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Shell and Pallet Morphology in Early Developmental Stages of *Teredo navalis* Linné (Bivalvia: Teredinidae)

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ABSTRACT

Dimensions of the shell and provinculum distinguish *Teredo navalis* larvae from the larvae of other bivalve mollusks. In the present scanning electron microscopic study of shell and pallet morphology during early ontogenetic stages of this species, the characteristic teredinid provinculum, with two interlocking pairs of small teeth and a wide central tooth and socket, was well-developed in shells 90 μm long. Provinculum length ranged from 44 to 51 μm during the larval period. Average lengths of provincular teeth of the left valve were 9.6 μm for the anterior tooth and 8.2 μm for the posterior tooth; in the right valve, lengths were 7.2 μm for the anterior tooth, 16.4 μm for the central tooth, and 6.6 μm for the posterior tooth. Larval shell height prior to metamorphosis was just under 230 μm.

Formation of a ligament pit preceded secretion of the dissoconch and development of the apophyses, condyles, and exterior denticulated ridges. Shell loss along the posterior margin of the right valve accompanied a shift in the axis of articulation from the dorsal to the posterior plane; subsequent secretion of the dissoconch restored bilateral symmetry. The initial triangular shape of the pallet blade became increasingly rectangular and finally elongate with growth along the distal margin.

Key words: Larvae; post-larvae; shell morphology; pallets; *Teredo navalis*; teredinid; shipworm.

INTRODUCTION

The common shipworm *Teredo navalis* Linné, 1758, is distributed worldwide in temperate waters (Turner, 1966, 1971; Abbott, 1974). This larviparous bivalve releases veligers at the straight-hinge stage of development (Sigerfoos, 1908; Grave, 1928; Jørgensen, 1946; Sullivan, 1948; Loosanoff & Davis, 1963; Loosanoff *et al.*, 1966; Turner, 1966, 1971; Scheltema, 1971; Turner & Johnson, 1971). Early morphology of *T. navalis* has been described with optical photomicrographs and gross shell dimensions at various developmental stages (Jørgensen, 1946; Sullivan, 1948; Imai *et al.*, 1950; Loosanoff & Davis, 1963; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971; Culliney, 1975). Jørgensen (1946) characterized the teredinid provinculum as having three teeth on the right valve and two teeth on the left valve; however, dimensions of the larval hinge teeth are not documented for this species. Growth rates of *T. navalis* during larval and post-larval stages were tabulated by Imai *et al.* (1950). Morphology of the shell and pallets of *T. navalis* during post-larval stages has not been described to date.

The present scanning electron microscopic study provides a comprehensive description of the morphological features of the shell and pallets of *T. navalis* during early developmental stages. Provinculum length and dimensions of provincular teeth of *T. navalis* larvae are compared with the same measurements of previously described teredinid larvae to facilitate identification of specimens isolated from plankton samples. Scanning electron microscopic methods for reproducible and consistent orientation of post-larval specimens are described. Details of the rapid changes in shell morphology during metamorphosis are elucidated with micrographs of sequential developmental stages.

MATERIALS AND METHODS

Adult specimens of *Teredo navalis* were collected from a subtidal stake of sweet gum (*Liquidambar styraciflua* Linné) located in a coastal bay near Wachapreague Inlet, Virginia. Larvae (initial shell stages) were removed from three of these adult shipworms and were reared in filtered (50 μm mesh) baywater (salinity range = 29.5 to 34.5‰; temperature range = 22 to 28 °C) using standard culture techniques (Loosanoff & Davis, 1963). During metamorphosis, animals colonized several pieces of conditioned wood that were floated in the culture tank.

Larval and post-larval samples were treated with a 5.25% sodium hypochlorite solution for 10 minutes to remove soft tissues (after Rees, 1950); disarticulated valves and pallets were rinsed several times with distilled water and were stored in 95% ethanol. Specimens were mounted on silver tape, were coated with approximately 600 Å of gold-palladium, and were examined using an ETEC Autoscan scanning electron microscope (SEM). Consis-

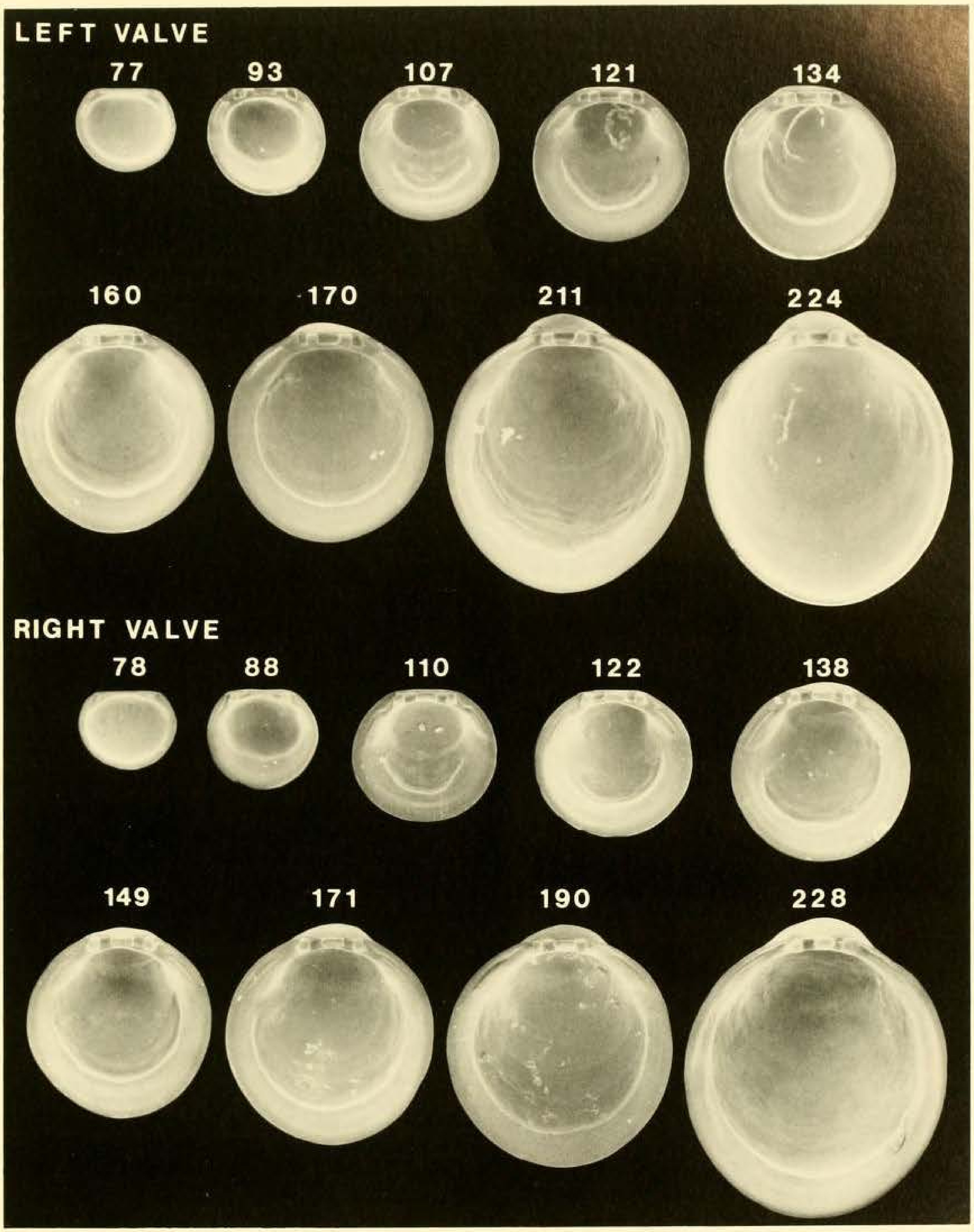

Figure 1. Scanning electron micrographs of disarticulated valves of *Teredo navalis* larvae. Numbers indicate greatest shell dimension in μm.

