Heard
1977

Malacological Review, *1977*, *10*: *59-70*

ANATOMICAL SYSTEMATICS OF *CRISTARIA PLICATA* (LEACH) (PELECYPODA: UNIONIDAE: UNIONINAE)[1,2]

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ABSTRACT

The anatomy of *Dispas plicatus* Leach, the type species of the Asian naiad genus *Cristaria* Schumacher, is described from 3 growth forms from a common population. The findings are employed in characterizing *Cristaria* as members of the Unionidae: Unioninae s.s., and in interpreting the phylogenetic position of that nominate subfamily within the Unionidae.

Significant character states include unipartite septa and water-tubes in the outer, marsupial demibranchs, dimorphic septal spacing between outer and inner demibranchs of females but not males and notably within the marsupial demibranchs, vestigial septal perforations, subtriangular, hooked glochidia and concentric beak sculpture. Specializations are reduction in the sizes of the supra-excurrent opening and the foot, and vestigial hinge dentition.

The Asian Lamellidentinae are proposed as being ancestral to the Unioninae s.s., among which *Cristaria*, in comparison to *Unio*, are considered to be derived. It is also suggested that the Anodontinae s.l. were derived from the Unioninae s.s.

INTRODUCTION

The generic-group taxon *Cristaria* Schumacher 1817 (type species, by monotypy: *C. tuberculata* Schumacher 1817) replaced by objective synonymy the name *Dispas* Leach 1815 (type, by monotypy: *D. plicatus* Leach 1815), which Laurenti (1768) had previously applied to a group of reptiles. Haas (1969a) characterized Recent members of this eastern and southeastern Asian group of freshwater mussels as comprising 2 subgenera (*Cristaria* s.s. and *Pletholophus*), 3 species and 2 subspecies. Modell (1964) cited *Cristaria* from Oligocene to mid-Miocene deposits in Japan, the Miocene to Upper Pliocene of northern Baikal and the Upper Pleistocene of northern China, and *Pletholophus* (treated as a genus of Unionidae:Anondontinae) from Oligocene beds in Japan. Haas (1969b) simply noted Tertiary to Recent *Cristaria* s.s. from eastern Asia, and only Recent *C. (Pletholophus)* in eastern and southeastern Asia.

Simpson (1900, 1914) placed *Cristaria* in the Unionidae:Unioninae:Heterogenae (the latter name represents a division of the Unionidae:Lampsilinae; see Heard & Guckert, 1970; Burch, 1975). The genus was subsequently classified in the Unionidae:Anodontinae by Thiele (1934), Haas (1969a,b) and Starobogatov (1970), and in the Unionidae:Hyriopsinae by Modell (1942, 1964), and in the Amblemidae:Hyriopsinae by Brandt (1974).

All of the above records and classifications were based on shell features, but, as noted by Heard & Guckert (1970), classifications of naiades based on hard-part morphology may differ significantly from those founded on soft-part anatomy and on reproductive features.

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[1] This investigation was supported, in part, by the Smithsonian Institution's "Waterborne Diseases of the Mekong River Drainage" research project.

[2] This paper is dedicated to Dr. J.P.E. Morrison in honor of his many contributions to malacology prior to his retirement on 31 July 1975.

The purposes of this report are to describe what I consider to be the systematically significant animal features of the type species of *Cristaria* and to provide an interpretation of the systematic position and affinities of this genus and of the subfamily of which it is a member.

MATERIAL AND METHODS

This report is based on a single collection of 16 animals made on 10 July 1971 from Kut Kwang, a lake about 0.5 km southwest of Ban Kut Kwang (7.2 km south of Khon Kaen on Highway 2), Khon Kaen Province, Thailand. The shells of these animals have been deposited in the U.S. National Museum of Natural History, and empty shells from the same collection are in the Thai National Reference Collection, Bangkok.

The methods employed here are those described by Heard (1975) and Heard & Vail (1976). Most anatomical features were revealed by gross dissection, although details of the structural organization of the demibranchs and also the sex of each individual were determined by histological sections.

