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DESCRIPTION OF GLOCHIDIA OF FIVE SPECIES OF FRESHWATER MUSSELS (HYRIIDAE: UNIONOIDEA) FROM SOUTH AMERICA.

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ABSTRACT

The glochidia of South American Hyriidae were first described and illustrated by Lea (1868); 52 years later Ortmann (1921), followed by Bonetto (1954, 1955, 1960a, b, 1961a–c, 1962a, b) and others, described the larva of various species. However, many larvae are still unknown. The valves of five glochidia of two different types are here illustrated and described: two fish-parasitizing glochidia with the presence of a S-shaped tooth in each valve, and three glochidia that do not parasitize fish, with valves devoid of teeth or spinulae. The valves are measured and compared in: (a) length, (b) height, (c) dorsal hinge length, (d) displacement of the ventral point in relation to the middle of the hinge, and (e) angle of the ventral point in relation to the center of the hinge. Statistics of these measurements are also provided. The internal anatomy of the glochidium of *Diplodon martensi* (Ihering, 1891) and *D. koseritzi* (Clessin, 1888) are briefly described. Some of the larvae illustrated were photographed with a scanning electron microscope and some were drawn using a biological microscope with camera lucida.

Key words: descriptions, Glochidia, Hyriidae, Unionoidea, South America.

INTRODUCTION

The larvae of freshwater bivalves of the superfamily Unionoidea, called glochidia, usually parasitize fish. The glochidia aid dispersal of the mollusk upstream. When the fish passes by, the larva adheres to its scales, fins or gills, becoming a temporary ectoparasite. A cyst is formed by the fish, where the glochidium completes its development to the postlarval phase. This period of parasitism, which lasts 10 to 30 days, is usually conditioned to the times of high water during the spring when the phenomenon called "piracema" occurs in South America.

The glochidia of South American species have morphological affinity with Australian species and differ from the remaining Unionoidea species that live in the holarctic region (Parodiz & Bonetto, 1963). Their characteristics aid the identification and classification of this group of mollusks in which juvenile and adult individuals often lack interspecific diagnostic criteria.

Two types of glochidia are known among South American Hyriidae – those with teeth that develop parasitically on fish, where they form a cyst inside which the glochidium completes its development until the postlarval phase; and those without teeth, which fully and directly develop inside incubating pouches called marsupia of the female, until the postlarval phase.

Variations occur in the teeth of fish-parasitizing glochidia – in the tribe Castaliini and in the subgenus *Diplodon* (*Australis*) (Bonetto et al., 1986) of the tribe Diplodontiti, the tooth is triangular, short, wide at the base, and shaped like a beak. They have no spines or terminal cusps. In the remaining Diplodontini and Prisodontini, the tooth is fine, elongate, and S-shaped, with terminal cusps (Parodiz & Bonetto, 1963).

The glochidia of South American species were first observed by Lea (1868), who described and illustrated the larvae of two *Diplodon* species ("*Unio*" *peculiaris* and *"U." firmus*). He mentioned the subtriangular contour and the ventral margin terminating in a point containing teeth. The teeth do not appear in the small figures drawn by Lea, and he did not offer a description of them. Ihering (1893: 47) commented on the wide differences in the form of South American glochidia compared to North American and European glochidia, and stated that the larvae observed

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by him did not have teeth or the adhesive filament which he called "bisso".

Ortmann (1921) described Hyriinae (= Hyriidae) larvae in more detail and observed for the first time the absence of teeth in many species. Furthermore, he pointed out that, when present, the teeth appear to be completely different from those of European species of the genus *Unio* and from the Anodontinae of Eurasia and North America; that is, they are long, fine and S-shaped, articulated at the base and without spinules. When describing *Castalia* glochidia, he mentioned that they appear to be different from those of *Diplodon* in having a shorter tooth, which is thicker at the base. He also observed that the toothless glochidia had growth bands on the borders of the valves, which probably represented the beginning of the permanent shell. He assumed that these glochidia developed in direct manner without a host fish. Bonetto (1955) confirmed the assumptions of Ortmann (1921) and stated that mature glochidia probably had an anatomical organization similar to that of glochidia in the post-larval stage after completing their parasitic development on fish and abandoning them.

