adhering to a flat surface, the edges of each succeeding, expanding layer curving downward over the preceding layer to afford firm attachment. The radial markings of the enigmas are comparable to markings on some balanomorph bases, which result from their interlocking contact with the compartmental plates of their shell walls. The stronger radials account for the sinuosity of the subcircular outline of enigmas, which is comparable to the rudely hexagonal outline of the basis of *Acasta cyathus*, relict from its six compartmental plates. This suggests that *Mclellania* may have had plates at an early stage of its growth.

2. Enigmas and the shells of thoracican cirripeds are both composed of calcite. According to Newman, Zullo, and Withers (1969:218), barnacle shells are predominantly calcite and contain no aragonite. Perhaps the report (Lowenstam, 1964:385) of aragonitic bases in the balanomorphs, *Catophragmus* and *Tetracrita*, is best regarded in the balance as no more than the ubiquitous exception.

3. Alternate light and dark layers are common to enigmas and thoracicans. In enigmas and in balanid bases, the alternate layers are prominent when exposed. Other thoracican lepadomorphs, such as *Scalpellum magnum* Darwin (1851, pl. 1: fig. 1e; see also Withers, 1953, pl. 52, fig. 7), show the alternation on the exterior. The specimen illustrated here (Plate 1: figure 10) was recovered by Blake Blackwelder from off-shore dredgings in the Atlantic Ocean, where it was associated with Yorktown age fossils. Withers (1953:302) does not report the species outside the Pliocene Coralline Crag of England.

4. The aggregates may have a function homologous to that of crowded groups of barnacles, in which larger specimens adhere to each other and sometimes overrun smaller specimens. Barnacles, according to Schäfer (1972:114), live crowded, not because of advantages of environment, but because cirripeds, although sessile, have retained internal fertilization and must be within reach of each other. The aggregate enigmas are anastomosed, but crowded barnacles, though tightly adherent, are not and cannot be anastomosed, because of the growth requirements of the compartmental plates of their shell walls. Inasmuch as there could hardly be an environmental advantage from closeness within the mercenarias, by extrapolation, it is assumed that sexuality is the compulsion. Fourteen (over 41%) of the 34 enigma specimens in mercenarias are aggregates; most of the single specimens are small to very small (Table 1), presumably not mature. The aggregates are all larger than the singles, not just because they are made up of more than one individual, but also because the individuals that make up the aggregates tend to be larger. The

aggregates may be the sexually mature, adult condition.

Obviously, *Mclellania* lived between the mantle and the shell of a bivalve. This it has in common with *Malacolepas* Hiro (1933:233-239), a lepadomorph cirriped described as living in and attached to shells of two genera of living bivalves, *Cucullea* and *Venerupis*, in Japanese waters. Of necessity, *Mclellania* and *Malacolepas* are homologous in the area of attachment; Newman, Zullo, and Withers (1969:217) have pointed out Darwin's determination of the homology of Lepadomorpha and Balanomorpha in this respect. It is difficult to assess from Hiro's description, but the homology may extend even further in the case of *Mclellania* and *Malacolepas*. In part, the specimens of *Malacolepas* are surrounded by calcareous tubes believed by Hiro to have been produced by the bivalves. His reasons are not particularly convincing in light of the two specimens of *Malacolepas* in *Venerupis* which "have a common cup around the basal parts" (Hiro, 1933:238). A consideration of possible homology with the *Mclellania* aggregates is inescapable, but without specimens I cannot go further. At least one other condition may be had in common: *Malacolepas* has no plates, a condition not uncommon in Lepadomorpha, but one, apparently, unknown in Balanomorpha. *Mclellania*, at some point in its existence (evolution or growth), must have had plates. No other explanation seems possible for the radial markings on the enigmas. Either the plates were lost at an early stage of growth or the soft parts were predisposed to replicate relict conditions in forming the hard parts of the enigmas. The fact remains that the aggregates could not have had plates. They were lost at some point in the evolution or during the growth of the enigmas within the protected environment of the *Mercenaria* interior.

This parallelism between forms in Balanomorpha and in Lepadomorpha is interesting, particularly so because of the possibility of parasitism in both. Parasitism is not rare in lepadomorphs, but I have not seen it recorded in balanomorphs. *Malacolepas* is said to be commensal (Hiro,

1933:233). Both *Malacolepas* and *McLellania*, living in the restrictive niche between the mantle and the shell of bivalves, must somehow be sustained by their hosts. In neither case can a positive benefit from the association be deduced, and the association is not certainly, demonstrably harmful. As recounted earlier, however, some evidence indicates that there may have been a constant effort by the mercenarias to overrun the enigmas. Empirically, I believe *McLellania* to have been a parasite. *Mercenaria* has survived and *McLellania* is extinct, but for a time this balanomorph evolved and produced a survival platform within *Mercenaria*.

