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PARASITISM AND THE UNIONACEA (BIVALVIA)

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CONTENTS

I. INTRODUCTION

The way organisms reproduce and disperse can have profound effects on genetic structure and demographic processes of populations (Emlen, 1973; Endler, 1977; Gaines & McClenaghan, 1980; Grant, 1981). Similarly, mode of reproduction and dispersal can play a major role in species longevity, geographic distribution, and rate of speciation (Mayr, 1971; Jackson, 1974; Stanley, 1975, 1979; Hansen, 1978, 1983). Freshwater bivalves of the superfamily Unionacea incorporate a parasitic stage in the life-cycle which involves an obligate relationship between a vertebrate host, usually a fish, and a highly modified larva, the glochidium. This parasitism is atypical, not only in that the Unionacea are the only members of the Class Bivalvia that are known to produce an obligate parasitic larva, but also in that these unionids are one of the few groups of parasitic organisms in which the larvae alone are parastic while the adults are free-living. This parasitic mode of reproduction appears to us to have had far-reaching consequences for morphological stasis, levels of phenotypic variability within a species, extent of species' geographic ranges, and rates of speciation among the unionids.

North American unionacean bivalves have undergone one of the most dramatic radiations encountered among freshwater invertebrates. Recent systematic descriptions recognize about 50 nominal genera and over 225 species and subspecies (Burch, 1975; Davis & Fuller, 1981). These bivalves are distributed over eight faunal regions, of which the Interior Basin (essentially the entire Mississippi River drainage) is by far the most diverse (Van der Schalie & Van der Schalie, 1950; Johnson, 1970). This radiation appears to involve mainly young taxa: old genera such as *Margaritifera* and *Anodonta* (Upper Cretaceous) contain rather few widely distributed species, while the species-rich

North American genera seem to be of Pliocene and Pleistocene origin (LaRoque, 1966; Haas, 1969; Davis *et al.*, 1981).

Despite the diversity and abundance of unionacean bivalves in freshwater communities, they remain among the least understood of benthic macro-invertebrates, even with regard to such basic life-history attributes as reproduction, development, dispersal, competition, and habitat selection. It is perhaps due to limited realization of the important consequences of their parasitic mode of reproduction that the basic biology of these bivalves remains poorly understood. Here I summarize the pertinent data dealing with various aspects of parasitism among mainly the North American Unionacea, and compare their reproductive and dispersive strategies to those practised by more thoroughly investigated parasites, as well as plants.

II. GLOCHIDIA AND HOSTS

(1) *The glochidium*

Glochidia develop from fertilized eggs which are maintained in variably modified gill brood-pouches of female (and hermaphroditic) unionaceans. When mature, the glochidium consists of two thin hinged valves which are drawn together by a single adductor muscle, and which enclose mantle cells, some supplied with sensory hairs (Fig. 1) (Arey, 1924; Wood, 1974a). Glochidia of bivalves of the genera *Unio*, *Anodonta*, and some endemic North American genera such as *Megalonaias* and *Quadrula* (see Table 1 for a classification of the genera mentioned in the text) additionally possess a long, thread-like structure which usually projects from specially modified cells at the centre of the mantle cavity, and which could have the dual function of a sensory and an attachment structure (Wood, 1974a). Glochidia are diverse in size, ranging from a minimum length of about 0·05 mm in *Margaritifera* to a maximum of about 0·4 mm in *Anodonta* (Baker, 1928). In terms of shape, glochidia are separable into three main types (see Fig. 2a–c).

(a) *Hooked.* These glochidia are characterized by possession of a well-developed hook-shaped, hinged projection at the ventral margin of each triangular-shaped valve. Each hook, or stylet, is additionally equipped with a series of smaller spines; these structures are thus highly adapted to pierce and secure attachment to the skin, scales, or fins of the host. Hooked glochidia are generally among the largest of the three types, and usually attach to the exterior and exposed parts of the fish host. They are characteristic of the unionid subfamily Anodontinae.

(b) *Hookless.* This category is composed of glochidia of most North American species. The glochidia are generally characterized by a rounded to subelliptical shape, and vary greatly in size. The ventral margin is usually rounded, and, while not equipped with stylets, is often reinforced and can bear a number of microstylets. Glochidia of this type are usually parasitic on the gill filaments of the host, but can attach to fins as well.

(c) *Axe-head.* Glochidia of this type are distinguished by a flaring ventral margin which gives them their characteristic shape. Axe-head glochidia are only known in species of the North American genus *Proptera*, and, while they seem most closely related to the hookless type, can exhibit four hooklike prongs, one at each corner of the shell (Coker *et al.*, 1921; Baker, 1928). Where these glochidia attach on the host is not known.
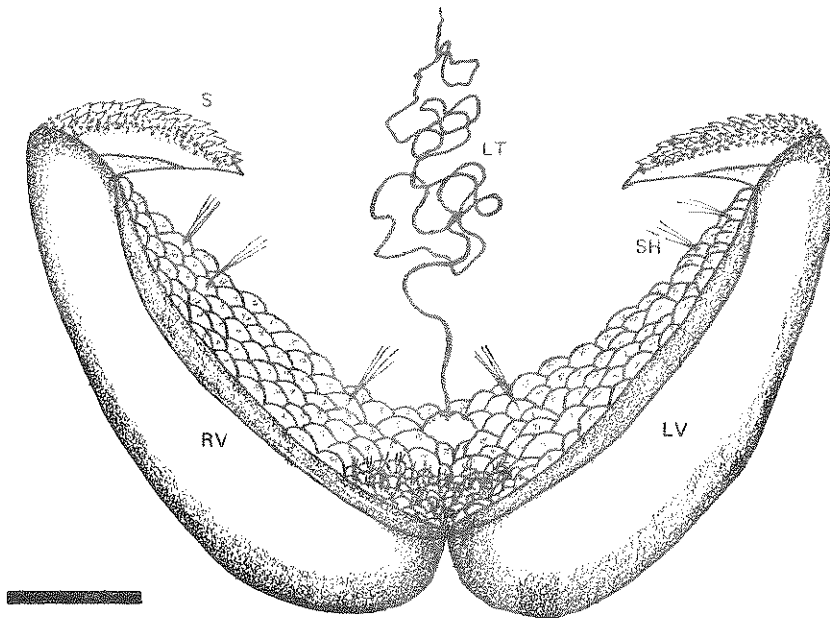
Fig. 1. Mature glochidium of *Anodonta cygnea*. LT = larval thread, LV = left valve, RV = right valve, S = stylet, SH = sensory hairs on the mantle cells (after Wood, 1974a). Scale bar = 50 μm.

