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Morphology and systematics of the Recent Japanese brachiopod *Shimodaia pterygiota* gen. et sp. nov. (Laqueidae : Terebratulida)

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Abstract. **A small, brightly coloured brachiopod, *Shimodaia pterygiota* n. gen. and n. sp., presently restricted to waters of less than 100 m depth off Shimoda, Izu Penninsula, and parts of Sagami Bay, Honshu, Japan, is described and illustrated. Previously mistaken for *Frenulina sanguinolenta* (Gmelin), *S. pterygiota* is shown to differ from all other known laqueid brachiopods in its unique combination of adult cardinalial and brachidial features. Investigation of the loop ontogeny of *S. pterygiota* reveals that, whereas juvenile axial, cucullate and annular loop phases are comparable to those in other laqueids, the adult phase is unusual in consisting of an incomplete annular phase resulting from resorption of the transverse band. Only one adult specimen from over 200 recovered to date shows resuturing of previously discrete (resorbed) ascending loop branches to form a conventional annular phase.**

Key words : Brachiopod, Japan, Laqueidae, loop ontogeny, Recent, *Shimodaia pterygiota* gen. et sp. nov.

Introduction

In 1986, a number of dead brachiopod shells were dredged from a depth of between 65 m and 71 m, about 3 km SSE of Shimoda, Izu Penninsula, Honshu, at localities close to an earlier reported occurrence (Harada and Mano, 1960) of the distinctive laqueid brachiopod, *Frenulina sanguinolenta* (Gmelin) (Figure 1 ; Table 1). While the shells of the 1986 collection exhibited a red/white, variegated pattern similar to that occurring in *Frenulina sanguinolenta*, they were generally somewhat smaller, and more rounded in shape (Figures 2-1—2-4). In addition, examination of dorsal valve interiors (Figures 2-5—2-6, Figure 3, Figure 7-1) revealed a morphology distinctly different from that occurring in *Frenulina* specimens of comparable size (Figure 4) and unlike that of any other previously described laqueid genus (MacKinnon, pers. comm., in Endo *et al*., 1994). Inspection by Saito (1996) of the original illustrations of the brachiopods described by Harada and Mano (1960), revealed that, morphologically, the specimens they collected were indistinguishable from the later collection, and it was concluded that Harada and Mano had misidentified the material they had collected. Consequently a restudy of the problematic brachiopod has been undertaken with a view to its formal naming, describing, and illustrating. A comparison of *S. pterygiota* to morphologically similar juveniles of other Recent laqueid brachiopods from the same region has also been undertaken in an attempt to establish evolutionary relationships of *S. pterygiota* to those other taxa.

Materials and methods

Over 200 specimens of *S. pterygiota* have been collected from 8 localities (Table 1). After opening the conjoined valves with a scalpel blade, valves were then placed in bleach solution and constantly monitored under a binocular microscope. Soft tissues were removed using domestic grade bleach (sodium hypochlorite : approximately 5% (v/v)), as described by Mackay *et al*. (1994). Immediately all tissue was dissolved, each specimen was then washed, allowed to dry, and then mounted on a SEM stub. Specimens were then coated with gold, or Pt-Pd alloy, prior to observation by scanning electron microscope (Leica Stereoscan 440 or Hitachi S-2400S). Apart from one specimen of *Laqueus rubellus* which is housed in the National Museum of Natural History, Washington D.C. (USNM 550341), all specimens are housed in the University Museum of the University of Tokyo (UMUT). Lengths of dorsal and ventral valves are indicated by the abbreviations L_{dv} and L_{vv} respectively.

