A REVIEW OF THE MORPHOLOGICAL FEATURES AFFECTING THE CLASSIFICATION OF CLITAMBONITIDINE BRACHIOPODS

by ANTHONY D. WRIGHT *and* MADIS RUBEL

ABSTRACT. It is difficult to provide a monothetic diagnosis of a clitambonitidine brachiopod, as any important feature (chilidium, deltidium, spondylium, etc.) of a 'standard' genus such as *Vellamo* may be absent from another stock that is nevertheless a quite acceptable member of the suborder. Critical examination is made of the morphological structures, particularly those associated with the vital functions of maintaining position relative to the substrate and of feeding. The pedicle foramen became sealed in numerous stocks; a sequence of stages from an open delthyrium via deltidial plates to a complete plate confirms a deltidium rather than a pseudodeltidium; the chilidium likewise varies from a large structure, the outer growing surface of which lies within the conch, to a more modest normal arrangement, a pair of chilidial plates or an open notothyrium. The spondylium supporting the ventral muscle field is variously modified or may only be simulated by a pseudospondylium; the dorsal muscle field is disported in various ways and, with other variable structures normally accorded taxonomic status like the ancillary cardinal process ridges and the presence of aditicules, illustrates the fundamental taxonomic tenet of features unstable in one group becoming stable and of taxonomic importance in another.

THE clitambonitidines form a distinctive group of articulate brachiopods which lived throughout the Ordovician and, although achieving world-wide distribution in the shallow seas of the time, are particularly associated with the Baltic faunas of Estonia and western Russia (Ingria), from which species were first described by von Schlotheim (1822). The outstanding study of the group was the very thorough review of these excellently preserved east Baltic brachiopods by Öpik (1934), which still stands as the leading research contribution; but a useful and easily accessible review is the contribution to the brachiopod *Treatise* volume by Williams (1965). The present article arises from our researches in preparation for the forthcoming revision of that *Treatise*. These highlighted the need for a critical review of the shell morphology, its understanding and interpretation especially with regard to classification within the group. In a further study, we are formally revising the classification of the group utilizing a cladistical approach and incorporating the morphological developments here recorded.

Williams (1965, p. H346) pointed out that although the clitambonitidines possess a unique assemblage of characters, the individual features themselves are typical of other contemporaneous groups and accordingly make the origin of the group uncertain. Thus there is little difficulty in recognizing a 'standard' clitambonitidine, such as the ubiquitous *Vellamo* (Text-fig. 1) with its wide hinge, ventri-biconvex profile and costellate exterior, long ventral interarea with convex deltidium perforated by a large foramen and a strong spondylium internally; the short dorsal interarea with well developed chilidium, and internally with a simple ridge-like cardinal process and laterally directed socket ridges. But within the accepted umbrella of the suborder, the morphologies stray far from this standard picture through the not uncommon absence of one or more of the definitive features, and the relationships of those early Ordovician stocks from Laurentia which lack a spondylium to those of Baltica with a strong spondylium are by no means certain.

The vital functions of any brachiopod are (1), to be able to open its valves to feed and (2), to maintain a life position on the sea floor, initially achieved by attachment to the substrate via the

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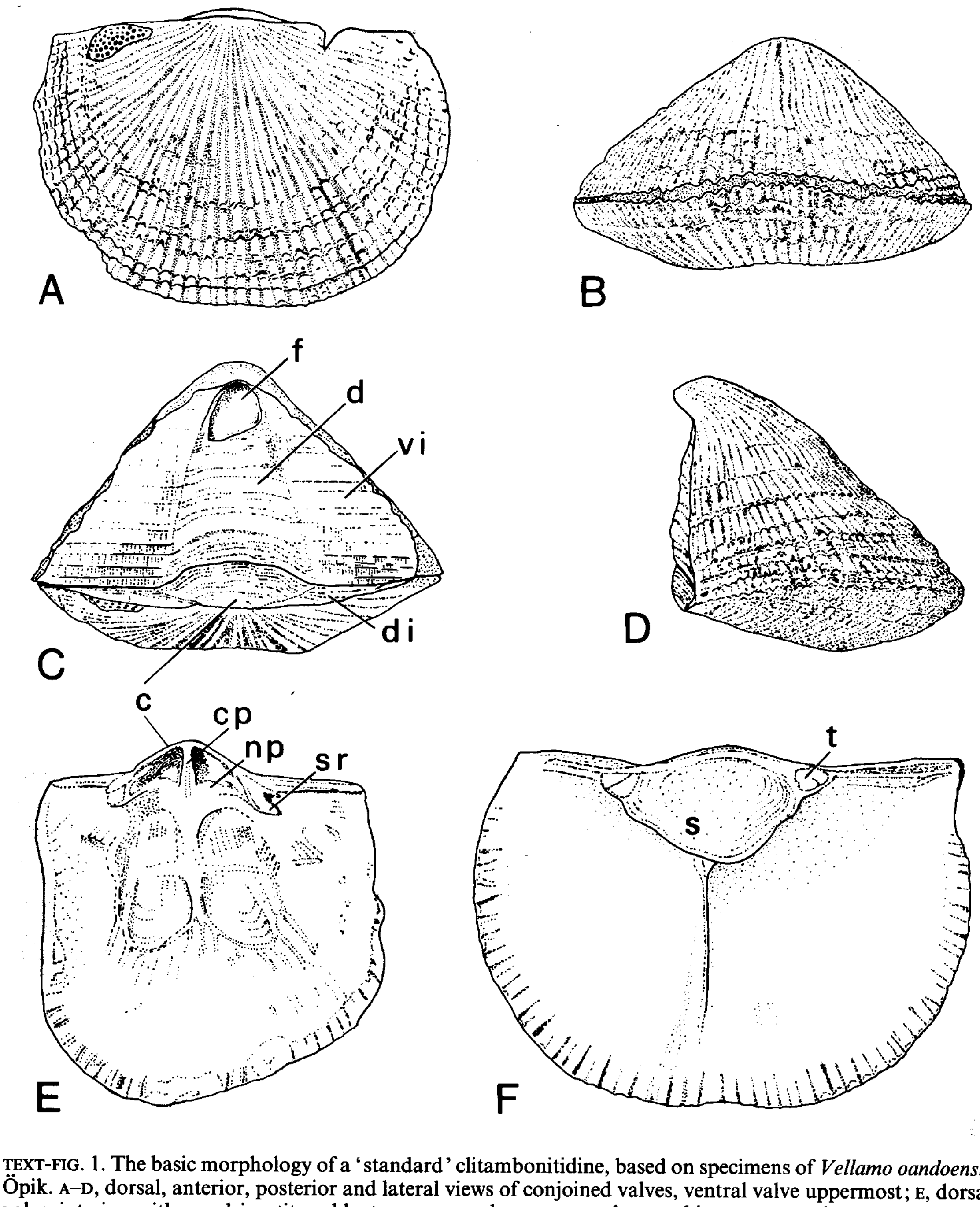

TEXT-FIG. 1. The basic morphology of a ‘standard’ clitambonitidine, based on specimens of *Vellamo oandoensis* Öpik. A–D, dorsal, anterior, posterior and lateral views of conjoined valves, ventral valve uppermost; E, dorsal valve interior with quadripartite adductor scars and some vascular markings preserved; F, ventral valve interior. The predominantly intercalated costellae of the dorsal valve are reflected as branching ribs on the ventral valve. c – chilidium; cp – cardinal process; d – deltidium; di – dorsal interarea; f – foramen; np – notothyrial platform; s – spondylium; sr – socket ridge; t – hingetooth; vi – ventral interarea. × 3 approx.

