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THE MANTLE FLAP IN THREE SPECIES OF *LAMPSILIS* (PELECYPODA: UNIONIDAE)

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ABSTRACT

The purpose of this study was to review the morphological and general activity bases of mantle flapping in the North American unionid subfamily Lampsilinae and to explore experimentally some factors that may account for this striking activity: flapping mussels resemble small swimming fish. Morphological studies (chiefly on preserved material of *Lampsilis ventricosa* and *L. fasciola*), occasional field studies (in several counties in northwest Arkansas), and prolonged aquarium studies on living *L. ventricosa*, *L. siliquoidea* and *L. brevicula brittsi* were carried out from 1962 to 1965. It was found that the mantle flaps which are an extension of the inner lobe of the mantle edge just anteroventrad to the branchial siphon, are a permanent feature of the mature female. Among the flaps of these 3 species, there exist structural similarities (presence of eyespot, innervation by branches of pallial nerves from the visceral ganglion) as well as differences in shape and pigmentation.

Flap movements are initiated by paired pulses which produce contractions starting at the tail base and move toward the eyespot ends of the flaps. A recovery phase follows, in which the flaps assume their former position, with the tails floating horizontally.

Flapping behavior also involves the coordinated function of foot, marsupia, valves and siphons to such an extent that the supposed normal spatial relationships between body and shell are much altered. For different species flapping involves different behavioral complexes as well as different relevant stimuli (in particular light intensity for *Lampsilis ventricosa* and water waves and jarring of substrate for *L. siliquoidea*).

Flaps occur only in mature female specimens, although juveniles and males have flap rudiments, and flap movements have been seen only in gravid, never in non-gravid females. Flapping occurs in prolonged periodical spells throughout the summer months and has been seen to accompany the gradual emptying of the ovisacs, and the shedding of conglutinates. Flapping has not been observed after spawning of glochidia.

Two earlier hypotheses concerning the function of flap movements in the Lampsilinae, i. e., the roles of the moving flaps as "lures" for host fish to the mussels' glochidia, and as aerators for the gills and marsupia, seem now to be only partly plausible. Because of the differences in aspect, in speed of flapping and in responsiveness to environmental stimuli among the different species, it is here suggested that these differences are possible adaptations to habits of peculiar host species of fishes. The bellows-like movement created by the paired pulses of all flap movements, regardless of species or of flapping frequency, might help the glochidia to remain suspended in the water for a period of time, and thus facilitate the vitally necessary contact with a host fish.

INTRODUCTION

Only a few genera of freshwater mussels, all in the American subfamily Lampsilinae[2] within the large and world-wide family Unionidae, are known to possess mantle flaps. These flaps (F) are appendages of the mantle, that are located anteroventrad to the branchial siphon (BS, Fig. 1). During late spring and through the summer months, female animals possessing such well-developed flaps may upend themselves in the substrate. Their mantle flaps are then extended (Fig. 2) and moved in a series of rhythmic pulsations. To the human observer they strongly suggest a small fish, complete with pigmented eyespots, stationary in the current and waving its flanks and tail.

Ortmann (1911) was the first to record observations of flap movements which he had seen best in *Lampsilis ventricosa* and *L. multiradiata* (*L. fasciola*). Studies on the natural history of freshwater mussels undertaken early in the century (e.g., Wilson & Clark, 1912; Coker et al., 1921) contain occasional references to lampsilid flap movements. Taxonomic treatments of the Unionidae (e.g.,

[2]The Lampsilinae are the only unionid subfamily entirely confined to North and Central America.
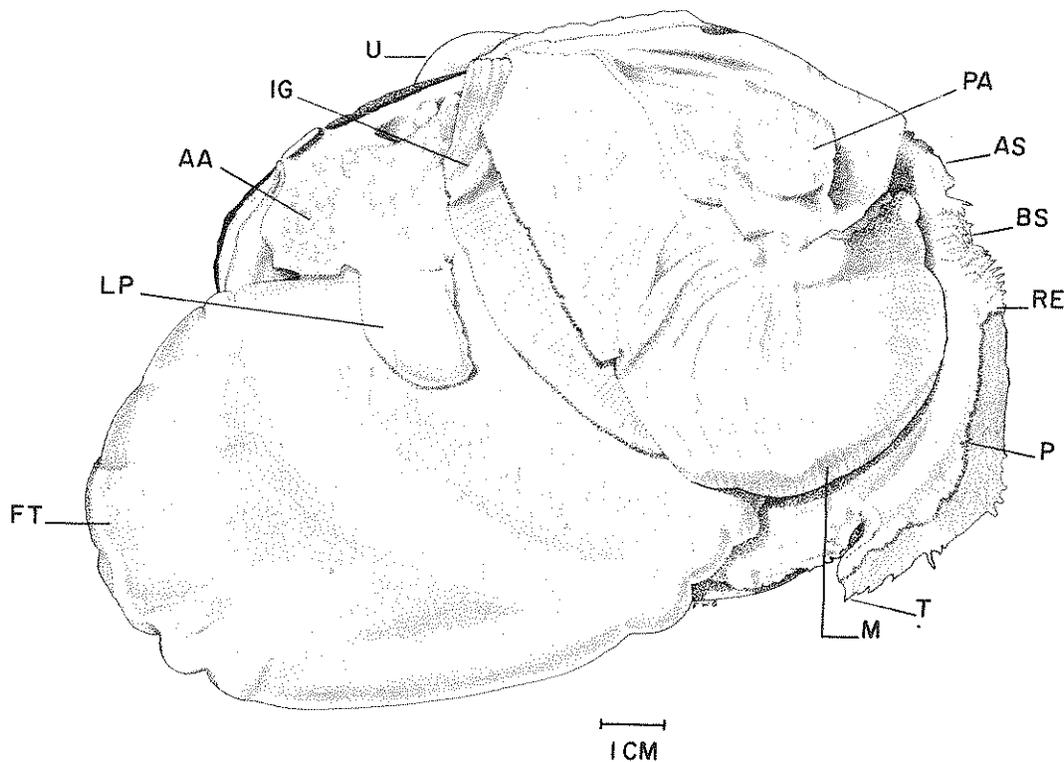

FIG. 1. *Lampsilis ventricosa* (Barnes). Drawing of preserved specimen, seen from the left side. Left valve and most of left mantle removed. Specimen collected from River Raisin, above Sharon Hollow, Washtenaw Co., Michigan, 1963. (For abbreviations, see p 228).
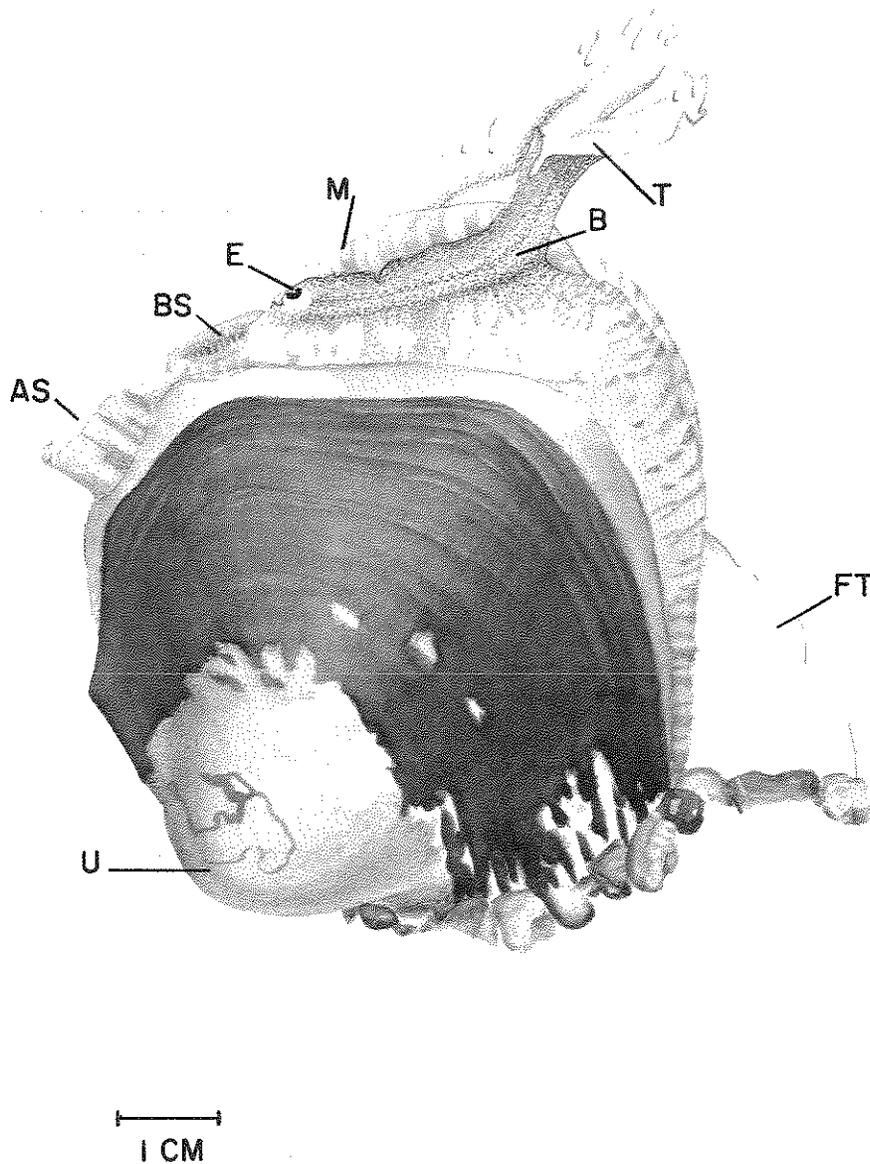
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FIG. 2. *Lampsilis ventricosa* (Barnes) in typical "headstand" position (rotated by 90°) during flapping behavior, drawn from the left side. Specimen collected from War Eagle Creek, Benton County, Arkansas, June 14, 1964. (For abbreviations, see p 228).

Scammon, 1906; Ortmann, 1911; Simpson, 1914; Walker, 1918) provide brief descriptions of the flaps' appearance.

Some authors (Ortmann, 1911; Howard & Anson, 1922; Welsh, 1933) have specu-lated that the unique lampsilid flaps and flap movements may be involved in fish-host relationships. Welsh (1933) carried out a brief experimental study of the mantle flaps with *Lampsilis nasuta* (*Ligumia nasuta*) in which he discovered

LIST OF ABBREVIATIONS

AA	anterior adductor muscle	M	marsupium (modified posterior portion of outer gill)
AE	"anterior" or eyespot end of flap		
AS	part of mantle modified as anal siphon	MA	mantle
B	base of flap	OSH	outer shell layer
BS	part of mantle modified as branchial siphon	OV	ovisac (water tube) of exposed marsupium
BT	basal tentacle	P	line of pigment on inner surface of mantle flap
CG	conglutinates		
DEF	distal edge of flap	PA	posterior adductor muscle
DM	distal edge of marsupium	PE	periostracum
E	eyespot	PG	pedal gape
ERF	edge of right flap	PO	pore
ESH	edge of shell	PS	pigment spot
ET	empty tube	RE	region which corresponds with location of eyespot on outer surface of right mantle flap
F	mantle flap		
FT	foot		
G	glochidia		
H	hinge region	RF	right mantle flap
ISH	inner shell layer	RM	right marsupium
IG	inner gill	RT	right mantle flap's "tail"
L	ligament	RV	right valve
LBS	location of branchial siphon	SAS	supra-anal-siphon
LF	left mantle flap	SG	secretory groove
LM	left marsupium	SP	siphonal partition
LP	labial palp	T	"tail" of mantle flap
LT	left mantle flap's "tail"	TE	tentacle
LV	left valve	U	umbo

a correlation between frequency of flap movements and decreasing light intensity. Lack of sufficient live material prevented Welsh from conducting further experiments.

The foregoing constitutes the slender bulk of work which has been published to date on lampsilid mantle flaps. The precise nature of the flap movements, their possible role in the mussel's life history, and in the distribution and speciation of the Lampsilinae, were unexplored. A feeling of some urgency accompanied the present study, because freshwater mussel populations are vanishing at an alarming rate in the U.S. (H. & A. van der Schalie, 1950). Living Lampsilinae are increasingly difficult to find, and may be unobtainable for such studies a decade hence.

It is the purpose of this communication (1) to describe flap movements of *Lampsilis ventricosa* (Barnes), as well as the species' characteristic "flapping behavior" complex (which is ostensively related to its general behavior inventory; (2) to summarize results of experimental studies of possibly relevant stimuli to flapping behavior in *L. ventricosa;* (3) to report comparative studies of *L. siliquoidea* (Barnes) and *L. brevicula brittsi* (Call), which reveal striking differences from *L. ventricosa* in flap morphology, in flapping behavior, and in stimuli relevant to that behavior; (4) to present evidence in support of certain conclusions which I have reached regarding the role of flapping behavior in the life history of these species; and (5) to suggest further hypotheses.

BACKGROUND

1. Taxonomic position of the Lampsilinae

Mantle flaps and flap movements are peculiar to the Lampsilinae, a subfamily

that has long been considered to contain the most advanced forms. As Walker (1917: 10) pointed out, the evolution of the Unionidae "has all been centered around the adaptation of the gills of the female for the care of the eggs until they are hatched." Evidence for Walker's generalization is patent in the distinguishing characteristics of the 3 subfamilies of the Unionidae: (1) the Unioninae are short-term breeders in which water tubes of all 4 gills serve as containers or ovisacs for glochidia; (2) the Anodontinae are long-term breeders in which only modified midsections of the water tubes of the outer gills serve as ovisacs (Ortmann, 1911); and (3) the Lampsilinae are long-term breeders in which only the posterior portion of each outer gill serves as a marsupium, the ventral borders of the latter extending below the distal edge of the inner gills, and often having a "beaded" appearance. Water tubes which become ovisacs in the Lampsilinae remain undivided, the whole tube serving as ovisac.

Ortmann (1911) believed that the Lampsilinae were the most highly evolved of the unionid subfamilies, not only because of the restriction of the marsupium to part of each outer gill, but also because of the prominent expression of sexual dimorphism in the shell, and the characteristic presence of special structures just in front of the branchial siphon: (1) the distinct, often large, conical papillae (or tentacles) found in *Ligumia* and *Villosa* (TE, Fig. 3) and (2) a lamellar keel or ribbonlike flap (the mantle flaps mentioned above), better developed in the female than in the male.

2. Mantle movements in other bivalves

Though mantle flap movements have been seen only in the Lampsilinae, generalized rhythmic movements of the mantle, independent of shell movements, occur in other bivalves. Redfield (1917: 233) investigated rhythmic mantle movements in at least 9 different species of lamellibranchs, and observed that in *Mya arenaria*, for example, a wave of con-
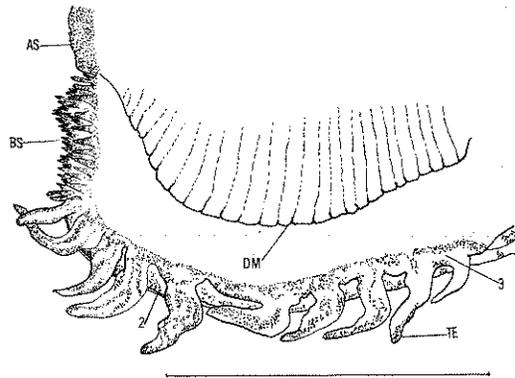

FIG. 3. *Villosa* (Lampsilinae); posterior left mantle edge, showing tentacles of unknown function anterior to branchial siphon (drawn from fresh specimen). 2, middle or second fold of mantle edge; 3, inner or third fold of mantle edge. Scale = 1 cm.

traction is seen to start at the distal end of the extended siphon, and to "move forward ending with the rise and fall of the mantle," about once a minute, in a freshly collected specimen. Pelseneer (1935) and Franc (1960) contended that such mantle movements favor circulation of water in the pallial cavity.

3. Modified mantle structures in other bivalves

Though mantle flaps per se are peculiar to the Lampsilinae, modified mantle structures are known in other bivalves, and include: eyes which rim the mantle of pectinid species and stud the siphonal tentacles of *Cardium*; a crown of tactile papillae around the branchial siphon (*Tapes*, *Corbula*, *Poromya*); and tactile papillae edging mantle borders (*Solenomya*, *Lepton*, *Pecten*). Among the Unionidae, in the Lampsilinae, there occur modified mantle structures of unknown function near the branchial siphon, such as "caruncles" or fleshy protuberances (*Carunculina*), and conspicuous tentacles and papillae (*Ligumia*, *Villosa*).

4. Factors which affect spawning in other bivalves

In the present study, the possible relationship of flaps, and flap movements of the Lampsilinae, to spawning of

glochidia will be considered. For fresh-water mussels as a whole, direct experimental evidence of factors which affect spawning is slight, though some efforts have been made to study them (Utterback, 1931). For marine bivalves, especially for several commercially valuable species, a number of factors have been implicated (Table 1).

5. Review of general neuroanatomy and sensory structures of *Lampsilis*

Since the present paper deals with a form of bivalve behavior, and since "... an organism's behavior is an expression principally of the capabilities of its nervous system" (Dethier & Stellar, 1964: 3), there follows a brief review

TABLE 1. Factors implicated in spawning* in some marine bivalves

Presumed spawning factor	Species	Investigator
Condition ("ripeness" of bivalve prior to spawning)	*Mytilus californicus*	Young, 1945
Spawning movements (shell)	*Ostrea* (♀)	Galtsoff, 1938a
Temperature (above 27° C, spawning appears to be inhibited)	*Ostrea edulis* *Crassostrea virginica*	Loosanoff & Engle, 1940
Lunar periodicity (uncertain whether light or water pressure is critical factor)	*Ostrea edulis* (♀)	Korringa, 1947
Sex of bivalve (differences in latent period between stimulus and spawning: ♂ are generally more responsive to stimulus than ♀)	*Ostrea* *Gryphea* (= *Crassostrea*) *virginica*	Galtsoff, 1938a Nelson & Allison, 1940
Sperm cells in surrounding water	*Mytilus californianus* *Ostrea* (*Crassostrea*) *virginica*	Young, 1945
Diantlin (an active principle in sperm cells of some bivalves)	Oysters *Mytilus californianus* *Tridacna*	Nelson & Allison, 1940 mentioned by: Fretter & Graham, 1964
Thyroxin, theelin (injections followed by emission of sperm)	*Ostrea gigas* (♂)	Galtsoff, 1940
Extracts of *Ulva*, a green alga, induces shedding of sperm	*Ostrea gigas* (♂)	Miyazaki, 1938
Neurosecretions (as suggested by effects of extirpation of cerebro-pleural and visceral ganglia)	*Mytilus edulis* *Chlamys varia*	Lubet, 1956
Mechanical stimulation (scraping and pulling of byssus; water turbulence)	*Mytilus californianus* *Cumingia tellinoides*	Young, 1945 Grave, 1927
Repeated stimuli (no response to 1st application of stimulus but to later ones)	*Mytilus californianus*	Young, 1945

*Spawning refers to emission of sperm or eggs

of the neuroanatomy of *Lampsilis*. The organization of the nervous system of *Lampsilis* closely resembles that of *Anodonta* (described by Simpson, 1884).[3]

Members of the genus *Lampsilis* possess a bilateral nervous system that includes the 3 pairs of ganglia characteristic of bivalves. A pair of cerebropleural ganglia are located on either side and slightly posterior to the mouth and to the anterior adductor and protractor muscles, where they are embedded in the tissue of the foot. Nerves from the cerebropleural ganglia extend into the mantle, viscera, anterior muscles, muscles of the foot and to the statocysts. A conspicuous connective passes under the esophagus and joins the 2 cerebropleural ganglia. Connectives extend from each cerebropleural ganglion to the fused pedal ganglia, deep in the muscle of the foot. Prominent connectives from each cerebropleural ganglion emerge posteriorly from the visceral mass, and approach each other just behind the posterior retractor muscle, where they shortly join the fused visceral ganglia.

The visceral ganglia are closely joined by a wide commissure to form a single large, butterfly-shaped ganglion (hereafter referred to as the visceral ganglion), located just under the superficial epithelium covering the ventral surface of the posterior adductor muscle. From this ganglionic complex arise many nerves which I have traced into the osphradia, gills, kidneys, pericardial cavity, posterior adductor muscle, rectum, inner and outer surfaces of the mantle in general, and by way of many branches and anastomoses into the siphons and flaps.[4]

As in other bivalves, sense organs, such as statocysts[5] and osphradia are found in *Lampsilis*. The statocysts are 2 tiny spherical cavities (each of which contains a sizeable statolith) at the ends of the statocyst nerves, deep in the foot tissue. The osphradia are 2 small patches of specialized epithelia next to the branchial nerve, just dorsal to the gills and ventral to the visceral ganglion.[6]

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[3]The summary which follows here is based on dissections made for this study, as described in "Materials and Methods," under "Anatomical Studies" (p 232).