Bonetto (1960a, b, 1961a–c), Bonetto & Ezcurra (1963, 1965) and Parodiz & Bonetto (1963) described 44 glochidia of different species based, in part, on his personal collection, on Ortmann's slides, and in part on fixed material belonging to various museum collections. Many glochidia have not yet been adequately described, especially with respect to dentition. Some belong to synonyms of ill-defined species, with the resulting presence of different types of larvae in the same "species".

More recently, Alvarenga & Ricci (1979) described the glochidium of *Diplodon besckeanus* (Dunker, 1849) from Rio de Janeiro. Mansur (1983) observed for the first time the glochidium of *D. koseritzi* (Clessin, 1888) and of *D. martensi* (Ihering, 1983) from the sub-basin of the Jacuí in South Brazil. Mansur & Campos-Velho (ms) described the glochidium of *Castalia martensi* (Ihering, 1891) from the same sub-basin. Martinez (1983) described the glochidium of *Castalia ambigua multisulcata* from Venezuela, a species considered by Mansur (1991) to be *C. orinocensis* Morrison, 1943.

The work intends to contribute to the knowledge of the biodiversity, morphology, and systematics of South American freshwater bivalve molluscs. Despite of their importance to the ecosystem and their close relation to fish, they are poorly known in term of the number and distribution of species, as well as in morphology. While the lack of knowledge continues, these animals suffer from rapid anthropic growth and invasion of exotic species.

MATERIALS & METHODS

Mature glochidia collected from the marsupia of gravid females were anesthetized with menthol crystals for 48 h. The tissues were removed with commercial sodium hypochlorite (8 drops for 10 ml deionized water for 5 min). The valves were cleaned by maceration in deionized water in test tubes for 2 days, with frequent fluid changes by means of a pipette. The material was dried on filter paper, and part of its was mounted on stubs, sputtered with gold, and photographed using standard scanning electron microscopy methods. The rest was mounted on permanent optic slides. The methods for these procedures and for the measurement of the glochidial valves were those of Mansur & Campos-Velho (1990). Live samples of the glochidia of *D. martensi* and *D. koseritzi* were observed directly under the optic and stereoscopic microscope with drops of diluted methylene blue (1/1000).

Diplodon martensi (Ihering, 1893) – Bom Jardim, a small tributary from the lower part of the Cai River, between Triúnfo and Montenegro cities, Rio Grande do Sul State, southern Brazil (latitude 29°50′01″S, longitude 051°20′21″W) (MCNF mol. 6218); *Diplodon kozeritzi* (Clessin, 1888) – In the lake "rio Guaíba" at the beaches Florida, Vila Elza, and Alegria, municipality of Guaíba, inside an area corresponding to 30°08′30′S and 30°09′24′S and 051°18′36″W and 051°19′18″W; at the Municipality of Porto Alegre at the bay Belem Novo, and Municipality of Viamão at the beaches of Itapuã and Porto das Pombas (MCT-PUCRS); *D. berthae* – Little lake Sheidt, near the Jacuí River and the town Cachoeira do Sul, RS (MCNF mol. 31976); *D. iheringi* – Small river Arroio do Conde, near Jacui River and the town São Jerônimo, RS (MCNF mol. 30698); *D. charruanus* – Canal from the lake Jacaré to the Taim Ecological Station, municipality of Rio Grande, RS (MCNF mol. 8633). All studied samples and slides were preserved in the mollusc collection of the MCNF (Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul) and collection of MCT-PUCRS (Museu de Ciências e

Tecnologia da PUCRS, Porto Alegre). Some slides from Ortmann's collection were studied in the INALI (Instituto Nacional de Limnologia, Santo Tome, Santa Fé, Argentina).

