

Mechanics of Glochidial Attachment (Mollusca: Bivalvia: Unionidae)

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ABSTRACT Glochidia are third-class levers in which the valves form the lever arms and the single adductor muscle produces the force. In this study the lengths of the lever arms and the areas of glochidial valves and adductor muscles were determined for 57 species of unionid glochidia. The position of the adductor muscle relative to the dorsal margin of the larval valve was also determined for each species. From these data and an analysis of the possible configurations of adductor muscle and valve dimensions, we determined that most of the glochidia within the Unionidae emphasize area of sweep during valve adduction. These glochidia possess long resistance arms and short force arms and generally had small-diameter adductor muscles. Other glochidia, however, were found to possess one or all of the following: short resistance arms, long force arms, and large-diameter adductor muscles. It is suggested that these glochidia are adapted for strength of valve adduction and that for these larvae a trade-off exists between strength of valve adduction and acceptable valve gape. Furthermore, this study suggests that the mode of attachment employed by glochidia has played a major role in the development of these bivalve larvae and has produced convergence in valve shape and adductor muscle size.

A review of the literature dealing with glochidia reveals that two areas of study representing two periods in the life history of these animals are emphasized. The first area is the portion of the life cycle that occurs within the marsupial gills of the female bivalve. Here the fertilized eggs are stored and develop into mature glochidia. Much work has been done to elucidate this developmental sequence (Flemming, 1875; Lillie, 1895; Matteson, '48; Yokley, '72; Wood, '74; Zale and Neves, '82). Glochidia removed from the marsupia of females have also been described for use in unionid systematics (Lea, 1858, 1863, 1874; Ortmann, '11, '12, '19; Clarke, '81, '85; Hoggarth, '88).

The second area of emphasis is the investigation of the conditions required for attachment to a host (usually to the gills, fins, or epidermis of a fish) (see Hoggarth, '88, Appendix A) and the examination of encapsulation, metamorphosis, and release as juveniles (Coker and Surber, '11; Arey, '21, '24, '32a,b; Howard and Anson, '22; D'Eliscu, '72; Isom and Hudson, '82, '84). We use the term encapsulation rather than encystment as it has been demonstrated that glochidia

are surrounded by tissue entirely of host origin (Arey, '21, '32a; Karna and Millemann, '78) rather than of glochidial origin (see Olsen, '74).

Few studies describe the interval between expulsion from the marsupial gills of the female and attachment to a host, even though it is during this period of the life cycle when the greatest mortality occurs (Young and Williams, '84), hence providing considerable opportunity for natural selection. Furthermore, work dealing with this admittedly brief period in the life cycle of the Unionidae is concerned primarily with the responses of glochidia to various stimuli (Lefevre and Curtis, '12; Arey, '21; Heard and Hendrix, '65).

It was our intent to reexamine the parasitic encounter between glochidia, the larval stage of the Unionacea, and their hosts by an examination of the mechanical limitations and benefits intrinsic to glochidial structure. Glochidia do not feed or engage

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in any significant activity other than to seek attachment during this period of their life cycle. Hence, we assume that selection will be concentrated on this activity with no competing functional constraints on morphology.

MATERIALS AND METHODS

We examined 134 glochidia from 57 species representing 23 genera of the Unionidae. Glochidia were removed from the gravid marsupia of female molluscs located in the collections of The Ohio State University Museum of Zoology (OSUM), University of Michigan Museum of Zoology (UMMZ: uncataloged collection), Illinois Natural History Survey (INHS), The University of Wisconsin Zoological Museum (UWZYM), and the personal collection of the senior author (M.A.H.).

Figure 1 demonstrates the measurements taken from each glochidium by using an ocular micrometer calibrated to 0.05 mm in a Bausch and Lomb dissecting microscope. Valve areas and adductor muscle cross-sectional areas were obtained from projections of micrographs of glochidia on the screen of a Hewlett Packard 9874A Digitizer by using HP Digitize Software with an HP 9825B computer. Only glochidia with tightly closed valves were measured and photographed to ensure that each glochidium was flat in relationship to the microscope stage (not tilted) and that each adductor muscle was fully contracted.

A least-squares regression analysis (NCSS 5.0, Hintz, '87) was performed to determine the relationship between the relative size of the glochidial adductor muscle and the degree of valve depression (dorsoventral reduction). Relative adductor muscle size was determined by dividing the area of the adductor muscle by the area of the valve. An index of valve depression was calculated by dividing the length of a glochidium by its height. These data are presented in Table 1. Drawings of representative glochidia have also been made to demonstrate valve shape and size and adductor muscle location and size.