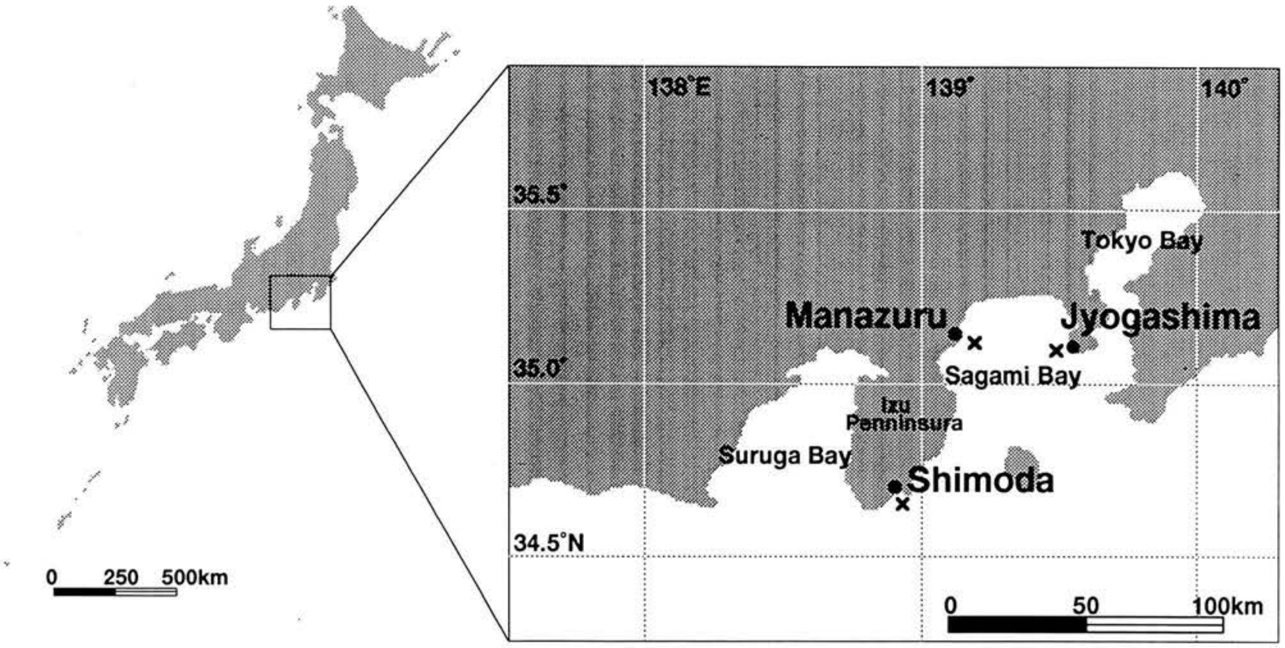

Figure 1. Locality map; localities at which *Shimodaia pterygiota* gen. et sp. nov. has been dredged indicated by (×).

Table 1. Locality data for *Shimodaia pterygiota* gen. et sp. nov.

Locality	Date	Station	Latitude	Longitude	Depth Range (m)
Off Shimoda	09.12.86	St. 4	N34°37.68′	E138°57.70′	65-71
	28.05.94	St. 4	N34°38.11′	E138°56.94′	52-57
		St. 7	N34°37.42′	E138°58.17′	73-98
		St. 8	N34°37.71′	E138°57.84′	67-81
	26.11.96	St. 1	N34°38.27′	E138°56.72′	36.8-45.5
		St. 2	N34°38.12′	E138°56.74′	46.0-47.3
Off Jyogashima	27.07.93	St. 3	N35°07′36′	E139°35′02′	80
Off Manazuru	05.09.94	St. 11	N35°08′12.5″	E139°11′20.7″	75-77

Systematics

Order Terebratulida Waagen, 1883
Family Laqueidae Thomson, 1927

Shimodaia gen. nov.

Type species.—*Shimodaia pterygiota* MacKinnon, Saito and Endo, sp. nov.

Diagnosis.—Small (<7.5 mm), ovate, commissure rectimarginate; beak erect, attrite; foramen submesothyrid; deltidial plates disjunct; dental plates present, pedicle collar broad; cardinal process inconspicuous, septal pillar arising (in adults) about midvalve, very long and narrow, strongly inclined anteroventrally, sometimes spinose distally, extending posteriorly as low ridge to unite with excavate inner hinge plates; adult loop annular with descending branches attached to septal pillar and ascending branches commonly incomplete, rarely forming a complete ring; juvenile axial loop phase with well developed septal flanges

Discussion.—*Shimodaia* resembles *Frenulina* in possessing red/white colour markings of the shell, but is readily distinguished from the latter genus (Figure 4) by its distinctive adult (incomplete) annular loop form (Figure 3) with prominent septal pillar, sessile septalium, and generally smaller adult size. Both the loop and cardinalia of *Shimodaia* are readily distinguishable from those in similar-sized juveniles of other larger sympatric laqueid brachiopods such as *Pictothyris picta* (Dillwyn) and *Laqueus rubellus* (Sowerby) (Figure 7). Juveniles of *S. pterygiota* and *Laqueus rubellus* are similar in

Figure 2. 1-8 *Shimodaia pterygiota,* gen. et sp. nov., 1-4: Ventral, dorsal, lateral, and anterior views of exterior of holotype, UMUT RB27390 (L_w7.05 mm), ×100. 5-6: Lateral and dorsal interior views of UMUT RB27394 (L_{dv}=6.2 mm), ×130 and ×100 respectively. 7: ventral interior view of UMUT RB27394b (counterpart of UMUT RB27394a) (L_v=6.4 mm), ×125. 8: Anterior oblique view of dorsal interior of UMUT RB27394a (L_w=6.4 mm), ×130.

