Greetings Dick!
Louise

Kraemer
1984

ASPECTS OF THE FUNCTIONAL MORPHOLOGY OF SOME FRESH-WATER BIVALVE NERVOUS SYSTEMS: EFFECTS ON REPRODUCTIVE PROCESSES AND ADAPTATION OF SENSORY MECHANISMS IN THE SPHAERIACEA AND UNIONACEA

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ABSTRACT

The soft bodies of mollusks provide the animals with a neuroanatomical context within which the plasticity and variability of the molluscan nervous system can be exploited. For the higher taxa of fresh-water bivalves, functional morphology not only of the reproductive systems (in the tradition of Ortmann, 1911), but also of nervous systems and sensors and effectors can account for much adaptive radiation of fresh-water bivalves in stable and in rapidly changing habitats.

Histological/neuroanatomical and behavioral evidence is presented here concerning several neural entities for (1) the hermaphroditic sphaeriacean bivalve *Corbicula fluminea*; and (2) several dioecious unionacean bivalves, genera *Lampsilis* and *Carunculina*. For *C. fluminea*, details of (a) gonoduct innervation; (b) development of "follicular ganglia" along with maturation of oogenic and spermatogenic follicles; and (c) peculiar, conjoined statocysts—are evaluated in their neuroanatomical context. For *Lampsilis*, details of (a) mantle ganglia organization and (b) separate, cislaterally innervated statocysts; and for *Carunculina*, innervation and behavior of the "thumb-twiddling" caruncles—are similarly evaluated.

The foregoing tend to corroborate and amplify characteristics of the reproductive process which distinguish the sphaeriacean and unionacean bivalves. Nervous systems of mollusks do frequently have clusters of neuronal soma at the periphery of even very small nerves, and some of these clusters can be demonstrated (as in the present study) to be associated with peculiar reproductive or locomotor behavior. It seems, therefore, that further investigations of molluscan nervous systems will provide important clues to the environmental past and phylogenetic history of these organisms and also to their adaptational future.

Key words: behavior; bivalve; gametogenesis; ganglia; nerves; reproduction.

For the fresh-water taxa of the class Bivalvia, a number of investigators, including Ortmann (1911), Walker (1917), van der Schalie (1952), Fretter & Graham (1964), Heard & Guckert (1970), Johnson (1970), Clarke (1973) and Burch (1973) have urged the use of anatomical characteristics of reproductive processes to separate/distinguish taxa. Davis & Fuller's (1981) immunological study lends support. In a different context, Hunter (1964, p. 90) notes ". . . bivalves of fresh waters show little of the adaptive radiation that gives particular interest to functional morphology in most groups of marine bivalves. The four major fresh-water families (i.e. Unionidae, Mutelidae, Corbiculidae, Sphaeriidae) are remarkably uniform in structure. . . ." I agree with the former workers and disagree with the latter worker on the basis of evidence and argument which follow.

In this paper, I will provide evidence from which I will argue that at least for the higher taxa of fresh-water bivalves, functional morphology not only of reproductive systems, in the tradition of Ortmann (1911), but also of *nervous* systems and sensors and effectors can account for much adaptive radiation of fresh-water bivalves in stable and in rapidly changing habitats. I will review findings from some of my studies of the morphology and behavior of the sphaeriacean bivalves, *Corbicula* cf. *C. fluminea* (Müller, 1774), and of certain unionacean bivalves, especially members of the genera *Lampsilis* and *Carunculina*. Emphasis will be on analyses of certain peripheral neural entities. I also will summarize findings which provide neuroanatomical context for the former entities, and which together relate to the bivalves' reproductive, spawning or locomotor capabilities. Finally, I will argue that functional anatomy studies of such peripheral neural elements in

bivalves are important not only in interpreting systematic position of these animals, but also in evaluating their capabilities for future adaptation.

METHODS AND MATERIALS

Living *Corbicula fluminea* used for this study were from the Arkansas River near Russellvill, Pope County, Arkansas, and from the Buffalo River in Madison County, Arkansas. *Lampsilis* spp. described here include those obtained as detailed in Kraemer (1970). *Carunculina texasensis* (Lea, 1857) specimens were obtained by Bob West (Arkansas Power and Light Co.) from Rock Creek (tributary of the Arkansas River in Pulaski county, Arkansas), maintained in aquaria and observed manifesting their peculiar spawning behavior in June 1981. Observations of their behavior are reported below in detail for two reasons: (1) no previous record has been found to exist in the literature; and (2) opportunity for making such observations becomes increasingly rare as populations of these animals disappear from heavily managed rivers of the United States. Preserved specimens of *C. texasensis* collected in Nueces River in Texas in August 1978 were provided by Mark Gordon (University of Arkansas); preserved specimens of *Carunculina glans* (Lea, 1834) were collected from the Illinois River in Washington County, Arkansas in October 1964.

Histological material was prepared as described elsewhere (Kraemer and Lott, 1977). Photomicrographs were made with a Leitz Ortholux microscope equipped with a 35-mm Leica camera, and with a Wild M5 Stereomicroscope in conjunction with a 35-mm Wild Mka 1 camera.

LIST OF ABBREVIATIONS

A	anus
AS	anal or exhalant siphon
BRS	branchial shelf, membrane which separates exhalant from inhalant or branchial chamber
BS	branchial or inhalant siphon
C	caruncle
CO	connective tissue capsule
CT	connecting tube between left and right statocysts of *Corbicula fluminea*
CVC	cerebro-visceral connective
DO	site of distal *pore* which appears in each ovisac of the marsupial gills near the culmination of mantle flapping/spawning behavior
E	"eyespot" of mature female *Lampsilis* mantle flap
EM	cross-section of embryo within the gonoduct of *C. fluminea*
F	foot
G	gill
GL	gonoduct/gonopore lip
GO	gonoduct
IG	inner gill
L	lumen
LBN	left branchial nerve
LC	left caruncle
LMF	left mantle flap of mature female *Lampsilis*
LMG	left mantle ganglion of mature female *Lampsilis*
LOG	left outer gill
LP	labial palp
LPN	left pallial nerve trunk
LV	left shell valve
M	posterior portion of left and right outer gills which are differentiated into marsupia for glochidia larvae
NC	nerve from cerebral ganglion innervating follicular "ganglion"
NF	nerve fibers
NP	neuropile-like aggregation of nerve fibers within the follicular "ganglion"
O	ovisac of gravid marsupial gill, charged with glochidia larvae
P	papilla
PA	posterior adductor muscle
RC	right caruncle
RM	right mantle lobe
RMF	right mantle flap of mature female *Lampsilis*
RPN	right pallial nerve trunk
RV	right shell valve
S	neuronal soma
SB	suprabranchial chamber
SE	sensory epithelium
SF	spermatogenic follicle
SL	statolith
SM	clump of mature sperm of sperm "morula"
SN	statocyst nerve
T	"tail" of mature female *Lampsilis* mantle flap
VG	visceral ganglion
VM	visceral mass