SHELLS

Three shell forms occurred in the material examined: 4 males and 4 females of a smaller, more alate type (Fig. 1), 3 males and 3 females of a larger, more ovate type (Fig. 2), and 1 male and 1 female of intermediate size and shape (see Table 1). The anatomies of these forms differed only in some size relationships, and, because the anterior and especially the posterior wing of the shell could have been broken off or worn down with increased age (such a condition is particularly notable in the unionid *Hyriopsis bialata* Simpson; pers. observ.), I believe that these variations reflect allometric changes. The anatomical descrip-

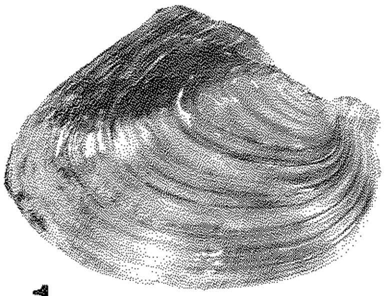
TABLE 1. Size relationships (mean ±1 standard deviation) in mm of 3 "forms" of *Cristaria plicata*.

Length	Form		
	Small, alate (N = 8[1])	"Intermediate" (N = 2)	Large, ovate (N = 6)
Shell length[2]	103.77 ± 10.57	130.50 ± 9.19	150.66 ± 8.53
Length of SO[3]	13.14 ± 2.35	11.30 ± 5.51	9.97 ± 2.24
Length of PS	25.81 ± 2.90	30.60 ± 4.38	31.38 ± 2.98
Length of EO	8.10 ± 1.47	8.95 ± 1.06	11.03 ± 0.90
Length of IO	14.87 ± 1.42	20.80 ± 0.99	26.12 ± 1.20

[1] In 1 female the supra-excurrent opening was obliterated by the pallial suture (total length: 46.3 mm).

[2] Up to 300 mm *fide* Haas (1969a). Thai specimens rarely exceed 160 mm in length (Brandt, 1974).

[3] EO = excurrent opening; IO = incurrent opening; N = number of specimens; PS = pallial suture; SO = supra-excurrent opening.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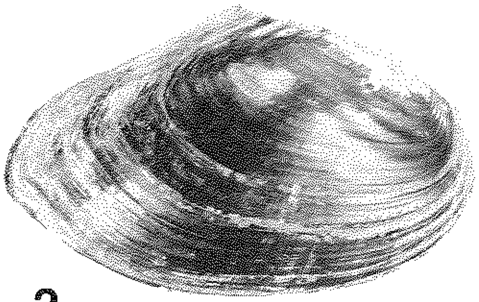
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FIGS. 1-2. Right valve of *Cristaria plicata.* FIG. 1. Small, alate form; 100.0 mm long. FIG. 2. Large, ovate form; 161.0 mm long. (Animals from these shells are depicted in Figs. 3-4.)

tion given here is common to the animals of all 3 shell forms unless stated otherwise.

Beak sculpture, reported by Simpson (1900,1914), Modell (1942), Haas (1969a,b) and Brandt (1974) to be initially double-looped and subsequently concentric single-looped ridges, was obliterated by decoriation in all but 1 specimen. The beak sculpture on this specimen consisted of fine, single-looped, low concentric ridges toward the ventral part of the beaks, and was followed onto the upper part of the disc by several low but wide, distantly spaced, concentric bars. However, although concentric, these ridges and bars were not parallel to the growth striae but lay at a slight angle to them (see Fig. 1).

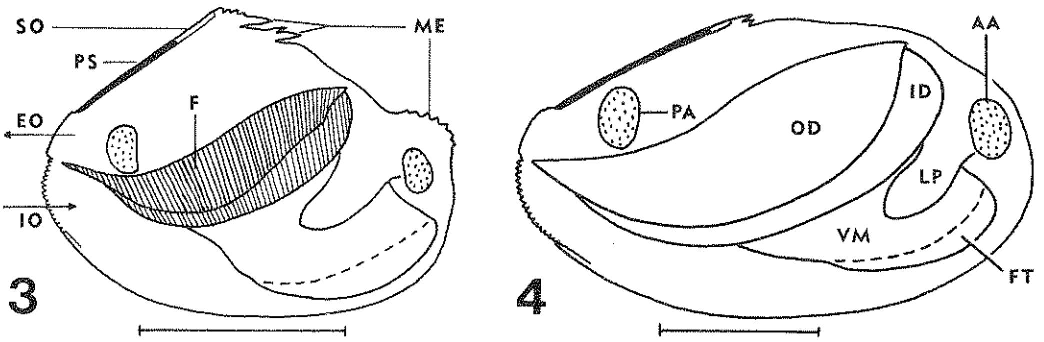
Prior workers presented varying descriptions of hinge dentition. Simpson (1900, 1914) recorded the presence or absence of a faint pseudocardinal tooth in each valve and the presence (or absence in "adult shells") of a single, short lateral tooth in each valve. Modell (1942, 1964) did not treat features of this genus or species, but noted a loss of the pseudocardinals within the Hyriopsinae, in which he placed *Cristaria* with *Hyriopsis.* Whereas Brandt (1974) cited obsolete pseudocardinals and strong, long, lamelliform laterals, Haas (1969a,b) previously considered all such prominences to be claustra, viz., structures presumably only analogous to hinge teeth. It is evident that there is considerable intraspecific variation in *C. plicata,* because all 16 shells examined here were entirely edentulous.