tent orientation for documentation of shape was obtained by positioning larval shells with points of the shell margin aligned in a plane normal to the electron beam of the SEM. [For further details of SEM methods for larval shells, see Fuller *et al.* (1989).] Similar orientation of post-larval valves was impossible because points along the post-larval shell margin do not lie in a single plane. Throughout the post-larval developmental period, however, points along the dorsoventral margin of the anterior slope (except those at the extreme ventral region) comprise a plane (figure 3). Thus, consistent orientation of post-larval shells was achieved by positioning specimens such that this plane was parallel to the electron optical axis. Additional adjustments were made so that dorsal and ventral condyles were at an equal working distance. Shells mounted for documentation of external shell mor-

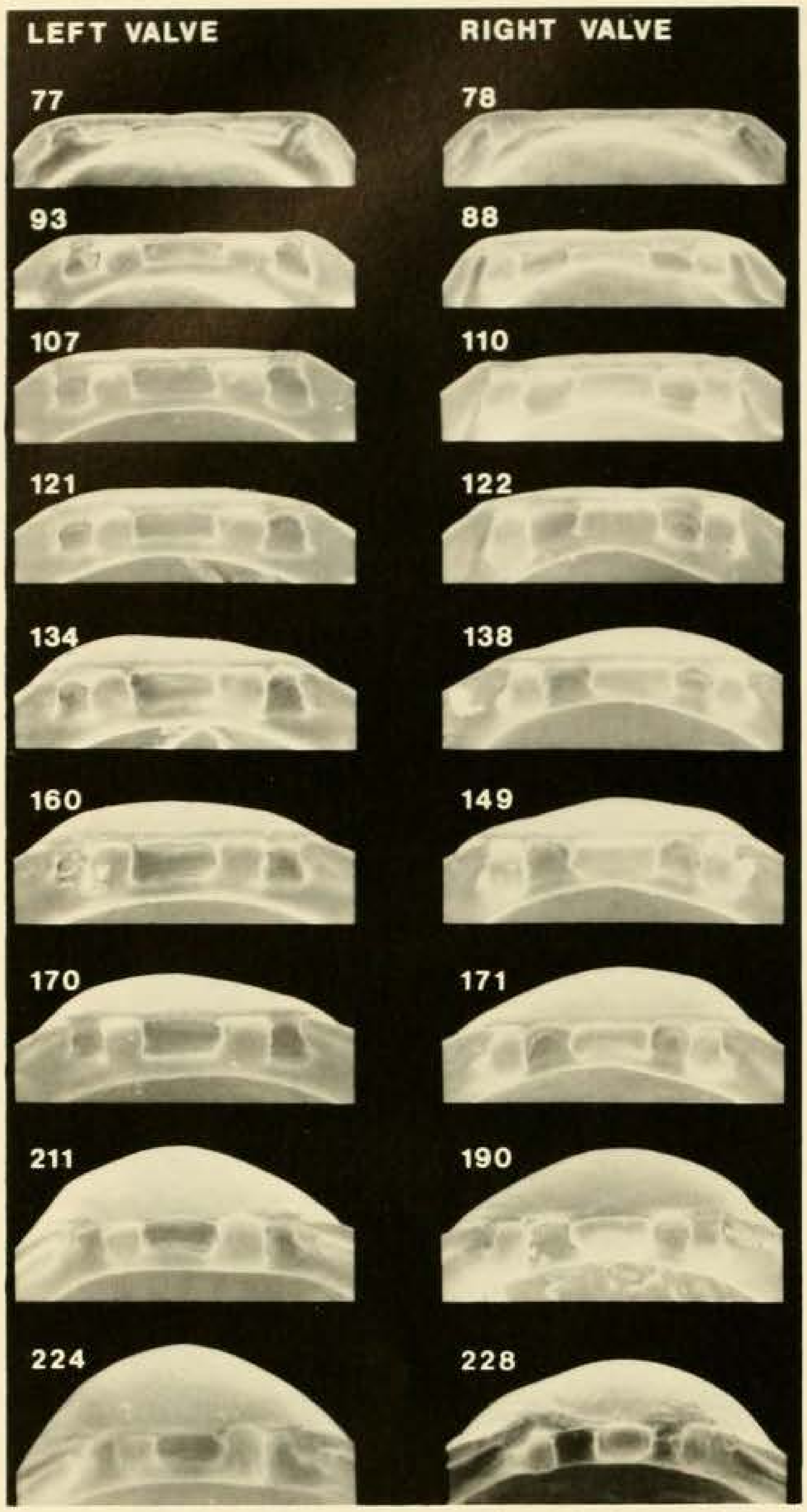

Figure 2. Scanning electron micrographs of the hinge of disarticulated valves of *Teredo navalis* larvae seen in figure 1. Numbers indicate greatest shell dimension in μm.

phology were placed with the condyles and posterior slope resting on a specimen mount, which was tilted slightly for maximal visibility of the external surface.

Shell height is defined as the greatest dorsoventral dimension. Shell length is defined as the greatest anteroposterior dimension roughly parallel to the hinge line in larval and early post-larval specimens; measurements of this dimension include the anterior and posterior slopes as they developed in late post-larvae. Shell nomenclature is taken from Turner (1966, 1971).

Outer surface morphology of the pallets was documented with the blade positioned approximately perpendicular to the electron optical axis. Pallet length is the distance between proximal and distal ends (see Turner, 1971:26, for pallet terminology).

RESULTS

Scanning electron micrographs of disarticulated valves and hinges of sequential ontogenetic stages of *Teredo navalis* larvae are shown in figures 1 and 2. Straight-hinge larval shells ranged from 77 to 87 μm long ($\bar{x} \pm$ SD = 81.5 ± 3.3 μm; n = 30) and from 66 to 70 μm high ($\bar{x} \pm$ SD = 66.6 ± 1.5 μm; n = 30). Larvae 90 μm long had a well-developed provinculum, with two interlocking pairs of small teeth and a wide, central tooth and socket. Provinculum length ranged from 44 to 51 μm ($\bar{x} \pm$ SD = 47.7 ± 1.7 μm; n = 21) during the larval period. Measurements of provincular teeth are summarized in table 1. A low umbo formed in shells approximately 120 μm long. During mid-larval stages, the longest valve dimension shifted from an anteroposterior to a dorsoventral axis; larvae were equidimensional at approximately 150 μm. Length of larvae just prior to metamorphosis ranged from 195 to 210 μm ($\bar{x} \pm$ SD = 202.0 ± 4.8 μm; n = 30); height was just under 230 μm at this stage.

The first morphological evidence of metamorphosis was formation of a ligament pit, which was observed when valves were approximately 230 μm high (figures 3, 4). Immediately following formation of the ligament pit, dramatic morphological changes occurred in the shell and hinge. An apophysis grew from a base beneath the anterior tooth and socket; this base extended below the entire hinge area and expanded at the posterior end to form an early dorsal condyle (figures 3, 4, height 240 μm, DC). Formation of the ventral condyle began with an inward protrusion of the ventral margin (figure 3, height 240 μm, VC). Shell loss along the posterior margin of the right valve began at this stage (figures 3, 5, height 240 μm). An initial denticulated ridge formed on the anterior margin of the shell exterior (figure 5, height 240 μm).

A shift in the axis of articulation from an anteroposterior to a dorsoventral orientation occurred when shell height was between 230 and 240 μm (figure 6). Loss of approximately 25 to 40 μm of the shell along the posterior margin of the right valve accommodated this shift (figures 5, 7). New ridges were added on the external surface of the anterior margin (figure 5, height 250 μm).