OBSERVATIONS OF NEURONAL STRUCTURES

A. Dioecious unionaceans (Fig. 1)

1. The mantle ganglia of female *Lampsilis ventricosa* (Barnes, 1823)

L. ventricosa is one of a number of indigenous fresh-water mussels which have developed a unique spawning apparatus and spawning behavior complex characteristic only of the mature gravid females of this dioecious group (Kraemer, 1970). In the mature gravid female, the water tubes of the posterior portion of each outer gill are filled with fully differentiated glochidia. Upending herself in the substrate, the mussel extends a pair of mantle flaps equipped with "eyespots" and "tails" from between the posterior margins of her shell valves. Charged marsupia are typically then protruded between the flaps. The mantle flaps are moved rapidly in *L. ventricosa*—up to three times per second— and to the human observer resemble a small swimming fish. Mantle flap movements are paired pulses which are initiated near the tail ends of the flaps and travel postero-dorsally toward the eyespot ends (Fig. 2). After several weeks of flap movements glochidia are discharged. The foregoing phenomena, as well as species variations (in which some
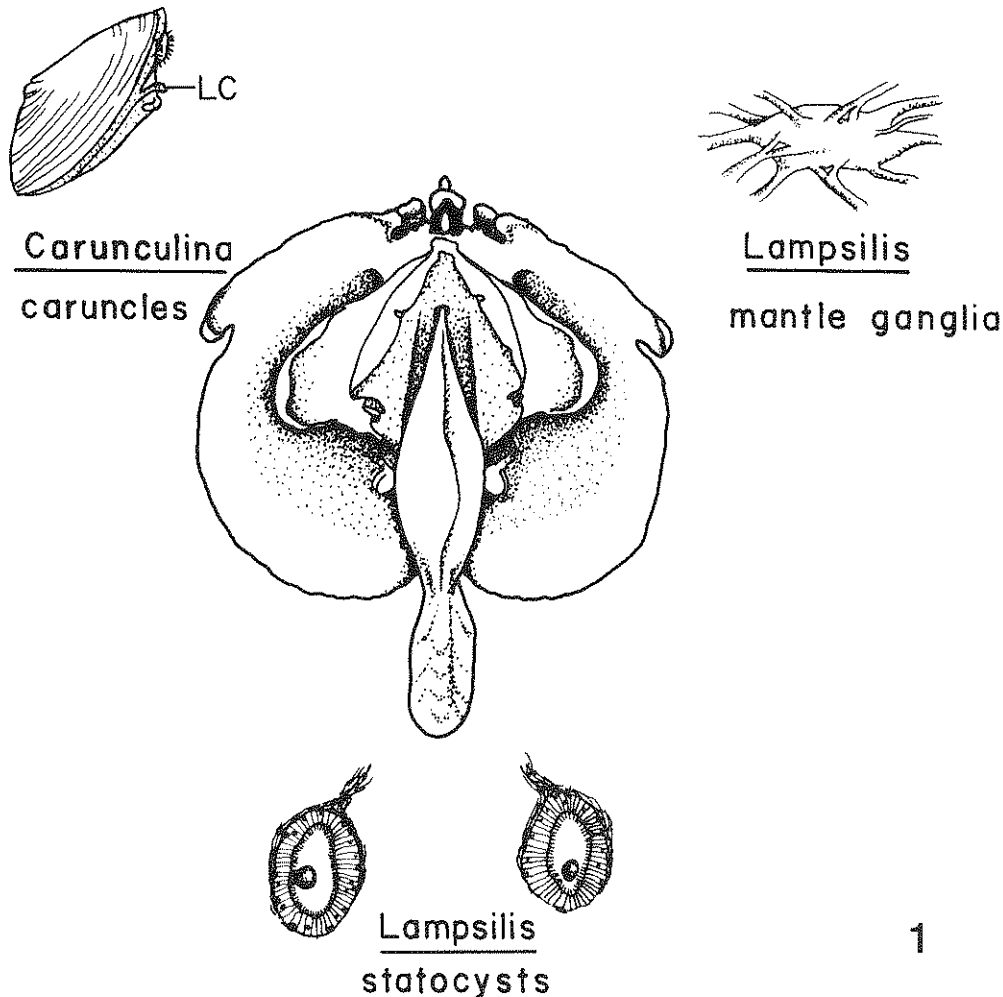

FIG. 1. Summary diagram indicating the peripheral neural entities of the unionacean bivalves *Lampsilis ventricosa* and *Carunculina texasensis*, discussed in the section of "Observations."
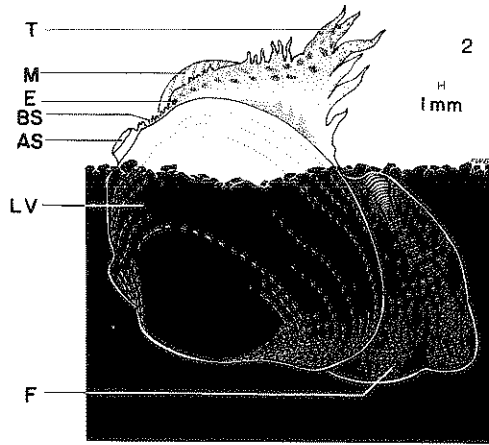
FIG. 2. Diagram of female *Lampsilis fasciola* during flapping behavior. Mantle flaps are protruded between the valves and pulsing mantle flap movements proceed from "tail" (T) to eyespot (E) end of flap. Posterior end of a gravid outer gill or marsupium (M) protrudes between flaps.

flaps and flap movements are *not* "fish-like") found in *Lampsilis radiata siliquoidea* (Barnes, 1823), *Lampsilis fasciola* (Barnes, 1834), *Lampsilis brevicula brittsi* (Simpson, 1900), have been detailed elsewhere (Kraemer, 1970, 1974).[1]

If the animal is completely removed from its shell valves and placed on its dorsal surface for dissection, one notes that the posterior mantle lobe edges are unfused (Fig. 3A). How then does the animal co-ordinate the movement of both flaps? Dissection in the area of the visceral ganglion and of its peripheral

pallial nerves reveals the presence of a pair of mantle ganglia in the mature female (Fig. 4A, 5A). Histological examination (Fig. 5B) verifies their ganglionic organization: a sheath of connective tissue enclosing a peripheral layer of neuronal soma, the latter surrounding a central neuropil. Similar mantle ganglia were not found in neuroanatomical dissections of mature specimens of male *L. ventricosa* (Fig. 4B), or in *Amblema plicata* and *Anodonta imbecilis*. They were not included in previously published figures of peripheral bivalve neuroanatomy (Duvernoy, 1852; Rawitz, 1887; Bullock & Horridge, 1965).

The mantle ganglia seem to be characteristic only of the mature female lampsilid mussel and their location is suggestive of association with mantle flap movements. Each is positioned in the mantle tissue near the "tail" end of a mantle flap, the point at which each mantle flap movement begins. It is possible that these mantle ganglia are the pacemakers for the mantle flap movements, or that they function to co-ordinate the mantle flap movements which are mediated by the visceral ganglion.

2. The "caruncles" of *Carunculina*

Carunculina parva is a hermaphroditic species (van der Schalie, 1970) which belongs to the same subfamily (Lampsilinae) as *Lampsilis*. In the mature animals a conspicuous pair of "caruncles" is developed, one on either side of the inner surface of the

[1]Davis & Fuller's (1981) article on genetic relationships among recent Unionacea of North America has just recently appeared. Davis and Fuller carried out an impressive immunological study of 52 unionacean species from 27 genera. They also assembled a thoughtful evaluation of noteworthy systems of unionacean classification against which to compare the evidence from their cladogram. With some of their extrapolations to functional morphology, however, I cannot agree. One sample (: 244) follows:

"For example, the probasal margins of *Lampsilis* are piscine in character; the implication is that predatory . . . fish species will attack the 'prey' represented by the mussel's mantle margins and will be showered with glochidia *if*, as is often true in the case of heterogeneous genera, discharge of parasitic larvae is through the marsupial wall and not through the excurrent mantle aperture."