In my limited acquaintance with arthropod literature I have not seen an account of anastomosed individuals, or aggregates. Within the Thoracica, a highly evolved sessile group of great diversity presumably descended from free-living progenitors, anastomosed individuals may represent a trend or possibly nothing more than plateless proximity.

The complexity and diversity of form and habitat of the Cirrhipedia, as noted by the specialists, is impressive, but the aggregate specimens of *McLellania* may be unique and add yet another component to the diversity of the class.

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## PLATE 1

*Mclellania aenigma*, new genus, new species

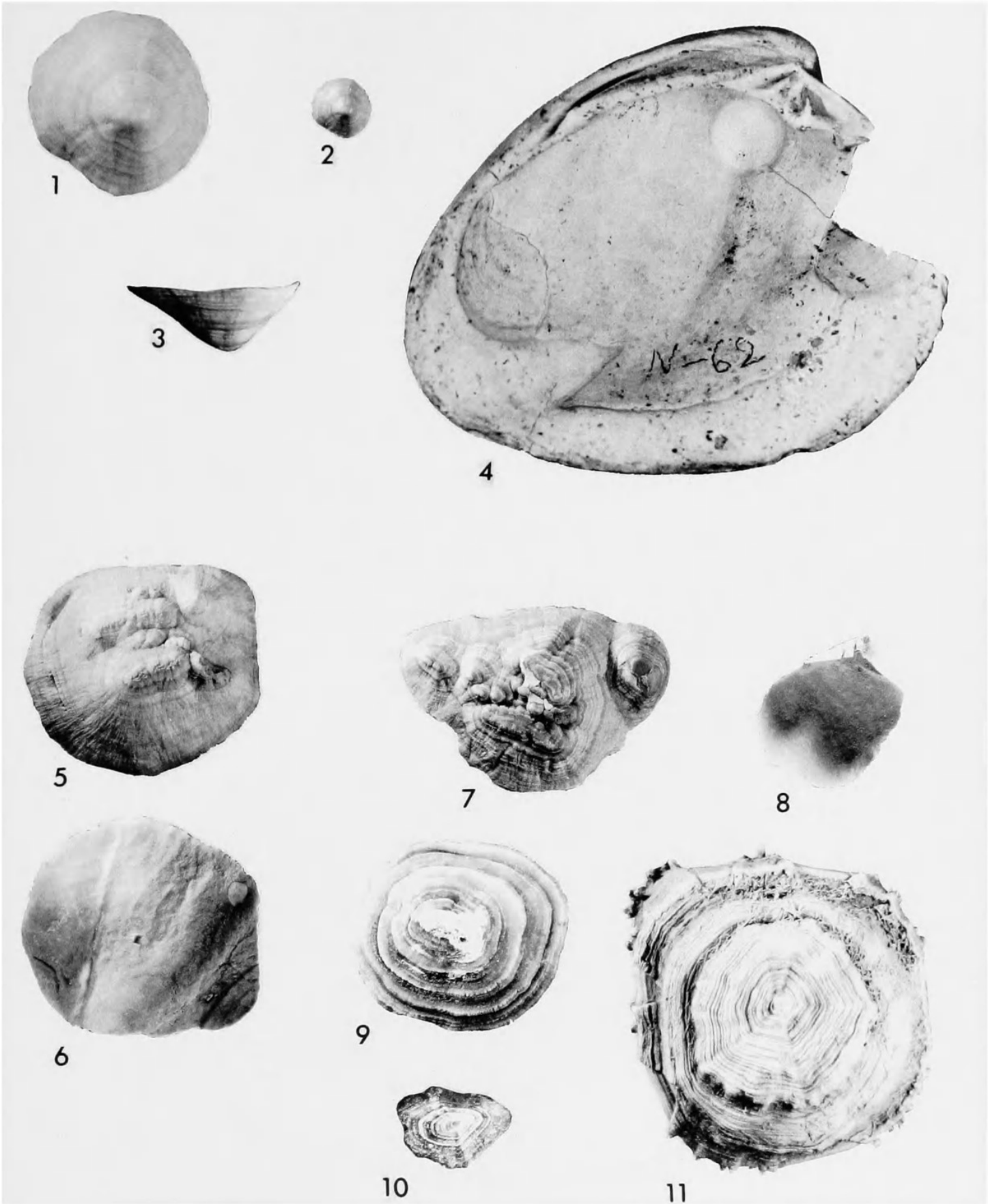
- 1–3. Holotype USNM 304378; 1, basal view,  $\times 3$ ; 2, basal view,  $\times 1$ ; 3, side view,  $\times 3$ .
4. Locus of holotype (the light circular depression under the umbo) in shell of *Mercenaria permagna*,  $\times 1$ .
- 5, 6. Aggregate paratype USNM 304379; 5, basal view, and 6, upper surface, showing xenomorphic markings derived from inner surface of a *Mercenaria*,  $\times 1$ .
7. Aggregate paratype USNM 304380, basal view,  $\times 1$ .
8. Aggregate paratype USNM 304381 from high under the umbo of a *Mercenaria*, upper surface,  $\times 1$ .
9. Paratype USNM 304382; highly weathered basal surface showing light and dark layers,  $\times 3$ .

