

The adaptive value of offspring size among freshwater mussels (*Bivalvia*; *Unionoidea*)

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Summary

1. The glochidia (larvae) of the freshwater mussels *Unionoidea* must attach to a host fish to pass through their parasitic stage. Glochidial size is species-specific: varying from *c.* 0.05 mm to *c.* 0.45 mm shell length.

2. There is a trade-off between size and number such that fertility is high in species with small glochidia and vice versa.

3. There appear to be no allometric constraints on glochidial size. Phylogenetic constraints seem to be of minor importance (perhaps with the exception of the *Margaritiferidae*). Furthermore, no influence can be shown for the breeding type (long- or short-term breeder) or the habitat type with respect to the water current. The number and type of marsupia (four marsupia, two marsupia, two marsupia on the posterior part of demibranchs) also does not seem to be related to glochidial size.

4. The morphological factor 'hook on the glochidial shell' and the ecological factor 'host range' (number of host fish families) are of importance. Glochidia with a hook are larger than unhooked ones. They frequently attach to tough host tissues and therefore have to be powerful. Glochidial size also increases as the host range increases. This relationship probably evolved because of an interplay of the duration of the parasitic stage and the host's immunological defences.

5. The analyses suggest that glochidial size is a crucial component in the evolution of a continuum of reproductive strategies among the *Unionoidea*. Representatives of one end of the continuum are the *Margaritiferidae* with small glochidia, high fertility, long parasitic stage, protracted growth on the host and narrow host range. They are highly specialized with respect to the habitat. Some *Anodonta* species represent the opposite end with large glochidia, low fertility, short parasitic stage with no growth being involved and large host range. They live in a variety of habitats.

Key-words: constraints, host range, reproductive strategy, selection, trade-off.

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Introduction

A life-history trait which is closely related to fitness is offspring size (Parker & Begon 1986; Lloyd 1987). Therefore, theoretical models on the evolution of offspring size usually assume that it is adapted to ecological requirements, i.e. it is optimized by a selective compromise, based on a positive correlation between offspring size, and survival of offspring and a trade-off between offspring size and number (Smith & Fretwell 1974; Brockelman 1975). However, the validity of such models would have to be taxonomically restricted considerably, if either offspring size or clutch size or even both traits are heavily constrained, as has been reported for numerous vertebrate and invertebrate

groups (Ashmole 1971; Blueweiss *et al.* 1978; Kaplan & Salthe 1979; Begon, Harper & Townsend 1986; Berrigan 1991; Skorping, Read & Keymer 1991; Stearns 1992).

The separate influences of various factors on life-history variation may be disentangled by comparative studies of closely related species (Murphy 1989; Harvey & Keymer 1991; Stearns 1992). Here such an analysis is performed on offspring size among freshwater mussels of the Superfamily *Unionoidea* (najads). This group is monophyletic (Davis & Fuller 1981), with similar gross morphology and ecology. The adults are filter feeders. The eggs develop into larvae (glochidia) in portions of the female gills which are permanently modified (as marsupia). After being

released into the water, the glochidia have to attach to a host fish where they pass through a parasitic stage, necessary for the metamorphosis into the juvenile mussel.

As shown in the Appendix, large differences exist between higher taxonomic groups (families or subfamilies resp.) in the number and type of marsupia, in the length of the breeding season and in the morphology of the glochidial shell. The species differ ecologically with respect to habitat and host range and morphological differences exist in body size and in glochidial size which is related to the stage of glochidial development.

In order to contribute further to the theory of offspring-size evolution using Unionoidea as a model group (i) interspecific variability of glochidial size is documented, (ii) the trade-off between size and number is analysed, (iii) the impact of possible constraints and of ecological factors on glochidial size is compared, and (iv) relationships between glochidial size and developmental mode on the host fish are investigated. The results lead to an explanation of the reproductive strategies involved in the complicated life cycle of this animal group.

Methods

This paper is based on both new data from three European species (if no sources are given) and on published records from holarctic mussels (mainly North America and Europe). The most important cited bionomic data for this study are presented in the Appendix.

GLOCHIDIAL SIZE

The size of glochidia is species- or genus-specific (Lefevre & Curtis 1912; Davis & Fuller 1981; Wächtler 1986; Nagel 1988). Here the length of the glochidial shell was used as a measure of size. For 65 species, data on the height of the shell are also available (Surber 1912; Clarke 1981; Yeager & Neves 1986; Nagel 1988). Eighty-two per cent of height variation is explained by length ($y = 0.03 + 0.92x$, $r = 0.91$, $P < 0.001$, the reduced major axis regression slope is $b = 1.02$). Thus, shell length apparently is a good predictor of glochidial size.

FACTORS POSSIBLY RELATED TO GLOCHIDIAL SIZE

Adult size

Literature records on the size of najads almost exclusively refer to shell length although this is a less precise measure than weight or body volume. The agreement between species of the relationships between length and live weight of soft parts has been tested for three species for which data were available from an earlier study (Bauer, Hochwald & Silkenat 1992). Analysis

of covariance showed that the relationship for *Margaritifera margaritifera* (L.) ($n = 60$) and *Anodonta piscinalis* (Nilsson) ($n = 26$) could not be distinguished ($F = 0.63$; NS), whereas *Unio crassus* (Philipsson) ($n = 32$) is slightly heavier ($F = 19.4$; $P < 0.001$). In the present study length data of 52 species could be used.

Fertility

In addition to published data on fertility (= number of glochidia in the marsupia of one female) of three species (and one subspecies) this parameter was estimated for *Margaritifera margaritifera*, *Unio pictorum* and *Anodonta piscinalis* as follows: gravid mussels were collected, measured along their longest axis and kept individually until they released the glochidia (see Bauer 1987c and Hochwald 1988 for further information). The mussels were then inspected, to ensure that all glochidia had been released. The glochidia were suspended in a definite amount of water (0.1–0.5 ml, depending on the concentration of glochidia) and several counts of abundance were made allowing an estimate of the total to be calculated. (The same counting method was applied to estimate the number of glochidia in the marsupia of one preserved female of *Lasmigona* sp. and one of *Leptodes fragilis* Rafinesque).

Phylogeny

An important problem in comparative analysis is non-independence of species values because species may share characteristics not through convergent evolution but because of shared ancestry (Pagel & Harvey 1988; Harvey & Keymer 1991; Skörping *et al.* 1991). Therefore, it is crucial for the interpretation of life history variation to take the phylogenetic relationships into account. However, because there is still disagreement on the classification system of the Unionoidea (Heard & Guckert 1971; Davis & Fuller 1981; Smith & Wall 1984), particularly on taxonomic levels above genera, three different classification systems have been considered here (Heard & Guckert 1971; Fuller 1974; Davis & Fuller 1981).

Morphology, breeding season and ecology

Among the criteria used for systematic classification are the morphology of the glochidial shell, the number and type of marsupial demibranchs and the length of the breeding season (Heard & Guckert 1971; Davis & Fuller 1981). The morphology of the glochidial shell is sharply distinguished by (a) the presence of a hook at the ventral margin in some groups and (b) its absence in others. Glochidia without a hook are restricted to the gills of their hosts, whereas hooked ones can attach to the host's fins and even scales (Davis & Fuller 1981).