ANATOMY

Mantle

The small anterior wing and the more prominent posterior wing of the small, alate shell form contained thin extensions of the mantle (Fig. 3: ME) that were dorsally crenulated and horizontally cleft, respectively. In the large, ovate form (Fig. 4) the wings of the shell were missing, the anterior mantle extension was absent, and the incised posterior mantle extension was reduced in size. The mantle extensions in the specimens of intermediate size and shape were only moderately developed.

A pallial suture (Figs. 3, 5: PS), about 3 times longer than the excurrent opening (EO), separated the latter from the supra-excurrent (supra-anal) opening (SO). The excurrent opening was about slightly more (alate form) to slightly less (ovate form) than 1/2 as long as the incurrent opening (IO), and was nearly 2/3 of (alate form) to slightly greater than (ovate form) the length of the supra-excurrent opening. The incurrent opening was only slightly (alate form) to about 2½ times longer (ovate form) than the supra-excurrent opening. These variations reflect changes in proportion with size (age): decrease in the supra-



FIGS. 3-4. Dextro-lateral aspect of the animal of *Cristaria plicata*, with the mantle removed from over the branchial chamber. FIG. 3. Small, alate form. FIG. 4. Large, ovate form. Scale: 50 mm for each figure. (Shells of these animals are shown in Figs. 1-2.) AA = anterior adductor muscle; EO = excurrent (anal) opening; F = filament; FT = foot; ID = inner demibranch; IO = incurrent (branchial) opening; LP = labial palp; ME = mantle extension into wing; OD = outer demibranch; PA = posterior adductor muscle; PS = pallial suture; SO = supra-excurrent (supra-anal) opening.

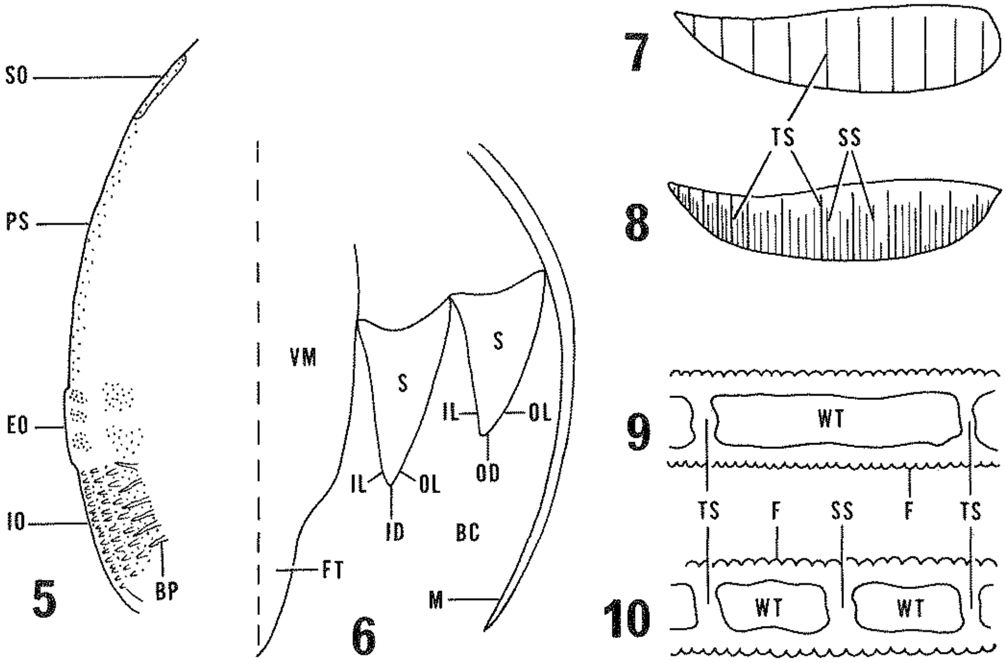
excurrent opening and concomitant increase in the pallial suture, slight elongation of the excurrent opening, and significant lengthening of the incurrent opening (see Table 1). The ventral margins of the mantle sheets were free (i.e., not conjoined) anterior to the incurrent opening.