[4]No attempt was made in this study to follow nerve fibers through the ganglia. Friedenfelt (1904) described much of the fine structure of the visceral ganglion in *Anodonta;* but Rawitz (1887) was the only investigator whom I found to have described pathways of nerve fibers through this ganglion (in *Mytilus*). Since Rawitz' work was done with primitive techniques, one is inclined to believe, with Bullock & Horridge (1965: 1396) that especially with reference to the cerebropleural and pedal ganglia, "the whole matter of pathways. . . must be regarded as requiring investigation *de novo.*"

[5]Statocysts have been experimentally implicated as organs of equilibrium (Buddenbrock, 1913, for *Chlamys varia*).

[6]The assertion (by Rawitz, 1887; Pelseneer, 1906) that the innervation of the osphradia is by way of connectives from the cerebropleural ganglia through the visceral ganglion, has recently been questioned (Bullock & Horridge, 1965). That osphradia function as chemoreceptors in bivalves has often been maintained (e.g., Pelseneer, 1906; Allen, 1923); but this claim has not, to my knowledge, been experimentally demonstrated. Bailey & Laverack (1963) reported that action potentials in the branchial nerve of a snail followed chemical stimulation of its osphradium. Aiello & Guideri (1964) suggest that regulation of water flow through the mussel (*Mytilus edulis*) may be due to a possible physiological connection between chemical stimulation of the animal's osphradia and subsequent nervous control of ciliary activity on the lateral epithelia of the gills.

Specialized photoreceptors have not been identified in the Unionidae, despite the fact that several species (including those of *Lampsilis*) are light, i.e., "shadow" sensitive (skioptic). Photoreceptors are known in some marine bivalves (reviewed by Franc, 1960).[7]

Tactile sensitivity in bivalves (noted in *Lampsilis,* too) is particularly localized in the siphonal papillae and in the anterior part of the foot. The innervation of such papillae has been studied in other species (e.g., by Galtsoff, 1964, in *Crassostrea virginica*). Franc (1960) reported that the siphons of *Mya* are sensitive to a pressure of 1 mg per 1 mm^2 of siphonal surface (Pieron, 1941) and noted that the foot of the Unionidae orients itself into the weakest of currents, being sensitive to the slightest differences in friction on either side of the foot.

MATERIALS AND METHODS

Field Collections: From the summer of 1962 through the summer of 1965, occasional collections were made of *Lampsilis ventricosa, L. siliquoidea* and *L. brevicula brittsi,* chiefly in the White River and its tributaries, in Washington County, northwest Arkansas (see Fig. 4). *L. ventricosa* exhibiting flapping behavior were observed on several occasions in June, 1962, and in June, 1963, in the White River. The best collection site was in that river near the Wyman Community. Very large (over 20 cm long) old specimens of *L. ventricosa* of both sexes were not difficult to find there prior to serious depletion of 2 fine shoals, apparently through drought and sewage pollution late in the summer of 1963. Other shoals which served as collection sites are now inundated by the backing up of the White River behind Beaver Dam. In

no instance were *Lampsilis* abundant. Several hours of searching would turn up 2-3 gravid females. Young individuals were seldom found. Specimens were collected usually on shoals of sand and gravel, in swift and in sluggish currents, in water ranging from clear to very turbid, and from depths of 1-3.5 feet.

Anatomical Studies: Dissections were made of fresh specimens of *Lampsilis ventricosa, L. siliquoidia, L. brevicula brittsi* as they became available, largely in the summer months. The neuroanatomy of preserved *L. ventricosa* and *L. fasciola* and of methylene blue preparations of fresh *L. ventricosa* was examined in some detail. Preliminary studies of flap and nerve histology were also made.

Aquarium Studies: For purposes of observation some mature female *Lampsilis* were maintained in aquaria throughout most of the year from the summer of 1962 through the summer of 1965. Individuals were held in aquaria in a variety of environments for as long as 12 months. Female mussels were kept in various ways: solitary, with others of the same sex, with males of the same species, with specimens of other species, and with fish of various kinds, including the black crappie, largemouth bass, and madtom. The aquaria used were of various sizes ranging from 2 to 50 gallons in capacity. Water temperature in some aquaria was allowed to fluctuate with normal room temperatures, but was held constant in others. Light conditions were varied from no daylight with only occasional artificial light (i.e., incandescent or fluorescent light) to natural daylight only. It was not possible for me to feed the animals adequately. In many instances, algae were allowed to grow on the sides of the tank, and were then periodically suspended in the water

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[7]Kennedy (1960) was able to demonstrate photoreceptive activity of the pallial nerve in *Spisula,* although he was not able to identify pertinent photoreceptor pigments there. (Photoreceptive function has not been demonstrated for cytochrome h̲, the hemoprotein he actually found present in high concentration in the pallial nerve of *Spisula*).
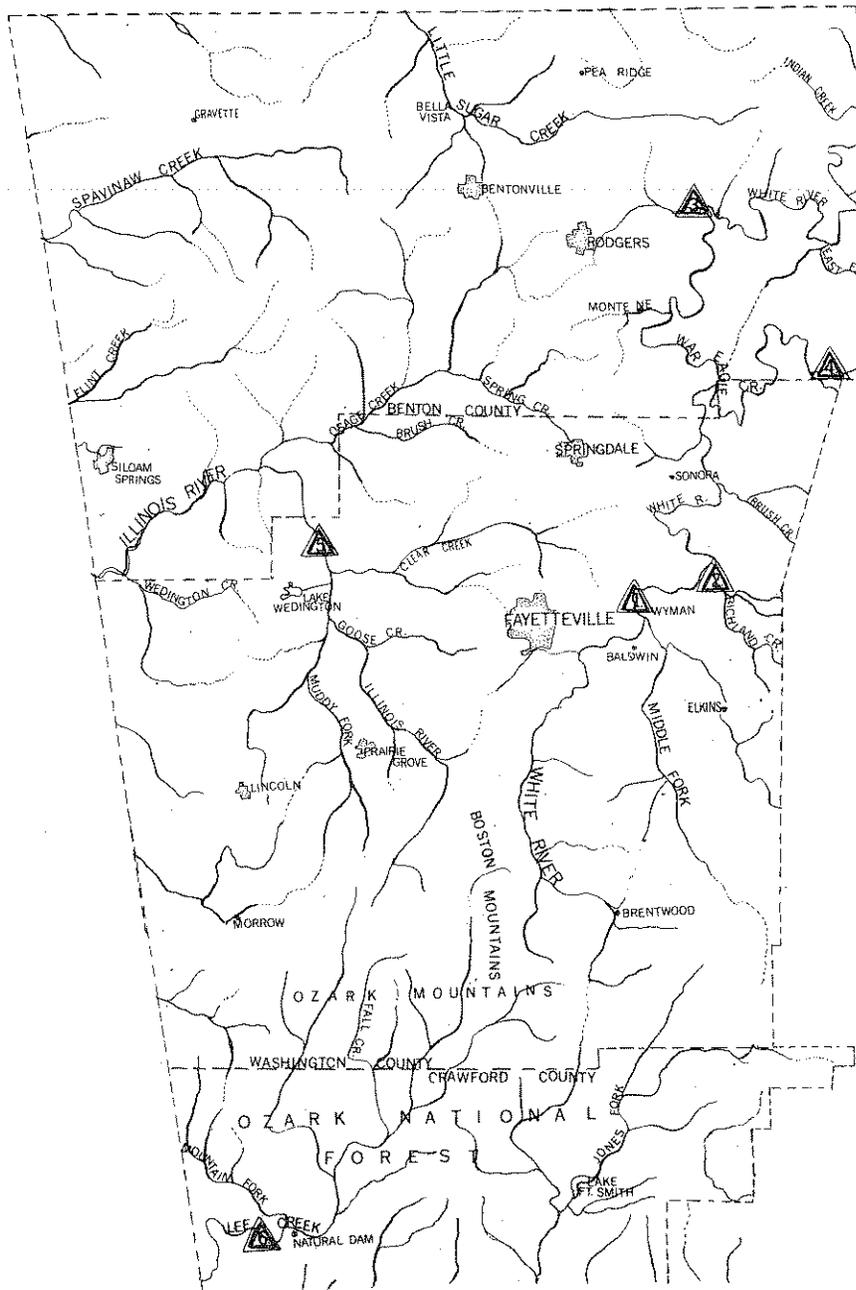
FIG. 4. Chief collection sites (triangles) in northwest Arkansas, for specimens used in this study. Map is from Arkansas Highway Dept., 1963. Scale shown here: 1 inch = approx. 10 miles.

by scraping the tank walls with a clean piece of nylon net.

Light Studies: *Lampsilis ventricosa, L. siliquoidea* and *L. brevicula brittsi* were subjected to initial exploratory light studies by means of a 3-way bulb (30, 70 and 100-Watts) suspended approximately 50 cm above the water surface. Changes in flapping behavior which accompanied change in light intensity were noted. Results of these studies coupled with data on diurnal flapping behavior (frequency of flap movements, response of flaps to natural light change at dusk and at dawn, etc.) in these same species indicated that *Lampsilis ventricosa* would be the most suitable animal for additional investigation. Subsequent light studies were carried out with a device (Variac) attached to a Weston AC voltmeter, which was used to vary the voltage through 200- and 300-Watt white frosted GE bulbs situated directly over the water surface at a distance of one meter. *Lampsilis ventricosa* were exposed both to successive increments and to successive decrements of light intensity at a variety of illuminations.

The preliminary studies with artificial light were partly made at natural fluctuating temperatures and partly at constant temperatures of 19-21° C. All of the later studies with *Lampsilis ventricosa* were performed at controlled temperatures (19-21° C). Almost all light studies were carried out at night, after dark, the later ones (reported in Table 14) between 7:30 and 11:30 p.m., from July 25 to August 16, 1965.

For convenience of measuring rapid flapping rates, and for ease of comparison, the frequency of flap movements has been expressed not as the number of moves per unit time, but as the duration of a fixed number of moves. The number was set at 30 after extended preliminary observations had indicated

that a smaller number would not allow for the animal's occasional spontaneous alterations of flap movement rate.

During prolonged observations of flapping behavior in the dark, a safelight (a red 25-Watt bulb) was used. A penlight or small torch was employed occasionally just to check on the occurrence of flap movements in the dark.

BEHAVIOR INVENTORY OF *LAMPSILIS*

Familiarity with the various categories of "normal" behavior such as locomotion, siphoning, adductor rhythms, responses to several kinds of external stimuli and spawning is indispensable to an evaluation of the flapping behavior in *Lampsilis*. In an attempt to apply to these mollusks a holistic approach – a regular part of the technique of the vertebrate ethologist – a behavior inventory, summarizing normal activities, is presented in Table 2, before the highly specialized attributes of flapping behavior are considered in detail.

A. FLAPPING BEHAVIOR IN *LAMPSILIS VENTRICOSA*

1. General morphology and location of the mantle flaps

Characteristic morphological features of *Lampsilis ventricosa* mantle flaps are shown in Fig. 5a, b. In this species, as in others of the Lampsilinae, mantle flaps are extensions of the mature female's anal and branchial siphon edges. In transverse section, the bivalve mantle edge is generally understood to consist of 3 lobes,[8] Fig. 6. Like the siphons, the mantle flaps are part of the inner lobes of the mantle edge (shown as lobe 3 in Figs. 7 and 8).

All 3 lobes of the mantle edge are modified in the flap region. This modification accompanies sexual dimorphism

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[8]This may be an arbitrary generalization. See Hillman's (1964: 8) article on "The functional morphology of the fourth [*sic!*] fold of the mantle of the Northern Quahog, *Mercenaria mercenaria.*"

TABLE 2. Summary, behavior inventory of adult female *Lampsilis* (as examined in *L. ventricosa* and *L. siliquoidea*)[a]

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
Adductor rhythms: (opening and closing of valves)	Tonic (slow) rhythm	Valves kept partly agape or completely closed, both for long periods. Less characteristic of gravid female just prior to spawning, than of juvenile or adult male during same period. Frequency of occurrence not influenced by light or temperature, except when animal is engaged in flapping.[b]	Muscle tissue: anterior and posterior adductor muscles which hold valves together, contain (1) tough, white smooth fibers which produce tonic rhythm; and (2) soft gray, translucent fibers ("fast" fibers) now known to be smooth fibers with peripheral twisted fibrils (reviewed by Hoyle, 1964, for *Anodonta*).
	Phasic (fast) rhythm	Quick closures, slower relaxations.[c] Active shell movements are altered, depending upon whether mussel is in increased state of excitability from rising water temp., accumulated metabolites in stagnant water, or whether it is a gravid female, spawning.[e]	Nervous control:[d] Control of both slow and fast rhythms appears to be intrinsic in the nerve ganglia, independent of peripheral stimulation. Rapid rhythm is controlled in each adductor by its nearest ganglion. Slow rhythm is controlled in each adductor muscle by combined effect of (1) the nearest ganglia which produce a tonus, and (2) the cerebropleural ganglia (which inhibit that tonus at intervals (Barnes, 1955).
Locomotion: (horizontal, or burrowing movement with foot in substrate)	Patterns of locomotion: (a) horizontal, valves at right angle to substrate, ligament dorsal; (b) burrowing: valves may be buried in substrate; only siphons' edges visible.	Elements of both horizontal[f] and burrowing movement are similar: (1) milky white foot is thrust out and forward between the valves; (2) foot's posterior, now heel-shaped portion is produced; (3) foot is then expanded, penetrates substrate, forms turgid hold; (4) valves open, close, mussel hunches, rocking down or forward into substrate.[g]	(According to Dawson, as described by Morton, 1964): for stages indicated in column #3: (1) external and internal anterior retractor muscles and transverse muscle fibers within the foot contract, compressing and lengthening the foot's blood sinuses; (2) further extension and heel formation is effected by contractions of the posterior retractor muscles; (3) expansion of the foot's volume occurs through massive blood flow into the foot's sinuses, and distal relaxation of the internal and external posterior retractor muscles.[h]

(See p 236 for footnotes a–h).

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
	Coincident conditions: (a) Substrate	In the absence of a yielding substrate (in aquarium), there may be keel-like protrusion of foot onto container's smooth bottom; foot then is further extended and expanded; but large animals cannot thus move into upright position, or complete the forward phase of locomotion. After a few days, foot is seldom extended; and the mussel may live thus for 4 months or more without attempting locomotion.	

[a] Applies to all unionids observed by author.

[b] I have noted periods of continuous rapid rhythm lasting 7-10 days, among gravid female lampsilid mussels maintained at ordinary room temperatures from April through September. Following spawning, however, a prolonged period of quiescence (7+ days) was always noted. Galtsoff (1964) noted a similar post-spawning characteristic for *Crassostrea virginica*.

[c] In *Anodonta cygnea* (Barnes, 1955) the sequence may be repeated 20 times an hour. My observations of *Lampsilis* are similar. The figure may be considerably higher during periods of flapping activity.

[d] The neurophysiological basis for the adductor rhythms is still unclear. To date, excitatory and inhibitory mechanisms have been found in mollusks only by stimulating whole nerve trunks or ganglia. Hoyle (1964: 327-328) commented that it "...has not been possible to make a nerve-muscle preparation of any molluscan muscle and feel sure that no synaptic junction in addition to the neuromuscular ones intervene."

[e] Galtsoff (1964) characterized these and additional subcategories of the rapid adductor rhythm for *Crassostrea virginica*, each accompanied by figures of kymograph recordings.

[f] The ligament (which dorsally joins the 2 valves of the shell) also functions in this context (Trueman, 1954).

[g] Fraenkels (1927) terms for locomotion in *Ensis* suggest a pattern similar to that observed in *Lampsilis* and in other unionids: (1) Grab-schritt (digging step), initial movements of the foot, consisting of 3 stages: (a) Keilform (wedge-like extension of the foot), (b) Hakenform (heel shape) i.e., further extension and downward thrust of foot into substrate and (c) Schwellform (turgid state) i.e., swelling of the foot as blood sinuses fill: and (2) Grabstufe (digging stage) the downward movement, which brings the animal further into the substrate.

[h] Such movements are not inefficient. A mature lampsilid mussel can accomplish the circuit of a 10-gallon aquarium (about 5 feet) in 5 hours.

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
Locomotion, extensive (min. distance of 6 in.) by gravid female:	(b) Time of day:	L. ventricosa was observed to travel mostly at night. Several specimens were observed a number of times daily from May into August; 29 of 35 travels occurred during the dark. L. siliquoidea showed a different pattern: of 31 such travels, 18 were between dusk and dawn, as against 13 in daylight.	
	(c) Temperature:	Temperature did not seem to be a factor. One specimen of L. ventricosa, kept at a constant temp. of 19° C, made 12 lengthy moves in a 3-month period, all between dusk and dawn.	
Siphoning: (water current flows into branchial and out of anal siphon)	Discharge: of material from rectum and cloaca via anal siphon. Intake: of water and suspended material through branchial siphon, over gills where cilia sort particles, etc.	In siphoning animal, steady current of water into branchial siphon, and out of anal siphon. Particles move from a. s. in steady stream or in sudden "sneezes." Siphoning stops when siphons close or withdraw in response to shadows, tactile or chemical stimuli (see below). In usual erect posture (ligament dorsal), siphons protrude (e.g., 1/2 cm in 15 cm-long animal) parallel to substrate.	Posterior edges of mantle, inner lobe of left and right mantle edges joined laterally, not medially, except for superficial fusion with suprabranchial septum. Innervated by branching siphonal nerves from visceral ganglion. No nerves pass directly from one side of siphon to other. (Both siphons are striped and mottled with orange and black pigments. Branchial siphon usually most brightly colored with 3+ rows of papillae within the lumen. Largest papillae, located in innermost row, are sensitive to tactile stimuli).
Responses to sensory stimuli:	Response to shadows	Siphons, especially anal siphon, close quickly, then open.[i] See also Table 3.	Little information available. Siphons and foot with ample nerve supply. Neuro-physiological mechanisms unknown.
	Response to tactile stimuli	Foot, especially anterior end, withdraws. Siphons, especially when papillae within branchial siphon are stimulated, close.[j]	

(See p 238 for footnotes i-j).