RESULTS

Diplodon martensi (Ihering, 1893)
(Fig. 1–3; Table 1a)

The glochidia of *D. martensi* are fish parasites. Their valves are articulated along the dorsal line, with an S-shaped tooth inserted internally close to the ventral point of each valve. The contour of the larva is subtriangular and similar to that of the parasitic glochidia described by Ortmann (1921a), Bonetto (1960a, b, 1961a–c, 1962a, b), Bonetto & Ezcurra (1965), and Alvarenga & Ricci (1979). The tooth ends with three grouped cusps, the central one being more elongate and translucent than the two lateral ones (Figs. 1–3). The outer surface of the valves is granulated, looking like an eggshell at 100 and 400 × magnification. It is perforated by minute pores visible at about 400 × magnification. Each pore is approximately 1 µm in diameter. The entire border of each valve is surrounded by a band that stands out from the general surface by being smooth (Figs. 1–3). The 40 measured glochidia of *D. martensi* varied in length from 0.28 to 0.32 mm (mode and mean 0.29); in height from 0.24 to 0.28 mm (mode and mean 0.25); and the dorsal hinge length from 0.20 to 0.23 mm (mode 0.21 to 0.22, mean 0.21). The displacement of the ventral point in relation to the middle of the dorsal hinge ranged from 0.2 to 0.5 mm (mode 0.4, mean 0.03); the angle of the ventral point in relation to the center of the dorsal hinge ranged from 12° to 19° (mode and mean 15°). The tooth length reached 0.10 to 0.11 mm (Table 1a).

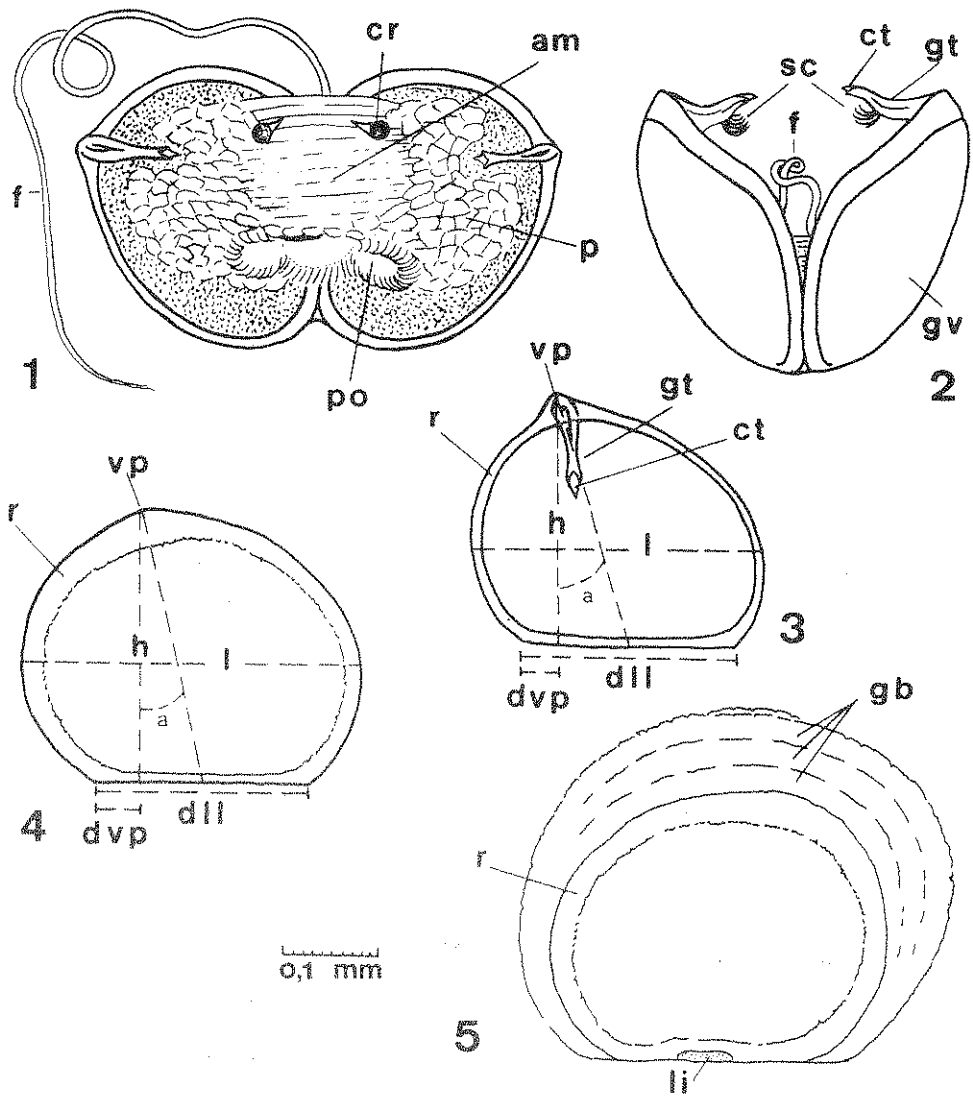
The glochidia of *D. martensi* have a central adductor muscle, a posterior ciliated organ, and a long anterior filament (Figs. 1, 2). This reaches approximately four times the length of the glochidial valve and, when not distended, is rolled up two full turns inside the glochidium. Close to the base of the filament is a pair of sensory "cirros" (term used by Bonetto, 1962a), which deeply stain with methylene blue. These "cirros" are shaped like aculei with a rounded base (Fig. 1). On the inner surface of each glochidial tooth is a tuft of sensory cilia (Fig. 2). The remainder of the pallial cavity of the glochidium is lined with large cells-phagocytes according to Dawydoff (1928), or of the mantle according to Harms (1909)-forming a tissue of spongy appearance.