The inner surface of the inner lobe of the mantle margin was simple (i.e., lacked papillae), except at the incurrent opening. The incurrent, branchial papillae (Fig. 5: BP) were usually tereted and only rarely bifid apically, and were arranged in 4 rows. The anterior-most row had the largest and fewest papillae, and the sizes decreased and numbers increased toward the posterior-most row.

The pigmentation pattern on the inner surface of the inner lobe of the mantle sheets was nearly constant in preserved animals (see Fig. 5). A faint dusting of brown pigment formed a very narrow band along the apex of the supra-excurrent opening (SO) and the adjacent pallial suture (PS). The low flaps of the excurrent opening (EO) had a white apex, small blotches of moderately concentrated black, melanistic pigment immediately anterior to the apex, and, anterior-most, large blotches of light dustings of melanin. The incurrent opening (IO) had a white background color that was covered by a faint to light dusting of melanin between the papillae, and by rust-orange pigment on the papillae (heavy concentration on the anterior-most row, to faint on the posterior-most row).

Demibranchs

The dorsal margin of the outer lamella (Fig. 6: OL) of the outer demibranchs (OD) was united for its entire length with the inner surface of the mantle, thereby creating a complete diaphragm that separated the branchial chamber from the suprabranchial chamber. The dorsal margin of the inner lamella (IL) of the outer demibranchs (OD) was joined for its entire length to the dorsal margin of the apposing outer lamella (OL) of the inner demibranchs (ID). The dorsal margin of the inner lamella (IL) of each inner demibranch (ID) was attached to the visceral mass (VM) for about its anterior-most 1/8 to 1/6 of its length in the alate form and 1/10 to 1/7 in the ovate form, was free from the visceral mass for the next posterior 1/3 to nearly 1/2 of its length in the alate form and about 1/2 in the ovate form, and was united, behind the visceral mass, with the dorsal margin of the other inner demibranch for nearly the posterior-most 1/2 of its length in the alate form and for nearly



FIGS. 5-10. Posterior mantle openings and gills in *Cristaria*. FIG. 5. Posterior mantle openings in a large, ovate *Cristaria plicata*, with pigmentation pattern (described in the text) and papillae shown. BP = branchial papillae; EO = excurrent opening; IO = incurrent opening; PS = pallial suture; SO = supra-excurrent opening. FIG. 6. Transverse aspect of 1 side of *Cristaria plicata*. BC = branchial chamber; FT = foot; ID = inner demibranch; IL = inner lamella; M = mantle; OD = outer demibranch; OL = outer lamella; S = interlamellar septum; VM = visceral mass. FIGS. 7-8. Dextro-lateral representations of the right demibranchs of *Cristaria plicata*, with the outer lamella removed to show heights and spacing of interlamellar septa. Fig. 7. Non-marsupial demibranch (all 4 in males, but only inner pair in females). Fig. 8. Marsupial, outer demibranch with organization of most females. SS = short septa (densely spaced); TS = tall septa (typically distantly spaced, but more crowded in posterior end of female outer demibranchs). FIGS. 9-10. Frontal aspect of parts of different demibranchs of *Cristaria plicata*. Fig. 9. Non-marsupial demibranch. Fig. 10. Marsupial region of female outer demibranch. F = filament (in transverse section); SS = short septum; TS = tall septum; WT = water-tube.

1/3 to almost 1/2 in the ovate form.

