MALACOLOGICAL

REVIEW

Fusconaia masoni (*Conrad* 1834) (*Bivalvia: Unionacea*) in
the Atlantic drainage of the southeastern United States.

S.L.H. FULLER

FUSCONAIA MASONI (CONRAD 1834) (BIVALVIA: UNIONACEA) IN THE ATLANTIC DRAINAGE OF THE SOUTHEASTERN UNITED STATES

Samuel L. H. Fuller

ABSTRACT

Fusconaia masoni (Conrad 1834), previously reported from the Savannah River system in Georgia and the Cape Fear River system of North Carolina, also occurs in the Ogeechee River system of Georgia. These are the first unequivocal records of this genus in the Atlantic drainage of eastern North America. A redescription of *F. masoni* is accompanied by discussions of its ecology, systematic relationships and zoogeography. Particular attention is paid to the systematic status of the closely allied genus *Lexingtonia* Ortmann 1914 and to the difficulty of classifying these genera and their relatives in any existing system of the Unionacea. The 2 genera (or their ancestors) probably entered the southern Atlantic drainage during confluence of the ancient Roanoke and Teays Rivers.

INTRODUCTION

Recent collections of freshwater mussels from the southeastern United States include specimens which conform to the concept of *Fusconaia* Simpson 1900 as advanced by Ortmann (1912: 239, 1919: 6). This material constitutes the first intimation that this genus occurs in the Atlantic drainage of eastern North America since Simpson (1900: 785; 1914: 868), unavoidably ignorant of its anatomy and beak sculpture, hesitantly placed *Unio pumilus* Lea 1838 from the Cape Fear River system of North Carolina in his section *Fusconaia* of the genus *Quadrula* Rafinesque 1820. Following Fuller (1971, 1972), this species is here referred to *Unio masoni* Conrad 1834 from the Savannah River system of Georgia and South Carolina, the earliest available and conchologically appropriate taxon whose type locality lies within the range of this species as currently understood. This species has occasionally been reported in the literature as a member of the genus *Pleurobema* Rafinesque 1819 or the genus *Lexingtonia* Ortmann 1914 (usually as *L. subplana* (Conrad 1837)).

Much of the present paper is devoted to a redescription of *Fusconaia masoni* (Conrad 1834), with notes on its ecology and systematic relationships, but of equal interest are the zoogeographic implications of these first unequivocal records of *Fusconaia* in the Atlantic drainage of the United States and Canada. Accordingly, the origins of *Fusconaia* and *Lexingtonia*, the nature of their close relationship, and the role of former stream confluence in their penetration of the Atlantic drainage are explored in some detail.

TERMINOLOGY AND PROCEDURES

Abbreviations: ANSP = Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A. MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. USNM = United States National Museum [National Museum of Natural History, Smithsonian Institution], Washington, D.C., U.S.A.

Terminology: The expression *tetragenous* will be used in this paper to denote mussels having marsupial structure in all demibranchs of the (female) gills; *digenous* will refer to those whose marsupial structure is restricted to the outer demibranchs.

The expression *fusconaiad* will refer to the unionine genera with subcylindrical egg masses (e.g., Figs. 5-7). Fusconaiad bivalves are *Fusconaia* (Ortmann, 1912: 239), *Lexingtonia* (Ortmann, 1914: 29; 1921: 84) and *Quincuncina* Ortmann 1922 (Ortmann, *in* Ortmann & Walker, 1923: 2). *Cyclonaias* Pilsbry 1922 is a possible 4th fusconaiad genus, since Ortmann (1919: 57-58) described subcylindrical egg masses in the outer demibranchs of *Rotundaria* [=*Cyclonaias*] *tuberculata* (Rafinesque 1820) and noted that its beak sculpture is a combination of the concentric, double-loop and zigzag types. Similar sculpture is also found in *Quincuncina* (Ortmann & Walker, 1923: 2-3).

Sterki (1898: 19, 28-29) described "cylindrical" egg masses from certain *Unio* now placed in *Strophitus* Rafinesque 1820 and *Cyprogenia* Agassiz 1852, but additional peculiarities of the egg masses, marsupia and other characters consign these genera to Ortmann's (1910, 1911, 1912) concepts of the subfamilies Anodontinae and Lampsilinae, respectively.

Collection and preparation of material: Most specimens were taken by hand and insensitized in 2 or 3 days' time with a Nembutal solution of less than 1% by volume in tap water (a variation of the method of van der Schalie, 1953). In the absence of a better fixative, the Cape Fear River specimens were killed and graded up in ethanol to a storage strength of 70% ethanol by volume, with minimal distortion of the soft parts. All other material was fixed in a formalin solution of about 5% by volume in tap water before storage in ethanol.

Both demibranchs of the left gill in every specimen were examined with transmitted light under 10X-60X power of a Bausch & Lomb dissecting microscope. The gill wall was teased away to reveal the structure and spacing of the interlamellar septa. The material has not been examined for histological evidence of the hermaphroditism known to occur in some *Fusconaia* (Sterki, 1898: 31; van der Schalie, 1970: 95).

Material examined: All specimens of *Fusconaia masoni* used in this study are deposited in the alcoholic collections of the Department of Malacology at the Academy of Natural Sciences of Philadelphia. Three populations were sampled:

1) Cape Fear River system: Cape Fear River drainage. Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles southwest of Slocomb and about 6 miles north-northeast of Fayetteville, Cumberland County, North Carolina. ANSP A2267 — 2 females; 19 September 1969; S. L. H. Fuller, collector. ANSP A2268 — 2 males; 11 June 1970; S. L. H. Fuller, collector. ANSP A2269 — 6 females (3 ovigerous); 11 June 1970; S. L. H. Fuller, collector.

2) Savannah River system: Brier Creek drainage. Mill Race at Georgia state route 23, about 2 miles north of Sardis, Burke County, Georgia. ANSP A2263 — 3 females (all ovigerous); 8 July 1971; S. L. H. Fuller, collector. ANSP A2264 — 1 male; 8 July 1971; S. L. H. Fuller, collector. ANSP A2265 — 2 females (1 ovigerous); 18 July 1971; S. L. H. Fuller, collector.