Table 1. *Classification of the genera mentioned in the text; classification principally according to Davis & Fuller (1981), number of species in each genus according to Burch (1975)*

Unionacea
  Margaritiferidae
       Margaritifera (3 species)*
  Unionidae
    Anodontinae
         Anodonta (14 species)*
         Alasmidonta (11 species)
         Strophitus (2 species)
         Lasmigona (5 species)
         Simpsoniconcha (1 species)
    Ambleminae
      Lampsilini
        Lampsilis (21 species)
        Proptera (3 species)
        Cyprogenia (2 species)
        Actinonaias (3 species)
        Obliquaria (1 species)
        Leptodea (4 species)
      Pleurobemini
        Elliptio (19 species)†
        Pleurobema (32 species)†
      Amblemini
        Quadrula (9 species)
        Megalonaias (1 species)

* North American species only.   † Apparently radiating genera with problematic taxonomy.
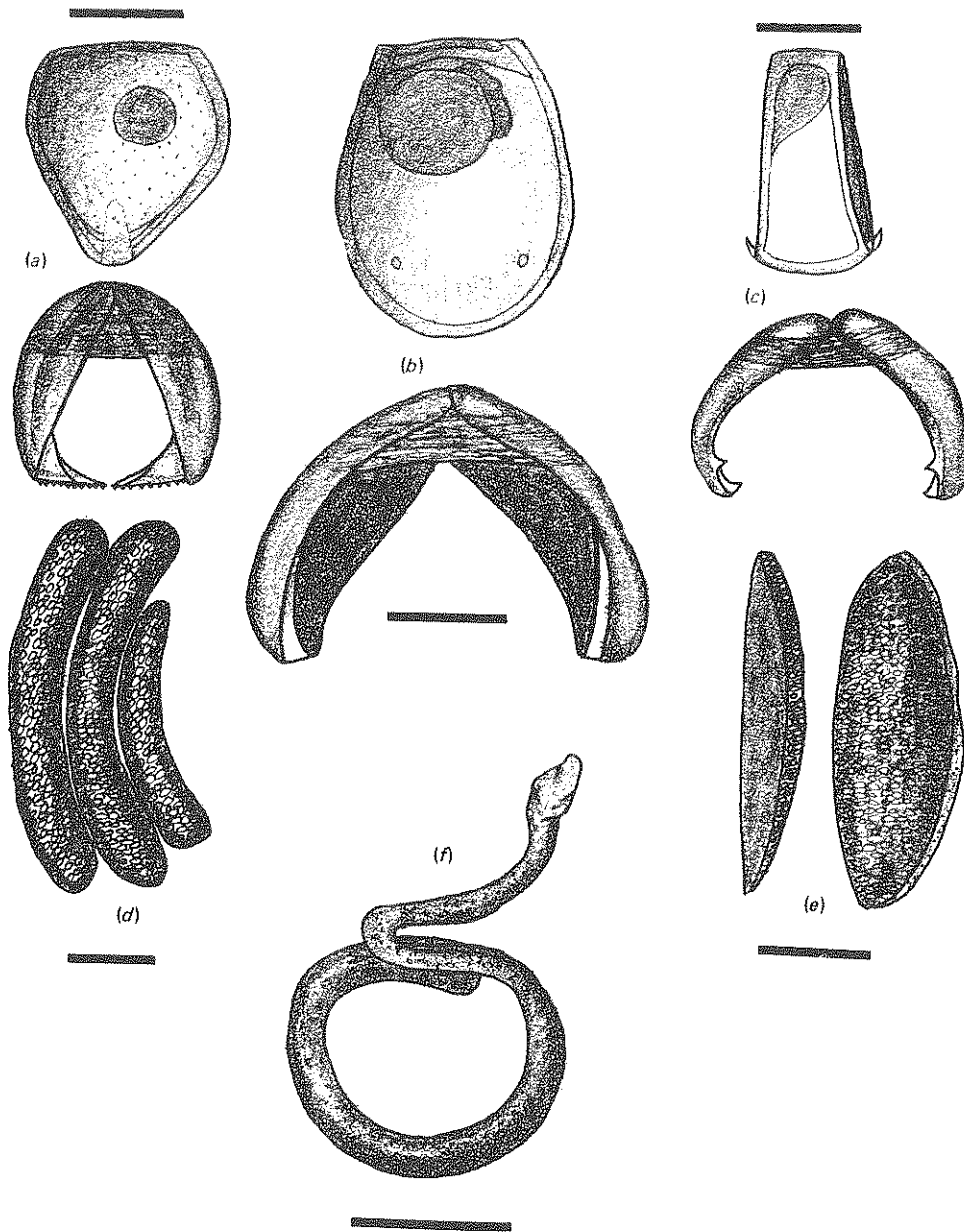
Fig. 2. Glochidia and glochidial conglutinates of various unionid species. (a) Top and side views of a hooked glochidium of *Lasmigona costata*, scale bar = 0·2 mm. (b) Top and side views of a hookless glochidium of *Elliptio complanata*, scale bar = 0·1 mm. (c) Top and side views of an axe-head glochidium of *Proptera alata*, scale bar = 0·1 mm. (d) Conglutinates of *Obliquaria reflexa*, scale bar = 2 cm. (e) Conglutinates of *Actinonaias carinata*, scale bar = 3 cm. (f) Conglutinate of *Cyprogenia alberti*, scale bar = 0·5 cm (a, c, d and e after Coker et al., 1921; f after Chamberlain, 1934).

