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THE MORPHOLOGY AND PALAEOBIOLOGY OF *LINNARSSONELLA GIRTYI* WALCOTT (ACROTRETID INARTICULATE BRACHIOPOD)

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ABSTRACT

The muscle scars, other morphological features and the ontogenetic changes in *Linnarssonella girtyi* are described. Evidence is presented to show that the pedicle is attached to the inner surface of the posterior end of the imperforate shell valve and that it comes out in between the posterior ends of the two valves but not through the aperture and canal of the perforate valve. From further evidence it is inferred that an exhalant current of water leaves the mantle recess in the posterodorsal region of the animal via the canal of the perforate valve. It is suggested that the perforate valve of *Linnarssonella*, previously regarded as the pedicle valve, is the brachial valve. The imperforate valve, previously regarded as the brachial valve, is the pedicle valve with a pedicle presumably attached to its posterior inner region.

INTRODUCTION

To Walcott's (1902, 1912) original description of acrotretid *Linnarssonella girtyi*, Bell (1941) added further information. Williams & Rowell (1965) gave further account in their contribution to the Treatise (Ed. Moore). The most detailed account including a statistical analysis based on acid-etched topotype specimens was given by Rowell (1966). The same acid-etched topotype specimens of the U. S. National Museum from locality8 8a, Late Cambrian limestone in the northern suburbs of Deadwood, Black Hills, South Dakota, formed the basis of the present study.

I wish to thank the following gentlemen of the Department of Paleobiology of the U. S. National Museum : Dr. G. Arthur Cooper, Senior Scientist, for permission to examine brachiopod specimens in his care and for providing some rare references ; Dr. Porter M. Kier, Chairman, for accommodation in his Department and for permission to publish my observations ; and Mr. Frederick Collier for many facilities during my stay in 1968.

TERMINOLOGY

The terms used in this account are as defined in an earlier paper on *Schizambon*. The purely descriptive term imperforate shell valve refers to the gently convex valve with no perforation, while the perforate valve is the taller valve with a siphonal canal that opens on the outer surface as the outer siphonal aperture and on the inner surface of the shell as the inner siphonal aperture. Tubercle refers to the bulging process just lateral to the pedicle attachment area at the posterior region on the inner surface of the imperforate valve. The anal levator is a tendinous muscular strand running approximately anteriorly from the posterior sector of the perforate valve to the posterior body wall. Procline, catacline and apsacline are terms referring to the inclination of the posterior sector relative to the commissure line as defined by Schuchert & Cooper (1932).

MORPHOLOGY

External features. As Walcott (1902, 1912) previously noted, the minute, broadly ovate to subcircular shells have their perforate valves taller than the other (text-fig. 1B). However, some may appear equally convex in lateral view (text-fig. 1A). The posterior sector of this perforate valve appears convex outward because of the change in inclination from an earlier slightly procline to a later weakly apsacline condition. This confirms Walcott's observations (1902, 1912) that the slope of the posterior sector is variable, varying its inclination from catacline to procline.

A subcircular area with faintly pitted appearance on the umbo seems different in texture from the rest of the shell valve. Although the state of preservation of the fossil does not allow firm determination whether this area is the larval shell, the probability cannot be ruled out. This 'larval shell' occurs at the posterodorsal angle

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of the perforate valve, often with its posterior edge jutting out above the outer siphonal aperture (Figs. 1A & 1B). It lies subperipherally at the posterior end of the imperforate valve.

The outer siphonal aperture, circular to oval in shape, generally lies within the larval valve (Fig. 1B). However, in some, its posterior edge nicks the posterior part of the larval valve in varying degrees (Figs. 1C-1E). The aperture usually faces posteriorly in young specimens but may face posterodorsally or posteroventrally in older ones.