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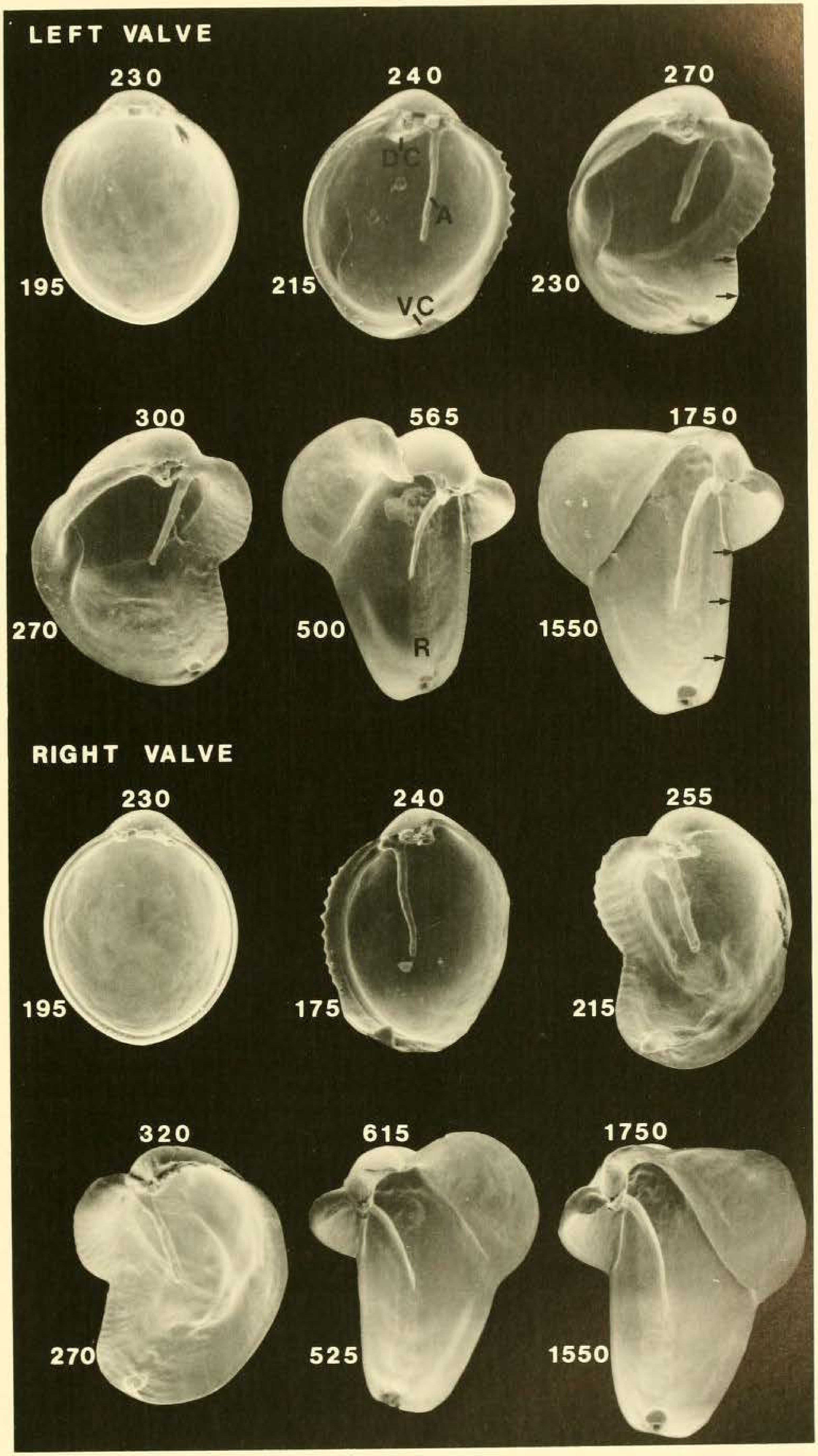
Figure 3. Scanning electron micrographs of disarticulated valves of *Teredo navalis* post-larvae. Numbers above the shells indicate shell height (greatest dorsoventral dimension); numbers beside the shells indicate shell length (greatest anteroposterior dimension). Dimensions are in μm and are accurate to within 5 μm. Arrows designate the dorsoventral margin of the anterior slope; points on this margin were aligned in a plane for consistent orientation of valves. A, apophysis; DC, dorsal condyle; VC, ventral condyle; R, umbonal-ventral ridge.


LEFT VALVE
230
195
240
DC
A
215
VC
270
230
300
270
565
500
R
1750
1550
RIGHT VALVE
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195
240
175
255
215
320
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615
525
1750
1550

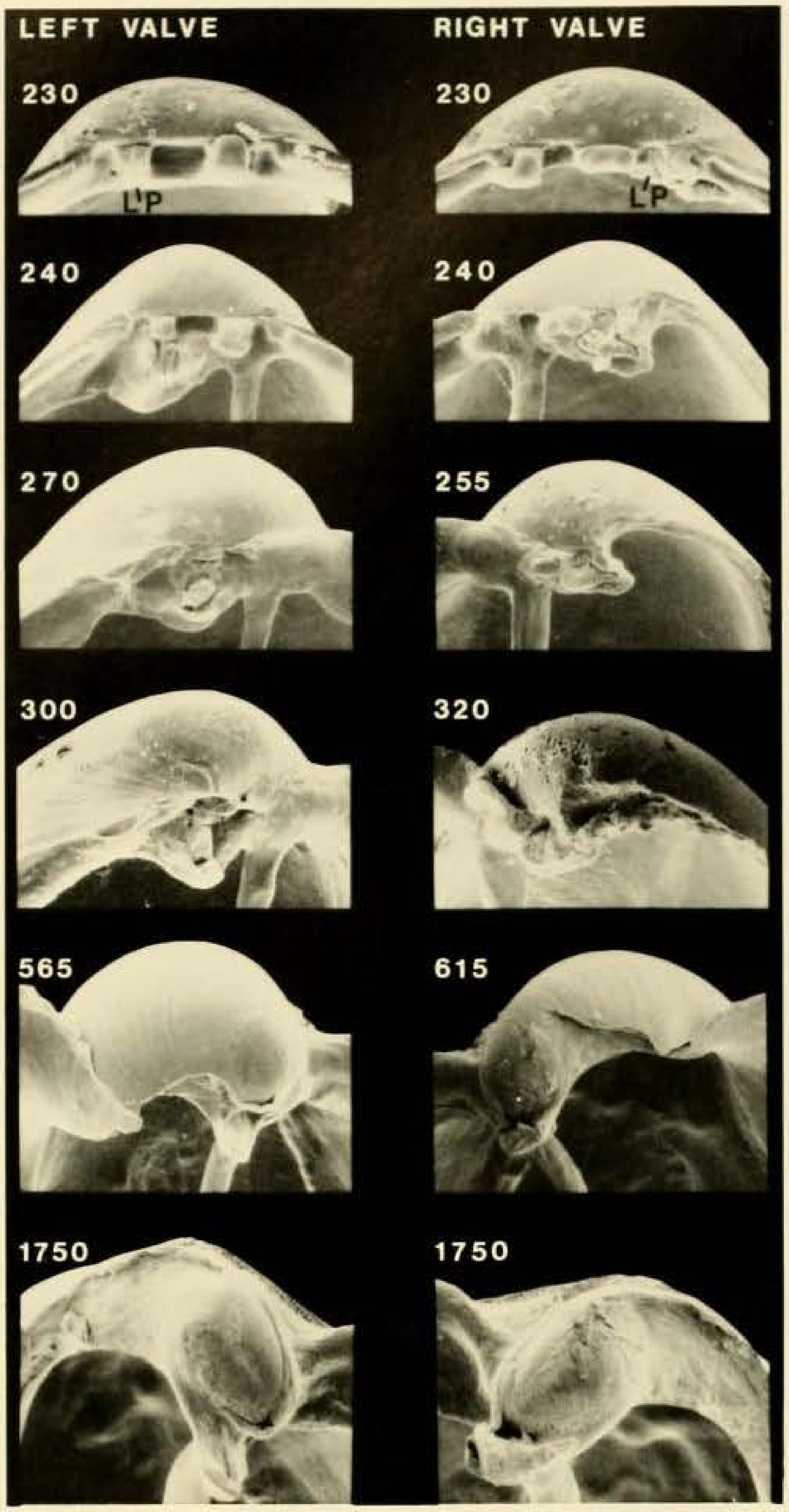

Figure 4. Scanning electron micrographs of the hinge of disarticulated valves of *Teredo navalis* post-larvae seen in figure 3. Numbers indicate shell height (greatest dorsoventral dimension) in μm. LP, ligament pit.