3) Ogeechee River system: Buckhead Creek drainage. Magnolia Springs outfall, about 3 miles south-southwest of Perkins, Jenkins County, Georgia. ANSP A2266 — 2 females (1 ovigerous); 18 July 1971; J. W. Richardson, collector.

RESULTS

Redescription of *Fusconaia masoni*: The shell is rather small, at least 64 mm (about 2 1/2 inches) in length; it is sub-rhomboid in outline, thin but strong, of rather great height (ranging from about 3/5 to about 4/5 of the length), moderately inflated (width about 2/5 of the length) and without apparent sexual dimorphism. The beaks are slightly prosogyrous, prominently elevated above the dorsal margin and located anteriad of center. The beak sculpture consists of 3 or 4 subconcentric bars of about equal weakness, almost straight and very weak across the disk, obsolete anteriorly and weakly tuberculate at the posterior ridge, where they turn sharply dorsad and quickly disappear. Later bars are no more than weak tubercles at the ridge. The adult shell is without sculpture. The brownish-yellow periostracum, sometimes partially obscured by foreign deposits, is decorated with concentric low folds and ridges, which presumably mark the ends of growth periods.

The posterior ridge is prominent and broadly rounded. The posterior slope is weakly concave and usually scored by 2 shallow grooves subparallel to the ridge, which cause little or no biangulation of the posterior margin. The hinge is yellowish-brown, rather broad, opisthodetic, short (about 1/4 of the shell length) and raised prominently above the dorsal margin for most of its length.

The dorsal margin descends posteriorly; before the beaks it is short, often descendant, and usually forms an obtuse but distinct angulation with the anterior margin, which is often very nearly straight. The ventral margin is an even,

shallow curve which meets the dorsal margin in a blunt point just below the mid-line. Older individuals may be slightly produced post-basally.

The hinge plate is rather narrow, extending about 1/2 of the shell length. The interdentum is short and (for a *Fusconaia*) very narrow. The nymphal callosities are conspicuous bars, about 1/2 of the length of the lateral teeth, which project sharply dorsad. The laterals are short (about 1/3 of the shell length), straight or very slightly decurved, blade-like and, descendant in the rear, set obliquely to the dorsal margin. There is one lateral in the right valve; 2 in the left, of which the lower is somewhat longer and more broad. There are 2 pseudocardinal teeth in the left valve; each is irregularly sub-deltoid, strong and conspicuously subdentate on its dorsal surface. The posterior tooth is sub-umbonal and the more strongly developed and subdentate. There is one pseudocardinal in the right valve and often a vestige of a sub-umbonal tooth on the interdentum. The right pseudocardinal is larger, longer and usually more peg-like than those of the left valve and is not subdentate. The interlocking surfaces of all teeth are variably rugose (particularly the pseudocardinals) or finely ribbed (particularly the laterals); rugosity extends onto the right interdentum.

The nacre is smooth throughout, with no unusual sulcations. The beak cavity is deep. The pallial line is narrow and faintly impressed; it forms an even curve subparallel to the shell margin, except for an occasional shallow concavity at the postbasal corner of the posterior adductor muscle scar. The anterior muscle scars are impressed, particularly along their posterior margins, but the posterior scars, although clearly outlined, are scarcely or not impressed. The dorsal muscle scar is an oblique grooved ridge on the interdentum within the beak cavity. The nacre is thickened and white over about the anterior 2/3 of the shell, especially at the bases of the pseudocardinal teeth and below and before the pallial line. The nacre becomes iridescent posteriorly and is often so thin that the growth rests in the periostracum show clearly through.

The free mantle margins are trilobate and undifferentiated, except at the anal and branchial apertures. The branchial bears 2 somewhat intermingled rows of papillae. Those of the inner row rise subapically from the inner lobe; they are longer, stouter, sub-tentaculate, fused to the mantle baso-laterally and spaced unevenly and discontiguously for the most part. Ordinarily they terminate simply, but biramous individuals are common; rarely the form is dendritic, with as many as 5 processes. Papillae of the outer row rise apically from the inner lobe; they are much shorter, more slender, comparatively stiff, scarcely fused to the mantle baso-laterally, arranged closely and at rather equal intervals and simple. In life the inner papillae are erected obliquely from the mantle and almost interdigitate across the branchial aperture; the outer papillae lie sub-parallel to the mantle, projecting posteriad. The papillae of the anal aperture resemble those of the outer branchial row; their disposition in 2 rows is obscure.

The branchial and supra-anal apertures approach twice the length of the anal. Although in life the inner lobes of the apposing mantle margins lie tangentially between the anal and branchial apertures (effecting their functional separation), there is no mantle fusion between them. There is a high and strong fusion of the inner lobes between the anal and supra-anal apertures. A similar connection closes the supra-anal dorsally for much of its height, and the remaining opening may be broken up by one or more additional fusions.

The inner demibranch is the greater in length and height; it hangs slightly below the outer behind and greatly below anteriorly, and it extends farther anteriad. Sweeping sharply dorsad, its anterior margin is truncate. Anteriad of the posterior margin of the foot, the dorsal margin of the inner demibranch is free of the

visceral mass, excepting a brief attachment anteriorly. The ventral margin of the inner demibranch is thickened and grooved; in the outer demibranch it is thin and sharp. Male water tubes comprise about 12 gill filaments; female, about 6. Male septa are delicate, the thickness being no more than the breadth of a single filament. Female septa are sturdy, with a thickness equal to the combined breadths of several filaments.

