

**ELLIPTIO MARSUPIOBESA, A NEW FRESH-WATER MUSSEL**  
(MOLLUSCA: BIVALVIA: UNIONIDAE)  
FROM THE CAPE FEAR RIVER, NORTH CAROLINA

SAMUEL L. H. FULLER

*Academy of Natural Sciences of Philadelphia*

**ABSTRACT.** — A new species of the fresh-water mussel genus *Elliptio* (Mollusca: Bivalvia: Unionidae) is described from the Cape Fear River of North Carolina. This species and *E. icterina* (Conrad 1834) form an advanced group characterized by reproductive capabilities significantly greater than their congeners'. Several working hypotheses emerge from discussions of the new species' ecology and ancestry, including the possibility that portions of the Cape Fear and neighboring river systems once formed a haven for unionid speciation isolated by an interglacial sea.

## INTRODUCTION

Two recent collections of naiades from the Cape Fear River near Fayetteville, southeastern North Carolina, include examples of an undescribed species which is most closely allied to the concepts of *Elliptio icterina* (Conrad 1834) advanced by Johnson (1970: 328-329) and Fuller (1971). These two species form a natural group within the genus which is in advance of their congeners in terms of reproductive capability. The new species differs from other *Elliptio* in certain characters of the shell and reproductive anatomy. The following description is accompanied by notes on the systematic relationships, ecology, and zoogeography of the new species.

## METHODS AND PROCEDURES

1. *Collection and preparation of material.* All specimens were taken by hand or with a Needham scraper of 3/16" mesh wire; relaxed in about two days' time with a Nembutal solution of less than 1% by volume in tap water (see van der Schalie, 1953); and, in the absence of a better fixative,

killed by grading up in ethanol to a storage strength of 70%.

2. *Sexing.* Individuals were sexed by examining clippings from each demibranch with transmitted light and under 1× to 30× magnification. The gill wall is readily teased away to reveal the structure and spacing of the interlamellar septa. In this species the septa of the outer (i.e., marsupial) female demibranchs are sturdy and set about every sixth gill filament, whereas those of the inner (i.e., non-marsupial) female demibranchs and of all male demibranchs are about twice as widely spaced and are conspicuously more delicate.

3. *Abbreviations.* ANSP — Academy of Natural Sciences of Philadelphia, Pennsylvania. CM — Charleston Museum, South Carolina. MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. USGS — United States Geological Survey, Washington, D.C.

4. *Locality data.* Those for the new species were prepared from two USGS topographic sheets: the 1950 edition of the "Slocomb [North Carolina]" quadrangle in the 7.5 minute series, and the 1959 edition of the "Saint Pauls [N.C.]" quadrangle of the 15 minute series.

5. *Terminology.* I prefer the expression *egg mass* to several ambiguous terms (e.g., "placenta" or "conglutinate") that have been used by authors in reference to the body of ova in a water tube. In describing the uncharged marsupium, *barren* is used in preference to "sterile," another misleading expression. *Elasticity* will mean the ability of the marsupium to distend during reception and incubation of ova.

*Elliptio marsupiobesa* new species

## TYPES

All known specimens of *Elliptio marsupiobesa* were collected by the author in North Carolina from Cape Fear River system: Cape Fear River drainage: Cape Fear River. All are designated as types.

(a) *Type locality*: 0.1 mile downstream from Carvers Creek, about 3 miles SW of Slocomb, and about 6 miles NNE of Fayetteville, Cumberland County (Latitude, 35° 8' 34" North; Longitude, 78° 51' 9" West). Specimens collected 11 June 1970 include the ovigerous female *holotype*, ANSP 324501, and *paratypes*, ANSP 324502 (one dead shell, seven males, three barren females, five ovigerous females). Two dead shells taken 19 September 1969 are *paratypes*, ANSP 324503.

(b) Additional *paratypes*, ANSP 324504 (one male, two barren females), were taken 16 June 1970 about 1 mile S of Tolar Landing and about 3 miles ENE of Tobermory, Bladen County.

(c) Another *paratype*, ANSP 324505 (dead shell), was taken 17 September 1969 about 1.25 miles ESE of Duart, Bladen County.

## ETYMOLOGY

The epithet *marsupiobesa* is derived from the Latin *marsupium* (pouch) and *obesus* (fat) and agrees adjectivally with *Elliptio*, which is feminine (Baker, 1964). The name refers to the swollen gravid marsupium of the new species, a character of greater systematic importance than the carinate posterior ridge, which reflects the marsupial condition.

## DESCRIPTION

The shell is of small to medium size, reaching 68.5 mm (almost 3 inches) in length; thin and strong (older individuals may be thickened anteriorly); elongate (height is consistently about one half the length); moderately to greatly inflated (width is consistently about one third the length and ranges from about three fifths to about four fifths of the height); cuneiform in outline; and without sexual dimorphism. The beaks are full, very slightly prosogyrous, prominently elevated above the dorsal margin, and located about one

quarter of the shell length from the anterior end. The posterior ridge is rather swollen and carinate. The posterior slope is narrow and distinctly concave. The disk is inflated and rounded along and above the midline. Greatest breadth occurs at or just behind the beaks; greatest height is at the beaks. The ligament is prominent, darkly pigmented, opisthodontic, and short (about one quarter the shell length).