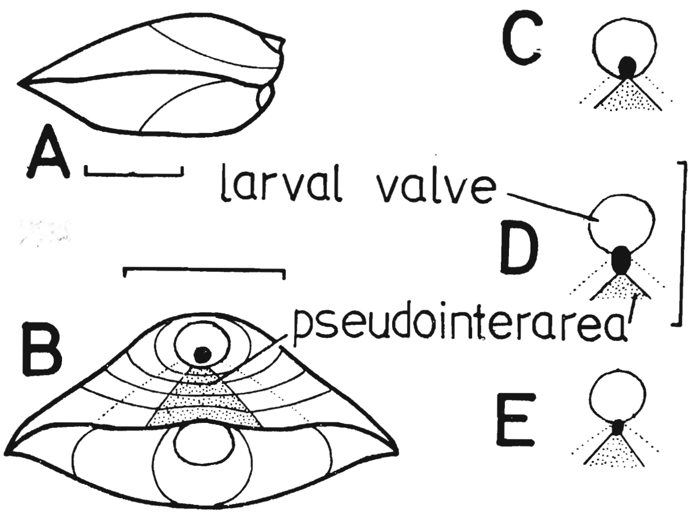

Fig. 1. *Linnarssonella girtyi* Walcott. Topotype specimens from locality 88a, Late Cambrian limestone of northern suburbs of Deadwood, Black Hills, South Dakota. All Scales = 0.5 mm.

A, B. Lateral and posterior views of specimens with the two valves remaining united after acid-etching. Perforate valve on top.

C, D, E. Three other positions of outer siphonal aperture (solid black) in relation to larval valve. The inner region of the pseudointerarea is stippled.

Seven perforate valves have outer siphonal apertures with the following dimensions in mm. :—0.023 (length), 0.023 (width); 0.030, 0.030 ; 0.037, 0.030 ; 0.037, 0.037 ; 0.045, 0.030 ; 0.045, 0.045 ; 0.075, 0.037. These measurements indicate that the aperture is either circular as Walcott (1912), Bell (1941) and Rowell (1966) previously reported, or oval with length exceeding the width in all specimens observed. The following measurements in mm. of the width of the outer aperture followed by the width of the shell (bracketed) in seven specimens show that the width of the aperture does not increase proportionately with the size of the specimen :—0.022, (1.23.) ; 0.030, (1.02) ; 0.037, (1.14) ; 0.045, (1.20) ; 0.052, (0.53) ; 0.052, (1.46) ; 0.060, (1.32).

A triangular median part on the outer surface of the posterior sector of the perforate valve has a different texture from the rest of the shell surface and was referred to as the false area by Walcott (1902, 1912) and pseudointerarea by other authors (Bell, 1941 ; Bell & Ellinwood, 1962 ; Williams & Rowell, 1965 ; Rowell, 1966). The pseudointerarea stretches both posteriorly and posterolaterally from the outer siphonal aperture, increasing in size in these directions. A smaller pseudointerarea (as measured by the angle of the sector) is usually associated with a smaller siphonal aperture.

Inner surface of the valves. The imperforate valve is subcircular in outline. Its width, however, usually slightly exceeds its length. The inner surface is bordered all round with a limbus except for the posteromedial region, where wide attachment areas for the pedicle occur (Fig. 2A). In its posterior half is a low median septum that bifurcates anteriorly some distance behind the anterior adductor scars. At the posterior end of this septum is the ventral pedicle attachment area for the attachment of the proximal end of the cuticle of the ventral wall of the pedicle. On each side of the ventral attachment area is a depression, representing presumably one of the two lateral pedicle attachment areas for the attachment of the proximal end of the cuticle in the lateral wall of the pedicle. Directly anterior to each of these two areas is the lateral attachment area for the attachment of the connective tissue and muscle of the proximal end of the lateral wall of the pedicle. These attachment areas are inferred from observations on *Lingula*, which *Linnarssonella* resembles in the morphology of the posterior end of the inner surface of the imperforate valve.