After several years of careful study, Kraemer (1970) elucidated the flapping behavior complex in living *Lampsilis* spp. and reported in detail from first hand knowledge on many aspects of the matter, including: (1) The probasal margins of *Lampsilis* spp. are not necessarily "piscine" in character, either in structure or function. (2) *No* evidence was found of fish "attacking" the mantle flaps. To the contrary, much evidence was accumulated that in stream environments mantle flap movements *cease* when fish appear in the vicinity of the moving flaps. (3) *No* evidence was ever found of glochidia being released in a "shower" from the ovisacs of the marsupia. Occasionally distal margins of marsupial ovisacs ruptured, and the glochidia from an ovisac would consequently be aborted, not as a "shower" but as a lump, a conglutinant. (4) The "*if*" in the Davis and Fuller sentence quoted above is ironic. Kraemer (*ibid.*) reports specifically that a tiny hole is seen to appear in the distal edge of each ovisac near the end of the flapping behavior complex. Further she reports that glochidia in a series of monitored ovisacs were seen to disappear from those ovisacs over a 12-h period. All circumstantial evidence indicated that the avenue for egress for glochidia was from the several holes described, and indeed not as an aborted conglutinant, *not* as a "shower," and most certainly not from the excurrent siphon.
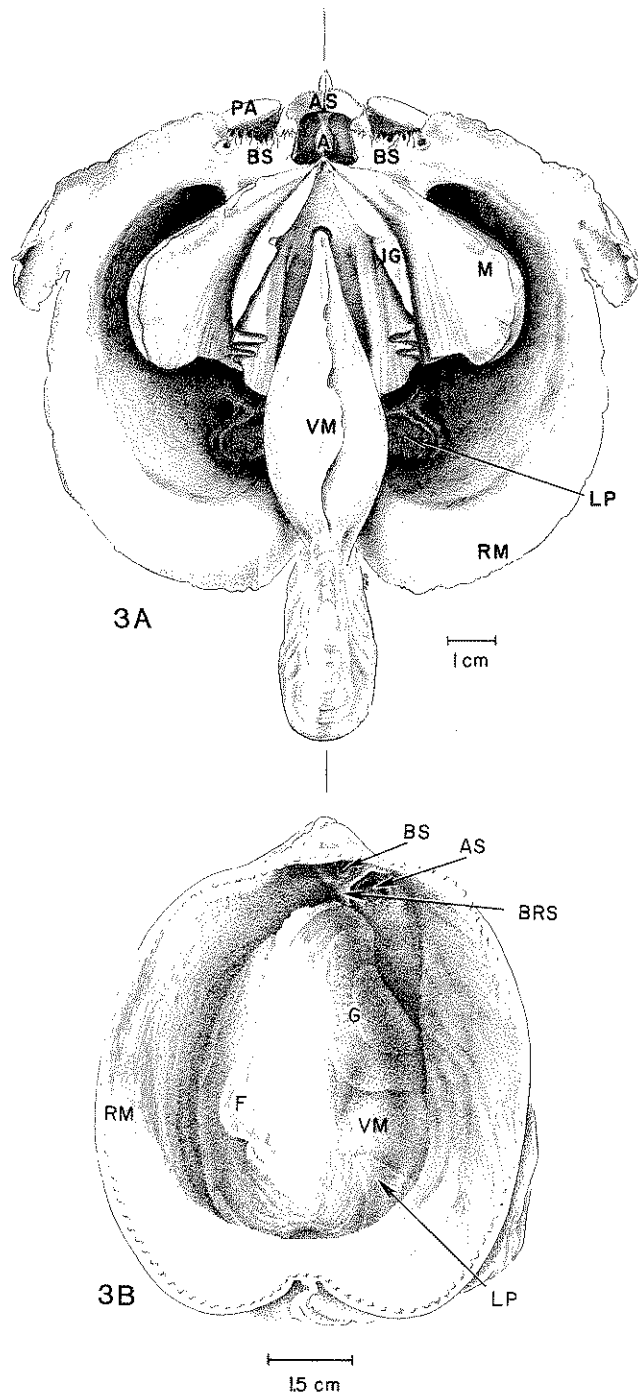
FIG. 3A. *Lampsilis ventricosa* (Barnes). Drawing of relaxed, preserved mature female specimen removed from its shell valves, placed on its dorsal surface and viewed from the rear. Note flaring mantle lobes, which show almost no fusion. Compare with B. From Kraemer, 1979. B. *Corbicula fluminea* (Müller). Drawing of relaxed fresh mature specimen removed from its shell valves, placed on its dorsal surface and viewed from the rear. Note thickened, fused posterior portion of mantle lobes, and narrowed pedal gape. Compare with A.
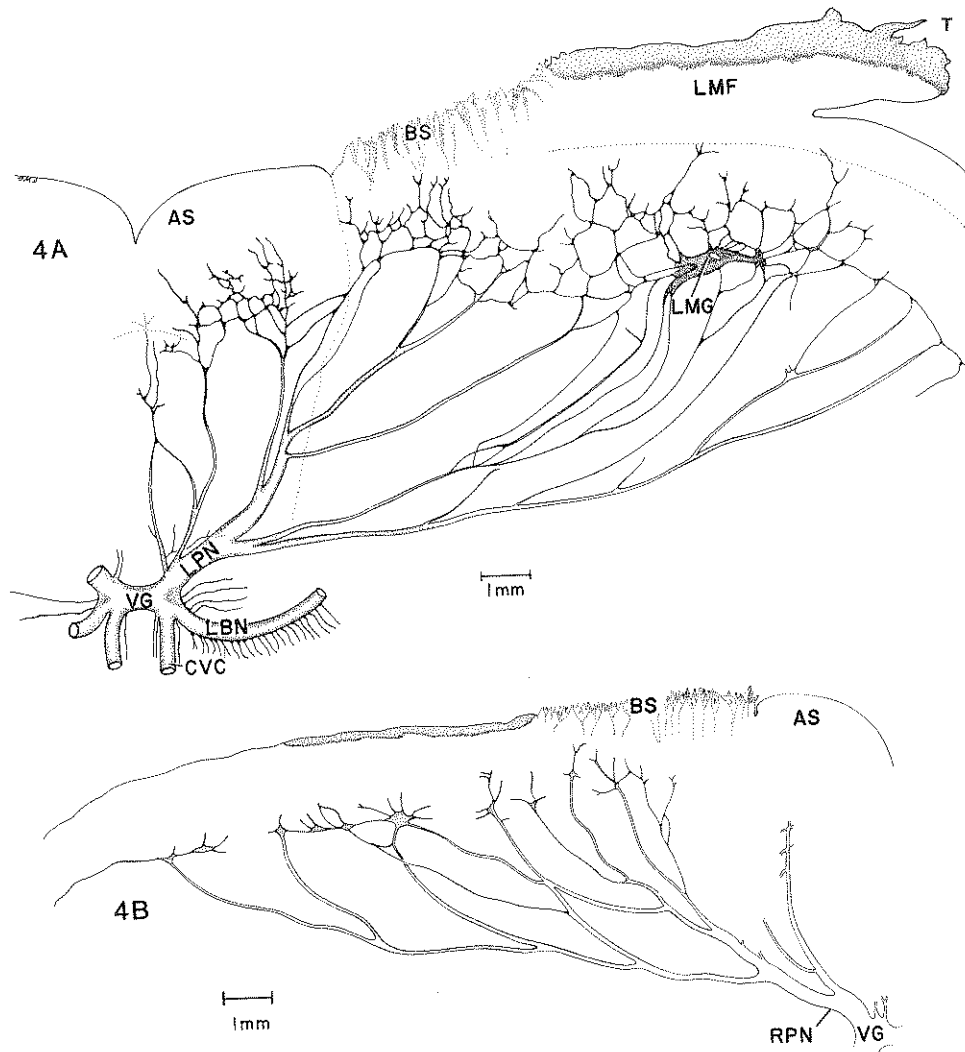
FIG. 4A. Drawing of dissection of posterior region of mantle of mature female *Lampsilis ventricosa*, showing visceral ganglion (VG), innervation of left rear mantle lobe and location of accessory mantle ganglion (LMG), adjacent to mantle flap "tail" (T). B. Drawing of dissection of posterior region of mantle of mature male *Lampsilis ventricosa*, showing visceral ganglion (BV) and innervation of right rear mantle lobe.

mantle margin, and anteroventrad to the branchial siphon (Simpson, 1914).

Prior to this study, I examined more than 25 specimens of *C. parva* to determine the locations of the "caruncles." Neuroanatomical dissections were made of four specimens. Distribution of posterior pallial nerves is shown in Fig. 7. No evidence of mantle ganglia near the "caruncles" was found.

In June 1981, two mature gravid individuals of the apparently dioecious species *Carunculina texasensis* were observed intermittently

for more than 5 h, as they showed the behavior described below. Bob West verified that the animals had been showing similar behavior for about two weeks. (Mantle edges of female *C. texasensis* are shown in Fig. 6.)

(a) *"Pulsing" behavior*: Lying on one valve or the other, or lying hinge down in the substrate, both mussels showed bouts of pulsing behavior which continued for 15 min, 30 min, 60 min, or more.