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
	Response to sudden jarring of substrate:	Siphons or siphons and foot withdraw, valves may close.k	
	Response to various chemicals:	Siphonal closure or withdrawal response, usually. See studies of Allen (1923, on Lampsilis and other unionids) and Hopkins (1931, on oysters).	
Spawning: (discharge of reproductive products).l	In male: discharge of sperm into water.	Discharge of sperm in clusters which exhibit rotary motion in water, described by Utterback (1931) for L. ventricosa.	
	In female: Discharge of glochidia, usually preceded and accompanied by flap behavior.	Discharge of glochidia from marsupia of female in clusters (conglutinates) having shape of ovisac, or singly. (Details in body of this paper).	

iBuddenbrock (1930) investigated the shadow reflex of Arca, Pecten, and especially of barnacles, and was concerned with the reflex as it relates to the shadow's intensity, to "adaptation," and to summation in response to a rapid succession of shadows.

jA sequence described by Allen for a number of unionid species (1923: 62) may be verified by repeatedly touching the inner circle of papillae with a fine probe: (1) Ventral siphon strongly stimulated. Both siphons close vigorously. Both reopen together. (2) Stimulus repeated soon. Both siphons close. Ventral reopens, then dorsal. (3) Stimulus again repeated. Dorsal siphon closes. Ventral not entirely closed, and reopens at once.

kThe response described here presents problems in experiments with mussels. E.g., Wenrich (1916; 298) wrote for Anodonta, "...precautions against vibrations to which the animals are very sensitive, were taken by supporting the experimentation-box by another box on the cement floor of a basement room, and placing wads of paper under the lower box, between the two boxes, and under the jar containing the animals."

lLatter (1891) described shedding of eggs from oviducts of Anodonta, the only account I have seen of this process. He recorded that eggs pass singly, in a steady stream through the oviduct and out of the genital aperture, their passage being aided by contractions of intrinsic foot muscles and ciliated lining of the oviduct itself. In about 50 seconds an egg would have moved to the posterior edge of the visceral mass, meeting the stream of eggs from the other side of the body, and then would pass back through the suprabranchial cavity to the cloaca. From the cloaca the eggs are moved forward into the "latticed recess" of the outer gills. Latter estimated the number of eggs thus passed in 10 days at about 500,000.
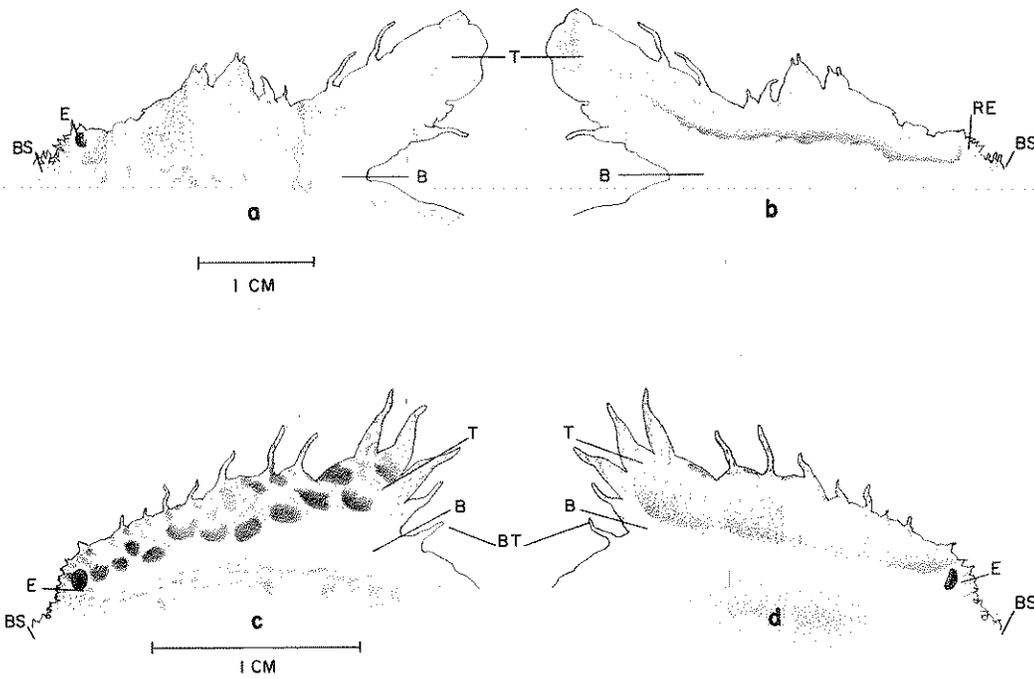
FIG. 5. Mantle flaps in 2 species of *Lampsilis*, drawn from preserved material. a, b, *L. ventricosa*; c, d, *L. fasciola*. The illustration shows the characteristic features of the outer (a, c) and inner surfaces (b, d) of the flap. Note the rather uniform pigmentation of outer surface, eyespot visible only on outer surface, and relatively narrow, truncated tail of *L. ventricosa*. Compare with many pigment spots on external surface, eyespot visible on both external and internal surface, and rather broad tail comprised of a number of large tentacles, in *L. fasciola*.
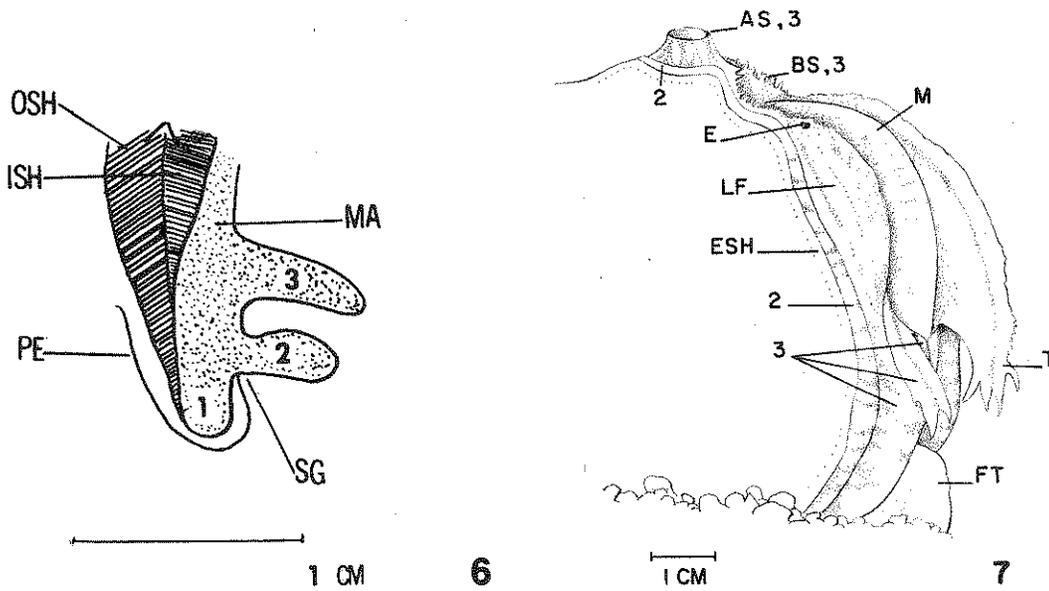
(See p 240 for legends to Fig. 6 and Fig. 7).

of the valves, whereby the rotundity of the female shell accomodates the marsupia as well as the thickened posterior mantle edges.

In the living, mature female animal, the outer mantle lobe (Fig. 6, 1) is much thickened in the siphonal and flap region, and is almost completely covered by the shell. The middle lobe (2) is very thin at the base of the anal and branchial siphons, but is evident as a rounded pigmented ridge, near the flaps (Figs. 7, 8). The inner lobes (3) not only form the flaps, but their protruding apposition under the flaps' "tails" is seen (especially in a rear view of flapping *L. ventricosa,* Fig. 8, B3) to cause an elevation of the tails.

2. Orientation of *Lampsilis ventricosa* to the substrate during flapping behavior [9]

When the mussel is engaged in flapping, its appearance is much altered from "normal" (Figs. 9a, b) by: (1) forward tilting of valves (a rotation of about 90°); (2) exaggerated posterior extension of foot; and (3) extreme protrusion of flaps, inner mantle lobes and marsupia (Fig. 9c).

Flapping behavior configuration alters not only the position of the animal relative to its substrate, but to the valves of its shell as well. The "anatomical correspondence" areas defined by Stasek (1963) for a number of bivalves, would not apply to *L. ventricosa* during flapping. (See Fig. 10).

For the foregoing reasons, conventional designations of "anterior," "posterior," "dorsal" and "ventral," become misleading; and thus terms which are meaningful within the special context of flapping behavior (as shown in Fig. 11) will be used in this paper. A summary contrasting orientation of *L. ventricosa* to its substrate during flapping behavior and during normal activity is presented in Table 3.

The typical position of flapping *L. ventricosa* illustrated in Fig. 9c is the only one I have noted for this species under natural conditions. Ortmann (1911) and Grier (1926) have presented general descriptions of this position. However, I have often observed that *L. ventricosa* in aquaria may exhibit flap movements when its valves are tilted up no more than 45° (Fig. 7), although such flap movements are slow, and occur at low light intensities.

3. Analysis of flap movements in *Lampsilis ventricosa*

Ortmann (1911), Wilson & Clark (1912), Grier (1926) and others noted that flap movements are very rhythmic and rapid in *L. ventricosa.* In the course of prolonged observations of flapping animals in aquaria during spring and summer months and from analysis of 16 mm moving pictures of some of these animals, I have determined that there are at least 2 principal categories of flap movements: (1) regular movements, observed at high flapping frequencies of

[9]Orientation of animal to substrate only is discussed here. Field observations (my own, 1962, 1963, and those of Ortmann, 1911) indicate that the flapping animals may orient themselves into the current. Present studies have not included an investigation of this factor.

FIG. 6. Diagram of transverse section of bivalve mantle edge. 1, outer lobe; 2, middle lobe; 3, inner lobe (from Morton, 1960). Scale shown indicates approximate size of a transverse section through posterior mantle edge of *Lampsilis ventricosa,* ♀, in a specimen 15 cm long.

FIG. 7. Semi-diagrammatic view of *Lampsilis ventricosa,* during slow flap movements in aquarium, from left rear side, indicating lobes of mantle edge. 2, middle lobe; 3, inner lobe and structures arising from it. Note that valves here are tilted by only 45°; the inner mantle lobes are pushed out against each other.
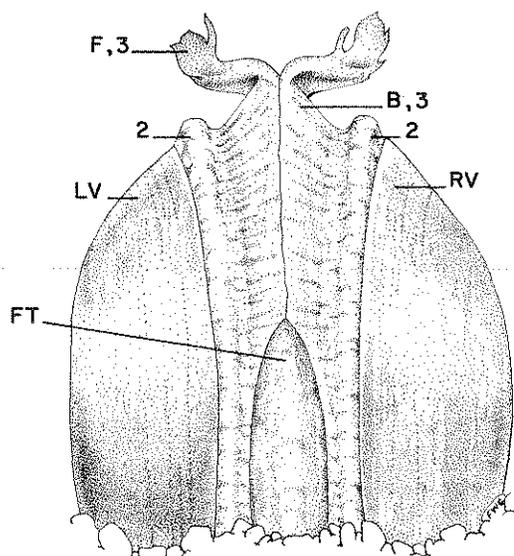
FIG. 8. Flapping in mature female *Lampsilis ventricosa*. Rear view during flap movements. Drawn from living animal. 2, 3, middle and inner lobes, respectively, of mantle edge. Note that the inner lobes below the mantle flaps are pushed tightly together.

60 or more moves per minute, and (2) slow movements, seen at rates of less than 30 moves per minute. The mantle flaps exhibit other types of movements too, though less often. All spontaneous flapping movements involve both mantle flaps.

Regular flap movements (Figs. 12, 13): Before the regular movement is begun, the tails of the flaps are spread apart, to float horizontally in the water, inner surface dorsal. The "anterior" ends (see Fig. 11) of the flaps, with white-rimmed black "eyespots"[10] on the external surface, are held together; or, if the marsupium protrudes, flaps are held close to the sides of the marsupium.[11] The movement starts with a quick strong contraction at the base of the flaps. The tails are thereby turned upward, and often clap together over the exposed edge of the marsupium. Now a pulse[12] moves from just in front of each of the tails, forward to the anterior, eyespot ends of the flaps. A lateral bulge is thus simultaneously produced in each flap; and as the pulse moves along, it increases in amplitude and causes each flap to be turned downward and outward. Finally the pulse reaches the eyespot end of each flap, pushing the whole flap-pair forward, and snapping the eyespot ends outward.[13] The slower recovery stroke of the regular movement now occurs. The tails relax and float out horizontally,

[10]The eyespot's function as a photoreceptor has not been demonstrated. Sufficient material for adequate pigment analysis was not available in this study, but chromatograms made from a couple of eyespots from very large (20 cm) specimens showed pink fluorescence above pigment sample, and dark, probably UV absorption spots 5-7 cm above pigment sample (Whatman' #1 paper, butidine solvent). Presence of porphyrins (characteristic for photosensitive pigments) may be indicated. Because no photoreceptive function has yet been demonstrated for the "eyespot," the term is inappropriate. It will be used throughout this study, however, because it is established in the literature, and because many lampsilids possess numerous other pigment spots.

[11]Because frequently one marsupium only protrudes during flapping behavior, the term "marsupium" rather than "marsupia" will be used in much of this description, although both of the marsupia protrude from time to time.

[12]A pulse is a superposition of sine waves of different frequencies, analogous to the motion generated by pushing up, then pulling down on a taut rope's end - not a wave or undulation, which would advance at a constant speed and amplitude.

[13]When one observes a flapping *L. ventricosa* in a turbid stream, the completion of the forward movement of the pulse is striking. On the internal surface of the flaps in this species, at a point corresponding with external location of the eyespots, there is a patch of white. To the human observer, the flash of the white patches is the most eye-catching part of the regular flap movements.
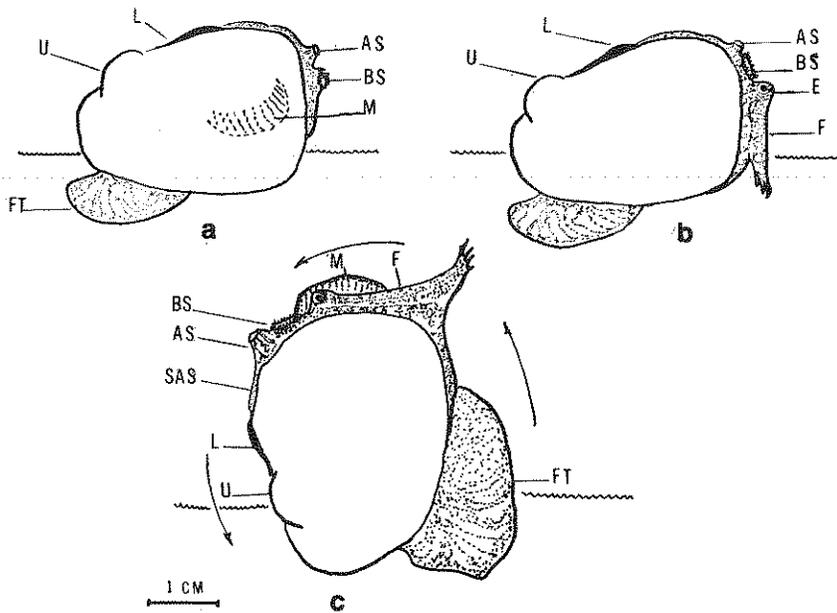
FIG. 9. Flapping in mature female *Lampsilis ventricosa*. Diagrams showing appearance while anchored in substrate, from the left side, a, during normal activity, flaps withdrawn; b, flaps visible; and c, during flapping behavior, showing "headstand" position with tilted valves, foot as prop, flaps and marsupium broadly protruding. Note "normal" position of marsupium (dotted) under shell in a.
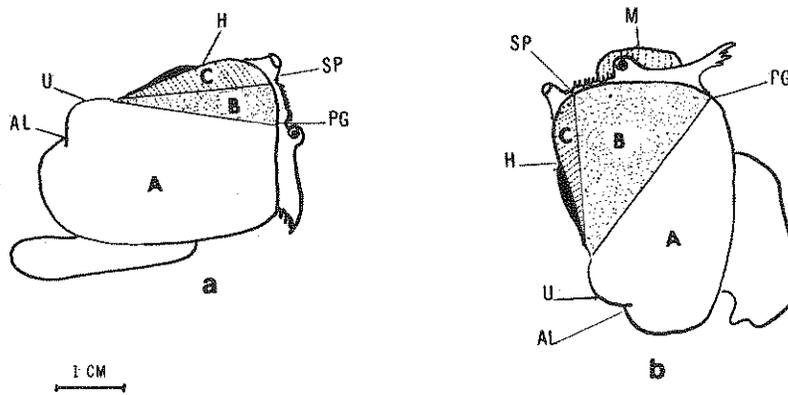
FIG. 10. Flapping in mature female *Lampsilis ventricosa*. Diagrams showing "anatomical correspondence" areas, defined by Stasek (1963) for bivalves, as they might be applied to *Lampsilis ventricosa* during: a, "normal" activity, and b, during flapping behavior. A, pedal margins, which extend from anterior limit (AL) of the infra-branchial chamber near the mantle isthmus of the animal to its pedal gape (PG); B, the inhalent aperture, extending from the pedal gape to siphonal partition (SP); and C, the exhalent aperture which extends from the siphonal partition to the limit of the suprabranchial chamber near the hinge (H).
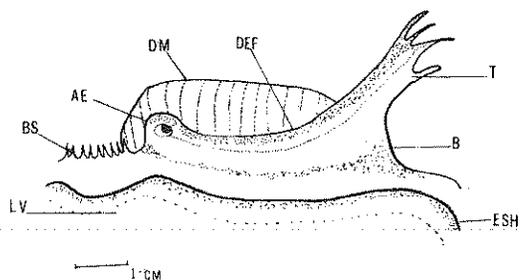
FIG. 11. Flapping in mature female *Lampsilis ventricosa*. Diagram of flap region showing terminology used in text (p 228) in analyzing movements of mantle flaps during flapping behavior. Note that the distal edge of marsupium and distal edge of flap is now "dorsal," while the eyespot end is "anterior" and the tail of the flap is "posterior."

the anterior ends move up against each other (or against the protruding marsupium), and both flaps are simultaneously pulled back and together.

Regular flap movements resemble swimming motions of a little fish, a resemblance first noted by Coker et al. (1921), and later by Howard & Anson (1922). This resemblance has prompted Welsh (1933) to refer to the flaps as "lures" for possible fish hosts to the mussel's glochidia. Regular flap movements have been observed at frequencies varying from 60 or slightly less to as much as 180 per minute. At 1 per second frequency, each recovery stroke requires about 0.6 seconds.

The slow movements (Figs. 14, 15): I have observed slow movements usually at low light intensities, and at frequencies of from 30 per minute down to less than one in 30 minutes. Before the slow movement starts, flaps are spread wide apart, the entire length of each floating out horizontally, inner sides uppermost in the water. The marsupium may not, but more often does, protrude between the flaps. When the movement begins, there is a contraction at the flap base; the tails move up and may touch medially; then a pulse moves forward from in front of the tails, which draws the eyespot

ends of the flaps upright, together, and backward.

In recovery, first the tails, then gradually the rest of the flaps relax and float out horizontally once more. At the end of the recovery stroke, the flaps have moved forward slightly, again.

Whereas it has been speculated that the minnow-like aspect produced by the rapid ("regular") movements of the flaps might attract possible fish hosts, and that these movements may serve to aerate the glochidia, slow movements of the flaps seem unqualified for either role. The slow movements can go on for hours at very low light intensities and obviously contribute little to aerate glochidia, nor do they give the impression of a swimming fish.

A prominent feature of the mussel's slow movements is the accompanying, broad exposure of the marsupium.

Other flap movement patterns: Other movement patterns noted in this study for *L. ventricosa* are: "fluttering" movements, "weak, regular" movements, and, rarely, "double" movements. The first 2 are described here.

Fluttering movements may be observed during periods of very low flapping frequency. They consist of slight, rapid contractions which course from eyespot to tail and from tail-base to eyespot, and involve just the distal, gray-pigmented parts of the flaps. Their passage along the flap is accompanied by minute darkenings of the pigment, and bendings of delicate papillae which fringe the free surface of each flap.

Weak regular movements may be seen during periods of prolonged, high flapping frequency (1 move/sec.). Initial contractions at flap-base, and the pulse subsequently generated, are much less strong than in the regular movements. The pulse does not cause the eyespot ends of the flaps to be thrust forward and to snap apart. The recovery stroke does not bring the flap edges upright and together. The effect of these weak regular movements is to produce a rhythmic, gentle "waving" of the flaps.

TABLE 3. Orientation of *Lampsilis ventricosa* during "normal" activity, contrasted with position during flapping behavior (compare with Fig. 9)

Body structure	Position during "normal" (non-flapping) activity	Position during flapping behavior
Valves	"Upright," i.e., umbones and ligament on top (dorsal).	Tipped (rotated anteriorly), often in "headstand," i.e., umbones are now near substrate, ligament vertically above umbones or even in a line forming an acute angle with substrate in front of the animal.
Foot	Used chiefly during locomotion: foot extended at front, then back, valves then hunching forward.	Posterior part of foot much extended to make wedge-shaped prop for animal's up-tilted valves.
Anal siphon	Dorsal and posterior; line ligament – anal siphon nearly parallel with substrate.	Dorsal to anterodorsal. Line ligament – anal siphon vertical to substrate.
Branchial siphon	Posterior, ventral to anal siphon. Distal edges projecting parallel to substrate (papillae may be touching medially).	Dorsal, posterior to anal siphon, distal edges may be turned medially, papillae touching.
Mantle flaps	If visible, located ventral to branchial siphon, not extending far from valves. Tails may or may not be hanging free, and ventral to rest of flap.	Dorsal, posterior to branchial siphon. Eyespot, "anterior" flap portion just posterior to branchial siphon. Tail, posterior portion, floating free, the whole flap pushed out from valves.
Inner lobe (3), at base of flaps	Distal edges touching medially, or withdrawn between the valves. If withdrawn, mantle flaps are not extended or visible.	Distal edges projecting at least 2 cm from valves (in specimen 10 cm long, touching each other medially at 60° angle to form peak under flap tails (see Fig. 8).
Marsupia (posterior portion of outer gills)	Ventral to posterior adductor and rectum. Kept within pallial cavity.	Pushed out between flaps, protruding 2 cm; distal edges dorsal. Posterior tubes of marsupium now anterior because of 90° rotation of animal. Marsupia may move "up" and "down" between flaps according to light intensity and frequency of movements.