The muscle scars in each posterolateral region of the imperforate shell valve comprise a large posterior adductor scar posteriorly placed and a more anterior flattened scar of the inferior oblique muscle. A line joining the posterior adductor scars roughly forms the base of a truncated triangle, which is the shape of the floor of the visceral cavity. At the truncated apex of this triangle lie a pair of large oval scars of the anterior adductors and a pair of more medially placed superior oblique muscle scars. In the gap between the anterior and posterior adductor scars on each side a large mantle canal, which may give rise to two or three branches, runs out of the visceral cavity into the mantle cavity. A pair of smaller trunks run out anteriorly from between the anterior adductor scars. An oval impression of the brachium lies in each anterolateral region of the mantle cavity. The inner surface of the shell shows a mosaic of fine pentagonal and hexagonal areas, which presumably copy the original surface texture of the shell. Long thin grooves presumably representing marks or impressions of setae or branches of mantle canals occur near the rim along the anterior half of the imperforate valve ; they are especially coarse in the anteromedial region.

The subcircular perforate valve is usually slightly wider than long. On the inner surface the morphology of the posterior region varies with the size of the specimen. In a large specimen (Fig. 2B) there is some reflex growth of the posterior edge of the shell to form an interarea. In each lateral region of the middle third of this is a transversely directed groove. In each postero-lateral region of the shell is an oval area which represents one of the two posterior subdivisions of the visceral cavity. It encloses two muscle scars, a large scar of the posterior adductor medially and a narrow scar of the superior oblique muscle laterally. Near the middle of the inner shell surface is a larger transversely oval anterior subdivision of the visceral cavity enclosing the anterior adductor scars and presumably also those of the brachial retractors (coarse dots). The scars of the anterior adductors are very faint in *Linnarssonella* specimens examined and distinct scars of separate brachial retractors are not distinguishable. The posterior edge of the anterior subdivision of the visceral cavity is notched by the large inner siphonal aperture. This is usually roughly triangular in shape with the apex pointing posteriorly. The posterior rim of this opening continues into a median ridge, which houses either a groove as Bell (1941) and Rowell (1966) have previously reported or a tube (Walcott, 1912 ; Rowell, 1966). This tube traverses the shell substance and opens on the outer surface as the outer siphonal opening. Posterior to the ridge is a faint scar of the inferred anal levator in the posteromedial region (Fig. 2B). Impressions of the proximal whorl of the brachia occur just outside the visceral cavity at each anterolateral region.

The sculpture on the inner surface of the valve is a mosaic of fine pentagons and hexagons and is especially prominent in the posterior region bounded by the two posterior adductors and the inner siphonal aperture.

Impressions presumably due to the setae or to the branches of mantle canals occur anteriorly and antero-laterally along the margin of the perforate valve as in the imperforate shell. Deeper and wider impressions occur near the median part of the valve, presumably indicating the presence of larger setae or larger branches of the mantle canal in this region.

Changes of the shell during ontogeny. In the life history of *Linnarssonella girtyi* there was presumably a succession of two shelled stages, namely the larval and the postlarval stages.