All members of the Unionoidea have two gills on each side. Therefore, the number of marsupia (a) is four, if all demibranchs are totally used for reproduction. Some groups restrict their marsupia to (b) the outer two demibranchs (two marsupia) and some groups further restrict them to (c) the posterior parts of the outer demibranchs. The number and type of marsupia might determine the total available marsupial volume, and therefore might have influenced the evolution of offspring size.

The length of the breeding season is the time during which the offspring are retained in the marsupium. It amounts to more than half a year in (a) long-term breeders, whereas it is completed after a few weeks in (b) short-term breeders (Heard & Guckert 1971; Nagel 1988). Since there is some evidence that the embryos absorb nutrients from the maternal organism (Yokley 1972), long-term breeders might be expected to produce more developed glochidia, which are usually larger than poorly developed ones (Harms 1907a, b, 1908).

Two ecological parameters are considered here. One is the degree of host specificity. There are only a few cases in which most or all host species are known (e.g. the *Margaritifera* and *Unio* species, *Anodonta cygnea* L., *Anodonta grandis* Say). However, the available data probably give an indication of the host range for higher taxonomic levels. Thus, the host range is given here as number of fish families represented as hosts by a mussel species: (a) one fish family, (b) two fish families, (c) three and more fish families.

The second ecological parameter is the habitat type with respect to the water current, (a) running water, (b) standing water, (c) both types of habitat. As glochidia are not able to swim actively a relationship between running/standing water and glochidial size might be expected. The chance of attaching to a host is highest for suspended glochidia. However, in standing water large glochidia will rapidly settle.

Developmental mode

First, the question was investigated as to whether the duration of the metamorphosis (= parasitic stage) depends on the developmental stage and thus the size of glochidia. The time of parasitism is expressed as day-degrees from the day of attachment until the day on which most young mussels dropped from the host. One experiment was run with brown trout (*Salmo trutta* L.) fingerlings infected with glochidia of *Margaritifera margaritifera*. Freshly released infective glochidia were suspended in a 20-litre bucket of heavily aerated water (c. 5000 glochidia per litre). Forty fish were placed in the bucket for 3 minutes so that c. 50 glochidia attached to the gills of one fish. The fish were kept in two 250-l aquaria at 8°C until metamorphosis of glochidia was completed.

Second, the available data on the growth pattern during the parasitic stage were evaluated by analysing

whether glochidia grow on their host or not, and if there is a relationship between growth and initial glochidial size.

DATA ANALYSIS

The statistical analyses were performed with the SPSS and SAS statistical packages. Before regression- or variance analyses the data were checked for normality or homogeneity of variances respectively. For mean values the confidence limit is given throughout.

Allometric relationships and the trade-off between glochidial size and number

Investigations of allometric relationships between adult body size (size of the species) and glochidial size, and of allometries and trade-offs in the relationships between female size, glochidial size and fertility were conducted. The trade-off between glochidial size and number was analysed as follows: for each group (species or subspecies), the mean female size and the mean fertility of the data given in Fig. 3 was calculated (Gould 1975; Kaplan & Salthe 1979) and the simultaneous influence of mean female size and of glochidial size on mean fertility was tested using a path analysis. The path coefficients (= beta) represent the magnitude of the direct effect of one independent variable on the dependent variable (= mean fertility), with the other independent variable in the equation held constant (Sokal & Rohlf 1981).

Phylogeny and glochidial size

Since the true branching phylogeny is not known for the Unionoidea, the following procedure was adopted: to identify the appropriate taxonomic unit for comparative analysis a three-level nested ANOVA was used (Stearns 1992). Group and subgroup categories included family, subfamily and genus. The appropriate unit is the one within which the trait (here glochidial size) varies little but among which it varies a lot, i.e. the unit where the mean values can be treated as statistically independent of other such values.

The impact of morphology, breeding season and ecology

The relationships of these parameters to glochidial size were analysed by using them as factors in one-way ANOVAs.

Comparison of the effects of phylogeny, morphology and ecology

A rough measure of the extent to which evolutionary history has constrained a character is provided by comparing species within those taxonomic or morphological units that are known to explain most of its variation (Harvey & Pagel 1991). Therefore, it was

investigated whether or not relationships between glochidial size and ecological factors reported across all species were also found within these units. (a) If the relationships cannot be confirmed within these units, they are probably a taxonomic artefact, i.e. they must be attributed to differences among lineages but not to adaptations within them. (b) If they are confirmed, this is evidence that the ecological factor in question in fact acts on glochidial size and evolutionary history has probably been of little importance in preventing adaptation. These analyses suggested that one morphological and one ecological factor could be of importance.

Both factors were used to control the effect of phylogeny (on glochidial size) for morphology and ecology. A two-way ANOVA was conducted with these factors to assess their simultaneous impact on glochidial size. Then the taxonomic units evaluated above (see 'phylogeny and glochidial size') were recompared for differences in standardized residuals of glochidial size using a one-way ANOVA. Standardized residuals were calculated as follows: for each cell, according to the morphological and ecological factor considered, the mean glochidial size was calculated. Then each species deviation from the mean was divided by the standard deviation of the residuals of the taxonomic unit. If the taxonomic units still differ with respect to the standardized residuals then phylogenetic constraints on glochidial size cannot be ruled out (Wootton 1987; Murphy 1989).

Results

GLOCHIDIAL SIZE

Roughly 240 species of the Unionoidea occur in North America and 11 in Europe (Davis & Fuller 1981; Nagel 1988). Data on glochidial size were found for 81 species. The size distribution is presented in Fig. 1.

ALLOMETRIC RELATIONSHIPS AND THE TRADE-OFF BETWEEN SIZE AND NUMBER

No allometric relationship between the shell length of a species and the size of its glochidia was found (Fig. 2).

The available data on fertility in relation to female size are presented in Fig. 3. As indicated in Fig. 1, the groups analysed here cover nearly the whole spectrum of glochidial size. Fertility is a positive function of female size and seems to be highest in species with small glochidia and vice versa. This is confirmed by a path analysis with the glochidial size of the species (or subspecies) and their means of Fig. 3, showing that mean fertility is positively related to mean female size ($\beta = 0.45$; $P < 0.001$), whereas it is negatively related to glochidial size ($\beta = -0.64$; $P < 0.001$).