Adult shell growth is without sculpture excepting one or two radial grooves on the posterior slope which cause little or no biangulation of the margin posteriorly. Alternation of deeply impressed growth rests and periods of inflated shell growth produces an undulate surface in some individuals. Beak sculpture consists of up to seven subconcentric, slightly wavy bars, which converge toward the posterior ridge, where earlier ones are greatly thickened, often weakly nodulose. The bars are increasingly closely spaced with age; older bars, which almost coalesce at the ridge, are complete; younger bars are obsolete posteriorly. The periostracum may exhibit minute malleations and scratches, which are scattered or arranged in rays; otherwise it is smooth and shiny, roughened along the margins and (in older individuals) on the posterior slope. Color of younger individuals is bright yellow-brown, often rayed with more or less evenly spaced dark green lines, which are most conspicuous below the disk on about the posterior one half of the shell; older specimens are uniformly dark brown or black.

The ventral margin is a weakly convex even curve, which may straighten posteriorly; anteriorly it ascends rather sharply, usually forming a distinct angulation with the dorsal margin just before the beaks. The dorsal margin is straight or a very weakly convex even curve; it forms a more or less weak angulation shortly behind the beaks and descends to meet the ventral margin in a blunt point or rostration at or just below the midline.

The hinge plate is narrow, weak, and rather long (about two thirds the shell length). The interdentum is very short and narrow. The nymphal callosities are blade-like bars about one half the length of the lateral teeth and project sharply dorsad. The laterals are short (about one third the shell length), straight or very slightly decurved,

blade-like, descendant in the rear, and subparallel to the dorsal margin; the lower of the two in the left valve is slightly the longer and more broad; the one lateral on the right valve is stronger than either on the left. The left valve has two pseudocardinal teeth; the right has one, often with a vestigial subumbonal tooth behind it on the interdendum. The right pseudocardinal is much like the posterior one on the left valve; it is longer and more blade-like than the comparatively short, squat, ragged, and amorphous anterior left pseudocardinal. Pseudocardinals may be subdentate distally; all teeth are variably rugose, especially on their interlocking surfaces.

The nacre is thick and usually white within the beak cavity and over about the anterior one half of the shell; it is particularly thickened below the pallial muscle scar. There may be discoloration or a faint to vivid flush of yellow, orange, or salmon color. Elsewhere the nacre is iridescent and much thinner; iridescence is pronounced outside the pallial muscle scar posteriorly. The pallial scar is a smooth curve subparallel to the ventral margin. Other muscle scars are variably suboval. Anterior scars are well marked and impressed; posterior scars are less distinct, but the posterior adductor is somewhat impressed anteriorly. Dorsal scars are clusters of tiny shallow pits on the interdentia within the beak cavities, which are very deep.

Free mantle margins are trilobate; differentiation is confined to papillation of the inner lobe at the anal and branchial apertures, which bear two rows of papillae. The branchial rows are somewhat intermingled; papillae of the inner row are longer, stouter, subtentaculate, fused to the mantle basolaterally, and spaced unevenly and discontinuously for the most part; ordinarily they terminate simply, but the rare individual is biamous. Papillae of the outer row are much shorter, more slender, comparatively stiff, scarcely fused to the mantle basolaterally, arranged closely and at rather equal intervals, and terminally simple. In life the inner papillae are erected obliquely from the mantle and almost interdigitate across the aperture; the outer papillae lie subparallel to the mantle, projecting posteriad. The papillae at the anal aperture resemble those of the outer branchial row; their disposition in two rows is obscure. The anal and supra-anal apertures are separated by a strong

fusion of the opposing inner mantle lobes; similar fusion closes the supra-anal for about the upper four fifths of its length. The branchial and supra-anal apertures are subequally long and about thrice the length of the anal.

The outer oral palpi are somewhat the larger; palpi extend posteriad slightly beyond the anterior margin of the inner demibranch. Dorsally and laterally the anus is protected by a simple hood. External aspects of the foot and visceral mass offer no peculiarities.

The demibranchs are subequal in size; the outer hang lower behind; the inner hang lower anteriorly and extend farther anteriorly. Distal demibranch margins are bilobate, indistinctly so in the outer pair. Proximal margins of the inner demibranch are free of the visceral mass for about the posterior two thirds of that portion of their length which lies before the posterior margin of the foot. Delicate septa are separated by about 12 gill filaments in the male and in the inner demibranch of the female; much stronger septa are about twice as closely spaced in the outer female demibranchs, which alone are marsupial. The marsupium is a smooth obese pad which extends the full length of the demibranch and retains the distal demibranch margin as a conspicuous rib. Egg masses are subelliptical, compressed, lamellar, flat, extremely broad (with about 25 somewhat staggered rows of ova at the broadest point), pointed at the ventral margin, pointed or (more rarely) bluntly attenuate at the dorsal margin, white, and fill most of the height of the water tubes. The egg is minute (about 0.2 mm in diameter), translucent, subspherical, with a subcentral opaque white embryo. The glochidium is unknown. Sexual maturity may be reached during at least the fourth year of life. Breeding begins in at least the early spring; possibly the ova overwinter in the marsupia.