4. **Behavior accompanying initiation of flap movements**

Lampsilis ventricosa often begins flap movements at dawn, with a characteristic behavior sequence (Table 4), the consequences of which are: (a) mussel has assumed "headstand"; (b) foot is prominently displayed as a luminous white heel, or prop, for uptilted valves; (c) flap movements markedly increase in frequency (from 30 moves/5-10 minutes, to 30 moves/30 seconds or less, i.e., they become from 10-30 times as fast, see Fig. 16), and (d) one marsupium or both marsupia protrude between flaps.
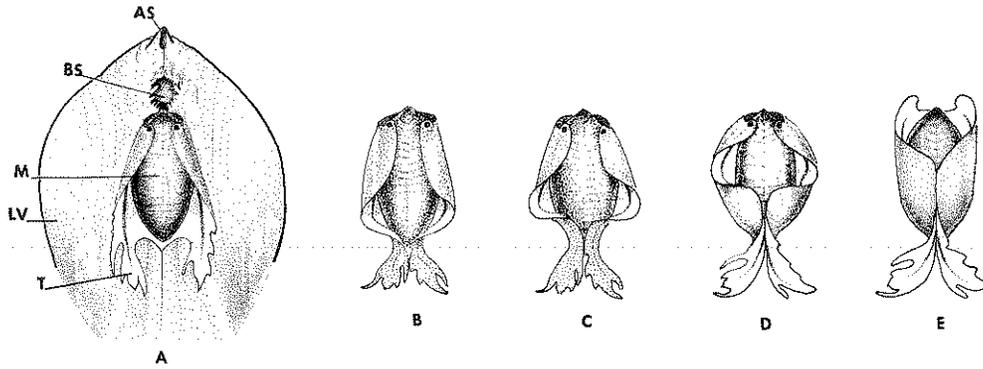
FIG. 12. Elements of the regular flap movements of *Lampsilis ventricosa*, viewed from above (semidiagrammatic). A, position at end of recovery stroke (tails floating out, eyespot ends against sides of marsupium); B, pulse begins near base of tails, outer margins fold over and meet at centerline; C, pulse (bulge) moving toward anterior eyespot end of each flap; D, pulse nearing eyespot ends of flaps; E, pulse at eyespot ends of flaps, pushing them outwards and forward horizontally.

TABLE 4. Summary of sequence of events in initiation of flap movements in gravid female of *Lampsilis ventricosa*

Step	Behavioral event	Approximate duration in minutes
1	Mussel in normal position (ligament dorsal).	--
2	Flaps are extended, until free edges of tails are exposed.	5-10
3	Flaps hang limply, ventral to branchial siphon.	5
4	Fluttering movements occur.	2
5	Pause.	2
6	Animal completely withdraws flaps; mantle lobes in siphonal region are squeezed together; mussel extends foot out and slightly backward in substrate and tips valves forward, toward umbones.	1
7	Valves open slightly; flaps are re-extended.	2
8	Repetition of steps 4 through 7, approx. 3 times.	20

Whenever flaps are withdrawn, the marsupium is moved down into the pallial cavity. The flaps then are re-extended, and move vigorously for 1-2 minutes before marsupium protrudes fully again.

Grier (1926) described an increase in flapping frequency in *L. ventricosa*, but not in the context of the animal's response to increasing daylight. He observed (:112): "At first the rate is quite slow, as if the creature were 'warming up' but rapid acceleration occurs to a maximum rate . . ." I have found that the rate of acceleration in flapping frequency is not always rapid, and that the "maximum" rate varies with each animal from
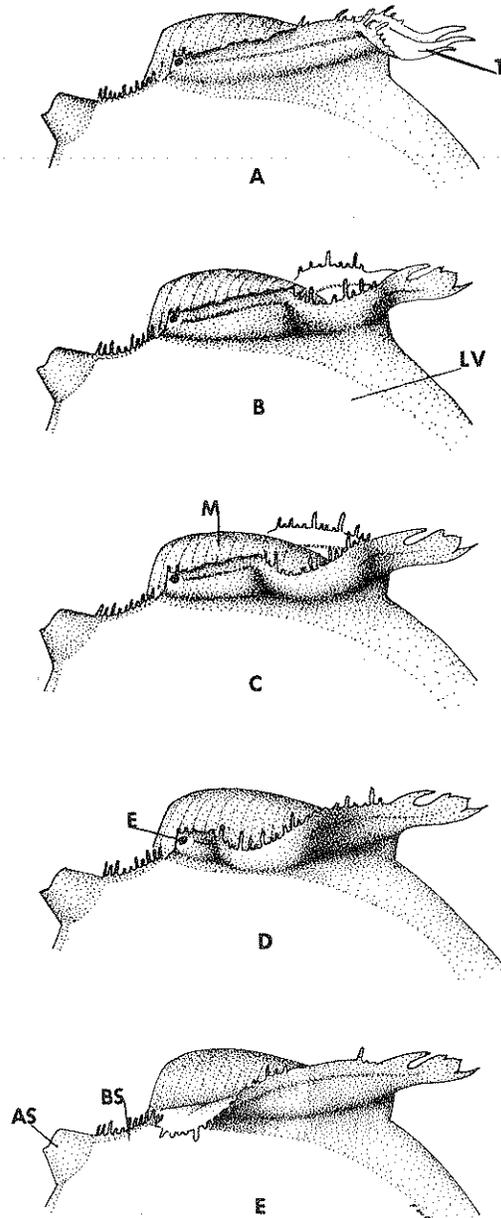
FIG. 13. Semidiagrammatic view of the regular flap movements of *Lampsilis ventricosa*, from the left side. Compare stages with Fig. 12. A, end of recovery phase (tails out, horizontally); B, beginning of "forward" pulse (note that it begins at base of tails); these are then brought upward and seem to clap together medially, over the protruding marsupium; C, pulse moves along each flap, causing a lateral bulge; D, pulse nears "anterior" eyespot end of flaps; E, pulse is at each flap end, pushes them outward and horizontally, also thrusting the flap-pair forward.
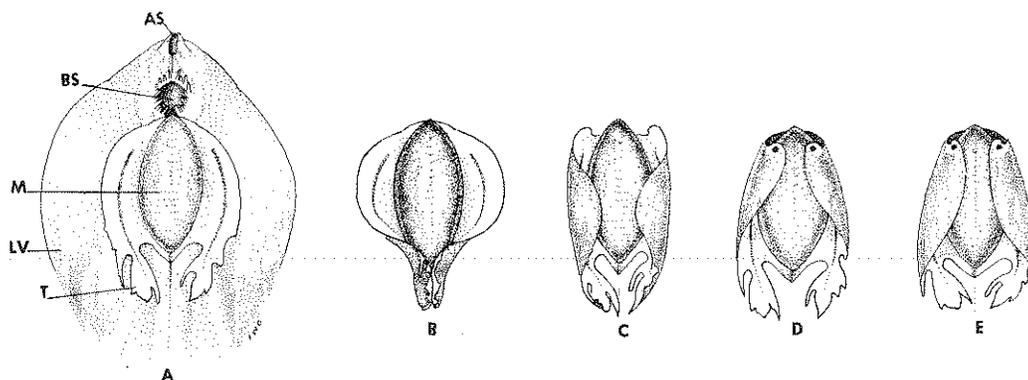
FIG. 14. Elements of the slow flapping movements of *Lampsilis ventricosa,* viewed from above. A, position of flaps at end of recovery stroke (flaps wide apart, floating horizontally, entire inner surfaces uppermost, marsupium widely exposed); B, pulse begins at base of flaps, bringing tails together medially; C, pulse moves forward, bringing mid-portion of flaps up medially; D, pulse nears eyespot ends of flaps, bringing them up close together with their anterior ends pulled back a little; E, end of forward pulse, most of flaps up, together and still backward.
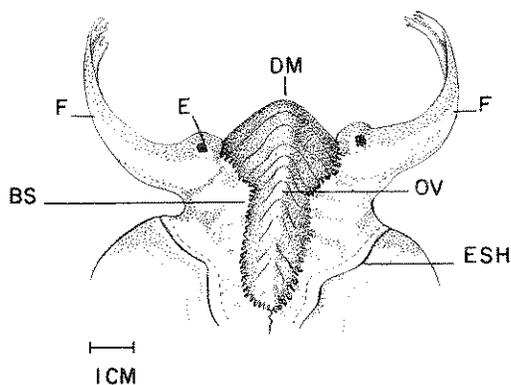
FIG. 15. "Head-on" view of flaps of *Lampsilis ventricosa* during slow movements; drawn from an animal in headstand position, looking from branchial siphon toward the flaps. Eyespot ends of flaps in foreground, free-floating flap-tails in rear. Note widely exposed marsupium. Only one marsupium is visible, the other one held within the branchial cavity.

one day to another (as well as from one time of day to another).

Variation in the daily time of onset of flap movements was noted in this study. Occasionally an animal would not initiate flap movements until mid-afternoon, even on a sunny day. Water temperature did not appear to be an immediate stimulus for initiation of flap movements. No differences were observed between specimens of *L. ventricosa* maintained in aquaria at normal, fluctuating temperatures, and others kept at a constant temperature of 19° C, in the lengths of their flapping periods, in the daily time of onset, or in behavior at onset of flap movements.

5. Behavior accompanying cessation of flap movements

This process may be observed in an undisturbed animal just before sundown (see Fig. 17), in rapidly fading daylight, when the mussel virtually reverses the warming up behavior it exhibited at sunrise (see Table 4). As the rate of flapping decreases from 1 movement/sec. to 1 movement/2 secs., there is a shift from the regular to the slow type of flap movement, the latter broadly exposing the marsupium. Flaps are drawn together, then withdrawn between the valves, as the animal gradually changes its angle of headstand orientation by hunching back down into the substrate. Flaps float out again and movements continue at the reduced rate. After a
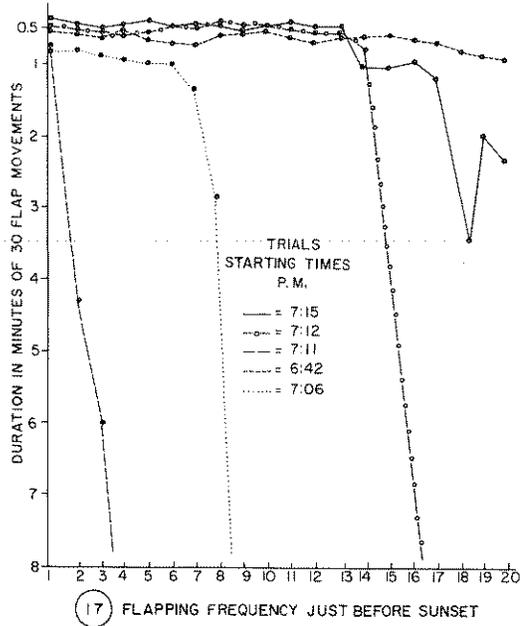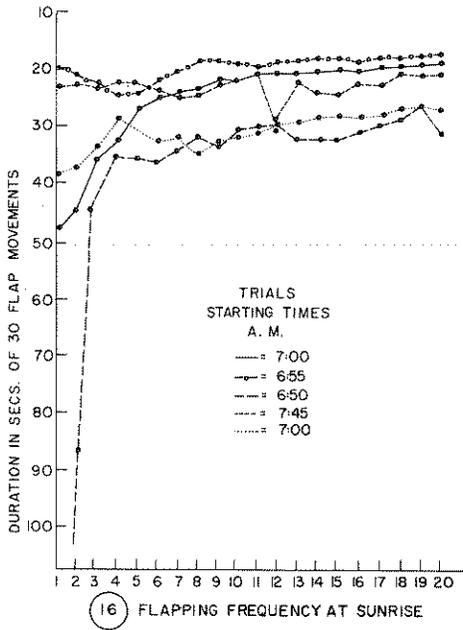
FIG. 16, 17. Flapping frequency of *Lampsilis ventricosa* at sunrise and sunset from 5 trials each, on different days in July and August, 1965. Each trial consisted of up to 20 consecutive counts (given in seconds in Fig. 16; in minutes in Fig. 17). Each of the large black dots represents a count, that is, the time span for 30 flap movements. Note that in 2 of the trials at sunset, movements did not cease, though movements perceptibly slowed in one of them.
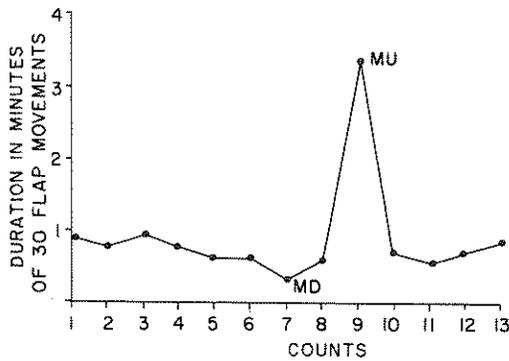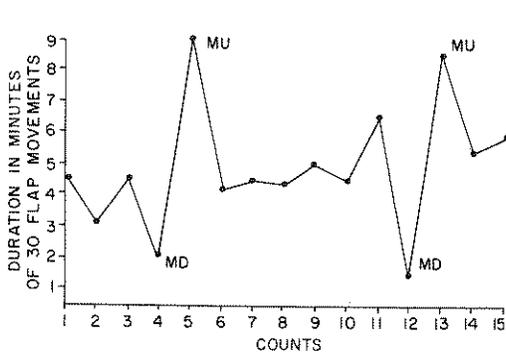
FIG. 18, 19. Alteration of flapping frequency (duration in minutes of 30 flap moves) which accompanies movements of marsupia in *Lampsilis ventricosa*. Trials comprised of 15, 13 consecutive counts in Figs. 18, 19 respectively. A count is the duration of 30 flap movements. Trials started at 3:40 p. m. on August 1, 1965 (Fig. 18) and at 10:45 a. m. on July 11, 1965 (Fig. 19). MD, marsupia moved down into pallial cavity; MU, marsupia moved up to protrude between flaps.

few minutes, flap withdrawal, valve closure, hunching down and flap re-extension are repeated. Finally, the flaps remain withdrawn, and the animal has assumed a normal siphoning position in the substrate.

6. Behavior accompanying diminution of flapping frequency (see Fig. 17)

Often the mussel maintains a headstand while its flap movements decrease in frequency with the oncoming dusk. Flap movements change to the slow pattern; the marsupia continue to protrude; and the flaps are spread more and more widely apart as daylight fades.[14]

7. Role of marsupia in flapping behavior of *Lampsilis ventricosa*

The marsupia of *L. ventricosa* affect flapping behavior in at least 4 ways:

(a) As a necessary condition for flapping behavior. The marsupia must contain glochidia. Among more than 40 living mature female *L. ventricosa* observed at length in this study, flap movements were seen only in gravid, though not in all gravid specimens.

(b) In increasing prominence of display. In the course of the 3- to 4-month summer season of flapping, *L. ventricosa* will, the first few weeks, show one marsupium or the other (seldom both) protruding just slightly between the flaps whereas in later weeks, one or both marsupia project prominently from between the flaps throughout the daily flapping periods. When both marsupia are

exposed, one is invariably thrust out more than the other, occupying a position closer to the siphons. The appearance of the 2 marsupia is neither quite side-by-side, nor quite one-behind-the-other (see Figs. 20, 21).

(c) In sharply altering frequency of flap movements (Figs. 18 and 19). The marsupia are occasionally spontaneously moved down into the pallial cavity and subsequently up between the flaps, during flapping movements. The downward movement is accompanied by a slight pause, then an increase in flapping frequency. Re-emergence of the marsupium is typically accompanied by a noticeable slowing of flap movements.

(d) In spawning of glochidia. Toward the end of several months of intermittent flapping behavior, a tiny hole appears in the distal margin of each visible ovisac (charged water tube in a marsupium); and within a week or less, the ovisacs are emptied of glochidia, ostensibly through these openings, during lengthened periods of flapping. Alternatively, the edge of one (or more) of the ovisacs may rupture, and the entire contents are shed as a conglutinate.[15] Figs. 20 and 21 show marsupia protruded (in the manner typically observed late in the season of flapping behavior). Location of pores in the ovisacs is shown in Fig. 22, and the gradual emptying of ovisacs, or spawning, is shown in Fig. 23. Because the ovisacs are transparent, and because individual ovisacs may have contents of different appearance,[16] it is

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[14]The animal may remain thus for hours in the dark. I have watched these movements for long periods at night, with a safe-light (a red, 25-Watt bulb). Slowest flapping rate recorded in this context: 30 flap movements in 36 minutes and 18.3 seconds (August 13, 1965).

[15]The conglutinate or mass of embryos expelled as a whole still has the shape of the ovisac. Conglutinates of *Lampsilis ventricosa* are the size, shape and color of a slivered almond. All those examined in this study consisted of well-developed glochidia, each larva usually still surrounded by its own membrane. Lampsilinae do not seem to abort conglutinates as readily as some other unionids. *Pleurobema*, for example, frequently shed many tiny, bright pink, splinter-shaped conglutinates within an hour after collection. These often consist largely of immature embryos.

[16]Differences in color and texture of ovisac contents are not as marked in *Lampsilis ventricosa* as they are in *Pleurobema* and other unionids (Lefevre & Curtis, 1910) where there can be brightly colored stratification of unfertilized eggs among the glochidia in the tubes of each marsupium.
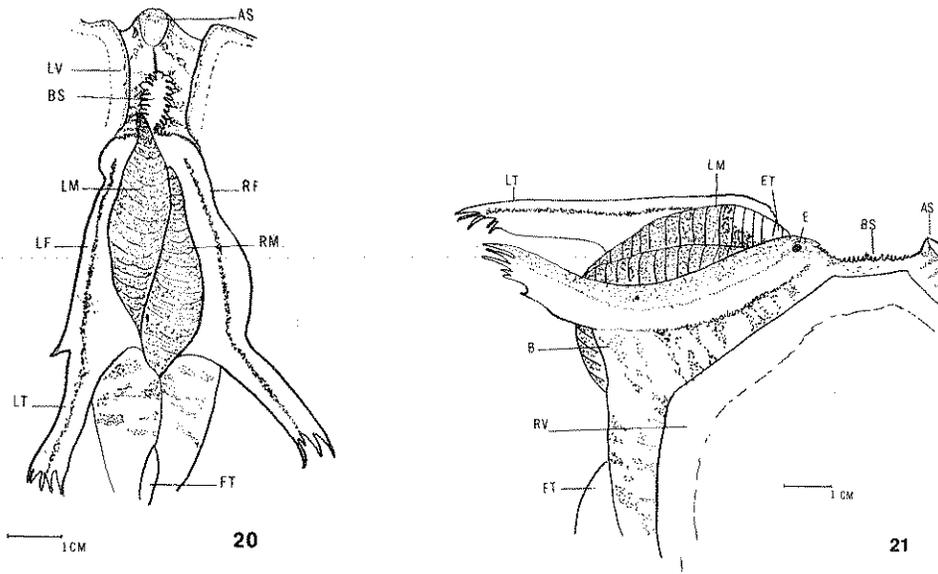
FIGS. 20-23. Marsupia of gravid female *Lampsilis ventricosa*.

FIG. 20. Protrusion of both marsupia, dorsal view (sketched on August 5, 1964, 10:30 p. m. artificial light (75 Watt incandescent bulb).