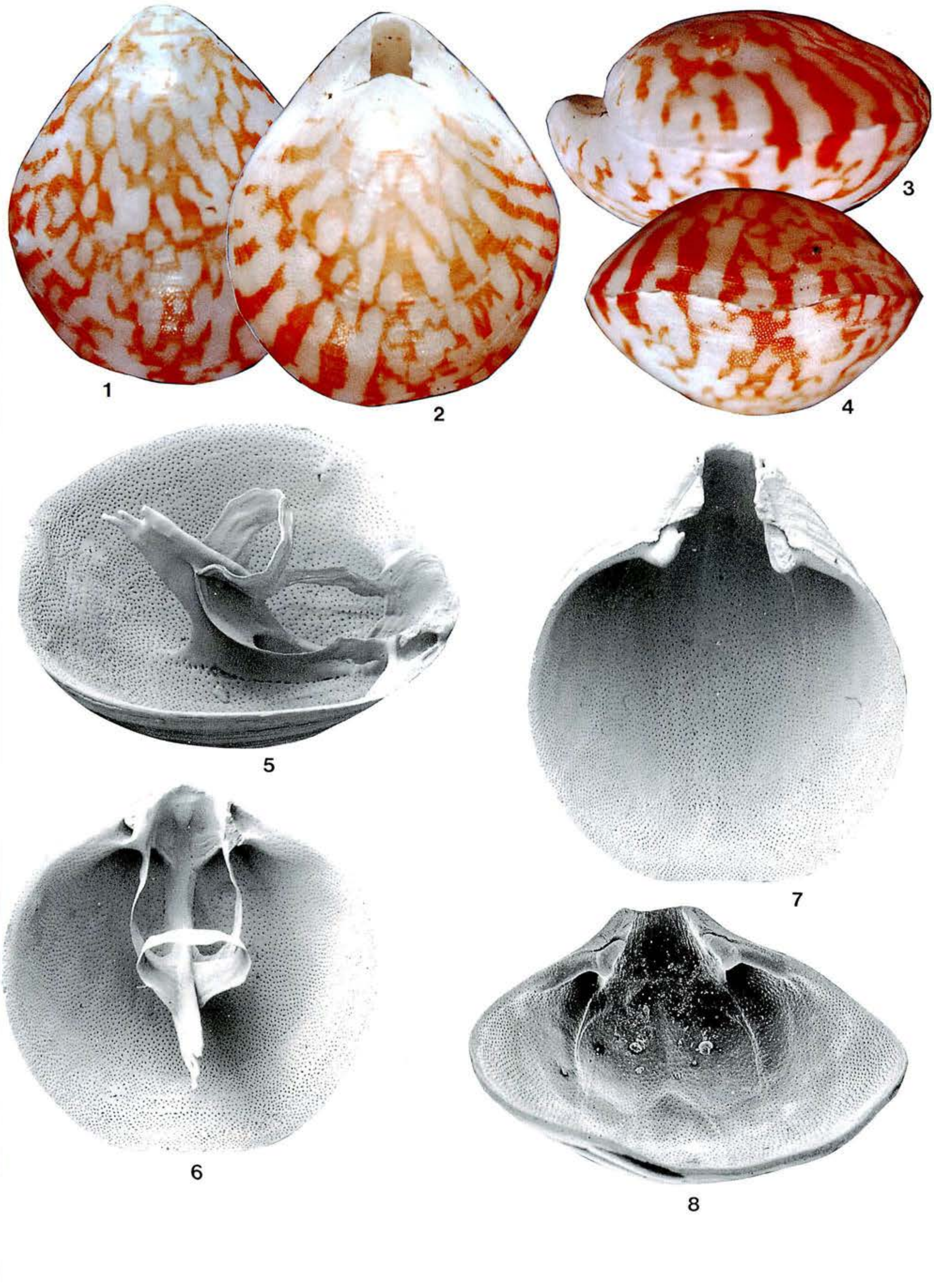
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Figure 3. Stereophotograph showing the incomplete annular (adult) loop phase of *Shimodai pterygiota*, gen. et sp. nov., UMUT RB19862 (L_{dv}=4.7 mm).