Both demibranchs are marsupial in the female. Egg masses occur in all water tubes of the ovigerous female, excepting a few lying farthest anteriad and posteriad. These uncharged regions may be more extensive in the inner demibranch. Egg masses extend most of the height of the water tubes. They are very sturdy; aborting under stress, some may break transversely, but their natural form is otherwise retained. There are about 30 to 50 sub-cylindrical egg masses in each demibranch. Ten strands of ova can usually be distinguished at the midpoint of the egg mass, where a layer of 4 strands is sandwiched between 2 layers of 3 strands each; in other words, 8 strands are more or less equally spaced around, and parallel to, the remaining 2. At its midpoint the mass is suboval in cross sectional outline, but, where the strands intermingle at the dorsal and ventral ends of the mass, 6 strands are often ranged more or less circularly and hexagonally about a central seventh. The egg is subspherical, variable in diameter (about 0.15 to 0.20 mm in preservation), translucent, with a subcentral opaque embryo, usually vividly pigmented with a red or orange-red color. The marsupia are slightly swollen; the outer one retains the sharp distal margin of the demibranch. The glochidium is unknown.

Outer oral palpi are larger than the inner; posterior margins of the palpi are fused for about the proximal 1/3 of their lengths. The palpi are sub-falciform in outline, longitudinally grooved on their apposing surfaces, bluntly attenuate distally and slightly overlap the anterior margins of the inner demibranchs.

Adductor muscles are irregularly sub-oval in cross section; the pedal retractors are tiny. The pallial musculature is thick and extensive. The dorsal muscles are short, strong bars set obliquely on the apposing surfaces of the mantle within the beak cavities. The foot is rather long and slender, curving slightly dorsad in life. The posture of the anal hood forces discharge ventrad into the suprabranchial cavity before the anal aperture; the hood has reflected lips with scalloped margins. The dorsal crest of the mantle between the lateral teeth is short, very high, and subrectangular in lateral outline.

Most of the animal is a soiled or yellowed white (the coloration intensified in preservation). In life, regions of heavy musculature are comparable to the ova in color; these include the pedal, pallial, adductor, papillary, and pedal protractor and retractor muscles. The mantle is darkly mottled among the bases of the papillae. A band of similar pigment lies sub-parallel to the mantle margin a short distance before the branchial papillae. Dark mottlings may occur about the animal generally.

Habitat: All Cape Fear River specimens of *Fusconaia masoni* were secured immediately downstream of a jam of fallen timbers and brush, which broke the current so that a sheltered, shallow area was created with a sand, mud and silt bottom. These conditions are at variance with the optimum for Mississippi basin *Fusconaia*, which, according to numerous authorities, prefer substrates of gravel or hard sand, often in swift and deep waters. Nonetheless, the Cape Fear material is less conchologically depauperate than specimens from Mill Race in the Savannah River system which is a tiny creek with a predominantly sand bottom. Specimens from the Magnolia Springs outfall in the Ogeechee River system were far larger and heavier than those at the latter 2 localities. The abundance of

pleurocerid snails in the outfall is another indication that this water is relatively pristine, well oxygenated and rich in calcium. Clearly, radical adjustment in habitat tolerance was involved as *Fusconaia* spread to the Atlantic drainage.

Host: Coker *et al.* (1921: 152-153) reported centrarchid and anadromous clupeid fishes as hosts of certain Mississippi basin *Fusconaia*, but the hosts of other members of the genus, including *F. masoni*, are unknown. Since the genus is so widespread, there is no reason to assume that Atlantic drainage hosts are related to those employed in the Mississippi basin in any way other than ecological suitability.

Parasites: Although infestation with *Unionicola* was commonplace among some naiad species associated with *Fusconaia masoni* (especially in the Cape Fear River), evidence of infection with neither water mites (Arthropoda: Acari: Unionicolidae) nor "distomids" (Platyhelminthes: Trematoda: Digenea) has been found in the *F. masoni* examined.

DISCUSSION

Systematic relationships

Superfamily: Although the larva of *Fusconaia masoni* is unknown, it is safe to assume that, as in other *Fusconaia*, the larva is a glochidium (see, e.g., Ortmann, 1919: 19). Accordingly, *F. masoni* is best placed in the superfamily Unionacea (see Heard & Guckert, 1971), but the correct family for this genus and species is uncertain.

Family: The better unionacean classifications, i.e., those of Ortmann (1910, 1911, 1912) and of Heard & Guckert (1971), based on imaginative analyses of a wide variety of somatic and reproductive characters, do not emphasize the role of ancestral fusconaiad mussels in a history in which one of the turning points among non-hyriid unionaceans was restriction of marsupial function to the outer demibranchs. This development, however, would have been a disaster had there not already begun a tendency toward the "elastic" marsupium, a device which permitted a reduction in the number of marsupial demibranchs without jeopardizing reproductive capacity. This chronology is reflected in genera like *Quadrula*, whose elastic marsupia accomodate broad egg masses, but which has not relinquished the marsupial function of the inner demibranch. Similarly, the tetragenous genera *Fusconaia* and *Quincuncina* reflect an intermediate stage in the development of marsupial elasticity, where a more narrow egg mass (i.e., the subcylindrical type) is necessitated by water tubes whose septa are capable of only moderate lateral extension. The genus *Lexingtonia* is the only surviving representative of one of the stocks whose marsupial demibranchs were reduced in number before adequate marsupial elasticity was realized; the relict distribution of this genus (see below) emphasizes the consequences of the lowered reproductive potential explicit in this unfortunate evolutionary experiment. Thus it appears that the elasticity of marsupial demibranchs has had greater biological significance than has had the number of them. I further suspect that, in most unionine stocks, marsupial elasticity had been developed before the number of marsupial demibranchs was reduced.

From the genetic point of view, the latter conclusion is an aprioristically logical one. The genetic change involved in the genesis of the elastic marsupium would be minor in that greater elasticity is effected merely by increasing the quantity of a single type of tissue (see Ortmann, 1911: 291). Loss of marsupial function in a demibranch, however, is a more complex, essentially qualitative adjustment, because the demibranch would have to be restructured and the ova

prevented from entering it. This would be a major genetic undertaking. Increased marsupial elasticity could easily and advantageously have developed at any time, regardless of whether or not reduction in number of marsupial demibranchs was happening concurrently, but the latter development was ever a disadvantage without the former.