The dark mantle pigment among the bases of the anal and branchial papillae (which are reddish) does not extend anteriorly into the mantle cavity. Immediately before the apertures there may be a narrow band of mantle pigment subparallel to the margin. In the apertural region the opposing faces of the mantle lobes are lightly pigmented. Most of the rest of the animal is a dirty white, but the mantle is primarily a dull yellow, which is accentuated in muscle tissue generally, and the gills may exhibit some dark pigmentation, especially when gravid.

## DIAGNOSIS

1. *Superfamily*. The larva of the new species is unknown, but, because naiades are currently represented in the United States only by Unionacea (as defined by Parodiz and Bonetto, 1963), I am confident that it is the glochidium of that superfamily.

2. *Family*. Since its marsupium is not confined to the inner demibranch, the new species belongs to the family Unionidae as defined by Ortmann (1910, 1911, 1912). Although Heard and Guckert (1971) removed certain genera from Ortmann's Unionidae to the family Amblemidae, this species conforms to their concept of the Unionidae, also, in that only its outer demibranchs are marsupial.

The only constant difference between the Unionidae and Amblemidae of Heard and Guckert is the number of marsupial demibranchs found in the members of each (two and four, respectively). I am not convinced that a single character is an adequate discriminant at the family level and will employ Ortmann's concept of the Unionidae in this paper.

3. *Subfamily*. The new species belongs in Ortmann's (1910, 1911, 1912) Unioninae because no qualitative changes occur in the structure of the gill during the breeding season.

4. *Genus*. A combination of additional characters places the new species in the genus *Elliptio* Rafinesque 1820. Shell shape is elongate and scarcely oblique (Figs. 1-3). Beak sculpture includes several strong, complete bars (Fig. 4). Marsupial structure is confined to the outer demibranchs (Fig. 7). The egg mass is compressed from front to rear. *Pleurobema* Rafinesque 1819 is an attractive alternative, but the well developed beak sculpture of the new species precludes its being placed in that genus.

5. *Intragenetic relationships*. *Elliptio marsupiobesa* is distinct from its congeners in several ways. The posterior ridge is full and carinate; it descends very slowly, meeting the margin posteriorly at or immediately below the midline, and an unusually narrow and concave posterior slope is effected (Figs. 1-3). Straight or weakly curved, the posterior portions of the dorsal and ventral margins converge rapidly, thus contributing to the char-

acteristically wedge-like outline of the shell, which is always highest at the beaks (Figs. 1-3). The fully charged marsupium is greatly swollen and extends the length and nearly the height of the (outer) demibranch (Fig. 7). The beaks are elevated well above the dorsal margin (Figs. 1, 2). The beak sculpture bars are greatly thickened at the posterior ridge (Fig. 4).

Certain other characters — not unique to the new species, but rare among Atlantic drainage *Elliptio* — are typical of *E. marsupiobesa*. The beaks are full and located close to the anterior end, the beak cavities are deep, and the posterior point is at the midline or just below (Figs. 1-3). The periostracum (particularly across the disk and in younger individuals) is shiny, rather brightly colored, and extremely smooth (Figs. 1-3). The shell is maximally broad at the beaks or immediately behind. Mantle pigmentation at the anal and branchial apertures scarcely extends anteriorly from among the bases of the papillae (Fig. 7).

*Elliptio icterina* is the only currently recognized member of the genus that can be mistaken for *E. marsupiobesa*. Typical forms of the two species are quite different, but the broad concept of *icterina* espoused by Johnson (1970: 328-329) includes posteriorly pointed shells — such as *Unio ocmulgeensis* Lea 1861 — which greatly resemble *marsupiobesa* in outline. However, no ecophenotype of *icterina* has the sharply keeled posterior ridge or the unusually narrow and concave posterior slope of *marsupiobesa*.

The marsupium and egg mass of *Elliptio icterina* were figured by Fuller (1971). The marsupium does not extend the full length of the (outer) demibranch. The egg mass is broad (sometimes subcircular and never reaching the top of the water tube), and the marsupial wall stretches to accommodate this great breadth. In contrast, the marsupium and egg masses of *E. marsupiobesa* occupy the entire (outer) demibranch (Fig. 7), the egg mass (Fig. 8) is higher and narrower, and the charged marsupium is less distended.

The beak sculpture bars of *Elliptio icterina* (Fig. 6) are weaker than those of *E. marsupiobesa* (Fig. 4), but its reproductive morphology represents a clear advance over the new species in terms of division of labor between reproductive and somatic

tissues in the outer demibranch, which, combined with broader egg masses and the more distended marsupium, yields more efficient and plentiful production of larvae. Thus it appears that *marsupiobesa* represents an earlier stage in the development within *Elliptio* of a group of species with greatly elastic marsupia and improved reproductive ability. In addition, *marsupiobesa* retains the number of beak sculpture bars found in southerly populations of the more primitive *E. complanata* (Lightfoot 1786) (compare Figs. 4, 5), whereas *icterina* has a somewhat smaller number of them (Fig. 6).