A sagittal ridge on the larval valve of the perforate

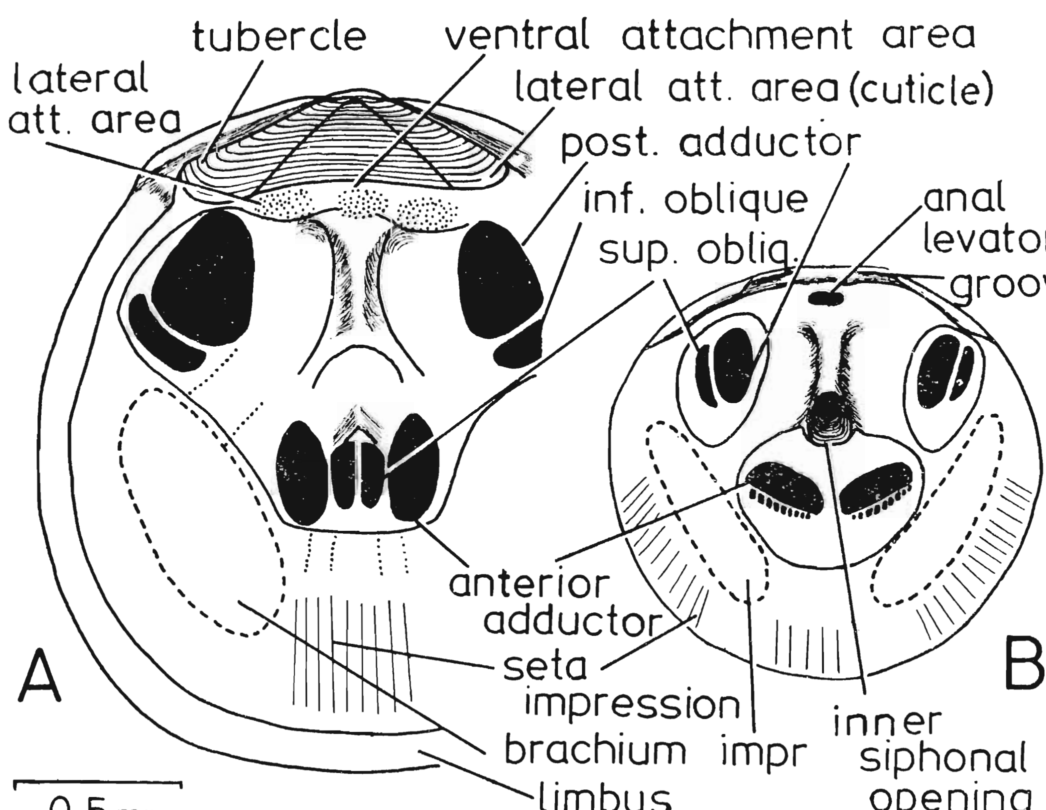

Fig. 2. *Linnarssonella girtyi* Walcott. Topotype specimens from locality 88a, Late Cambrian limestone of northern suburbs of Deadwood, Black Hills, South Dakota.

A. Inner view of imperforate valve.

B. Inner view of perforate valve.

valve presumably indicates the plication of the early postlarval stage imprinted on the thin larval shell. This plication, recognisable in the younger postlarval stages, is matched by the presence of a median sulcus flanked by two longitudinal ridges on the larval valve of the imperforate shell. This again is presumably the imprinting effect of the early postlarval sulcation on the thin larval valve. The fold and sulcus are gradually reduced during the later stages.

The fully formed larval valve, which indicates the size of the larva at the time of settlement, is a thin oval plate with its width slightly exceeding its length (Figs. 1B, C, D, E). It seems to have a pitted outer surface and thus differs in texture from the postlarval shell formed after settlement. Eleven larval valves of the topotype specimens from Walcott's locality 88a of South Dakota (Late Cambrian) have the following dimensions :

Perforate (per) or imperforate (imp) valve	imp	imp	imp	imp	per	per	imp & per
Length (μm)	143	150	150	165	150	150	180
Width (μm)	157	157	165	165	172	157	180
Length/width	0.91	0.96	0.91	1.0	0.89	0.96	1.0
Frequency	1	1	3	2	1	1	2

The larval valves in the last column are from a joined pair of perforate and imperforate valves presumably belonging to the same individual.

The postlarval shell undergoes several modifications during growth. In the youngest perforate valve examined (USNM topotype locality 88a, specimen No. 20) the siphonal canal is almost non-existent, and the outer and inner siphonal apertures are almost one and the same opening 0.030 mm. wide and 0.045 mm. long. In a larger specimen the small inner siphonal aperture still lies very near the posterior edge of the shell with its posterior and anterior edges in line with the corresponding ends of the posterior adductor scars (text-fig. 3A). A short siphonal canal, perforating the shell substance directly beneath the posterior sector of the larval valve and of the early postlarval valve, connects the inner and the outer siphonal apertures. With further growth of the postlarval shell the canal becomes longer and the inner siphonal aperture becomes wider than the outer one. While the outer aperture remains more or less constant in size, which varies from 0.023 mm. to 0.060 mm. in width in specimens of up to 1.32 mm. in shell width, the inner aperture becomes larger with increase in shell size. Measurements of the width in mm of the inner siphonal aperture in topotype specimens of various sizes (shell width in mm. in brackets) are as follows :—0.030, (smallest) ; 0.082, (0.53) ; 0.135, (1.35) ; 0.180, (1.47).