If it is assumed that chronologically (not morphologically) primitive characters best reflect natural relationships, then among most (if not all) surviving unionine groups, marsupial incubative capacity is a systematic character more significant than the number of marsupial demibranchs. Accordingly, use of the latter character in the Heard & Guckert (1971) system as a discriminant between and among families is suspect. Specifically, in placing *Fusconaia* and *Quincuncina* in the tetragenous Amblemidae and *Lexingtonia* in the digenous Unionidae, Heard & Guckert have disguised what I feel is a much closer relationship among the 3 genera. In placing all 3 close to one another in the same subfamily (i.e., Unionidae: Unioninae), Ortmann was, I suspect, much closer to the truth. I would prefer, in addition, to see the fusconaid stage in unionacean evolution given taxonomic recognition at some supra-generic rank, much as Heard & Guckert, in recognizing an amblemid subfamily Gonideinae, have also recognized the stage in the development of the interlamellar septum that is reflected in the dorsally perforate septa of *Gonidea angulata* (Lea 1838) of the western United States and Canada (Ortmann, 1916). Creation of a new subfamily or tribe for the fusconaiad genera seems warranted. Formal introduction of such a taxon, however, is beyond the scope of the present study, whose primary goal is not to gather materials toward another higher unionacean classification.

Subfamily: In the Ortmann system of the naiades, *Fusconaia masoni* would be placed in the Unioninae, because gill structure undergoes no qualitative changes during the breeding season; for example, the sharp distal margins of the outer demibranchs remain so when the organism is gravid (Fig. 11). Although the feature is not universal among unionine genera, it should be added that the *F. masoni* breeding season appears to be short: ovigerous females were secured 11 June, but those taken 19 September were barren.

Genus: *Fusconaia masoni* is a fusconaiad mussel by virtue of its subcylindrical egg mass (Figs. 5-7) and water tubes. *Lexingtonia* is the only genus which can be confused with *Fusconaia*, but the latter has less well developed beak sculpture (Table 1, Fig. 10) and the tetragenous marsupial condition (Table 1, Fig. 11). Although there are cases of a digenous mussel's displaying ova in both demibranchs, this condition rarely involves tetragenous marsupial structure (Ortmann, 1919: 71). Since all known females of *F. masoni* have tetragenous marsupial structure, this species should not be thought an atavistic *Lexingtonia*. Apparently the only fusconaid genus in the Apalachicola River system, where it is endemic, (the tetragenous) *Quincuncina* can be distinguished from either genus on account of its remarkable shell sculpture.

Fusconaia masoni has additional peculiarities characteristic of — but not confined to — the genus. The shell is sub-rhomboidal in lateral outline, the posterior ridge is well developed, and umbones are raised well above the lateral margin (Figs. 8-9). The palpi extend somewhat beyond the truncate anterior margins of the inner demibranchs (Figs. 2, 11), and the branchial papillae are dendritic for the most part (Fuller, 1971). Much of the musculature and reproductive tissue is highly colored in life.

Specific identity: Referral of Atlantic drainage *Fusconaia* to *Unio masoni* Conrad 1834 of the Savannah River system is discussed by Fuller (1972).

Intrageneric relationships: Juveniles of *Fusconaia escambia* Clench & Turner
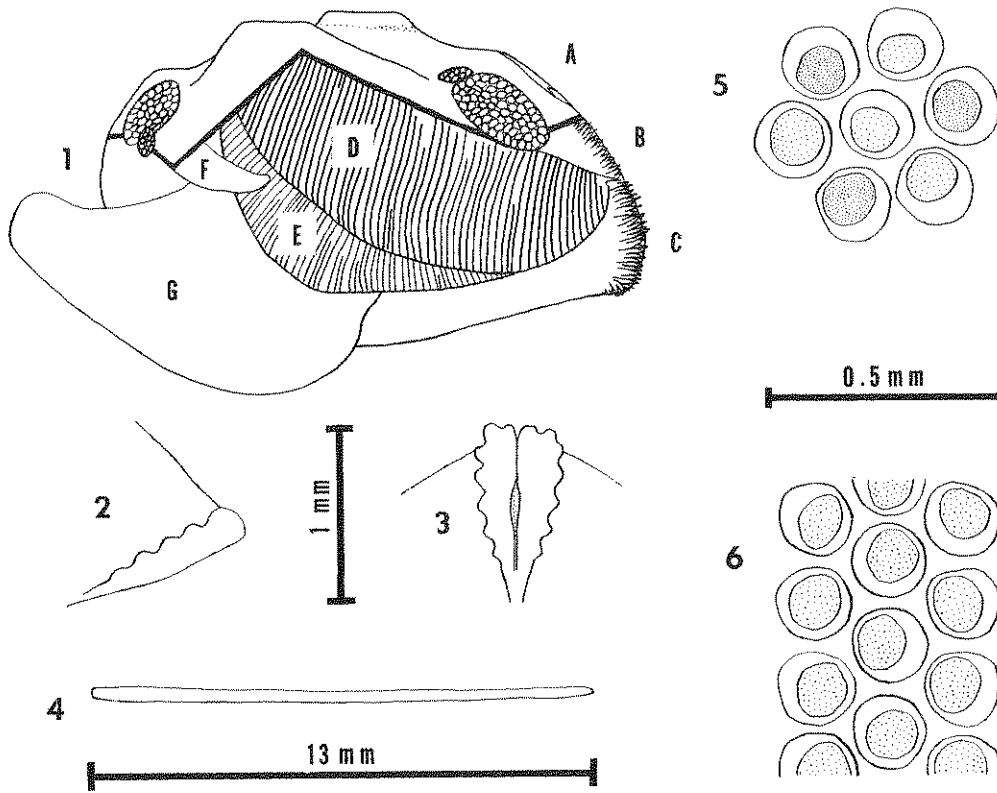
FIGS. 1-6. *Fusconaia masoni* (Conrad 1834), ♀, ANSP A2269, Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles SW of Slocomb and about 6 miles NW of Fayetteville, Cumberland County, North Carolina, 11 June 1970. 1, Animal, left lateral view with mantle removed at adductor muscles and along heavy line. A-C, supra-anal, anal and branchial apertures, respectively. D-E, outer and inner demibranchs, respectively. F, outer oral palpus. G, foot. 2X. 2-3, Anal hood, lateral and posteroventral views, respectively. 4, Egg mass. 5. Egg mass, transverse cross section near dorsal or ventral end of egg mass as shown in Fig. 4. 6, Egg mass, lateral view near longitudinal midline.