pedicle. It would seem reasonable that structures associated with these functions are likely to be the more important in morphological diversification and that the systematics should be based on this. In the case of the clitambonitidines, the delthyrium and notothyrium are typically closed by convex plates (e.g. *Vellamo*), although these are unknown in some stocks (*Oslogonites*), which are presumed to have had open delthyria and notothyria. Other stocks, like *Atelelasma*, in which the delthyrium is largely open, developed incomplete plates along its margins. The entire plate in the delthyrium of the ventral valve has variously been called a deltidium (e.g. Wright 1964; Harper 1989) or pseudodeltidium (e.g. Öpik 1934; Williams 1965) and, if this plate is incomplete along the anterior margin of the pedicle foramen, the parts have been termed lateral plates (Cooper 1956). According to Williams (1965, p. H346), the pedicle remained functional throughout the life of most clitambonitidines. Although there is no doubt that the collar-like extension of the pedicle foramen in *Kullervo* (Wright 1964, pl. 10, figs 19–20) indicates a functional pedicle throughout life in this case, despite its distortions (Wiman 1907, pl. 1, figs 1–4), the plugging of the pedicle foramen in adult shells is not uncommon, and certainly is not restricted to *Antigonambonites* as implied by Williams (1965, p. H346) but occurs variably in other genera such as *Clitambonites* itself (Pl. 4, fig. 6), *Clinambon*, *Estlandia* and *Raunites*. Study of the developmental stages of sealing of the foramen in these forms together with the pattern of the growth lines in specimens of *Vellamo* shows how the plates accreted and indicates the nature of the plate. The difference between deltidium and pseudodeltidium is not one of semantics, but is of fundamental importance in any attempt to ascertain the affinities of the stocks.

THE DELTIDIUM

According to the glossary of morphological terms in the *Treatise* (Williams and Rowell 1965), a deltidium (p. H143) is defined as the 'cover of the delthyrium formed by conjunct deltidial plates, line of junction of plates visible'. Where the deltidial plates are fused, and the median line of junction is lacking, the term 'symphytium' is used (p. H154), but this is fundamentally the same structure. A pseudodeltidium (p. H151) is defined as a 'single, convex or flat plate affording variably complete cover of delthyrium but *invariably* closing apical angle when foramen is supra-apical or absent and *always* dorsally enclosing apical foramen' (our italics). The significance of this is discussed by Williams and Rowell (1965, p. H88), but morphologically the pseudodeltidium always isolated the pedicle from the dorsal valve, and either occurs or does not occur; by contrast, a deltidium grew by increments gradually to fill the delthyrium in front of the pedicle.

In essence then, to recognize a pseudodeltidium we need to be able to confirm the presence of a strip of pseudodeltidium separating the foramen from the remainder of the delthyrium. Accepting that preservation commonly leaves something to be desired so that it has not been possible to study the plate in all genera, and that *Antigonambonites* remains problematical, the available evidence noted below all indicates the plate to be a deltidium.

In some clitambonitidines, such as the Atelelasmatinae and Anomalorthinae, the delthyrium is open or with only selvages of shell along the lateral margins. Williams (1965, p. H346) interpreted this state as probably indicating that the pseudodeltidium failed to develop 'during the differentiation of the young shell'. But this growth pattern is typical of a deltidium, not of a pseudodeltidium which, as noted, always defines the front of a pedicle foramen. The absence of a delthyrial cover is also noted by Williams (*in* Whittington and Williams 1955, p. 412) in at least some young specimens of a species of the more standard *Kullervo*.

Vellamo is a genus with a large foramen extending anteriorly from the apex of the delthyrium where the spondylium may or may not show the scar of a pedicle callist. The foramen has a somewhat variable degree of regularity in its outline, and small forms may lack the standard deltidium. The type specimen of *Vellamo parva* Öpik, 1934 is one such small form, 14 mm wide, in which the usual large foramen of the genus is not enclosed at the front by the deltidium which is present only as a pair of plates along the lateral margins of the delthyrium. A specimen of *Vellamo* *simplex* (Pl. 1, fig. 7) shows well preserved growth lines on the deltidium which illustrate how the deltidial plates developed, initially as small plates occupying the antero-lateral corners of the delthyrium. The growth lines show the addition of increments extended further towards the midline until the plates abutted; subsequently secretion took the form of continuous convex strips of calcite arching across the width of the delthyrium to form a deltidium, the growth lines of which are continuous with those across the adjacent interarea. The form of the growth lines makes it quite clear that the structure could not have been produced by resorption of continuous strips of a deltidium, but that it gradually accreted as indicated. Many specimens of *Vellamo* in the Öpik (1934) collection in Tallinn illustrate this growth pattern, which has also been observed in *Clitambonites*. The deltidium of *Clinambon anomalis* (Pl. 1, fig. 8) again shows how the deltidial plates accreted before joining at the front with continuous strips across the deltidium, but this specimen also shows well the gradual sealing of the foramen within the deltidium; the secretion to the posterior of the foramen additionally confirms that the direct contact of the pedicle with the apex in the manner of a strophomenid pseudodeltidium was lacking. The mode of sealing of the foramen at the posterior of the deltidium in a specimen of *Estlandia* (Pl. 2, fig. 4) is less obvious. The sealed posterior part, presumably where the foramen was originally situated, is depressed relative to the frontal portion; across its middle is a topographically higher arcuate band of shell. Internally this part is smooth, lacking any indication of the presence of a foramen in the young stages.

Kullervo displays varying stages of a deltidium. Cooper (1956, p. 528) noted the presence of a vestige in the apex of a delthyrium which is figured by him (1956, pl. 80, figs 2, 7–8; pl. 99, fig. 45), and a similar vestige is also present in figures of Williams (*in* Whittington and Williams 1955, pl. 39, figs 58–59). This apical vestige is also present in shells with a well defined foramen and deltidium as figured by Öpik (1934, pl. 35, fig. 4*a*; text-fig. 39) and Wright (1964, pl. 10, figs 16, 19). In other specimens the foramen would appear to reach the extreme apex (Wright 1964, pl. 10, fig. 4) and may be sealed (Öpik 1934, pl. 35, fig. 6).

Thus it is easy to see how the delthyrial structure in *Apomatella*, with small deltidial plates, could evolve into that of *Clitambonites*, *Clinambon*, *Vellamo*, etc., with their fully fledged deltidia. Where evidence is currently lacking is in forms like *Antigonambonites* and *Raunites*, which simulate the strophomenids in their resupinate profiles and in having a commonly minute foramen situated close to the apex of the valve which became sealed early; the chances of obtaining the necessary very earliest stages to study early growth in such forms are currently remote.

VALVE HINGING

While the delthyrium is concerned primarily with the pedicle and relations with the substrate, it is in direct contact with the hinge line about which the valves open to feed, and moreover is located in the middle of the ventral area which records the growth of the hinge line. Externally, the clitambonitidines are strophic, wide-hinged forms with interareas well developed on both valves; that of the ventral valve is commonly long and varies in attitude from apsacline to procline. The

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EXPLANATION OF PLATE 1

Figs 1–6. *Kullervo panderi* (Öpik). Two valves showing relationships of aditicules between interior and exterior shell surfaces. 1–3, RMS Br136961; Kohtla-Järve, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); 1–2, exterior and interior of dorsal valve; ×3; 3, enlarged tilted view to show details near the anterior margin; ×6. 4–6, QUB 26139; Küttejõu, Estonia; Kukruse Stage (CII); anterior, ventral and postero-dorsal views of ventral valve; all ×6.