The outer lamellae of both inner and outer demibranchs were higher than the inner lamellae (see Fig. 6), and each lamella of the inner demibranch was higher than the corresponding lamella of the outer demibranch. The interlamellar septa (S) in the inner demibranchs were higher than those in the outer demibranchs in 12 of the 16 animals, and slightly lower in the others.

The interlamellar connections in all 4 demibranchs of both males and females were developed as septa (Figs. 6-10: S, SS, TS) that ran parallel to the filaments (Fig. 3: F). The septa showed 3 kinds of variation: tall (about 4/5 to 9/10 as high as the inner lamella) or short (about 1/10 to 7/10 as high as the tall septa), comparatively distant or dense spacing, and imperforate or perforated constitution. The tall septa (TS) were distantly spaced in all demibranchs of both sexes (Figs. 7-10), but were more crowded in the posterior 1/5 of the female outer demibranchs. Several short septa (SS) occurred between consecutive tall septa throughout the outer demibranchs of most females (Fig. 8) but only for the middle 3/5 and 1/10 of the length of these demibranchs in 1 alate and 1 "intermediate" female, respectively; in all of these cases the short septa were densely spaced. Short septa in all non-marsupial demibranchs were rare and of sporadic distribution. The water-tubes (Figs. 9-10: WT) were flanked laterally by about 20 filaments (F) between distantly spaced septa, by about 10 filaments between the tall septa in the posterior 1/5 of female outer demibranchs, and by only about 6 filaments between densely spaced septa (Table 2). Most septa in all demibranchs of both sexes were continuous and complete (i.e., imperforate), although the densely spaced septa in the female outer demibranchs had a faint trace of a vertical row of up to 11 apparently closed performations. Rarely, a single, small, open performation was found in a densely spaced septum in the middle or anterior of 3 female outer demibranchs, and also in a middle, distantly spaced septum of some outer (1 specimen) and inner demibranchs (3 specimens) of some males.

All septa and water-tubes of all demibranchs of both males and females were simple, i.e., not vertically divided as in the marsupial demibranchs of the Unionidae:Anodontinae (see Heard & Guckert, 1970; Heard, 1975). None of the 8 females was gravid, but comparison of the structural organization of the 4 female demibranchs suggests that the marsupia are located in just the outer demibranchs, and perhaps only in the region of the densely

TABLE 2. Numbers of filaments flanking water-tubes in different demibranchs of *Cristaria plicata* (mean ± 1 standard deviation; based on 10 water-tubes for each condition).

Shell form Part of demibranch	Outer Demibranchs		Inner Demibranchs	
	Males	Females	Males	Females
Small, alate				
Central, dorsal	24.90 ± 4.04	6.40 ± 1.58	24.20 ± 5.83	23.70 ± 2.21
Central, ventral		6.60 ± 2.12		
Posterior, dorsal		11.00 ± 2.40		
Posterior, ventral		6.10 ± 1.37		
"Intermediate"				
Central, dorsal	21.70 ± 3.59	6.50 ± 1.08	23.20 ± 4.49	21.00 ± 3.13
Central, ventral		6.50 ± 1.58		
Posterior, dorsal		10.50 ± 2.32		
Posterior, ventral		5.20 ± 0.79		
Large, ovate				
Central, dorsal	20.00 ± 3.94	6.20 ± 1.47	21.40 ± 3.20	24.50 ± 3.75
Central, ventral		6.70 ± 1.77		
Posterior, dorsal		10.20 ± 2.39		
Posterior, ventral		6.10 ± 1.37		

spaced septa as is the case in many other mussels in southeastern Asia (Heard, unpubl.).

Labial palpi

The palpi (Fig. 4: LP) were slightly more than 1/3 to nearly 1/2 as long as the inner demibranchs, and were not contiguous with them. The outer member of each palp was laterally attached to the inner surface of the mantle for about 1/3 to nearly 2/3 of its length in the alate form, and for slightly more than 1/2 of its length in the ovate form. The 2 members of each palp were dorsally joined together for almost their entire length in all forms.

Foot

These naiades were collected from near the center of a large, shallow lake (< 2 m maximum depth). The substrate in which the animals were nearly completely buried was a very soft muddy silt. A very conspicuous anatomical feature of all of the animals was a very small foot, which suggests that they are poor burrowers except in such soft substrates. I did not find this species in harder, sand substrates at more than 150 other localities (mostly streams, and some other lakes) in northeastern Thailand.

