MORPHOLOGICAL CHARACTERS OF GLOCHIDIA OF UNIONIDAE AND THE TAXONOMIC SIGNIFICANCE①

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Abstract Comparative morphology of glochidia of 18 unionid species was studied. Characters including shape, size, decoration and pore of shells, hook, spines, sensory hairs as well as larval thread are more or less different among species. These characters are considered to be significant for species identification and phylogenetic analysis.

Key words Glochidia, Unionidae, Taxonomic significance

1 Introduction

Traditionally, the classification of unionid mussels was principally based on shell characters, but shells were greatly variable under different environmental conditions and hence, they can hardly reflect the phylogenetic relationships of these groups.

Freshwater unionids have highly specialized larvae, the glochidia which develop from fertilized eggs in modified gills of female unionids. After maturing, the glochidia are discharged from maternal shells into water, and further undergo development if they encounter the appropriate hosts. For classification, the parasitism and morphology of glochidia, and their relations to hosts are considered by malacologists. Recently, more and more attention has been focused on the glochidial morphology, especially their microstructures, which enable more complete descriptions for most species and provide valuable information for phylogenetic analysis of Unionidae. Species of the family are rich in mid-lower basins of Changjiang River, but very few studies on glochidia were conducted. In recent years, the glochidial morphology of 18 species and marsupial types of 21 species of Unionidae in China were studied by the authors (Wu, 1998; Wu et. al., 1999, 2000). The purpose of the present work is to explore some morphological characters of glochidia for species identification and for phylogenetic analysis of higher taxa.

The materials were collected from Poyang Lake, ponds of Nanchang, Jiangxi Province, Baoan Lake, Wanghu Lake of Hubei Province and Dongting Lake of Hunan Province (Tab.1).

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Tab.1 Sampling localities and dates of gravid unionids

Species	Locality	Date
Unioninae		
Unio douglasiae	Poyang Lake	'96,4—6.
Acuticosta chinensis	Poyang Lake	'96,10.
Acuticosta aurora comb.nov. (= Parreysia aurora)	Poyang Lake	'92,6.
Schistodesmus lampreyanus	Poyang Lake	'97,5.
Arconaia lanceolata	Poyang Lake	'96,4.
Lanceolaria eucylindrica	Poyang Lake	'96,11.; '97,6.
Lanceolaria gladiola	Poyang Lake	'96,11.; '97,6.
Lanceolaria grayana	Poyang Lake	'97,8.
Cuneopsis pisciculus	Poyang Lake	'97,7—8
Cuneopsis heudei	Poyang Lake	'97,7—8
Lamprotula cornuum-lunae	Poyang Lake	'97,7.
Lamprotula caveata	Poyang Lake	'97,7.
Aculamprotula fibrosa gen. et comb. nov. (= *Lamprotula fibrosa*)	Wanghu Lake	'97,11.
Hyriopsis cumingii	Ponds, Nanchang	'97,9.
Anodontinae		
Anodonta woodiana woodiana	Poyang Lake	'96,6.
Anodonta pacifica	Baoan Lake	'96,8.
Anodonta lucida	Ponds, Nanchang	'98,1.
Anodonta angula	Dongting Lake	'64,6.
Anodonta arcaeformis	Poyang Lake	'96,3—4
Cristaria plicata	Ponds, Nanchang	'95,11.; '96,5.
Lepidodesma languilati	Poyang Lake	'84,8.

2 Marsupial types and revision

During breeding season, the outer two or all four gills of female unionids are used as brood pouch, generally termed as marsupium. Simpson (1900,1914) divided the marsupia of different unionids into two groups, exobranchial and endobranchial. The former was further separated into eight types, viz., heterogenae, digenae, mesogenae, ptychogenae, eschatigenae, diagenae, homogenae and tetragenae. In our observation on 21 species, only homogenae and tetragenae were found. The former includes *Unio douglasiae*, *Acuticosta chinensis*, *Acuticosta aurora*, *Schistodesmus lampreyanus*, *Lanceolaria eucylindrica*, *Lanceolaria gladiola* and *Lanceolaria grayana*. Their marsupia are thin and long, only somewhat swollen without thickened ventral margins when embryos are contained. Embryos exist with conglutination in marsupia (Lefever, 1910). Most of the conglutination are white in color, but some are yellow or red. Similar characters of marsupia were observed in *Arconaia lanceolata*, *Cuneopsis pisciculus* and *Cuneopsis heudei*, except that there are no conglutination. Conglutination is also absent in *Hyriopsis cumingii*, *Anodonta*, *Cristaria plicata* and *Lepidodesma languilati*. However, when employing embryos, all of their marsupia show smooth and pad-like with thickened ventral margins. As glochidia matured, the colors of their marsupia are brownish, and the glochidia are diffuse. Another type is tetragenae, including the species of *Lamprotula*

only.