(2) *Brood pouches*

As mentioned above, the glochidia are maintained within variably modified brood pouches within the gills of the unionaceans. The simplest condition is encountered in the genus *Margaritifera* in which all four demibranchs are marsupial, and lamellae are separated by randomly arranged trunks of intralamellar connective tissue (Davis & Fuller, 1981). This tetragenous condition seems to have become progressively modified by increasing the number and organization of the intralamellar connectives, by restricting the marsupium to the outer pair of gills (ectobranchous and homogenous), and by further restricting the marsupium to the basal region (longenous, ptycho-branchous), the middle region (mesogenous), and the posterior region (heterogenous) of the outer demibranchs (Davis & Fuller, 1981). Concomitant with this reduction of marsupial size is a reduction of the number of glochidia contained in the marsupium. For example, a homogenous anodontine such as *Leptodea fragilis* was estimated to contain 2225000 glochidia within its demibranchs, while a heterogenous lampsiline, *Lampsilis siliquoidea*, held about 129000 glochidia; Coker *et al.* (1921) mention that the number of glochidia varies in different species from about 75000 to 3000000. A reduction in the number of glochidia might at first seem counterproductive to chances of successfully infecting the host, but, as with most parasitic organisms, this reduction is often accompanied by adaptations that promote the probability of host encounter and infection (see below).

It is necessary to point out that modification of the gills into marsupia, and retention of larvae through various stages of development, is not restricted to unionacean bivalves. A review of brood protection is presented by Sellmer (1967), who reached two main conclusions, as follows.

(1) Some form of brood protection has arisen repeatedly and independently among the Bivalvia, including the freshwater family Sphaeriidae.

(2) By far the largest percentage of incubatory bivalves are less than $\frac{1}{2}$ inch long, and brood protection was proposed by Sellmer (1967) to be a reproductive strategy that enhances survival of a few offspring by releasing them at an advanced stage of development, which is especially critical among small bivalves which are physiologically constrained as to the number of eggs they can produce. Clearly, unionaceans do not fall in this second category, not only because of their large adult size, but also because of the large number of larvae present in the marsupium. Thus, while unionaceans exhibit similarities to other bivalves with respect to incubation of larvae, this adaptation is likely the result of an entirely different set of selective forces.

(3) *Release of glochidia*

Unionaceans can be divided into two categories according to the length of time glochidia are maintained within the brood pouches. Long-term breeders (bradytictic) generally reproduce during the middle and latter parts of the summer, glochidia develop during the autumn and early winter, and are not released from the marsupia until the following spring and early summer. Coker *et al.* (1921) noted that considerable variability can exist within a bradytictic population as to timing of release of glochidia. Short-term breeders (tachytictic) compress the entire reproductive cycle into a roughly 5-month period from April to August, and usually release their glochidia later than the

bradytictic group. Members of the genus *Margaritifera* seem unique in that they can complete two reproductive cycles, releasing glochidia in March and August (Wood, 1974*b*). With respect to bradytictic breeders, experiments indicate that, while glochidia removed from the marsupia during autumn (when they have just matured) can be induced to attach to fish hosts and metamorphose, they require a longer period of parasitism than glochidia which are released the following spring (Corwin, 1920; Coker *et al.*, 1921; Tucker, 1928). Trdan & Hoeh (1982) have proposed that differences in timing of glochidial release among sympatric unionacean species could have resulted from competitive interactions among such unionaceans for a limited number of hosts: the same host is used sequentially by different unionaceans with sequential release times. However, timing of glochidial release can also be a critical factor determining probability of host infection (see below).

Discharge of glochidia occurs in several different ways, which reflect to a certain extent various adaptations involved in either attracting the fish host and/or increasing the probability of attachment (see below). In most species, the glochidia pass from the marsupia into the suprabranchial canal, and are discharged through the excurrent siphon. When released in this fashion, the glochidia are more or less bound together by mucus, which either dissolves soon after their discharge, or maintains the glochidia within so-called conglutinates (Fig. 2*d–f*) which are variously shaped and coloured (Ortmann, 1910; Arey, 1924; Baker, 1928). Glochidia that possess larval threads are usually extruded in tangled masses which form loosely organized webs (Wood, 1974*b*). Among the lampsilines, glochidia are discharged in irregular masses through special holes at the base of the brood pouches, and are released through the incurrent siphon by rapid adduction of the shell valves (Ortmann, 1910; Baker, 1928).

When glochidia are expelled from the brood pouch, further development is contingent upon attachment to a suitable host. Telda & Fernando (1969) determined that survival in the absence of a fish host was temperature-dependent, but that less than 1% of the glochidia of *Lampsilis radiata* survived longer than 36 h at 20 °C, 144 h at 12 °C, and 216 h at 10 °C. In terms of prevailing temperatures at the time of release, Telda & Fernando (1969) estimated that glochidia would remain competent to attach to fish hosts for a period of about 2 days after discharge. Personal observations on expelled conglutinates in aquaria indicate that glochidia are highly susceptible to attack by a variety of microorganisms, presumably attracted by the mucus that surrounds them, thus further limiting survival time when not attached to a host.

Three species (*Anodonta imbecilis*, *Strophitus undulatus*, and *Obliquaria reflexa*) have been described as completing metamorphosis within the marsupium, thus bypassing the parasitic stage entirely (Lefevre & Curtis, 1911, 1912; Howard, 1914). Lefevre & Curtis (1912) and Howard (1914) postulated that components of the mucus in which the glochidia are embedded can serve as nourishment for the glochidia, which are not expelled until they have reached a juvenile stage. However, these observations have not been duplicated (e.g. Tucker, 1927), and both *A. imbecilis* and *S. undulatus* glochidia are known to parasitize a number of hosts (Fuller, 1974; Trdan & Hoeh, 1982). Tucker (1927) hypothesized that the facultative parasitism exhibited by *A. imbecilis* could be a response to environmental conditions, but this remains to be ascertained.