"Pulsing" behavior is the term I am applying to the following: In opposing short pigmented
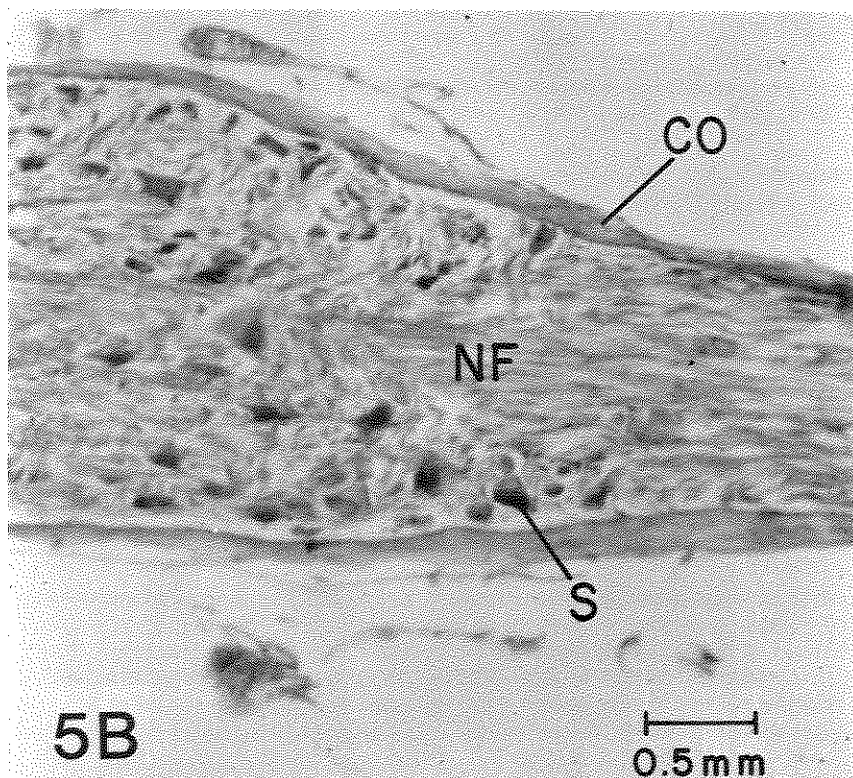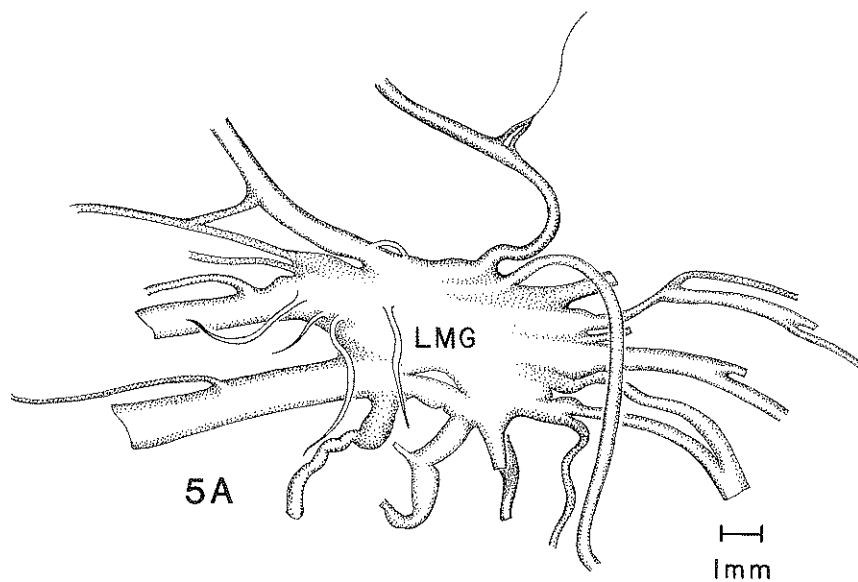
FIG. 5A. Drawing of accessory mantle ganglion, removed from left mantle lobe of specimen of *Lampsilis ventricosa*, shown in Fig. 3A. B. Sagittal section of mantle ganglion removed from rear left mantle lobe near "tail" of mantle flap of mature female specimen of *Lampsilis ventricosa*.
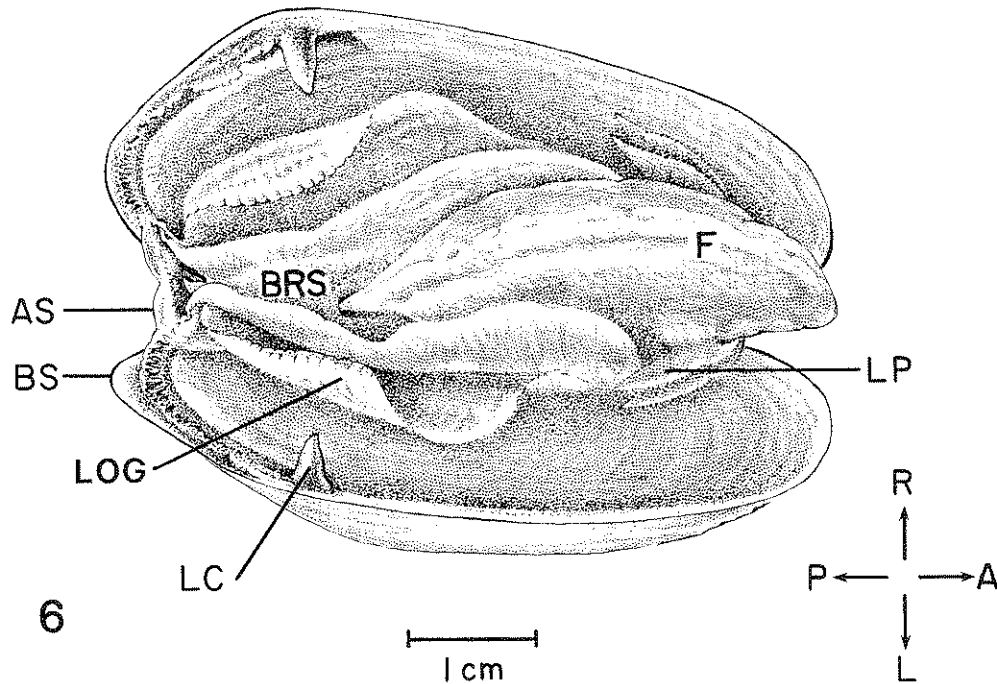
FIG. 6. Drawing of preserved mature female *Carunculina texasensis* to show left (LC) and right caruncles on inner surface of mantle antero-ventral to branchial siphon.

sectors of the inner lobe of each mantle edge, immediately adjacent to the branchial siphon, paired movements began as synchronous pulses and passed quickly along the mantle edges to the region of the two caruncles. The pulses were rapid, about 3/sec. They were followed by a one- or two-second pause, then repeated. Pulses occurred typically in groups of three, but often varied up to seven or more. As the paired pulsing movements passed along the thin membranous flanges of the inner mantle lobes, round, white, bead-like distal edges of the ovisacs of the gravid marsupial gill of the animal could be seen exposed between the lobes. The effect was a kind of rippling "smile" of the mantle edges.

During the few hours available for observation, other pulses were seen (in the mantle lobe areas) which moved in the opposite direction, from caruncle region to branchial siphon. These occurred less frequently and their relation to the "pulsing" behavior described above could not be determined.

(b) *Caruncular behavior*: Following a course of pulsing behavior, first one "caruncle" and then the other extended from between the mantle lobes. The caruncles were white, completely unpigmented and elongate, with very much the *shape* of "thumbs." That is, each caruncle was somewhat splayed distally, tapered, and cylindrical near its point of attachment on the inner surface of the mantle lobe.

The first thumb-like caruncle to emerge was observed to move in a rotary plane at right angles to the longitudinal axis of the animal. When the second caruncle emerged, both caruncles rotated, frequently touching each other at their distal "thumb" tips. Viewed from the side through the aquarium glass, one caruncle rotated clockwise about its base, the other counter-clockwise (Fig. 8A, 8B, 8C). From time to time, the thumb-like caruncles would reverse their respective rotary movements. The rotary caruncular movements continued at an even rate of about 1/sec for 15 min or more. The longest sequence observed lasted 1 h. In several instances caruncular movements ceased as the caruncles were withdrawn and the paired pulsing movements of the mantle edges resumed.

When the animal lay on its dorsal surface in the substrate, and its moving caruncles were viewed from a postero-ventral aspect, the
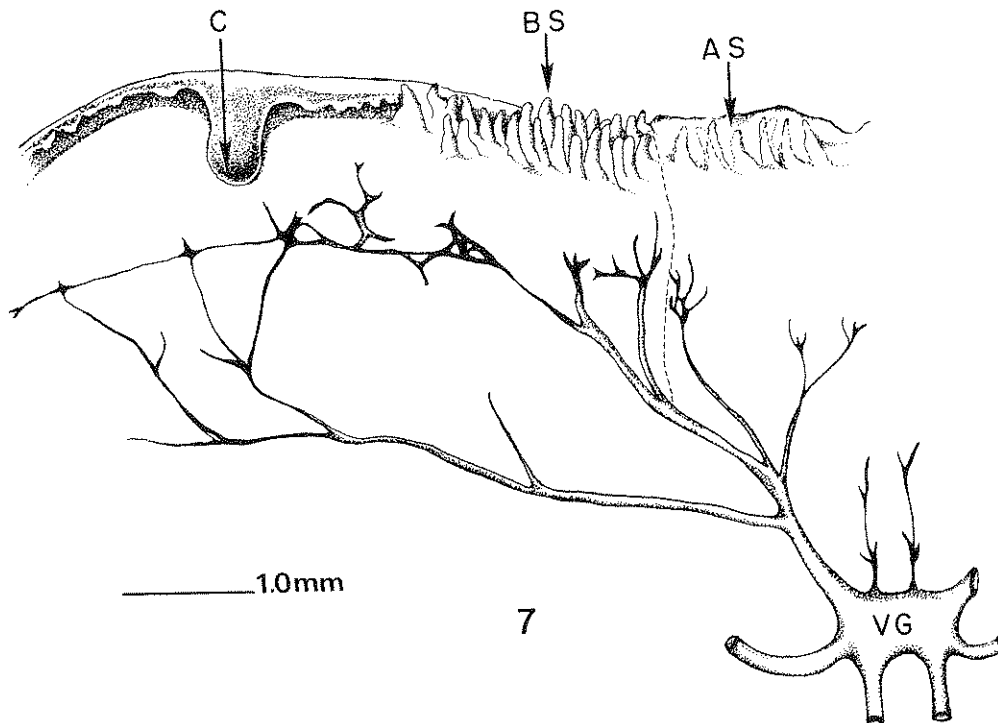
FIG. 7. Drawing of posterior region of mantle of *Carunculina parva*, showing the visceral ganglion (VG), innervation of right rear mantle lobe and location of "caruncle" (C).

caruncles resembled a pair of opposing, twiddling thumbs (Fig. 8D). J. P. E. Morrison (personal communication) had used the expression "thumb twiddling" years ago in commenting on the movement of *Carunculina* caruncles. Until the observations described above, however, I had neither seen, nor encountered a detailed description of such movement. Now it is obvious to me that Morrison's characterization of "thumb twiddling" is apt for the caruncular movements.

It seems likely that the pulsing movements and caruncular movements of *Carunculina* mantle edges have a spawning function similar to the mantle flap behavior complex of *Lampsilis* (Kraemer, 1970), although the movements of *Carunculina* are differently initiated and displayed. It seems possible that peripheral aggregation of neuronal soma may be found where pulsing movements are initiated, near the ventral edges of the branchial siphon.