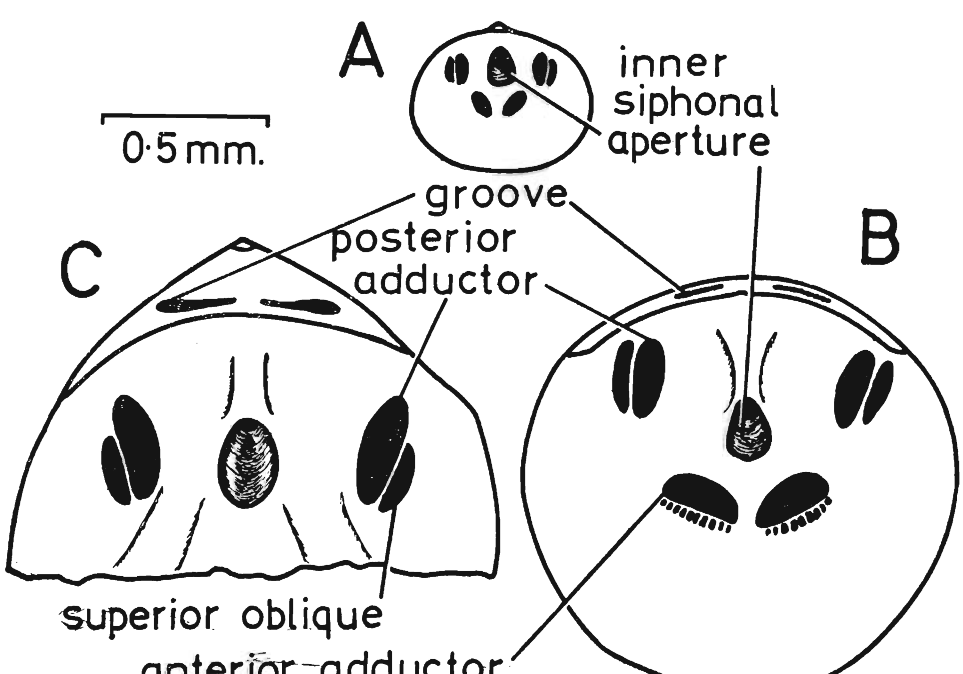

Fig. 3. Perforate valves of different sizes in *Linnarssonella girtyi* Walcott to illustrate ontogenetic changes. Topotype specimens from locality 88a, Late Cambrian limestone of northern suburbs of Deadwood, Black Hills, South Dakota.

A, B, C. Small, larger and largest (incomplete) specimens. Note the increase in size of inner siphonal aperture, the increase in distance of muscle scars from the posterior edge of the shell, and the absence of siphonal canal and of interarea in A, and the relative size of these in B and C.

On the inner surface of the siphonal tunnel are circular markings which presumably represent the successive positions of the inner siphonal aperture or the anterior end of the siphonal tube in its forward growth or migration.

In a young specimen (Fig. 3A) there is little reflexion of the posterior edge of the perforate valve and hence no recognisable interarea. With further growth of the postlarval shell an interarea forms and extends over a sector equal to about a quarter of the circumference. In this flat, wide interarea a pair of socket-like transverse grooves develop (Figs. 3B & 3C).

As in other inarticulates, there was some apparent movement of the muscle scars anteriorly during ontogeny. For instance, the posterior adductor scars occur nearer the posterior edge in a smaller specimen than in a larger one (text-fig. 3). This presumably indicates not only a rapid growth of the posterior sector of the shell behind the adductors but also an actual spread of muscle fibres anteriorly. The inferior oblique muscle scar seems to have moved forward also.

The median plate of Rowell (1966), which is interpreted in this study as the pedicle attachment area and its track, was measured in 15 imperforate shell valves of varying sizes (Fig. 4). The plot of its width and length against shell length indicates that there is a proportional increase in both width and length with increase in shell length, as in recent *Lingula anatina*.