The marsupial type has been regarded as an important character in the classification of families or subfamilies of Unionacea (Simpson, 1900, 1914; Davis et al., 1981; Heard et al., 1970). However, Simpson's descriptions on marsupial types of several Chinese unionids were incorrect (Tab.2). For example, he assigned the species of *Acuticosta*, *Arconaia* and *Lanceolaria* to endobranchial group, and those of *Schistodesmus*, *Cuneopsis* and *Lamprotula fibrosa* (= *Aculamprotula fibrosa* gen. et comb. nov.) (Wu et al., to be submitted) to tetragenae. Actually, they are all homogenae. *Lamprotula* is a special genus with marsupia different obviously from other genera of Unioninae. Based mainly on the marsupial characters, Moore (1969) and Hass (1969) put this genus into Ambleminae.

Tab.2 Marsupial types of unionids in China

Species	Author's Observation	Simpson's Description
Unio douglasiae	homogenae	homogenae
Acuticosta chinensis	homogenae	endobranchiae
Acuticosta aurora	homogenae	endobranchiae
Schistodesmus lampreyanus	homogenae	tetragenae
Arconaia lanceolata	homogenae	endobranchiae
Lanceolaria eucylindrica	homogenae	endobranchiae
Lanceolaria gladiola	homogenae	endobranchiae
Lanceolaria grayana	homogenae	endobranchiae
Cuneopsis pisciculus	homogenae	tetragenae
Cuneopsis heudei	homogenae	tetragenae
Lamprotula scripta *	tetragenae	tetragenae
Lamprotula cornuum-lunae	tetragenae	tetragenae
Lamprotula caveata	tetragenae	tetragenae
Aculamprotula fibrosa	homogenae	tetragenae
Hyriopsis cumingii	homogenae	homogenae
Anodonta woodiana woodiana	homogenae	homogenae
Anodonta pacifica	homogenae	homogenae
Anodonta lucida	homogenae	homogenae
Anodonta angulata	homogenae	homogenae
Anodonta arcaeformis	homogenae	homogenae
Cristaria plicata	homogenae	heterogenae
Lepidodesma languilati	homogenae	heterogenae

* from Wei (1994)

3 Morphological characters of glochidia and taxonomic significance

3.1 Glochidial types

Glochidia may be divided into three types: hooked, hookless and axed. The authors have examined the glochidia of 18 unionid species and found that most of them were hooked except hookless larvae of *Lamprotula* and *Hyriopsis* (Tab. 3). This character is important in the classification in the Unionidae (Modell, 1964; Hass, 1969; Heard et al., 1970; Davis et al., 1981). Lefever (1910) and Ortmann (1918) reported that the glochidia of *Unio* from North America and Africa were hookless, while Heard et

al. (1970) believed that Ortmann's description was based on immature specimens and pointed out that hooks appeared only at final developmental stage of the larvae in some species. Wood (1974) mentioned the hookless glochidia from British *Unio*, but Pekkarinen (1995, 1996a) found that the glochidia of European species are hooked. The glochidia of *Unio douglasiae* in China were determined to be hooked by the authors. This result is identical to other reports from Asia (Wei et al., 1994; Park, 1995).