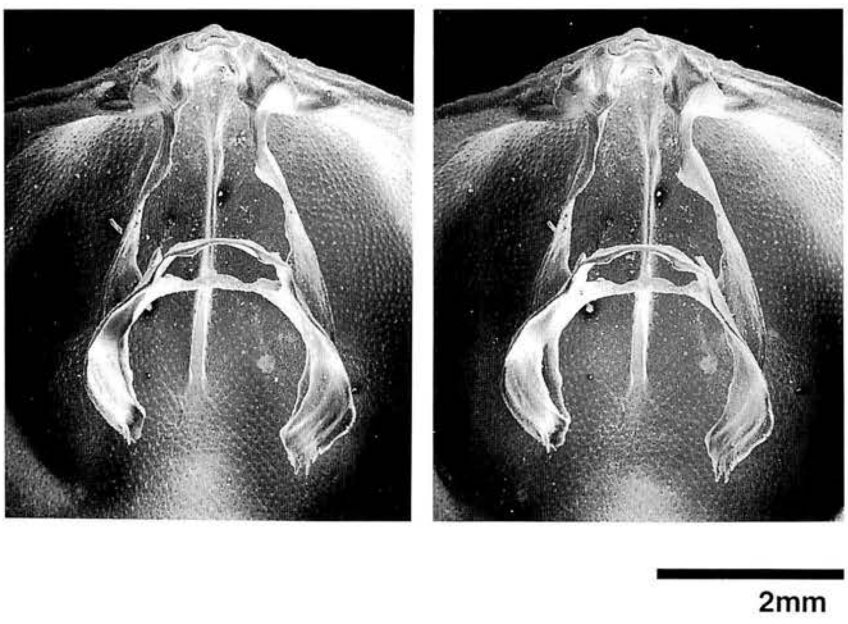


Figure 4. Stereophotograph showing the adult bilateral loop phase of *Frenulina sanguinolenta* (Gmelin), UMUT RB27395 (L_{dv}=6.6 mm).

that both share an inconspicuous cardinal process and sessile septalium, but the post-juvenile loop ontogeny of *L. rubellus* is much more extensive and complicated. As noted by Saito (1996), Harada and Mano (1960) observed mature gonads in specimens between 5 mm to 7 mm in ventral valve length, and Saito (1996) also noted crowding of growth lines around shell margins in specimens with a ventral valve length greater than 5 mm, thus the possibility that *Shimodaia* might represent the juvenile stage of some larger brachiopod is discounted.

Etymology.—Named after the town of Shimoda, Izu Peninsula, Honshu, Japan.

Shimodaia pterygiota sp. nov.

Figures 2-1—8, 3, 7-1

Frenulina sanguinolenta, Harada and Mano, 1960, p. 37-39, fig. 1-7.
'Frenulin' sp., Endo *et al.*, 1994, tables 1, 3, 6 and text-fig. 7.
'Frenulina' sp., Saito 1996, p. 492, fig. 6-1—8.

Material.—Holotype : UMUT RB27390. Paratypes : UMUT RB27391, UMUT RB27392.

Diagnosis.—As for genus.

Description.—Small, moderately biconvex, with subcircular dorsal valve and subelliptical ventral valve ; maximum width and thickness around midvalve ; commissure straight. Beak attrite, suberect ; pedicle foramen submesothyrid ; deltidial plates no wider than teeth, subtriangular and disjunct. Exterior shell surface smooth ; strongly mottled colouration consisting of a median and two lateral bands that are dominantly red-mottled, with intervening bands of white mottling.

Ventral valve interior with strong teeth supported by well developed dental plates ; lateral umbonal cavities deep. Floor of delthyrial cavity lined by wide, impunctate, pedicle collar. Weakly to moderately impressed ventral muscle field, posterolaterally confined by dental plates, extending anteriorly from front edge of pedicle collar to about midvalve.

Dorsal valve interior with high, narrow, but robust, anteroventrally projecting septal pillar. Anteroventral extremity of septal pillar either blade-shaped or spinose and may reach to ventral valve floor. Descending lamellae extending between crura and septal pillar. Ascending lamellae arising from posterodorsal edge of septal pillar as two curved, wing-like processes. Processes widest proximally at attachment to septal pillar, and tapering distally ; distal extremities rarely reuniting to form a ring. Septal pillar extending posteriorly as low ridge to merge with, steeply inclined, and dorsally convergent, inner hinge plates which do not quite fuse together medially, thus forming a sessile septalium. Prominent inner socket ridges and narrow outer socket ridges defining deep sockets. Crura short, with indistinct crural bases. Dorsal pedicle adjustor muscle scars well impressed on inner hinge plates. Low boss developed in some gerontic specimens just anterior of posteromedianly located myophore. Indistinct, elongate oval, adductor muscle scars located on valve floor on either side of septal pillar.

Dimensions (mm).—

Specimen	Length	Width	Thickness
UMUT RB27390(Holotype)	7.05	6.0	5.15
UMUT RB27391(Paratype)	6.65	5.75	4.70
UMUT RB27392(Paratype)	6.55	5.85	3.25

Scatter diagrams showing length/width and thickness/width differences between *Shimodaia pterygiota* sp. nov. and *Frenulina sanguinolenta* are shown in Figures 5A and 5B.

Occurrence.—A list of localities at which *S. pterygiota* has been collected is given in Table 1. *S. pterygiota* is especially abundant off Shimoda where it occurs with *Pictothyris picta*. At other stations in and near Sagami Bay, off Manazuru and off Jyogashima, *S. pterygiota* was collected along with *P. picta* and *Laqueus rubellus*.