*Scalpellum magnum* Darwin

10. Upper latus, USNM 304386, of fossil from off-shore dredging in the Atlantic Ocean,  $\times 3$ .

*Acasta cyathus* Darwin

11. Basal view of USNM 7842 figured by Pilsbry (1916, pl. 57: figs. 1, 1a–b) showing basis and interlocking edges of capitulum,  $\sim \times 10$ .

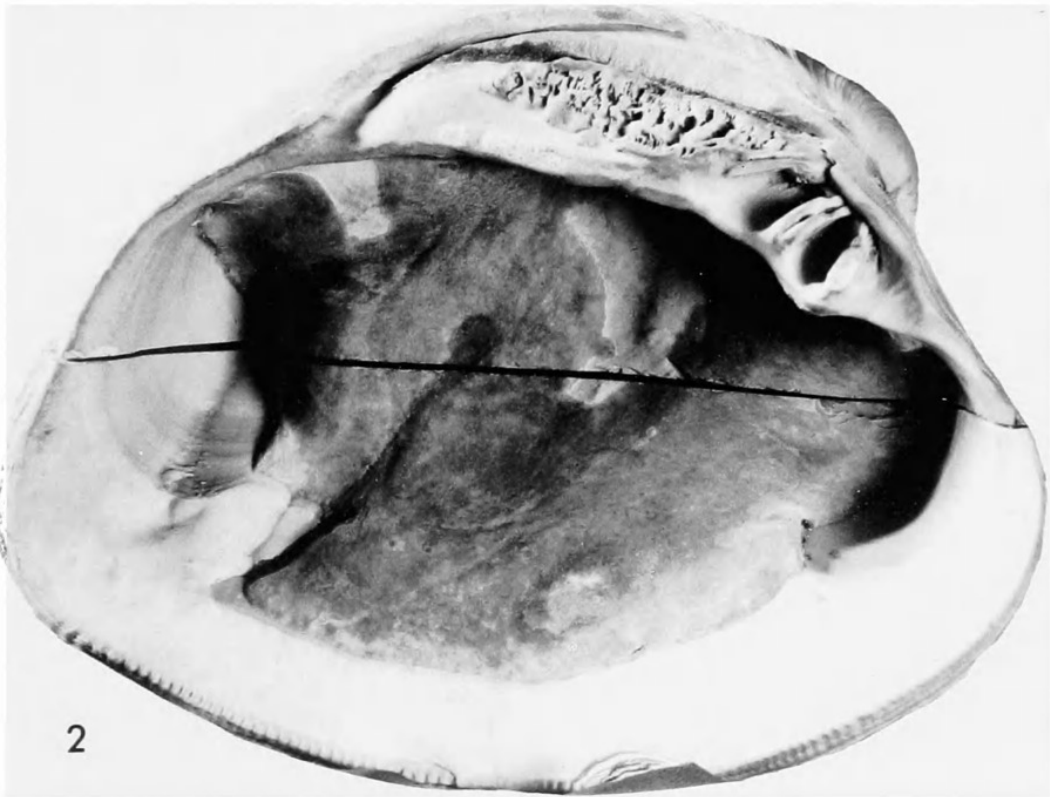


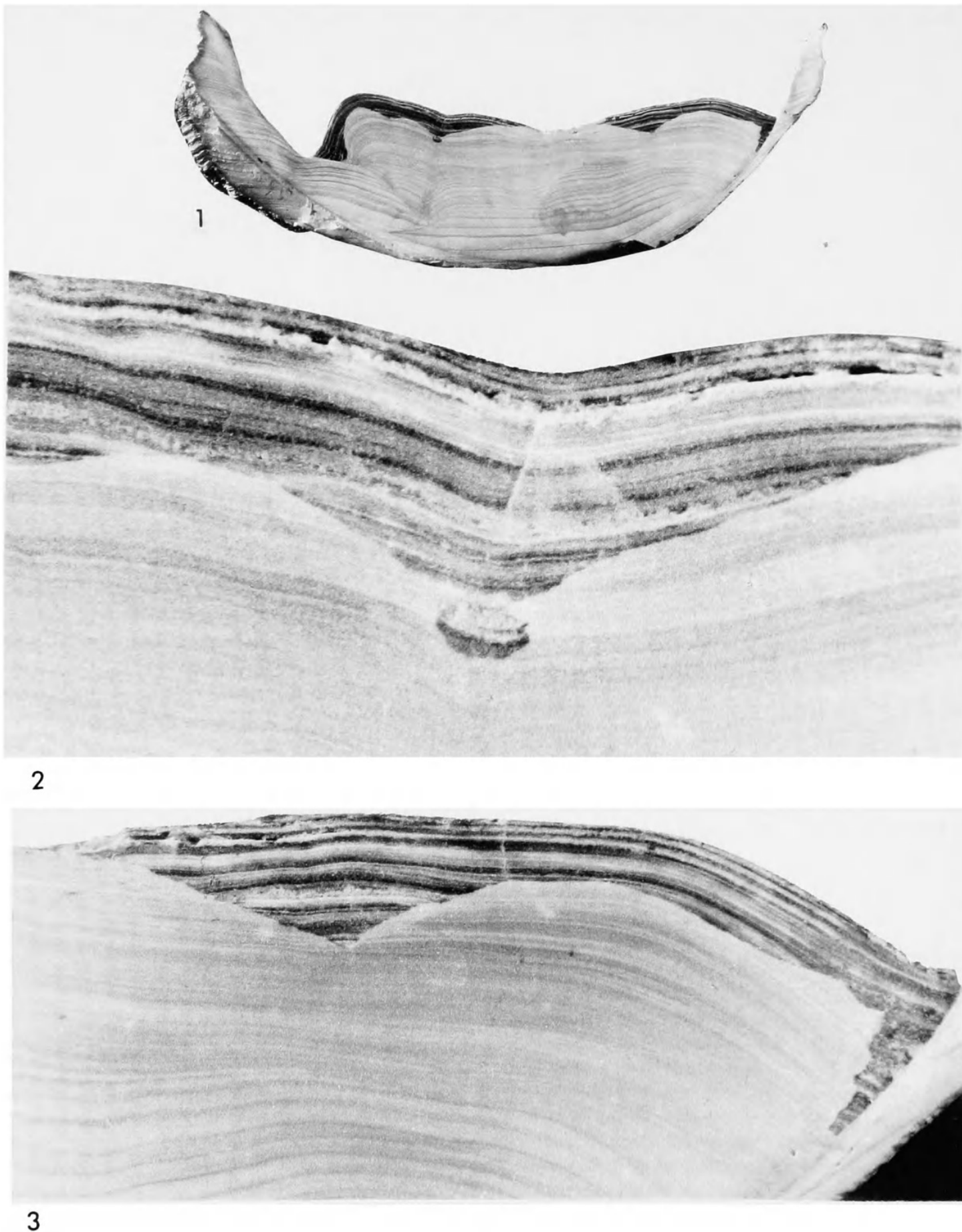


**PLATE 2**

*McLellania aenigma*, new genus, new species

1. Paratype USNM 305108 embedded in juxtaposition to anterior adductor muscle scar in right valve of *Mercenaria corrugata* "tridacnoides" from 4 miles (6.4 km) northwest of Williamston, North Carolina,  $\times 1$ .
2. Aggregate paratype USNM 305107 embedded in and covering greater part of inner surface of left valve of *M. corrugata* "tridacnoides" from 15 miles (24 km) above Bell's bridge, Tar River, North Carolina; showing position of cross-section,  $\times 1$ .





### PLATE 3

*Mclellania aenigma*, new genus, new species

1-3. Aggregate paratype USNM 305107 embedded in left valve of *Mercenaria corrugata* "tridacnoides"; 1, cross-section at level of adductor muscle scars,  $\times 1$ ; 2, posterior portion of cross-section,  $\times 5$ ; 3, anterior portion of cross-section,  $\times 5$ .





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