Diplodon berthae Ortmann, 1921
(Figs. 6–8; Tables 1b)

The species was considered by Parodiz (1968) as a synonym of *D. piceus* (Lea, 1860). The larva was first observed by Ortmann (1921) when describing the species. He described the larva as a fish parasite with teeth, but did not provide illustrations, because it was presumed immature. The larva is a little smaller and similar to that of *D. martensi* in shape, but its teeth are more curved inward and have a more reinforced base. One tooth has a concavity at the base (Fig. 7), and the opposite tooth has a small prominence at the same place (Fig. 8). The dimensions of the larva ranged from 0.24 mm to 0.28 mm in length (mode 0.27, mean 0.26) and 0.21 mm to 0.25 mm in height (mode and mean 0.23), with a dorsal hinge length of 0.17 mm to 0.21 mm (mode 0.19, mean 0.18). The displacement of the ventral point is 0.02 mm to 0.06 mm (mode 0.05, mean 0.04), and the angle of the ventral point in relation to the center of the dorsal hinge is 05° to 16° (mode 13°, mean 12°) (Table 1b).

Diplodon koseritzi (Clessin, 1888)
(Figs. 4, 5; Tables 1c)

The glochidium presents a pair of articulated valves on the dorsal hinge and has no teeth. It has a sub-oval contour, similar to that of other non-parasitic glochidia previously described by Bonetto (1960a, b, 1961a–c, 1962a, b) and Bonetto & Ezcurra (1962, 1965). The outer surface is similar to that of *D. martensi* glochidia and is also perforated with pores. The border that surrounds each valve is wider in glochidia newly hatched from the egg and is also less smooth, occasionally showing concavities and pores. An adult *D. koseritzi* specimen collected in December had some glochidia still in the marsupium, with three growth bands in addition to the normal rim or border of the larval shell (Fig. 5). These bands do not occur on the line of valve articulation and reach the greatest height on the ventral margin, where they all reached 0.09 mm, in addition to the normal border. The existence of growth bands in addition to the nor-