Fig. 7. *Vellamo simplex* Öpik; IGT Br511; Kohtla, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); posterior view of conjoined valves showing detail of areas, including growth of deltidium; ×6.

Fig. 8. *Clinambon anomalus* (Schlotheim); IGT Br524; Rakvere, Estonia; Ordovician (Caradoc), Keila Stage (DII); posterior view of conjoined valves showing detail of areas, including sealing of foramen; ×6.

PLATE 1


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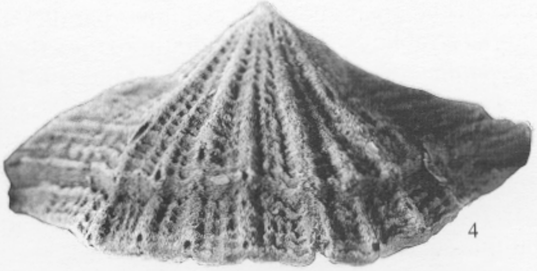
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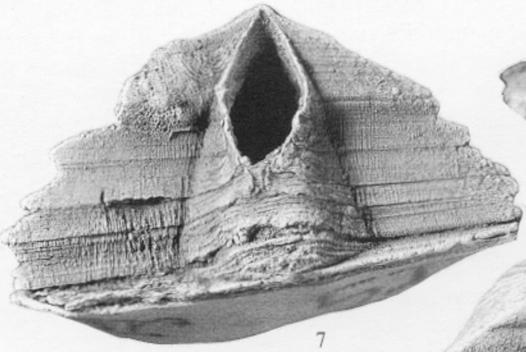
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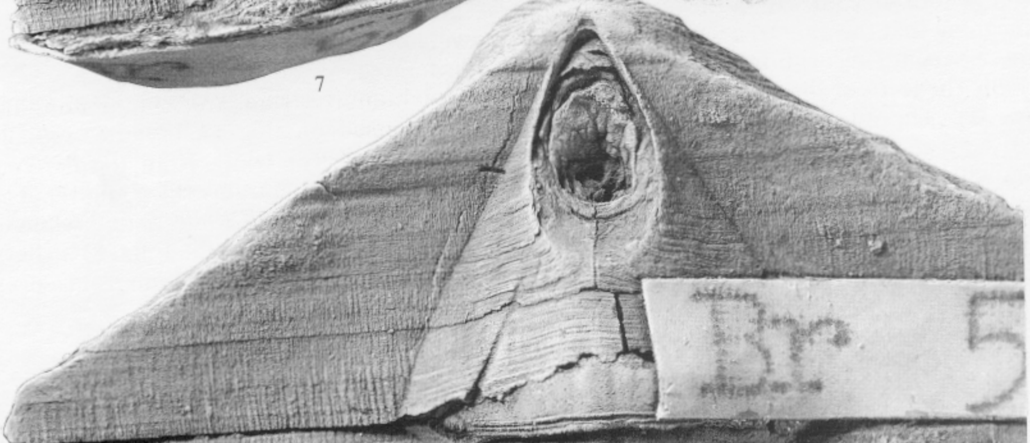

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WRIGHT and RUBEL, *Kullervo, Vellamo, Clinambon* surface of the areas shows growth lines parallel to the hinge, tracks perpendicular to this and, less commonly, oblique grooves radiating from the apex like the margins of the delthyrium, as in *Antigonambonites* (see Pl. 3, fig. 6 and Öpik 1934, pl. 31, fig. 3*c*) and *Tritoechia* (Ulrich and Cooper 1938, pl. 33, fig. 24). In well preserved material, this surface detail on the ventral valve is commonly more strongly developed in the sector closer to the delthyrium (Pl. 1, figs 7–8) in a manner reminiscent of the perideltidial areas of the orthotetidines. As with the deltidium, a strong chilidium is typically developed in the 'standard' forms; the variations in this stucture are discussed below (p. 63). In the figure of *Clinambon* (Pl. 1, fig. 8) the margin of the deltidium is seen overlying the large chilidium so that when the valves opened, the chilidium would have slid further beneath the deltidium. The shallow grooves near the lateral edges of the chilidium are matched by corresponding grooves in the deltidium, demonstrating that the two structures may reflect each other closely, as has been noted for *Vellamo* and other groups of brachiopods (Wright 1981, p. 349).

Teeth and spondylium

The teeth of clitambonitidines are deltidiodont (Jaanusson 1971, p. 35; pl. 1, fig. 5). In this context the specimen of *Estlandia* (Pl. 2, figs 2–4) is of interest. The teeth, emerging from beneath the interarea, are double structures in this genus. The inner part, along the lateral edge of the deltidium, stands high at the hinge-line and is separated from the main part of the tooth by a groove, essentially corresponding to the delthyrial margin on the surface of the interarea, and which runs down the inner surface of the tooth to mark the crural fossette. The antero-dorsal edge of the tooth curves dorsally, so that the distal end stands above the projected continuation of the interarea. The significance of this is that for growth to take place in such a structure resorption of the proximal part of the tooth is necessary. Thus although basically a deltidiodont tooth, the need to resorb the proximal part of the tooth as it grew would make it more akin to the hook-like type of cyrtomatodont tooth that characterizes the Spiriferacea (Jaanusson 1971, p. 35). This pattern Wright (1979) felt was closer to a deltidiodont tooth than to the knob-like cyrtomatodont tooth of the terebratulides and rhynchonellides, and suggested 'advanced deltidiodont' for what he regarded as a deltidiodont tooth with resorption, a phenomenon which characterizes the dorsal structures in deltidiodont orthides like *Dicoelosia* and *Rhipidomella*. Professor Jaanusson (pers. comm.) has also observed the hook-like growth of the teeth on *Estlandia* shells, but only in older shells; he interprets this as meaning that the interarea would have ceased growing by this stage and accordingly it would not be necessary for resorption in the manner of the Spiriferacea.

Internally the teeth of the hinge are supported by a spondylium in a 'standard' clitambonitidine (Text-fig. 1F). The muscle scars of the ventral valve are located on this spondylium, radially disposed, with the median adductors commonly separated by a clear break from the flanking diductors with the adjustors next to the line of the teeth at the lateral margins (Pl. 3, fig. 1). The principal modifications to the muscle surface are best seen in *Clinambon* and *Kullervo* and relate to the breaks in slope along the outer edges of the adductor scar. In *Clinambon* (Pl. 4, fig. 8) a sharp crest, which may even be acute in profile, separates the essentially V-shaped spondylium from a deep

