

# SHELL MORPHOGENESIS OF *ALVEINUS OJIANUS* (BIVALVIA: KELLIELLIDAE) AND TAXONOMIC SIGNIFICANCE OF THE EARLY FEATURES

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## ABSTRACT

The ontogenetic development of hinge, ligament and other morphological features of a paedomorphic bivalve mollusc *Alveinus ojanus* (Yokoyama, 1927) of 1.8–2.0 mm shell length have been examined by light and scanning electron microscopy. At a shell length of 200–220 µm, the provinculum of *A. ojanus* bears eight or nine larval denticles, the primary ligament pit and the cardinal tooth-complex 3a–3b, which is located anteriorly. Subsequent to the latter the cardinal tooth I forms. The lateral tooth Lp1 develops in the juvenile stage at a shell length of 700–1150 µm. In adult *A. ojanus*, the provincular denticles are reduced, tooth-complex 3a–3b and tooth Lp1 develop with little change, and the ligament pit is broadened due to the hinge plateau. A comparison of morphogenesis of *A. ojanus* with that of related families shows differences from the Arctidae but similarities with some Veneridae. The most significant morphological features of the larval and juvenile shell, which suggest taxonomic relationship of *A. ojanus* (and, possibly, other kelliellids) with the Arctidae and Veneridae, appear to be: dentition of the provinculum; distinctness and location of the primary ligament pit; topology and sequence of formation of the cardinal teeth.

## INTRODUCTION

In the ontogenetic development of bivalve molluscs, consisting of four to nine stages (Waller, 1981; Malakhov & Medvedeva, 1985; Mouëza, Gros & Frenkiel, 1999), the pelagic larval stage and subsequent juvenile stage are of great importance both for understanding the species ontogeny and for clarifying the taxonomic status and phylogenetic relationships of a taxon. However, our knowledge of larval morphological features and their significance for bivalve taxonomy (usually based on the adult characters alone) is contradictory. From one point of view, these features have a high morphological similarity that allows taxa to be distinguished only at high taxonomic rank (Malakhov & Medvedeva, 1986; Goodsell *et al.*, 1992; Cragg, 1996). On the other hand, larval and early postlarval stages, especially of commercially important species, can be identified at the specific level (Rees, 1950; Yoshida, 1953, 1964; Miyazaki, 1962). At the same time, the phylogenetic and taxonomic significance of the juvenile morphological features of most bivalves, including common species, are still insufficiently studied.

This is also true for *Alveinus ojanus* (Yokoyama, 1927), a small bivalve of 1.8–2.0 mm shell length belonging to the family Kelliellidae. It is widespread in the shallow bays of the Sea of Japan as well as off the Pacific coast of Japan (Habe, 1953, 1977; Scarlato, 1981; Kafanov, 1991). From our data, it is also distributed from the South Kuril Strait and Aniva Bay in the Sea of Okhotsk to the Gulf of Thailand in the South China Sea. Forms similar to *A. ojanus* also inhabit the Red and Arabian Seas (Oliver & Zuschin, 2001). *Alveinus ojanus* is common in sandy muds at depths of 2–22 m, where its density may exceed 1000 per m<sup>2</sup>. Regular recruitment makes it possible to find all ontogenetic stages in settlements of adults. But, despite this wide distribution and available data on the morphology of adult and some early ontogenetic stages of *A. ojanus* (Tanaka, 1982; Sakai & Sekiguchi, 1992), as well as other species of the Kelliellidae

(Knudsen, 1970; Bernard, 1989; Warén, 1989; Hayami & Kase, 1993), their taxonomic status is still debated, as indeed is that of the whole family Kelliellidae (Allen, 2001).

In the present study, we examine the shell ontogeny of *A. ojanus* from the pediveliger stage to the adult and compare its development with that of related taxa.

## MATERIAL AND METHODS

Larval, juvenile and adult specimens of *A. ojanus* from Amursky Bay and Vostok Bay in the Sea of Japan were used in this study. Larvae were sampled using a 96-µm plankton net in August–September, 2000 and 2001. Juveniles and adults were collected with a dredge from the research vessel *Lugovoye* in September 1999 and sampled with a hand drag and by SCUBA diving to 12–14 m depth in July–September, 2000 and 2001.

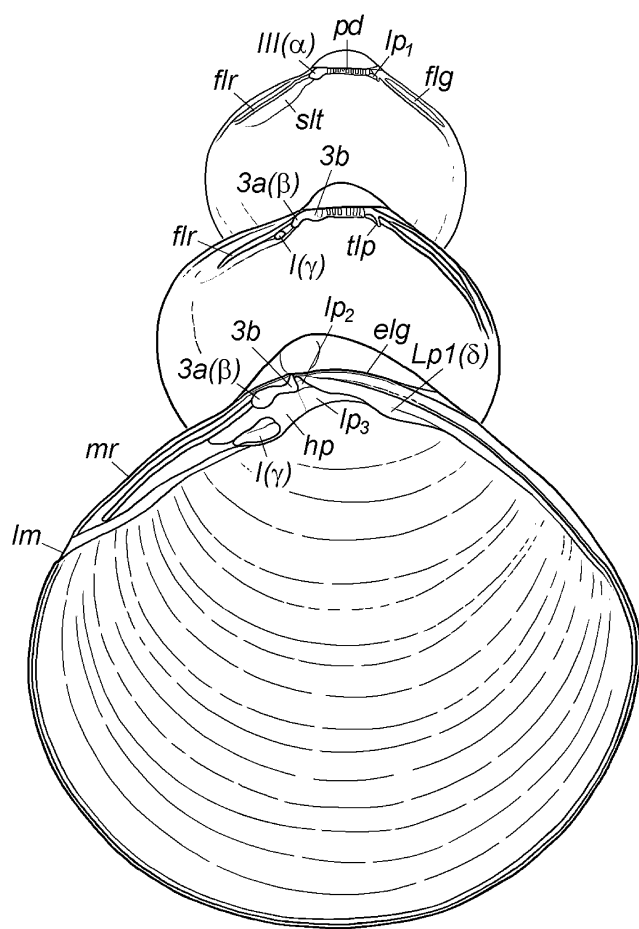
Larvae, juveniles and adults of *A. ojanus* were preserved in 96% ethanol. Specimens were cleaned with a 5–10% solution of sodium hypochlorite to remove the soft tissues. The shells were thoroughly rinsed with distilled water and then dehydrated in a series of ethanol solutions: 70, 80, 90 and 96%. The shell morphology of *A. ojanus* was studied by light and scanning electron microscopy.