Table 2. *Fish hosts, number of unionid parasites, and host diet (unionid data from Fuller, 1974; diet data from Hynes, 1970; Ney, 1978; and Townsend, 1939)*

Fish host	No. of unionid species	Host diet*
Pomoxis annularis (white crappie)	17	I, L, C, F
Lepomis macrochirus (bluegill)	13	I, C, F
Micropterus salmoides (largemouth bass)	12	I, F
Lepomis cyanellus (green sunfish)	12	I, F
Stizostedion canadense (sauger)	12	I, F
Aplodinotus grunniens (drum)	11	I, C, M
Pomoxis nigromaculatus (black crappie)	10	I, L. F
Ambloplites rupestris (rock bass)	6	I, F, C
Perca flavescens (yellow perch)	6	I, F, C, M

* I = insects, L = insect larvae, C = crustaceans, F = fishes, M = molluscs.

(4) Hosts

With the exception of *Simpsoniconcha ambigua*, which parasitizes a salamander (*Necturus maculosus*: Howard, 1951), all unionids and margaritiferids are parasitic on fishes. While a large variety of fish are parasitized, examination of lists of hosts such as those provided by Coker *et al.* (1921) and Fuller (1974) reveals that some groups, such as the centrarchids (sunfishes, basses), serve disproportionately as hosts. For example, the white crappie (*Pomoxis annularis*) hosts 17 species of glochidia, the largemouth bass (*Micropterus salmoides*) hosts 13, the bluegill (*Lepomis macrochirus*) and the green sunfish (*L. cyanellus*) host 13 and 12 species, respectively, and the black crappie (*P. nigromaculatus*) serves as host for ten species. Other species of fish which are not included in the Centrarchidae but which host similarly large numbers of glochidia are the sauger (*Stizostedion canadense*) with 12, the drum (*Aplodinotus grunniens*) with 11, and the yellow perch (*Perca flavescens*) with six. It is important to point out that these numbers should be considered minima, since they largely represent host species for the unionaceans of commerical interest examined by the U.S. Bureau of Fisheries Laboratory at Fairport, Iowa. Host identity is not known for by far the largest percentage of North American unionaceans.

Why certain fish are much more heavily parasitized with respect to numbers of unionacean species becomes clear with an examination of both host diet and behaviour. Much has been made of the relationship between molluscivorous fish and their unionacean prey. Fuller (1974) termed the interaction 'mutualistic at worst' since such fish as the drum and catfish can become heavily infested when feeding on larvigerous females, thereby "unwittingly propagating their food supply" (Coker *et al.*, 1921; Townsend, 1939). Yet an examination of three species of sunfish, for example, reveals a pattern of glochidial infestation that is opposite from that predicted by diet (Sadzikowski & Wallace, 1976); the molluscivorous pumpkinseed (*Lepomis gibbosus*) only serves as host to two unionid species according to Fuller (1974), while the largely vegetarian and insectivorous bluegill and green sunfish host 13 and 12 species, respectively. In fact, the five most commonly parasitized fish are omnivorous, insectivorous, and piscivorous rather than molluscivorous (Table 2). This apparent contradiction will be pursued further below.

The intensity of infection of hosts by unionacean larvae is generally low (Evermann & Clark, 1918; Coker *et al.*, 1921; Wiles, 1975; Dartnall & Walkey, 1977; Trdan, 1981). For example, a survey of seven hosts of *Lampsilis radiata siliquoidea* by Trdan (1981) indicated both a low incidence of infection among the hosts (average 8% of host fish surveyed) and a low intensity of infection of those hosts parasitized (average of 13 glochidia/host). However, data collected by Surber (1912), Coker *et al.* (1921), Telda & Fernando (1969), and Dartnell & Walkey (1979) indicate that some host populations can exhibit 100% infection, and that an individual host can be infected by almost 4000 glochidia. Trdan (1981) proposed that such high infections result from high levels of host specificity, necessitating concentration of glochidia on the available hosts. Also, factors such as relative unionacean and fish population densities, and levels of host immunity (Fustish & Milleman, 1978; Meyers *et al.*, 1980) should be considered as contributing to these rates of infection.

(5) *Glochidial attachment*

Glochidia are remarkably unselective in attachment. Tactile stimuli from pieces of paper, slivers of wood, hairs, and pieces of plastic are sufficient to induce such attachment (Arey, 1921; Coker *et al.*, 1921; Wood, 1974*b*), but chemical stimuli are required to prolong the attachment until the host tissue encysts the glochidium by epithelial proliferation (Arey, 1921; Heard & Hendrix, 1964; Lukasovics & Labos, 1965; Telda & Fernando, 1969; Wood, 1974*b*). Glochidia that do not receive these chemical cues after attachment can release themselves (e.g. Wood, 1974*b*), but this is not always possible if attachment occurs on a fish species that does not serve as its host. Glochidia seem to be incapable of selecting the proper host; when presented with a number of suitable and unsuitable hosts, the degree of infestation is not significantly different, but all unsuitable hosts will slough off glochidia after a period of 4–7 days (Davenport & Warmuth, 1965; Telda & Fernando, 1969; Fustish & Milleman, 1978). The reaction of the host to the parasite could be an important factor in the determination of specificity of these bivalves and other host–parasite systems (e.g. Baer, 1951; James, 1971; Kennedy, 1975). This becomes especially apparent when closely related hosts such as the basses *Roccus americanus* and *R. chrysops*, and the salmon *Onchorhynchus kisutch* and *O. tshawytscha* exhibit drastically different reactions to glochidia of the same bivalve species (Telda & Fernando, 1969; Fustish & Milleman, 1978).