FIG. 21. Protrusion of both marsupia seen from right side (sketched on August 15, 1964, 8:00 a. m. in natural light). Several water tubes (ovisacs) in left marsupium, near branchial siphon (BS) looked partly empty.
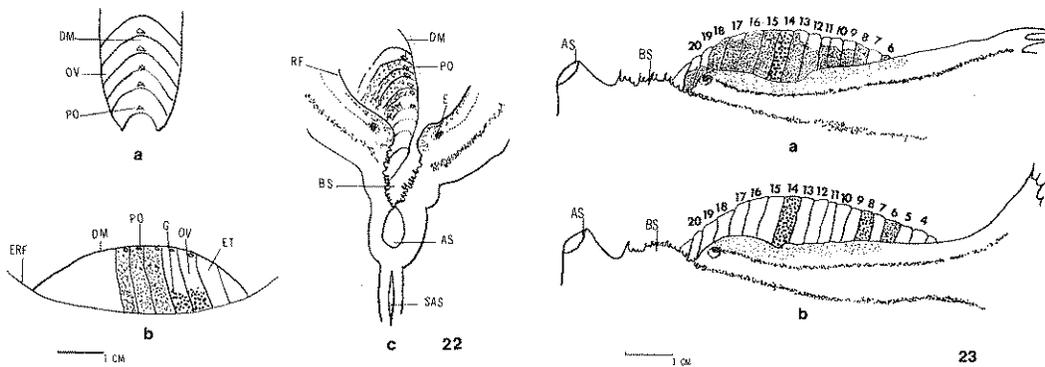
FIG. 22a, b, c. Location of pores in ovisacs (water tubes of posterior portion of outer gill). a. "Anterior" part of exposed marsupium, showing "edge-on" view of marsupial border; ovisacs empty. Orientation as in Fig. 15. b. Lateral view, slightly tipped to show pores on border. c. Exposed marsupium of flapping animal, sketched from anterior (eyespot) end of flaps.

FIG. 23. Spawning. Left mantle flap and exposed right marsupium, seen from left side, on 2 successive days. Ovisacs are numbered to show that between time when upper sketch was made, (6:30 a. m., Sept. 2, 1964) and time of lower sketch (8:30 p. m., Sept. 3, 1964), a number of water tubes (serving as ovisacs) had discharged their glochidia, probably via pores (not sketched here). No conglutinates were shed during that time.

possible to observe the emptying of various tubes in a marsupium, from day to day (Fig. 23).

8. Characteristic flapping periodicities

The times when *Lampsilis ventricosa* exhibits flapping may be summarily categorized as follows:

(a) Flapping season: extends for about 4 months from late spring onwards through the summer. I have records for a few Arkansas specimens which exhibited flapping behavior intermittently from June through September while in aquaria (see Tables 13 & 14).

(b) Flapping period: consists typically of a week or less in which the mussel exhibits flapping behavior at least part of every day. I have observed 6-8 such periods in individual specimens kept in aquaria at normal temperatures throughout a flapping season. A flapping period is frequently preceded by extensive locomotion, i.e., the mussel makes a circuit or two of the aquarium, before tilting up to a headstand (flapping position). Flapping periods are separated by several days to several weeks or more when no flapping occurs.

(c) Flapping day: is a day of flapping activity, which often begins at dawn; the flap movements finally cease or radically diminish in frequency just before sundown. Table 5 is a record, for one specimen of *Lampsilis ventricosa*, of 4 flapping periods, including a total of 18 flapping days, during which the animal was checked continually for flap movements. These data seem typical for *L. ventricosa*, in that they indicate the following: (1) frequency of flap movements varies throughout the day, and from one day to another; (2) flapping frequency does not increase or decrease uniformly through the day; (3) a flapping day is usually inaugurated at sunrise and tapers off just before sunset (Graph, Fig. 24, taken from Table 5).

I have further observed (at controlled and uncontrolled temperatures) that during any day of a flapping period, *Lampsilis ventricosa* is more likely to exhibit flapping activity at sunrise or just before sunset than at any other times of the 24 hour day.

B. EFFECT OF PHOTIC STIMULI ON THE FLAPPING BEHAVIOR OF *LAMPSILIS VENTRICOSA*

Early studies of the general (non-flapping) behavior of *Lampsilis ventricosa* included observation of the marked response of both siphons, but especially of the anal siphon to sudden shadows (skioptic response). Table 6 shows a typical series of responses by the anal siphon of a specimen of (non-flapping) *L. ventricosa* to repeated shadows. The anal siphon soon becomes "habituated" to the shadow stimulus. That is, the anal siphon shows a waning response to the repeated stimulus, not evidently occasioned by sensory adaptation or muscular fatique, inasmuch as the "habituated" siphon is still responsive to other (e.g., tactile) stimuli.

Later studies of the flapping behavior of *Lampsilis ventricosa* indicated the flapping animal's evident sensitivity to photic stimuli. Table 7 contrasts the observable responses of mantle flaps to photic stimuli (as well as to tactile stimuli, local water waves, jar of substrate, and temperature fluctuations) during flapping behavior, with responses of siphons during normal activity. The reader is reminded of the fact that both siphons and mantle flaps are part of the third (inner) lobe of the mantle edge, and that both are innervated by nerves from the visceral ganglion.

Simple preliminary experiments revealed that *Lampsilis ventricosa* can apparently be induced to increase its flapping frequency in response to light of increasing intensity.[17]

A series of experiments was then

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[17]*Lampsilis ventricosa* does alter its flapping frequency in apparent response to sudden, artificial changes in light intensity. The following is taken from notes made on July 7, 1964, regarding an aquarium specimen maintained at normally fluctuating temperatures: "A hot (100° F) sunny day. Water temperature up to 33° C. Mussel had been flapping in extreme headstand all through the day. Movements very rapid (up to 10 sec. for 30 movements).

TABLE 5. Average flapping frequency* for one specimen of *Lampsilis ventricosa* at various times of day in natural light only, at a constant water temperature of 19° C, during 4 flapping periods, from July 2 to August 18, 1965

Flapping periods	Date 1965	Duration in seconds of 30 movements at different hours							
		6-8 h	8-10 h	10-12 h	12-14 h	14-16 h	16-18 h	18-20 h	20-22 h
	7/2								20. 0
1	7/8		15. 2	17. 2	19. 7 17. 6	17. 8 18. 1 17. 5	18. 0	54. 6	
	7/9	25. 2	16. 8		16. 5	24. 6 19. 9		32. 9 105. 8	
	7/10	19. 9		46. 7 28. 7	26. 4		30. 5	36. 5	
	7/11	21. 5 21. 6		56. 0		332. 3			
	7/12	43. 7		486. 8$^{(3)}$				479. 0	
2	7/27	23. 1	27. 5	27. 0		30. 7	2:39. 5		
	7/28							481. 2$^{(4)}$	
	7/29	29. 7		32. 4	34. 6	44. 4	46. 4	170. 4$^{(3)}$	
3	8/1	33. 2		125. 3		347. 3		900. 9$^{(3)}$	
	8/2	24. 6	25. 4					39. 3	
	8/3	93. 9		108. 4				605. 3$^{(1)}$	
	8/4							464. 0$^{(1)}$	
4	8/12					29. 7 26. 7		293. 0$^{(1)}$	
	8/13	22. 5		22. 0	22. 7	23. 3	30. 7	401. 1$^{(1)}$	
	8/14	30. 6	25. 6	24. 6		31. 1	34. 7	1110. 0$^{(1)}$	
	8/15	30. 8		35. 5	38. 4	303. 4$^{(4)}$			
	8/16							131. 6$^{(9)}$	
	8/17	42. 8							

*Frequency is expressed as average duration of 30 flap movements in a series of 20 trial counts. In 11 instances fewer counts (10) were made (superscripts in parentheses).

[17](contd.) Still flapping at 8:00 p. m. Turned on light over aquarium at 9:00 p. m. Mussel had tilted back down toward normal position in substrate. No flap movements. Marsupia withdrawn. 9:30 p. m., animal in headstand, flapping rapidly. (30 movements in 10 seconds). " I later found an evident correlation between the beginning, continuation and termination of a flapping period, and the proclivity of a mussel for exhibiting such artificially induced movements.

TABLE 6. Successive responses of anal siphon of a gravid *Lampsilis ventricosa* to a sequence of shadows (1 sec. each). Total time for all trials tabulated, 7 minutes

Trial	Shadow* sec.	Siphon closure	Recovery time** in seconds
1	1	Immediate, complete	26.1
2	1	Immediate, complete	23.5
3	1	Immediate, complete	15.9
4	1	Immediate, complete	23.3
5	1	Immediate, complete	30.3
6	1	Immediate, complete	37.3
7	1	Immediate, complete	15.1
8	1	Immediate, complete	18.6
9	1	Immediate, partial	8.5
10	1	Immediate, partial	8.1
11	1	Immediate, partial	7.5
12	1(x3)	Delayed, partial	16.3
13	1(x3)	Delayed, complete	21.1
14	1(x3)	Delayed, complete	16.8
15	1(x4)	More delayed, partial	15.5
16	1(x8)	Still more delayed, partial	9.3
17	1(x20)	No response. Anal siphon remained open	

*Shadows were presented more than once (numbers in parentheses) in trials 12-16 before siphon closed.

**Recovery time is period between closure of anal siphon in shadow response and re-opening.

carried out, (a) to test the assumption that photic stimuli can alter mantle flap behavior in *L. ventricosa*, and, if photic stimulation could be experimentally demonstrated, (b) to examine certain parameters of the photic response.

The experiments covered a considerable range of light intensities (0.3-22.5 foot candles). They were performed at night, with a single light source (see Materials and Methods), and at a constant water temperature of 19° C. Observations included short time checks (10 timed counts or less of 30 movements each), and long ones (20-such trial counts). They were conducted when the animal was in a headstand or almost a headstand position; after days of vigorous flapping, and after days of flapping inactivity; and at the beginning, middle, and end of flapping periods. Preconditions of 8 experiments are summarized in Table 8. Table 9 is a summary of the results of the 8 experiments.

At light intensities greater than 3.7 foot candles, alterations of flapping frequencies in response either to increments or decrements of light were not consistent. In the light intensity interval from 2.3 foot candles to 0.8 foot candles, flapping frequencies were consistently altered, increasing in response to small or large increments of light (Fig. 25), decreasing in response to small or large decrements of light (Fig. 26). The above experimental results make it seem likely that the "warm-up" and "slow-down" character of flapping behavior typically exhibited by *L. ventricosa* at sunrise and just before sundown, respectively (compare Figs. 16 & 17), is a photic response.

C. COMPARATIVE STUDIES WITHIN THE GENUS *LAMPSILIS*

Comparative studies were made of the flapping behavior of *Lampsilis siliquoidea* and *L. brevicula brittsi* in order

TABLE 7. Comparison of responses to various stimuli of mantle flaps (during flapping behavior) and of siphons (during normal activity) in *Lampsilis ventricosa*

Stimulus	Response of Mantle Flaps	Response of Siphons
Photic		
a. Repeated shadows (sudden light decrements)	Shadow response present, as slight pause (0.1 sec.) in flap movements (some indication that shadow response may be inhibited at a high flapping frequency). *	Shadow response present, especially for anal siphon, except after repeated responses to shadows (Table 6).
b. Gradual decrement (as at sundown)	"Headstand" maintained, moves slow, change from "regular" to "slow" pattern, flaps are spread wide apart, marsupia exposed; OR: headstand abandoned, flapping slows, then ceases; flaps and marsupia withdrawn.	No consistent observable response to natural gradual increments or decrements of light intensity. Siphons may be wide open, or closed, in dim or in bright light, day or night.
c. Darkness	If flapping, moves are in "slow" pattern, marsupium (-ia) exposed.	
d. Gradual increment (as at sunrise)	Assumption of headstand, extension of flaps, onset of flap movements, change from "fluttering" to "slow" to "regular" pattern (the last a protective configuration, i.e., marsupia mostly covered by flaps).	
Tactile		
Stroking of relevant structures with fine probe	Negligible; flapping frequently unaltered, even when moving flaps are touched.	Anal siphon: negligible; branchial siphon: innermost row of papillae in lumen sensitive, siphon may close.
Local water waves	No observable response in *L. ventricosa* (marked response in *L. siliquoidea* and *L. brevicula*).	No observable response.
Sudden jarring of substrate	Animal may pause and then either continue or withdraw flaps, then siphons, abandon "headstand" and stop altogether.	Siphons may close, then withdraw; foot may also withdraw, and valves may close.
Temperature fluctuations		
Diurnal variations vs. constant temperature	None noted (although Grier, 1926, claimed temperature response for this species).	None noted.

*I have made several observations of *L. ventricosa* during periods of very high flapping frequency (as high as 3 movements per second), when the mussel gave no recognizable response to shadows. One such observation was made on June 22, 1963, in the White River near Wyman, Washington County, Arkansas, on a large (20 cm long) gravid female, angled in a headstand, into the current, and flapping in full mid-afternoon sun, in approx. 18 in. of water. For more than an hour, I made repeated attempts to induce the shadow reflex in the flapping animal. There was, however, no closure of siphons nor any apparent diminution of flapping frequency. Such observations as these indicate that high flapping frequency may inhibit the siphonal shadow reflex.

to distinguish elements of flapping be-
havior common to these 2 species and to
L. ventricosa, as well as to determine
any flapping characteristics peculiar to
one or more of these species.

Flaps and Flapping Behavior in *Lampsilis siliquoidea*

1. Flapping position and gross flap morphology

In *L. siliquoidea,* flapping position in
characteristically a rotation of only about
50°; the flaps are heavily pigmented, with
less conspicuous eyespots than those of
L. ventricosa, and with elaborate de-
velopment of flap tail portions (Table 10;
Figs. 27, 28).

2. Flap movements in *L. siliquoidea*

These are similar to the "regular"
movements of *L. ventricosa.* The moves
begin with contractions at the base of
each flap's tail, and progress as paired
pulses toward the eyespot. The pulse
pulls the eyespot end of each flap later-
ally. Recovery phase of the movement
brings first the eyespot ends, then the
rest of the flaps together once more.
Flap movements in this species differ
from those of *L. ventricosa* as follows:

a. There are no movements compar-
able in configuration to the "slow" move-
ments of *L. ventricosa* in the flapping
behavior repertoire of *L. siliquoidea.*

b. Frequency of flap movements is
much lower in *L. siliquoidea* than in *L.
ventricosa.* I have recorded rates up to
180 per minute for *L. ventricosa,* com-

pared with a maximum for *L. siliqoidea*
of 29.7 per minute.[18]   *L. ventricosa,*
also, exhibits a much greater range of
flapping frequencies.

c. Spontaneous flap moves in *L. sili-
quoidea* are preceded by definite, twitch-
ing contractions of basal tentacles (BT,
Figs. 27, 28) just under the flap tails,
followed by a slight pause.

d. Spontaneous flap moves typically
occur in pairs in *L. siliquoidea.* Howard
& Anson (1922: 71) also noted this charac-
teristic of *L. siliquoidea* flap movements,
describing them as ". . .regular undula-
tions [*sic!*] of two rapidly succeeding
waves lasting 2 seconds, each taking
approximately a second to pass from the
anterior ventral lobes to the eyespots."[19]

e. A single flap movement (i.e., a
simultaneous movement of both flaps)
may be readily induced in *L. siliquoidea*
(but not in *L. ventricosa*) by sudden jar-
ring of the substrate or by water waves
in the immediate vicinity of the flaps,
such as can be caused by fin movements
of a fish.[20] Such flap responses cannot
be induced by stroking the flaps with a
fine probe. The single flap movement
occurs when the flaps are extended and
either moving rhythmically,[21] or not
moving. These mechanically induced flap
movements are thus readily dis-
tinguished from spontaneous movements
(Table 11).

3. Characteristic flapping periodicities of *Lampsilis siliquoidea*

a. Flapping season lasts through the
spring and summer months. My earliest

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[18]The most extensive recordings of daily flapping frequency for a single specimen of *L. sili-
quoidea,* cover the period from April 25 to July 23, 1963. Average number of movements per
minute for 10 minute counts were tabulated several times daily. Average flapping frequency
throughout this period was between 4 and 5 moves per minute.

[19]"Anterior ventral lobes" are the tails of the flaps. The speed these authors record is faster
than that I measured for *L. siliquoidea.*

[20]An attempt to measure the stimulus causing this response was unsuccessful. Tuning forks
(512, 384 and 324 cycles per second) set to vibrating in and near the aquarium containing flap-
ping *L. siliquoidea* did not stimulate the single flap movement response described above.

[21]If the single flap move is induced during spontaneous movements, their rhythm is broken.
Further, ability of flaps to respond to water waves or to jarring with the single flap movement
diminishes with prolonged stimulation, then ceases, so that several minutes must elapse be-
fore the single-flap-move response can be induced again.