TABLE 1. Contrasting features of *Fusconaia* and *Lexingtonia* (Ortmann, 1912: 239; 1914: 29; 1919: 6; 1921: 84; Boss & Clench, 1967: pl. 15, fig. 1).

Character	Genus	
	Fusconaia	*Lexingtonia*
Beak sculpture	3-4 weaker bars	6-9 stronger bars
Marsupium	tetragenous	digenous

1956 resemble Atlantic drainage fusconaids, but the adult *F. escambia* is so high as to be almost square, and its shell is far more solid, with a massive hinge plate (Clench & Turner, 1956: pl. 7, figs. 3-4). Known only from the Escambia and Yellow Rivers of the eastern Gulf drainage (Johnson, 1969: 35), *F. escambia* is more reminiscent of *Fusconaia* of the western Gulf drainage and the Mississippi basin.

Fusconaia masoni is conchologically unlike *F. succissa* (Lea 1852), which is rather widespread in the eastern Gulf drainage west of the Apalachicola River system (Clench & Turner, 1956: 151-152, pl. 7, fig. 5). The vivid coloration in reds and oranges of musculature and reproductive tissues of *Fusconaia* in general is muted in the occasional *F. succissa*, which may be extensively flushed with browns and blacks (Ortmann, 1923: 74). This darker pigmentation occurs in *F. masoni* and is commonplace in the group of *F. barnesiana* (Lea 1838) of the upper Tennessee River drainage (Ortmann, 1917: 61-62). Possibly these 3 forms constitute a natural group within the genus.

Unio utriculus Lea 1845 is the other Carolinian mussel placed by Simpson (1900: 787) in his section *Fusconaia*. The shell (Lea, 1848: pl. 1, fig. 3) bears little resemblance to a fusconaiad, and Simpson (1914: 787) later referred this form to *Pleurobema*. Lea (1848: 69) wrote that his original specimens came "...from North Carolina, and no doubt from one of the tributaries of the Tennessee River." Johnson (1970: 300) agreed that *utriculus* is not of the Atlantic drainage. The species' generic position is uncertain because its anatomy remains unknown.

Finally, I must call attention to the similarity between *Fusconaia flava* (Rafinesque 1820) of the Mississippi basin and less depauperate populations of *F. masoni* (such as the one in the Magnolia Springs outfall). The similarity is so striking as to provoke the suspicion that these 2 taxa are conspecific, *F. masoni* being only the Atlantic drainage form of *F. flava* and expressing the latter's conchological character in only the most favorable habitats.

Similar species: Aside from the occasional similarity to *Fusconaia flava*, *F. masoni* is conchologically closest to Atlantic drainage populations of *Lexingtonia*. As discussed above, characters of the beak sculpture and soft anatomy (Table 1) will separate the genera in question, but excellent material is required. These features of most museum specimens are destroyed; this has led to the perennial confusion of *Lexingtonia* with other genera (rarely with *Fusconaia*) and to the failure to recognize *F. masoni* as a unique entity.

Status of *Lexingtonia*: As indicated above, I view *Fusconaia* and *Lexingtonia* as distinct genera representing fundamentally different lines of naiad evolution. On the other hand, we but imperfectly understand the evolutionary history of North American Unionacea. Since mussels exhibit few variable morphological features, generic concepts commonly depend upon very few characters. We lack additional data (histological, cytogenetic, immunological) which might extend or reject some of the many concepts that are currently recognized. A broader concept of *Fusconaia*, for example, might reasonably embrace subgenera *Fusconaia s.s.* and *Lexingtonia*. In any case, no viewpoint which recognizes the clear biological differences between *Fusconaia* and *Lexingtonia* would discredit the zoogeographic ideas advanced below.