In shells approximately 255 to 275 μm high, the ventral condyle had developed into a prominent knob, and the provinculum was no longer recognizable (figures 3, 4). Rapid growth along the ventral margin increased the depth of the valves and caused articulated shells to become nearly spherical. Protrusion of ventral condyles further separated right and left valves. Five to 12 ridges covered the external surface of the anterior slope (figure 5, height 265/275 μm). Demarcation of the posterior slope began in valves 300 μm high (figures 3, 5). Posterior margins of right and left valves were symmetrical; unequal secretion of the dissoconch along this margin restored earlier asymmetry of the valves (figure 8).

External growth lines marked the pronounced ventral extension of the valves (figure 5, height 330/295 μm). As development continued, the posterior slope became more prominent (figure 3, height 565/615 μm). The umbonal-ventral ridge appeared on the interior surface of the shell (figure 3, height 565/615, 1,750 μm). The dorsal condyle developed (figure 4, height 565/615 μm) from the early expanded base of the apophysis (figure 4, height 240, 270/255, 300/320 μm) and was positioned posterior to the apophysis (figure 9). At a shell height of approximately 1 mm, the posterior gape was well-developed (figure 10).

The external surface of the anterior slope of both valves was sculptured with closely-spaced, denticulated ridges in early post-larvae. Subsequent ridges were more widely-spaced, so that the relationship of shell length to number of ridges over the entire post-larval period was logarithmic (figures 5, 11). In contrast to early post-larval ridges with uniform denticles, late post-larval ridges had fine denticles in the anterior section, while large, coarse denticles marked posterior ridges (figure 5, height 610/490, 855 μm). In addition, these late post-larval ridges formed a sharp angle at the ventral junction of the anterior and posterior sections of the anterior slope.

The earliest pallets were removed from animals with a shell length of approximately 240 μm. The pallet blade at this stage was triangular, with the margin of the inner face extending further distally than that of the outer face (figure 12, 75 μm). The shape of the blade became more rectangular with additional growth of the inner margin (figure 12, 125/110 μm). Inner and outer margins of the pallet blade elongated, and the margin of the outer face became considerably more concave than that of the inner face (figure 12, 200/195, 285/265, 485/470 μm).

Throughout development of the pallets, each pair had a symmetrical shape. Close examination of an individual pallet, however, revealed that the ventral surface was longer than the dorsal surface of the blade. The resulting asymmetry of the blade was increasingly evident as ventral and dorsal surfaces rounded and the dorsal distal tip extended further than the ventral distal tip (figure 12, 715/795, 1,025/1,035 μm). Further growth was greatest in a distal direction, resulting in an elongate shape of pallets approximately 1,500 μm long (figure 12).

Pallet length increased more rapidly than shell length during initial post-larval stages. After anterior and posterior slopes were well-developed, pallet length and shell length increased at approximately equal rates (figure 13).

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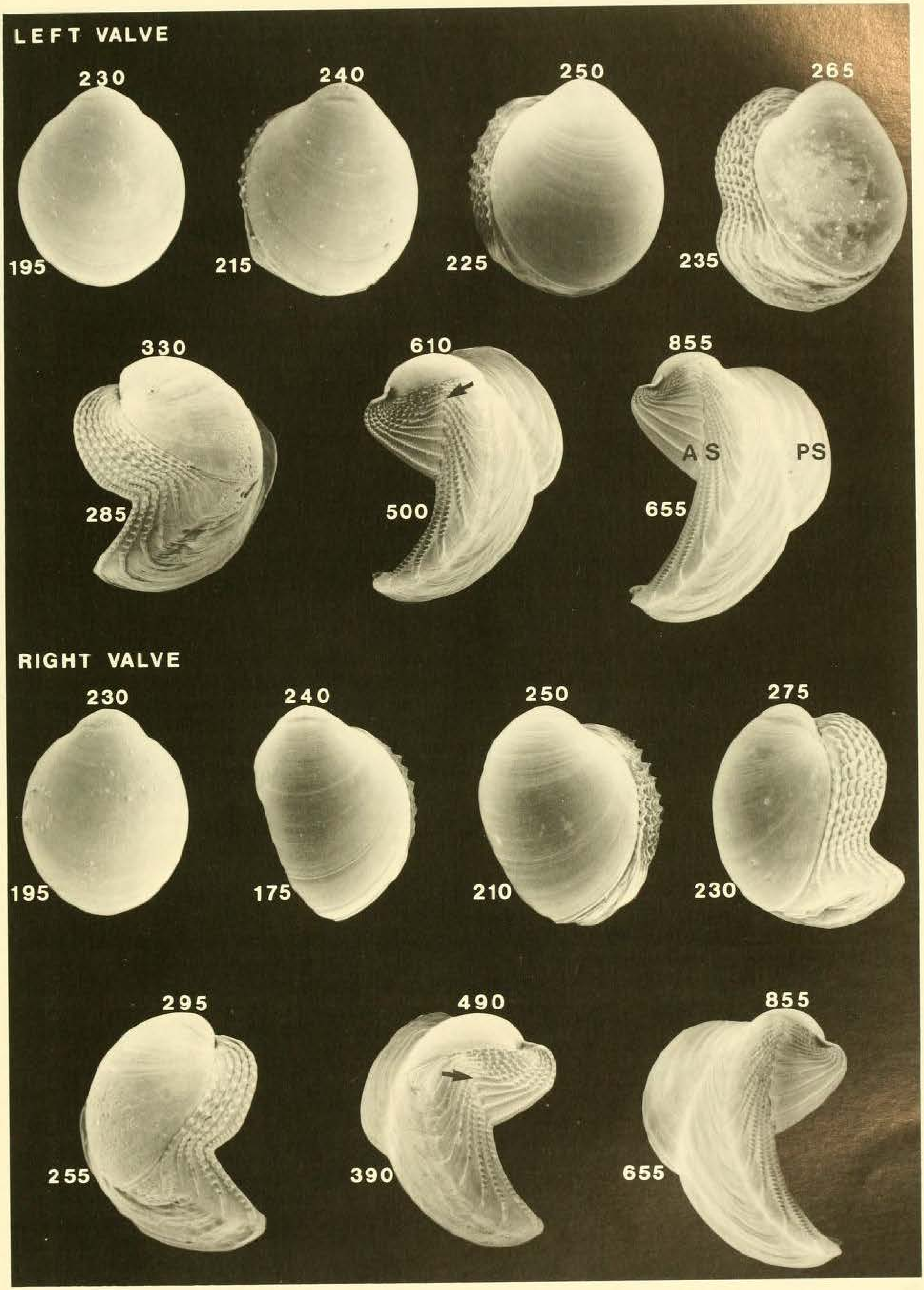
Figure 5. Scanning electron micrographs of the exterior surface of disarticulated valves of *Teredo navalis* post-larvae. Numbers above the shells are shell height (greatest dorsoventral dimension); numbers beside the shells are shell length (greatest anteroposterior dimension). Dimensions are in μm and are accurate to within 5 μm. Arrows mark late post-larval ridges, which are comprised of both fine and coarse denticles. AS, anterior slope; PS, posterior slope.