The peculiar marsupia and beak sculptures of *Elliptio marsupiobesa* and *E. icterina* are unknown elsewhere in the genus. The group typified by *E. complanata* is most like the *marsupiobesa* group in adult shell characters, but the beak sculpture bars of *complanata* (Fig. 5) are scarcely thickened at the posterior ridge. Moreover, the charged marsupium of *complanata* is relatively inelastic, containing narrow egg masses (Fuller, 1971).

*Elliptio waccamawensis* (Lea 1863) is reminiscent of *E. marsupiobesa*. Endemic to Lake Waccamaw and neighboring canals in the Waccamaw River system immediately to the south of the Cape Fear system along the Carolina coast, this species, also, has a carinate posterior ridge and, occasionally, very high and full beaks. The ridge, however, descends rapidly to form a nearly postbasal biangulation of the margin. Moreover, the posterior slope is often weakly sculptured, which persuaded Johnson (1970) to place this species close to *E. crassidens* (Lamarck 1819) and its relatives. Although the anatomy of *waccamawensis* has not been described, close relationship between *marsupiobesa* and that species is doubtful.

The adult shell of *Elliptio marsupiobesa* resembles those of certain Floridian taxa included by Simpson (1900: 712-719, 1914: 627-650) in his group of *Unio buckleyi* Lea 1843, an heterogeneous collection, some of whose members were distributed quite differently by Johnson (1970). A record of *U. buckleyi* in South Carolina published by Mazyck (1913: 24) is surely spurious. Mazyck had seen *buckleyi* but had not personally collected it in South Carolina, and the only material in the Charleston Museum that is labeled *buckleyi* is from Florida. There are several reasons why Mazyck's record was probably based on another's mistaken

authority. First, Ortmann (1912: 270) wrote an anatomy representative of the *buckleyi* group, with a description of its peculiar, not quite double-looped beak sculpture; although many details of their reproductive morphology have not been described, this sculpture alone is sufficient to separate members of the true *buckleyi* group from *Elliptio* beyond peninsular Florida. Second, the *buckleyi* group is such a distinctive assemblage that Heard and Guckert (1971) placed *buckleyi* in *Popenaias Frierson* 1927. Third, there is no possibility that *marsupiobesa* is an introduction from Florida: Cornell (personal communication) reports that no Floridian fishes have been stocked in North Carolina.

## ECOLOGY

1. *Breeding season.* Gametogenesis and fertilization commence during late summer among *Elliptio complanata* in the Altamaha River system of Georgia, ova develop over the winter in the marsupia, and their glochidia are released in the late spring (Raulerson and Burbanck, 1962; see Johnson, 1970: 398). I have *complanata* from the Delaware River system in New Jersey exhibiting fully formed egg masses as early as 24 April, and Ortmann (1919: 104) reported glochidia as early as 7 June, and through 11 July, in Pennsylvania. Although breeding in *complanata* can be repressed by cold (Matteson, 1948), these data imply that latitude has little or no influence upon the length or timing of the season in this species.

*Elliptio marsupiobesa* contained fully formed egg masses on 11 June, which suggests that its breeding season may closely approximate that of *E. complanata*. On the other hand, I have *E. icterina* from the Savannah River system in South Carolina exhibiting this condition as late as 20 July. Thus the breeding season of *icterina* appears to be somewhat out of phase with those of *marsupiobesa* and the more primitive *complanata*. This would tend to support my suspicion that *marsupiobesa* is less advanced than *icterina*.

A difference in breeding season was possibly among the mechanisms isolating the ancestors of *Elliptio marsupiobesa* and *E. icterina*, or, more probably, the latter's apparently delayed season may have evolved independently after geographic isolation. Perhaps *icterina* is developing the lengthy

season characteristic of the Anodontinae and Lampsilinae. True bradytaxis is known in the unionine genera *Megaloniais* Utterback 1914 and *Popenaias* Frierson 1927 (Heard and Guckert, 1971).

2. *Host*. Searching among numerous species of fish, Matteson (1948) was unable to find a gluchidial host for *Elliptio complanata* other than the yellow perch, *Perca flavescens* (Mitchill 1814). However, Davenport and Warmuth (1965) demonstrated that it cannot be assumed that a mussel is restricted to the host that is dominant in nature. Certainly the enormous range of *complanata* suggests that it employs more than one host, and Raulerson and Burbanck (1962) implied that this is true in the Altamaha River system.

The ancestors of *Elliptio marsupiobesa* could hardly have competed advantageously with those of the highly successful *E. complanata* for hosts used simultaneously by both. Since their breeding seasons appear to be in phase, one infers that at least their primary hosts are different. On the other hand, if *marsupiobesa* and *E. icterina* can afford to employ common (or closely related) hosts because their seasons are staggered, I suggest that

these may be darters (*Etheostoma* Rafinesque 1819), the only group of fish I have observed at certain small creek stations where *icterina* was collected.