3. Statocysts of *Lampsilis ventricosa*

As reported earlier (Kraemer, 1978a) each of the paired statocysts is a small translucent globe (about 2 mm in diameter in an animal 12 cm long). The two statocysts are widely separated from each other. Each is embedded deep in the latero-mid-posterior portion of the foot. Each statocyst is attached to a statocyst nerve which branches from the cis-lateral cerebro-pedal connective. The statocyst nerve penetrates the connective tissue capsule of the organ, and branches among the tall ciliated columnar epithelial cells which line the capsule (Fig. 9A, 10A). The central cavity of the statocyst contains one or more hard statoliths.

Slow stepping movements of the foot of *Lampsilis* during normal locomotion may be responding to information from the distally placed statocysts.

During the flapping behavior complex

8A

B

C

0.5 cm

8D

2.5 mm
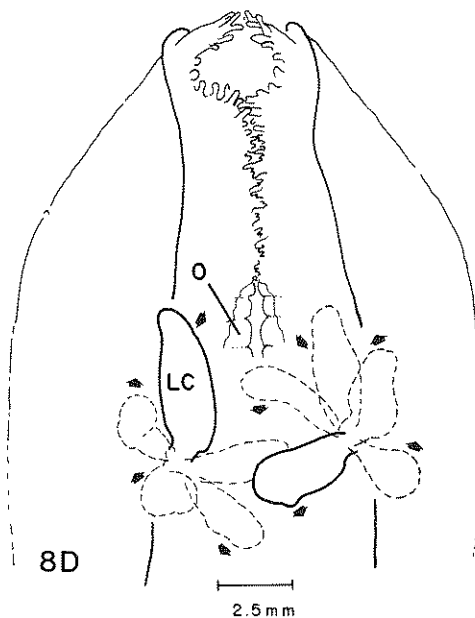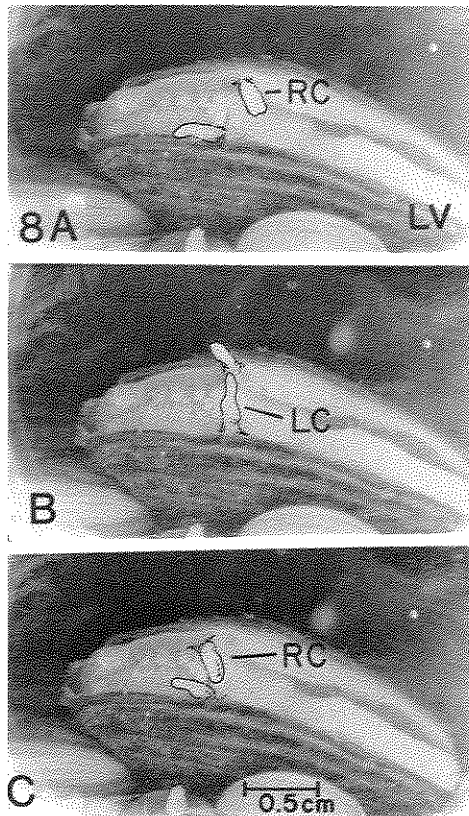
which accompanies spawning of glochidia in *L. ventricosa*, the female typically assumes a prolonged "headstand," in which the foot functions as a vital prop (Kraemer, 1970). In this instance too, *L. ventricosa* statocysts are well suited to aid the animal in maintaining its spawning "stance."

B. Monoecious sphaeriaceans (Fig. 11)

    1. Innervation of the gonoduct "lips" in *Corbicula fluminea*

Even before there is any histological evidence of gamete or gonad development in young clams (2–3 mm long), the lips of the two gonoducts are well differentiated (Kraemer, 1978b). Not until the clam has undergone further development of its gonads (4–6 mm specimens), however, does one see extensive innervation of the gonoduct lips. Many nerve fibers branch directly from each cislateral cerebro-visceral connective as it emerges from the visceral mass at the level of each gonoduct opening (Fig. 12A).

    2. Follicular ganglia of *Corbicula fluminea*

Oocyte development begins in small animals (4–6 mm long) when gametocytes differentiate in close association with the basement membranes of the gut and the digestive glands. A developmental sequence may be traced in which slender oogenic follicles elongate and ramify through the visceral stroma; the follicles later become crowded with enlarged oocytes; the oocytes subsequently appear stalked. Eventually, the oogenic follicles appear to be mostly empty of oocytes, and also may contain what appear to be young embryos (Fig. 12B). Not until the oogenic follicles are well developed is there histological differentiation of spermatogenic follicles (Kraemer, 1978b). Spermatogenic follicles are never more than one-fourth as numerous as the oogenic follicles and are located mostly peripheral to the oogenic follicles.

←——

FIG. 8. Sequence (A, B, C) of photographs showing caruncular movements in *Carunculina texasensis,* taken through aquarium glass, June 11, 1981. Animal is lying on its left shell valve. Note that right caruncle (RC) is showing counter-clockwise movement and left caruncle (LC) is showing clockwise movement. D. Diagram of caruncles from dorsal aspect, illustrating "thumb twiddling" movements of the opposed caruncles.
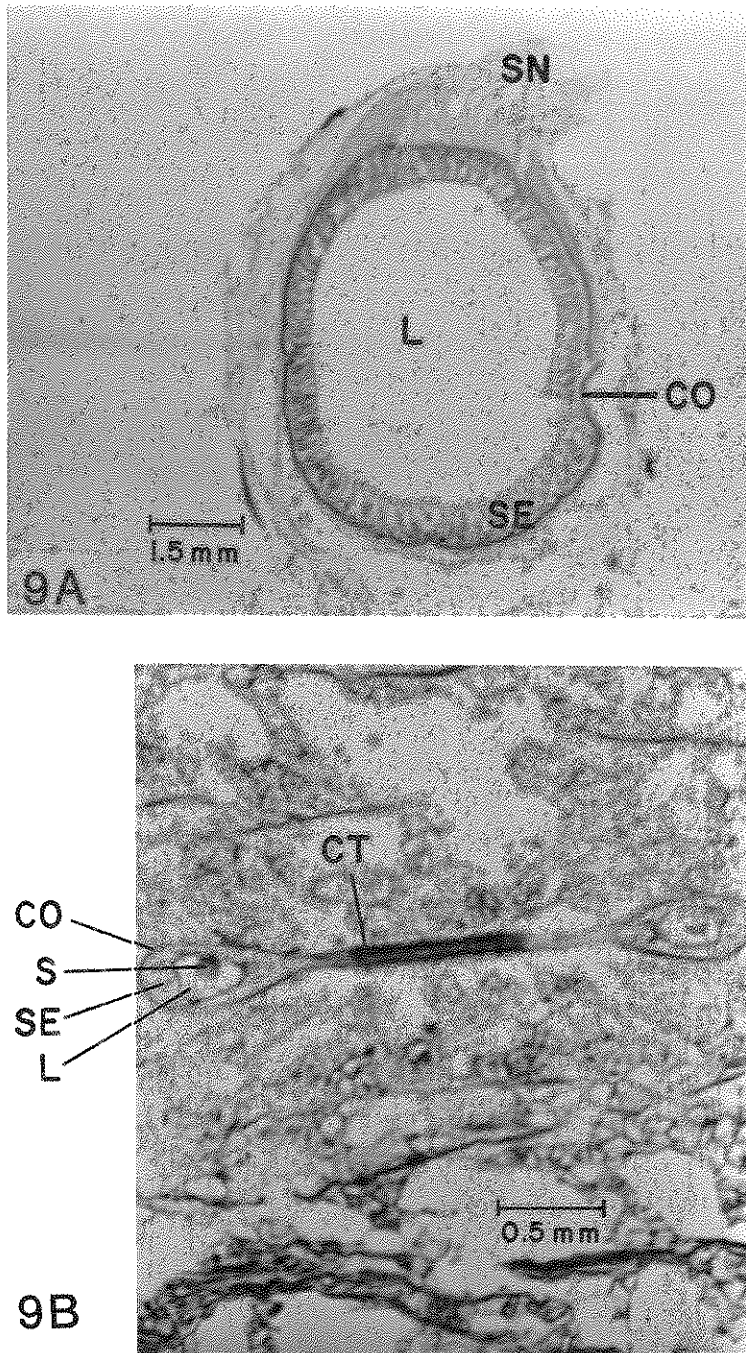
FIG. 9A. Sagittal section through left statocyst of *Lampsilis ventricosa*, showing attached statocyst nerve (SN), connective tissue capsule (CO), sensory epithelium (SE) and lumen (L). Break in the tissue on the right side of the statocyst capsule was the site through which the hard statolith "popped" during sectioning of the tissue. From Kraemer, 1978a. B. Cross-section of *Corbicula fluminea*, through region of visceral mass near pedal ganglion, showing unusual statocysts in the midline of the body, conjoined by a tube (CT). From Kraemer, 1978a.
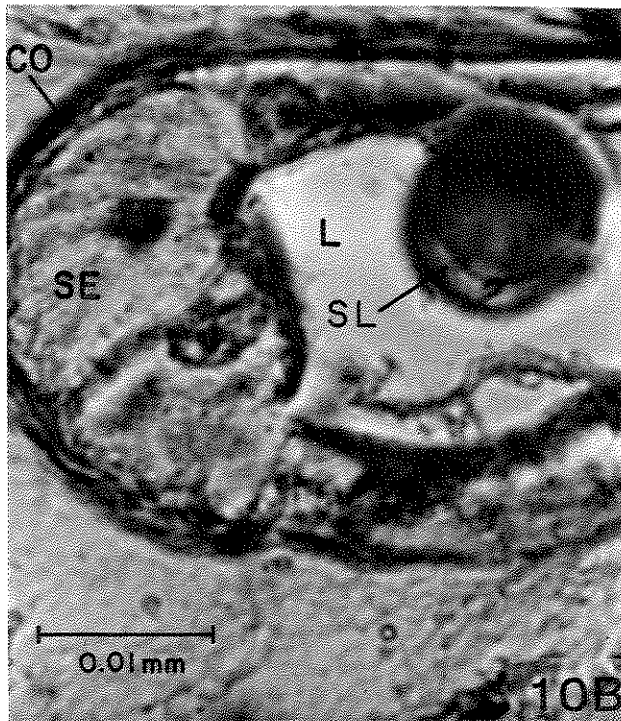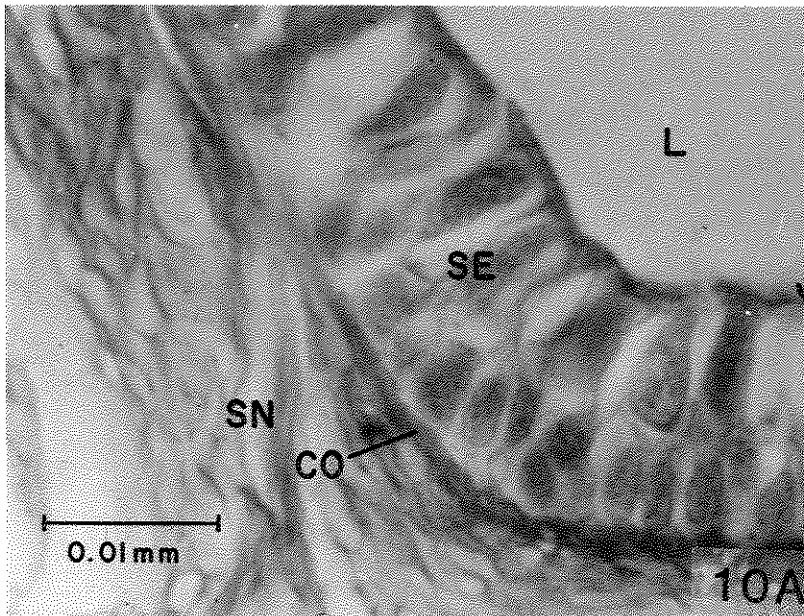
FIG. 10A. Photomicrograph of sensory epithelium (SE) of statocyst of *Lampsilis ventricosa*, showing innervation by neuronal fibers of statocyst nerve (SN). B. Photomicrograph of right statocyst of *Corbicula fluminea*, showing epithelium (SE) and statolith (SL) A, B from Kraemer, 1978b.