When the limited data of *Lasmigona* sp. and *Leptodes fragilis* are included in the analysis, the values

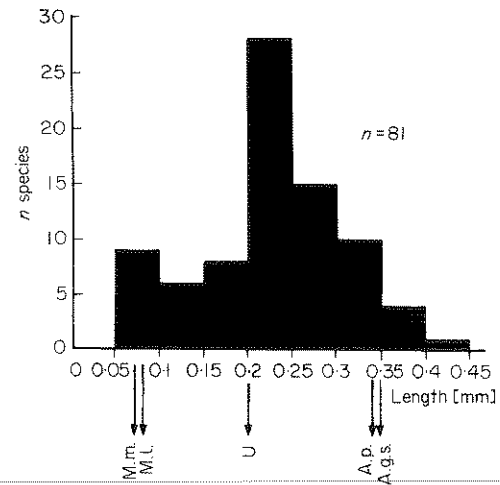


Fig. 1. Frequency distribution of shell lengths of glochidia of 81 species of the Unionoidea. Eighty species are from North America and Europe and one (*Margaritifera laevis* Haas) is from Japan. (The abbreviations refer to the data presented in Fig. 3: M.m. = *Margaritifera margaritifera*, M.l. = *Margaritifera laevis*, U = *Unio*, A.p. = *Anodonta piscinalis*, A.g.s. = *Anodonta grandis simpsonia* Lea). (Sources as in the Appendix.)

of the path coefficients hardly change (female size: $\beta = 0.48$; $P < 0.05$; glochidial size: $\beta = -0.59$; $P < 0.01$). Thus, the number and type of marsupial demibranchs (four: *Margaritifera*; two: *Unio*, *Anodonta*, *Lasmigona*; two at the posterior end of the outer demibranchs: *Leptodes fragilis*) seem to be of little importance for fertility compared to female and glochidial size.

PHYLOGENY AND GLOCHIDIAL SIZE

Data on the host range are only available for less than half of the species shown in the Appendix. Furthermore, the margaritiferids are somewhat atypical with respect to many characters (Bauer 1992; Chesney, Oli-

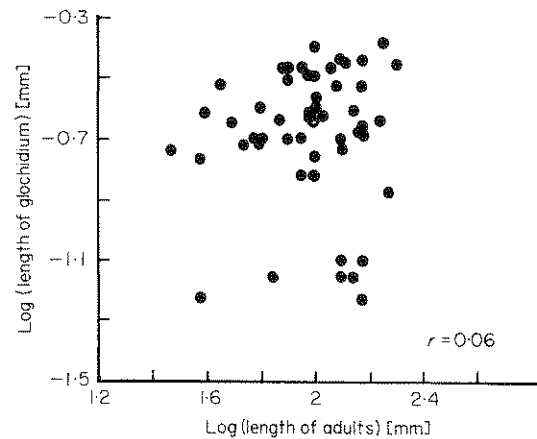


Fig. 2. Test for allometric relationships between species size and glochidial size. (Each point refers to one species. Correlation coefficient: $r = 0.06$). (Data in part from Surber 1912; Howard 1915; Awakura 1968; Meyers & Millemann 1977; Buchanan 1980; Clarke 1981; Nagel 1988).

ver & Davis 1993). Both factors may obscure the final conclusions about the impact of phylogeny when it is simply analysed across all data. Therefore, this analysis has been conducted four times within each taxonomic classification system: with all data ($n = 81$), with the data set where information on the host range is available ($n = 33$), with each of these data sets but with the margaritiferids excluded ($n = 77$ or 30 resp.). The results are approximately identical in all cases. The appropriate taxonomic level of analysis is subfamily (and family in the system of Fuller 1974). These taxonomic units (families or subfamilies resp.) account for most of the variation in glochidial size (Table 1); they will be considered below.

THE IMPACT OF MORPHOLOGY, BREEDING SEASON AND ECOLOGY

The presence or absence of a hook on the glochidial shell has a considerable influence (Table 2). Hooked glochidia are much larger than unhooked ones (0.3 ± 0.02 mm versus 0.18 ± 0.02 mm). The factor 'marsupial demibranchs' also contributes to differences in glochidial size, although without showing a trend in relation to the marsupia (four marsupia: 0.17 ± 0.04 mm; two demibranchs used as marsupia: 0.29 ± 0.02 mm; two marsupia at the posterior part of outer demibranchs: 0.19 ± 0.02 mm). Length of the breeding season is not related to glochidial size.

Both ecological factors considered here exhibit a significant influence on glochidial size when all data are considered (Table 2). A continuous increase in glochidial size with increasing host range is evident (one fish family: 0.13 ± 0.05 mm; two fish families: 0.2 ± 0.05 mm; three and more fish families: 0.27 ± 0.04 mm). Glochidia of species specialized for running water are smaller than glochidia of the other groups (running water: 0.19 ± 0.04 mm, standing water: 0.31 ± 0.06 mm, both habitats: 0.25 ± 0.03 mm).

COMPARISON OF THE EFFECTS OF PHYLOGENY, MORPHOLOGY AND ECOLOGY

The impact of ecological factors within taxonomic or morphological units

Data for which analyses are possible are presented in Table 3. The result of the increase in glochidial size with increasing host range, as gained from all data is largely confirmed. Within the family Unionidae (system Fuller 1974) glochidial size increases with increasing host range (one fish family 0.16 ± 0.06 mm; two families 0.2 ± 0.05 mm; three and more families 0.27 ± 0.04 mm). The same occurs within the subfamilies Ambleminae (system Davis & Fuller 1981) (one fish family 0.16 ± 0.05 mm; two families 0.16 ± 0.04 mm; three and more families 0.22 ± 0.01 mm), Lampsilinae (one or two fish families,