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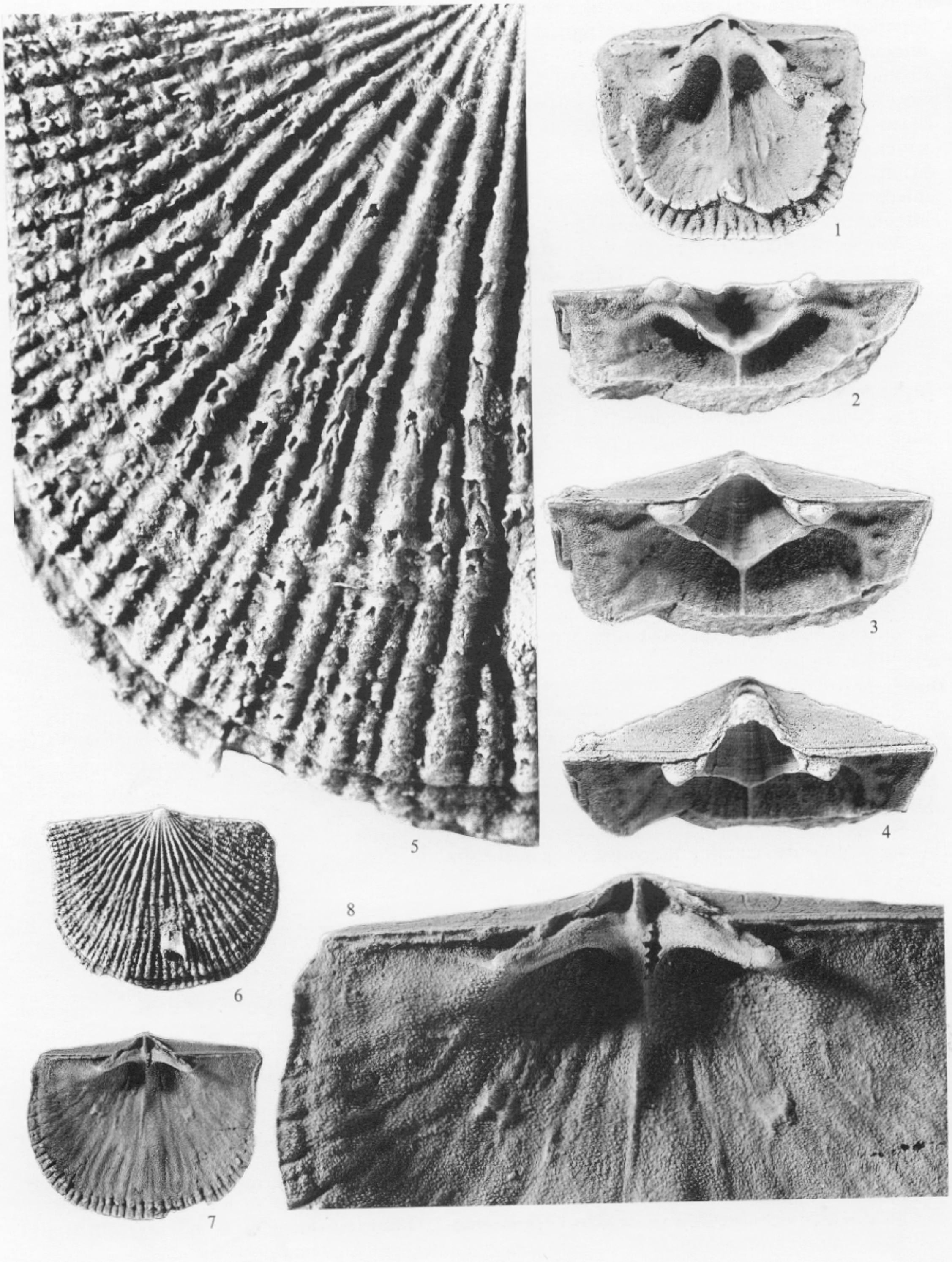
EXPLANATION OF PLATE 2

Figs 1–8. *Estlandia marginata* (Pahlen). 1, RMS Br68369; Türisalu, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); interior of dorsal valve showing strong subperipheral rim and *vascula terminalia*; × 3. 2–4, IGT Br553; Kohtla, Estonia; Kukruse Stage (CII); anterior, dorsal and posterior views of incomplete ventral valve to show mantle canals, double tooth, spondylium and deltidium; all × 3. 5–8, RMS Br68368; Türisalu, Estonia; Kukruse Stage (CII). 5, dorsal valve showing detail of surface ornament, × 10; 6, exterior, and 7, interior of valve; both × 2; 8, details of cardinalia and the granular internal surface; × 6.

PLATE 2



WRIGHT and RUBEL, *Estlandia marginata*

subelliptical median portion bearing the adductor scars. A similar but less exaggerated pattern is found in *Ilmarinia*, and it may be that the deep median depression is a reflection of the procline interareas which characterize these two genera. The condition in *Kullervo* (Pl. 3, fig. 5) is quite distinct and was referred to by Öpik (1934, p. 162) as a hemisyrinx. Here the median adductor scars are almost roofed over by a pair of plates to form a chamber (hemisyrinx). Although easily damaged, the plates are separated by only a narrow slit for two-thirds or so of the spondylium, with wider access to the chamber only at the front. Presumably therefore the adductor muscles only extended from the front of the chamber across the body cavity to the dorsal valve. It is difficult to interpret any function for the upper surface of the plates apart from serving as an additional attachment surface for diductor muscles which would then have extended almost to the median line.

Williams (1965, p. H346) regarded the development of the spondylium as being 'related as it is in its forward extension to the exaggerated growth of the ventral interarea' but this very plausible explanation is somewhat of an oversimplification. Amongst other brachiopods, forms with exceptionally long interareas like *Terebrirostra* and *Onchotreta* do not have spondylia; those orthotetidines with long interareas may have well developed dental plates (*Meekella*) or a spondylium (*Geyerella*) or they may not (*Diplanus*, *Tropidolasma*, *Goniarina*); and, conversely, forms with well developed spondylia commonly do not have long interareas (as in *Stenocisma* and some Palaeozoic rhynchonellides like *Camerophorina*, in addition to most pentamerides). One is back here to the fundamental of opening and closing the valves and thus the relative positions of especially the diductor muscles for leverage purposes; if the interarea is long, reflecting a particular relationship with the substrate, raising the ventral muscle field on a spondylium is only one method of bringing the ventral attachment of the diductors closer to the cardinal process. An alternative, as seen for example in *Tropidolasma*, is to carry the dorsal seat of diductor attachment up into the extended ventral umbo on an elongated cardinal process. There are no suggestions that the function of a spondylium was other than to bear the muscles in a raised position off the floor of the valve and closer to the fulcrum along the hinge line in a relatively deep ventral valve. As an adaptation to valve articulation, the structure arose independently in various brachiopod stocks. In the 'standard' clitambonitidine, the structure is a spondylium simplex, formed from union of the dental plates fused on to a single median septum. This is modified in the gonambonitaceans into a spondylium triplex, with a pair of lateral septa extending from below the spondylium towards the valve floor on either side of the median septum. In *Antigonambonites*, with its closely opposed valves and spondylium lying close to or sessile on the valve floor, the lateral septa are quite prominent (Pl. 3, fig. 4), while the medium septum may be poorly developed or even absent. In *Estlandia* and *Kullervo*, with their deeper ventral valves and well developed median septum, the lateral septa are present only as low ridges on the underside of the spondylium (Pl. 2, fig. 2; Pl. 3, figs 1–2) with the lateral septa only reaching the valve floor in the umbonal region (Öpik 1934). The spondylium in

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EXPLANATION OF PLATE 3

Figs 1–2. *Estlandia pyron* (Eichwald) *silicificata* Öpik; NHM BB5234; Aluvere, Estonia; Ordovician (Caradoc), Jõhvi Stage (DI). 1, direct and 2, anterior, views of a silicified ventral valve interior showing the pedicle callist and the lateral septa of the spondylium triplex; ×2.