By the time spermatogenic, as well as oogenic follicles, are well differentiated, paired aggregation of apparent neuronal soma appear at the *confluence* of male and female follicles, usually at four locations: (1) in the postero-ventral part of the visceral mass near a large vertical loop of the intestine; (2) the mid-ventral portion of the visceral mass dorso-lateral to the pedal ganglion; (3) in the mid-anterior region of the visceral mass, postero-dorsal to each cerebral ganglion; and (4) in the mid-dorsal region of the visceral mass not far from cerebro-visceral connectives and gonoducts. I have tentatively named these clusters of neuronal soma "follicular ganglia" (Kraemer, 1978b). In addition to the apparent neuronal soma, each putative follicular ganglion was seen to enclose a dense neuropil-like core and to be innervated by slender nerves from neighboring ganglia (cerebral, pedal) (Fig. 13). A cavity of unknown function, lined with well-differentiated, ciliated cuboidal epithelium was observed in many of the follicular ganglia.

Possible function of the "follicular ganglia" may be to co-ordinate gamete production and subsequent internal and/or self-fertilization. Circumstantial evidence in support of this hy-
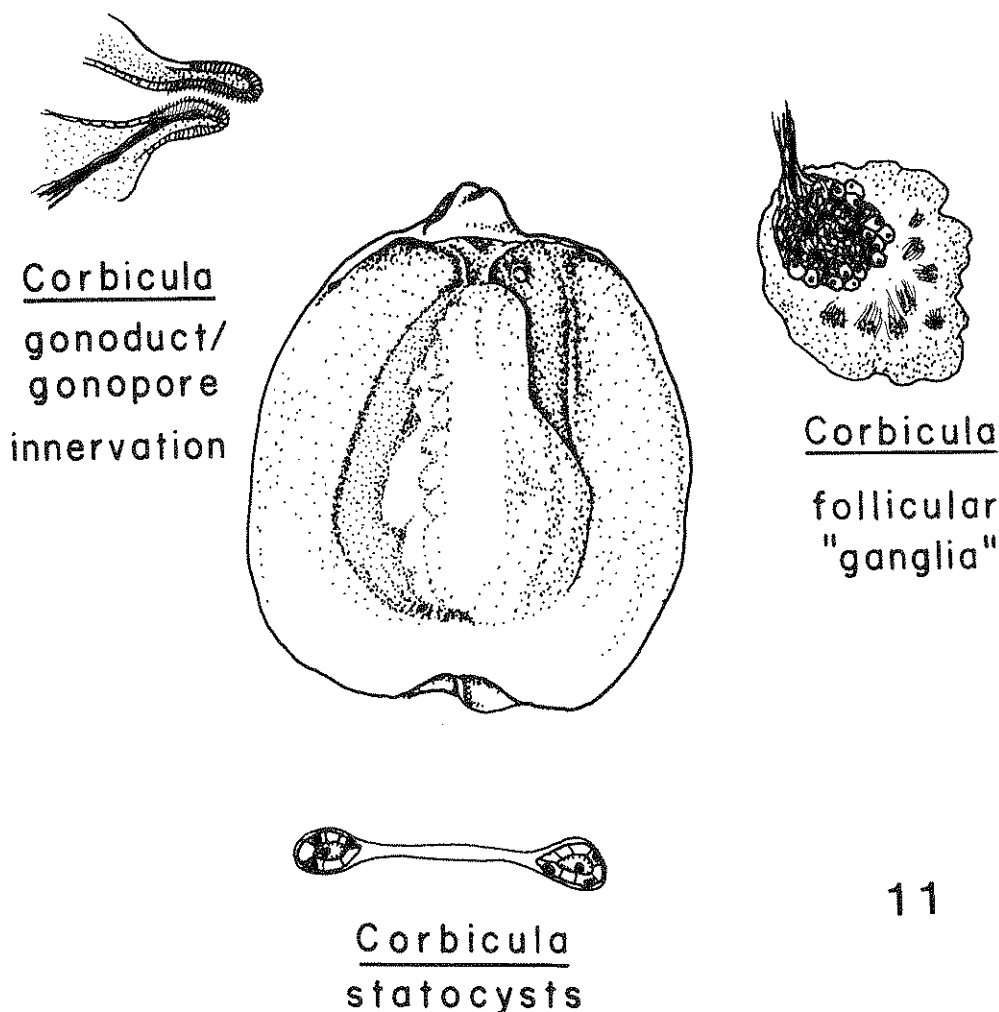

Corbicula
gonoduct/
gonopore
innervation

Corbicula
follicular
"ganglia"