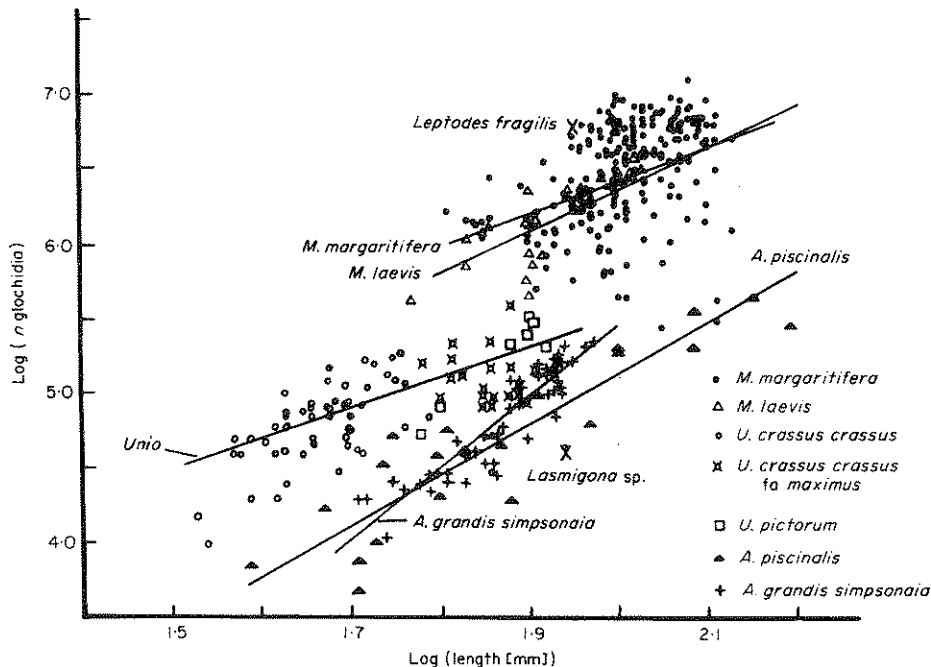


Fig. 3. Relationship between female size (shell length) and fertility (number of glochidia produced). Each dot refers to one individual. (Data for *Margaritifera laevis* from Awakura 1968, for *Unio crassus* from Hochwald 1988, for *Unio crassus* fa *maximus* from Engel 1990 and for *Anodonta grandis simpsonaia* from Hanson, Mackay & Prepas 1989). The lines in the figure and the following statistics refer to least square regressions. As within *Unio* the glochidia are of identical size, only one regression is calculated for this genus. (See Fig. 1 for glochidial size.) *Margaritifera margaritifera*: $n = 209$; $y = 2 + 2.2x$; $r = 0.39$; $P < 0.001$. *Margaritifera laevis*: $n = 29$; $y = 0.62 + 2.86x$; $r = 0.82$; $P < 0.001$. *Unio*: $n = 83$; $y = 1.5 + 2x$; $r = 0.67$; $P < 0.001$. *Anodonta piscinalis*: $n = 22$; $y = -1.59 + 3.37x$; $r = 0.91$; $P < 0.001$. *Anodonta grandis simpsonaia*: $n = 54$; $y = -4 + 4.75x$; $r = 0.91$; $P < 0.001$. *Lasmigona* sp.: glochidia 0.38 mm. *Leptodes fragilis*: glochidia 0.08 mm.

Table 1. Taxonomic distribution of variance in glochidial size from nested ANOVA. Three different classification systems are used. Within each system one analysis is conducted with all data (ALL), one is conducted with those species for which information on the host range is available (HR). These analyses are then repeated with the margaritiferids omitted (NM). The system of Davis & Fuller (1981) consists of one family, the system of Fuller (1974) of two: Margaritiferidae and Unionidae

Classification system	Data	Percentage of variation explained by		
		Family	Subfamily	Genus
Heard & Guckert (1971)	ALL	6.4	63	2.8
	NM	0	68	2.3
	HR	1.6	66	8.3
	NM	0	60	6
Fuller (1974)	ALL	56	38	2
	NM		64	5
	HR	41	37	8
	NM		63	11
Davis & Fuller (1981)	ALL		78	4
	NM		74	0.8
	HR		78	4
	NM		76	2

Table 2. ANOVA-summary showing the influence of morphological factors and breeding season (presence or absence of a hook on the glochidial shell, number and type of marsupia, short-term breeder-long-term breeder) and ecological factors (host range, habitat type according to water current) on glochidial size

Factor	<i>n</i>	<i>F</i>	<i>P</i>
Hook	81	60	<0.001
Marsupia	81	23.6	<0.001
Breeding season	73	2.8	NS
Host range	33	9.8	<0.001
Habitat	53	5.7	<0.01

0.14 ± 0.05 mm; three families 0.24 ± 0.03 mm) and Anodontinae where this trend is evident but not significant (two fish families 0.28 ± 0.04 mm; three and more families 0.35 ± 0.04 mm, *P* = 0.052). For glochidia with hooks there is a tendency to be bigger as the host range increases (two fish families 0.24 ± 0.1 mm; three and more families 0.31 ± 0.09 mm). This relationship is significant for glochidia without hooks (one fish family 0.13 ± 0.04 mm; two families 0.14 ± 0.04 mm; three and more families 0.23 ± 0.02 mm). The same pattern, though not significant, is found for the unit 'marsupial demibranchs': four marsupia, one fish family 0.1 ± 0.08 mm, two and more families 0.19 ± 0.06 mm (*P* = 0.052); two marsupia, one or two fish families 0.24 ± 0.06 mm, three families 0.3 ± 0.07 mm.

The ecological factor 'habitat' does not show any significant influence on glochidial size within these taxonomic or morphological units, although there are more data available dealing with this factor compared to data on host range (Table 3).

The combined impact of morphology, ecology and phylogeny

The results gained so far suggest that the morphological factor 'hook' and the ecological factor

'host range' are closely related to glochidial size (Fig. 4). This is confirmed by a two-way ANOVA with these factors (33 species). As there are no hooked glochidia with only one fish family, the groups 'one' and 'two fish families' had to be combined. The analysis shows a significant influence of the factors 'hook' (*F* = 26; *P* < 0.001) and 'host range' (*F* = 11; *P* < 0.01) on glochidial size (*R*² = 0.62). There is no significant interaction between them (*F* = 1.3; NS). (All other combinations of morphological and ecological factors yield lower values of *R*².)

When the effect of phylogeny is controlled for morphology (hook) and ecology (host range), it still seems to be significant. Table 4 shows that the standardized residuals (residuals = species' deviations from the means shown in Fig. 4) differ among those taxonomic units representing most of the variation of glochidial size (Table 1). However, this is due to the exceptionally small glochidia of the three *Margaritifera* species. When they are excluded, the effect of phylogeny vanishes (Table 4).

DEVELOPMENTAL MODE

As Table 5 shows, the duration of the parasitic stage is inversely related to glochidial size. The large glochidia of *Pseudanodonta complanata* (Rossmässler) and *Anodonta cygnea* require only 200–300 day-degrees to complete development into the young mussel, whereas the small glochidia of *Margaritifera* need more than 1000 day-degrees.

Growth during the parasitic stage is negligible in the overwhelming majority of najad species (Harms 1907a,b, 1908; Lefevre & Curtis 1912). However, there are five remarkable exceptions, three *Margaritifera* species (the most primitive group) and two Lampsiinae (the most advanced group), *Proptera laevissima* (Lea) and *Plagiola donaciformis* (Lea) (Surber 1912;

Table 3. ANOVA summary showing the influence of ecological factors on glochidial size within taxonomic and morphological units. The subfamily Anodontinae is identical in all classification systems considered here. The Lampsilinae are identical in the system of Heard & Guckert (1971) and Fuller (1974), and consist of species with two marsupia at the posterior end of the outer demibranchs

Data analysed	Factor	<i>n</i>	<i>F</i>	<i>P</i>
Unionidae (Fuller 1974)	Host range	30	5.7	<0.01
Ambleminae (Davis & Fuller 1981)	Host range	21	5.1	<0.05
Anodontinae	Host range	9	5.4	NS
Lampsilinae	Host range	9	7	<0.05
hook +	Host range	12	1	NS
hook -	Host range	21	6.3	<0.001
4 marsupia	Host range	9	5.5	NS
2 marsupia	Host range	15	2	NS
Unionidae (Fuller 1974)	Habitat	49	2.7	NS
Anodontinae	Habitat	19	0.64	NS
Ambleminae (Fuller 1974)	Habitat	9	0.23	NS
Ambleminae (Davis & Fuller 1981)	Habitat	30	0.5	NS
Lampsilinae	Habitat	13	0.02	NS
hook +	Habitat	23	0.23	NS
hook -	Habitat	30	4.3	NS
4 marsupia	Habitat	13	2.7	NS
2 marsupia	Habitat	27	0.2	NS

Awakura 1968; Karna & Milleman 1977; Young & Williams 1984b; Buddensiek 1991). All belong to the group whose very small glochidia (Margaritiferidae: 0.06 mm, 0.07 mm, 0.08 mm; Lampsilinae: 0.06 mm, 0.1 mm) are clearly separated from the remaining species (Fig. 1). Their final size (at the end of the parasitic stage) is 0.36–0.5 mm in the case of the Margaritiferids. For the Lampsilids the reported data indicate a shell length between 0.3–0.35 mm.