ANALYSIS AND RESULTS

Obliquely striated muscle was long considered a form of smooth muscle. However, demonstration that it also uses a sliding filament contraction mechanism (Hanson and Lowry, '61) and a better understanding of

its three-dimensional structure have led to a present consensus that it is a form of striated muscle (see Rosenbluth, '72; Toida et al., '75; and Hoyle, '83, for reviews). Z-lines are absent but are replaced functionally by "dense bodies." Oblique striations occur because the myofilaments are staggered rather than aligned, so that the striations form an acute (sometimes as sharp as 1°) angle to the long axis of the fiber.

The adductor muscle of a glochidium is a flexor spanning an angle (gape), with the hinge (pivot) separating right and left valves (lever arms). As in the case for many flexors, the adductor provides the force in a third-class lever system in which the resistance (here considered to be primarily the surrounding medium, assuming that the resistance of the hinge is minimal and constant among species) is considered to be concentrated at the ventral margins of the valves. Attachment devices, such as the large styliform hooks of the triangulate glochidia (Fig. 2), the lanceolate hooks of the axe-head glochidia (Fig. 3j), and the denticulate flange of a majority of subelliptical glochidia (Fig. 3), are restricted to the ventral margin of the valve (see Hoggarth, '88, for micrographs of these structures).

At first glance, positioning the adductor muscle appears to present a trade-off between gripping force and closing velocity. In the first instance, the adductor should be ventrally placed, thereby maximizing its moment arm; in the latter, the muscle should be close to the hinge so that a small contraction will induce a large angular displacement of the ventral edge of the valve. We ask, however, if this is a correct description of the selection on adductor muscle placement?

Like the more familiar cross-striated muscle, obliquely striated muscle contains cells, or fibers, composed of linear series of contractile units (Heffelfinger, '69; Zs.-Nagy and Labos, '69). The properties of sarcomeres have been analyzed recently by Gans and co-workers (Gans et al., '85; Gans and De Vree, '87). We do not intend to review that analysis, but some of its points are of special concern to the present situation.

Contraction is effected when bonds between interdigitating thick and thin filaments of the sarcomeres are activated to draw the filaments centripetally past each other. The tension generated depends on the number of bonds between thick and thin fila-

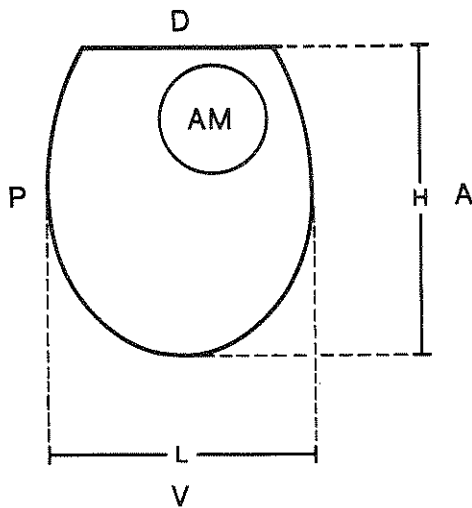


Fig. 1. Glochidium demonstrating height (H) and length (L) measurements and adductor muscle (AM) position within the valve. A, anterior; D, dorsal; P, posterior; V, ventral.

ments, and is, therefore, proportional to the degree of overlap per half-sarcomere. Isometric contractions at various degrees of overlap produce the familiar length-tension curve with a plateau of peak tension in the zone of maximum overlap.

The analysis presented by Gans and co-workers assumes that all sarcomeres within a given muscle are equivalent, and we will further assume sarcomeric equivalency among species of glochidia. For equivalent sarcomeres, force is proportional to cross-sectional area. Thus, for the muscle as a whole, force is proportional to the number of sarcomeres arranged in parallel (i.e., force increases with an increase in cross-sectional area of the muscle). For a given load, speed is proportional to the number of sarcomeres in series (i.e., the contractions of individual sarcomeres are additive and time is constant). Assuming the resting gape of the glochidium is constant, an adductor further from the pivot must have longer fibers with more sarcomeres in series and thus should be intrinsically faster. Conversely, an adductor nearer to the pivot must have shorter fibers, and assuming the volume of the muscle is constant, will have more sarcomeres in parallel and thus should produce greater force.

The situation is further complicated by several other considerations. First, acceleration of the valves depends on force applied.

Second a given gape can be bridged by fibers containing either a few fully extended or many partially contracted sarcomeres. Excursion and peak isometric tension are the same in both cases, but the latter can begin contraction closer to the plateau region. Third, the effective force (i.e., the portion of total force that induces rotation rather than translation) varies with the angle of attachment and increases with adduction of the valves as the angle of attachment approaches an ideal 90° . These various considerations suggest numerous options that could be played against each other. However, in all cases it would appear that bigger is better, because the larger the cross-section of the adductor muscle, the more force it can apply at any point in its excursion.