Glochidia, once attached to the host, become encysted within 20–36 h (Arey, 1921; Coker *et al.*, 1921; Tucker, 1927), or as soon as 2–3 h after attachment (Telda & Fernando, 1969). During encystment, glochidia grow to varying extents, ranging from a sevenfold increase for the tiny glochidia of *Margaritifera margaritifera* (Murphy, 1942) to no increase for glochidia of *Elliptio complanata* and *Lampsilis radiata* (Matteson, 1948; Telda & Fernando, 1969). Metamorphosis is completed after a period ranging from 6 days to 6 months, depending in the species and temperatures during development (Young, 1911; Howard, 1914; Coker *et al.*, 1921; Tucker, 1927; Telda & Fernando, 1969; Dartnall & Walkey, 1979; Trdan & Hoeh, 1982). How the glochidium breaks out of its cysts after metamorphosis is not yet fully understood (e.g. Telda & Fernando, 1969), although Arey (1932) ascribes it to some activity of the metamorphosed glochidium itself. Shedding of glochidia can occur over a short period of time (Murphy, 1942; Matteson, 1948) or a long one (Telda & Fernando, 1969).

III. UNIONIDS AS PARASITES

One of the most fundamental aspects of any host–parasite system involves the ability of the parasite to make contact with the host, and, in the cases of narrow specificity, the degree of certainty with which the suitable host can be infected. As can be expected from such a diverse group, North American unionaceans exhibit a wide variety of adaptations which promote both the probability of contact as well as the probability of contact with the correct host. Perhaps among the least specialized adaptations are those that only involve synchronization of the timing of reproduction to correspond to availability of the host.

Freshwater fish often have predictable cycles of migration and behaviour, which involve movements from deep to shallow water in lakes, spawning migrations during the spring, aggregational behaviour during reproductive periods, and movement of anadromous hosts such as the salmon into fresh water (Hynes, 1970). The best-documented relationship involving critical timing of release of glochidia involves *Anodonta implicata* and its anadromous host, the alewife (*Alosa pseudoharengus*). Alewives spend a relatively short period of time in fresh water, but the reproductive and developmental cycles of *A. implicata* are so well synchronized with the spawning run that the species can infect, metamorphose, and drop off the host before it leaves the freshwater habitat (Davenport & Warmuth, 1965). As another example of synchronization, many tachytictic unionacean species time release of glochidia to correspond with nesting behaviour of the host, during which time the host becomes highly territorial (e.g. Hynes, 1970; Gross & Nowell, 1980) and thereby very predictable in its presence. My own observations in rivers during the nesting period indicate that nests are often constructed in sand patches within a unionacean community, thereby rendering both the fish and its offspring highly susceptible to infestation. Also, the mode of nest construction and maintenance, which involves displacement of sediment with fins, is likely to promote attachment of glochidia lying on the sediment surface. The high rate of infestation of fishes that exhibit nesting behaviour, such as the centrarchids, is thus far from accidental. Such examples of timing of reproduction and release of infectious stages to correspond with periods of high host density and/or predictable behaviour of hosts are common among other host–parasite systems as well (Hawking, 1975; Kennedy, 1975, 1976; Holmes, 1976).

Another adaptation unionaceans frequently exhibit which promotes probability of host contact involves mimicry of food items. The first such adaptation involves various modifications of the glochidial conglutinates to resemble food items of the host such as worms, leeches and grubs (Fig. 1 *d*, *e*). Perhaps the most most remarkable example was described by Chamberlain (1934) for *Cyprogenia alberti*. The marsupium of this species is highly curved, and, when gravid, contains bright red, wormlike conglutinates (complete with a slightly bulbous head region, see Fig. 1 *f*) which vary in length from about 2 to 5 cm. These conglutinates are partially extruded from the excurrent siphon and were readily ingested by fish, all of which were noted to have been infected on the gills shortly after this meal (Chamberlain, 1934). Members of the genera *Elliptio*, *Lampsilis*, and *Pleurobema* release conglutinates that resemble leeches and flatworms (my observations), which not surprisingly constitute a major portion of the diet of such hosts as the yellow perch and the white crappie (Allen, 1935; Townsend, 1939; Ney,
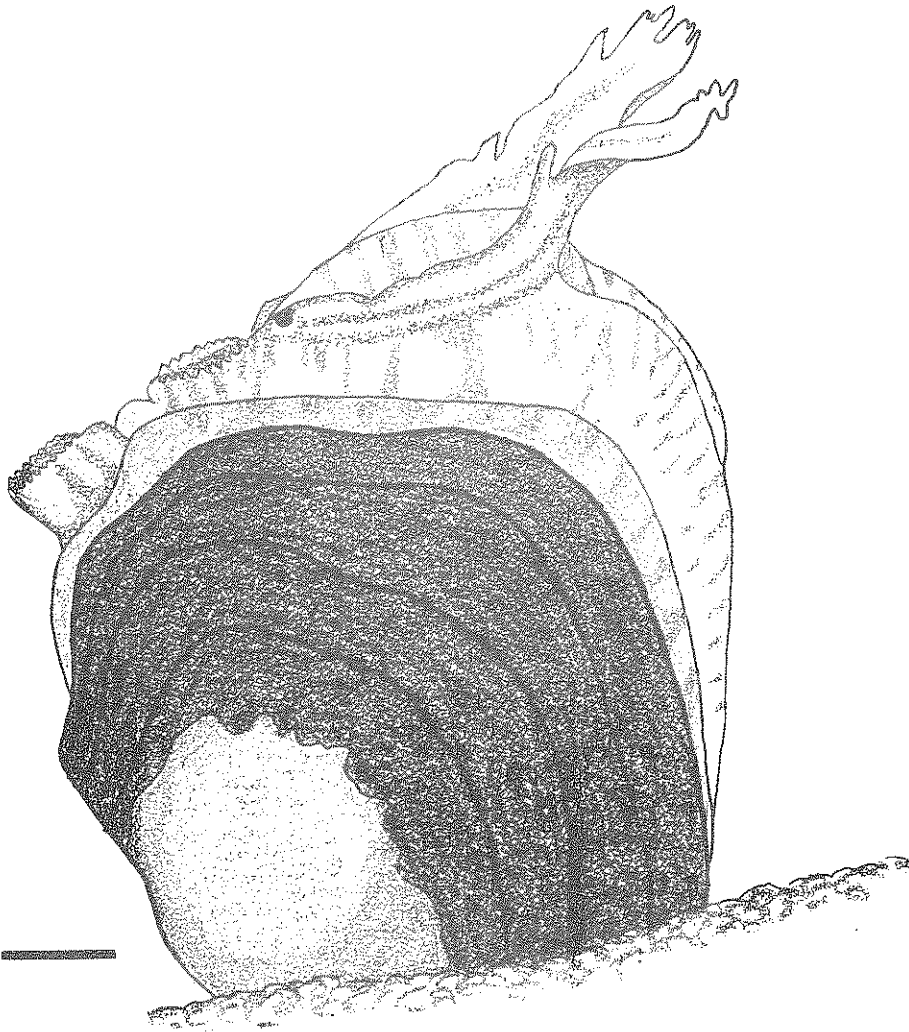
Fig. 3. Highly modified mantle edge of a female *Lampsilis ventricosa* which exhibits a fish-like lure
complete with eye spot and tail. Scale bar = 1 cm (after Kraemer, 1970).