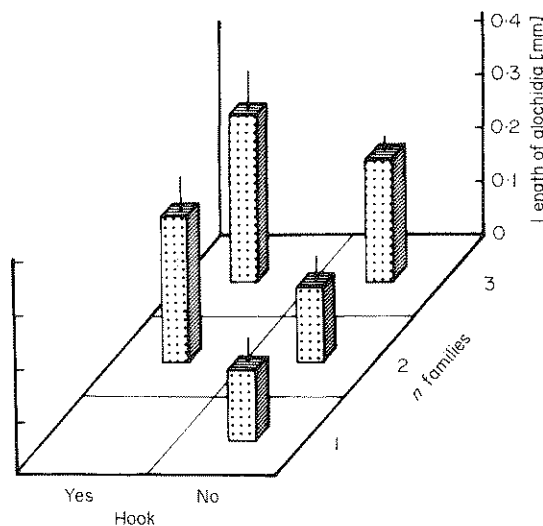


Fig. 4. Average length of glochidia (+c.i.) of 33 species in relation to the size of the host range (number of fish families) and the presence or absence of a hook.

Discussion

THE FRAMEWORK OF TRADE-OFFS AND CONSTRAINTS

A trade-off which is frequently observed above the species level is the negative relationship between offspring size and offspring number (Berrigan 1991; Stearns 1992). This trade-off was also found here (Fig. 3).

As shown in Fig. 2, allometric constraints on glochidial size cannot be binding. The same seems to be true for phylogenetic constraints since: (i) the impact of ecology (host range) is not only evident across all species (Table 2), but also within other taxonomic or morphological units (Table 3), indicating that evolutionary history has been of minor importance in preventing change of glochidial size; (ii) when the margaritiferids are excluded the impact of phylogeny (Table 1) vanishes when it is controlled for morphology and ecology (Table 4). The glochidia of the margaritiferids (0.07–0.08 mm) are smaller than expected for the group 'unhooked—one fish family' (Fig. 4). One reason may be that some members of this group in reality may exploit more than one fish family, whereas the host range of the genus *Margaritifera*, which has been investigated thoroughly, surely encompasses only one fish family (Awakura 1968; Bauer 1987b; Karna & Millemann 1977). A second reason may be that the margaritiferids are indeed constrained by phylogeny. They form the most

Table 4. Comparison of standardized residuals of taxonomic units after factoring out the morphological effect 'hook' and the ecological effect 'host range'. Chi²-values in brackets refer to a Kruskal-Wallis analysis. With the species considered here the subfamilies of Fuller (1974) and Heard & Guckert (1971) are identical

Data analysed	Factor	<i>n</i>	<i>F</i> (χ^2)	<i>P</i>
All	2 families (Fuller 1974)	33	249	<0.001
	5 subfamilies (Fuller 1974) (= Heard & Guckert 1971)	33	67.7	<0.001
	3 subfamilies (Davis & Fuller 1981)	33	(8.6)	<0.05
Without Margaritiferids	4 subfamilies (Fuller 1974) (= Heard & Guckert 1971)	30	0.6	NS
	2 subfamilies (Davis & Fuller 1981)	30	(0.8)	NS

Table 5. Glochidial size and duration of the parasitic stage in day-degrees of Central European species

	Size (mm)	<i>T</i> (°C)	Day degrees	Author
<i>Pseudanodonta complanata</i>	0.34	8	240	Hüby (1988)
		12	180–192	
<i>Anodonta cygnea</i>	0.34	16	304	Claes (1987)
		20	240	
		25	200	
<i>Unio tumidus</i>	0.2	17	544	Maass (1987)
		20.5	410	
<i>Unio pictorum</i>	0.2	17	493	
<i>Margaritifera margaritifera</i>	0.07	8	1600	Own data Hruska (1992)
		15.5–17	1300–1430	

T, temperature at which the experiment was run.

primitive group, which, despite its wide distribution and high phylogenetic age, is of very low diversity (Smith 1980; Chesney *et al.* 1993).

Of the morphological factors, the presence or absence of a hook on the glochidial shell is of particular importance (Table 2). Hooked glochidia are confined to larger size classes (Fig. 4). Presumably the underlying mechanisms must be sought in relation to the point of attachment to the host. Unhooked glochidia attach to the soft tissues of the gills, whereas hooked glochidia frequently attach to fins and scales and therefore have to be more powerful to pierce these tough tissues (Davis & Fuller 1981).

GLOCHIDIAL SIZE AND ECOLOGY

In contrast to the habitat type, whose impact on glochidial size (Table 2) vanishes within taxonomic and morphological units (Table 3), the increase in glochidial size with increasing host range seems to be a true relationship (Tables 2 & 3; Fig 4). This can be attributed to the interplay of the host response and the duration of the parasitic stage. Investigations on the host response show that the host produces specific antibodies against the glochidia some weeks after infection (Arey 1932; Meyers, Millemann & Fustish 1980; Bauer 1987a; Bauer & Vogel 1987; Claes 1987). Large glochidia, which, at the beginning of parasitism are highly developed, are able to complete their metamorphosis into young mussels within a short period

of time (Table 5). They have probably already left the host before a specific immune response is initiated. Therefore, there is little selective pressure to adapt to a particular host taxon and accordingly the host range may be extended. Small glochidia are only poorly developed when they are released by the female mussel (Harms 1907a,b, 1908), which is probably the reason for the long duration of the parasitic stage (Table 5). Hence, it follows that small glochidia are likely to be exposed to the antibodies of the host. In order to minimize this host response they have to adapt very closely to the host. There are some indications that masking (= due to biochemical adaptation the parasite is protected from being recognized by the host as foreign, Sprent 1962) may be an important process in this context (Arey 1932; Baer 1951). It seems reasonable that such a highly specific adaptation can only be achieved for a few closely related host species, i.e. hosts with a very similar protein structure to which the protective mechanism of the glochidia could adapt during evolutionary time and in this way lead to high host specificity.

REPRODUCTIVE STRATEGIES OF THE UNIONOIDEA

Although there is one common type of life cycle for all Unionoidea, the reproductive mode differs considerably. This becomes evident in the variation of such important traits as glochidial size, fertility, host

range, site of attachment to the host and developmental mode (i.e. duration of the parasitic stage, growth on the host). As shown, glochidial size is closely related to all these traits. Thus, the adaptive value of the variation in reproductive parameters is essentially the question of to what degree and through which factors glochidial size is optimized and to what degree it is constrained.

The main constraint discovered so far is the presence or absence of hooks on the glochidial shell (Fig. 4). However, within these two categories, glochidial size can apparently respond freely to selection. Thus, a great deal of the variation of the reproductive mode must be considered as adaptive.

Since there are only few data available on the ecology and life history of Unionoidea, an approach to selective processes acting on this animal group is only possible at a very simplistic level. From this point of view the following forces can be expected to select for small glochidia: (i) the advantage of high fertility, particularly since the chance of glochidia contacting a host are extremely low (Young & Williams 1984a; Hochwald 1988; Bauer 1989; Jansen & Hanson 1991); (ii) the advantage of minimizing the waste of resources by production of unsuccessful glochidia. As most glochidia fail to attach to a host, the waste of resources increases as glochidial size increases, all other factors being equal.