The system of larval, juvenile and definitive teeth notation used in this study is based both on Bernard (1895) and Rees (1950). We also designated a sequence of the tooth formation in the right valve by means of a Greek letter (Fig. 1).

## RESULTS

The morphogenetic series of *A. ojanus* reveals the main stages of its ontogeny, showing changes of the shell outline, umbo, provinculum, hinge, ligament and other morphological features. Beginning at the late larval stage of 170–190 µm shell length (Fig. 2A, B), the equivalent larval shell is rounded and the umbo is rather high, almost symmetric or slightly inclined anteriorly. The provinculum bears eight or nine large and for

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**Figure 1.** The shell shape, morphology and hinge nomenclature of the right valve of *Alveinus ojanus* in larval, juvenile and definitive (adult) stages. Numerals and abbreviations: *I*( $\gamma$ ), central cardinal tooth forming third; *III*( $\alpha$ ), dorsal non-separated cardinal tooth forming first; *3a*( $\beta$ ), anterior cardinal tooth forming second as a result of bifurcation of tooth *III*; *3b*, posterior cardinal tooth developing as a result of bifurcation of tooth *III*; *Lp1*( $\delta$ ), posterior lateral tooth forming after the cardinal teeth; *flg*, flange groove; *flr*, flange ridge; *lm*, lunular margin; *lp1*, primary ligament pit; *lp2*, secondary ligament pit; *lp3*, definitive ligament pit; *mr*, marginal shell ridge; *elg*, external ligament groove; *hp*, hinge plateau; *pd*, provincular denticles; *slt*, sublunular thickening; *tlp*, tooth-like projection of the posterior margin of the ligament pit.

the most part rectangular denticles; one to three denticles, which are usually located in the central part of the provinculum, may be narrow. The first cardinal tooth *III*( $\alpha$ ) appears as a rounded knob in the anterior part of the provinculum of the right valve. This knob grows anteriorly, changing into the narrower, long, slightly curved, second cardinal tooth *3a*( $\beta$ ), which terminates subprovincularly on the thickened inner shell wall (Fig. 1, *slt*). Anterior and ventral to tooth *3a*( $\beta$ ), the third cardinal tooth *I*( $\gamma$ ) forms on the thickened inner wall (Fig. 3B). Therefore, formation of the cardinal teeth of the right valve occurs during the relatively short ontogenetic phase when shell length increases from 170–180 to 200–220  $\mu\text{m}$ .

In the left valve (Fig. 3A), the anterior part of the provinculum merges smoothly with the shell margin. On the thickened inner shell wall, the plateau of the cardinal tooth *II*( $\alpha$ ) is located anterior and ventral to the provinculum. This oval or elongate tooth occupies the posteroventral part of the plateau and is separated from the shell margin by the narrow deep pit for tooth *3a*( $\beta$ ). The anteroventral margin of the plateau merging

with the shell margin forms a notch for tooth *I*( $\gamma$ ) of the right valve.

In the right valve, along its smoothly rounded anterodorsal margin there is a flange-like ridge. In the left valve, a groove fits this ridge. At the posterodorsal margin of the right valve, there are two flange ridges separated by a groove. One ridge of the left valve inserts between these when the valves are closed. The distinct triangular or trapezium-shaped primary ligament pit is located at the posterior end of the provinculum and isolated by ridges anteriorly, dorsally and posteriorly. The ridge of the posterior margin of the pit forms a small, pointed, tooth-like projection (Figs 1, *tlp*; 3A) oriented ventrally or somewhat posteriorly.

At a length of 300–450  $\mu\text{m}$  (Fig. 2C, D), the shell is almost regularly rounded. The provinculum becomes inclined; its anterior end is lower than the posterior one. The provincular denticles are partly reduced; the pointed projection of the posterior margin of the primary ligament pit merges with the thickened posterior end of the shell. A larger triangular secondary ligament pit appears (Figs 1, *lp2*; 3D). The external ligament is very thin; the nymph base is indistinct.