1978). A related adaptation involves a variety of modifications of the mantle edge below
the incurrent siphon to act as lures for the host. This adaptation is almost entirely
restricted to the Lampsilini, which exhibit modifications of this mantle flap, ranging
from a rather simple highly coloured patch in *Lampsilis radiata* to the complex structure
of *L. ventricosa* which closely resembles a small fish complete with eye spots and a tail
(Fig. 3; see Kraemer, 1970, 1979). Gravid lampsiline females further exhibit a
particular behaviour, which involves exposure of the shell well above the substrate and
prolonged pulsations of the mantle edges, which Kraemer (1970) assumed to both attract
the fish host and keep the glochidia suspended once released. Again, there is a good
correlation between this type of mimicry and host diet; five of the six known hosts of
L. ventricosa, for example, are largely piscivorous.

Other adaptations that promote host contact involve the release of glochidia within mucilaginous networks which remain suspended in the water above the bivalve (Matteson, 1948; Yokley, 1972), and release of glochidia which remain infective for long periods of time; for example, Murphy (1942) was able to keep glochidia of *Margaritifera falcata* alive for 11 days at 11 °C outside the marsupium.

Despite these adaptations, host specificity among unionaceans seems to be rather low. For example, the 43 unionid and margaritiferid species listed by Fuller (1974) parasitize an average of 4·5 fish hosts each; one species, *Anodonta grandis*, parasitizes over 30, and the host list seems to grow with each detailed observation (e.g. Trdan & Hoeh, 1982). In contrast, narrow specificity seems to be fairly widespread among parasites, presumably as a result of a history of coevolution between the parasite and its host (Kennedy, 1975; Waage, 1979; Fox & Morrow, 1981; Thompson, 1982). For example, Janzen (1980) found that, of 110 species of beetle larvae, almost all (83 spp.) fed on seeds of only one plant, and that only four species utilized more than four hosts (see also Price, 1980, for other examples of extreme host specialization). Narrow specificity can entail associated costs, however, since it often restricts the geographic range of the parasite and can be especially costly if unsuitable hosts are encountered frequently.

Low host specificity among unionaceans could be the result of an inability to predict the exact identity of the fish attracted to the various lures, which is highly likely considering the catholic nature of freshwater fish diets. Such long host lists apparently do not result from summations of hosts over locally specialized populations (see Fox & Morrow, 1981; Thompson, 1982): Trdan & Hoeh (1982) found that two populations of *A. grandis* naturally parasitized 16 hosts, and parasitized and metamophosed from a total of 21 hosts in the laboratory. Unfortunately, it has never been determined whether all 33 hosts of *A. grandis*, for example, are equally ranked according to percentages of glochidia that complete metamorphosis, and are thus equally acceptable as hosts for this bivalve. Trdan (1981) presents some data for degree of parasitism of a number of fish hosts of *Lampsilis radiata siliquoidea*, and, while there seem to be significant differences in the mean intensity of infection, no data about differences in successful metamorphosis on those hosts exists. Parasites for which this aspect has been studied usually exhibit a wide range of host suitability (Dogiel *et al.*, 1964; Leong, 1975), and suitability can be a complex function involving several variables (Holmes, 1976). Specificity among unionaceans does appear to some extent to be a dynamic phenomenon in that the geographic range of a unionacean can be larger than that of its primary host (e.g. Wiles, 1975), and in that recently diverged unionaceans endemic to certain drainages parasitize recently diverged hosts (Kat, 1983 a).

IV. DISPERSAL, DIVERSIFICATION AND SPECIATION

The success of freshwater bivalve groups such as the Sphaeriidae, Corbiculidae, and Dreissenidae underlines the fact that parasitism is not a necessary consequence of the invasion of freshwater habitats by the Bivalvia. Why then has this unique system persisted among the Unionidae and, if the facultative parasitism supposedly exhibited by *Anodonta imbecilis* and *Strophitus undulatus* is real, why has there not been a unionacean group that has secondarily evolved away from this seemingly unpredictable and costly means of reproduction? A partial answer to these questions can, I believe,

be gained by examining the advantages of parasitism to unionaceans vis-à-vis non-parasitic freshwater bivalves.