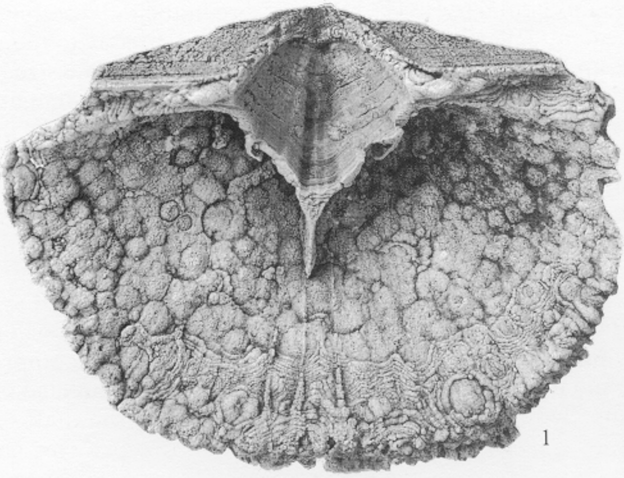
Figs 3, 7. *Lacunarites ilmatar* Öpik; IGT Br605; Paldiski, Estonia; Ordovician (Llanvirn), Kunda Stage (BIII). 3, ventral valve exterior, ×3; 7, detail showing fila and aditicules; ×10.

Figs 4, 6. *Antigonambonites planus* (Pander); River Lava, Vassilkovo, Ingria, Russia; Ordovician (Arenig), Volkhov Stage (BII). 4, IGT Br982; ventral valve interior; showing sessile spondylium triplex; ×2. 6, IGT Br983; posterior view of conjoined valves showing features of the interareas; ×3.

Fig. 5. *Kullervo lacunata* Öpik; Kohtla, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); IGT Br598; ventral valve interior showing spondylium with hemisyrinx; ×3.

Fig. 8. *Ladogiella imbricata* Öpik; Vassilikovo, Ingria, Russia; Ordovician (Llanvirn), Kunda Stage (BIII); IGT Br464; ventral valve exterior, ×5.

PLATE 3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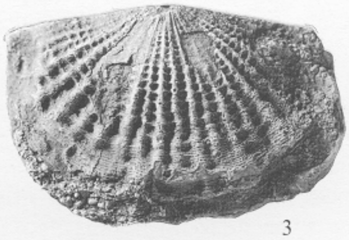
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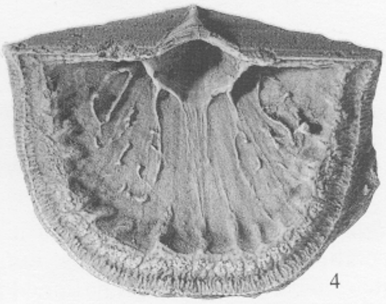
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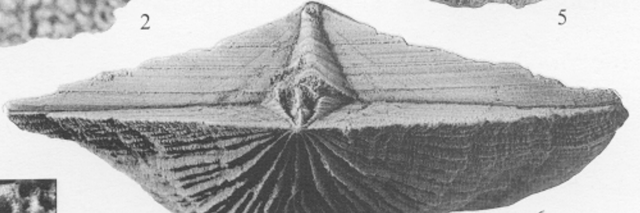
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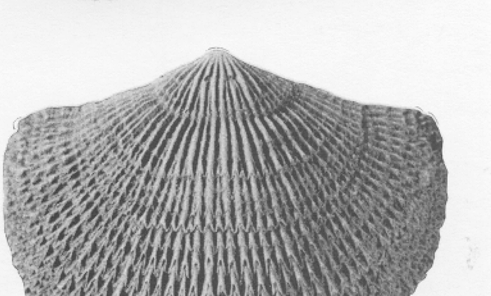
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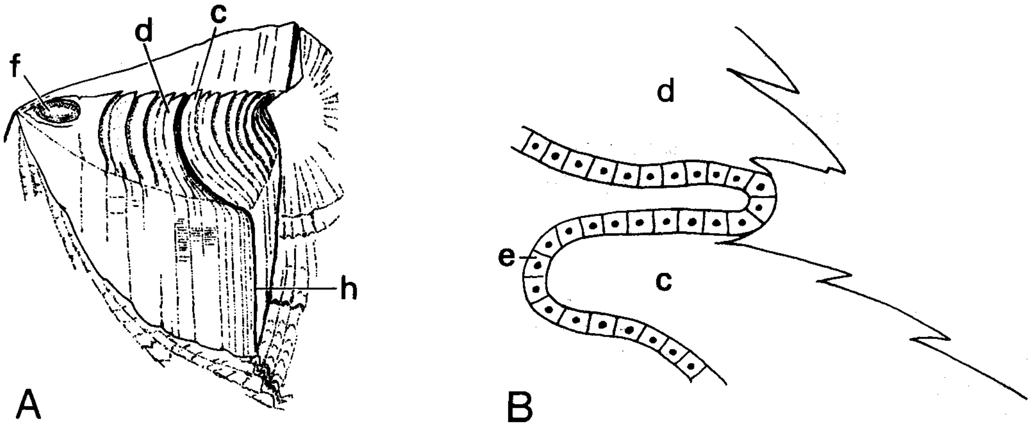
WRIGHT and RUBEL, clitambonitidine brachiopods

Anomalorthis is sessile; according to Williams (1965, p. H347), the structure in the Polytoechiidae is a pseudospondylium, differing in that the dental plates do not unite, but extend directly to the valve floor with the muscle field between built up by shell thickening. In *Polytoechia* itself, the structure, with median septum and dental plates continuous to the valve floor, strongly simulates a spondylium triplex. But the opposite is also true: a well developed spondylium triplex, with its lateral septa reaching the valve floor, strongly simulates a pseudospondylium. Öpik (1934, p. 28) regarded *Polytoechia* as having a true spondylium triplex, and suggested (p. 29) that the spondylium may have originated independently in different brachiopod stocks, a view borne out by the diverse forms, even including a lingulate (*Spondylotreta*), which possess this structure.

The cardinalia

The clitambonitidine cardinalia typically forms an anchor-shaped structure (Pl. 5, fig. 2) comprising the chilidium, socket ridges and sockets, and notothyrial platform, with a posteriorly directed plate-like cardinal process and an anteriorly directed median septum that together form the shaft of the 'anchor'.

Chilidium. A chilidium is usual; in *Clinambon* it is particularly strong, this being a reflection of its association with an unusually long dorsal interarea. *Clitambonites* itself has a large, high, semicircular chilidium with flattened lateral margins, well demarcated from the dorsal interarea (Pl. 5, fig. 1). The imbricate nature of the main shell surface is reflected in that of the chilidium, which is intriguing as its surface laminae are undercut *towards* the umbo and away from the hinge line. Thus the impression is of younger shall having been laid down on the external surface of the earlier shell. The deltidium of *Clitambonites* has its shell layers undercut away from the umbo and towards the hinge line as would be expected. In other words, the lamellose arrangement of the deltidium is stacked in the same direction as that of the chilidium. The latter is tucked in below the front of the deltidium (Text-fig. 2), so that in life the part of the chilidium currently being secreted was *within* the conch and with the shell-secreting outer epithelium lining what would subsequently become an external surface. The outer epithelia of the ventral and dorsal valves are fused in this area, but only as far as the edges of the notothyrium/delthyrium in these protremate shells. Lateral to the



TEXT-FIG. 2. Sketches of (A) the postero-median part of the hinge region of *Clitambonites* to show the orientation of the growth laminae on the deltidium and chilidium, and (B) a longitudinal section showing the envisaged relationships of the shell secreting outer epithelium to the edges of the deltidium and chilidium during growth. c – chilidium; d – deltidium; e – epithelium; f – foramen; h – hinge line.

chilidium, the lamellae pass into the non-lamellose growth lines of the interarea; this in life was underlain by mantle (Wright 1994). The same type of stacking on the chilidia is present, but not so pronounced, in forms like *Clinambon* and *Ilmarinia*. Some specimens of *Vellamo* show the feature but in many it is difficult to observe more than the general presence of growth lines.