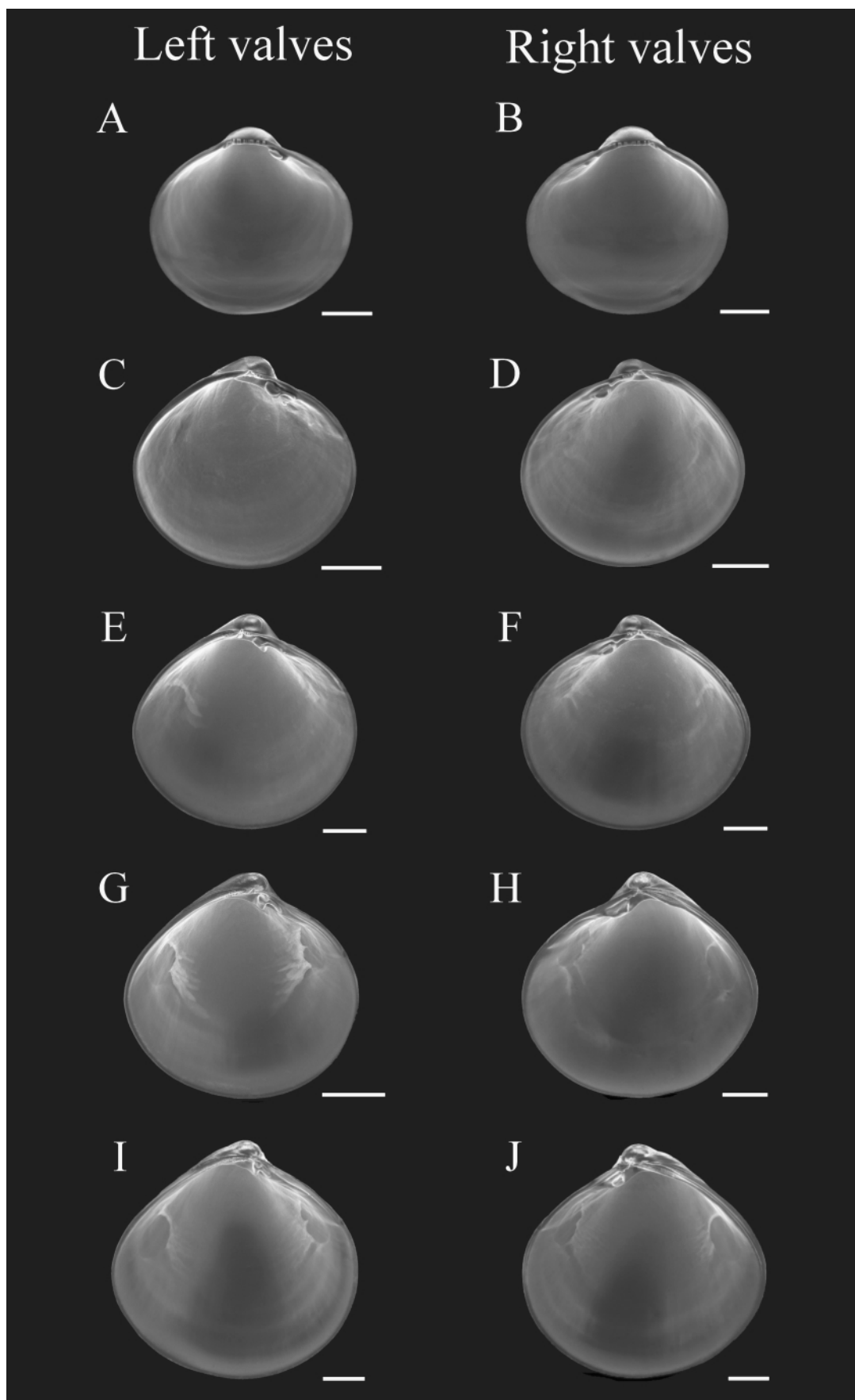
Anterior to the ligament pit, the hinge plateau begins to form (Fig. 1, *hp*). In the right valve, this occurs by the ventral dilatation of the provinculum as well as its merging with the cardinal teeth *3a*–*3b*. Tooth *3a* is more elongated than in the previous stage. It joins the thickened anterodorsal margin of the shell. The third cardinal tooth *I*( $\gamma$ ) becomes oval-triangular in shape.

In the left valve, the hinge plateau develops by the ventral dilatation of the provinculum and formation of tooth *4b*, as well as by the dorsal and posterior expansion of the plateau of cardinal tooth *II*, which joins the bottom of the secondary ligament pit and base of the posterior flange ridge. At first, on the anteroventral part of the hinge plateau, a ridge forms that connects tooth *II* with the thickened anterodorsal shell margin. The ridge then grows in height and changes into the narrow, slightly curved tooth *2a*, which is apically rounded.

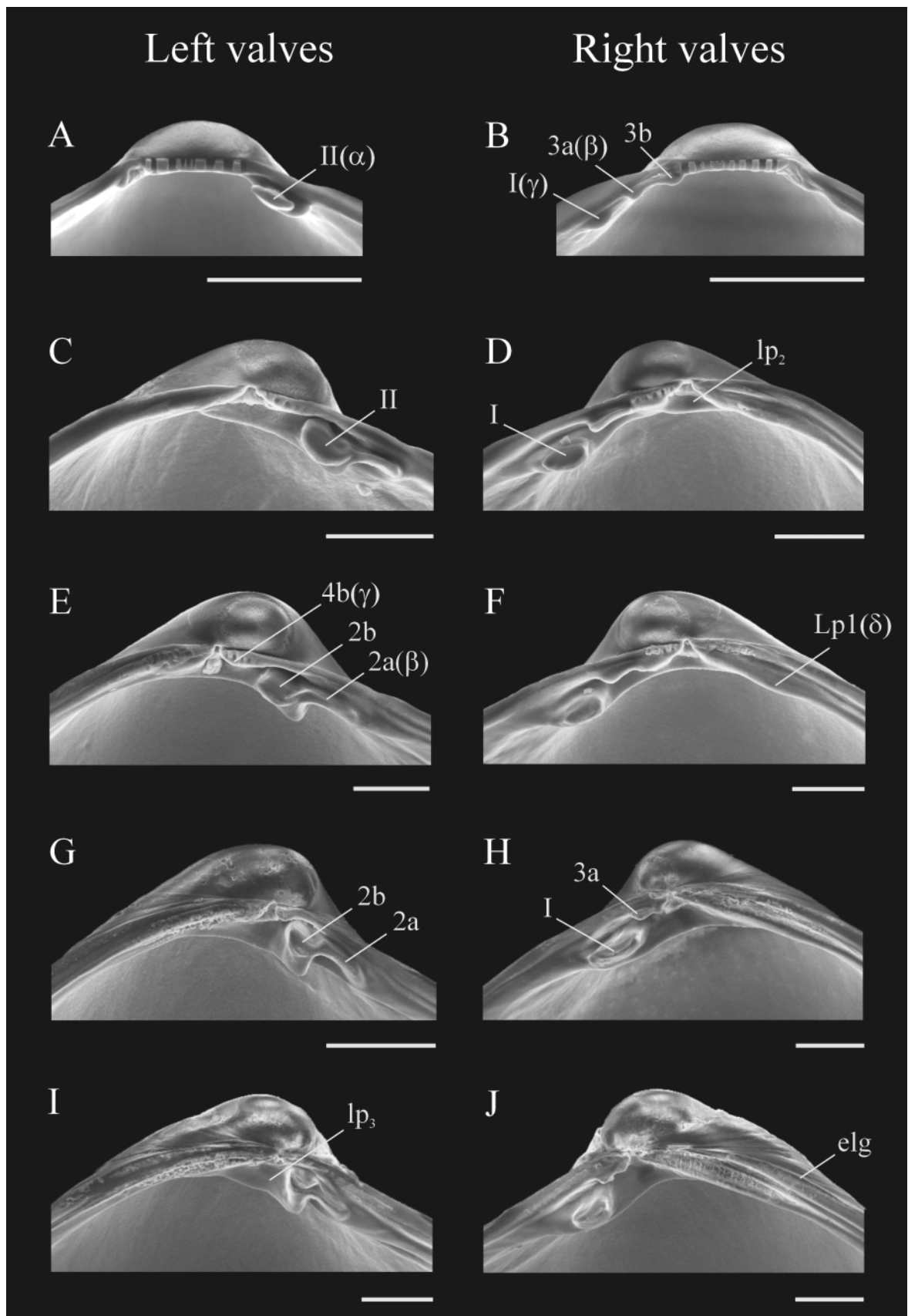
At a length of 500–700  $\mu\text{m}$  (Fig. 2E, F), the shell becomes triangular-rounder; the pointed umbo is inclined anteriorly. In the right valve, there is a distinct lateral tooth *Lp1*( $\delta$ ) posterior to the ligament pit (Fig. 3F). This begins as a marginal ridge of the pit and continues posteroventrally as an inner flange ridge. The hinge plateau of the right valve is considerably wider than the plateau of the previous stage. Joining with the base of the lateral tooth, the plateau forms the bottom of the ligament pit (Fig. 1, *lp3*). In the left valve tooth *2a*–*2b* becomes S-shaped (Fig. 3E).