LEFT VALVE
230
195
240
215
250
225
265
235
330
285
610
500
855
AS
PS
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RIGHT VALVE
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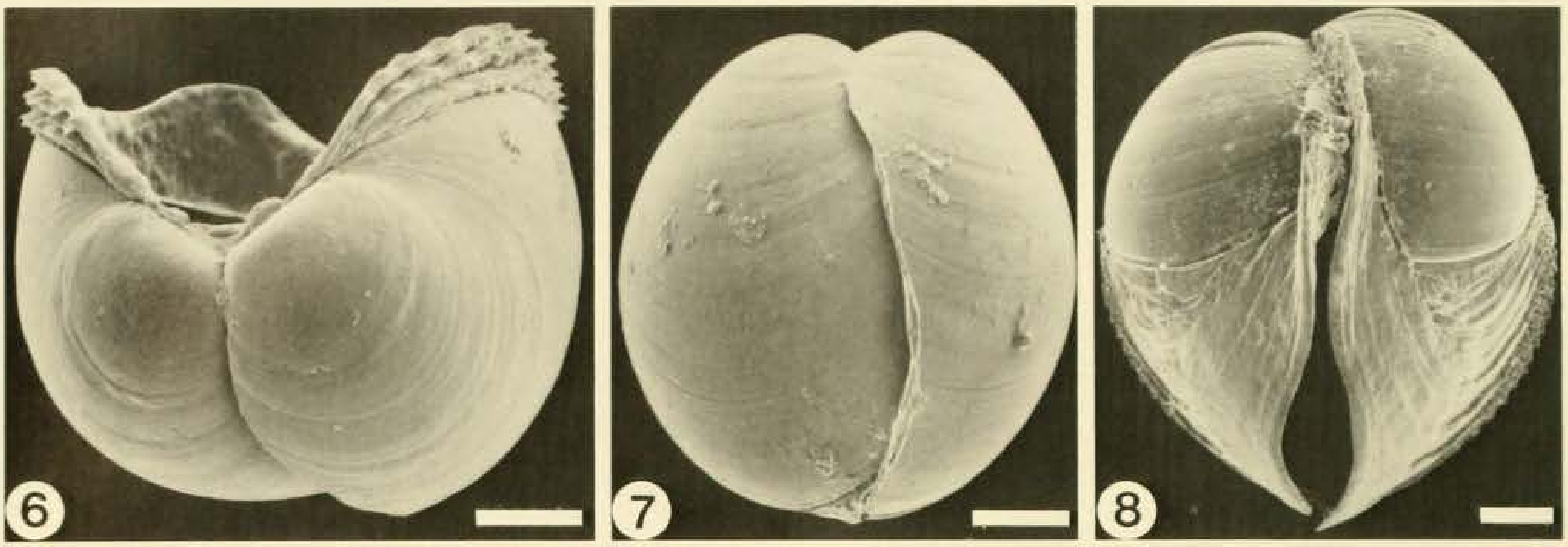
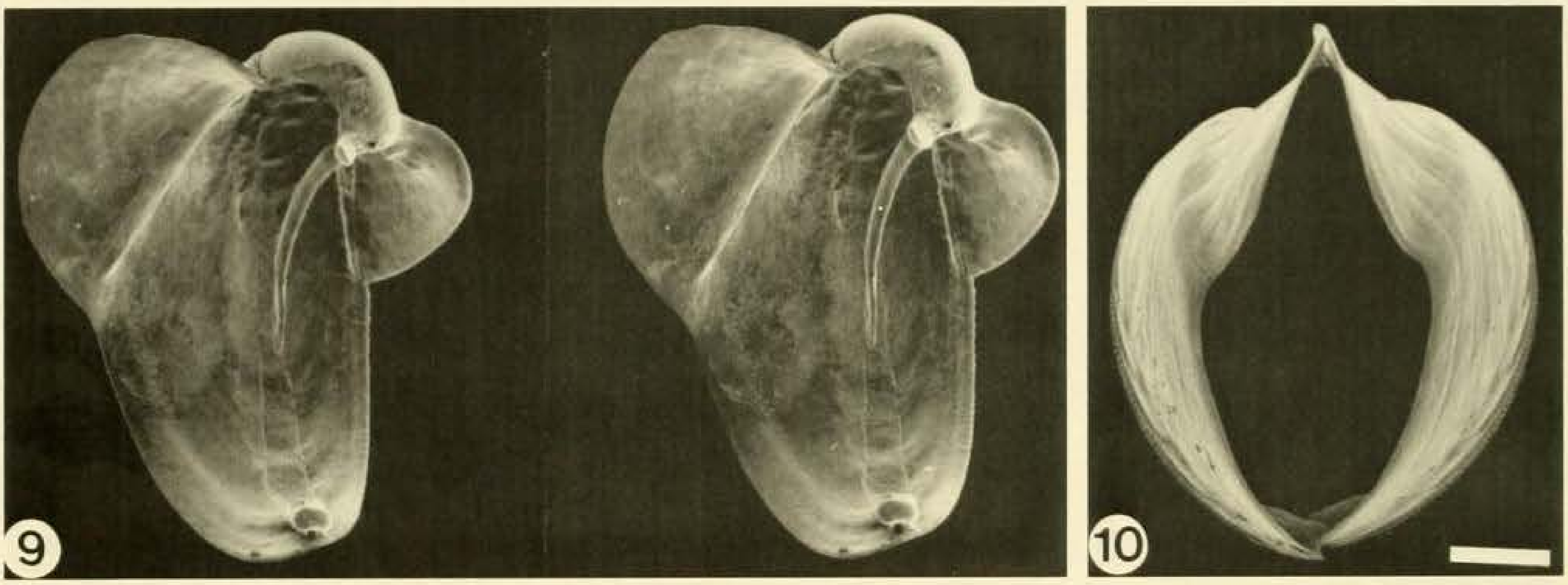


Figures 6–8. Scanning electron micrographs of early post-larval shell specimens of *Teredo navalis*. **6.** Dorsal view after the shift in axis of articulation to a dorsoventral orientation. Scale bar = 50 μm. **7.** Posterior view after the shift in axis of articulation to a dorsoventral orientation. Scale bar = 50 μm. **8.** Posterior view when symmetry of right and left posterior margins is nearly complete. Scale bar = 50 μm.



Figures 9, 10. **9.** Scanning electron micrographs of a left valve of a post-larval specimen of *Teredo navalis*. Stereo pair was taken with an 8° angular displacement between exposures. **10.** Scanning electron micrograph of an articulated post-larval shell specimen of *Teredo navalis*; posterior view. Scale bar = 200 μm.

DISCUSSION

LARVAL DEVELOPMENT

Previously reported shell dimensions of *Teredo navalis* larvae are summarized in table 2. Dimensions of straight-hinge larvae in the present study were consistent with those in previous descriptions. Mean provinculum length of *T. navalis* in the present study was 47.7 μm, close to the 51.3 μm mean given by Culliney (1975) and within the 45 to 50 μm range given by Chanley and Andrews (1971). Umbones appeared when larvae were about 120 μm long, similar to the 123.3 μm mean length reported by Culliney (1975) and within the 110 to 150 μm length range given by Sullivan (1948), but larger than the 95 to 100 μm length range found by Chanley and Andrews (1971). Shell length and shell height were equal when larvae of this species were approximately 150 μm, which was the size given by Imai *et al.* (1950) but was larger than the 123 and 122 μm sizes of equidimensional larvae found by Culliney (1975) and Mann and Gallager (1985), respectively. Size at metamorphosis was smaller than that reported by Sullivan (1948), Imai *et al.* (1950), and Mann and Gallager (1985) and approximately the same as that reported by Loosanoff and Davis (1963), Loosanoff *et al.* (1966), Chanley and Andrews (1971), and Culliney (1975). Difficulty in achieving consistent shell orientation due to great convexity of the valves during late larval stages may account for the discrepancies among measurements. Measurements of disarticulated valves, aligned with the shell margin in a plane, would improve accuracy.