FIGS. 1–3. Glochidium of *Diplodon martensi* (Ihering, 1893), of parasitic type, with "S" shaped teeth. 1. Ventral view of internal organization. 2. Frontal view, profile of teeth. 3. Glochidial valves in lateral view.
FIGS. 4, 5. Glochidium of *Diplodon koseritzi* (Clessin, 1888), non-parasitic glochidium type: 4. In lateral view, 5. With growth bands, in post-larval stage found within the marsupium.
Abbreviations: a — angle; am — adductor muscle; r — rim; l — length; *li* — ligament; *cr* — *cirrus*; ct — cusps of glochidial tooth; dll — dorsal hinge length; dvp — displacement of the ventral point in relation to the middle of the dorsal line length; f — filament or flagellum; gb — growth bands; gt — glochidial tooth; gv — glochidial valve; h — height; p — phagocytic cells; po — posterior cilliary organ; sc — cilia; vp — ventral point.

mal border of the glochidium, and the presence of a ligament, reveals that after they hatch from the egg, the glochidia start their post-larval development while incubated inside the marsupium (Figs. 4, 5). The glochidia measurements were as follows (without counting the growth bands): length from 0.32 mm to 0.35 mm (mode and mean 0.34); height, 0.27 to 0.29 mm (mode 0.28, mean 0.27); dorsal line length, 0.20 to 0.22 mm (mode 0.20 to 0.21, mean 0.20); displacement of the ventral point in relation to the mid-

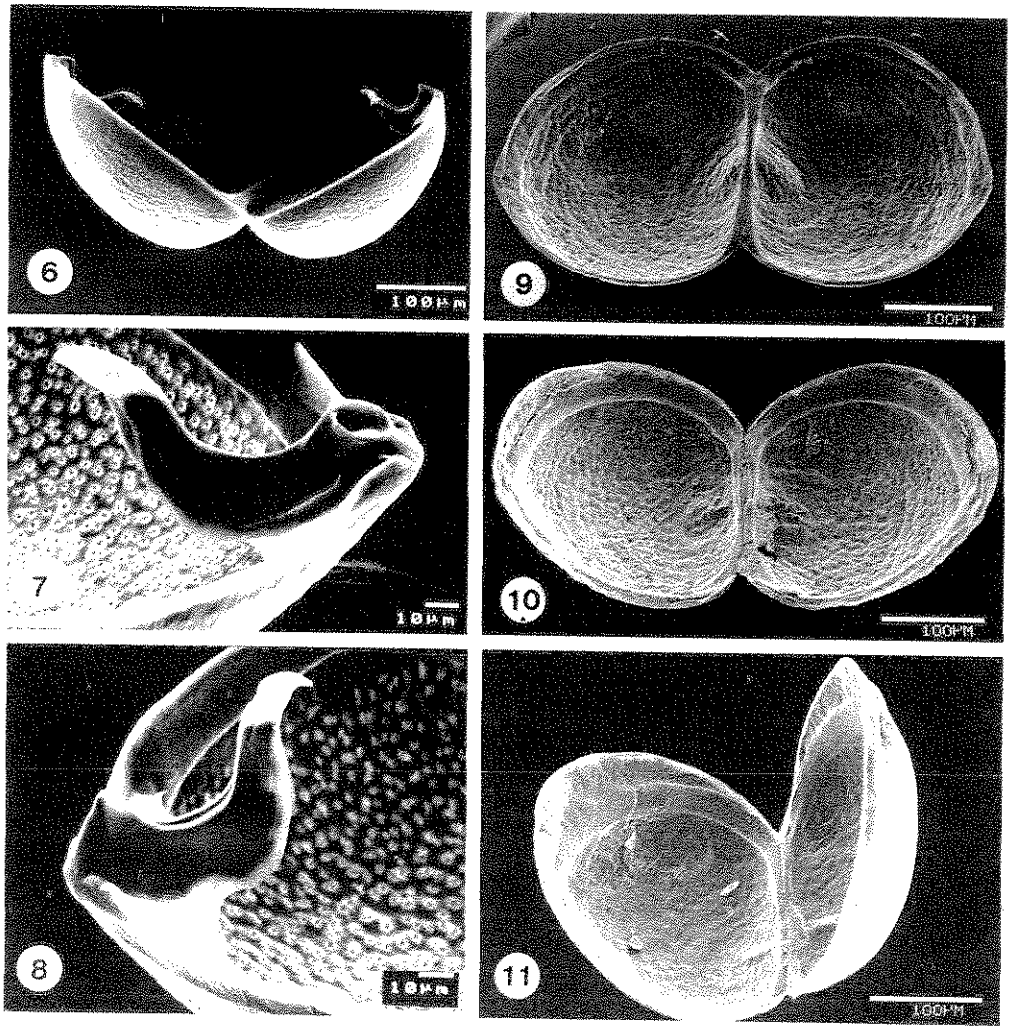
TABLE 1. Statistics of glochidia measurements