Other clitambonitidines, such as *Antigonambonites* and *Estlandia*, possess smaller, less pronounced and more triangular chilidia on which the growth lines are undercut on the side of the hinge line (in those specimens where preservation is sufficient to allow the direction to be determined). In these cases the growing edges would have been external, i.e. not concealed within the conch by the deltidium, and lined internally by outer epithelium in the usual way.

In addition to these two arrangements of the chilidia, in other clitambonitidines the notothyrium was either flanked by chilidial plates as in *Tritoechia* or, as with *Oslogonites*, completely lacking any calcareous plates within an open notothyrium. The various forms of the structure have accordingly been used as a basis for differentiating stocks.

Socket ridges. The socket ridges extend latero-anteriorly from within the limits of the notothyrium (Pl. 5, fig. 1), coming away from the underside of the chilidium and forming a ridge lying along the lateral extensions of the notothyrial platform, defining the sockets medianly and commonly culminating in a small ventrally projecting process. The amount of associated shell deposition may produce a quite different appearance as seen in the contrasting cardinalia of the two specimens of *Estlandia marginata* figured as Plate 2, figures 1 and 7. The heavy ridges seen in figure 1 coupled with the strong subperipheral rim suggest that this is gerontic specimen. This must remain a possibility, but from the viewpoint of size rather than presumed age the specimen of figure 7, with its more slender socket ridges and barely developed subperipheral rim, is clearly the larger of the two, being nearly 4 mm the wider.

Notothyrial platforms. The notothyrial platform in a standard clitambonitidine is well developed. At the front it is undercut, apart from in the middle sector where it passes anteriorly into a strong median ridge to produce the characteristic anchor-shaped cardinalia (Pl. 5, fig. 2). But there is considerable variability. In species of *Vellamo* the undercutting may or may not occur. In *Oslogonites* and *Progonambonites* the notothyrial platform is short, barely extending beyond the hinge line, is concave forward and sharply truncated anteriorly, with any low median ridge between the adductor pairs rising anterior to, and not continuous with, the platform (Rubel 1963, pl. 1, fig. 2; pl, 3, fig. 1). Despite the variation, what does appear valid is that, while in most forms the platform is built up to be almost flush with the dorsal interarea, in *Polytoechia* and its allies the platform is only weakly developed or, at best, depressed well below the interarea. It may not be coincidence that the polytoechiids also lack the generally strong chilidium of the other clitambonitidines.

Cardinal process. The cardinal process is a simple, generally narrow and prominent ridge in the centre of the notothyrial platform which extends towards, and may fuse with, the inner surface of the chilidium. The cardinal process is not always present, but its absence as a generic character is unreliable. For example, its use as a feature separating *Oslogonites* from *Progonambonites* (Williams 1965, p. H355) is not valid, for although the latter genus does have a cardinal process, *Oslogonites* is described by Rubel (1963, p. 92) as being either with or without a weak cardinal process. Again, the cardinal process in some specimens within the *Hemipronites-Ladogiella* complex may be absent, yet it is present in others, and cannot therefore be used as a means of differentiating the two genera. This situation resembles that of the punctate orthide *Paurorthis*, another example of an early stock which lacks the stable development of a cardinal process so that its presence or absence is of little taxonomic significance.

Taxonomic use has also been made of the presence of subsidiary or ancillary cardinal process ridges which flank cardinal process in some forms, so that they are said to characterize specific genera. Thus, for example, in the subfamily Clitambonitinae (Williams 1965, p. H348) they form part of the diagnoses of *Clinambon*, *Iru* and *Ladogiella*, while, by contrast, *Vellamo* is diagnosed as having a simple cardinal process. However, the recognition of these ridges, termed *Seitenleiste* by Öpik (1934, p. 213), appears simply to reflect their degree of development, and even within a population they may be strongly or imperceptibly developed, as may readily be seen by comparing the two specimens of *Ilmarinia dimorpha* illustrated in Plate 4, figures 1–4. Regarding the specific case of *Vellamo*, ancillary ridges are clearly visible on many species of the genus in the Öpik (1934) collection, and indeed are apparent from his figures (e.g. 1934, pl. 13, figs 1, 5). The structures were also clearly figured for *V. sulculata* by Wright (1964, pl. 10, figs 2, 5), who specifically noted the presence of two muscle scars on either side of the cardinal process for which he suggested (p. 236) that the inner pair (which extend up on to the side of the cardinal process) were for attachment of the diductor muscles and the outer pair for the accessory diductor or possibly dorsal adjustor muscles. The division of the notothyrial platform into three areas on either side of the median cardinal process in the figured specimen of *Ilmarinia* (Pl. 4, fig. 2), *Iru* (Öpik 1934, pl. 4, fig. 3) and other forms suggests that in fact all three muscles may be sited on the notothyrial platform. The delimitation of the various scars by ridges would appear to be dependent on the amount of differential secretion beneath the muscle and at its lateral margins. In gerontic valves this difference could be expected to be greater, but other morphological factors affecting the function of the diductors, such as a procline interarea, may also be contributory to the relative amounts of shell secretion and hence the relative emphasis of the ancillary ridges.

Thus we have serious misgivings about the taxonomic value of these ridges which display a high degree of variability that is shared also with other internal structures currently accepted as characterizing different genera. To evaluate the taxonomic significance of such variable features will require the future statistical treatment of large samples.

Adductor field

The dorsal adductor field in genera such as *Clitambonites*, *Ilmarinia*, *Clinambon* and *Ladogiella* is typically quadripartite, with the anterior and posterior pairs being separated by a clearly defined ridge perpendicular to the median ridge. But, because of variability, the scars of some specimens of such genera take on a different aspect caused by strong radial ridges traversing the scars, so that the appearance is of a posterior pair disposed lateral to the anterior pair (compare *Ilmarinia* of Öpik 1934, pl. 19, fig. 3 with fig. 4 or pl. 18, fig. 2; and *Ladogiella* in pl. 42, fig. 1 with fig. 2). These radial ridges occur commonly external to the muscle field in well preserved and particularly gerontic specimens and characterize the pinnate mantle canal system. Their presence across the muscle scars in some specimens may reflect their earlier strong development on the floor of the mantle cavity before the body cavity with the muscle scars advanced over it. The significance of this is that in some clitambonitidines, such as *Kullervo*, the adductor scars do appear to be arranged radially (Öpik 1934, pl. 35, figs 1–2) and have been described as subpetaloid. But in such valves the posterior part

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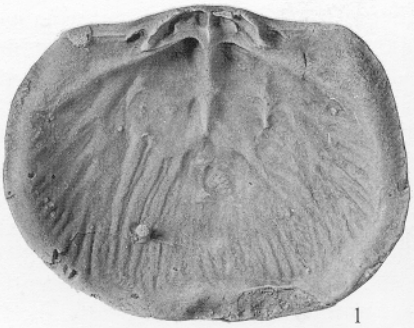
EXPLANATION OF PLATE 4

Figs 1–4. *Ilmarinia dimorpha* Öpik; Üksnurme, Estonia; Ordovician (Caradoc), Oandu Stage (DIII); detail of cardinalia of two dorsal valves to show variation in development of ancillary ridges. 1–2, QUB 26137. 1, valve interior; × 1·5; 2, details of the cardinalia; × 5. 3–4, QUB 26138; 3, valve interior; × 1·5; 4, tilted to show details of the cardinalia; × 5.