Scheltema (1971) summarized previous descriptions of teredinid larvae from the North Atlantic. He emphasized that features included in these early descriptions, such as larval size ranges and color, are not always sufficient for positive identification of unknown species. On the other hand, differences in external shell surface sculpture revealed by scanning electron microscopy distinguished

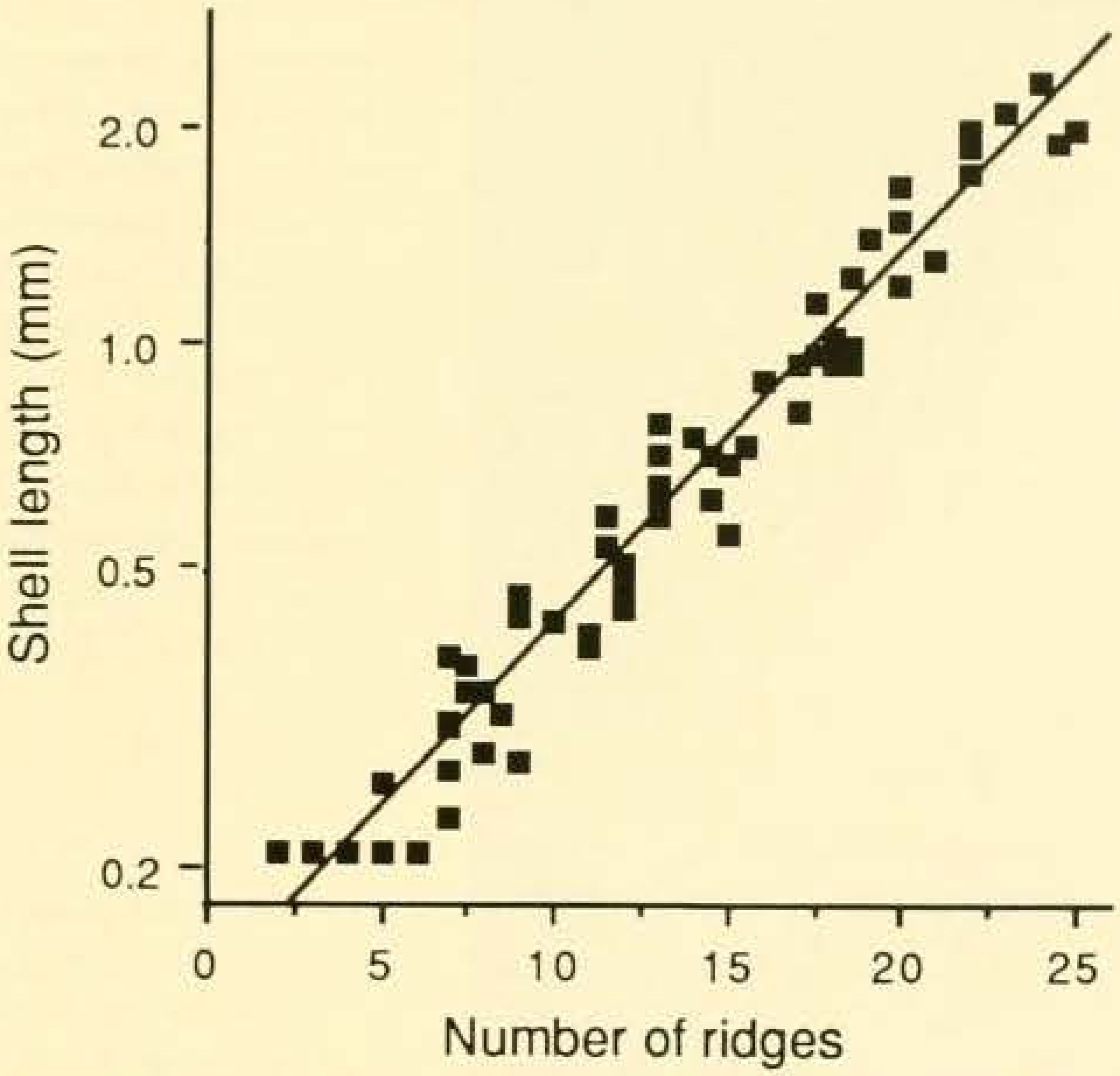


Figure 11. Relationship between shell length (greatest antero-posterior dimension) and number of (early and late post-larval) ridges on the exterior surface of shells of *Teredo navalis*. Regression equation is $y = -0.28 + 0.08x$; $r^2 = 0.93$.

several species of the Teredinidae (Scheltema, 1971; Turner & Boyle, 1975; Calloway & Turner, 1979). Also, Turner and Johnson (1971) illustrated the distinct nature of the velum in two teredinids and suggested use of this character as an aid in species identification.

The value of hinge structures for identification of larval bivalves is well-documented (Jørgensen, 1946; Sullivan, 1948; Rees, 1950; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971; Le Pennec, 1980; Lutz *et al.*, 1982; Jablonski & Lutz, 1983). In teredinids, provinculum length is constant throughout the larval period (Rees, 1950); therefore, identification of teredinid species based on provinculum length can be made without regard to larval size or stage of development. In specimens of *T. navalis* larvae examined in the present study, dimensions of provincular teeth showed individual variation but were independent of developmental stage or size.

Provinculum length of *Teredora malleolus* (Turton, 1822) (= *Teredo thomsonii* Tryon; Turner, 1966; Scheltema, 1971) is approximately 70 μm (Rancurel, 1965: fig. 1) and of *T. navalis* averages 47.7 μm (present study); therefore, larval specimens of *T. navalis* and *T. malleolus* are easily distinguishable on the basis of provinculum length. Furthermore, measurements and shapes of individual teeth of *T. malleolus* reported by Rancurel (1965) differ from shapes and dimensions of teeth of *T. navalis* in the present study.

Scanning electron micrographs of a disarticulated right valve of *Lyrodus pedicellatus* (Quatrefages, 1849), another larviparous teredinid, were presented by Turner and Johnson (1970: figs. 1, 2). Although measurements of teeth from these micrographs are approximate, measurements of the length of the central tooth relative to the anterior and posterior teeth indicate distinct differences in the provinculum of the right valve of *T. navalis* and *L. pedicellatus*.

Dimensions of provincular teeth of *T. navalis* also differ from those of *Bankia martensi* (Stempell, 1899) (table 1). The most striking difference in the provinculum of these two species, however, is the shape of the anterior tooth of the right valve, which is J-shaped in *B. martensi* and rectangular in *T. navalis* (B. Campos, personal communication). A J-shaped anterior tooth is also noted in the provinculum of the right valve of *Bankia setacea* (Tryon, 1863) (Quayle, 1951: fig. 8).

METAMORPHOSIS

Lutz and Hidu (1979) suggested that development of the ligament pit was among the earliest morphological changes that occur in planktonic bivalves during metamorphosis. Further evidence of the early formation of the ligament pit is seen during metamorphosis of *Teredo navalis*. In this species, the ligament pit formed ventral to the hinge structure in post-larval shells approximately 230 μm high. Secretion of the dissoconch and formation of apophyses, dorsal and ventral condyles, and external ridges occurred subsequently, when shipworms were approximately 240 μm high.