L. R. KRAEMER
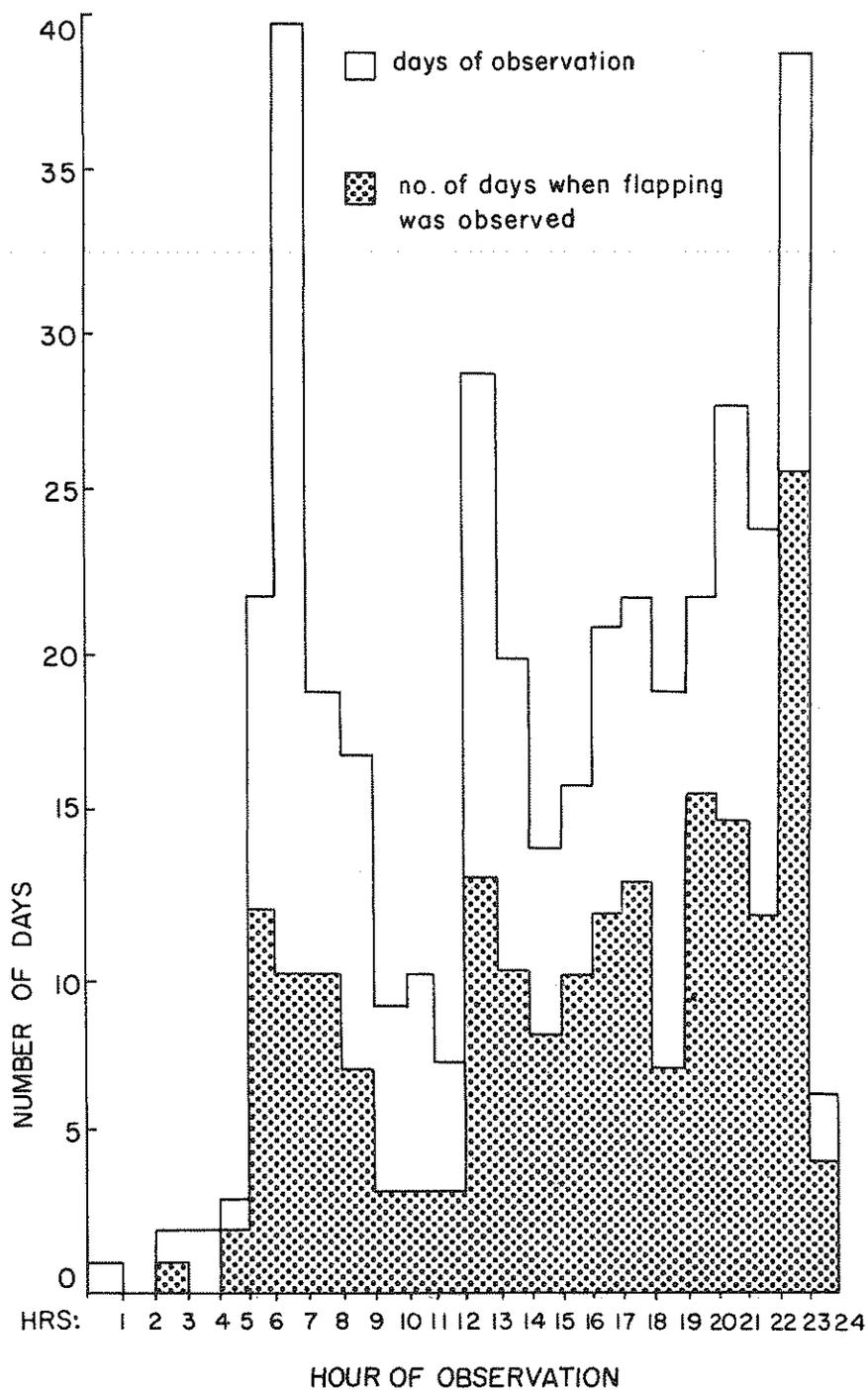
FIG. 24. Flapping activity of *Lampsilis ventricosa*. Times of 24-hour day, during 4 flapping periods (compare with Table 5), when flap movements occurred. Constant water temperature of 19° C.
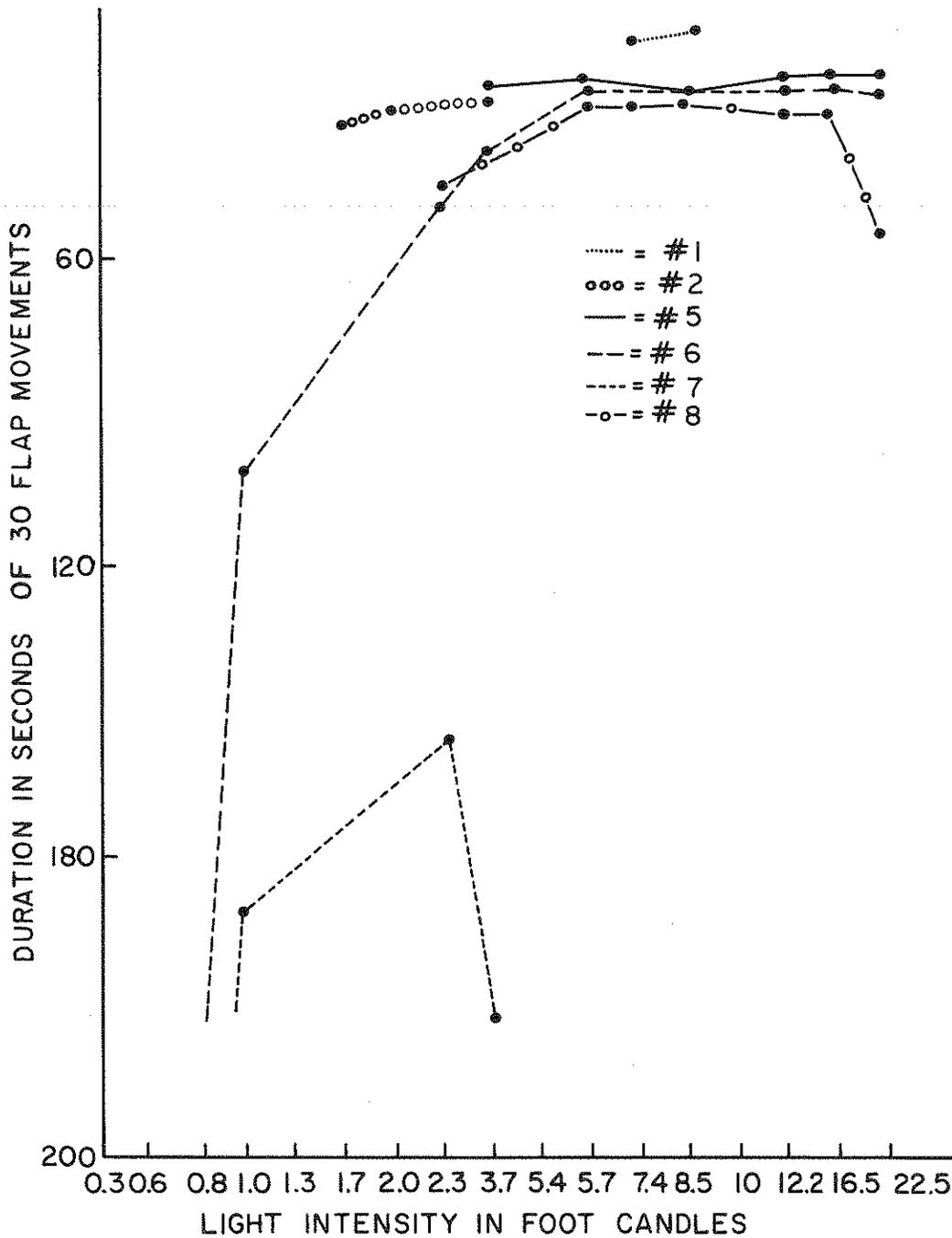
FIG. 25. Response of mantle flap movements of *Lampsilis ventricosa* to increasing light intensities. Data taken from experiments recorded in Tables 8 and 9. At low light intensities (between 0.8 and 2.3 foot candles) flapping frequency increased in response to light increments (compare with speedup of activities at sunrise, Fig. 16).
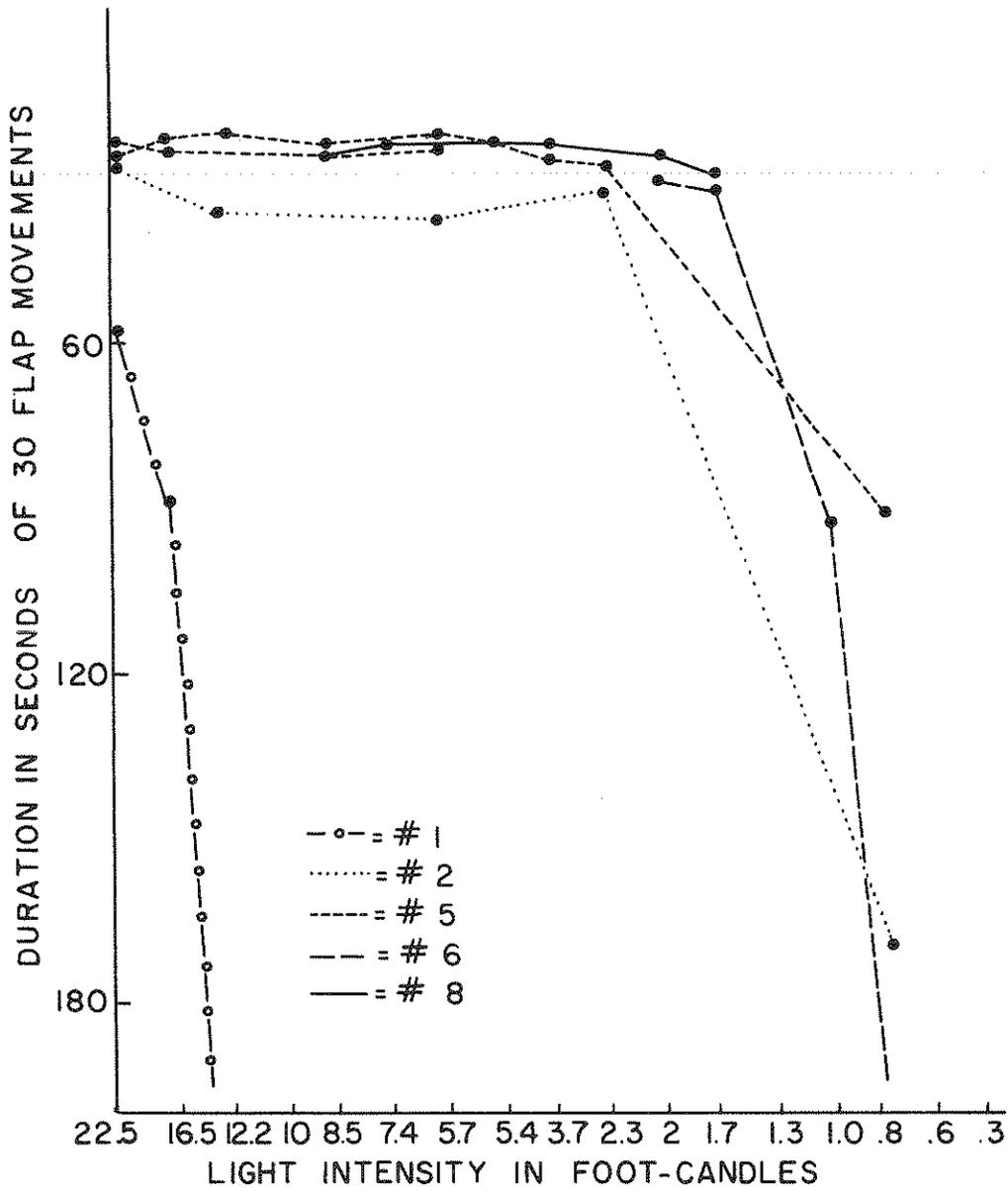
FIG. 26. Response of mantle flap movements of *Lampsilis ventricosa* to decreasing light intensities. Data taken from experiments recorded in Tables 8 and 9. At low light intensities (between 2.3 and 0.8 foot candles) flapping frequency decreased in response to light decrements (compare with slowing or stoppage of activity at sunset, Fig. 17).
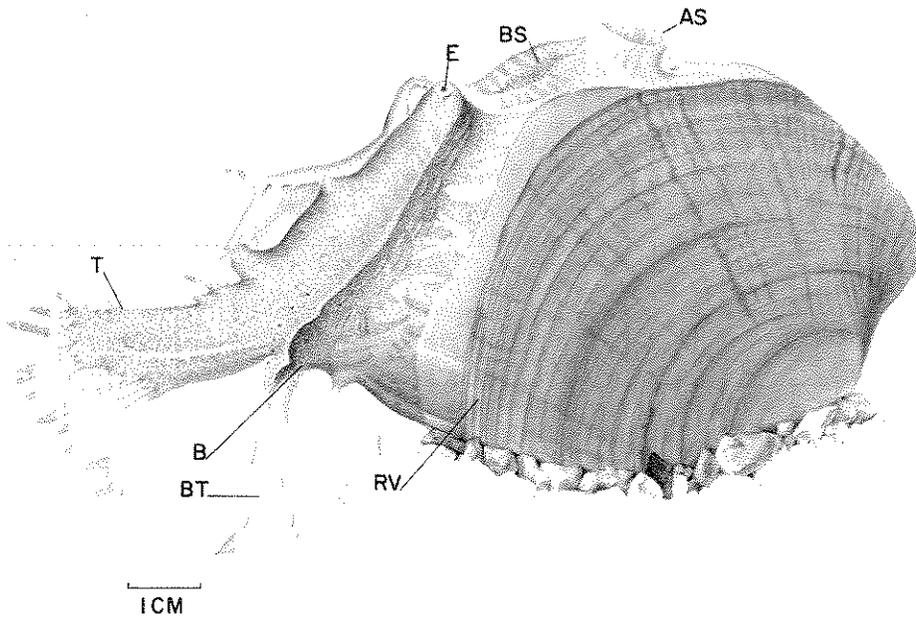
FIG. 27. *Lampsilis siliquoidea,* during flapping behavior, drawn from the right side. Note the position of the animal in a typical flapping stance: while the valves are somewhat tilted forward, the animal is not in the headstand so often seen in *L. ventricosa*. Note also that the edges of the branchial siphon (BS) are held horizontally and not vertically as in *L. ventricosa*.
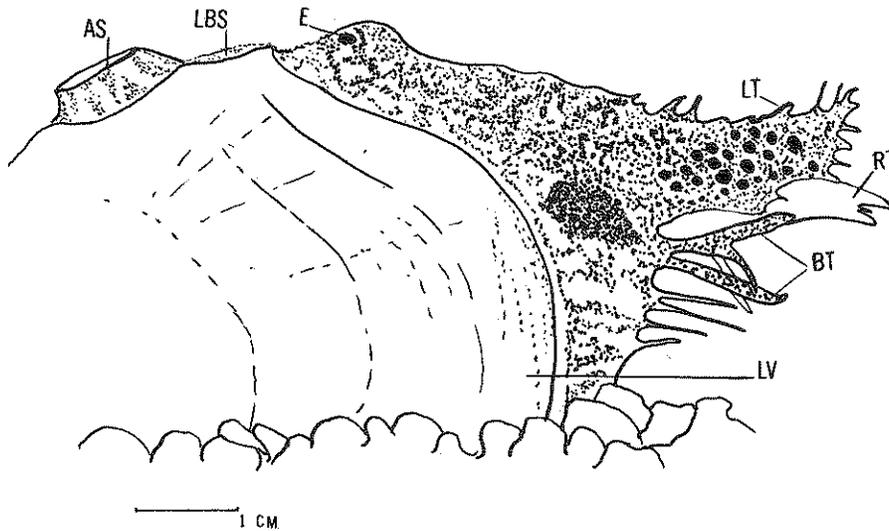
FIG. 28. *Lampsilis siliquoidea* in flapping position, seen from the left side, showing typical, ornate pigmentation especially in tail region of flaps. Branchial siphon not visible from this angle. Specimen from War Eagle Creek, Benton County, Arkansas, July 5, 1964.

TABLE 8. Summary of conditions under which 8 experiments on photic stimulation of flap responses by artificial light were carried out during July and August, 1965*

Experiment	Date (1965)	Prior — Time relative to flapping period	Locomotion	Headstand	Flapping speed in natural light (in min. for 30 moves)	Duration of experiment (p.m.)	Sequence of light intensities in foot candles (read across page)	No. of trial counts at each light intensity
1	7/25	2 days before onset	yes	yes	none	8:05 – 11:00	8.5 7.4 5.4 / 3.7 2.0 1.7	20
2	7/28	during 2nd day	yes	yes	10	7:50 – 11:00	1.7 1.7 2.0 / 1.7 1.0 / .6	20 / 10
3	7/29	near end	no	yes	15	8:00 – 11:00	.6 / .3	10 / 2
4	7/31	1 day before onset	no	45° angle	none	8:10 – 11:00	10.0 / 10.0	20 / 10
5	8/12	1st day	yes	yes	4	7:30 – 11:30	22.5 16.5 12.2 / 8.5 5.7 3.7 / 5.7 8.5 12.2 / 16.5 22.5 16.5 / 5.7 2.3 / .8	20 / 10
6	8/13	2nd day	no	yes	6	7:15 – 10:50	.8 1.3 2.3 3.7 / 5.7 8.5 12.2 / 16.5 22.5 12.2 / 5.7 2.3 .8	10
7	8/14	3rd day	no	yes	18	7:30 – 11:00	.8 1.3 2.3 3.7	10
8	8/16	before last day	no	yes	10	7:50 – 9:50	2.3 3.7 5.7 8.5 / 12.2 16.5 / 22.5 / 1.65 / 12.2	10 / 8 / 10 / 2

record for flapping activity in this species is April 25, and the latest record August 15.

b. Flapping periods are not as distinct in *L. siliquoidea* (Table 12) as they are in *L. ventricosa* (Tables 13 and 14). For example, in 69 days of daily observations of a specimen of *L. siliquoidea* (maintained in an aquarium at naturally fluctuating temperature and light conditions), intermittent flapping activity was recorded during 52 days.

c. A flapping day. *L. siliquoidea*, unlike *L. ventricosa*, may often start or stop flapping activity several times a day. In a series of recorded observations (Table 12) the start-stop pattern was noted on 43 out of 52 days (or 84.6% of the time during which flapping was observed). Such a pattern was seen less than 50% of the time in similar series of observations on *L. ventricosa* (Tables 13 and 14).

Flapping activity in *L. siliquoidea* occurred much less often in the morning than in the mid-afternoon (2-5 p.m.) or late evening from 10-11 p.m. (see Fig. 29).[22] Characteristics of a flapping day for *L. siliquoidea* as contrasted with *L. ventricosa* are summarized in Table 15. Table 16 presents a few records of occasions on which I timed an animal's flapping frequency for 10 consecutive minutes in very dim light and for a like period in bright light.

Flaps and Flapping Behavior in *Lampsilis brevicula brittsi*[23]

1. Flapping position and gross flap morphology

L. brevicula brittsi is a small, thin-shelled species. Externally the flap is little (2.5 cm long in a specimen 6 cm long), dark gray, has inconspicuous eye-spot and an elaborate tail which has a number of tentacles and a prominent pigment spot (Fig. 30). Marsupia protrude between the flaps, their dorsal-most edges scalloped, uneven (not smooth as in *L. ventricosa*). Flapping position is less than a headstand (i.e., rotated only by 45° - 75° instead of 90°) and the animal is typically dug deeper into the

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[22]Late evening observations were made by means of a 25-Watt red bulb or with a penlight. Of 130 recorded observations between midnight and noon, flapping was noted 50 times (31%). Of 260 observations made between noon and midnight, flapping was observed 146 times (56%). As regards observations made on 39 days between 10-11 p.m., the animal was flapping vigorously 66.6% of the time.

[23]Flap movements of this species were observed through spring and summer of 1964 only, whereas flapping individuals of *L. ventricosa* were alanyzed through 4 seasons, and those of *L. siliquoidea* through 3 seasons.

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*General conditions of the experiments which are summarized in Table 8.
a. Water temperature 19°C throughout.
b. Length of experimental periods was limited naturally: at high light intensities, though without measurable increase in water temperature, prolonged exposure would bring about pause in regular flap movements, then fluttering movements, finally a halt. At low light intensities, moves slowed to negligible rate. Movements were considered to have stopped if there was a pause longer than 10 minutes between movements.
c. Experiments were all conducted at night, to control light conditions. Animal could not be moved to a darkroom because of its sensitivity to "jarring"; such a move might have stopped its flap movements, which may then not have been resumed for days.
d. The number of counts made (time for 30 moves) was large because the animal's response to altered light intensities by marsupial movements is often accompanied by alteration in flapping.
e. Observations concern a single animal because, even with 8-10 mature females kept, there was seldom more than one animal flapping for long periods. This same animal's flapping behavior, when not exposed to artificial illumination constituted the control. Movements in the darkness were observed with a red 25-Watt safelight.

TABLE 9. Average flapping frequency* of a specimen of *Lampsilis ventricosa* at various light intensities

Experi- ment no.	Light intensity (in foot candles)																
	22.5	16.5	12.2	10.0	8.5	7.4	5.7	5.4	3.7	2.3	2.0	1.7	1.3	1.0	.8	.6	.3
1						114.6 36.8											
					25.0←26.3	→24.6 → 24.7			25.2 ——→27.2→30.1								
2											53.0 32.4← 34.4	→34.9 —— →94.5 —————→292.6					
3																	568.0→1728.1
4				104.0 140.2													
5	33.2 25.1→ 24.5→23.7 24.2← 24.1 →25.3				→25.5 —— 26.7←	→24.8 25.0← 25.4	→26.5		→28.4					→92.2		
6	28.1← 26.9← 27.8 →36.9				27.0←	27.1← 38.3→		40.4← 50.2 33.8→				104.6←		52.3 2178.3 255.6 →171.0		
7									279.3←110.9				201.6←		572.2		
8	58.7← 33.0←33.3 89.6 427.7				30.6←	30.8←		29.9← 47.6								

*Frequency is expressed as average duration of 30 movements; time is expressed in seconds, the numbers are averages from up to 20 consecutive counts of 30 moves each.

Arrows indicate whether a particular frequency followed an increment (←) or a decrement (→) of light.

TABLE 10. Comparison of flapping position and gross flap morphology in *Lampsilis siliquoidea* and *L. ventricosa*

Flapping feature	*L. siliquoidea*	*L. ventricosa*
Position		
valves:	typically not a headstand; animal usually tilted (i.e., rotated forward) at 45° angle. (Figs. 27, 28)	typically a headstand, especially at higher flapping frequencies. Animal tilted (rotated anteriorly) at 90° angle to substrate. Foot serves as prop. (Fig. 2)
branchial siphon:	edges often held horizontally	edges not often held horizontally
marsupia:	do not protrude prominently between the flaps	do protrude prominently between the flaps, especially later in flapping season, at time of regular moves with high flapping frequency, and at times of very "slow" flap movements; marsupia may move up and down with changes in light intensity
Appearance (in flapping animal)		
tail:	long, broad, prominently fringed with many basal tentacles	truncated, with few or no basal tentacles
eyespot:	raised, dark, not prominent on external surface of flap; visible though smaller on internal surface	prominent, often raised, dark, and surrounded by white ring; not visible on internal surface of flap
outer flap surface:	often dark, reddish brown, with rows of dark brown spots. Prominent dark spots near tail base and on tail	uniform, medium-light gray; not spotted. Line of pigment on inner surface shows through
inner flap surface:	a rosy peach, especially in tail region of flap. Line of pigment, extending from eyespot to tail, may be present	pale gold to pink, with prominent black line of pigment extending from just behind area corresponding to exterior location of eyespot to tail tip

substrate.

2. Flap movements

They resemble those of *L. siliquoidea*, beginning as a pair of pulses at the base of the flap tails, moving simultaneously toward the eyespots, causing the eyespot portions of the flaps to turn laterally. Recovery stroke brings first the eyespot ends, then the rest of the flaps together in apposition once more.

Movements occur in groups of 2 or more, the flaps moving at slightly higher frequencies than those of *L. siliquoidea*.