Suppose, however, that the number of sarcomeres is limited. If parallel fibers attach further from the hinge, and if the resting gape is constant, then the fibers must be longer, and the sarcomeres must be rearranged from in-parallel to in-series (see especially Fig. 4 in Gans and De Vree, '87). This consideration leads to the nonintuitive conclusion that if the volume of the muscle is a constant among species, then its position relative to the hinge is largely irrelevant. Hence, gape reduction produces a double benefit. Not only can more sarcomeres be retained in parallel, but the change in the angle of attachment increases the effective force. Thus, the trade-off is not between speed and grip, but between gape (area swept) and grip (holding on).

Thus far we have assumed that each valve of the shell constitutes a straight, ridged lever, and that the valves unite at the hinge to form a "<" (Fig. 4a). However, this shape incorporates an insuperable disadvantage: at full closure there is no space to contain the animal. A space for the animal's body is easily provided by curvature of the valves. If the curvature is localized so that the valves acquire an angle, then the longitudinal section of a closed glochidium is an attenuate vase shape (Fig. 4b). If the curvature is gradual and the valves more or less crescentric, then the longitudinal section is elliptical (Fig. 4c) or oval (Fig. 4d).

In the vase-shaped configuration, if the adductor attaches dorsad to the bend, the wide angle of divergence permits a relatively long muscle (compared to the "<"-shaped configuration) and maximizes sarcomeres in series. Placement of the muscle

TABLE 1. Relative adductor muscle cross-sectional area and index of valve depression for glochidia of the unionidae¹

Species	Catalog No.	L/H	A/V	L/H	A/V
<i>Anodonta cygnea</i>	OSUM:20911.2	1.04	18	1.00	14
		1.05	18	1.00	11
		1.05	13	1.05	12
		1.00	17		
<i>A. beringiana</i>	OSUM:3711.2	1.00	13	0.95	17
		1.00	14	1.00	15
		1.00	12		
<i>A. kennealyi</i>	OSUM:52882.2	1.00	11	1.05	16
		1.05	12		
<i>A. g. grandis</i>	OSUM:50838.14	1.11	12	0.96	12
		1.00	14	1.00	14
		1.00	17		
<i>A. g. corpulenta</i>	OSUM:38468.6	1.00	15	1.04	11
<i>A. c. cataracta</i>	OSUM:19136.2	0.95	17	1.00	15
		0.96	15		
<i>A. doliaris</i>	OSUM:26405	1.00	13	1.00	15
		1.05	13		
<i>A. suborbiculata</i>	OSUM:13634	1.14	12	1.10	10
<i>A. imbecillis</i>	OSUM:4432.3	1.00	14	0.97	10
	UWZY:24971.1	0.97	13	1.06	12
	UMMZ:Uncataloged	1.00	19	1.14	23
<i>A. californiensis</i>		1.13	23		
<i>Anodontoides ferussacianus</i>	OSUM:3379	1.08	12		
<i>Simpsoniata ambigua</i>	UWZY:22658	0.93	10	0.93	9
	UWZY:22662	0.87	8		
	UWZY:22672	0.93	11		
<i>Strophitus u. undulatus</i>	OSUM:13880	1.25	22	1.24	21
	OSUM:28082.2	1.29	24		
<i>S. u. tennesseensis</i>	OSUM:33381.2	1.23	26		
<i>Alasmidonta marginata</i>	OSUM:53152	0.82	7	0.88	11
	M.A.H.:724.1	0.91	8	0.83	11
		0.92	11		
<i>A. viridis</i>	OSUM:21506	1.20	30		
<i>Pegias fabula</i>	OSUM:41308.3	1.08	59		
<i>Lasmigona costata</i>	M.A.H.:385	0.87	9	0.94	12
	M.A.H.:882.1	0.95	11		
	INHS:2308	0.91	7		
<i>L. complanata</i>	INHS:1923	0.92	11		
<i>L. compressa</i>	OSUM:16039.4	1.17	22	1.17	22
		1.24	25		
<i>Magnoniata nervosa</i>	OSUM:21794	0.86	11		
<i>M. boykiniana</i>	OSUM:51107.4	0.75	8		
<i>Tritogonia verrucosa</i>	M.A.H.:654.2	0.80	15		
<i>Quadrula c. cylindrica</i>	OSUM:26318.11	1.00	17	0.92	16
<i>Q. p. pustulosa</i>	OSUM:45174.1	0.75	6		
<i>Amblema p. plicata</i>	OSUM:19676.21	1.08	14	0.93	11