Corbicula
statocysts

11

FIG. 11. Summary diagram indicating the peripheral neuronal entities of the sphaeriacean bivalve *Corbicula fluminea,* discussed in the section of "Observations."
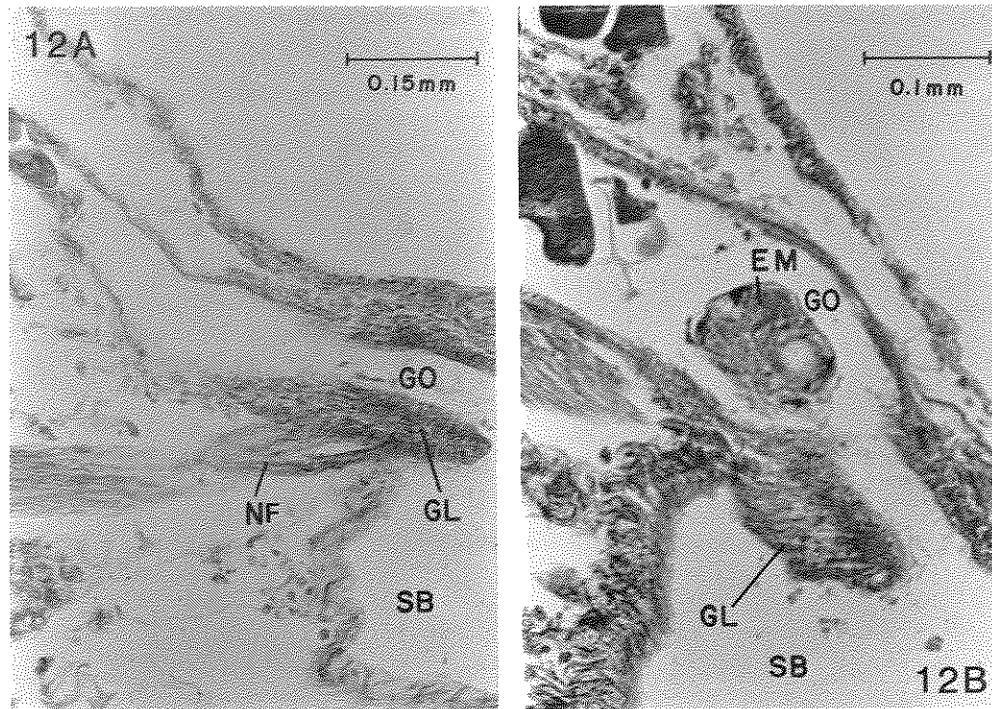
FIG. 12A. Photomicrograph of sagittal section of *Corbicula fluminea* through region of gonoduct lips (GL), showing innervation by means of neuronal fibers (NF) from cerebrovisceral connective. From Kraemer, 1978b. B. Photomicrograph of sagittal section of *Corbicula fluminea* through region of gonoduct lips (GL), showing section of embryo (DM) in the lumen of the gonoduct (GO).

pothesis includes the repeated observation of embryos within follicles near the follicular ganglia, and the subsequent appearance of embryos in the gonoduct (Fig. 12B) from where the embryos could be traced into marsupial chambers of the inner gills.

Studies on the follicular ganglia of *Corbicula fluminea* are continuing. Currently, I do not know whether, once the follicular ganglia have differentiated, they regress or are maintained by the animal.

3. Statocysts of *Corbicula fluminea*

Statocysts in this animal contrast sharply with those of *L. ventricosa* (Kraemer, 1978a). Their position in the dorsal part of the foot near its border with the visceral mass is comparable to that of *L. ventricosa*. Where the statocysts of *L. ventricosa* are displaced laterally, however, *C. fluminea* statocysts are close together in the midline of the body, and are horizontally *conjoined* by a connecting tube (Fig. 9B) The statocysts are tiny (about 100 μm in diameter in a 4-mm clam). Each is

surrounded by a connective tissue capsule and lined with cuboidal epithelium (Fig. 10B). Within the cavity of each statocyst is a single large statolith. Innervation of the statocysts has not been worked out.

Conjoined by a fluid-filled tube, the statocysts of *C. fluminea* seem well suited to detecting the rapid forward-and-back, side-to-side movements which its foot manifests. As already noted (Kraemer, 1978a), it seems reasonable to hypothesize that other bivalved mollusks capable of rapid foot movements also may have conjoined statocysts.

DISCUSSION AND CONCLUSIONS

Contrasting features of the peripheral neuroanatomy of certain sphaeriacean and unionacean bivalves discussed in the following paragraphs are summarized in Table 1.

If we compare a relaxed specimen of *L. ventricosa* alongside a similar specimen of *C. fluminea* lying ventral side up, similar to the manner in which we typically view the an-
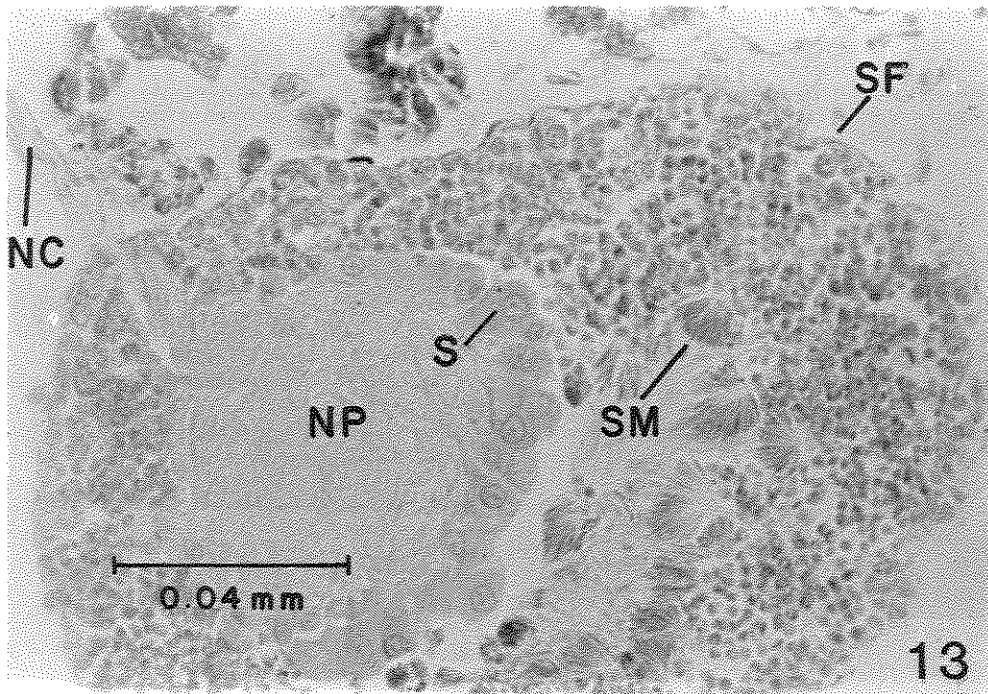
FIG. 13. "Follicular ganglion" section from anterior region of visceral mass of *Corbicula fluminea*, posterior and slightly dorsal to cerebral ganglion. Note innervation by means of nerve fibers (NC) from cerebral ganglion, many neuronal-like soma (S) at periphery of "ganglion," and its location within a well-developed spermatogenic follicle. From Kraemer, 1978b.

TABLE 1. Summary of peripheral neuronal complexes discussed in "Observation" section which account for differences in functional morphology of nervous systems in representative species of the Unionacea and Sphaeriacea, respectively.

Neural complex	Unionacea: *Lampsilis ventricosa* *Carunculina texasensis*	Sphaeriacea: *Corbicula fluminea*

Reproductive neuronal structures	In mantle:
	    L. ventricosa: paired mantle ganglia in mature female near flaps antero-ventral to branchial siphon. (Figs. 4A, 5)
	    C. texasensis: paired "caruncles" in mature female antero-ventral to branchial siphon. (Figs. 6, 7, 8)
		In visceral mass:
		    C. fluminea: development of innervation of gonoduct lips on postero-dorsal surface of visceral mass. (Fig. 12A)
		    C. fluminea: development of pairs of follicular "ganglia" at confluences of oogenic with spermatogenic follicles, within visceral mass. (Fig. 13).

Statocysts	*L. ventricosa:* paired statocysts widely separated, each innervated by nerve from cislateral cerebropedal connective. (Figs. 9A, 10A)	*C. fluminea:* pair of conjoined statocysts in midline of visceral mass immediately dorsal to pedal ganglion. (Figs. 9B, 10B)

atomy of a complex bilaterally symmetrical animal (Fig. 3), it is at once evident that the former shows almost no fusion of the mantle lobes, and that the posterior mantle lobe ends are flared elaborately into the mantle flaps of the mature female. During normal siphoning and locomotor behavior, the unfused mantle lobes of *Lampsilis* spp. expose these animals to their river environment. During spawning behavior, which involves prolonged periods of the "headstand" and the flapping behavior complex (Fig. 2), the gravid female is even

more exposed generally to the water. By contrast, the fused thickened posterior mantle edges of *Corbicula* form a deep protective siphonal pocket and greaty narrow the pedal gape of the clam. The clam consequently is much less exposed (Fig. 3B). Moreover, the strong dentition of the heavy, rather inflated, ridged shell valves and the mantle sutures which "stitch" the lobes together to form a foramen for the adductor muscles (Kraemer, 1977), further protect the internal organs.

If spawning function is considered, a marked contrast between unionacean and sphaeriacean bivalves is observed. Distribution of the parasitic glochidial larvae has quite obviously become a function not only of the modified outer marsupial gills of female *Lampsilis* spp. and *Carunculina* spp., but also of the posterior mantle lobes. Mantle flaps and mantle ganglia of *Lampsilis* spp. function in the spawning process, as do the highly innervated, "thumb twiddling" caruncles and pulsing, membranous mantle edges of *Carunculina* spp.