Frierson (1927: 44) and Johnson (1970: 300) interpreted *Lexingtonia* as a subgenus of *Pleurobema* which has a compressed egg mass (Ortmann, 1919: 71). As long as reproductive characters are thought to be conservative, the nature of the egg mass should be accorded diagnostic value at the generic level, at least. Identification of *Lexingtonia* with *Pleurobema* involves a broad generic concept which obscures important biological differences. Were there supporting evidence
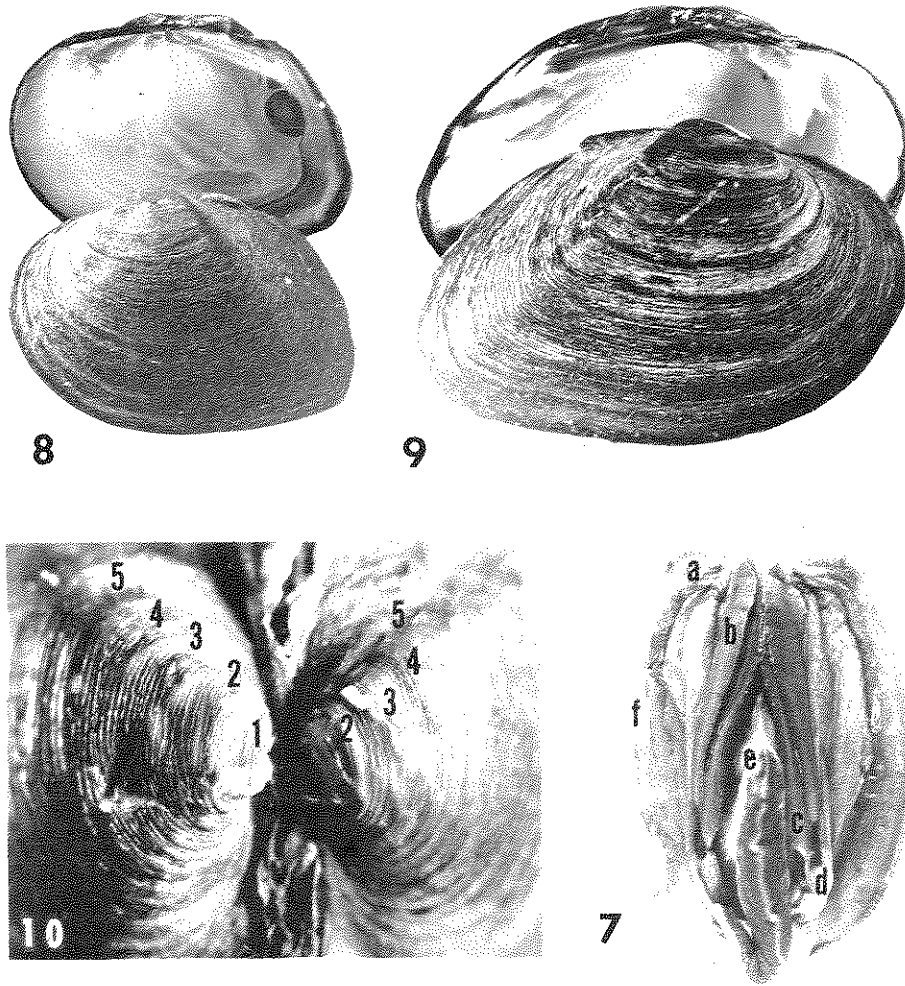
FIGS. 7-10. *Fusconaia masoni* (Conrad 1834), ♀, ANSP A2269, Cape Fear River, 0.1 mile downstream from confluence with Carvers Creek, about 3 miles SW of Slocomb and about 6 miles NW of Fayetteville, Cumberland County, North Carolina, 11 June 1970. 7, Animal, ventral view with mantle reflected dorsad. a, papillae of left branchial aperture. b, ovigerous left outer demibranch (note sharp distal margin). c, ovigerous right inner demibranch. d, right outer oral palpus. e, foot. f, left mantle. 1.25X. 8, Length 39.0 mm, height 27.5 mm, width 16.5 mm. Age about 10 years. 1.25X. 9, Length 53.0 mm, height 33.5 mm, width 20.0 mm. Age about 13 years. 1.25X. 10, Beak sculpture. Asymmetrically disposed and developed annuli 4-5 probably are not true juvenile umbonal bars. 6.25X.

from a variety of disciplines, the entire system of Ortmann's (1910, 1911, 1912) Unioninae might be overhauled to advantage. Unfortunately, the conservative approach based only upon certain (usually conchological) characters has not been consistently applied. For instance, Johnson and Frierson both distinguished between *Pleurobema* and *Elliptio* Rafinesque 1820, whose similar egg masses (Ortmann, 1912: 263, 269, 271) imply closer relationship than exists between *Pleurobema* and any fusconaiad genus.

Zoogeography

Fusconaia has invaded previously glaciated areas to a lesser extent than ecologically comparable genera like *Pleurobema*. Although rather common in the Lake Ontario drainage (Harman, 1970), *Fusconaia* evidently has failed to become established in the St. Lawrence River system; early St. Lawrence records (as in Simpson, 1900) apparently depended upon confusion with *Pleurobema*. *Fusconaia* does not occur elsewhere in the Atlantic drainage north of the terminal moraine (numerous authorities). Recognition of *F. masoni* in the Cape Fear, Savannah and Ogeechee River systems confirms occurrence of the genus in the Atlantic drainage south of the moraine. *Fusconaia* has been reported throughout the Mississippi basin and the Gulf drainage (numerous authorities).

It is unlikely that absence of *Fusconaia* from the Apalachicola River system (Clench & Turner, 1956: 106) is due to extinction, because of the rich naiad fauna revealed by them. Accordingly, it is certain that *Fusconaia* did not reach the Atlantic drainage through the generally accepted confluence of Savannah River system headwaters with those of the Chattahoochee River, a major tributary of the Apalachicola in northwestern Georgia. Although the fusconaid genus *Quincuncina* is represented in the Apalachicola system, it is inconceivable that even a remarkable depauperization could have realized *F. masoni* from an ancestor close to the heavily sculptured *Quincuncina*. Limited fossil evidence bears only negatively on these points: La Rocque (1967: 169) recorded a single naiad (possibly *Lampsilis* Rafinesque 1820) from Pleistocene deposits at Ladds in Bartow County, northwestern Georgia, within the Etowah River watershed of the Coosa-Alabama River system.

There are certain avenues and mechanisms of dispersal which have *not* afforded *Fusconaia* any access to the Atlantic drainage. (1) Modern *Fusconaia* clearly did not enter the Atlantic drainage during the presumed confluence of the Susquehanna River system with headwaters of the Monongahela River in the Ohio River drainage of central Pennsylvania (see Ortmann, 1913: 368-371). (2) According to Pilsbry (1897), fossil mussels from Pleistocene (Henderson, 1935: 94) deposits near the Delaware River at Fish House in Camden County, southern New Jersey, include no fusconaiads and show affinities to the modern Great Lakes fauna. Simpson (1894) reported no fusconaiads among fossil mussels from Toronto, Canada. There is, then, no indication that fusconaiads have ever inhabited the Atlantic drainage north of the terminal moraine. (3) Mesozoic or early Tertiary invasion of Virginia, the Carolinas and Georgia by ancestors of modern Atlantic drainage fusconaiad genera is unlikely, because the present fauna reflects nothing of the inevitable radiation of so ancient a stock. (4) Human introduction of glochidially infected host fish is out of the question, because fusconaiad mussels were being described from the Atlantic drainage long before inauguration of fish stocking at the close of the last century (Cornell, pers. comm.) as an aid in wildlife management. Moreover, human introduction could not account for the great range of fusconaiads in the southern Atlantic drainage as represented by Johnson (1970: 301-302), some of whose records of "*Pleurobema*" *masoni* include *Fusconaia*, as well as *Lexingtonia*. (5) As noted above, *F. masoni* is not an atavistic *Lexingtonia*. (6) Although still resurrected from time to time, the notion that overland transport by animals is important in naiad distribution was discredited by van der Schalie (1945).