The outer shell surface, covered by the brownish translucent periostracum, bears very thin and almost regular commarginal grooves. The large, oval, crescentic lunule is located in a weakly marked depression and delimited by a groove and a border, which terminate close to the point of greatest convexity of the anterior shell margin (Fig. 1, *lm*). The external ligament, located in a narrow groove beneath the umbo (Fig. 1, *elg*), consists of one layer, formed by the thickened dark brown periostracum. The internal ligament represents the elastic resilium, occupying the posterior half of the hinge plateau.

The juvenile development of *A. ojanus* is complete at a shell length of 700–1150  $\mu\text{m}$  (Figs 2G, H; 3G, H). The shell outline and configuration of the cardinal teeth remain the same as in the previous stage. At the same time, teeth *3a*, *I* and *Lp1* continue to increase in height, i.e. towards the opposite valve. The larval denticles are almost entirely reduced. The hinge plateau of the right valve is broadened ventrally; its distal margin becomes S-shaped like plateau in the adult shell. In the left valve, tooth *4b* is reduced; the flange ridge increases in height similar to the lateral tooth of the right valve. The ventral margin of the hinge plateau becomes smoothly concave. On the inner surface of both valves there are distinct scars of the anterior and



**Figure 2.** Left and right valves of larval, juvenile and adult *Alveinus ojanus*. Scale bars: **A, B** = 50  $\mu$ m; **C–F** = 100  $\mu$ m; **G–J** = 200  $\mu$ m.



**Figure 3.** Hinge of the left and right valves of the larval, juvenile and adult *Alveinus ojanus*. Scale bars: **A–F** = 50 μm; **G–J** = 100 μm. Numerals are the same as given in Figure 1. II(α), anteroventral non-separated tooth of the left valve; 2a(β), anterior and 2b, posterior teeth forming as a result of bifurcation of tooth II; 4b(γ), posterior tooth of left valve.

posterior adductors. The scar of the anterior retractor is separated from the adductor scar. The pallial line devoid of a sinus may be seen in some views.

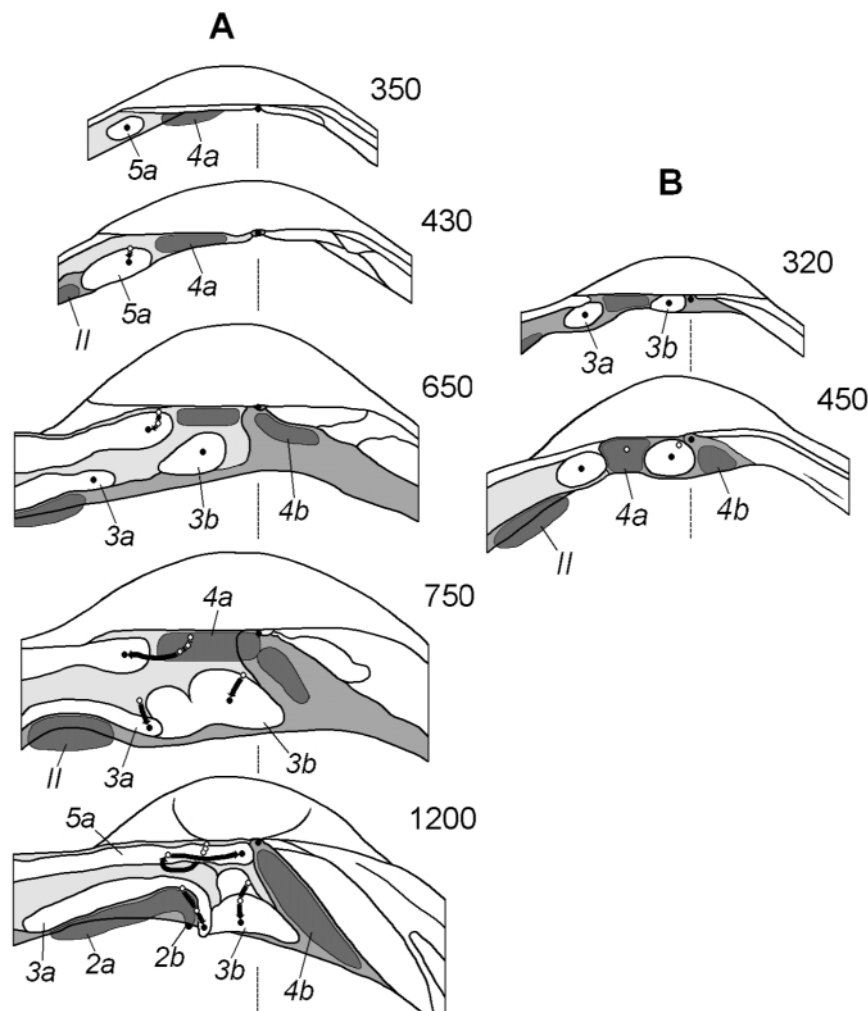
In the right valve of the adult shell, there is a comparatively broad hinge plateau with tall pointed teeth 3a, I and Lp1 (Fig. 3J). The primary ligament pit is well marked. The bottom of the secondary ligament pit merges with the base of the hinge plateau. The nymph is short; the groove of the external ligament is weakly pronounced. There is a tall pointed tooth 2b in the left valve (Fig. 3I). Tooth 4b is usually reduced but in some specimens it can be seen as a small projection anterior to the primary ligament pit. In both valves the anterodorsal and posterodorsal shell margins bear flanges extending antero-ventrally up to the lunular margin.