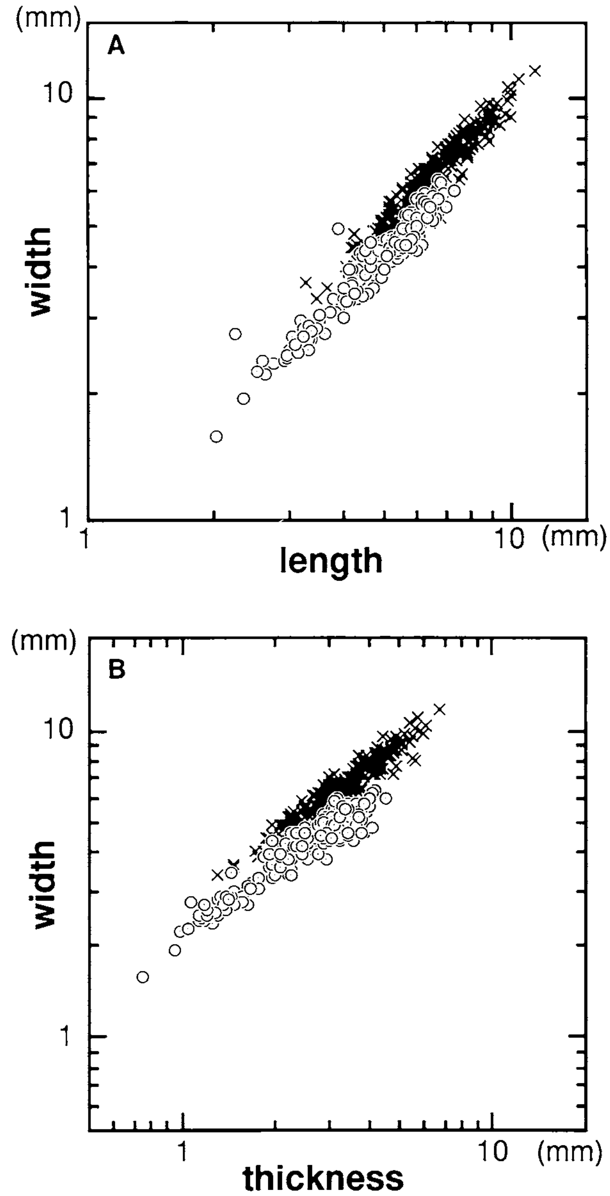


Figure 5. Scatter diagrams of **A** : length to width, and **B** : thickness to width, in *Shimodaia pterygiota* (×) (n=259), and *Frenullna sanguinolenta* (⊙) (n=230). Specimens of *F. sanguinolenta* used in this study were collected from "Tori-ike" cave, off Shimoji Islet, Miyako Island, Okinawa, at between 12 m and 40 m depth.

Etymology.—From the Greek *pterygion*, wing, referring to the wing-like ascending loop branches of the brachidium in adult forms.