<i>Fusconata ebena</i>	OSUM:34335.112	1.00	3	
<i>Psychobranichus fasciolaris</i>	M.A.H.:586	0.88	8	7
<i>Cyprogenia aberti</i>	OSUM:48067	1.38	5	7
		1.33	8	
		1.30	6	
<i>Actinonaias l. carinata</i>	M.A.H.:842.1	0.90	7	11
<i>A. pectorosa</i>	OSUM:24337	0.91	9	
<i>Obovaria retusa</i>	UMMZ:Uncataloged	0.76	6	
<i>O. olivaria</i>	OSUM:51282	0.84	7	8
<i>O. subrotunda</i>	M.A.H.:659.2	0.74	7	7
<i>O. jacksoniana</i>	OSUM:50233.7	0.77	7	8
<i>O. unicolor</i>	OSUM:47696.3	0.77	8	
<i>Leptodea fragilis</i>	M.A.H.:658	0.75	7	
<i>Patamilus atatus</i>	OSUM:1983.58	0.61	12	13
<i>P. purpuratus</i>	OSUM:52335.4	0.56	14	13
		0.56	13	13
		0.83	11	12
		0.81	9	4
		0.75	4	6
<i>Medionidius conradicus</i>	OSUM:55466	0.76	7	7
<i>Venustachoncha ellipsiformis</i>	UMMZ:Uncataloged	0.70	8	
<i>Villosa vibex</i>	UMMA:Uncataloged	0.75	12	
		0.78	6	
<i>V. i. iris</i>	UMMZ:Uncataloged	0.78	6	
	OSUM:55828.4	0.78	6	
<i>Lampsilis t. teres</i>	UWZY:25024.1	0.74	5	
<i>L. r. radiata</i>	M.A.H.:897.1	0.85	10	
	M.A.H.:897.2	0.88	8	
<i>L. r. luteola</i>	M.A.H.:845	0.83	8	9
		0.81	12	
<i>L. ventricosa</i>	OSUM:55976	0.90	7	11
		0.85	6	
<i>L. fasciola</i>	OSUM:25467	0.92	13	
<i>L. altilis</i>	OSUM:34764.7	0.82	10	11
<i>Epioblasma triquetra</i>	M.A.H.:588.2	1.11	26	
	M.A.H.:700.1	1.00	24	
<i>E. brevidens</i>	OSUM:20380.91	1.00	18	14
<i>E. metastrata</i>	OSUM:27506.2	1.06	15	
<i>E. othcaloogensis</i>	OSUM:19032.2	1.14	16	
<i>E. lenior</i>	OSUM:15584.4	1.00	18	
<i>E. capsaeformis</i>	OSUM:3964.5	1.13	18	
	OSUM:42007	1.07	17	
	OSUM:43166	1.00	14	14
<i>E. walkei</i>	OSUM:15595.51	1.10	22	18
		1.14	21	23
<i>E. rangiana</i>	M.A.H.:632.1	1.00	20	

¹Key to the abbreviations: L/H, length/height; A/V, cross-sectional area of adductor muscle area of glochidial valve; OSUM, The Ohio State University Museum of Zoology; UWZY, The University of Wisconsin Zoological Museum; UMMZ, The University of Michigan Museum of Zoology; INHS, The Illinois Natural History Survey Collection; M.A.H., the personal collection of M.A. Hoggarth.