In view of these considerations, it is clear that penetration of the Atlantic drainage by *Fusconaia* was realized exclusively by dispersal across the Appalachian Mountains on glochidially infected hosts. The assumption that the Tennessee River drainage has contributed directly to the Atlantic drainage naiad fauna does

furnish an explanation of the fact that *Lexingtonia* has been recorded in only these 2 drainages. However, in spite of the slight resemblance of *F. masoni* to *F. barnesiana*, there is no geological evidence that an Atlantic drainage river system has ever captured Tennessee headwaters or that mussels could have entered the Atlantic drainage by subterranean migration of hosts in the Appalachians.

Johnson (1970: 379) called attention to the similarity of *Villosa constricta* (Conrad 1838) of the Atlantic drainage to *V. vanuxemensis* (Lea 1838) of the Tennessee and Cumberland River drainages. This would support a theory of Tennessee and Atlantic drainage intercourse were it not that a close anatomical relationship between these *Villosa* has not been demonstrated and that the genus is represented in the Ohio River drainage (see Ortmann, 1919: 261-270).

A more credible explanation of the known distribution of *Lexingtonia* assumes that the ancestral Mississippi basin fusconaiad stock had already differentiated in the directions of modern genera by the early Pleistocene, when there arose an opportunity to invade the Atlantic drainage as the ancestral Roanoke River system broke through the Appalachians in western Virginia and captured headwaters of the Teays (ancestral New) River, after which the Roanoke suffered piracy by the early James River system (Ross, 1969, gave a detailed chronicle of these events). This opportunity was exploited by precursors of *Fusconaia* and *Lexingtonia*, and the remarkably similar adult shells of modern Atlantic drainage fusconaiads developed as common responses to the unaccustomed rigors of life in the mud and sand floors of the comparatively turbid, sluggish and lime-poor streams of the Piedmont and Coastal Plain. Meanwhile, the ancestors of *Fusconaia* speciated successfully throughout the Mississippi basin and spread to the Gulf drainage. This was accomplished at the expense of the *Lexingtonia*-type, which appears to have died out beyond the Atlantic drainage except for the relict *L. dolabelloides* (Lea 1840) of the Tennessee drainage (see Ortmann, 1921: 83-85).

This account has the added advantage of (1) suggesting why shells of *Lexingtonia dolabelloides* resemble Mississippi basin *Fusconaia* more than fusconaiads of the Atlantic drainage; (2) indicating why *Lexingtonia* has never been detected in the Ohio River drainage; and (3) precluding dissection of Ortmann's concept of *Lexingtonia* on the unwarranted assumption that it embraces convergent organisms of different lineages in the Atlantic and Tennessee drainages.

No other theory so persuasively accounts for the distributions (Johnson, 1970: 301, 379-380) of *Villosa constricta* and another exclusively Atlantic drainage species, *Pleurobema collina* (Conrad 1836). These species must have evolved from ancestors which entered the Atlantic drainage through the Roanoke and James River systems and spread southward — but not so far as the Savannah system, so there is no possibility that they reached the Atlantic drainage from the Apalachicola system.

Lasmigona subviridis (Conrad 1835) is another species whose distribution reflects former confluence of the Atlantic and ancestral upper Ohio River drainages. This species occurs in the New and Greenbrier Rivers of the latter drainage and throughout the Atlantic drainage from the Hudson River system of New York through the Savannah River system, but *Lasmigona* is not represented in the Apalachicola River system (Johnson, 1970: 282, 285, 345-346). *L. subviridis* doubtless originated in the Atlantic drainage, failed to reach the Apalachicola and, as originally proposed by Ortmann (1913: 372), used the Roanoke-Teays confluence for *westward* dispersal.

SUMMARY

Notice is taken of the first fully substantiable records of the freshwater mussel genus *Fusconaia* Simpson 1900 (Mollusca: Bivalvia: Unionacea) in the Atlantic

drainage of eastern North America. Detected in the Cape Fear, Savannah and Ogeechee River systems (i.e., in Georgia and North Carolina), the specimens are identified with *Unio masoni* Conrad 1834 from the Savannah system. The term fusconaiad is introduced and defined. The organism is redescribed under the combination *Fusconaia masoni* (Conrad 1834). Characters of the beak sculpture and reproductive anatomy confirm the generic diagnosis and are required to separate this species from Atlantic drainage populations of the closely related *Lexingtonia* Ortmann 1914. The glochidial host of *F. masoni* is unknown. The difficulties in classifying the fusconaiad genera below the superfamily level are discussed. The legitimacy of a generic concept of *Lexingtonia* is defended. It is proposed that precursors of modern Atlantic drainage *Fusconaia* and *Lexingtonia* migrated from the ancestral New River drainage during its former confluence with the Roanoke River system.

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LITERATURE CITED

BOSS, K. J. & CLENCH, W. J. 1967. Notes on *Pleurobema collina* (Conrad) from the James River, Virginia. *Occ. Paps. Molls.*, 3(37): 45–51, pl. 15.

CLENCH, W. J. & TURNER, R. D. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwanee River. *Bull. Fla. St. Mus.*, *biol. Sci.*, 1(3): 97–239, pls. 1–9.