A change in host presents a physiological problem that is presumably less difficult if the old and new hosts are closely related. *Perca* Linnaeus 1758 and *Etheostoma* belong to the same family (Percidae), and it is possible that percid fishes have played an important rôle in speciation within *Elliptio*. On the other hand, Coker *et al.* (1921) showed that systematic position does not necessarily determine the relationship between mussel and host. Accordingly, the notion that a darter is an important host for *E. marsupiobesa* is particularly attractive because of the benthic habits of these fishes. In adding that Foster and Jankowski (personal communication) reported two *Etheostoma*—*E. fusiforme* (Girard 1854) and *E. olmstedii* Storer 1842—living sympatrically with *marsupiobesa*, I must emphasize that I insist upon none of the conjectures advanced in this section or the last. They are provided essentially as a provocation to the experimentalist interested in furthering understanding and conservation of mussels through better

FIGURE 1.—*Elliptio marsupiobesa* new species. Female holotype. ANSP 324501. Cape Fear River, 0.1 mile downstream of Carvers Creek, about 3 miles SW of Slocomb, and about 6 miles NNE of Fayetteville, Cumberland Co., North Carolina. Length, 51 mm; height, 27 mm; width, 18.5 mm. About 1.8×. Note elevated beaks, carinate posterior ridge, and convex posterior slope.

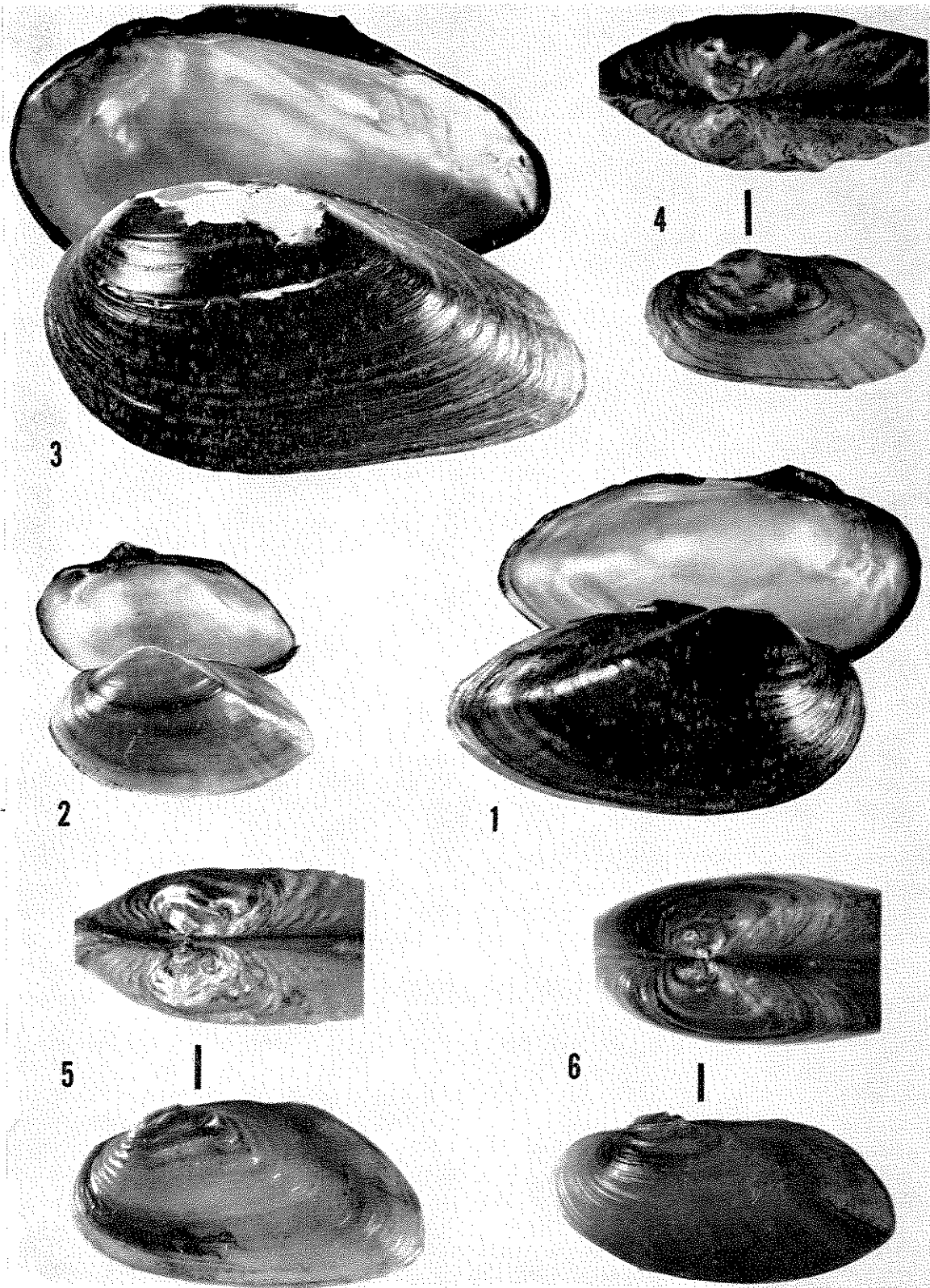
FIGURE 2.—*E. marsupiobesa*. Dead paratype. ANSP 324502. Same locality. Length, 31.5 mm; height, 18 mm; width, 11 mm. About 1.8×.