Opposing forces are: (i) the advantage of a broad host range for large glochidia. This advantage may increase the chance of glochidia contacting a suitable host and it will enable the species to live in a variety of habitats, i.e. in habitats with different fish faunas; (ii) the high mortality risk of small glochidia: fish develop immunity to glochidia after a number of previous infections (Arey 1932; Bauer 1987a). Therefore, small glochidia develop mainly on young fish, i.e. fish which have only been infected a few times or not at all. Due to their long parasitic stage they are subject to all mortality factors acting on these young fish. Moreover species with small glochidia will metamorphose into small young mussels which take a long time to grow up. But it is advantageous to reach the adult stage as soon as possible as young mussels are subject to high mortality rates (Young & Williams 1984a), whereas survivorship of adults is high (Negus 1966; Bauer 1987c; Laura, Burch & McArthur 1990). Selection for large young mussels should be particularly intense in habitats where juvenile growth rates are low (Sibly & Calow 1986). This applies for example for *Margaritifera* (Buddensiek 1991) which prefers trout streams poor in nutrients (Murphy 1942; Bauer *et al.* 1992).

All these variables interact to produce a continuum of reproductive strategies. Consider the distribution of glochidial size (Fig. 1). At the upper limit are some *Anodonta* species with a low fecundity and a low host specificity, living in a variety of habitats (Davis & Fuller 1981). Representatives of the opposite strategy are the

Margaritifera species with very small glochidia, a high fecundity and a very restricted host range. Only the subfamily Salmoninae contains suitable hosts for this group (Awakura 1968; Bauer 1987b; Karna & Millemann 1977) and they are restricted to trout streams. The disadvantage of small young mussels is avoided by the growth of glochidia on the host of up to 0.5 mm. Thus, the overwhelming amount of energy required for the young mussel stems from the host, whereas the adult mussel invests very little in a single glochidium. As the distribution of glochidial size indicates (Fig. 1), the majority of species adopt a strategy between these extremes with glochidia between 0.2 and 0.25 mm. To what degree adaptations play a role that promotes the probability of host encounter and infection (Kat 1984) is unknown for most species.

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References

- Arey, L.B. (1932) A microscopical study of glochidial immunity. *Journal of Morphology*, **53**, 367–378.
- Ashmole, N.P. (1971) Sea bird ecology and the marine environment. *Avian Biology*, Vol I (eds D. Farner & J. King), pp. 223–286. Academic Press, New York.
- Awakura, T. (1968) The ecology of parasitic glochidia of the freshwater pearl mussel *Margaritifera laevis*. *Scientific Reports of the Hokkaido Fish Hatchery*, **23**, 1–17.
- Baer, J.G. (1951) *The Ecology of Animal Parasites*. Univ. Illinois Press, Urbana.
- Bauer, G. (1987a) The parasitic stage of the freshwater pearl mussel. II. Susceptibility of brown trout. *Archiv für Hydrobiologie*, Suppl. **76**, 393–402.
- Bauer, G. (1987b) The parasitic stage of the freshwater pearl mussel. III. Host relationships. *Archiv für Hydrobiologie*, Suppl. **76**, 413–423.
- Bauer, G. (1987c) Reproductive strategy of the freshwater pearl mussel. *Journal of Animal Ecology*, **56**, 691–704.
- Bauer, G. (1989) Die bionomische Strategie der Flußperlmuschel. *Biologie in unserer Zeit*, **3**, 69–75.
- Bauer, G. (1992) Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology*, **61**, 425–436.
- Bauer, G., Hochwald, S. & Silkenat, W. (1992) Spatial distribution of freshwater mussels: the role of host fish and metabolic rate. *Freshwater Biology*, **26**, 377–386.
- Bauer, G. & Vogel, C. (1987) The parasitic stage of the freshwater pearl mussel. I. Host response to glochidiosis. *Archiv für Hydrobiologie*, Suppl. **76**, 393–402.
- Begon, M., Harper, J. & Townsend, C.R. (1986) *Ecology*. Blackwell Scientific, Oxford.
- Berrigan, D. (1991) The allometry of egg size and number in insects. *Oikos*, **60**, 313–321.
- Blueweiss, L., Fox, H., Kudzma, V., Nakashima, R.P. & Sams, S. (1978) Relationships between body size and some life history parameters. *Oecologia*, **37**, 257–272.
- Britton, J.C. (1979) *The Freshwater Bivalve Mollusca of the*