TABLE 11. Comparison of spontaneous "regular" flap movements with me-
chanically induced movements in *Lampsilis siliquoidea*

Spontaneous movements	Mechanically induced movements
normal flap movements as described for *L. ventricosa*	the same aspect for individual move
preceded by twitching of basal tentacles	not so preceded
occur typically in pairs (less often triple, rarely single moves)	are single
—	produced in response to jarring of substrate or to local water waves
—	provokable in absence of spontaneous flapping

1st flopping period
2nd flopping period
3rd flopping period
4th flopping period
cumulation of 4 flopping periods
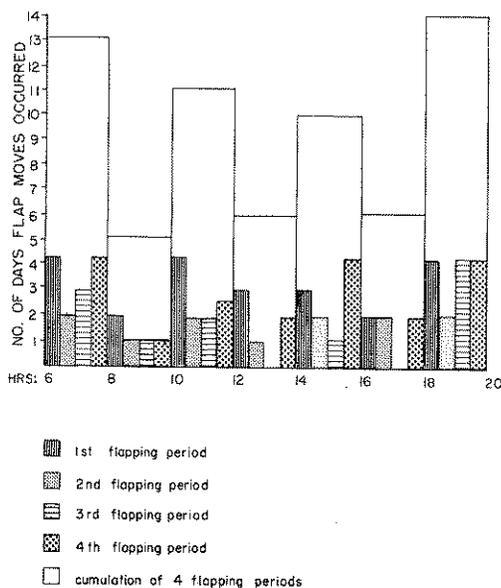
FIG. 29. Diurnal flapping activity in *Lampsilis siliquoidea*.

Flap movements may be mechanically induced in *L. brevicula brittsi*, as they are in *L. siliquoidea*. The fortuitous observation described below indicates how flap movements induced mechanically (e.g., by water waves) may facilitate mantle flap activity by *L. brevicula brittsi*.

On August 11, 1964, a specimen of *L. brevicula brittsi* had come to a position not more than 5 cm away from a specimen of *L. siliquoidea*, in one of my aquaria. At 11:00 a.m., both animals were exhibiting flap movements, almost flap-tail to flap-tail.[24] The very regular alternation of movements, first by one animal then the other, caused me to time several flapping sequences of the 2 animals (Table 17).

L. brevicula brittsi maintained a flapping frequency about twice that of *L. siliquoidea* throughout. Neither the characteristic twitching of the basal tentacles which precedes spontaneous flapping in *L. siliquoidea*, nor the typical paired movements were observed at that time. It seemed probable that the movements of *L. siliquoidea* were being mechanically stimulated by the movements (local water waves) of *L. brevicula brittsi* nearby. *L. brevicula brittsi*, in turn, may have been responding at least

[24]Two mature female specimens of *Lampsilis ventricosa*, at the opposite end of the same aquarium, exhibited no flap movements at that time.

FIG. 30. Various flapping positions in *Lampsilis brevicula brittsi*. Specimen collected from War Eagle Creek, Washington County, Arkansas, on July 5, 1964. Sketched: a, August 4, at 7:00 a.m.; b, August 5, at 6:30 a.m.; c, August 1, at 11:00 a.m.

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TABLE 12. Diurnal flapping activity of a specimen of *Lampsilis siliquoidea* at seasonal fluctuating temperatures and natural light[X], from April 25 to July 2, 1963

Date (1963)	Hour of the day																							
	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
4/25																					*			
26						*															*		*	
27					*																	*	*	
28											*			*	*					*			*	
29																				*			*	
30																				*		*	*	
5/ 1																								
2																								
3															*	*								
4												*		*			*	*		*				
5												*	*	*	*			*	*		*			
6													*	*	*			*		*				
7					*																			
8																			*			*		
9			*				*	*			*		*		*		*							
10											*			*		*		*						*
11																			*		*		*	
12															*			*		*		*		
13						*	*	*										*	*		*			
14														*										
15																								
16																								
17																					*			
18																								
19																								
20																								
21																								
22																								
23																						*		
24																								
25							*	*	*	*		*	*								*	*		*
26								*			*		*		*							*		
27											*		*		*				*		*			
28											*							*		*			
29																		*		*			
30															*			*		*		*
31				*						*		*											
6/ 1												*									*	
2																	*				*	
3								*		*		*										

part of the time to the movements of its neighbor. The animals did not then seem to be maintaining independent spontaneous mantle flap rhythms.[25]

3. Time of flapping activity of *L. brevicula brittsi*

The flapping season lasts through the

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[25]This behavior continued through the day. Another series of 20 minute-count trials was made beginning at 10:30 p.m. on the same date, with results much the same as those recorded in Table 17.

Table 12. (Contd.)

Date (1963)	Hour of the day																							
	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
6/ 4								′	′				′				′			′		′		
5						′		′												′			′	
6	′											′				′						′ ′		
7						′		′				*	*				*		′ *		*		*	
8						′		′		′			′						′ *		′ *			
9					*	′		′ ′		′					′ ′				′	*	′	*		
10					*	′				′		′							′ ′	′	′			
11																								
12					*	*	*	* ′ ′					*				*	*			*		*	
13			′	*		*	*	*	′		′		*			*		′		*		*	
14					*		*				′	*	*		*		′ ′			*		*	
15				′	*		*		′			′				′ ′				′ ′		*	*
16				′					′			′								′ ′ ′			
17		′ ′			′ ′		′					*	′	*				′	*		*		
18			′		′		′			′							′ ′	′		′ ′		
19					*	′							*		*		*	*		*		*	′
20			′		′										*				′				
21					*						*			*		*		*	*		*		
22			′		*	*	*		*		′										′ ′		
23			′		′			′			*		*	*							′		
24				′		′				*		*		*		*	*			*		
25				′ ′		′					*				*					*		
26				*								*			*			*		*		
27				′		′			*			*				*		′ *		*		
28					′ *	′		*	′	*		′				*			*			
29				*			′			*		*		*		*					*	
30				′					′								′					
7/ 1				*			*		*		*	′									′	
2						′						*			′						′	
Summary																								
Flapping	0	0	1	0	2	12	10	10	7	3	3	3	13	10	8	10	12	13	7	16	15	12	26	4
Not flapping	1	0	1	2	1	10	30	9	10	6	7	4	16	10	6	6	9	9	12	6	13	12	13	2
Total	1	0	2	2	3	22	40	19	17	9	10	7	29	20	14	16	21	22	19	22	28	24	39	6

′ = No flapping occurred.

* = Flap movements occurred.

x = After dark observations were made with a small penlight.

spring and summer months. For a single specimen my earliest record of flapping activity was June 5, and the latest, September 3. There is not enough information at the present time for meaningful comparisons of eventual "flapping periods" of *L. brevicula brittsi* with those of other species. Specimens of *L. brevicula brittsi*, like *L. siliquoidea*, however, are capable of vigorous flapping in the dark (as seen with a 25-Watt safelight).

A Note on Flaps and Flapping Behavior in *Lampsilis fasciola* Rafinesque

L. fasciola is of interest, because, as H. & A. van der Schalie (1963) have

TABLE 13. Diurnal flapping activity[X] of a specimen of *Lampsilis ventricosa* maintained at seasonal, fluctuating temperatures, from June 29 to September 11, 1964, with some observations in artificial light

Date (1964)	Hour of the day																		
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
6/29														*					
7/ 3			*																
8					*											*			#
9		*	*	*	*	*	*	*	*	*	*	*	*	*	*				
10																			#
11	´	´	´																
12	´																		
13		´																	
14–22																			
23					*														
26									*										
28		*																	
29		´																	
30		´																	
31		´																	
8/ 1		´																	
2			*	*	*	*	*	*	*	*	*	*	*	*	´	´			
4		*	*	*	*	*	*	*	*	*	*	*	*	*	´	#			´ #
5	*	*												´ #	´ # ´			´	
7		´																	
8		´																	
9		´																	
10		´																	
11		´																	
15				*	*	*	*	*		*				´ #	#				
16				*	*	*	*	*	*			*		´	´				
17		*																	
18		´																	
19		*						´											
28			*	*															
31		*	*																
9/ 1			*				*	*	*	*	*	*	*						
2		*	*	*	*	*	*	*	*	*	*	*							
3																#			
10							(conglutinates shed)												
11							(conglutinates shed)												

[X] No observations were made between midnight and 5 a. m.

* Flap movements occurred, in natural light (after dark observations were made with a small penlight).

´ Flap movements did not occur, in natural light.

+ The same animal as that used in the previous light experiments.

x No observations were made between midnight and 6 a. m.

* Flap movements occurred, in natural light (after dark, checks were made with 25-Watt red safelight).

´ No flap movements occurred, in natural light (after dark, checks were made with 25-Watt red safelight).

Flap movements occurred, in artificial light (incandescent bulb, at different light intensities).

IR Flap movements occurred, in dim natural light plus artificial infra-red source. These preliminary studies with infra-red light were insufficient to yield conclusive results.

TABLE 14. Flapping activity of a specimen of *Lampsilis ventricosa*[+] maintained at 19° C under varying conditions of light, from July 2 to August 24, 1965[X]

Date (1965)	Hour of the day																	
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
7/ 2																	*	
3					/		/			/	/	/						
5									/	/	/				/	/		
6					/				/									
8					*				*	*	*	*	*	*	*	*	*	
9	/	*		*				*	*				*	/	/			
10	*				*	*								*				/#
11		*			*	*			*	*	/			/	/	/	/	
12	*		*	/	*	/	/			/	/			*		/	/	
13	/	/		/					/				/					
14		/		/		/	/			/	/					/		
15		/		/	/			/					/		/			
16		/						/	/				/					
17		/			/	/	/	/						/				
18		/							/									
19	/				/		/						/					
20		/			/	/	/						/					
21		/			/	/	/							/	/			
22		/		/	/	/	/						/	/	/			
23		/			/	/	/			/	/			/	/			
24		/								/		/						
25				/										/#	#	#	#	
26	/			/						/				/	/	/		
27		*		*	*	*			*	*	*	*		/	/			
28	/				/						/	/	*	#	#	#	#	
29	*				*	*	*			*	*	*		*	#	#	#	
30	/		/		/	/	/				/			/				
31	/				/	/	/				/			/	/	#	#	#
8/ 1		*			*					*				*	#	#		
2	*			*	IR	IR	IR	IR	IR	IR			*/					
3	*			*	*	*	*	*	*	*	*		*					
4	/			/						/	*			*	#	#		
5	/									/				/				
6	/			/					/					/				
7	/						/						/					
8	/				/	/	/							/	/			
9	/						/			/				/	/	/	/	
10		/			/	/				/				/	/	/	/	/
11		/								/							/	
12		/						/		*				*		.		
13		*			*	*	*	*	*	*	*	*		*	#	#	#	#
14		*		*	*	*	*		*	*	*	*		*	#	#	#	#
15		*			*	*	*		/	/	*		/					
16		/			/	/	/		/	/	/			*	#	#		
17		*		/		/	/		/	/	/	/		/	/	/		
18	/				/	/	/			/	/			/				
19	/					/							/					
20		/			/	/	/			/	/	/		/	/			
21		/			/	/				/	/			/	/	/	/	
22	/				/	/	/			/	/			/	/	/	/	
23	/																	
24	/				/	/	/			/	/			/				

TABLE 15. Characteristics of a flapping day for *Lampsilis siliquoidea* and for *L. ventricosa*

Flap activity	*L. siliquoidea*	*L. ventricosa*
Time of onset	any time of day	often at dawn
Pattern through daylight hours	starts, stops, starts; often 3 or more times a day	starts, speeds up flap movements at dawn, flaps through day, slows down or stops at dusk
Pattern after dark	may show more vigorous flap moves (especially from 10-11 p.m.) than in daylight	if flapping, moves are of slow pattern
Response to experimental light conditions	no consistent definite responses noted*	consistently, at low illuminations flapping frequency slows in response to light decrements and speeds up with light increments

*Limited experimental efforts only were made to check the effect of various light intensities on flap movements of *L. siliquoidea* (see Table 16).

pointed out, it has a curiously circumscribed distribution in some areas of Michigan. This species exhibits fairly rapid, regular mantle flap movements. I had the opportunity to observe a number of *L. fasciola* in the River Raisin, upstream from Sharon Hollow, Washtenaw County, Michigan (see also footnote 40), in August, 1962. The 9 flapping females seen at that time were all clearly visible in the main channel at water depths from 1.5 to 2 feet. Movements of their flaps were such that all must have been in a headstand position. The movements were rapid and regular. In appearance, the flaps (Figs. 5c, d) are similar to those of *L. siliquoidea* (Figs. 27, 28), with elaborate pigmentation and many basal tentacles.

DISCUSSION AND CONCLUSIONS

In the course of this study, it has been found that:

(1) Mantle flaps in *Lampsilis ventricosa*, *L. siliquoidea*, *L. brevicula brittsi* and *L. fasciola* have common structural features:[26] (a) all are extensions of the third or inner lobe of the posterior mantle edge anteroventrad to the branchial siphon; (b) all possess the same general configuration with a pigmented spot (the eyespot) just posterior to the branchial siphon, and a free-hanging tail; (c) pigmentation of the external flap surface is generally more elaborate and always different from that of the internal surface; (d) innervation of the mantle flaps (examined in *L. ventricosa* and

[26]These morphological characteristics are found also in *Lampsilis cariosa*, of which a number of preserved specimens were examined for this study.

TABLE 16. Flapping frequency averages (average No. of moves/min. for 10 min.) in dim light and in bright (incandescent) light for *Lampsilis siliquoidea*

Date: April 1964	Time P. M.	Frequencies/min.	
		dim light	bright light
26	8:30	4.4	5.3
27	9:15	6.1	1.3
	10:30	13.8	10.8
28	7:30	5.1	5.4
29	7:10	3.5	3.5
30	7:15	1.1	0.8
	9:30	2.2	2.3

L. fasciola) is by way of branches of pallial nerves extending from the visceral ganglion.

(2) Mantle flaps in the above species differ morphologically in (a) external pigmentation, which may be a uniform gray (*L. ventricosa*), or heavily spotted (*L. siliquoidea*, *L. brevicula brittsi* and *L. fasciola*); (b) development of the tail, which may be truncated and slender, as in *L. ventricosa*, or broad and elaborately fringed with tentacles, as in the other 3 species; (c) appearance of the eyespot, which may be prominent, ringed with white, and confined to the external flap surface (*L. ventricosa*), or inconspicuous and visible on external and internal flap surfaces (as in the other 3 species).

(3) Flap movements as studied in *L. ventricosa*, *L. siliquoidea* and *L. brevicula brittsi* all comprise (a) paired pulses which are initiated as contractions at each tail base and move toward the eyespot ends of the flaps; and (b) a recovery phase in which the flaps assume their former position, often with tails floating free and horizontally in the water.

(4) Flapping behavior in the above 3 species is not limited to flap movements, but involves the coordinated function of many body structures, to such an extent that the supposed normal relationships between body and shell are much altered.

(5) Flapping involves different behavioral complexes in different species, e.g., headstand (upending by 90°), regular and slow flap movements, spontaneous marsupial movements, changes in flapping frequencies at dawn and dusk, and diurnal flapping pattern in *L. ventricosa* - contrasted with not so pronounced a headstand (forward rotation of 50°), regular double flap movements, no slow movements, no noticeable spontaneous marsupial movements, crepuscular to nocturnal flapping pattern in *L. siliquoidea*.

(6) Flapping behavior in these species involves different stimulus modalities, especially light for *L. ventricosa*, and water waves and jarring of substrate for *L. siliquoidea*.

(7) The special characteristics of flap movements in the species studied here, fit into the larger context of the total behavior repertoire of the non-flapping animal: (a) mantle movements independent of shell movements do exist in various bivalve genera (as found by Redfield, 1917, for *Mya*, *Modiolus*, *Mytilus*, *Solenomya*, *Ensis*, *Cumingia* and *Yoldia*); (b) extreme heel formation of the foot, in serving as a prop for some flapping lampsilids, can logically be viewed as an exaggeration of a phase of normal bivalve locomotion (the *Hakenform* and *Schwellform* of Fraenkel, 1927); (c) alterations of flapping frequency in response to alterations of light intensity show similarities to the animal's general skioptic (shadow) sense, which mediates siphon withdrawal in many bivalves; (d) marked response of extended or moving mantle flaps of mussels such as *L. siliquoidea* to jarring of substrate and to water waves is more difficult to identify although bivalves are notoriously sensitive to jar, the most widely observed response being siphon withdrawal and valve closure.

(8) Despite the fact that mantle flaps respond to different stimuli in different species and that flap movements can occur for a whole season previous to

TABLE 17. Sequence and number of flap movements during 20 1-min. periods for 2 specimens of *Lampsilis* whose moving flaps were approximately 5 cm apart; in aquarium, at natural temperatures. Trials started at 11:00 a.m. on August 11, 1964

Trial	Species*	Consecutive flap movements during 1 minute**	Total flap movements
1.	L. b.	/ / / / /	5
	L. s.	/ /	2
2.	L. b.	/ / / / / /	6
	L. s.	/ / /	3
3.	L. b.	/ / / / / /	6
	L. s.	/ / /	3
4.	L. b.	/ / / / / /	6
	L. s.	/ /	2
5.	L. b.	/ / / / / /	6
	L. s.	/ / /	3
6.	L. b.	/ / / / /	5
	L. s.	/ / / /	4
7.	L. b.	/ / / / / /	6
	L. s.	/ /	2
8.	L. b.	/ / / / / /	6
	L. s.	/ / /	3
9.	L. b.	/ / / / / / /	7
	L. s.	/ / / /	4
10.	L. b.	/ /	2
	L. s.	/ / /	3

spawning, they apparently do accompany spawning of glochidia in all species in which the movements have been observed. The foregoing statement is supported by the following evidence from this study: (a) flaps occur only in mature female specimens, whereas juveniles and males have flap rudiments; (b) flap movements have been seen only in gravid, never in non-gravid females (although not all gravid females maintained in aquaria for months showed flap movements); (c) flap movements have been seen in association with gradual emptying of the ovisacs and with shedding of conglutinates; (d) flap movements have not been observed after shedding of glochidia.

* * *

Grier (1926) and Welsh (1933) are the only previous investigators known to me to have undertaken experiments with flapping Lampsilinae. Grier contended he had induced increasing frequency of flap movements in a specimen of *Lampsilis ventricosa* by experimentally increasing water temperature. My own observations do not support his finding.

Welsh (1933) made a brief series of

Table 17. (contd.)

Trial	Species*	Consecutive flap movements during 1 minute**		Total flap movements
11.	L. b.	/ / / / / / /		7
	L. s.	/ / /		3
12.	L. b.	/ / / / /		5
	L. s.	/ / /		3
13.	L. b.	/ / / / /		5
	L. s.	/ / / /		4
14.	L. b.	/ / / / /		5
	L. s.	/ /		2
15.	L. b.	/ / / /		4
	L. s.	/ / /		3
16.	L. b.	/ / / / / /		6
	L. s.	/ /		2
17.	L. b.	/ / / / /		5
	L. s.	/ / /		3
18.	L. b.	/ / / / / /		6
	L. s.	/ /		2
19.	L. b.	/ / / / / /		6
	L. s.	/ / / /		4
20.	L. b.	/ / / / /		5
	L. s.	/ /		2

*L. b. = Lampsilis brevicula brittsi; L. s. = Lampsilis siliquoidea.

**/ = one flap movement.

determinations of the time required for 10 flap movements in a specimen of *Lampsilis nasuta* (*Ligumia nasuta*) over a range of 9 decreasing light intensities, as a consequence of which he observed (1933: 755) that ". . .light did play an important role in determing the frequency of these rhythmical contractions." Though his graph plotting frequency of flap moves against light intensity (here reproduced as Fig. 31) looks as though the animal had increased its frequency in response to increasing light intensity, it had in fact decreased its flapping frequency in response to decreasing light intensity, the data being arranged in inverse order. His numerical data (:755) are here reproduced (Fig. 32). Welsh found (:756) that the flapping rhythm of his specimen "was interrupted at low light intensities and ceased entirely [sic!] after a short exposure to an illumination of about 0.2 foot-candles." My own prolonged observations of *Lampsilis ventricosa* would indicate that *Ligumia nasuta* may actually possess a far more complex response to light than Welsh was able to discover
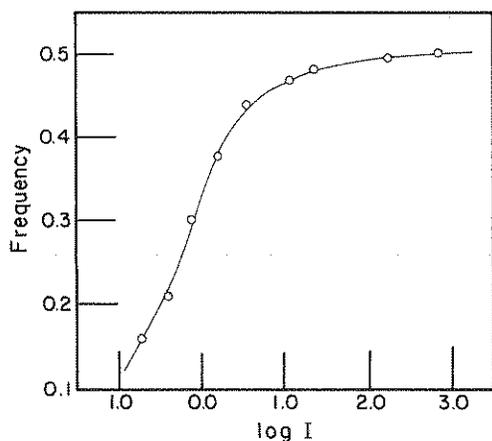
FIG. 31. Frequency of flapping in "*Lamp-silis*" (= *Ligumia*) *nasuta* from Welsh (1933: 755-756. Note that exposure was in reverse order, i.e., with decreasing light intensity, as indicated by his explanation of the graph: "Plot of data showing frequency of movement (number of movements per second) of the mantle flaps of *Lampsilis nasuta* plotted against the logarithm of the light intensity. Observations were begun at the highest illumination. "

from his more limited opportunity for study.