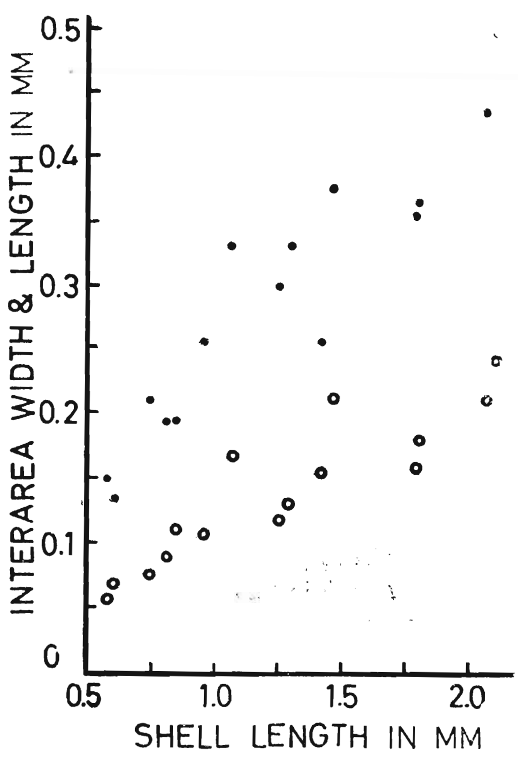

Fig. 4. Plot of the widths (dots) and lengths (circles) of the middle part of interarea (median plate of Rowell (1966) against shell lengths in 15 topotype specimens of *Linnarssonella girtyi* Walcott from locality 88a, Late Cambrian limestone of northern suburbs of Deadwood, Black Hills, South Dakota.

DISCUSSION

In addition to the anterior and posterior adductors reported by Walcott (1902, 1912), scars of the superior and inferior oblique muscles and of the anal levator were observed. However, there was no clear indication of the brachial levator, which occurred in *Schizambon* (Chuang, 1971) and in *Crania* (Blochmann, 1892).

Walcott's (1902, 1912) report of the strong cardinal area with well-defined "pseudodeltidium" on the imperforate valve was confirmed by Bell (1941), who, calling it "platform", presumed that it was for muscular insertion and also for the reception of the projecting margin of the perforate valve in articulation. Rowell (1966), working on acid-etched topotype specimens, further confirmed Bell's observations and called Bell's platform "median plate" flanked by propareas. The grooves on these propareas, according to Rowell, took part in valve articulation. In this study, however, it is considered that the anterior part of both Rowell's median plate and propareas serve as attachment area for the pedicle. Its great resemblance to the attachment area in *Lingula* provides sufficient evidence for the inference in this study that the imperforate shell valve is the pedicle valve to which the pedicle is presumed to have been attached in life. Consequently, the perforate shell valve is here regarded as the brachial valve. Walcott's "pedicle opening" and "pedicle tube" (1912, p. 666) are here considered as the siphonal aperture and siphonal canal for the exit of an exhalant current issuing from the mantle recess of the mantle cavity.

The lophophore of *Linnarssonella* presumably consisted of two spirolophous coils with their tips pointing towards the perforate shell valve. Presumably the filter-feeding system fits into Rudwick's (1960) inhalant type and had two inhalant streams entering the mantle cavity at the anterolateral region on each side as in *Crania* (Orton, 1914 ; Atkins and Rudwick, 1962). But in addition to having an exhalant current emerging anteromedially as in *Crania*, *Linnarssonella* presumably had another exhalant current of filtered water issuing through the siphonal canal out of the outer siphonal aperture on the surface of the perforate valve. This exhalant current could have resulted if the two lateral exhalant currents of *Crania*, instead of leaving the shell, were to enter on either side the mantle recess, which occurs in both *Crania anomala* and *Linnarssonella*. This inference is derived from some experiments with live *Crania anomala* (Chuang, 1974).