LARVAE

Haas (1922) described and illustrated subtriangular, hooked glochidia from Chinese *Cristaria plicata*, as did Inaba (1941) and Higashi & Hayashi (1964) from Japanese material. Only Haas mentioned the presence of a larval thread, and only Inaba noted the existence of minute spines on the hooks. The larval valves in each study were higher (up to 338 μm) than long (up to 309 μm). In addition, Higashi & Hayashi recorded the presence of glochidia in November through March and their absence in the rest of the year, and estimated up to 500,000 glochidia per animal of 100-135 mm in length.

Eight of the present 16 animals were females, and the rest were males; no hermaphrodites were present. Morphologically mature gametes were present in each animal, but none of the females was gravid.

OTHER FEATURES

No digenetic trematode larvae or aspidogastrean trematodes were found in any of the 16 mussels, but nymphal and adult stages of an unidentified unionicolid water-mite were observed between the demibranchs of 14 of the animals.

DISCUSSION

Intraspecific variation

Basing his description on specimens from China, Haas (1922) provided a prior anatomical account of *Cristaria plicata*. The present findings agree with those of Haas except in terms of the relative size of the posterior mantle openings and pallial suture, his report that the inner lamella of the inner demibranchs was attached to the visceral mass, and his statement that the marsupia occupied the entire outer demibranchs. Moreover, although he described general variation in septal height and spacing (without mention of presence or absence of perforations), Haas' illustration of a marsupial demibranch shows the absence of short septa in both ends.

The discrepancy between these accounts of the attachment of the inner demibranchs to the visceral mass or their detachment from it is enigmatic. Interspecific, congeneric variation in this feature is otherwise known only in the Nearctic genus *Strophitus* (Unionidae: Anodontinae; Heard & Fuller, unpubl.), but intraspecific variation has not been hitherto reported.

Interspecific variation

Knowledge of interspecific anatomical variation in *Cristaria* is provided by Haas' (1922) description of Taiwanese *C. discoidea* (Lea), the type species of the subgenus *Pletholophus*, and by Inaba's (1941) description of glochidia from Korean material of the same species. Wings and mantle extensions are lacking in *C. discoidea*. Although there is dimorphic septal spacing between the inner (distant) and outer (dense) demibranchs of females, short septa are evidently entirely absent. The glochidia are smaller (up to 277 µm high and 259 µm long) than in *C. (C.) plicata*. As also for the latter, Haas reported the attachment of the inner demibranchs to the visceral mass, failed to note the presence or absence of septal perforations, and concluded from non-gravid animals that the entire outer demibranchs serve as marsupia. Haas stated that his *C. discoidea* had been poorly preserved, but, if his findings are accurate, this is the first known case among naiades of congeneric variation in the presence or absence of short septa in marsupial demibranchs.

Generic comparisons

Other Asian mussels with subtriangular, hooked glochidia are members of *Anodonta, Inversidens, Lanceolaria, Simpsonella* and *Unio;* all but *Inversidens* are known to possess dimorphic septal spacing (Haas, 1922; Inaba, 1941; Higashi & Hayashi, 1964). Of these, the edentulous *Anodonta* have tripartite marsupial septa and water-tubes and variations of concentric beak sculpture (Ortmann, 1910a, 1912; Burch, 1975; Heard, 1975), and *Unio* have unipartite marsupial structure, complete hinge dentition and variations of zigzag beak sculpture (Haas, 1922; Heard & Vail, 1976). *Lanceolaria* and *Simpsonella* also have zigzag sculpture and presumably unipartite marsupial structure (see Haas, 1922), but, whereas *Lanceoloaria* have complete dentition, *Simpsonella* have only vestigial hinge teeth. *Inversidens,* with complete dentition but of unknown pattern of beak sculpture, have not been anatomically described, and reports on the larvae in this nominal genus are inconsistent. Inaba (1941) described subtriangular, hooked glochidia from the type species, *I. brandtii* (Kobelt), whereas Higashi & Hayashi (1964) recorded subovate, hookless glochidia from purportedly the same species; these workers described both kinds of larvae from among several alleged congeners of *Inversidens.* Such congeneric variation is unknown elsewhere among the naiades, and it is likely that both misidentification and misclassification created this confusion.