## DISCUSSION

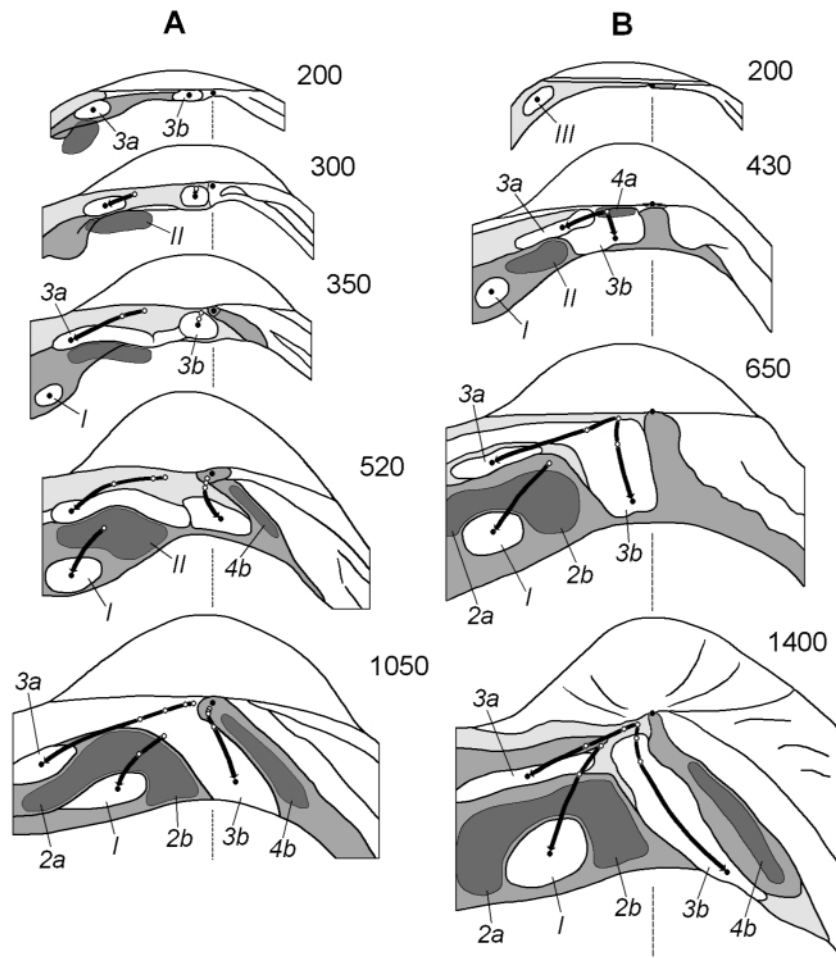
The suggested phylogenetic relationships between the family Kelliellidae, to which *A. ojanus* is referred, and morphologically similar families are contradictory. In a taxonomic system based

on the conchological features of adults, the family Kelliellidae as well as the families Arctidae and Trapeziidae belong to the superfamily Arcticoidea. The Arctidae, represented by the only living species *Arctica islandica* (Linnaeus, 1767), may be considered as an ancestral group (Keen, 1969). From other data (Scarlato, 1981; Starobogatov, 1992), the Kelliellidae forms a superfamily and, together with another two (Arcticoidea and Veneroidea) or three (Arcticoidea, Gaimardioidea and Glossoidae) superfamilies, is included in the suborder Venerina. In this case, in addition to the Arctidae and Trapeziidae, the Gaimardiidae, Glossidae, Veneridae and Vesicomidae are sister families, and the Veneridae may be considered as the ancestral group. There are other viewpoints on the relationships of the Kelliellidae, in which the Vesicomidae (Knudsen, 1970; von Cosel & Salas, 2001) or Glossidae (Allen, 2001) are believed to be morphologically close to the Kelliellidae.

We examined the shell ontogeny of *A. ojanus* from the pediveliger to the adult mollusc. Such data on the ontogenetic stages of closely related taxa, including *Kelliella*, could greatly increase the quantity of common features and reveal general developmental traits typical of major phylogenetic lines of the Bivalvia.



**Figure 4.** Topology, directions of growth and sequence of formation of the cardinal teeth. **A.** *Arctica islandica* (after Lutz *et al.*, 1982). **B.** *Meretrix lusoria* (Röding, 1798) (after Sakai & Sekiguchi, 1992). Dots show the growth centres of the cardinal teeth; open circles indicate the growth centres of previous stages; vectors connecting the growth centres of different stages show directions of tooth growth. The shaded outlines indicate topology of the cardinal teeth of the left valve. Numerals: II, auteroventral non-separated teeth of the left valve; 2a, anterior and 2b, posterior teeth forming as a result of bifurcation of tooth II; 3a, anterior and 3b, posterior teeth developing as a result of the divergent growth of tooth III or forming in two different centres and located dorsal to tooth I; 4a, anterior tooth of the left valve usually located anterior to the ligament pit; 4b, posterior tooth of the left valve which occupies a part of the juvenile or definitive ligament pit of the right valve; 5a, anterior teeth of the right valve located dorsal to tooth 3a. Shell-length stages (µm) are indicated.