The interpretation of pedicle and brachial valves in this study is the reverse of the previously accepted one but is supported by the following considerations :—

1. Both the imperforate valve of *Linnarssonella girtyi* and the cemented pedicle (ventral) valve of *Crania anomala* have an entire triangular floor for the visceral cavity, this floor fusing with the valve.
2. In *Linnarssonella* there are in between the two anterior adductor scars, two scars of the superior oblique muscles on the imperforate valve as on the pedicle valve of *Crania anomala* (Joubin, 1886 ; Blochmann, 1892).
3. Outside the posterior adductor scar on the imperforate valve of *Linnarssonella* is a scar of the inferior oblique muscle as on the ventral valve of *Crania* (Joubin, 1886 ; Blochmann, 1892). However, while this is at the lateral or anterolateral angle of the posterior adductor in *Linnarssonella*, it is at the posterolateral in *Crania*.
4. The roof of the visceral cavity fuses with the perforate valve in three separate regions in *Linnarssonella* as with the dorsal valve of *Crania* (Blochmann, 1892 ; Chuang, 1974). In both, the anterior part houses the anterior adductors, while each of the posterolateral parts contains a posterior adductor and a superior oblique muscle. Walcott (1902 p. 601 ; 1912, p. 666) had actually noted the anteromedian subdivision of the roof of the visceral cavity in *Linnarssonella urania* Walcott, when he remarked : "A partial cast of the interior of the ventral valve shows a small visceral area in front of the pedicle opening." This meant that on the perforate valve, which Walcott regarded as the ventral valve, the visceral cavity occurred in front of the inner siphonal aperture. But he did not notice the other two subdivisions.
5. The space below that part of the perforate shell not in contact with the roof of the visceral cavity in *Linnarssonella* is a recess of the mantle cavity analogous to the mantle recess in *Crania* (Orton, 1914 ; Chuang, 1974). However, while there is no dorsal outlet through the valve from this mantle recess in *Crania*, there is a siphonal canal running obliquely through the shell substance. One end of this canal communicates with the mantle recess at the inner siphonal aperture, while the other end opens on the outer surface of the shell as the outer siphonal aperture.

However, *Crania* differs from *Linnarssonella* in not having a pedicle and areas for its attachment. There is at the posterior end of the imperforate valve of *Linnarssonella* a region with well-defined areas for attachment of the various parts of the proximal end of the pedicle as in recent *Lingula*. The attachment areas in *Linnarssonella* only differ in length-width ratio from that of recent *Lingula*. The anterior part of Walcott's "pseudodeltidium" (1902, 1912) and of Rowell's "median plate" and "pseudointerarea" (1966, p. 18) is here considered as attachment area for the proximal end of the pedicle. Rowell (1966, p. 19) however, presumed that the pedicle in *Linnarssonella* was attached to the depressed region at the extreme anterior end of the apical process of the perforate valve.

While in most topotype specimens at the U. S. National Museum the outer siphonal aperture is situated inside the larval valve (Fig. 1B), other variations occur (Fig. 1C, D, E). This variability in its position seems to indicate that its formation involves a certain degree of reabsorption. It is formed presumably during the larval stage as a posteromedial notch, since even in a rare case where it almost lies entirely in the postlarval valve, it still occupies a small part of the larval valve (Fig. 1E). Its formation as a notch at the posterior margin of the larval valve followed by the conversion of the notch into an aperture by growth of the posterior part of the mantle medially seems necessary because of the profound disturbance in shell formation in the sector behind the outer aperture. This sector, which is the false area of Walcott (1902, 1912) or pseudointerarea of other authors (Bell, 1941 ; Bell & Ellinwood, 1962 ; Williams & Rowell, 1965 ; Rowell, 1966 ; and others), is the result of disturbed secretion of the later-formed mantle according to Williams & Rowell (1965) and Rowell (1966).

The edges of the central flat area of the pseudointerarea form an angle of about 90 degrees at the outer siphonal aperture in specimens where this is large, but the angle is about 80 degrees in specimens with a small outer aperture. This seems to provide evidence in support of the presumption that the pseudointerarea is a region of disturbed shell secretion, the larger outer aperture leading to a larger area of disturbed shell secretion.

The inner siphonal aperture was in a state of continuous growth during the entire postlarval life, since it increased in size and also moved forward with increasing size of the postlarval valve.