Among other anatomically described generic groups of Asian unionids, the larvae of *Cuneopsis* and *Schistodesmus* are unknown, the glochidia of *Acuticosta* are subovate and hookless but possess 2 tuberculated, truncated projections, and the glochidia of *Chamberlainia, Hyriopsis, Lamellidens, Physunio, Pseudoparreysia, Trapezoideus* and *Uniandra* (=*Contradens*) are subovate and hookless. All of these mussels have unipartite marsupial organization and dimorphic septal spacing, and at least *Hyriopsis, Lamellidens, Physunio, Trapezoideus* and *Uniandra* have perforated marsupial septa (Ortmann, 1911, 1916, 1917; Prashad, 1918a,b, 1919a; Haas, 1922; Bloomer, 1931; Woodward, 1964, 1965; Heard, 1974).

Although *Cristaria* and *Unio* differ in beak sculpture and hinge dentition, *Cristaria* are most similar to *Unio* in terms of larval and animal features. Included among the latter are septal perforations, which, however, appear to be secondarily vanishing in *C. plicata.* On the other hand, the perforations may be of seasonal occurrence, as has been suggested for them in *Unio* (see Heard & Vail, 1976).

Subfamilial comparisons

Heard & Guckert (1970) characterized subfamilies of Nearctic naiades according to differences in anatomy, period of larval incubation, and presence or absence of hooks on the larval shell. Intrasubfamilial variation in larval form is known among mussels only in the Unionidae:Lampsilinae (viz., celtiform and hookless but 4-spined glochidia in *Proptera,* and subovate, hookless and lacking spines in all other groups; Ortmann, 1912), and Modell's (1942, 1964) and Brandt's (1974) placement of *Cristaria* with *Hyriopsis* in the Hyriopsinae seems unwarranted because the glochidia of *Hyriopsis* are subovate and hookless.

Subtriangular, hooked glochidia of the kind found in *Cristaria* are characteristic of the Unionidae:Unioninae s.s. [as restricted by Morrison (1955) and Heard & Guckert (1970); *non* Simpson (1900, 1914), Ortmann, 1910a, 1912), Modell (1942, 1964), Haas (1969a,b), *nec* Burch (1975)] and Anodontinae s.l. [*sensu* Ortmann, Heard & Guckert and Burch (=Anodontinae s.s. + Alasmodontinae *sensu* Modell, Morrison and Haas)]. Unionine *Unio* and anodontine *Strophitus* have in common dimorphic septal spacing and at least seasonally perforated marsupial septa (Heard & Vail, 1976, and Heard & Fuller, unpubl., respectively), but only the Anodontinae s.l. possess a tripartite marsupial organization with imperforate septa in all but some *Strophitus.* Morrison's (1955) listing of the tripartite condition for all Unionidae is in error. Although reduced hinge dentition is common among anodontine groups (see Haas, 1969a,b; Burch, 1975), unipartite marsupial structure relates *Cristaria* to the Unioninae s.s. (*sensu* Heard & Guckert), in which group this genus is herein placed.

Familial groupings

The present findings on dimorphic septal spacing between outer and inner demibranchs of female but not male *Cristaria plicata* support Haas' (1922) report that *C. plicata* and *C. discoidea* are exobranchous. That the marsupia occur in only the outer demibranchs confirms *Cristaria* as members of the Unionidae (*sensu* Heard & Guckert, 1970).

Ensidens, Harmandia, Indonaia, Lamprotula, Parreysia, Pilsbryoconcha, Pseudodon, Ptychorhynchus, Rectidens, Scabies and *Solenaia* (=*Balwantia*) are Asian members of the tetragenous Amblemidae (*sensu* Heard & Guckert, 1970), with subovate, hookless glochidia except in *Indonaia,* whose larvae are of uniquely heightened shape and have hooks (Ortmann, 1910b; Ghosh, 1918; Prashad, 1918b, 1919a,b; Haas, 1922; Woodward, 1969; Heard, 1974; Brandt, 1974).