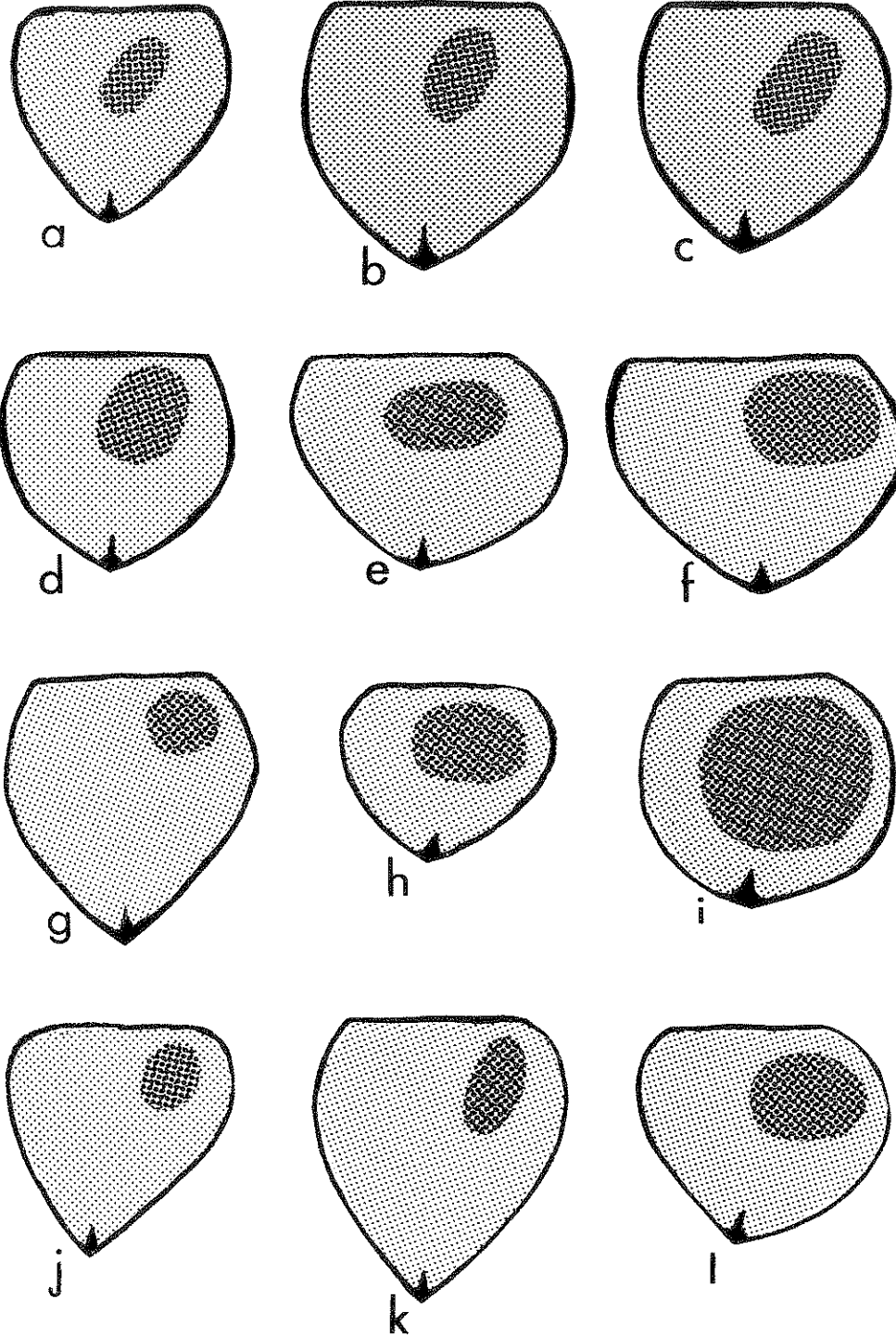


Fig. 2. Glochidia of the Anodontinae: a, *Anodonta imbecillis*; b, *A. g. grandis*; c, *A. g. corpulenta*; d, *Anodontoides ferussacianus*; e, *Strophitus u. undulatus*; f, *S. u. tennesseensis*; g, *Alasmidonta marginata*; h, *A. viridis*; i, *Pegias fabula*; j, *Lasmigona complanata*; k, *L. costata*; l, *L. compressa*. Bar length = 100 μ m.