Table 1. Lengths (distance across center of tooth and parallel to hinge line) in μm of provincular teeth of *Teredo navalis* and *Bankia martensi*.[1]

Position	*Teredo navalis*		*Bankia martensi*	
	Range	$\bar{x} \pm$ SD	Range	$\bar{x} \pm$ SD
	Left valve (n = 9)		Left valve (n = 10)	
Anterior	8.8–10.2	9.6 ± 0.5	8.5–12.8	9.1 ± 1.0
Posterior	7.7–8.6	8.2 ± 0.3	4.2–8.5	6.4 ± 1.0
	Right valve (n = 12)		Right valve (n = 9)	
Anterior	6.3–8.3	7.2 ± 0.6	4.2–6.4	5.2 ± 1.2
Central	13.7–18.2	16.4 ± 1.1	14.9–17.0	16.4 ± 0.8
Posterior	6.0–7.0	6.6 ± 0.3	4.2–8.5	5.9 ± 1.0

[1] Data on *Bankia martensi* were provided by B. Campos, Universidad de Valparaíso, Viña del Mar, Chile. Specimens were sampled from Valparaíso Bay, Chile.

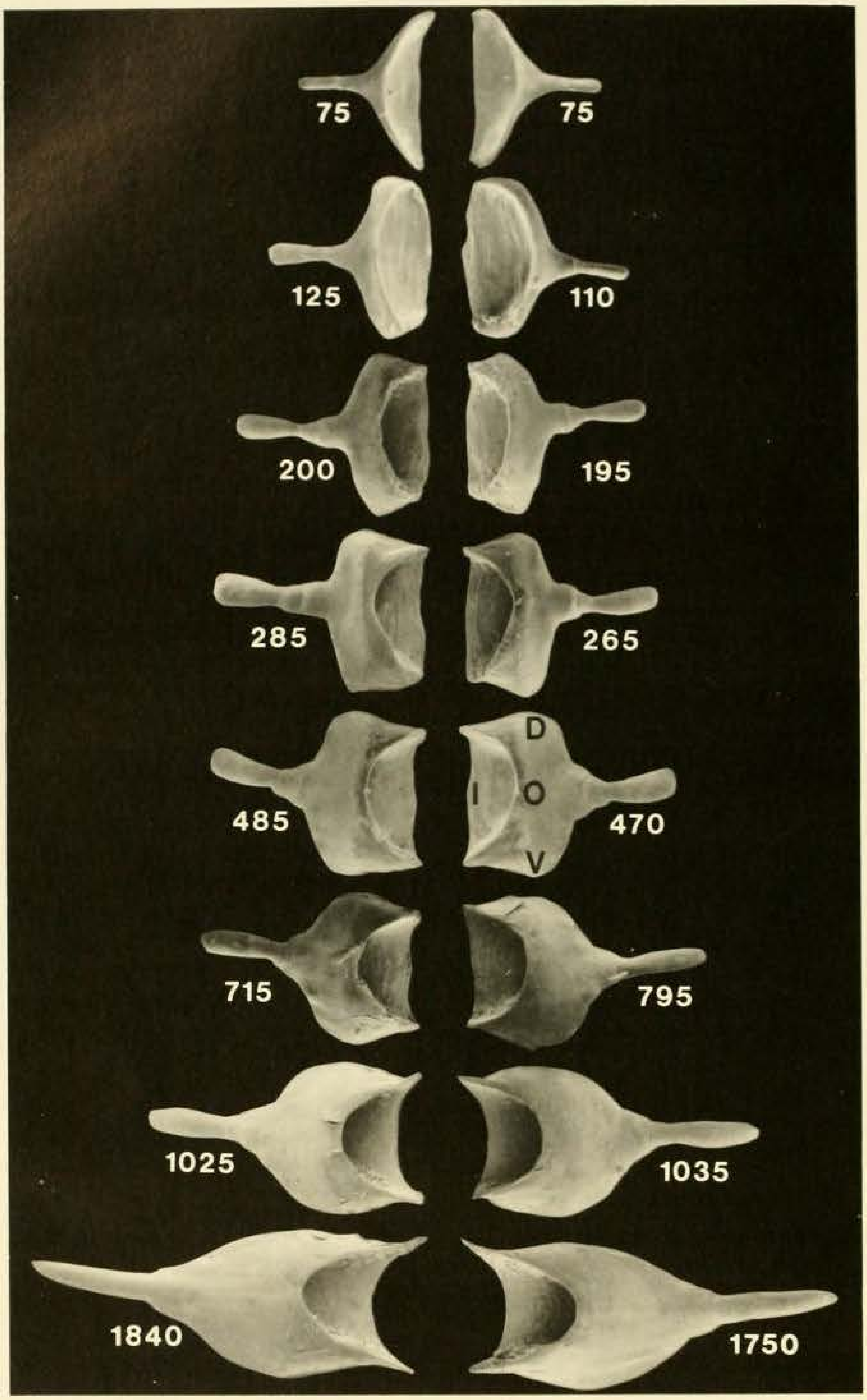


Figure 12. Scanning electron micrographs of the outer face of pallets of *Teredo navalis* post-larvae. Micrographs of similarly-sized right and left pallets are not necessarily from the same individual. Numbers indicate distance between distal and proximal ends in μm. I, inner margin; O, outer margin; D, dorsal surface; V, ventral surface.

In *T. navalis*, major modifications of the shell enable post-larvae to penetrate wood. Preparation for these changes begins in mid-larval stages with increased growth along the ventral shell margin, so that the new axis of articulation is oriented along the longest shell dimension. The shift in axis of articulation from the dorsal to the posterior plane is accomplished by shell loss along the posterior margin of the right valve. Quayle (1959) described similar shell loss along the posterior margin of the right valve of *Bankia setacea* following settlement and suggested that the loss was due to shell erosion. The shift occurs rapidly in *T. navalis*; shells approximately 230 μm high articulated along an anteroposterior axis, and shells approximately 240 μm high articulated along a dorsoventral axis. Subsequent adjustments for this rearrangement, however, occur more gradually with growth of the animal. These include further separation of the valves by an inward protrusion of the condyles until shells articulate against the condyles rather than against dorsal and ventral shell margins. Also, depth of the shell valves increases until articulated shells are nearly spherical. Separation of the valves allows extension of the foot and siphons.

The sudden shift in the axis of articulation is followed by an abrupt change in the orientation of growth axes. Growth axes of the anterior section of the anterior slope are roughly similar to larval growth axes. Growth at the extreme ventral margin of the dissoconch, however, is roughly perpendicular to the larval shell margin (figure 9).