Tab.3 A comparison of glochidial morphology of 18 unionid species

Species	Shape	Hook	Shell surface	Spine	ID[1] (μm)	OD[2] (μm)	Sensory hair	Conglutination
Unio douglasiae	wide triangular	triangular	shallow pits	3—4 rows	6.5	3.0	3 pairs	present
Acuticosta chinensis	gourd-shaped	ridge and wing fused	shallow pits	25—26 rows	3.3	1.6	3 pairs	present
Acuticosta aurora	gourd-shaped	ridge and wing fused	shallow pits	28 rows	3.3	1.6	3 pairs	present
Lanceolaria eucylindrica	wide triangular	triangular	pits	"V" pattern	13.9	3.8	3 pairs	present
Lanceolaria gladiola	wide triangular	triangular	pits	irregular	8.2	3.8	3 pairs	present
Lanceolaria grayana	wide triangular	triangular	shallow pits	"V" pattern	—	—	—	present
Cuneopsis pisciculus	elongated triangular	anchor-shaped	deep pits	irregular pattern	16.64	3.84	4 pairs	absent
Lamprotula cornuum-lunae	semi-elliptical	hookless	pores	absent	—	—	4 pairs	absent
Lamprotula caveata	semi-elliptical	hookless	shallow pits	absent	10.2	2.6	4 pairs	absent
Aculamprotula fibrosa	elongated triangular	anchor-shaped	pits	2 rows	12.9	3.8	-	absent
Hyriopsis cumingii	semi-elliptical	hookless	pores	absent	11.2	3.8	2 pairs	absent
Anodonta woodiana woodiana	elongated triangular	anchor-shaped	pores	2 row	13.5	4.1	4 pairs	absent
Anodonta pacifica	elongated triangular	anchor-shaped	pores	3 row	12.8	3.3	4 pairs	absent
Anodonta lucida	elongated triangular	anchor-shaped	pores	2 row	—	—	4 pairs	absent
Anodonta angula	elongated triangular	anchor-shaped	pores	irregular	—	—	4 pairs	absent
Anodonta arcaeformis	semicircle	anchor-shaped	pores	3 rows	absent	absent	-	absent
Cristaria plicata	elongated triangular	anchor-shaped	pores	2 rows	11.2	4.9	4 pairs	absent
Lepidodesma languilati	elongated triangular	anchor-shaped	shallow pits	2 rows	—	—	4 pairs	absent

1) Inner thread diameter
2) outer thread diameter

Wei et al. (1994) and Park (1995) reported the glochidia without hook in *Lamprotula caveata* and *Lamprotula scripta* from China and *Lamprotula gottschei* from Korea. For the former two species, Wei et al. also found dendriform and suckerlike structures on ventral margins of the glochidia. However, there were no similar structures in our materials of *Lamprotula cornuum-lunae* and *Lamprotula caveata*, only

membranous flanges were found on the ventral shell margins, similar to the larvae of *Margaritifera margaritifera* reported by Pekkarinen (1996b).

3.2 Colors of glochidia

Acuticosta chinensis, *Acuticosta aurora*, *Lanceolaria* and *Aculamprotula* have whitish glochidia. However, *Unio*, *Cuneopsis*, *Lamprotula* and Anodontinae have brown glochidial shells. Park (1995) and Pekkarinen (1995, 1996a) also noted that the glochidia of different unionid taxa had different shell colors. In comparison with their results, it shows that shell colors of glochidia of a species from different geographical locations were coincident, meaning that shell colors of unionid glochidia are basically invariable.

3.3 Shapes of Glochidia

There are five kinds of the glochidial shapes, viz. elongated triangular, wide triangular, semi-elliptical, semicircle and gourd-shaped, in eighteen unionid species (Fig.1). Shapes of different taxa are relatively stable. In Anodontinae, the larvae are elongated triangular except semicircle ones of *Anodonta arcaeformis*. Semi-elliptical larvae were found in *Lamprotula*, *Hyriopsis* and *Margaritifera*, and wide triangular larvae in *Unio* and *Lanceolaria*. These results are similar to the reports from other country or area (Wood, 1974; Rand, 1982; Park, 1995; Pekkarinen, 1995, 1996a,b; Wei et al., 1994). It should be pointed out that *Acuticosta* have gourd-shaped larvae, which is regarded to be special in comparison with other taxa.

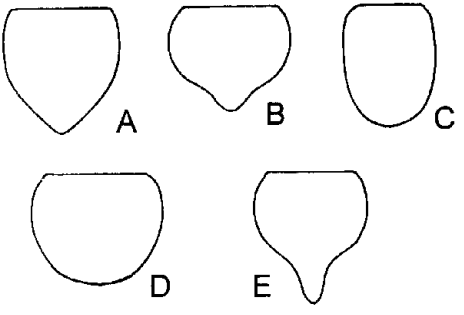

Fig.1 External shapes of glochidia
A: elongated triangular; B: wide triangular; C: semi-elliptical; D: semicircle; E: gourd-shaped

3.4 Size of glochidia

Size of glochidia of some unionids are presented in Tab.4. It shows that sizes are obviously different among species, especially among the genera. Davis et al. (1981) applied the glochidial index (Gln.: shell length × shell height) to divide the glochidia into three kinds: large size having Gln. ranging from 0.078 to 0.1225 with the average of about 0.1; middle size ranging from 0.0073 to 0.0867 with the average of about 0.047; and the small size less than 0.0036. According to Davis's criterion, Anodontinae have large glochidia, Ambleminae and Unioninae have middle glochidia, and Margaritiferidae have small glochidia. Although the glochidial sizes are somewhat variable geographically, glochidial size are recognized relatively stable in taxa of subfamilies.