Figs 5–7. *Clitambonites squamatus* (Pahlen); NHM BB68557; N Estonia; Ordovician, ?Kukruse Stage (CII). 5, ventral valve interior; × 2; 6, interarea viewed from exterior to show sealed foramen; × 4; 7, internal view of spondylium and deltidium showing smooth surface lacking any trace of foramen of young stages; × 4.

Fig. 8. *Clinambon anomalus* (Schlotheim); NHM B5858, Davidson collection; 'Reval, Russia. Ordovician'; [?Keila Stage (DII), Caradoc, N Estonia]. Ventral valve, view of interior to show spondylium; × 1·5.

PLATE 4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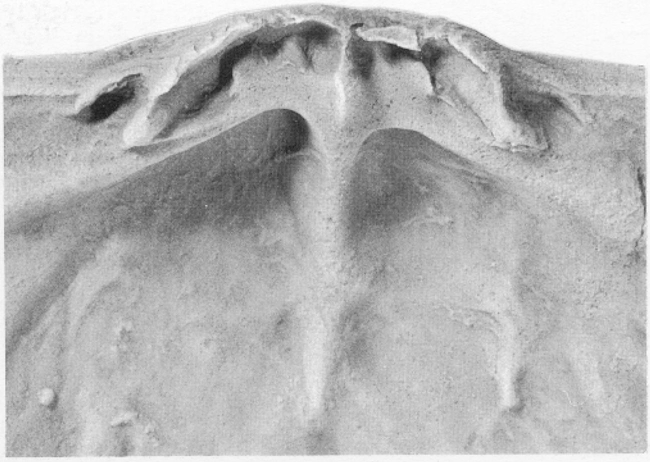
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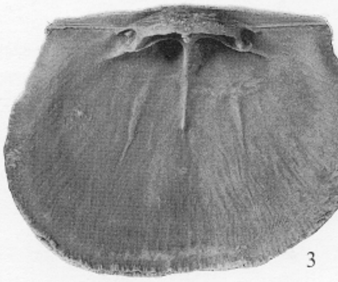
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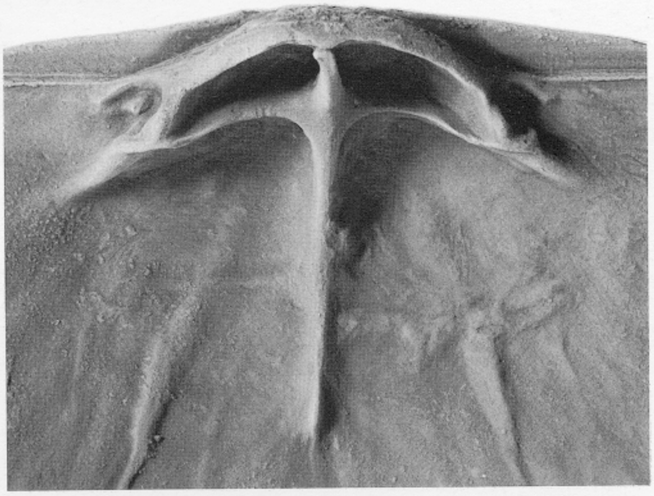
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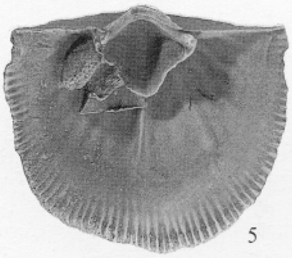
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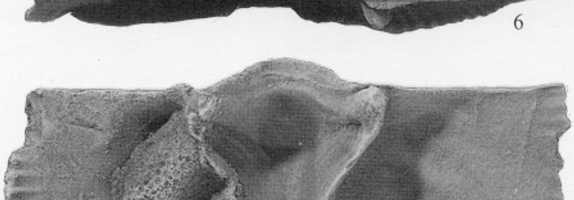
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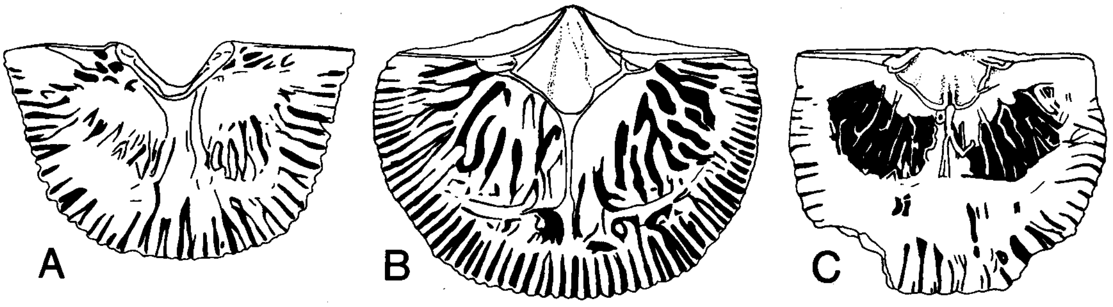
WRIGHT and RUBEL, *Ilmarinia*, *Clitambonites*, *Clinambon* of the scar shows no clear traces at all, and the figure of a different species (Öpik 1934, pl. 36, fig. 2) shows a pattern tending towards quadripartite, although the ridges separating anterior from posterior scars still have a basically radial disposition, being oriented antero-laterally in a manner developed to a certain extent in some *Vellamo* (Öpik 1934, pl. 12, fig. 7). In the more radial disposition as figured for *Kullervo* by Öpik (1934, text-fig. 52) the anterior pair is apparently larger than the posterior pair. The posterior scars appear as long narrow tracks, whilst the medianly situated anterior scars are tear-shaped. However, if the latter reflects the movement of an advancing muscle attachment, it may be that it is the smaller scar. The gonambonitids and the polytoechiids also have radially arranged adductor scars and in these cases the anterior pair is smaller than the posterior pair. This relative length of the adductor scar pairs has been used as a taxonomic character and, unlike members of these two families, *Clitambonites* and the majority of clitambonitidine genera have a posterior adductor pair which is shorter than the anterior pair. Nevertheless, the size difference is not always clear-cut and some stocks, such as *Vellamo*, are variable in this character both between and within species.

This emphasizes what appears to be a well-known tenet of taxonomy; that a feature variable in one group and therefore of little use in classification becomes consistent in another stock, when it provides that certainty for identification and also for classification.