Loop ontogeny

In order to clarify the taxonomic position of the present

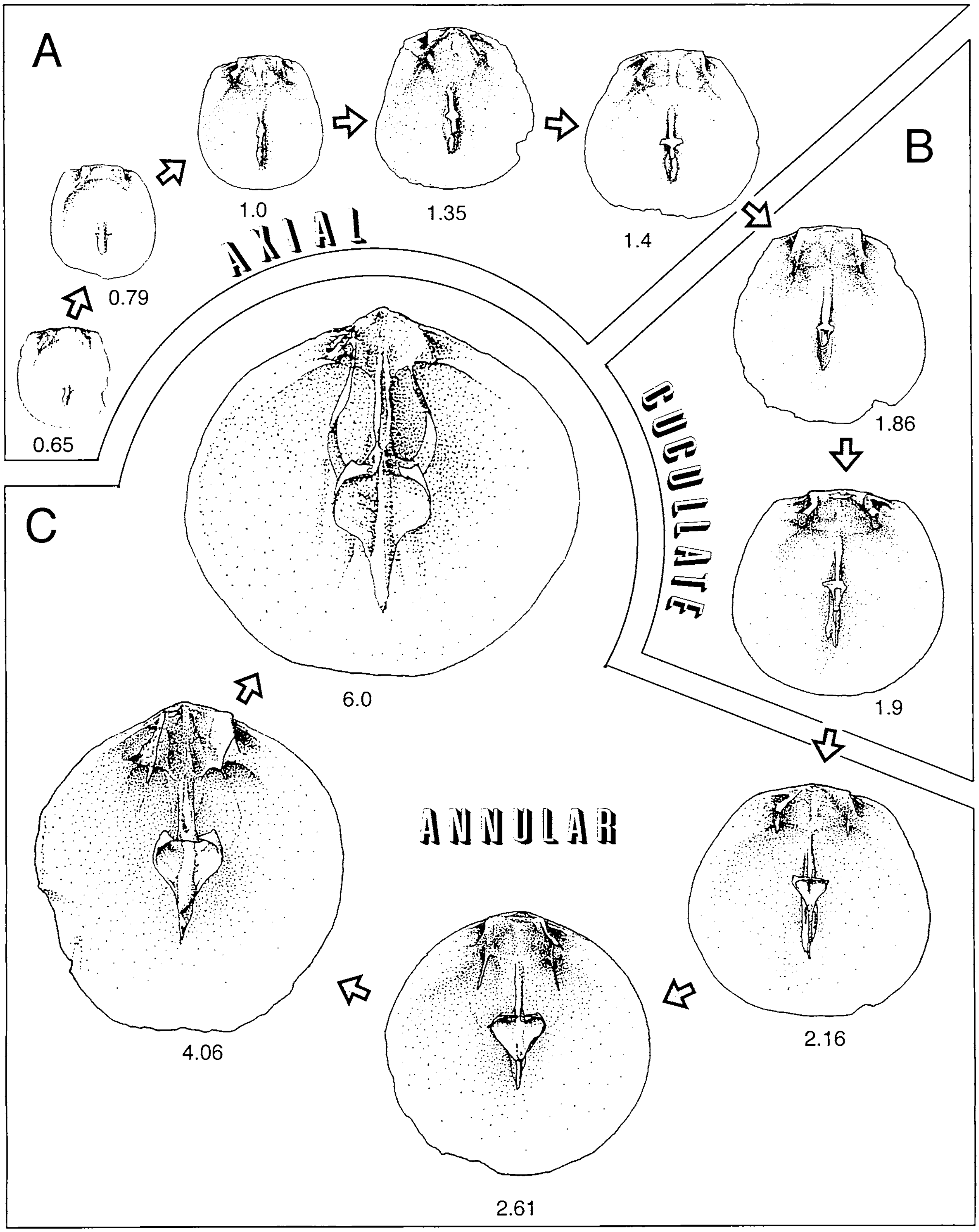


Figure 6. *Shimodaia pterygiota*, gen. et sp. nov. Ontogenetic series showing axial (A), cucullate (B), and annular (C) phases of loop development. Lengths of dorsal valves given in mm. beside each specimen.

species, loop ontogeny was investigated. The terminology applied by Richardson (1975), MacKinnon (1993), and Saito (1996) to transient loop phases is used herein. An ontogenetic series is shown in Figure 6A-C.

Axial Phase (early): In the smallest specimen investigated (dorsal valve length = 0.65 mm) the only distinctive features of the dorsal valve interior are sockets, defined by strong inner socket ridges, a narrow, peg-like, septal pillar that projects at a low angle toward the anterior commissure, and sporadic punctae; no muscle scars are discernible at this stage. The septal pillar, at this stage around 130 μm in length and 50 μm wide, arises at about 0.6 valve length, is antero-ventrally directed, and is composed of nonfibrous calcite.

Axial Phase (late): At 0.79 mm length, the rudiments of the septal flanges appear at the posterior basal margin of the septal pillar; the flanges are nonfibrous. At the distal end of the septal pillar a dense cluster of very small fibrous terminal faces, indicative of vigorous localised epithelial cell generation, is recognisible.

Between lengths 1.0 mm and 1.4 mm, the septal pillar becomes larger and more blade-like, and the septal flanges have migrated anteriorly to reach about halfway along the posterior edge of the septal pillar. The zone of very small fibres at the distal end of the septal pillar becomes elongated in the sagittal plane, and secondary layer fibres begin to extend from the valve floor up both sides of the septal pillar. In the median depression between the strong socket ridges, a pair of subquadrate dorsal pedicle adjustor muscle scar are discernible, and larger but less well-defined adductor impressions appear on the valve floor on either side of the septal pillar.

Cucullate Phase: Between lengths 1.4 mm and 1.9 mm, a shallow groove forms in that part of the distal edge of the septal pillar just anterior of the septal flanges. As growth proceeds, the laterally extended, wing-like septal flanges (which are migrating anteriorly) overlap the groove, thereby forming a narrow hood with a V-shaped cavity and flat-topped roof.

Annular Phase: By length 2.2 mm, differential growth along the anterodorsal edges, and resorption of the posterior section, of the hood gives rise temporarily to a ring. In addition, a pair of very small, anterior projecting crura emerge from the anteriormost edges of the inner socket ridges.