The most-cited advantage of parasitism to unionaceans is that of dispersal, and since unionaceans spend such a short time in association with their host compared to the duration of the free-living stage (which in the case of *Margaritifera margaritifera* can approach 100 years; Cox, 1969), dispersal could be one of the main functions of the parasitic association. Dispersal as a process has been best studied in plants, and it is constructive to draw several analogies between particular aspects of animal-dispersed seeds in plants and fish-dispersed unionaceans. One of the largest advantages to plants of being dispersed by mammals and birds rather than by wind or water is that the habitat in which the seed is deposited becomes much more predictable (Ridley, 1930; van der Pijl, 1972; Harper, 1977). Likewise, dispersal mediated by fishes that are habitat-specific will tend to reduce the unpredictability of the freshwater habitat as it applies to juvenile unionaceans. For example, glochidia that parasitize fish with a preference for habitats with muddy bottoms will have a much larger probability of encountering a mud substrate when they metamorphose than one consisting primarily of rocks, but high levels of phenotypic plasticity characteristic of unionaceans (e.g. Ortmann, 1920; Johnson, 1970; Kat & Davis, 1983*a*) can compensate for habitat unpredictability to some extent, in that it allows some modification of shell shape to suit the particular substrate where the bivalve develops.

Freshwater bivalves that rely on passive dispersal are analogous to wind-dispersed plants, in that habitat predictability is greatly reduced. Such predictability becomes especially critical when long-distance dispersal is involved. The geographic range of many unionaceans has expanded over long distances in the rather short time since the retreat of the Wisconsinan glaciers, and these bivalves have consequently repopulated large areas of previously glaciated territory in central Canada and the northern Atlantic Slope region (Athearn & Clarke, 1961; Clarke, 1973; Kat & Davis, 1983*b*). This is also true of sphaeriids and especially of a corbiculid that has spread over much of the North American subcontinent in the short time since it was introduced (Sinclair, 1971; Clarke, 1973; Kraemer, 1979; Kat, 1982*a*), but these bivalves are comparable to weeds in that they are largely hermaphroditic, presumably capable of self-fertilization (Thomas, 1959), resistant to desiccation (Ingram, 1941), extremely tolerant of a wide range of pollutants (Diaz, 1974; Fuller & Richardson, 1977; Horne & McIntosh, 1979), and capable of living and reproducing in ephemeral habitats (Thomas, 1963). Inter-drainage distribution among such bivalves is probably accidentally mediated by a wide variety of animals such as insects, amphibians, and water birds (Kew, 1893; van der Schalie, 1945), which can be attracted to a variety of aquatic habitats not necessarily suitable for unionacean bivalves.

As a rule, the unionaceans have much more stringent habitat requirements partly because of their slow rate of development to reproductive maturity and long lifespan (Coker *et al.*, 1921). It is therefore advantageous to form an association with a fish that largely shares those habitat requirements, so that dispersal over long distances occurs with much more habitat fidelity.

Why the association between the dispersal agent and the dispersant became a parasitic one among the unionaceans rather than one involving only attachment as in plant burrs

is not yet understood. Ellis & Ellis (1926) were able to raise glochidia artificially through metamorphosis on a solution of sugars, salts and amino acids, and therefore concluded that, while parasitism is not absolutely necessary, it does provide the glochidium with nourishment, protection against bacteria and protozoa (by encystment), and the opportunity of dispersal. Very little is known about how the glochidia obtain nourishment from their hosts, and in the cases in which there is little or no size increase of the glochidium during attachment to its host (e.g. *Elliptio complanata*: see Matteson, 1948), whether very much nourishment is taken at all. In such cases the association between fishes and unionids might fall in the grey area between phoresy (attachment without parasitism for purposes of transport: see Farish & Axtell, 1971; Binns, 1982) and parasitism. It is intriguing to note that there exist a number of similarities between 'good' phoretics, such as mites, and glochidia: phoretic mites include a 'waiting stage' in their life-cycle during which behaviour and morphology are geared towards attachment to the dispersant, they synchronize life-cycles with those of their hosts, and exhibit specificity in dispersant choice (Binns, 1982). Considerable work with the nutritional requirements of glochidia of a variety of unionid species is necessary to determine the relative importance of parasitism versus dispersal, and whether unionid species can be classified into groups that stress one or the other.

In contrast to their marine counterparts, diversification in terms of shell shape has been rather limited among the Unioneacea, and the semi-infaunal mode of life that characterized the earliest fossil unionaceans (Haas, 1969) is still almost exclusively represented in this freshwater group. Such basic marine bivalve adaptations as mantle fusion are entirely absent among the unionaceans, which instead seem to have diversified mainly along lines of reproduction (Walker, 1917) and host attraction. It could of course be argued that freshwater bivalves were not exposed to the degree of predation that presumably constituted strong selection for mantle fusion and the radiation of infaunal marine bivalves (Stanley, 1977), and that low levels of substratum stability in lentic systems would select against bivalves that could not actively migrate and re-burrow (e.g. Kat, 1982b), but it is also reasonable to postulate that the semi-infaunal life is in fact consequential to the development of parasitism and brood protection. An examination of Sellmer's (1967) list of brood-protecting bivalves reveals that, besides their small size, there exists a striking relationship between the development of brood protection and siphon length: by far the majority of bivalves that have modified their intralamellar spaces to serve as marsupia also have short siphons and/or unfused mantle edges, and are consequently all shallow infaunal to epifaunal. This pattern could perhaps be attributed to the substantial reduction in efficiency of water flow down long siphons introduced by frictional forces along the siphonal walls, so that the further pressure drop associated with water flow through gills containing larvae and mucus cannot be tolerated (water flow through the bivalve mantle cavity is generated by the action of ctenidial cilia; water is drawn in via the incurrent siphon and must pass through the gills and into the suprabranchial chamber before it can be expelled through the excurrent siphon). By the same reasoning, it might not be possible to generate sufficient pressure up a long excurrent siphon to expel the mucus-bound glochidial conglutinates important in attracting fish hosts, and semi-infaunal bivalves might be better able to detect hosts than infaunal bivalves. The applicability of these hypotheses could be tested by examining

adaptations possibly existing among marine groups such as the highly modified Terenidae (shipworms) and Clavagellidae (flower-pot clams) that have long siphons, but that also incubate larvae through various stages of development.