FIGURE 3.—*E. marsupiobesa*. Female paratype. ANSP 324504. Cape Fear River, about 1 mile S of Tolar Landing and about 3 miles ENE of Tobermory, Bladen Co., N.C. Length, 67 mm; height, 36 mm; width 24 mm. About 1.8×. Note slightly decurved postbasal production.

FIGURE 4.—*E. marsupiobesa*. Dead juvenile paratype. ANSP 324505. Cape Fear River, about 1.25 miles ESE of Duart, Bladen Co., N.C. Length, 14 mm; height, 7 mm; width, 4 mm. Lateral view, about 4.4×; dorsal view, about 10.5×. Note the number of beak sculpture bars (at least seven), of which several are very strongly developed at the posterior ridge.

FIGURE 5.—*E. complanata* (Lightfoot 1786). Juvenile. Savannah River system: Savannah River drainage: Upper Three Runs Creek at South Carolina state route 125, about 7 miles SE of Jackson, Aiken County, S.C. Length, 16 mm; height, 8.5 mm; width, 4 mm. Lateral view, about 4.8×; dorsal view, about 9.6×. Beak sculpture bars (about as many as in *E. marsupiobesa*, Fig. 4) are scarcely more strongly developed at the posterior ridge than elsewhere. About five bars of this type were shown by Marshall (1890: fig. 6) for *complanata* from the Hudson River system; about seven of the same type, by Reardon (1929: pl. 4) for specimens from the Potomac River system. Reduction in number of bars appears to have accompanied this species' exploitation of previously glaciated areas.

FIGURE 6.—*E. icterina* (Conrad 1834). Juvenile. Savannah River system: Brier Creek drainage: Mill Race at Georgia state route 23, about 2 miles N of Sardis, Burke County, Georgia. Length, 28 mm; height, 14 mm; width, 7.5 mm. Lateral view, about 2.6×; dorsal view, about 4.4×. Beak sculpture bars number about four (distinctly fewer than in *E. marsupiobesa*, Fig. 4, and southern *E. complanata*, Fig. 5); only the elder two are (slightly) more strongly developed at the posterior ridge than elsewhere.



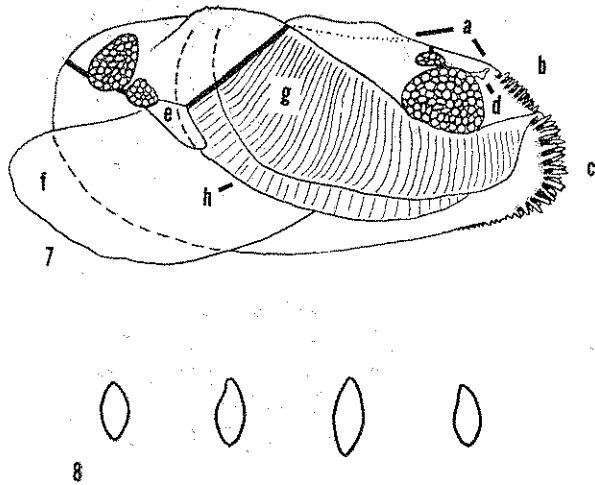


FIGURE 7.—*Elliptio marsupiobesa* new species, partially aborted ovigerous female (ANSP 324502), mantle removed along heavy line and proximal margins of outer palpus (e) and demibranch (g). a-c, supra-anal, anal, and branchial apertures, respectively. d, anal hood. f, foot. h, inner demibranch. About 1.5×. Crenulation of the mantle margin immediately anterior of the branchial aperture was probably induced by fixation in ethanol and has not been observed in formalin-fixed *E. icterina*.

FIGURE 8.—*Elliptio marsupiobesa*, egg masses in transverse cross section. About 1.5×.

knowledge of the identities of their hosts.

3. *Parasites.* The outer demibranchs of a single specimen of *Elliptio marsupiobesa* (an ovigerous female paratype) exhibit darkly pigmented inclusions which are probably damaged teleiochrysalides of a water mite (Arthropoda: Acari: Unionicolidae). Several species of *Unionicola* Haldeman 1842 were associated with Cape Fear River naiades in the area I examined, but Mitchell's (1955) work indicates that the specific identity of a mite cannot necessarily be inferred from its position on a mussel. Since no adults were found in any *marsupiobesa*, it is likely that the parasite is one of the Unionicolidae whose adult stage is free-living.

"Blistering" of the nacre and fraying of the distal gill margins in some individuals of *Elliptio marsupiobesa* suggest attack by mites and infection with "distomids" (Platyhelminthes: Trematoda: Aspidogastriidae). However, no aspidogastriid

flatworms were observed in any *marsupiobesa*.

4. *Habitat.* I intend that certain chemical and physical aspects of the Cape Fear River will be more fully discussed in a subsequent paper on its naiad fauna, but a brief account of the preferred habitat of *Elliptio marsupiobesa* is included here. River water was rather soft and exhibited circum-neutral pH and signs of eutrophication at the type locality, where most individuals of the new species (and of other mussels) were taken in a muddy sand bottom immediately below a log jam. This loosely packed substrate with an admixture of silt contrasts sharply with the more firm and pristine sands which form the river floor in most of the area examined. Additional specimens of *marsupiobesa* were collected at other stations primarily where the favored substrate type recurred.