3.5 Shell surface

Two cases on shell surface of glochidia have been recognized in our materials, of which one possesses pores and the other has deep or shallow pits. Most glochidia of subfamily Unioninae, including *Unio douglasiae*, *Acuticosta chinensis*, *Acuticosta aurora*, *Lanceolaria*, *Cuneopsis pisciculus*, *Lamprotula caveata* and *Aculamprotula fibrosa*, were observed without pores but pits. However, all of the Anodontinae have pores on the shell. It implies that the presence of pores or pits may be used for the classification of subfamilies, although there are certain exceptions, such as *Lamprotula cornuum-lunae* and *Hyriopsis cumingii* in Unioninae with pores on shell surface and *Lepidodesma languilati* in Anodontinae with shallow pits.

Tab.4 Glochidial indices of unionids

Species	Gln	Localities	Authors
Unio douglasiae	0.020	Poyang Lake, China	Wu et al., 1999a
Unio crassus crassus	0.048	Germany	Engel, 1989
Acuticosta chinensis	0.026	Poyang Lake, China	Wu et al., 1999a
Acuticosta aurora	0.025	Zhejiang, China	Wu et al., 1999a
Lanceolaria eucylindrica	0.040	Poyang Lake, China	Wu et al., 1999b
Lanceolaria gladiola	0.039	Poyang Lake, China	Wu et al., 1999b
Lanceolaria gladiola	0.041	Hubei, China	wei et al., 1994
Lanceolaria acrorhyncha	0.042	Korea	Park, 1995
Cuneopsis pisciculus	0.053	Poyang Lake, China	Wu et al.,1999b
Lamprotula cornuum—lunae	0.043	Poyang Lake, China	Wu et al., 1999b
Lamprotula scripta	0.038	Liangzhi Lake, China	Wei et al., 1994
Lamprotula caveata	0.037	Liangzhi Lake, China	Wei et al., 1994
Lamprotula caveata	0.036	Poyang Lake, China	Wu et al., 1999b
Aculamprotula fibrosa	0.059	Wanghu Lake, China	Wu, 1998
Hyriopsis cumingii	0.054	Jiangxi, China	Wu et al., 1999b
Anodonta woodiana woodiana	0.077	Jiangxi, China	Wu, 1998
Anodonta woodiana woodiana	0.088	Nanhu Lake, China	Wei et al., 1994
Anodonta woodiana woodiana	0.070	Korea	Park, 1995
Anodonta pacifica	0.080	Baoan Lake, China	Wu, 1998
Anodonta lucida	0.061	Jiangxi, China	Wu, 1998
Anodonta angula	0.076	Dongting Lake, China	Wu, 1998
Anodonta arcaeformis	0.19	Poyang Lake, China	Wu, 1998
Anodonta arcaefomis flaveltincta	0.119	Korea	Park, 1995
Anodonta anatina	0.126	Germany	Pakkarinen, 1995
Anodonta anatina	0.110—0.141	Finland	Pakkarinen, 1995
Anodonta cygnea(= *piscinalis*)	0.095	Russia	Pakkarinen, 1995
Anodonta cygnea	0.105	Russia	Pakkarinen, 1995
Anodonta cygnea	0.0945	Germany	Pakkarinen, 1995
Anodonta cygnea	0.108—0.118	Finland	Pakkarinen
Anodonta implicata	0.119	Canada	Wiles, 1975
Anodonta catracta	0.146	Canada	Wiles, 1975
Anodonta sp.	0.097—0.135	Poland	Pakkarinen
Cristaria plicata	0.081	Jiangxi, China	Wu, et al., 1999b
Cristaria plicata	0.060	Hubei, China	Wei et al., 1994
Lepidodesma languilati	0.131	Poyang Lake, China	Wu, 1998
Elliptio complanatus	0.045	Canada	Wiles, 1975
Lampsilis radiata	0.083	Canada	Wiles, 1975
Hyridella drapeta	0.076	Australia	Atkins, 1979

Various sculptures of glochidial shells were found in Unionidae, including numerous spines in *Cristaria plicata* glochidia, hairs in *Anodonta pacifica*, radial scriptures around the pits in *Lanceolaria* and fine decoration in *Aculamprotula fibrosa*. All of them are especially obvious under SEM. These characters are also regarded as taxonomic significance.