Inclusion of a parasitic stage in the life-cycle of unionaceans can have important ramifications on the rate of speciation in this group as compared with non-parasitic bivalves. Bush (1974, 1975 a, b) has extensively reviewed the genetics of host race formation and speciation, and mentions two genetic components that appear to play a primary role in many parasitic host shifts: genes controlling host recognition and selection, and genes involved with survival once contact has been made with the host. Bush (1975 b) and Day (1974) mention that the ability of a parasite to survive on a new host might require only few genetic changes, and that the genetic variation needed to establish a new host race could already be present in the parasite population (see Walliker, 1983). In addition to these host shifts, divergence among widely distributed host populations (e.g. Avise & Smith, 1972; Biette et al., 1981) could lead to coevolutionary genetic divergences among parasite populations (Wright, 1971; Kennedy, 1975). An example of this process has probably occurred among the unionaceans of Lake Waccamaw, North Carolina. This lake contains a diverse and largely endemic unionacean and fish fauna, members of which seem closely related to species occurring in the surrounding drainages (Hubbs & Raney, 1946; Davis et al., 1981; Kat, 1983 a). Isolation of a unionacean species in a restricted basin such as Lake Waccamaw in which only one of its several hosts is present could lead to evolution of host-recognition and survival gene complexes (Bush, 1975 a, b) highly specific to that particular host's biochemistry and immunology. Concurrent genetic divergence of the endemic host from its ancestors outside the restricted basin could accelerate the process of divergence between unionacean taxa. Examination of one of the endemic species in Lake Waccamaw, Lampsilis sp., has indicated that it probably diverged (based on genetic distances over 14 loci) from an ancestral species outside the lake about 1.3×10^5 years ago (Kat, 1983 a), a figure that agrees well with the age of the lake. This host-related divergence among parasites is analogous to racial differentiation with respect to pollinators in plants, in which floral morphology differences among plant races are correlated with pollination by such diverse pollinators as bees, moths and hummingbirds in different regions of the species' geographic range (Grant & Grant, 1965).

The type of host parasitized can also have a large effect on the rate of divergence among populations in widely distributed species. For example, Elliptio complanata primarily parasitizes the yellow perch, which is limited to fresh and slightly brackish water, exhibits territorial behaviour, and generally remains restricted to areas within a single river (Mansueti, 1960; New, 1978). Consequently, populations of E. complanata from neighbouring drainages and even from different sections of a single drainage can exhibit considerable molecular genetic and morphological differences, especially among recently established peripheral populations (Kat, 1983 b; Kat & Davis, 1983 b). This indicates that gene flow among such populations is rare. In contrast, populations of Anodonta implicata and Lampsilis ochracea, which parasitize anadromous and salt-tolerant hosts, exhibit remarkably little divergence between populations located at even opposite extremes of their geographic ranges (Table 3; see Kat & Davis, 1983 b; Kat, 1983 a). This demonstrates that habitats that are isolated for species that parasitize freshwater hosts (which presumably carry glochidia between drainage systems largely by chance)

Table 3. *Influence of host type : genetic characteristics of unionid populations occurring at opposite geographic range extremes. (Genetic data from Kat & Davis, 1983 b; host data from Townsend, 1939; Mansueti, 1960; Hynes, 1970)*

Unionid	Host tolerance	Percentage of alleles shared among populations	Genetic identity
Anodonta implicata	A	90·4	0·968 ± 0·014
Lampsilis ochracea	A	88·2	0·954 ± 0·005
Lampsilis radiata	FBS	80·7	0·943 ± 0·011
Elliptio complanata	FB	79·5	0·938 ± 0·016

* A = anadromous, S = salt-water tolerant, B = brackish-water tolerant, F = restricted to fresh water.

are less so for species that parasitize saltwater-tolerant or anadromous hosts (which presumably carry glochidia between drainage systems with greater frequency), and that species in the first category are much more likely to differentiate by allopatric divergence than species in the second category. It is also interesting to note that behaviour of pollinators can similarly have a considerable influence on the probability of gene flow among plant populations. For example, Schmitt (1980) demonstrated that bees typically fly short distances, resulting in very localized pollen dispersal, while butterflies frequently bypass nearby plants and can potentially distribute pollen among plant demes. Bee-pollinated plants are therefore analogous to freshwater-host-distributed unionaceans in that they have greater potential for local differentiation.

V. SUMMARY

It is proposed that the incorporation of a unique parasitic stage in the life-cycle of unionaceans which involves an obligate relationship between a vertebrate host, usually a fish, and a highly modified larval stage, the glochidium, has had far-reaching consequences with respect to overall morphology, extent of species' geographic ranges, and rate of speciation in the group.

Glochidia are separable into three main types with respect to overall shape and attachment features, and are retained in variously modified brood pouches. When mature, glochidia are released in several different ways which reflect various adaptations involved in either attracting the fish host and/or increasing the probability of attachment. Glochidia do not seem capable of host selection, and the reaction of the host to the parasite seems to be the main factor in determining specificity. Release of glochidia is synchronized to correspond to periods of predictable host availability, such as during spawing migrations and nesting behaviour. Other adaptations include modifications of glochidial conglutinates to mimic host food items, and modifications of the unionacean mantle edges to attract hosts. In all cases, a good correlation exists between the type of lure used and host food preferences, but, despite these adaptations, host specificity among unionaceans seems low.

Parasitism among unionaceans is postulated to be mainly advantageous in terms of predictability of dispersal by habitat-specific hosts, but parasitism is hypothesized to entail constraints in terms of the degree to which shell shape and life-habit can be diversified among unionaceans. The type of host parasitized is considered to affect the

rate of diversification among populations and speciation among unionaceans: those that parasitize strictly freshwater hosts are more likely to exhibit highly individualistic populations in different drainages with respect to molecular genetic and soft-part characters, while those that parasitize anadromous or saltwater-tolerant hosts show little differentiation among widely distributed populations.

VI. ACKNOWLEDGEMENTS

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