a. *Diplodon martensi* (Ihering, 1893)					
n = 40	Range	Mode	Mean	s	cv%
Length	0.28–0.32	0.29	0.297	0.0114	3.8396
Height	0.25–0.28	0.25	0.258	0.0095	3.2166
DLL	0.20–0.23	0.21–0.22	0.214	0.0093	4.3435
DVP	0.02–0.04	0.04	0.035	0.0071	20.3026
A°	12°–19°	15°	15	1.39	8.99
b. *Diplodon berthae* Ortmann, 1921					
n = 26	Range	Mode	Mean	s	cv%
Length	0.24–0.28	0.27	0.26	0.0092	3.47
Height	0.21–0.25	0.23	0.23	0.0089	3.89
DLL	0.17–0.21	0.19	0.18	0.0112	5.97
DVP	0.02–0.06	0.05	0.04	0.0114	24.83
A°	05°–16°	13°	12	2.4446	20.11
c. *Diplodon koseritzi* (Clessin, 1888)					
n = 40	Range	Mode	Mean	s	cv%
Length	0.32–0.35	0.34	0.34	0.0081	2.4041
Height	0.27–0.29	0.28	0.276	0.0065	2.3697
DLL	0.20–0.22	0.20–0.21	0.205	0.0059	2.8885
DVP	0.01–0.05	0.04	0.033	0.0111	33.6337
A°	10°–18°	12°	13	2.01	14.42
d. *Diplodon iheringi* Simpson, 1900					
n = 35	Range	Mode	Mean	s	cv%
Length	0.26–0.30	0.28	0.28	0.0096	3.41
Height	0.23–0.25	0.24	0.24	0.0058	2.41
DLL	0.17–0.21	0.20	0.19	0.0120	6.37
DVP	0.02–0.06	0.05	0.04	0.0098	21.87
A°	5°–15°	10°	10	1.99	18.93
e. *Diplodon charruanus* (Orbigny, 1835)					
n = 26	Range	Mode	Mean	s	cv%
Length	0.27–0.29	0.28	0.28	0.0061	2.20
Height	0.22–0.25	0.25	0.24	0.0091	3.77
DLL	0.18–0.20	0.19	0.19	0.0074	3.93
DVP	0.04–0.06	0.05	0.05	0.0082	16.34
A°	9°–15°	12°	12	1.74	14.11

DLL, Dorsal hinge length; DVP, Displacement of the ventral point in relation to the middle of the hinge length; A°, Angle of the ventral point in relation to the center of the hinge.

dle of the dorsal line ranged from 0.01 mm to 0.05 mm (mode 0.04, mean 0.03); angle of the ventral point in relation to the center of the dorsal line ranged from 10° to 18° (mode 12°, mean 13°) (Table 1c). The ventral point was distinguished with difficulty by being highly rounded even in newly hatched glochidia, this being the probable reason for the wider variation in the angle.