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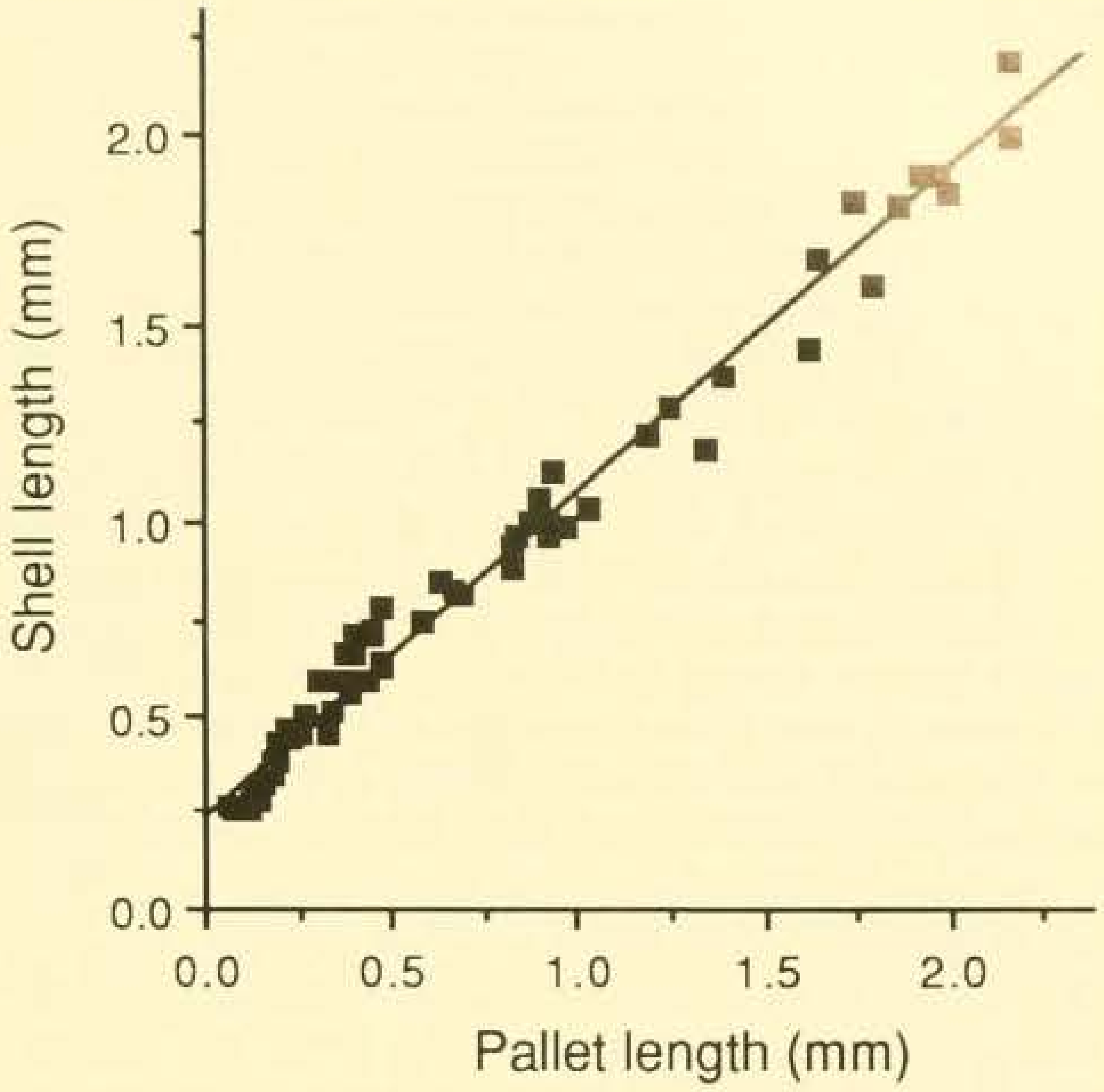

Figure 13. Relationship between shell length (greatest anteroposterior dimension) and pallet length (distance between proximal and distal ends). Each point represents an individual animal; when right and left values differed, the average was used. Regression equation is $y = 0.23 + 0.84x$; $r^2 = 0.99$.

Table 2. Summary of literature reports on larval shell dimensions (in μm) of *Teredo navalis* at: (1) time of release from parent; (2) appearance of umbones; (3) equidimensional stage; and (4) metamorphosis. For comparative purposes, l = anteroposterior dimension; h = dorsoventral dimension; p = provinculum length.

Source	Release	Umbones	Equi-dimensional	Metamorphosis
Grave (1928)	l = 85–90 h = 70–75	—	—	—
Jørgensen (1946)	l = 80 ($\bar{x}$)	—	—	h ≈ 250
Sullivan (1948)	h × l ≈ 80 × 95	l = 110–150	—	h × l ≈ 250 × 220
Imai *et al.* (1950)	l = 85 ($\bar{x}$) h = 72 ($\bar{x}$)	—	≈150	l = 215 ($\bar{x}$) h = 235 ($\bar{x}$)
Loosanoff and Davis (1963)	h × l = 70 × 80 (min) l = 90 (max) l = 85–95 (average)	—	—	l > 200 l = 190 (min) h = 206 (min) l = 200 (max) h = 231 (max)
Loosanoff *et al.* (1966)	h × l = 70 × 80 (min) l = 90 (max)	—	—	l > 200
Chanley and Andrews (1971)	l = 70–90 (min) p = 45–50	l = 95–100	130–140	l = 190–>200

Culliney (1975)	l = 87.7 ($\bar{x}$);
	range = 77–95
	h = 75.4 ($\bar{x}$);
	range = 66–85
	depth range = 55–57
	p = 51.3 ($\bar{x}$);
	range = 46–54
		l = 123.3 ($\bar{x}$)
		h = 123.3 ($\bar{x}$)
		depth = 90
			≈123	[1]l = 205.5;
				range = 200–216
				h = 239.2;
				range = 192–260
				depth = 190

Mann and Gallager (1985)	l = 89.3 ($\bar{x}$) h = 76.1 ($\bar{x}$)	—	≈122	[2]l = 212.1 h = 230.0

Present study	l = 81.5 ($\bar{x}$);
	range = 77–87
	h = 66.6 ($\bar{x}$);
	range = 66–70
		l = 120	≈150	l = 202.0 ($\bar{x}$);
				range = 195–210

[1] Pediveliger.

[2] First appearance of pediveliger.

EXTERNAL SHELL MORPHOLOGY

Numerous, closely-spaced denticulated ridges cover the external surface of the anterior slope of early post-larval shells of *Teredo navalis*. Although the number of ridges found in early stages is variable, observations show a consistent decrease in total number of ridges after formation of the posterior slope (compare figure 5, right valves, heights 275 and 295 μm). This decrease suggests that early post-larval ridges are obliterated as late post-larval ridges (ridges with both fine and coarse denticles) are added at the anterior shell margin.

Hill and Kofoid (1927) described the function of exterior ridges of the adult shell of *T. navalis*. By carving in an anterior direction, shipworms deepen burrows with the fine serrations on anterior ridges; at the same time, posterior ridges with coarser teeth increase the diameter of the burrow. Slightly curved early ridges have uniformly sized denticles (figure 5, height 330/295 μm). As described by Sigerfoos (1908) for *Bankia gouldi* (Bartsch, 1908), a difference in spacing at the dorsal and ventral ends of the shell of *T. navalis* gradually increases the curvature of a single ridge until a sharp right angle forms at the junction of the anterior and posterior sections of the anterior slope. In *T. navalis*, fine denticles form in the central portion of the ridge at this stage (figure 5, height 610/490 μm). Successive ridges are comprised of only fine denticles on the anterior section and only coarse denticles on the posterior section of the anterior slope (figure 5, height 855 μm).

PALLET DEVELOPMENT

Pallet morphology during early post-larval developmental stages was one of the characters used in determining phylogenetic relationships of species within the family Teredinidae (Turner, 1966). Unfortunately, development of pallets is described for only a few species. Pallets of *Lyrodus pedicellatus* were described by Isham and Tierney (1953) from first appearance until an estimated length of 80 μm. Rancurel (1955) described developmental stages of pallets approximately 400 μm long and larger for *Teredora malleolus*. Early pallet blades of both *Teredo navalis* in the present study and of *L. pedicellatus* described by Isham and Tierney (1953) are initially triangular in shape and then grow distally. Early pallets differ in the two species, however, in that the stalk of the pallets in *L. pedicellatus* is thin and transparent, while the stalk of the pallets in *T. navalis* is calcified and opaque. Also, in *L. pedicellatus* the stalk forms before the blade (Isham & Tierney, 1953: fig. 20), whereas the earliest pallets examined of *T. navalis* had a blade (figure 12, 75 μm). In *T. malleolus*, the blade of pallets nearly 600 μm long is circular in cross-section and, with subsequent elongation, develops a medial fissure (Rancurel, 1955: fig. 4; Turner, 1966). In *T. navalis*, the blade of pallets approximately 700 μm long is circular in cross-section and then becomes elongate, but development of a fissure does not occur (figure 12).

The degree of individual and environmental variation in pallet morphology of adult *T. navalis* was demonstrated by Miller (1923). Turner (1966) stated that two pallets removed from an individual shipworm often showed unequal erosion, breakage, and deformation. Pallets in the present study were less subjected to effects of an adverse environment because of controlled culture conditions and collection at an early age. In general, sampled pallets had similar morphology, and sequential developmental stages were consistent. A striking symmetry of opposing pallets was observed throughout the post-larval developmental period (figure 12).

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