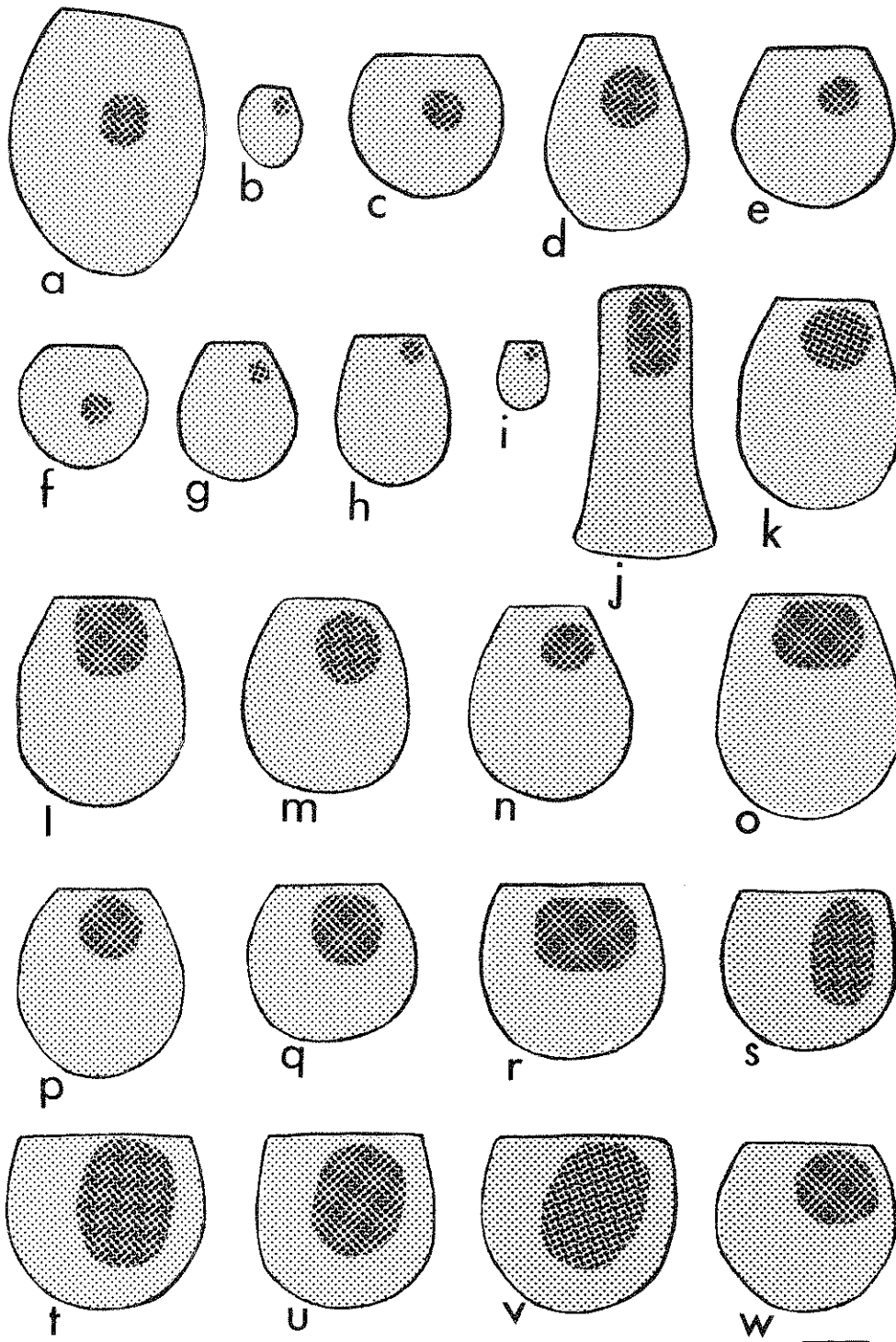
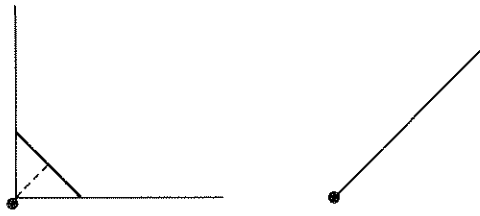
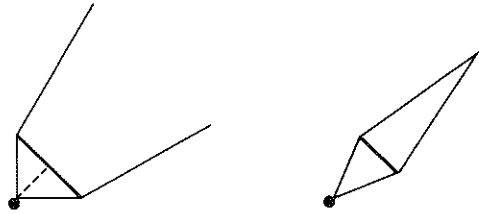


Fig. 3. Glochidia of the Ambleminae and the Lampsilinae: a, *Magnoniais nervosa*; b, *Tritogonia verrucosa*; c, *Quadrula c. cylindrica*; d, *Q. p. pustulosa*; e, *Amblema p. plicata*; f, *Fusconaia ebena*; g, *Ptychobranthus fasciolaris*; h, *Obovaria subrotunda*; i, *Leptodea fragilis*; j,

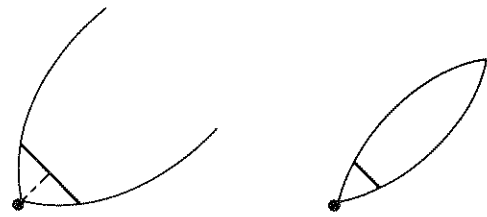
Potamilus alatus; k, *Villosa i. iris*; l, *V. vibex*; m, *Lampsilis r. luteola*; n, *L. ventricosa*; o, *L. fasciola*; p, *L. altilis*; q, *Epioblasma triquetra*; r, *E. brevidens*; s, *E. lenior*; t, *E. metastriata*; u, *E. capsaeformis*; v, *E. walkeri*; w, *E. rangiana*. Bar length = 100 μ m.



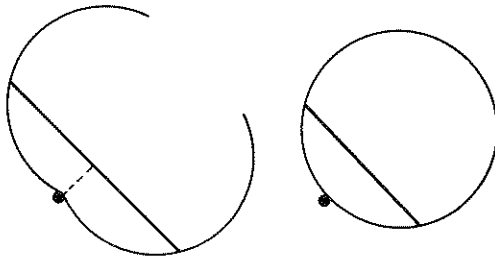
a "Ideal Lever"



b Bent Valve



c Curved Valve



d Extreme Curvature

Fig. 4. Valve shape. For any given adductor muscle length, moment arm, and valve length, valve shape affects the mechanics of valve adduction. Valves of all shapes are drawn to the same absolute length. Note that, for a given moment arm, a globular shape requires a longer muscle to effect any opening, and even a long muscle affords only a small gape.

ventrad to the bend, while increasing the moment arm, permits a relatively short, broad muscle increasing sarcomeres in par-