3.6 Shapes of hook and spines

Hooks in most glochidia were anchor-shaped, with two delicate wings stretching from the middle of hook to the rim of shell. The distal end of ridge is blunt in *Unio* and *Cuneopsis* (Fig.2A), and tapered in

Anodontinae (Fig.2B). In the glochidia of *Lanceolaria*, hooks appear triangular, with wings stretching from the distal end of ridge of shell (Fig. 2C). In *Acuticosta*, hooks are very special. The wings and ridge are fused, on which there are numerous delicate spines (Fig. 2D).

The number of spines and their arrangement on ridge are also different in different species (Tab. 3). Although the spines and styli continuously vary in size and thus, cause error during counting, yet the number of the spines is relatively constant in a species. Generally, the patterns of spines are two or three rows, but irregular arrangement of spines are also present in certain species.

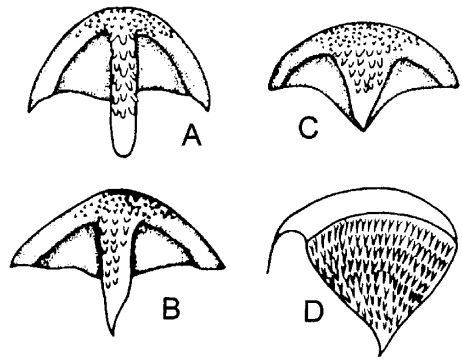

Fig.2 Hook types of glochidia
A, B: anchor-shaped; C: triangular;
D: ridge and wing fused

3.7 Sensory hairs

Lillie (1895) supposed the glochidia of *Anodonta* bearing four sensory hairs. Tand (1982), Wood (1974) and Pekkarinen (1995, 1996a) reported that the glochidia of *Anodonta* and several genera of unionidae had four pairs of hairs. Same results were obtained by the authors in five *Anodonta* species, including the non-parasitic glochidia of *Anodonta arcaeformis*. Park (1995) found that there were three pairs of sensory hairs in the glochidia of species of *Unio* and *Lanceolaria*, while only two pairs in *Lamprotula gottschei*. From our material, three paired sensory hairs in *Unio*, *Acuticosta* and *Lanceolaria*, and two paired hairs in *Hyriopsis cumingii* were present. However, in *Lamprotula*, glochidia bearing four paired sensory hairs were clearly observed, which was obviously different from Park's result. In fact, it is not easy to observe the sensory hairs of preserved specimens.

3.8 Larval thread

Not every species of Unionidae has larval thread. As early as 1889, Schierholz found the glochidia of *Pseudanodonta complanata* without larval thread (Wood, 1974). Lefever (1910) considered larval thread as a character of *Unio* and *Anodonta*, because no larval thread was found in those bivalves producing hookless glochidia. Wood (1974) reported that there was larval thread in immature larva of *Margaritifera margaritifera*, but it disappeared rapidly as the embryo developed. Larval threads are not necessarily present even in a genus. For instance, Rand (1982) discovered larval thread in *Anodonta cataracta*, but none in *Anodonta implicata*. In our specimens, all glochidia have larval threads except for non-parasitic species. Among the examined species, two kinds of larval threads were recognized, of which one is thicker with diameters 6.4μm or more for inner thread and 3.0 μm or more for outer thread, the other obviously thinner.

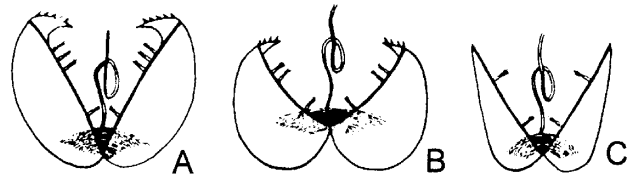

Fig.3 Number and location of sensory hairs
A: four pairs; B: three pairs; C: two pairs

In conclusion, morphological characters including shape, size, decoration and pore of shells, hook, spines, sensory hairs and larval thread are more or less different among species. Characters that are considered to be significant for species identification and phylogenetic analysis are listed in Tab. 4.

Tab.4 Some morphological characters of marsupium and glochidium of Unionidae

Structure	Character
Marsupia	Endobranchial or exobranchial
Conglutination	Present or absent
Glochidial size	Large, middle or small
Glochidial shape	Triangular, semi-elliptical, gourd-shaped or semicircle
Shell surface	Pores or pits
Sculpture of surface	Radial nicks, spines or decoration
Hook	Present or absent
Hook shape	Triangular, anchor-shaped or ridge and wing merge into a single whole
Sensory hairs	Two pairs, three pairs or four pairs
Spines	Two rows, three rows or irregular
Inner thread diameter	Thick or thin
Outer thread diameter	Thick or thin

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