Two hypotheses have been advanced by other investigators concerning the probable functions of flapping in these animals. First, the speculation by Ortmann (1911) and others (e.g., Coker et al., 1921) who followed him, that the flap movements help to aerate the glochidia, and second, the hypothesis subscribed to by Coker et al. (1921), Howard & Anson (1922), and Welsh (1933), that the moving flaps are in effect mimicking minnows and serve as lures to host fish. The first hypothesis seems, in the light of the study presented here, to be qualifiedly plausible. Regular movements of *Lampsilis ventricosa* (carried on intermittently for several months during the summer) especially those at high frequencies, do appear to create a lively water current over the bulging marsupia, though the slow movements certainly do

not. But in species such as *L. siliquoidea*, in which flapping movements are much slower, and the marsupia do not commonly protrude, the relation of flapping to gill or marsupial aeration would hardly seem to be of much consequence.

The second hypothesis is an intriguing idea, but it has many shortcomings. Admittedly, to the human observer watching rapid regular movements of an upended *L. ventricosa*, particularly on an eye-level with the eyespots of the flaps, the resemblance of the moving flaps to some small fish is striking. However, a flapping *Lampsilis ventricosa* exhibiting slow movements does not present a fish-like appearance, neither does a mussel such as *L. siliquoidea*, which does not characteristically assume a headstand, does not commonly protrude its marsupia (suggesting the rounded body of a fish), does not flap in a fish-like fashion, and does not have prominent eyespots.

It seems most plausible to reason that if host fishes are attracted to the flaps, it would be movements per se, rather than a fish-like appearance which might attract them. All of the species observed at length in this study (*L. ventricosa, L. siliquoidea, L. brevicula*), have been maintained from time to time with possible host fish such as the largemouth bass (*Micropterus salmoides*) and the black crappie (*Pomixis nigromaculatum*). The crappies upon occasion would make darting movements toward the tails of the moving flaps. At other times, a fish would loiter nearly motionless for hours in the vicinity of the tails of the moving flaps. If the fish were attracted by the flapping (though their presence always seemed merely fortuitous to me) the presence of the fish in the neighborhood of the moving flaps would insure their exposure to any glochidia discharged.

The differences between mussel species in flapping postures, appearance, optimal time of flapping activity [27] and

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[27]Such differences might coincide with periods of activity of potential fish hosts, such as described by Davis (1962).

Times in Seconds for Ten Movements of the Mantle Flaps of Lampsilis with Their Averages, and the Frequency (Number of Movements per Second) at Each of Several Intensities of Illumination. Temp. 21.3° C.

Intensity (Foot-candles)	0.20	0.41	0.83	1.66	3.6	12.0	23.0	180.0	689.0
Time (secs.) for 10 movements	65.0	48.0	28.6	24.5	22.5	21.2	21.0	20.1	20.0
	61.0	46.8	30.5	25.8	22.3	20.9	20.8	20.1	20.0
	62.0	49.2	32.2	27.4	22.2	21.4	20.8	20.1	20.2
	63.5	48.6	35.2	26.6	22.1	21.5	20.6	20.1	20.4
	61.8	46.7	33.0	26.4	21.9	21.8	20.9	20.5	20.1
			32.5	27.6	22.6	21.5	20.9	20.2	19.7
			30.8	27.6	23.4	21.2	21.0	20.4	19.6
			35.0	27.4	23.6	21.5	20.6	19.9	19.8
			36.0	27.0	23.3	21.0	20.6	20.4	20.0
			38.0	25.6	23.6	21.2	21.2	20.1	19.8
Averages	62.66	47.86	33.18	26.59	22.75	21.32	20.84	20.19	19.96
Frequency	0.159	0.210	0.301	0.376	0.439	0.469	0.481	0.495	0.502

FIG. 32. Numerical data from Welsh (1933).

the manner in which they respond to environmental stimuli suggests possible adaptations (still in need of much study) to habits of peculiar fish-host species.[28]

I would like to suggest another explanation for the flapping movements of lampsilids. A simple if partial hypothesis for the flap movements may be suggested by the diagram (Fig. 33) here. It shows an aquarium which Lefevre & Curtis (1910) constructed for the purpose of infecting host-fish with glochidia. The tank has a cross-hatched arrangement of perforated connecting pipes on the bottom, which were fed by a vertical inlet pipe of similar diameter. The purpose of this apparatus was to prevent glochidia, when introduced into the tank, from settling helplessly on the bottom, and to keep them suspended in the water, so that they might more readily come into contact with fish-hosts already in the tank. Similarly, I suggest, the bellows-like movement created by the paired pulses of all flap movements, regardless of species or flapping frequency or regularity, would help the glochidia to remain suspended in the water for a period of time, and thus facilitate the vitally necessary contact with a host fish. Regrettably, I did not experiment with the adequacy of flap generated currents to sustain glochidia in a mid-water position. This certainly should be done.

Ancillary problems arising from this

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[28] However, I am loathe to subscribe to anthropomorphic generalizations: what looks like fish to us need not necessarily do so to fish themselves. Further, empirical evidence - some almost paradoxical in the light of earlier hypotheses - should not be ignored. *L. ventricosa*, flapping at high speed in full sun in the stream or in the aquarium has never been observed in the course of this study to "attract" any local creatures, any more than any other piece of the scenery. Also, this animal flaps very slowly for long periods in the dark. Under such circumstances, the nature of the "attraction" for a fish-host would be difficult to imagine. *Lampsilis siliquoidea*, which flaps in a similar manner day and night (i.e., with its own characteristic slower but "regular" movements), responds quickly to any local water movement including the movement of a fish's fin by interrupting its regular flap movements, with no detectable response by the fish. *Lampsilis fasciola* studied for a week in the River Raisin, July, 1967 repeatedly ceased flapping movements in response to movements of fish or crayfish in the immediate vicinity of the flaps.
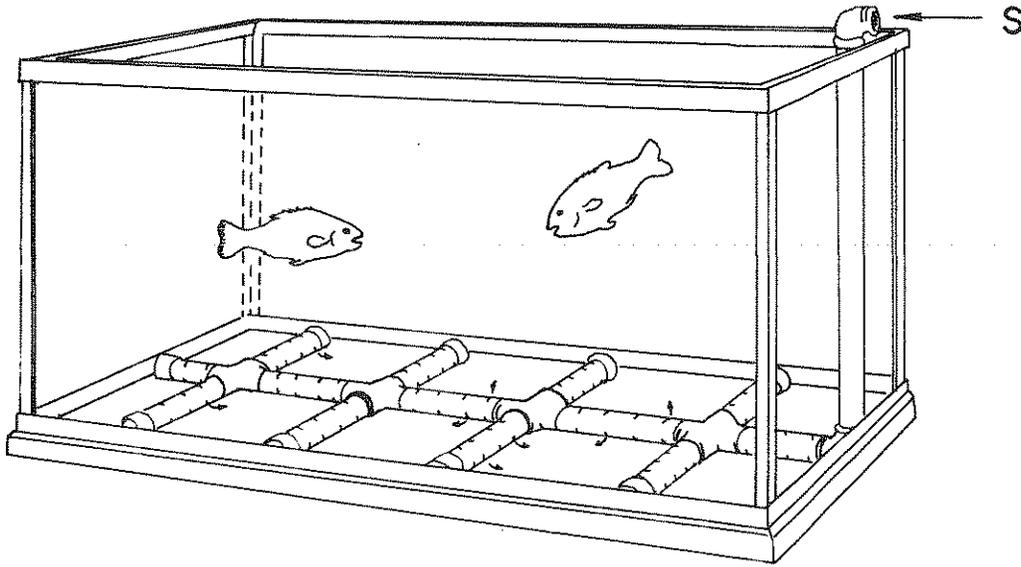
FIG. 33. Apparatus designed by Lefevre & Curtis (1910: 166) "for keeping glochidia suspended in water while fish are being exposed to them for gill infections." The force of the tap water entering at S and issuing in fine jets from perforations in the bottom grid is so regulated as to insure an even distribution of glochidia within the water, while preventing them from rising to the top and escaping with the overflow.

study fall into 2 groups, those related to mechanisms within flapping Lampsilinae, primarily, and those of broader taxonomic ramification such as species distribution, and fish-host relationships. In the first group would be included:

(a) The study of microscopic anatomy of the flaps, combined with neuroanatomical studies of the animal. Such studies, including a search for neurosecretory material, are in progress.

(b) Physiological studies of the mechanism whereby increasing light at low illuminations can increase or induce flapping behavior, and decreasing light at low illuminations can slow down or inhibit flapping behavior, as is the case in *L. ventricosa*. Particularly light (shadow) sensitive areas should be searched for in the mantle flaps and in

neural entities such as the visceral ganglion or pallial nerve. Relationships between the siphonal shadow reflex and mantle flap response to altered light intensity might be investigated and measured in a single species. Careful efforts could be made to extract pigments (especially from eyespots of *L. ventricosa*) and perhaps to ascertain the reaction spectrum of the mantle flaps.[29]

(c) Neurosecretory substances known to control spawning in other organisms could be injected into the mussels, such as the "shedding substance" investigated by Chaet et al., (1964) from radial nerves of starfish, in order to determine whether flapping behavior could thus be induced in *Lampsilis*.

(d) The mechanism whereby some lampsilids alter their flapping behavior

[29]Conly-Dillon (1965: 346) in his work on spectral sensitivity of eyes of the scallop *Pecten maximus*, injects a word of caution into an analysis of his findings: ". . .the possibility is not excluded that other light-sensitive structures, perhaps located directly within the nervous system itself, may be contributing to the spectral sensitivity of the animal."

in response to jarring of substrate or to water waves, should be investigated, along with the relationship between this response and the general bivalve response to jarring.

In the second group would be included:

(a) Tests of the hypothesis that flap movements help to keep glochidia afloat, employing lighting techniques (Westphal, 1965) to make the glochidia visible, and devising means to collect larvae at varying distances above the flapping animal.

(b) Further field studies, perhaps on a species such as *Lampsilis fasciola*, for which some living material is still available.

(c) Systematic fish host studies, especially with a view toward matching the flapping behavior repertoire of a given species of *Lampsilis* (time of maximum flapping frequency, etc.) with the behavior of the fish species.

(d) Further comparative studies among the species here investigated (*Lampsilis ventricosa* was contrasted with *L. siliquoidea* and *L. brevicula brittsi*) and other Lampsilinae, to discover the parameters of relevant flapping stimuli within the subfamily as a whole.

There is urgency in making these studies because of the decline of mussel populations so often noted in American streams. The urgency is accentuated by the need for substantial numbers of experimental and sacrificial mussels if the experimental analyses are to be adequately replicated in well designed, statistically significant studies.

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RÉSUMÉ

LE VOILE PALLÉAL CHEZ 3 ESPÈCES DE LAMPSILIS
(PELECYPODA, UNIONIDAE)

L. R. Kraemer

L'objet de cette étude est de passer en revue les bases morphologiques et d'activité générale des battements des voiles palléaux chez les unionides d'Amérique du Nord, de la sous-famille des Lampsilinae, et d'explorer expérimentalement certains facteurs qui peuvent compter pour cette activité frappante: les mollusques battant leurs voiles ressemblent à des poissons en train de nager. Les études morphologiques (principalement sur du matériel fixé de *Lampsilis ventricosa* et de *L. fasciola*) les études occasionnelles dans la nature (dans plusieurs régions du Nord-Ouest de l'Arkansas), et les études prolongées en aquarium sur *L. ventricosa, L. siliquoidea* et *L. brevicula brittsi* ont été menées de 1962 à 1965. On a trouvé que les voiles palléaux, qui sont une extension du bourrelet interne du bord du manteau antéroventral au siphon branchial, sont un fait permanent chez les femelles matures. Parmi les voiles de ces 3 expèces, il existe des similitudes de structure (présence de tâches "oculaires" pigmentées, innervation par les branches des nerfs palléaux en provenance du ganglion viscéral), aussi bien que des différences dans la forme et la pigmentation.

Les mouvements des 2 voiles débutent par des pulsations couplées qui produisent des contractions partant de la base des franges et se propagant vers l'extrêmité où se trouvent les tâches pigmentées. Il s'ensuit une phase de repos, pendant laquelle les voiles reprennent leur position initiale, avec les franges flottant horizontalement.

Le comportement du battement entraine aussi des fonctions coordonnées du pied, du marsupium, des valves et des siphons, à un point tel que les relations spatiales que l'on peut considérer comme normales entre le corps et la coquille, sont profondément altérées. Pour les différentes espèces, le battement nécessite différents types de comportements de même que différents stimuli adéquats (en particulier, intensité lumineuse pour *Lampsilis ventricosa* et agitation de l'eau et tremblement du substrat pour *L. siliquoidea*).

Le voile n'existe que chez les femelles matures, bien que les juvéniles et les mâles en aient des rudiments; les mouvements du voile n'ont été observés que chez les exemplaires gravides, jamais chez les non-gravides. Le battement se produit périodiquement tout au long des mois d'été et on l'a vu accompagner le vidage graduel des ovisacs et le rejet de larves glochidium conglutinées. Le battement n'a pas été observé après l'émission des larves.

Deux anciennes hypothèses concernant la fonction des mouvements du voile en mouvement agissant soit comme leurre pour les poissons qui sont les hôtes des larves glochidium, soit comme aérateurs des branchies et du marsupium, semblent maintenant n'être que partiellement plausibles. Compte-tenu des différences existantes dans l'aspect, dans la vitesse de battement et dans la réponse aux stimuli chez les diverses espèces, on pense pouvoir suggérer que ces différences sont des adaptations possibles aux modes de vie d'espèces particulières de poissons-hôtes. Le mouvement de soufflet, créé par des pulsations couplées pour tout battement du voile, quelles que soit les espèces et la fréquence de battement, pourrait aider les larves glochidium à demeurer en suspension dans l'eau pendant un certain temps et ainsi leur faciliter le contact vital nécessaire avec un poisson-hôte.

                                                         A. L.

RESUMEN

EL REPLIEGUE PALEAL EN LAS ESPECIES DE *LAMPSILIS*
(PELECYPODA: UNIONIDAE)

L. R. Kraemer

El propósito de este estudio fué revisar las bases morfológicas y de actividad general del repliegue y aleteo del manto en las especies norteamericanas de uniónidos de la subfamilia Lampsilinae, y explorar experimentalmente algunos factores que pueden contarse en esa actividad: el aleteo del manto simula un pequeño pez nadando. Estudios morfológicos, (principalmente de material conservado de *Lampsilis ventricosa* y *L. fasciola*), estudios ocasionales en el campo (en algunos condados del noroeste de Arkansas), y prolongados estudios en acuarios sobre individuos vivos de *L. ventricosa*, *L. siliquoidea* y *L. brevicauda brittsi*, se realizaron desde 1962 a 1965. Se comprobó que los repliegues alígeros del manto, que son una expansión del lóbulo interno del borde paleal anteroventral al sifón, constituyen un caracter permanente de las hembras maduras. Entre los repliegues de las 3 mencionadas especies existen similaridades estructurales (presencia de manchas oculares, ramificación de nervaduras paleales del ganglio visceral) así como diferencias en forma y pigmentación.

El aleteo se inicia en pulsaciones pares que producen contracciones, empezando en lo que correspondería a una base caudal y moviéndose hacia la terminación del repliegue con manchas oculares. Sigue una fase de reposo, en la que el repliegue asume su posición anterior, con la cola flotando horizontalmente.

El comportamiento envuelve también la función coordinada del pie, marsupia, valvas y sifones en forma tal que las supuestas relaciones espaciales normales entre el cuerpo y la concha estan muy alteradas. En diferentes especies el aleteo implica diferentes complejos de comportamiento, así como tambien los diferentes estímulos pertinentes (en particular intensidad luminosa para *Lampsilis ventricosa*, y sacudidas del substrato por los movimientos del agua en *L. siliquoidea*).

Los repliegues aparecen solamente en ejemplares de hembras maduras, aunque las juveniles y los machos presentan rudimentos; los movimientos del repliegue se han observado sólo en la hembras grávidas, nunca en las no grávidas. El aleteo ocurre por turnos periódicos durante el verano y se ha visto que acompañan la descarga gradual de los ovisacos y el derrame de conglutinados. No se observaron después de la liberación de las gloquidias.

Dos previas hipótesis concerniente a la función de estos movimientos del repliegue paleal de los Lampsilinae, que indicaban ser ya un cebo para peces que hospedan las gloquidias, o un sistema ventilador para las bránquias y marsupia, sólo en parte parecen ser verosímiles. Las diferencias en aspecto, velocidad de aleteo, y respuesta a los estímulos ambientales en diferentes especies, sugiere posible adaptaciones a los hábitos de las especies particulares de peces huéspedes. Los movimientos como de fuelle que se crean en las pulsaciones de los repliegues del manto, sin tener en cuenta especies o frecuencia del aleteo, podrían ayudar a la gloquidia a permanecer suspendida en el agua por cierto tiempo, facilitando así el contacto vital necesario con el pez hospedador.

J. J. P.

АБСТРАКТ

МАНТИЙНЫЙ КЛАПАН У ТРЕХ ВИДОВ *LAMPSILLIS* (PELECYPODA: UNIONIDAE)

ЛУИЗА Р. КРЕМЕР

В настоящей статье дается обзор морфологии и деятельности мантийного клапана у северо-американских унионид из семейства Lamsilinae, а также приводятся данные экспериментального исследования некоторых факторов, которые могут объяснить эту интересную активность. Движение мантийного клапана несколько напоминает небольших плавающих рыбок.

Морфологические исследования (главным образом на фиксированном материале по *Lampsilis ventricosa* и *L. fasciola*), случайные полевые наблюдения (в некоторых районах северо-западного Арканзаса) и длительное аквариальное изучение живых *L. ventricosa, L. siliquoidea* и *L. brevicula brittsi* проводились в период с 1962 по 1965 гг.

Было найдено, что мантийные клапаны моллюсков, которые представляют собой выросты внутренней лопасти края их мантии и находятся антеро-вентрально от бронхиального сифона, всегда имеются у половозрелых самок. Среди клапанов указанных выше моллюсков, существуют как структурное сходство (наличие глазных пятен, иннервация ветвями мантийных нервов, отходящих от висцерального ганглия), так и различия (в общей форме и пигментации).

Движения этих клапанов вызываются парной пульсацией, благодаря их сокращениям, которые начинаются с их хвостовой части и идут вперед, к тем концам клапанов, где имеются глазные пятна. Затем следует обратная фаза, когда клапаны приходят в исходное положение, и концы их располагаются горизонтально.

Работа клапанов включает также координированные движения ноги, марзупиев, створок и сифонов, в той степени, в какой предполагаемое нормальное пространственное отношение между телом и раковиной наиболее выгодно. Для различных видов колебания клапанов связаны как с различными поведенческими комплексами у моллюсков, так и стимулами из внешней среды (особенно таких, как интенсивность света для *Lampsilis ventricosa* и движение воды или вибрация субстрата для *L. siliquoidea*).

Клапаны развиваются только у половозрелых самок, в то время как у молоди и у самцов бывают только их рудименты. Движения клапанов наблюдаются только у беременных самок. Движение клапанов может происходить длительно в течение всех летних месяцев и сопровождаться постепенным опорожнением яйцевых сумок и высеванием конглютинатов. После выхода глохидиев движение клапанов прекращается. Ранее высказанные гипотезы, относительно роли движения клапанов у Lampsilinae, видимо, справедливы лишь отчасти. Так, считалось, что движение клапанов служит "приманкой" для рыб-хозяев глохидиев и что это движение служит для аэрации жабр и марзупиев. Различие в скорости движения клапанов и в отношении к факторам среды у различных видов моллюсков предполагает возможность существования адаптаций жизнедеятельности моллюсков к особенностям образа жизни различных рыб-хозяев.

Движения, напоминающие работу мехов для раздувания, обусловленные парной пульсацией всего аппарата клапанов (вне зависимости от вида моллюска или от частоты колебаний клапанов), может помогать глохидиям оставаться в течение некоторого времени в воде во взвешенном состоянии и таким образом облегчать жизненноважную для них возможность контакта с рыбами-хозяевами.

Z. A. F.