**Figure 5.** Topology, directions of growth and sequence of formation of the cardinal teeth. **A.** *Pitar morrhuanus* (Linsley, 1848) (after Goodsell *et al.*, 1992). **B.** *Mercenaria mercenaria* (after Goodsell *et al.*, 1992). Numerals are the same as given in Figure 4. I, Central tooth of the right valve; III, dorsal non-separated tooth of the right valve. Shell-length stages ( $\mu\text{m}$ ) are indicated.

However, of the possible sister families, only in the Arctiidae (Lutz *et al.*, 1982) and Veneridae (Le Pennec, 1973, 1980; Goodsell *et al.*, 1992; Sakai & Sekiguchi, 1992; Evseev, Kolotukhina & Semenikhina, 2001) has the morphology of the larval and juvenile stages been studied. Therefore we make a comparison with these.

#### Arctiidae

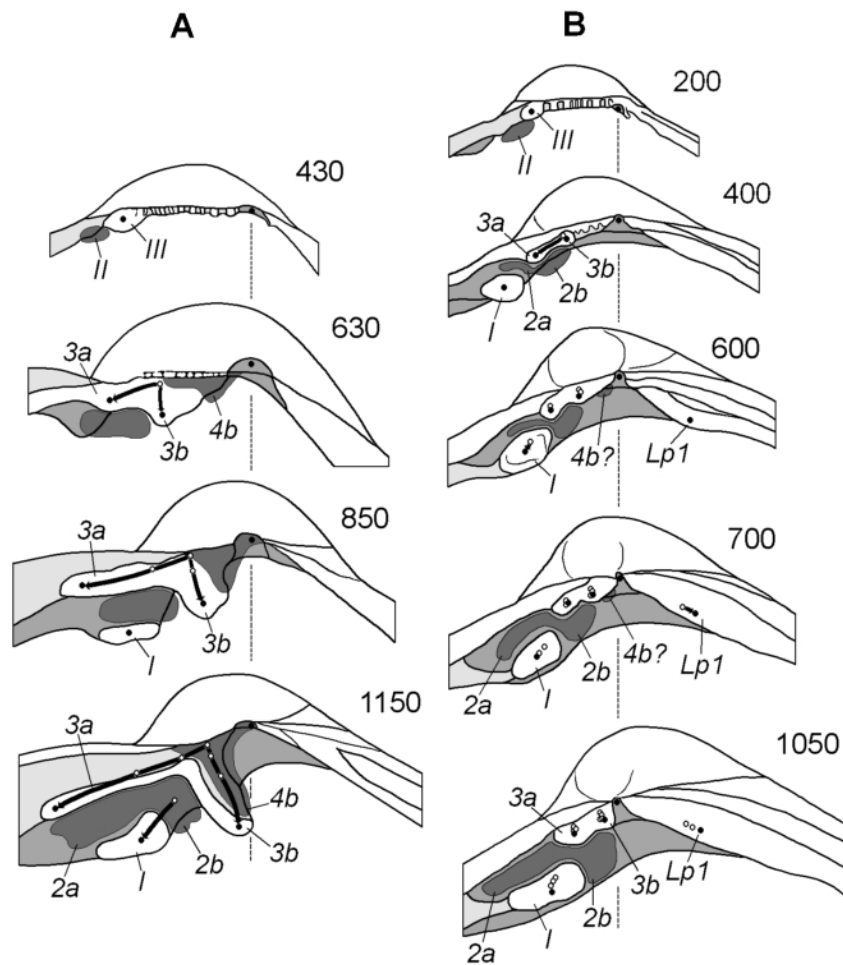
The larval and early juvenile shells of *Ar. islandica* are devoid of provincular denticles (Fig. 4A). The primary ligament pit appears after metamorphosis; it is not located posteriorly as in *A. ojanus*. In the right valve, the hinge begins to develop with the formation of cardinal tooth 5a, which is located subprovincularly. During the subsequent juvenile stages, the growing tip of tooth 5a is displaced anteriorly and merges with the thickened shell margin. Subsequent to the reduction of tooth 4a in the left valve, tooth 5a lengthens posteriorly and overgrows the pit of tooth 4a. The isolated cardinal teeth 3a and 3b appear simultaneously and join together at a shell length of 750–850  $\mu\text{m}$ . At a shell length exceeding 1500–2000  $\mu\text{m}$ , the anterior part of tooth 3a separates from the posterior part, which joins with tooth 3b and occupies the central part of the hinge plateau. Tooth I is absent. The juvenile stage of *Ar. islandica* is completed by the formation of the anterior and posterior lateral teeth.

A comparison between the early postlarval and juvenile stages

of *A. ojanus* and *Ar. islandica* shows that the distinguishing (and perhaps phylogenetically significant) features of the former are: (a) the presence of the larval provincular denticles in the early juvenile stages; (b) the posterior location of the primary ligament pit; (c) the place of formation of the first cardinal tooth of the right valve relative to the provinculum; (d) the sequence of formation of the cardinal teeth of the right valve which begins with tooth III( $\alpha$ ) bifurcating into 3a( $\beta$ ) and 3b and ending with tooth I( $\gamma$ ). Such distinctions in the early stages of ontogeny may indicate the absence of a close taxonomic relationship between the Kelliellidae and the Arctiidae.

#### Veneridae

In the family Veneridae, there are two types of larval hinge (Le Pennec, 1980): (1) without provincular denticles (the subfamilies Venerinae, Callistinae, Pitarinae, Meretricinae and Chioninae) (Figs 4B, 5A, B) similar to *Ar. islandica*; (2) with provincular denticles (the subfamily Tapetinae) (Fig. 6A, B) as in *A. ojanus*. In the early stages of development of some taxa of the Chioninae, Venerinae and Callistinae, the anterior subprovincular area of the right valve is occupied by tooth III. At the same stage in other taxa of the first type (Pitarinae and Meretricinae), tooth III is already bifurcate and the subprovincular area is occupied by tooth 3a, while the second cardinal tooth (3b) is located in the centre of the provinculum anterior to the ligament pit.