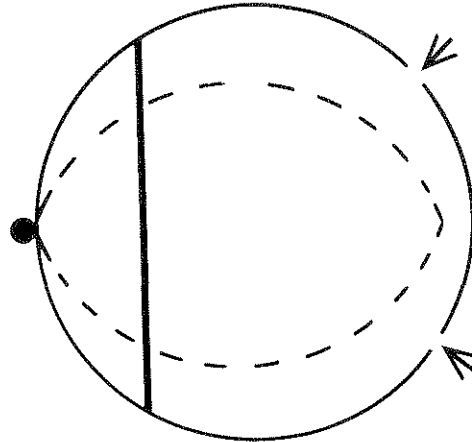


Fig. 5. The small gape of the globular glochidium in Figure 4 can be expanded by shell depression, i.e., shortening the portion of the shell ventrad to the muscle (at arrows). The closed glochidium, dotted lines, superficially resembles the curved shell of Figure 4, but has a shorter radius of curvature and shorter resistance arm.

allel. Similar arguments, but with a gradual rather than sharply divided range of changes in characteristics of the muscle, hold for gently curved and oval shells.

The arguments presented above identify a number of testable hypotheses relative to glochidial attachment during an encounter with a host. If selection is for forceful grip, then a large-diameter muscle is necessary. Therefore, if the number of sarcomeres is limited, diameter should be favored over length, and gape will be reduced. However, forceful grip is also promoted by a relatively short resistance arm. Regardless of the position of the muscle, both force and gape are improved by depression of the valves (Fig. 5). Hence, large-diameter adductors and depressed shells are complimentary and should occur together.

If selection is for maximum gape and sweep area, then the adductor should be relatively close to the hinge, permitting maximum separation for any extension. A decreasing effective force, together with packaging problems, including the position of other larval tissues and room for circumferential expansion of the adductor during contraction, may establish a limit for proximity to the hinge. With these constraints, a large gape can be achieved only by elongation of the muscle. If the volume of the muscle is held constant, then its diameter must decrease, and glo-

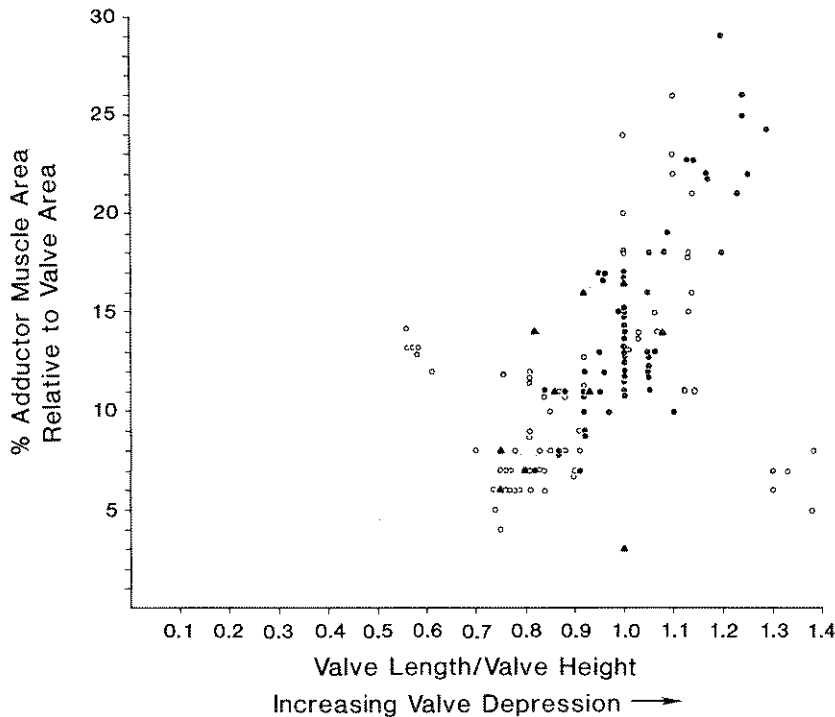


Fig. 6. Adductor muscle size increases with increased glochidial valve depression. Closed circles represent members of the Anodontinae, triangles the Ambleminae, and open circles the Lampsilinae; all

subfamilies of the Unionidae ($r = .800$, $P < .001$, $n = 134$). The glochidium of *Pegias fabula* was not plotted but was included in the regression analysis. (See Table 1 for the data used to construct this figure.)

chidia with small-diameter adductor muscles may also have long resistance arms.

Figure 6 demonstrates that our predictions hold true for most glochidia examined. The least-squares regression for the relationship between degree of valve depression and relative adductor size is significant ($r = .800$, $P < .001$, $n = 134$) and shows that glochidia with the longest resistance arms have the smallest adductor muscles, whereas morphologically depressed glochidia have the largest adductor muscles.