In his description of *Linnarssonella girtyi*, Walcott (1912, p. 666) remarked : "The cast of the interior of the pedicle tube is usually broken off . . .", thus indicating that the presumed pedicle had not been observed inside the canal of the perforate valve. The presence of a pedicle is inferred in this study from the pedicle attachment area on the inner surface of the posterior region of the imperforate valve similar to the one on the pedicle valve of a recent lingulid. Rowell (1966) believed that the pedicle in *Linnarssonella* was attached to the extreme anterior end of the apical process on the inner surface of the perforate valve and that it passed through the canal to leave the valve at the outer siphonal aperture (Fig. 5A). However, in this study, it is presumed that the pedicle was attached to the inner surface of the posterior end of the imperforate valve and that it passed out of the valve posteriorly through the gape between the two valves at their posterior end (Fig. 5C). Direct measurement of the width of the pedicle attachment area shows that the proximal region of the pedicle, if it is of the type found in recent lingulids, has a lateral diameter 3 1/2 times that of the inner siphonal aperture and about 10 times that of the outer aperture of the perforate valve. This makes it impossible for both the apertures and the canal to accommodate the pedicle. Moreover, it is highly improbable that it could bend at a right angle to enter the inner siphonal aperture and travel the length of the siphonal tube before emerging from the outer siphonal aperture of the valve directly opposite (Fig. 5B).

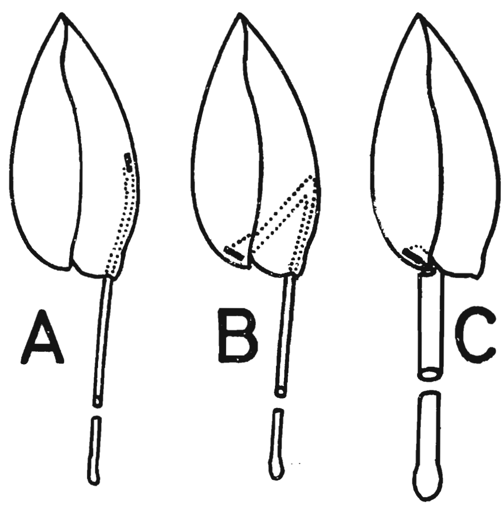

Fig. 5. Diagrammatic representation of the possible attachment areas (—) and methods of exit of the pedicle in *Linnarssonella girtyi* Walcott. The size of the pedicle in A and B is slightly exaggerated for ease of illustration.

A. Pedicle, attached to the extreme anterior end of the apical process of the perforate valve, passes through siphonal canal and emerges from the outer aperture of perforate valve (based on Rowell, 1966)

B. Pedicle, attached to the inner surface of the posterior region of the imperforate valve, enters siphonal canal of perforate valve to emerge from its outer siphonal aperture. This method of exit is considered unlikely in this study.

C. Pedicle, attached to the inner surface of the posterior region of the imperforate valve, passes out posteriorly between the two valves. This is considered most likely in this study.

The similarity of the pedicle attachment area between *Linnarssonella* and *Lingula* seems to point to a similar type of pedicle. Since the pedicle in the latter is bulbous and is embedded in sand or mud, it is presumed that a similar mode of anchorage occurred in *Linnarssonella*.

A kind of articulation between the posterior part of the shell valves in *Linnarssonella* has been postulated by some authors. Bell (1941, p. 235), who first noted it, presumed the presence, at the posterolateral margins of the perforate valve, of "teeth" which fitted into deep furrows in the imperforate valve. Examination of acid-etched specimens in this study did not confirm the presence of these "teeth". Williams & Rowell (1965, p. H96) believed that the grooves on the inner surface of the posterior end of the imperforate valve functioned as sockets for the edge of the perforate valve in the articulation. This, they added, served to restrict and inhibit the relative rotational and sliding movements of the valves. However, observations of the acid-etched valve pairs that remain attached to each other presumably in their natural position in this study seem to indicate that the so-called "articulation" is confined to a mere resting of the posterolateral rim of the perforate valve on the corresponding region of the imperforate valve. The posteromedial part of the perforate valve only spans like a bridge the depressed, grooved posteromedial region or median plate of Rowell (1966), which by analogy to recent *Lingula* is the track of pedicle attachment area. It is not clear whether the tubercle on each side of the pedicle attachment area is high enough to stop any sliding movements between the two valves by being placed anterior or posterior to the posterolateral rim of the perforate valve.

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