COKER, R. E., SHIRA, A. F., CLARK, H. W. & HOWARD, A. D. 1921. Natural history and propagation of fresh-water mussels. *Bull. U.S. Bur. Fish.* [for 1919–1920], 37: 75–181, tables 1–4, text figs. 1–14, pls. 5–21. Issued as Document 893 on 2 May 1921.

FRIERSON, L. S. 1927. *A classified and annotated check list of the North American naiades*. Baylor Univ. Press, Waco, Texas. p 1–111.

FULLER, S. L. H. 1971. A brief field guide to the fresh-water mussels (Mollusca: Bivalvia: Unionacea) of the Savannah River system. *ASB* [Association of Southeastern Biologists] *Bull.*, 18(4): 137–146, text figs. 1–14, 1 pl.

FULLER, S. L. H. 1972. Type locality of *Unio pumilus* Lea 1838 (Bivalvia: Unionidae). *Nautilus*, in press.

HARMAN, W. N. 1970. New distribution records and ecological notes on central New York Unionacea. *Amer. Midl. Natur.*, 84(1): 46–58, text figs. 1–2, maps 1–8.

HEARD, W. H. & GUCKERT, R. H. 1971. A re-evaluation of the Recent Unionacea (Pelecypoda) of North America. *Malacologia*, 10(2): 333–355, text figs. 1–3.

HENDERSON, J. 1935. Fossil non-marine Mollusca of North America. *Spec. Paps. geol. Soc. Amer.*, 3: vii, 1–313.

JOHNSON, R. I. 1969. Further additions to the unionid fauna of the Gulf Drainage of Alabama, Georgia, and Florida. *Nautilus*, 83(1): 34–35.

JOHNSON, R. I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope region. *Bull. Mus. Comp. Zool.*, 140(6): 263–450, tables 1–4, text figs. 1–5, pls. 1–22.

LA ROCQUE, A. 1967. Pleistocene Mollusca of the Ladds Deposit, Bartow County, Georgia. *Bull. Ga. Acad. Sci.*, 25(3): 167–187.

LEA, I. 1848. Description of new freshwater and land shells. *Trans. Amer. Philos. Soc.* (new ser.), 10(1): 67–101, pls. 1–9.

ORTMANN, A. E. 1910. A new system of the Unionidae. *Nautilus*, 23(9): 114–120.

ORTMANN, A. E. 1911. A monograph of the najades of Pennsylvania [Parts I and II]. *Mem. Carnegie Mus.*, 4(6): 279–347, text figs. 1–8, pls. 80–89.

ORTMANN, A. E. 1912. Notes upon the families and genera of the naiades. *Ann. Carnegie Mus.*, 8(2): 222-365, text figs. 1-28, pls. 18-20.
ORTMANN, A. E. 1913. The Alleghenian Divide, and its influence upon the freshwater fauna. *Proc. Amer. Philos. Soc.*, 52(210): 287-396, pls. 12-14.
ORTMANN, A. E. 1914. Studies in najades [Part 3]. *Nautilus*, 28(3): 28-34.
ORTMANN, A. E. 1916. The anatomical structure of *Gonidea angulata* (Lea). *Nautilus*, 30(5): 50-53.
ORTMANN, A. E. 1917. A new type of the naiad (or nayad) genus *Fusconaia*. Group of *F. barnesiana* Lea. *Nautilus*, 31(2): 58-64.
ORTMANN, A. E. 1919. A monograph of the naiades of Pennsylvania. Part 3. Systematic account of the genera and species. *Mem. Carnegie Mus.*, 8(1): 1-384, text figs. 1-34, pls. 1-21.
ORTMANN, A. E. 1921. The anatomy of certain mussels from the upper Tennessee. *Nautilus*, 34(3): 81-91.
ORTMANN, A. E. 1923. The anatomy and taxonomy of certain Unioninae and Anodontinae from the Gulf Drainage. *Nautilus*, 36(3): 73-84.
ORTMANN, A. E. & WALKER, B. 1923. A new genus and species of American naiades. *Nautilus*, 36(1): 1-6, 1 pl.
PILSBRY, H. A. 1897. Geology of the mussel-bearing clays of Fish-House, New Jersey. *Proc. Acad. Natur. Sci.* [for 1896], 48: 567-570.
ROSS, R. D. 1969. Drainage evolution and fish distribution patterns in the southern Appalachians of Virginia. *In:* Holt, P. C., Ed., The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. *Res. Div. Monogr. Va. Polytech. Inst.*, 1: 277-292, text figs. 1-5.
SIMPSON, C. T. 1894. On some fossil unios and other fresh-water shells from the drift at Toronto, Canada, with a review of the Unionidae of northeastern North America. *Proc. U. S. natn. Mus.* [for 1893], 16: 591-595.
SIMPSON, C. T. 1900. Synopsis of the naiades, or pearly fresh-water mussels. *Proc. U. S. natn. Mus.*, 22(1205): viii, 501-1044, pl. 18.
SIMPSON, C. T. 1914. *A descriptive catalogue of the naiades, or pearly fresh-water mussels.* Bryant Walker, Detroit, Michigan. p xii, 1-1540.
STERKI, V. 1898. Some observations on the genital organs of Unionidae, with reference to classification. *Nautilus*, 12(2): 18-21 and 12(3): 28-32.
VAN DER SCHALIE, H. 1945. The value of mussel distribution in tracing stream confluence. *Paps. Mich. Acad. Sci., Arts, & Lett.*, 30: 355-373.
VAN DER SCHALIE, H. 1953. Nembutal as a relaxing agent for mollusks. *Amer. Midl. Natur.*, 50(2): 511-512.
VAN DER SCHALIE, H. 1970. Hermaphroditism among North American freshwater mussels. *Malacologia*, 10(1): 93-109, tables 1-3, text figs. 1-27.

SAMUEL L. H. FULLER

Department of Limnology
Academy of Natural Sciences of Philadelphia
Philadelphia, Pennsylvania 19103, *U.S.A.*