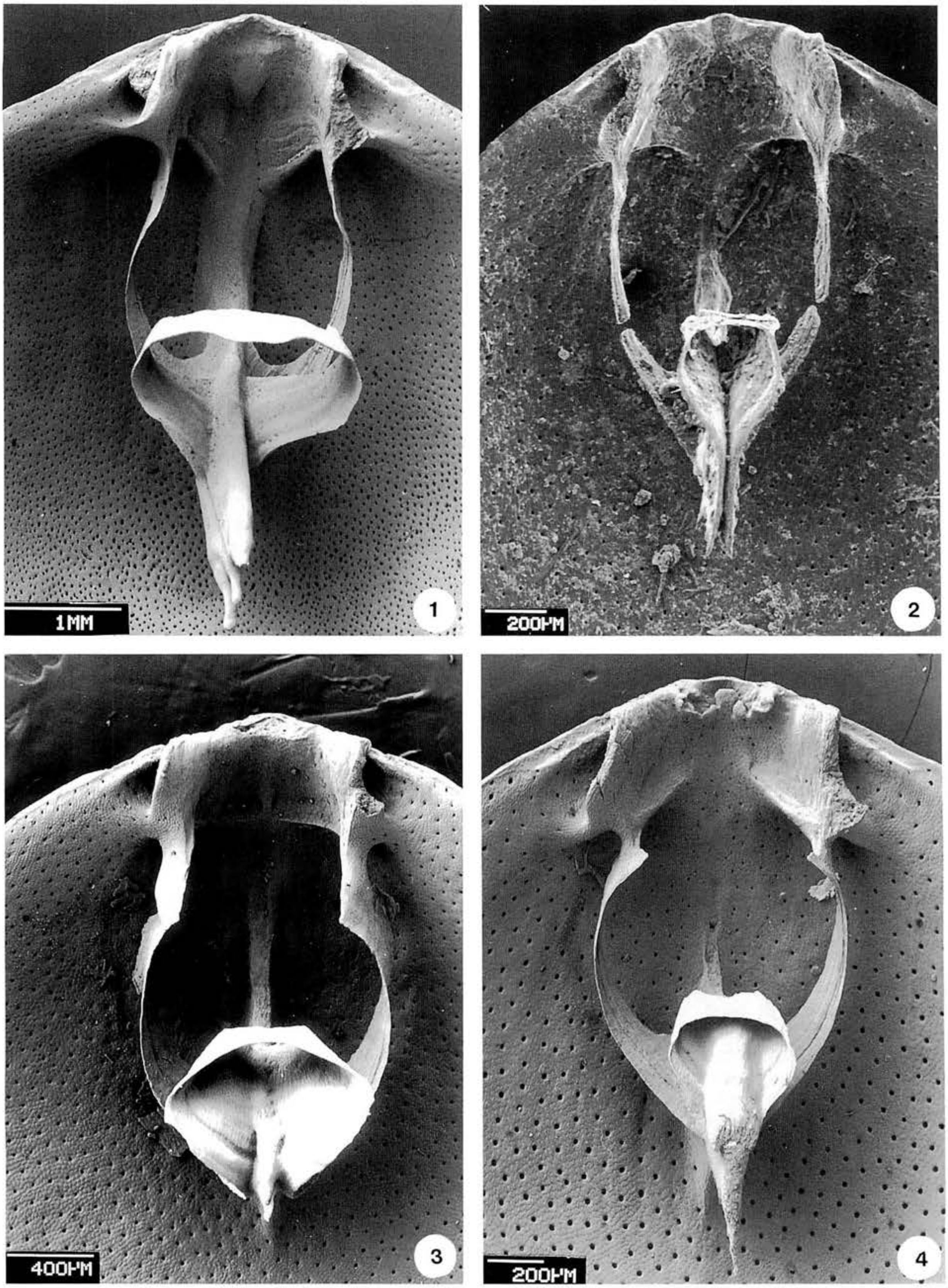
Incomplete Annular Phase: By length 2.6 mm the brachidial ring is broken due to resorption (not breakage) of the very narrow transverse band. The crural outgrowths continue to lengthen and beneath the crura, a pair of excavate inner hinge plates appear. From length 2.6 mm, and larger, the remaining ventrally curved parts of the ascending elements of the brachidium, and the septal pillar to which they are attached, continue to grow. The distal extremity of the septal pillar may become spinose, but it remains nonbifurcate. By about length 4.0 mm, the descending branches of *Shimodaia* are fully formed, running as arcuate branches from crura to septal pillar.

In one large specimen of dorsal valve length 6.0 mm (Figure 2-6, Figure 7-1), the ascending loop branches were observed to have reunited ventrally, but this specimen is, so far, unique. Usually, in adult specimens, the distal extremities of the ascending lamellae are separated by a gap. Similar incomplete annular loop phases have been reported by MacKinnon, *et al.* (1993) in the New Zealand mid-Cenozoic terebratellids *Praemagadina campbelli* and *Magadina squiresi*. Likewise an incomplete annular loop is found in Cretaceous *Magas* Sowerby, and in Cenozoic *Bouchardia*. However, all four taxa display various fundamental morphological dissimilarities to *Shimodaia* and, consequently, are not considered to be closely related to the latter.