On the other hand, reproduction in the monoecious sphaeriacean, *C. fluminea*, has involved elaborate innervation of the gonoduct lips via the cerebro-visceral connectives and development of a series of "follicular ganglia" associated with confluences of mature oogenic and differentiating spermatogenic follicles. These follicular ganglia, each innervated by nerves from nearby pedal or cerebral ganglia, are structures concomitant with the hermaphroditic process in *C. fluminea*. Thus, both the follicular ganglia of *C. fluminea* and the modified neuronal structures of *Lampsilis* and *Carunculina* spp. mantle edges clearly are associated with reproduction in the two very different kinds of animals.

Differences in the organization of the statocysts may be of more fundamental systematic significance. As organs implicated primarily in trophic activity of the organisms, conjoined statocysts of the relatively quick-moving *Carunculina* may signify a quite different environmental/adaptational history than that suggested by the widely separate, cislaterally innervated statocysts of the slower-moving *Lampsilis* spp. In *Lampsilis* spp., function of the statocysts also is implicated in the long "headstand" which accompanies the spawning process of flapping behavior.

These studies on the functional morphology of peripheral neural entities amplify an interesting peculiarity of molluscan neuronal organization *i.e.* the cell bodies of molluscan neurons are not confined to their ganglia. On the contrary, neuronal soma spread along many of a mussel or clam's nerves, and frequently aggregate in small clusters at the distal ends of even the smallest nerves. Prosser (1973: 648) comments ". . . nerve cell bodies are common in the peripheral nerves of many molluscs. . . ." Beyond such casual references, one searches the literature in vain for discussion of this phenomenon.

Functionally, what is the role of such peripheral aggregations of neuronal soma? Tauc (1966: 388) observed that ". . . if evolutionary rank may be assigned on the basis of dominance that the central nervous system exerts over peripheral events the Mollusca head the list of all invertebrates. . . ." That this view is not consistently adhered to is indicated by Prosser's comment (1973: 648) that ". . . in *Aplysia*, a gill disconnected from central ganglia contracts to local tactile stimulation and this response, mediated by peripheral plexus, can be habituated. . . ."[2]

As an alternative to the piecemeal approach to the study of mollusks, I have here tried to marshall evidence from neuro-anatomical/histological and behavioral studies to argue that disparate and differently organized peripheral neural entities integrate the reproductive process in the monoecious sphaeriacean bivalve *Corbicula fluminea*, and in the essentially dioecious unionacean bivalves *Lampsilis* and *Carunculina* spp. Behaviorally, these animals are very different (Figs. 14, 15). Physiological data are needed to connect and verify the tentative conclusions presented here. Logistical difficulties associated with careful physiological study of such small clusters of unmyelinated neurons, however, render the latter less than appealing preparations for rigorous experimental exploitation. It also is humbling to realize that Bullock's comment in 1965 (:451) is still patently true: ". . . the gulf between our present level of physiological understanding and the explanation of behavior . . . is wider than the gulf between atomic physics and astronomy and is indeed the widest gap between disciplines in science. . . ."

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[2]Such preparations have been much exploited by physiologists. For example, Lukowiak & Sahley (1981) report that they have demonstrated "associative learning" in a reduced-siphon-mantle-gill-abdominal ganglion preparation of *Aplysia*.
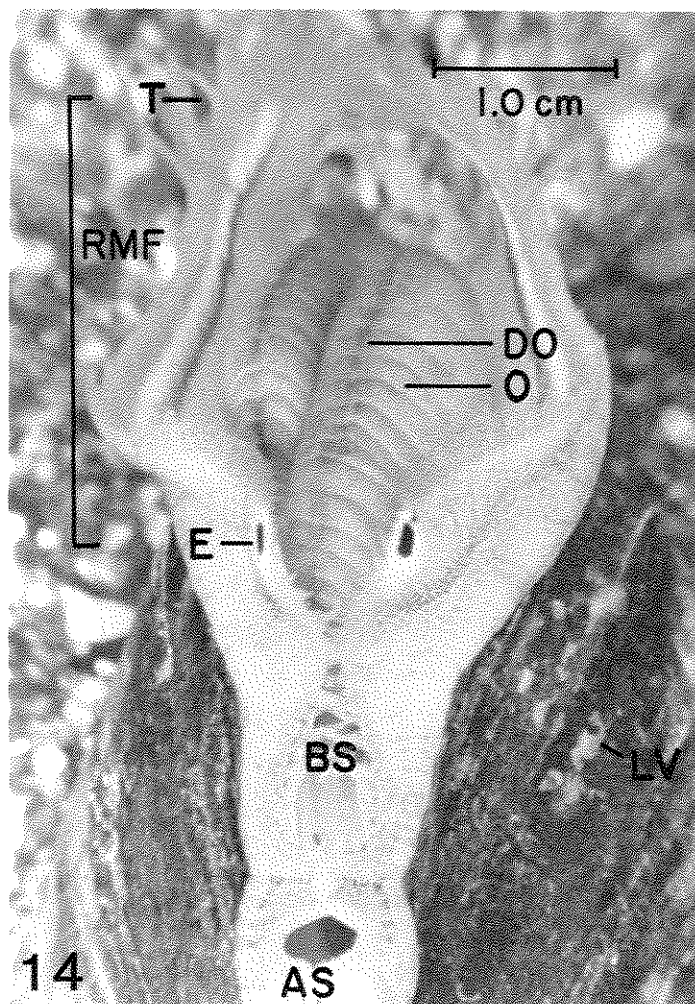
FIG. 14. Photograph from posterodorsal aspect of *Lampsilis ventricosa*, living mature gravid female, during flapping behavior. Note that posteroventral surfaces of both charged marsupial gills are pushed out of the mantle cavity and between the mantle flaps (E, T). The dark line in the distal edge (DO) of each ovisac (O) indicates the location of the "pores" seen by Kraemer (1970) through which glochidia appear to be discharged.

As a final comment, one may observe that the soft bodies of mollusks provide the animals with a neuroanatomical context within which the plasticity and variability of the molluscan nervous system may be exploited. This is demonstrably true of the developmental twisting of gastropod nervous systems and of the neurophysiological virtuosity displayed by the large, sentient surface of cephalopods. It also is observable among the bivalves, the *acéphales,* which eschewed an anterior "brain" and developed large, fused ganglia at their posterior ends along with an extensive system of peripheral nerves. It seems reasonable to expand investigations into the organization and function of various molluscan nervous systems as a means of interpreting the phylogenetic history of the higher taxa. Such studies also offer, *sui generis*, the opportunity for their pursuers to understand adaptational capacity and to predict direction of response to environmental change among the higher taxa of mollusks.
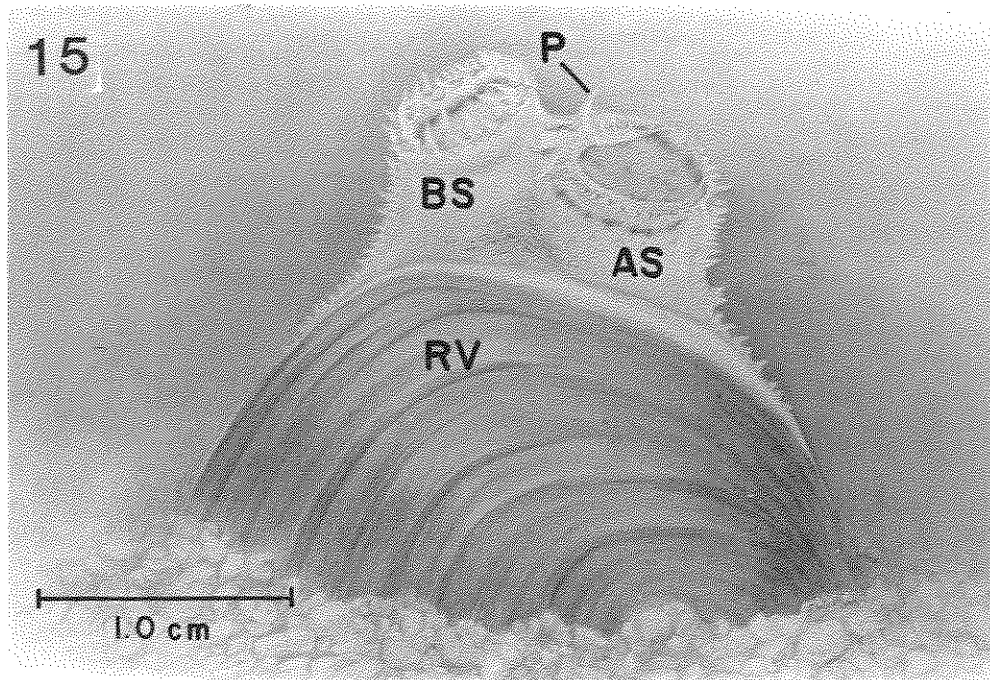
FIG. 15. Drawing of living *Corbicula fluminea* showing characteristic appearance of the animal's muscular siphons which protrude between the shell valves as tubes from the siphonal pocket within.

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