The recent released glochdium of *D. koseritzi* has the same morphological caracteristics of the young bivalve picture for *D. variabilis* by Parodiz & Bonetto (1963). It can move using its foot. No hooks or spines were observed on the valves. The foot is well developed and is able to stretch the length of the shell. Behind the foot, two short branchial filaments are visible on each side. The mantle borders are evident and thick. Many broods were observed within marsupia under a stereomicroscope. The egg has a transparent membrane, permiting the observation of the embryo, which is a white mass in its first phase. Later, small, white valves appear. When the embryos are more



FIGS. 6–8. Glochidium of *Diplodon berthae* Ortmann, 1921, of parasitic type, with "S" shaped teeth. 6. Frontal view of gaping glochidial valves. 7, 8. Details of glochidial teeth.
FIGS. 9–11. Glochidium of non-parasitic type, with gaping valves. 9. Glochidium of *D. iheringi* Simpson, 1914; 10, 11. Glochidia of *Diplodon charruanus* (Orbigny, 1835), found in the marsupium, in post-larval stage. 10. With poorly developed growth bands. 11. With well-developed growth bands.

developed and ripe to be released, the valves become pale yellow and the border is visible without hooks. The valves close and open when stimulated mechanically and the foot moves between them, even inside the egg.

Diplodon iheringi Simpson, 1900
(Fig. 9; Table 1d)

Specimens of this species were erroneously considered to be *D. charruanus* or *D. koseritzi* by Bonetto & Dreher-Mansur (1970). The glochidia are similar to those described above but slightly smaller in height and angle, with the following measurement ranges: 0.26 to 0.30 mm in length (mode and mean 0.28 mm); 0.23 to 0.25 mm in height (mode and mean 0.24 mm); 0.17 to 0.21 mm in dorsal hinge length (mode 0.20, mean 0.19 mm); 0.02 to 0.06 in the displacement of the ventral point (mode 0.05, mean 0.04); and the angle from 5° to 15° (mode and mean 10°). The ven-

tral point is not very pointed but more distinguishable than that of *D. koseritzi*. The rim of the glochidial valves very conspicuous and thick. Well-developed growth bands were observed on some larvae inside the marsupium.

Diplodon charruanus (Orbigny, 1835)
(Fig. 10–11; Table 1e)

The larvae of *D. charruanus* from the Taim canal are relatively small, measuring (without growth bands) from 0.27 mm to 0.29 mm in length (mode and mean, 0.28 mm); height was 0.22 mm to 0.25 mm (mode 0.25 mm, mean 0.24 mm); their dorsal hinge length ranged from 0.18 to 0.20 mm (mode and mean 0.19 mm); the displacement of the ventral point in relation to the middle of the dorsal line ranged from 0.04 mm to 0.06 mm (mode and mean 0.05 mm); and the angle of the ventral point in relation to the center of the dorsal line ranged from 9° to 15° (mode and mean 12°). The ventral point is also rounded, even in newly hatched glochidia, but more distinguished than those in *D. koseritzi*. Some of the recent delivered glochidia of the same female had developed growth bands and a small ligament (Figs. 10, 11).

DISCUSSION AND CONCLUSIONS

On the basis of the dimensions reported by Ortmann (1921a), Bonetto (1960a, b, 1961a–c, 1962a, b), Bonetto & Ezcurra (1965), and Alvarenga & Ricci (1979) for parasitic glochidia and those described herein, we conclude that *D. martensi* glochidia are close to the largest glochidia known, that is, those of *D. paulista* Ihering, 1893, the measurements of which are: 0.32 mm in length, 0.26 to 0.27 mm in height, 0.22 mm in dorsal line length, 0.03 mm in ventral point displacement, 18° to 19° obliquity angle, and 0.10 mm in tooth length. The glochidia of *D. martensi* have a considerable height in relation to length, but are less high than those of *D. piceus* (Lea, 1860), with a length and height of about 0.28 and 0.29 mm (Ortmann, 1921). They are proportionally larger than the glochidia of *D. besckeanus* (Dunker, 1849) and, even though they achieve the length of *D. multistriatus* (Lea, 1831) and *D. decipens* Ortmann, 1921, the latter are a little less high, with a respective height of 0.22 and 0.24 mm. The glochidia of *D. imitator* Ortmann, 1921, with a length and height of approximately 0.27 and 0.28 mm and a tooth length of 0.09 mm, are similar to *D. martensi* in height but are less elongate than the latter.