There are two clusters of points in Figure 6 that are not explained above. The cluster to the left of the linear relationship represents the larvae of the genus *Potamilus* (Fig. 2j). This glochidium is characterized by extreme anteroposterior valve reduction (producing the axe-head shape) and recurved lanceolate hooks (see Hoggarth, '88). The mechanical aspects of valve reduction and its consequences, including the reduction of fluid drag during valve adduction, are not at issue here. However, we suggest that glo-

chidia of this type have taken a step toward increasing speed during valve adduction in order to increase the angular momentum applied to penetration devices.

The cluster to the right of the linear relationship in Figure 6 and the triangle near the bottom of the graph represent morphologically depressed glochidia with relatively small adductor muscles (Fig. 3f). These are the glochidia of *Fusconaia ebena* (triangle) and *Cyprogenia aberti* (circles). The position of these points on the graph may best be understood in terms of a peculiar host attraction device employed by these species. The glochidia are expelled from the female in gelatinous masses within which the glochidia are positioned, valves gaping outward from the matrix. Similar structures are also found in *Strophitus*, a genus that likewise has morphologically depressed glochidia (Fig. 2e). This conglomerate of matrix and glochidia may be brightly colored and may best be described as wormlike. These glochidia therefore can be described as "preposi-

tioned" for attachment. We suggest that large valve sweep is of minor importance to the glochidia of these species because their hosts pick them up and move them into the gill chamber. Positioning the adductor muscle ventrally between depressed valves simultaneously increases the force arm and produces a better angle of attachment while permitting an acceptable gape. These first two effects also increase effective force and may compensate for a small-diameter muscle.

DISCUSSION

Following exposure to tactile stimulation, glochidia rapidly close their valves. However, permanent closure is often preceded by the repeated closing and opening of the valves referred to as "clapping" or "winking" (Lefevre and Curtis, '12; Arey, '21). This activity has led to the erroneous belief that glochidia could swim like members of the genus *Pecten*.

A glochidium will rapidly clap its valves together when mildly stimulated. This stimulation could be caused by a passing fin, the action of passing through the gill chamber of a fish, the presence of small concentrations of fish blood in the near environment of the glochidium, or many other examples of lesser importance to successful parasitism. During this initial period of parasitism, the more rapid the response and the larger the sweep the greater the probability for success. When contact is made, however, a glochidium immediately and rapidly adducts its valves, which increases tactile stimulation on the hair cells and produces continuous contraction of the adductor muscle. As contraction increases, the valves and/or hooks damage the tissues of the host, which produces the chemical stimulation required to ensure continued attachment until encapsulation occurs (Heard and Hendrix, '65).

The scenario above reveals two separate periods during attachment. First is the period of initial stimulation when a glochidium quickly adducts its valves and, second, the period following this initial response when the action of the glochidium is directed toward tenacious valve adduction. We have shown that adaptation toward one period reduces adaptation toward the other.

Following expulsion from the marsupial gills, glochidia gape widely, ready to close repeatedly and rapidly when stimulated. Glochidia with long resistance arms that are

adapted for large area of sweep have an advantage during this period. (We should note that the presence of paramyosin provides a biochemical augmentation of the gripping strength of any glochidial adductor regardless of its position.)

The other major group of glochidia are characterized by large adductor muscles and depressed shells. These glochidia are adapted for gripping strength. It is important to note that most of the glochidia in this group are members of the subfamily Anodontinae. The lampsiline genus *Epioblasma* is the only exception. The anodontine glochidia are generally found attached to exterior surfaces of their hosts (i.e., fins and epidermis) rather than to the more protected gill filaments. It is suggested, therefore, that selection for gripping strength occurred in these glochidia because they attach to hosts in areas where there is a tendency to be dislodged. Although little work has been done on attachment selectivity, such work that has been done (Dartnall and Walkey, '79; Dudgeon and Morton, '84) shows that anodontine glochidia selectively attach to the fins used in active swimming (tail and pectoral fins) rather than to the pelvic, anal, or dorsal fins. This selectivity may be a result of the probability of contact (actively moving fins sweep more area and come in contact with glochidia more often than the other fins), but these fins would also produce turbulence that would tend to dislodge a glochidium prior to encapsulation.

This analysis shows that the size of the adductor muscle and the relative dimensions of glochidial valves are selected on the basis of mode of attachment. Where modes of attachment are similar, as in the case of *Fusconaia ebena* and *Cyprogenia aberti* or the members of *Epioblasma* and the depressed anodontine glochidia, adductor muscle size and shell dimensions are also similar. Glochidia with high shells and small adductor muscles are likewise found in all three subfamilies and further demonstrate that these glochidial valve characters are of functional significance rather than of phylogenetic significance.

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