- Savannah River Plant*. Academy of Natural Sciences, Philadelphia.
- Brockelman, W.Y. (1975) Competition, the fitness of offspring, and optimal clutch size. *American Naturalist*, **109**, 677–699.
- Buchanan, A.C. (1980) *Mussels of the Meramec River Basin, Missouri*. Missouri Department of Conservation, Jefferson City.
- Buddensiek, V. (1991) *Untersuchungen zu den Aufwuchsbedingungen der Flußperlmuschel Margaritifera margaritifera in ihrer frühen postparasitären Phase*. PhD thesis, Tierärztliche Hochschule Hannover.
- Chesney, H.C.G., Oliver, P.G. & Davis, G.M. (1993) *Margaritifera durrovensis* Phillips, 1928: taxonomic status, ecology and conservation. *Journal of Conchology*, **34**, 267–299.
- Claes, M. (1987) *Untersuchungen zur Entwicklungsbiologie der Teichmuschel Anodonta cygnea*. Ms thesis, Tierärztliche Hochschule Hannover.
- Clarke, A.H. (1973) *The Freshwater Molluscs of Canada*. National Museum of Canada, Ottawa.
- Clarke, A.H. (1981) The freshwater mollusc of the Canadian Interior Basin. *Malacologia*, **13**, 495 pp.
- Davis, G.M. & Fuller, S.L.H. (1981) Genetic relationships among recent Unionacea of North America. *Malacologia*, **20**, 217–253.
- Engel, H. (1990) *Untersuchungen zur Autökologie von Unio crassus in Norddeutschland*. PhD thesis, Tierärztliche Hochschule, Hannover.
- Fuller, S.L.H. (1974) Clams and mussels. *Pollution Ecology of Freshwater Invertebrates* (eds C.W. Hart & S.L.H. Fuller), pp. 215–273. Academic Press, New York.
- Gould, S.J. (1975) On the scaling of tooth size in mammals. *American Zoologist*, **15**, 351–362.
- Hanson, J.M., Mackay, W.C. & Prepas, E.E. (1989) Effect of size selective predation by muskrats on a population of unionid clams. *Journal of Animal Ecology*, **58**, 15–28.
- Harms, W. (1907a) Über die postembryonale Entwicklung von *Anodonta piscinalis*. *Zoologischer Anzeiger*, **31**, 801–814.
- Harms, W. (1907b) Zur Biologie und Entwicklungsgeschichte der Flußperlmuschel. *Zoologischer Anzeiger*, **31**, 814–824.
- Harms, W. (1908) Die postembryonale Entwicklung von *Unio pictorum* und *Unio tumidus*. *Zoologischer Anzeiger*, **32**, 693–703.
- Harvey, P.H. & Keymer, A.E. (1991) Comparing life histories using phylogenies. *Philosophical Transactions of the Royal Society London*, **332**, 31–39.
- Harvey, P.H. & Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press.
- Heard, W.H. (1975) Sexuality and other aspects of reproduction in *Anodonta*. *Malacologia*, **15**, 81–103.
- Heard, W.H. & Guckert, R.H. (1971) A re-evaluation of the recent Unionacea of North America. *Malacologia*, **10**, 333–355.
- Hochwald, S. (1988) *Untersuchungen zur Populationsbiologie und Fortpflanzungsbiologie der Bachmuschel (Unio crassus)*. Ms thesis, Universität Bayreuth.
- Howard, A.D. (1915) Some exceptional cases of breeding among the Unionidae. *Nautilus*, **29**, 4–11.
- Hruska, J. (1992) The freshwater pearl mussel in South Bohemia: Evaluation of the effect of temperature on reproduction, growth and age structure of the population. *Archiv für Hydrobiologie*, **126**, 181–191.
- Hüby, B. (1988) *Zur Entwicklungsbiologie der Fließgewässermuschel Pseudanodonta complanata*. PhD thesis, Tierärztliche Hochschule Hannover.
- Jansen, W.A. & Hanson, J.M. (1991) Estimates of the number of glochidia produced by clams (*Anodonta grandis*) attaching to yellow perch, and surviving to various ages in Narrow Lake, Alberta. *Canadian Journal of Zoology*, **69**, 973–977.
- Kaplan, R.H. & Salthe, S.N. (1979) The allometry of reproduction: an empirical view in salamanders. *American Naturalist*, **113**, 671–689.
- Karna, D.W. & Millemann, R.E. (1977) Glochidiosis of salmonid fishes. III. *Journal of Parasitology*, **63**, 728–733.
- Kat, P.W. (1984) Parasitism and the Unionacea. *Biological Reviews*, **59**, 189–207.
- Laura, G.L., Burch, J.L. & McArthur, J.V. (1990) Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicularia fluminea* and *Elliptio complanata*, in a coastal stream. *Freshwater Biology*, **24**, 409–416.
- Lefevre, G. & Curtis, W. (1912) Studies on the reproduction and artificial propagation of freshwater mussels. *Bulletin of the Bureau of Fisheries*, **756**, 1–190.
- Lloyd, D.G. (1987) Selection of offspring size and other size versus number strategies. *American Naturalist*, **129**, 800–817.
- Maass, S. (1987) *Untersuchungen zur Fortpflanzungsbiologie einheimischer Süßwassermuscheln der Gattung Unio*. PhD thesis, Tierärztliche Hochschule Hannover.
- Meyers, T.R. & Millemann, R.E. (1977) Glochidiosis of salmonid fishes. I. *Journal of Parasitology*, **63**, 728–733.
- Meyers, T.R., Millemann, R.E. & Fustish, C.A. (1980) Glochidiosis of salmonid fishes. IV. Humoral and tissue responses of coho and chinook salmon to experimental infection with *Margaritifera*. *Journal of Parasitology*, **66**, 274–281.
- Murphy, G. (1942) Relationships of the freshwater pearl mussel to trout in the Truckee river. *California Fish and Game*, **28**, 89–102.
- Murphy, M.T. (1989) Life history variability in North American breeding tyrant flycatchers: phylogeny, size or ecology? *Oikos*, **54**, 3–14.
- Nagel, K.O. (1988) *Anatomische, morphologische und biochemische Untersuchungen zur Taxonomie und Systematik der europäischen Unionacea*. PhD thesis, Gesamthochschule Kassel.
- Negus, C.L. (1966) A quantitative study of growth and production of unionid mussels in the river Thames. *Journal of Animal Ecology*, **35**, 513–532.
- Page, M.D. & Harvey P.H. (1988) Recent developments in the analysis of comparative data. *Quarterly Review of Biology*, **62**, 413–440.
- Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size: effects of environmental and maternal phenotype. *American Naturalist*, **128**, 575–592.
- Skorping, A., Read, A.F. & Keymer, A.E. (1991) Life history covariation in intestinal nematodes of mammals. *Oikos*, **60**, 365–372.
- Sibly, R.M. & Calow, P. (1986) *Physiological Ecology of Animals*. Blackwell Scientific Publications, Oxford.
- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.
- Smith, D.G. (1980) Anatomical studies on *Margaritifera margaritifera* and *Cumberlandia monodonta*. *Zoological Journal of the Linnean Society*, **69**, 257–270.
- Smith, D.G. & Wall, W.P. (1984) The Margaritiferidae reinstated: a reply to Davis & Fuller 1981. *Occasional Papers on Molluscs*, **64**, 321–330.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman, San Francisco.
- Sprent, J.F.A. (1962) Parasitism, immunity and evolution. *The Evolution of Living Organisms* (ed. G. W. Leeper), pp. 149–165. Melbourne University Press, Melbourne.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press.

- Surber, T. (1912) *Identification of the Glochidia of Freshwater Mussels*. Bureau of Fisheries Document No. 771. Government Printing Office, Washington.
- Wächtler, K. (1986) Zur Biologie der Flußperlmuschel *Margaritifera margaritifera*. Entwicklung, Gefährdung, Ausichten. *Naturwissenschaften*, **73**, 225–233.
- Wootton, J.T. (1987) The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. *Evolution*, **41**, 732–749.
- Yeager, B.L. & Neves, R.J. (1986) Reproductive cycle and fish hosts of the rabbits foot mussel, *Quadrula cylindrica strigillata* in the upper Tennessee river drainage. *American Midland Naturalist*, **116**, 329–340.
- Yokley, P. (1972) Life history of *Pleurobema cordatum*. *Malacologia*, **11**, 351–364.
- Young, M. & Williams, J. (1984a) The reproductive biology of the freshwater pearl mussel in Scotland. I. Field studies. *Archiv für Hydrobiologie*, **99**, 405–422.
- Young, M. & Williams, J. (1984b) The reproductive biology of the freshwater pearl mussel in Scotland. II. Laboratory studies. *Archiv für Hydrobiologie*, **100**, 29–43.
- Zale, A.L. & Neves, R. (1982) Reproductive biology of four freshwater mussel species in Virginia. *Freshwater Invertebrate Biology*, **51**, 17–28.