Discussion

On external characteristics alone (in particular red/white variegated shell coloration, shell size, and shape), *Shimodaia pterygiota* most closely resembles *Frenullna sanguinolenta* and has in the past been confused with the latter species (e.g. Harada and Mano, 1960), however the present-day geographic distributions of the two species do not overlap. While *Shimodaia pterygiota* appears to be confined to the Izu Penninsula/Sagami Bay area, Honshu, *Frenulina sanguinolenta* is very widely distributed in tropical or near-tropical waters of the Pacific Ocean, including the Hawaiian Islands, Ryukyu and Ogasawara Islands of Japan, the Philippines, Sulu Archipelago, the Moluccas, New Caledonia, Tahiti, Tonga, and parts of northeastern, western, and southern Australia (Richardson, 1973). The largest specimen of *S. pterygiota* yet collected is about 7 mm in length (ventral valve), whilst the largest specimen of *F. sanguinolenta* currently available for study (from Japanese waters) is about 12 mm in length. Bivariate scatter diagrams showing the relationships between length/width, and thickness/width in over 200 specimens of both species reveal distinct differences in relative growth proportions (Figure 5). While there is close correspondence in the plots of length/width in both species, the plots of width/thickness (and length/thickness) reveal some discrepancy between the two species. Juvenile *F. sanguinolenta* are ovate in outline, whereas adult specimens tend to become subcircular; specimens of *S. pterygiota*, however, tend to remain ovate in outline throughout ontogeny.

Certain aspects of loop development in *S. pterygiota* have already been discussed by Saito (1996), as '*Frenulina*' sp., and compared with loop development in other Japanese laqueoid brachiopods, including *Frenulina sanguinolenta, Pictothyris picta*, and *Laqueus* sp. All three taxa pass through juvenile axial and annular loop phases comparable to those occurring in juvenile *Shimodaia*, but they do not then proceed to the adult (incomplete) annular phase characteristic of *Shimodaia*, and their later phases of loop ontogeny extend well beyond the axial and annular phases which they have in common with *Shimodaia*. As pointed out by Saito (1996), *Shimodaia* possesses a confusing mix of morphological characters in the dorsal valve interior. In the possession of steeply dipping inner hinge plates which converge on a low median septum to form a sessile septalium, and an inconspicuous dorsal diductor muscle attachment site (myophore), the cardinalia of *Shimodaia* (Figure 7-1) resemble those occurring in young *Laqueus rubellus* (Figure 7-2), as well as *Laqueus* sp. studied by Saito (1996). However, the septal pillar of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both juvenile *Laqueus* species becomes distinctly bifurcate along the anteroventral, growing edge by early in the axial loop phase (Figure 7-2), whereas the septal pillar of *Shimodaia* remains nonbifurcate throughout life (Figure 7-1). On the other hand, the septal pillars of both *Frenulina sanguinolenta* (Figure 7-3) and *Pictothyris picta* (Figure 7-4) remain essentially nonbifurcate throughout ontogeny, as occurs in *Shimodaia* but, in adult specimens of both *P. picta* and *F. sanguinolenta* (Figure 4), the cardinalia bear disjunct, subhorizontal, inner hinge plates elevated well above the valve floor. In addition, at the adult stage, the cardinal process is strongly differentiated in *Pictothyris*, and rather less well so in *Frenulina*. Thus, in summary, *Shimodaia* differs from juvenile *Laqueus* principally in the nonbifurcation of the septal pillar, whereas the main differences between *Shimodaia* and juveniles of both *Frenulina* and *Pictothyris* lie in the cardinalia, particularly the size and disposition of the inner hinge plates and the extent of definition of the cardinal process.

Because the foregoing morphological data concerning differences between *Shimodaia* and the other three taxa is so limited, there is little point in speculating as to which of the three, if any, is the most likely ancestor. Theoretically any one of the three taxa under consideration, i.e. *Laqueus*, *Frenulina*, or *Pictothyris*, could be the direct ancestor of *Shimodaia* but the issue could be resolved in the near future through appropriate molecular studies.

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Figure 7. 1-4. Comparative views of cardinalia and axial loop phases in 1 : *Shimodaia pterygiota* gen. et sp. nov., UMUT RB27394a (L_{dv} = 6.2 mm). 2 : *Laqueus rubellus* (Sowerby) USNM 550341 (L_{dv} = 2.4 mm). 3. *Frenulina sanguinolenta* (Gmelin) (L_{dv} = 4.0 mm). 4. *Pictothyris picta* (Dillwyn) (L_{dv} = 2.7 mm).