**Figure 6.** Topology, directions of growth and sequence of formation of the cardinal teeth. **A.** *Venerupis aurea* (after Le Pennec, 1973). **B.** *Alveinus ojanus*. Numerals are the same as given in Figures 4 and 5. Shell-length stages ( $\mu\text{m}$ ) are indicated.

In the left valve of taxa of both types there is usually one subprovincular tooth II, this is in contrast to *Ar. islandica*, in which the second subprovincular tooth 4a appears in early postlarval stage. Thus, the development of the cardinal teeth in venerid taxa of the two types begins identically: tooth III or its derivatives (3a and 3b) appear first in the right valve and tooth II develops in the left valve. However, in other species these teeth form at different stages (Table 1), for example, in the larval stage of *Mercenaria mercenaria* (Linnaeus, 1758) (Goodsell *et al.*, 1992) and in the juvenile stage of *Venerupis aurea* (Gmelin, 1791) (Le Pennec, 1980).

The subsequent development of the juvenile cardinal teeth of venerid taxa also continues on different paths. If tooth III (Chioninae, Tapetinae) develops first, the following change in form occurs by simultaneous growth anteriorly (tooth 3a) and ventrally (tooth 3b). But in some taxa (Chioninae) tooth 3b forms on the hinge plateau as in *A. ojanus*, whereas in others (Tapetinae) tooth 3b develops first and then its plateau appears. If in the early postlarval stage tooth III is already represented by its derivatives (3a and 3b), an isthmus forms between them (Fig. 5A), similar to that in the Arcticidae. Thus, at 300–450  $\mu\text{m}$  (Table 1), tooth III may consist of 3a–3b as a result of growth in two directions (Chioninae, Tapetinae) or of 3a+3b which develop by merging of the two centres of growth (Pitarinae and, probably, Meretricinae). At the same stage, tooth I appears in the right valve.

In the left valve of some taxa (Meretricinae), development of

the cardinal teeth begins with teeth II and 4a. In other taxa (Pitarinae), cardinal tooth II forms first and tooth 4a is absent in their ontogeny. Tooth 4b either forms simultaneously with the bifurcation of tooth II into 2a and 2b or somewhat later, but after changes in tooth III and after the appearance of tooth I in the right valve. The anterior lateral teeth form in the final stage of the juvenile development of venerids.

#### *Comparison of the morphological features of the taxa examined*

Differentiation in the early ontogenetic stages indicates that there are different phylogenetic lines of venerids some of which may be morphologically close to both the Kelliellidae and the Arcticidae. In a comparison of ontogenetic development (Table 1), the Pitarinae and Chioninae appear closer to the Arcticidae, especially at the larval stage. Differences are more pronounced in juvenile development, in which tooth 5a is formed in the Arcticidae ontogenetically later, while tooth I is absent but, in the ontogenies of *A. ojanus* and *V. aurea*, similar features are those by which *A. ojanus* and *Ar. islandica* are distinguished. For instance, the provinculum of *A. ojanus* and of *V. aurea* bears larval denticles, rudiments of which are seen in the juvenile stage. The primary ligament pit of both taxa is located posteriorly. The cardinal teeth III and I appear first, and tooth III is located at the provinculum. The sequence of formation of the other cardinal teeth is the same in both taxa.



**Table 1.** The ontogenetic stages and sequence of the hinge formation of *Alveinus ojanus* (Kelliellidae) and sister taxa belonging to the Arctidae (Lutz *et al.*, 1982) and Veneridae (Le Pennec, 1973; Goodsell *et al.*, 1992).

Stage	Taxa				
	<i>Arctica islandica</i> (Arctidae)	<i>Pitar morrhuanus</i> (Veneridae: Pitarinae)	<i>Mercenaria mercenaria</i> (Veneridae: Chioninae)	<i>Venerupis aurea</i> (Veneridae: Tapetinae)	<i>Alveinus ojanus</i> (Kelliellidae)
170–200 µm	Provinculum without denticles; ligament pit indistinct	PD-II = 190 µm; without denticles; ligament pit distinct; 3a(α) subprovincular?	Provinculum without denticles; ligament pit indistinct; III(α) subprovincular	PD-II = 200 µm; provinculum with denticles; ligament pit distinct	PD-II = 170–190 µm; provinculum with denticles; ligament pit distinct; III(α) provincular
200–300 µm	PD-II = 260 µm; formation of ligament pit	3b(β) provincular; II	PD-II = 240 µm; formation of ligament pit; 3b(β); II	III(α) provincular; II	<b>3a(β)–3b, I(γ); II</b>
300–450 µm	5a(α) subprovincular; 4a provincular	3a+3b, I(γ)	<b>3a–3b, I(γ); 4a provincular</b>	<b>3a–3b(β), I(γ)</b>	Reduction of provincular denticles; 4b?, 2a–2b
450–700 µm	3b(β), 3a(γ); II, 4b	4b, 2a–2b	2a–2b, reduction of 4a	Reduction of provincular denticles; 4b	Lp1(δ)
700–900 µm	<b>3a+3b; reduction of 4a</b>		4b	2a–2b	Reduction of 4b?
1000–1400 µm	2a–2b; La1, La3, Lp1, Lp3; La2, Lp2	La1, La3; La2			

PD-II, prodissoconch of the late pediveliger; 2a–2b, non-separated anterior and posterior cardinal teeth formed as a result of half bifurcation of the cardinal tooth II; 3a and 3b, separated anterior and posterior cardinal teeth; 3a–3b, non-separated anterior and posterior cardinal teeth formed as a result of half bifurcation of the cardinal tooth III; 3a+3b, joining anterior and posterior cardinal teeth; La1 and La3, anterior inner and outer lateral teeth of the right valve; La2, anterior lateral teeth of the left valve; Lp1 and Lp3, posterior inner and outer lateral teeth of the right valve; Lp2, posterior lateral tooth of the left valve. Other abbreviations are the same as given in Figures 1 and 4. Bold font indicates similar stages of development in the different taxa.

However, in the ontogenetic development of *A. ojanus* and *V. aurea* there are some differences which, while phylogenetically insignificant, should be taken into account in making a comparison between the larval and juvenile stages with the definitive ones. These differences concern the general morphology of the shell, its sculpture, ligament and shape of the cardinal and lateral teeth.