Parodiz (1968) considered *D. berthae* to be synonymous with *D. piceus* (Lea, 1860) and denotes this species as "the black form" of the Uruguay River. Specimens from the Sheidt Lagoon identified as *D. berthae* fully fit the description of this form. We prefer to retain the species *D. berthae* as valid for the Atlantic basin of southern Brazil, because the species *D. piceus* from the Uruguay River was confused with other species by Bonetto (1964, 1965) and Haas (1930, 1969).

Comparing the dimensions given by Ortmann (1921), Bonetto (1960a, b, 1961a–c, 1962a, b), and Bonetto & Ezcurra (1962, 1965) for non-parasitic glochidia, we state that *D. koseritzi* is among the largest, comparable to those of *D. hasemani* and *D. hildae*. In turn, the larvae reported as being *D. iheringi* Simpson *sensu* Bonetto (1961b) also have dimensions close to those of the glochidia measured here (i.e., 0.31 mm in length, 0.26 mm in height, 0.20 mm in dorsal line length, 0.02 to 0.03 mm in dorsal hinge displacement and a 15° to 17° angle). During a visit to the National Institute of Limnology, Santa Fé, Argentina, it was possible to examine material identified by Bonetto as *D. iheringi* for Guaíba, which were identical to the specimens of *D. koseritzi*. The dimensions of the glochidia were less than those of the specimens we measured, because they were immature or incomplete, with the border of the embryonic valve barely outlined. In turn, the *D. iheringi* of Bonetto (1961b) is synonymous with *D. charruanus*, according to Bonetto & Dreher-Mansur (1970).

The glochidia of *D. charruanus*, according to Ortmann (1921), measuring 0.31 mm in length and 0.26 mm in height, do not fully fit the dimensions of the specimens described here, and he did not mention the presence of growth bands. According to Bonetto (1962b), the glochidia of this species have growth bands and measure 0.30 mm in length, 0.26 mm in height, 0.18 mm in dorsal hinge length, a displacement of the ventral point of 0.03 to 0.05 mm, and an obliquity angle ranging of 9° to 14°. The glochidia samples of the species of the Taim canal are a little smaller than those mentioned by Bonetto (1962b), but in general the measurements fit with *D. charruanus* especially considering the angle.

Ortmann (1921) also described the glochidia of *D. hildae*, which measured 0.29 to

0.30 mm in length, 0.26 mm in height not counting the growth bands, and 0.34 to 0.35 mm in length by 0.28 to 0.29 mm in height counting the growth bands. On the basis of the above data, it is probable that the specimens of *D. charruanus* are closer to those of *D. hildae* than to those of *D. koseritzi*.

Internally, the hooked glochidia of Hyriidae differ little from those of the remaining Unionoidea described by Dawidoff (1928) and Harms (1909). The nonhooked glochidia about to be released from the gravid female look like young bivalves or the postlarva of the hooked glochidia after completing the parasitic phase in the fish (Parodiz & Bonetto, 1963). The young bivalve can move with its foot on substratum. Even embryos ready or about to be released but still enclosed by the egg membrane, have a foot between the hook-less valves. No information is available on the complete organogenesis of glochidia that do not parasitize fish and which develops directly in the marsupium of the gravid female just before the postlarval phase. The presence of growth bands in some recently released non-fishparasitic glochidia show that they can grow as post-larvae during a short time in the marsupia.

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