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Appendix

Life history data used to investigate the impact of phylogeny, morphology and ecology on glochidial size. European species are marked by*. Data on *Margaritifera laevis* are from a Japanese population, the remaining species occur in North America. The taxonomy is according to Fuller (1974). Four marsupia = Margaritiferidae and Ambleminae; two marsupia = Unioninae and Anodontinae; two marsupia at the posterior part of outer demibranchs = Lampsilinae; —, no records

Species	1 = long-term breeder 2 = short-term breeder	1 = with hook 2 = without hook	Habitat 1 = running waters 2 = standing waters 3 = generalist	Host range n fish-families	Glochidial-size (mm)	Source†
Margaritiferidae						
<i>Margaritifera margaritifera</i> *	2	2	1	1	0.07	20
<i>Margaritifera laevis</i>	2	2	1	1	0.08	4
<i>Margaritifera falcata</i>	2	2	1	1	0.07	9
<i>Cumberlandia monodonta</i>	—	2	1	—	0.055	3
Unionidae						
Ambleminae						
<i>Amblema plicata</i>	1	2	3	7	0.2	2, 11, 6
<i>Fusconaia ebena</i>	1	2	3	2	0.15	2
<i>Fusconaia flava</i>	1	2	1	—	0.15	7
<i>Quadrula metanerva</i>	2	2	1	2	0.175	2, 11, 6
<i>Quadrula pustulosa</i>	2	2	3	3	0.23	2, 11, 6, 1
<i>Quadrula quadrula</i>	2	2	1	1	0.078	7, 12
<i>Quadrula cylindrica</i>	2	2	1	1	0.22	11, 14
<i>Quadrula granifera</i>	2	2	—	—	0.29	2
<i>Quadrula heros</i>	2	2	—	—	0.26	2
<i>Quadrula solida</i>	2	2	—	—	0.16	2
<i>Quadrula trigona</i>	2	2	—	—	0.16	2
<i>Potamida litoralis</i> *	—	2	3	—	0.21	19
<i>Cyclonajas tuberculata</i>	2	2	1	—	0.27	12
Unioninae						
<i>Elliptio complanata</i>	2	2	3	1	0.2	10
<i>Elliptio icterina</i>	2	2	3	—	0.2	10
<i>Elliptio dilatata</i>	2	2	3	4	0.2	12
<i>Pleurobema cordatum</i>	2	2	1	2	0.14	11, 6, 5
<i>Pleurobema coccineum</i>	2	2	3	—	0.15	11
<i>Unio crassus</i> *	2	1	1	3	0.2	19, 18
<i>Unio pictorum</i> *	2	1	3	3	0.22	19, 16
<i>Unio tumidus</i> *	2	1	3	2	0.21	19, 16
<i>Unio gibbosus</i>	2	1	—	—	0.2	1
Anodontinae						
<i>Anodonta cataracta</i>	2	1	3	—	0.36	1
<i>Anodonta corpulenta</i>	—	1	—	—	0.35	2
<i>Anodonta gibbosus</i>	2	1	—	—	0.378	8
<i>Anodonta couperiana</i>	2	1	2	—	0.294	8
<i>Anodonta kennerlyi</i>	1	1	3	—	0.3	12
<i>Anodonta pegyae</i>	2	1	3	—	0.261	8
<i>Anodonta imbecillis</i>	1	1	2	2	0.23	8, 6
<i>Anodonta beringiana</i>	—	1	3	2	0.29	8
<i>Anodonta cygnea</i> *	1	1	2	7	0.35	19, 15
<i>Anodonta woodiana calipyos</i>	—	1	—	—	0.3	8
<i>Anodonta piscinalis</i> *	1	1	3	—	0.34	19
<i>Anodonta woodiana lauta</i>	—	1	—	—	0.29	8

Appendix (continued)

Species	1 = long-term breeder 2 = short-term breeder	1 = with hook 2 = without hook	Habitat 1 = running waters 2 = standing waters 3 = generalist	Host range n fish-families	Glochidial-size (mm)	Source†
<i>Anodontinae (continued)</i>						
<i>Anodonta grandis</i>	1	1	3	9	0.41	2, 6
<i>Anodonta grandis simpsoni</i>	1	1	3	—	0.35	7
<i>Anodonta hallenbeckii</i>	—	1	—	—	0.28	8
<i>Anodonta japonica</i>	—	1	—	—	0.26	8
<i>Alasmidonta calceola</i>	1	1	—	—	0.3	2
<i>Alasmidonta viridis</i>	1	1	3	2	0.3	12
<i>Alasmidonta marginata</i>	1	1	1	—	0.34	12
<i>Anodontoides ferrussacianus</i>	1	1	3	2	0.32	7, 12
<i>Arcidens confragosus</i>	1	1	2	4	0.355	2, 11, 6
<i>Lasmigona complanata</i>	1	1	3	3	0.29	2, 11, 6
<i>Lasmigona costata</i>	1	1	3	—	0.36	1
<i>Lasmigona compressa</i>	1	1	1	—	0.35	2, 7
<i>Pseudanodonta complanata*</i>	1	1	1	3	0.34	17
<i>Strophitus edentulus</i>	1	1	3	—	0.35	2
<i>Lampsilinae</i>						
<i>Lampsilis anodontoides</i>	1	2	3	1	0.18	2, 11, 6
<i>Lampsilis ligamentina</i>	1	2	—	—	0.22	2
<i>Lampsilis luteola</i>	1	2	—	—	0.25	2
<i>Lampsilis iris</i>	1	2	—	—	0.24	2
<i>Lampsilis capax</i>	1	1	—	—	0.15	2
<i>Lampsilis fasciola</i>	1	2	—	—	0.24	13
<i>Lampsilis fallaciosa</i>	1	2	—	—	0.2	2
<i>Lampsilis higginsii</i>	1	2	—	—	0.21	2
<i>Lampsilis trabalis</i>	1	2	—	—	0.19	2
<i>Lampsilis ovata</i>	1	2	3	3	0.25	7
<i>Lampsilis gracilis</i>	1	2	—	—	0.07	1
<i>Lampsilis radiata siliquoidea</i>	1	2	3	3	0.25	7
<i>Leptodes fragilis</i>	1	2	3	1	0.08	6
<i>Ligumia subrostrata</i>	1	2	—	—	0.27	11
<i>Ligumia recta</i>	1	2	3	—	0.23	1, 6, 7
<i>Villosa nebulosa</i>	1	2	1	2	0.2	13
<i>Villosa vanuxemi</i>	1	2	1	1	0.21	13
<i>Villosa fabalis</i>	1	2	1	—	0.17	12
<i>Villosa iris</i>	1	2	3	—	0.23	12
<i>Modiolus conradicus</i>	1	2	—	—	0.22	13
<i>Obovaria olivaria</i>	1	2	1	2	0.18	12
<i>Obovaria subrotunda</i>	1	2	3	—	0.2	12
<i>Truncilla donaciformis</i>	1	2	—	2	0.06	2, 6
<i>Plagiola elegans</i>	1	2	—	—	0.06	2
<i>Plagiola securis</i>	1	2	—	—	0.31	2
<i>Proptera laevissima</i>	1	2	—	2	0.1	2
<i>Proptera alata</i>	2	1	1	—	0.22	7
<i>Dromus dromus</i>	1	2	—	—	0.19	2
<i>Actinonaias carinata</i>	1	2	1	—	0.22	12

†Sources: 1, Lefèvre & Curtis 1912; 2, Surber 1912; 3, Howard 1915; 4, Awakura 1968; 5, Yokley 1972; 6, Fuller 1974; 7, Clarke 1973; 8, Heard 1975; 9, Karna & Milleman 1977; 10, Britton 1979; 11, Buchanan 1980; 12, Clarke 1981; 13, Zale & Neves 1982; 14, Yeager & Neves 1986; 15, Claes 1987; 16, Maass 1987; 17, Hüby 1988; 18, Hochwald 1988; 19, Nagel 1988; 20, Bauer 1987b.