#### ZOOGEOGRAPHY

*Elliptio marsupiobesa* has no close relatives in the Mississippi basin or (possibly excepting *E. icterina*) in the Gulf drainage. Derivation of the new species doubtless reflects those peculiarities of the geological and ecological histories of the Cape Fear and nearby river systems that blocked the latitudinal dispersal of seven Atlantic drainage naiad species, according to data in Johnson (1970).

I infer from Haas' (1969: N422) work that the presumably ancestral genus *Protelliptio* Russell 1934 arose in North America by the Tertiary and modern *Elliptio* probably did not emerge before the Pleistocene. However, Johnson (1970: 306) identified *E. pachyodon* Pilsbry 1953, a Pliocene species from peninsular Florida, with the Recent *E. crassidens*. Whether or not this synonymy can ever prove correct, it is apparent that the ancestors of at least some modern species of *Elliptio* had differentiated before the Pleistocene — and are perhaps older than the genus itself.

On the other hand, *Elliptio waccamawensis*, for example, is surely no older than Lake Waccamaw, which came into being during the last quarter of the Pleistocene (C. W. Cooke in Hubbs and Raney, 1946). The presence in southeastern North Carolina of this endemic species and of *E. marsupiobesa* (possibly endemic) is not the only evidence that the mussel fauna of the Waccamaw, Cape Fear, and neighboring river systems has had a re-



markable Quaternary history. For example, there occurs in the Cape Fear proper an *Elliptio* — referable to *Unio perlatus* Lea 1863 and equated by Johnson (1970: 331) with *E. arctata* (Conrad 1834), a native of the eastern Gulf drainage — that exhibits peculiarities in reproductive morphology (unpublished data) which distinguish it from all other Atlantic drainage *Elliptio* that I have been able to examine.

My impression is that a region including the Cape Fear River basin was isolated, probably by inundation, for a period long enough to promote naiad speciation. This degree and kind of isolation would have been most recently realized during the earlier and more extensive Pleistocene marine invasions of the Carolinian Coastal Plain. The maximal interglacial seas seem to have cut the upper Cape Fear system off from Coastal Plain fresh waters other than small portions of the Neuse and Pedee systems which encroached from the north and south, respectively (see, e.g., Johnson, 1970: pl. 1). Alternatively, it must be remembered that the origins of the earlier Carolinian Coastal Plain Pleistocene terraces have been in dispute; for example, Richards (1950) reported no marine fossils from these deposits.

As in the relationship between *Elliptio pachyodon* and *E. crassidens*, it can be assumed that the ancestral stock of marsupially elastic *Elliptio* existed before isolation of the Cape Fear region occurred: the advance in reproductive capability of *E. marsupiobesa* and *E. icterina* beyond that of their congeners argues a lengthy period of development. Inundation probably separated this stock into smaller and larger portions — the ancestors, respectively, of *marsupiobesa* and *icterina*. The comparatively small *marsupiobesa* gene pool stagnated (only the beak sculpture became, in part, more strongly developed), whereas the precursors of the more widespread *icterina* evolved toward superior reproductive capacity.

According to Johnson (1970: 329-330), the range of *Elliptio icterina* includes certain river systems of the eastern Gulf drainage and extends from peninsular Florida through the White Oak River system of North Carolina, but, as I have implied elsewhere (Fuller, 1971), this species cannot always be distinguished from the conchologically similar

*E. complanata* on the basis of museum specimens whose soft parts and beak sculptures have been destroyed. Consequently, it cannot presently be ascertained that *icterina* has successfully invaded the proposed original area of speciation of *E. marsupiobesa*, nor can we take for granted the apparently restricted range of the new species: it may easily have passed among adjacent river systems by estuarine, flood, or stream capture dispersal of host fish. Although this species is known only from the Cape Fear system, the Pedee system has never been thoroughly worked for naiades, and the widespread collecting by Walter (1956) in the Neuse system was not intensive enough to reveal more than one or two species at most of his stations.

However, the supposition that *Elliptio marsupiobesa* originated in (and is yet limited to) a circumscribed area is supported by its carinate posterior ridge. This characteristic is typical of endemic naiades, including *E. waccamawensis* and a large number of species (representing several genera) from the Altamaha River system of Georgia.

#### ACKNOWLEDGMENTS

The support of E. I. DuPont de Nemours & Company during field work and research into the identity of the new species was most important. These colleagues have allowed examination of material in their charges (often on loan): K. J. Boss (MCZ), R. Robertson (ANSP), and A. E. Sanders (CM). Communications with J. H. Cornell (North Carolina Wildlife Resources Commission) and N. R. Foster, E. K. S. Jankowski, and J. J. Loos (all ANSP) have provided valuable ichthyological information. R. W. Haug and J. M. Chance (both ANSP) have allowed free access to their data on Cape Fear River water chemistry. An early draft of the manuscript was improved in response to the criticism of R. Robertson. The final manuscript was typed by Miss L. A. Paul. J. Harasewych took the excellent photographs. In spite of this generous assistance, all errors are the responsibility of the writer.