Unfortunately, the nominal Asian genera *Arcidopsis, Arconaia, Caudiculatus, Ctenodesma, Diaurora, Discomya, Elongaria, Lepidodesma, Nannonaia, Oxynaia, Pressidens, Prohyriopsis, Protunio, Pseudobaphia, Radiatula, Rhombuniopsis, Schepmania* and *Unionetta* are known only from adult shell characters (see Haas, 1969a,b), and neither their relations to *Cristaria* nor even their familial memberships can yet be determined. Patterns of beak sculpture in these groups are: concentric in *Pressidens* and *Rhombuniopsis,* zigzag in *Ctenodesma, Diaurora, Oxynaia, Radiatula* and *Unionetta,* and unknown in the rest. All have complete hinge dentition, except in *Pseudobaphia* (laterals reduced) and *Lepidodesma* (all teeth vestigial).

Phylogenetic affinities

Despite discordance between shell and animal classifications of mussels, caused by convergence in either or possibly both sets of characters, and insufficient information about many mussels, it is possible to advance interpretations of the systematic position of (1) *Cristaria* within the Unioninae s.s. and (2) the nominate subfamily within the Unionidae.

I consider the following features in *Cristaria* to be derived character states in comparison to the alternative conditions in *Unio,* the only other currently known group of unionine naiades: concentric beak sculpture, a nearly edentulous hinge, incipient elongation of the marsupial region of the outer demibranchs, incipient secondary loss (?) of septal perforations, incipient loss of the supra-excurrent opening due to elongation of the pallial suture below it, and reduced size of the foot. Even after omission from consideration of the conspicuous specializations (viz., reductions of the dentition, supra-excurrent opening and foot), *Cristaria* can be treated as "more advanced" than *Unio.*

Evaluation of the features of Asian groups necessitates a reinterpretation of the affinities of unionids as proposed by Heard & Guckert (1970: 343). Those workers concluded that the Unioninae s.s. may have evolved as a side branch of the line leading directly from the Pleurobeminae to the Anodontinae s.l., but they overlooked the existence of the Lamellidentinae Modell, 1942 (=Hyriopsinae =Contradentinae, both Modell, 1942). Members of that Asian group, containing *Chamberlainia, Hyriopsis, Lamellidens, Physunio, Pseudoparreysia, Trapezoideus* and *Uniandra,* are anatomically similar to the Unioninae s.s. in that all have unipartite marsupial structure, dimorphic septal spacing in the outer demibranchs and perforated marsupial septa, but differ from them by generating subovate, hookless glochidia (Ortmann, 1911, 1916, 1917; Prashad, 1918a,b, 1919a; Haas, 1922; Bloomer, 1931; Woodward, 1964, 1965; Heard, 1974). In addition, at least *Hyriopsis* and *Physunio* have long-term larval incubation (Heard, unpubl.), a feature of *Cristaria* (see Higashi & Hayashi, 1964) but not *Unio* (Heard & Vail, 1976). Finally, all lamellidentines but *Hyriopsis,* with delicate concentric ridges, have zigzag beak sculpture, and all have complete hinge dentition (Haas, 1969a; Brandt, 1974).

Asian (or other?) Lamellidentinae probably gave rise independently to the Unioninae s.s. of the Eastern Hemisphere and to the Nearctic Pleurobeminae (=Popenaiadinae) and Lampsilinae. These evolutions, for which detailed documentation will be published separately, involved changes in septal structure and organization and also marsupial size in the outer demibranchs in the latter 2 groups, and in larval form in the derivation of the Unioninae s.s. The Anodontinae s.l. (represented throughout the Northern Hemisphere, but of significantly greater generic and species diversity in the Nearctic Region) were most likely derived from the Unioninae s.s. through the assumption of tripartite marsupial organization and, in the majority of species, by elongation of the marsupia and loss of septal perforations. Indeed, tripartite marsupia comprise the only significant structural feature (of animal or shell) that distinguishes the anodontine *Strophitus* from the unionine *Cristaria.* That *Hyriopsis* and *Physunio* have long-term larval incubation, whereas most unionines (viz., *Unio*) display short-term incubation, does not invalidate these conclusions. Duration of incubation is a generic feature among pleurobemines and lampsilines (see *Popenaias* and *Obliquaria,* respectively, in Heard & Guckert, 1970), and some of the lamellidentine groups may yet be shown to be of the short-term habit.

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