The shell outline and sculpture are the significant taxonomic features of adults but, in the larval and juvenile stages, these may be underdeveloped or already reduced, or they may be present in some stages but absent in others. For example, in species of the Tapetinae, Chioninae and Callistinae, the shell acquires the adult outline at a length exceeding 2–3 mm. If the adult sculpture consists of commarginal and radial ribs, commarginal ribs, which differ in their morphology and structure from these of the adults, develop first (Evseev *et al.*, 2001).

The shape of the cardinal teeth and their location relative to each other or to the ligament pit, which are also significant taxonomic features of the adult venerids, vary widely. For example, teeth 3a and 3b of adult Chioninae and Tapetinae may be lamellar, massive, straight, curved, bifurcated by the longitudinal groove, long or short. They are also distinguished in the juvenile stage (Figs 5B; 6A). At the same time, in other species, formation of the definitive shell and cardinal teeth as well as the commarginal or later radial ribs occurs heterochronically, i.e. at a different time in ontogeny.

For instance, in *V. aurea* (Le Pennec, 1973) tooth III develops in the juvenile stage at a shell length of *c.* 300 µm. In *Protothaca euglypta* (Sowerby, 1914) (Evseev *et al.*, 2001) and *A. ojanus* it forms at the larval stage of 180–200 µm. During subsequent development tooth III bifurcates into 3a and 3b. In *V. aurea* and *P. euglypta* this bifurcation occurs in the juvenile stage at a shell length of 400–600 µm. In *A. ojanus*, tooth III begins to bifurcate almost simultaneously with its formation, at a shell length of *c.* 200 µm, and remains underdeveloped up to the end of the juvenile stage at 600–700 µm shell length. In adult *A. ojanus*, the outlines of teeth 3a–3b are similar to the juvenile ones. Tooth 3a, as well as the lateral tooth and tooth I, is several times higher than tooth 3b. Therefore, in adult *A. ojanus*, the shell outlines,

commarginal sculpture and size of all teeth remain in the juvenile state, in contrast to these of the Tapetinae and Chioninae.

The ligament of larvae and early postlarvae of the Tapetinae and Chioninae, as in other venerid taxa (Ansell, 1962), consists of the internal elastic resilium and external thin periostracal junction (fusion layer) connecting valves along the provinculum. In juveniles and adults, the thickened fusion layer has inner layers functioning as a resilium (Owen, 1958). The primary internal resilium, which is partly reduced in the juvenile stages, is usually absent in adults. The adult ligament of *A. ojanus* consisting of the thin fusion layer and internal resilium, differs from the juvenile ligament by the length of the fusion layer (Fig. 1) and the size of the resilium which occupies, not only the extended secondary ligament pit, but also the posterior part of the hinge plateau. Also, the primary ligament pit of adult *A. ojanus*, unlike species of the genus *Kelliella* (Clausen, 1958; Bernard, 1989; Warén, 1989; Hayami & Kase, 1993; Allen, 2001; Oliver & Zuschin, 2001), is not overgrown.

The anterior lateral teeth typical of most venerid taxa are absent in the Tapetinae and Chioninae. No posterior lateral teeth are found in venerids. Thus, the posterior lateral tooth of *A. ojanus*, developing in the final stage of juvenile morphogenesis like the anterior lateral teeth of venerids, is an ontogenetically later structure than the cardinal teeth. On the other hand, it develops from the inner flange ridge similar to that of the Arctidae, but neither in the Veneridae nor in the Arctidae do the teeth originating from flanges look like the tall narrowly pointed peak directed towards the opposite valve. It is possible that this peculiarity of the lateral teeth of *A. ojanus* is typical of the genus *Alveinus*. In other kelliellids (e.g. *Kelliella miliaris* and *K. japonica*), the posterior lateral tooth is absent. In addition, their cardinal tooth-complexes 3a–3b and 2a–2b differ in topology and configuration, tooth 4b is developed and the hinge may be without the cardinal tooth plateau. However, both *Kelliella* and *Alveinus* are small-sized and bear the submarginal groove in the right valve and ridge in the left valve.

Thus, the most significant morphological features of the larval and juvenile shell, which suggest taxonomic and phylo-



genetic relationships between *A. ojanus* (and, possibly, other kelliellids) with the Arcticiidae and Veneridae, appear to be: (a) dentition of the provinculum; (b) distinctness and location of the primary ligament pit; (c) topology and sequence of formation of the cardinal teeth. Of features of adult *A. ojanus*, the following characters may be used for taxonomy: (d) general shell shape and (e) umbo shape; (f) convexity and (g) internal morphology of the anterodorsal and posterodorsal shell margin; (h) colour and character of the periostracum.

In their taxonomic and phylogenetic importance, the larval, juvenile and adult features of *A. ojanus* are not all equivalent. Some of them form before others and are useful only in taxa of high rank (families or superfamilies). These are cardinal teeth I, tooth 4b? and their complexes 2a–2b and 3a–3b, the topology and configuration of which allow discrimination between the Kelliellidae and related families. Dentition of provinculum and location of the primary ligament pit seem to have similar taxonomic rank. However, these morphological features are not yet sufficiently studied in related families. Other characters developing in later ontogenetic stages are less important compared with previous ones. The lateral tooth of *A. ojanus*, which forms after the cardinal teeth and which is absent in *Kelliella*, as well as the general ovate trigonal shell shape and relatively high bevelled umbo, may be considered to be generic features. The lustrous brown periostracum of *A. ojanus* is characteristic of the species. At the same time, some features of *A. ojanus* maybe a consequence of its paedomorphic development. Besides a small body size, these are the underdeveloped tooth 4b?, larval flange hinge in the form of the submarginal fine groove in the right valve and the ridge in the left valve, as well as the non-overgrowing pit of the primary ligament. These juvenilized characters may be used as distinguishing features when comparing the paedomorphic taxa with non-paedomorphic ones and as taxonomic features at generic or species ranks when comparing the paedomorphic taxa of the same phylogenetic line.

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