## LITERATURE CITED

- BAKER, H. B. 1964. *Elliptio* Feminine. — *Nautilus*, 78 (1): 33.
- COKER, R. E., A. F. SHIRA, H. W. CLARK, and A. D. HOWARD. 1922. Natural History and Propagation of Fresh-Water Mussels. — *Bulletin of the Bureau of Fisheries* (for 1919-1920), 37: 75-181, tables 1-24, text figures 1-14, plates 5-21. Previously issued 2 May 1921 as Document No. 893.
- DAVENPORT, D., and M. WARMUTH. 1965. Notes on the Relationship between the Freshwater Mussel *Anodonta implicata* Say and the Alewife *Pomolobus pseudoharengus* (Wilson). — *Limnology and Oceanography*, 10 (Supplement): R74-R78.
- FULLER, S. L. H. 1971. A Brief Field Guide to the Fresh-Water Mussels (Mollusca: Bivalvia: Unionacea) of the Savannah River System. — *ASB* [The Association of Southeastern Biologists] *Bulletin*, 18(4): 137-146, text figures 1-14, 1 plate.
- HAAS, F., and contributors. 1969. Superfamily Unionacea. — *Treatise on Invertebrate Paleontology*, Part N, Volume 1 (of 3), Mollusca 6, Bivalvia: N411-N470, text figures D15-D60.
- HEARD, W. H., and R. H. GUCKERT. 1971. A Re-evaluation of the Recent Unionacea (Pelecypoda) of North America. — *Malacologia*, 10(2): 333-355, text figures 1-3.
- JOHNSON, R. I. 1970. The Systematics and Zoogeography of the Unionidae (Mollusca: Bivalvia) of the Southern Atlantic Slope Region. — *Bulletin of the Museum of Comparative Zoology*, 140(6): 263-450, tables 1-4, text figures 1-5, plates 1-22.
- MARSHALL, W. B. 1890. Beaks of Unionidae Inhabiting the Vicinity of Albany, New York. — *Bulletin of the New York State Museum*, 2(9): 167-189, figures 1-18.
- MATTESON, M. R. 1948. Life History of *Elliptio complanatus* (Dillwyn, 1817). — *American Midland Naturalist*, 40(3): 690-723, tables 1-2, text figures 1-16.
- MAZYCK, W. G. 1913. Catalog of Mollusca of South Carolina. — *Contributions from the Charleston Museum*, No. II: xvi+1-39.
- MITCHELL, R. D. 1955. Anatomy, Life History, and Evolution of the Mites Parasitizing Fresh-Water of Mussels. — *Miscellaneous Publications, Museum of Zoology, University of Michigan*, No. 89: ii+1-41, tables 1-7, figures 1-6.
- ORTMANN, A. E. 1910. A New System of the Unionidae. — *Nautilus*, 23(9): 114-120.
- . 1911. A Monograph of the Najades of Pennsylvania [Parts I and II]. — *Memoirs of the Carnegie Museum*, 4(6): 279-347, text figures 1-8, plates 80-89.
- . 1912. Notes upon the Families and Genera of the Najades. — *Annals of the Carnegie Museum*, 8(2): 222-365, text figures 1-28, plates 18-20.
- . 1919. A Monograph of the Naiades of Pennsylvania. Part III. Systematic Account of the Genera and Species. — *Memoirs of the Carnegie Museum*, 8(1): 1-384, text figures 1-34, plates 1-21.
- PARODIZ, J. J., and A. A. BONETTO. 1963. Taxonomy and Zoogeographic Relationships of the South American Naiades (Pelecypoda: Unionacea and Mutelacea). — *Malacologia*, 1(2): 179-213, tables 1-4, maps 1-3, text figures 1-17.
- RAULERSON, C. L., and W. D. BURBANCK. 1962. The Life-Cycle and Ecology of *Elliptio hopetonensis* Lea (Abstract). — *ASB* [The Association of Southeastern Biologists] *Bulletin*, 9(2): 39.
- REARDON, L. 1929. A Contribution to Our Knowledge of the Anatomy of the Fresh-Water Mussels of the District of Columbia. — *Proceedings of the United States National Museum*, 75(2782): 1-12, plates 1-5.
- RICHARDS, H. G. 1950. Geology of the Coastal Plain of North Carolina. — *Transactions of the American Philosophical Society* (New Series), 40(Part 1): 1-83, tables 1-10, figures 1-76.
- SIMPSON, C. T. 1900. Synopsis of the Naiades, or Pearly Fresh-Water Mussels. — *Proceedings of the United States National Museum*, 22(1205): viii+501-1044, plate 18.
- . 1914. *A Descriptive Catalogue of the Naiades, or Pearly Fresh-Water Mussels* (Bryant Walker, Detroit), pp. xii+1-1540.
- VAN DER SCHALIE, H. 1953. Nembutal as a Relaxing Agent for Mollusks. — *American Midland Naturalist*, 50(2): 511-512.
- WALTER, W. M. 1956. Mollusks of the Upper Neuse River Basin, North Carolina. — *Journal of the Elisha Mitchell Scientific Society*, 72(2): 262-274, table 1, text figure 1.

## REVIEWERS OF THIS PAPER:

George M. Davis, Department of Malacology, Academy of Natural Sciences of Philadelphia.

C. W. Hart, Jr., Department of Limnology, Academy of Natural Sciences of Philadelphia.