MANTLE CANALS

The mantle canals, well known for the clitambonitidines as a result of the classic work of Öpik (1934), are characterized by displaying the pinnate pattern of Williams (1956). This was further emphasized by Williams (1965, p. H132), when he described them as being 'decisively' pinnate. It is therefore somewhat surprising to find that the overall pattern in the ventral valves of at least *Apomatella*, *Ladogiella* and *Neumania* is apparently saccate, with faintly developed vascula media sweeping around laterally in an arc to contain the gonocoeles. The *Ladogiella* specimen (IGT Br464) figured by Wright (1994, fig. 1F) is the same as that illustrated by Öpik (1934) as his plate 43, figure 1*b* and diagrammatically in his text-figure 13. In the text-figure description, Öpik stated that the bow-shaped vascula arcuata and ovarian markings were completely missing, and the radiating canals are depicted as being strong and continuous. This continuity is not, however, seen in his photograph, where the canals of the central areas fade across an ill-defined band before reaching the vascula terminalia. A different conclusion is reached from Wright's photograph, where the zone of uncertainty is seen as arcuate ridges, interpreted as arcuate vascula media, behind which terminate the canals of the central areas, interpreted as the site of gonocoeles. In the postero-lateral areas, certainly on the left-hand side of this specimen, the canals do radiate directly into the vascula terminalia so that the arcuate vascula media do not extend as far as these parts of the valve. Text-figure 3B is drawn from Wright 1994, figure 1F. Likewise, the photograph of *Apomatella* figured in the same paper as figure 1C again shows clearly, albeit faintly, arcuate vascula media enclosing ovarian markings; the vascular markings of this specimen (RMS Br74575) are drawn here as Text-figure 3A. Additional support for the presence of the saccate condition in the ventral valves of *Apomatella* and *Neumania* is seen in the figures of these genera illustrated by Rubel and Popov (1994). *Apomatella* again shows strong vascula media curving away at the front of the spondylial septum, although they fade and are difficult to trace laterally (Rubel and Popov 1994, pl. 1, figs 5, 16). Nevertheless, the clear, irregular ridges of the ovarian scars do not cross their smooth lateral continuation to reach the vascula terminalia, which is suggestive of the presence of arcuate vascula media along these smooth areas. The gonocoele areas in *Neumania* again stop against somewhat more clearly defined smooth arcuate vascula media, sketched in Text-figure 3C (based on the Rubel and Popov figure of IGT Br968; 1994, pl. 2, fig. 8). A form closely related to *Apomatella* is *Atelelasma*. Cooper (1956) figured the impression of a ventral valve interior which he identified as *Atelelasma* aff. *A. perfectum* Cooper (pl. 79, fig. 3), and although he makes no comment on the mantle canals, this figure clearly shows the saccate arrangement with arcuate vascula media which

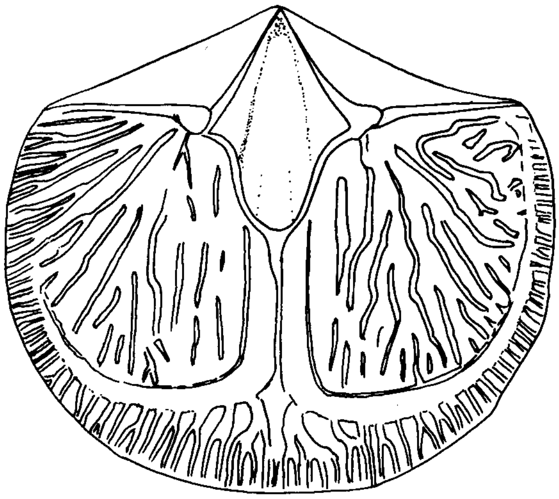


TEXT-FIG. 3. The mantle canal systems in the ventral valves of *Apomatella*, *Ladogiella* and *Neumania*, interpreted as indicating the saccate condition. Uncoloured areas are topographically positive or poorly preserved; black areas are topographically negative. A, *Apomatella ingrica* (Pahlen), based on Wright 1994, fig. 1C; B, *Ladogiella imbricata* Öpik, based on Wright 1994, fig. 1F; C, *Neumania erecta* (Pander), based on Rubel and Popov 1994, pl. 2, fig. 8.

appear to be directed laterally towards the antero-lateral margin. The saccate condition is also to be seen in the specimen of *Hemipronites tumidus* figured by Schuchert and Cooper (1932, pl. 8, fig. 10), who further drew attention to the similarity of the ovarian impressions to those of *Orthis*, etc. in their description. It is now clear that along with *Ladogiella* and *Hemipronites* (which we find hard to differentiate generically) the Atelelasmatinae are characterized by a saccate mantle canal system in the ventral valve (Text-fig. 4) in which arcuate vascula media confine the gonocoeles anteriorly and anterolaterally but which do not appear to confine them posterolaterally, where the radiating canals pass directly into the vascula terminalia, thus suggesting the onset of the pinnate pattern which characterizes the bulk of the clitambonitidine genera.

More fundamental to the understanding of the soft tissue distribution in extinct brachiopods generally and in protremates in particular has been the discovery of mantle canals lining the internal surface of the interareas in the procline clitambonitidines *Apomatella*, *Clinambon* and *Ilmarinia*. This demonstrated that the interareas of these strophic shells was lined with mantle and thus that the fusion of the mantle lobes and the start of the body cavity occurred not at the ends of the hinge

TEXT-FIG. 4. Generalized diagram to show the disposition of the mantle canals in those clitambonitidines which possess a saccate pattern in the ventral valve. The arcuate vascula media fade posterolaterally and the evidence so far available suggests that these may either break down laterally, with a pinnate pattern developing in the posterolateral angles (left-hand side), or may narrow but continue to the posterior margin (right-hand side). It may well be that both arrangements occur.



lines, as in extant telotremates, but at the edge of the delthyrium (Wright 1994). The problems of finding mantle canals beneath apsacline interareas were discussed in that paper, so that it is interesting to note their occurrence in a specimen of *Estlandia* (Pl. 2, fig. 2). Coming out from below the teeth at the lateral edges of the spondylium in this specimen are a pair of strongly developed mantle canals which extend across the valve floor in the usual way. The posterior branches of these canals, however, extend to the inner surface of the interarea which is marked by a series of nodes close to the hinge line. Though less impressive than the above noted mantle canals recorded from the procline areas of *Apomatella* and *Ilmarinia* (Wright 1994, fig. 1C–D, I–J), these impressions on apsacline shells confirm that, as predicted, the interareas of these strophic shells were also lined with mantle from the extremities of the hinge line medianly to the teeth and it is the teeth therefore which mark the lateral edges of the body cavity. Indeed, once pointed out, it is fairly obvious from the main canal system across the valve floors in these shells that the body cavity in the ventral valve must have been defined laterally by the position of the teeth and anteriorly by the edge of the spondylium.

ORNAMENTATION AND HOLLOW COSTELLAE

At present, there are no known smooth-shelled clitambonitidines, and apart from a single costate species, *Neumania costata* (Pander, 1830), the entire order possesses a costellate shell. The costellae arise by either branching or intercalation, or both; while their coarseness varies from the fine strophomenoid-like ribbing of *Raunites* (Pl. 5, fig. 5) to the coarse ribbing of *Vellamo*. The concentric ornament, by contrast, is highly variable (e.g. Pl. 2, fig. 5; Pl. 5, fig. 6), so that in addition to fine growth lines, there may be regular or irregular fila, and/or lamellae and imbrications. In combination with the radial ornament, a reticulate pattern may develop, as in *Kullervo* (Pl. 1, fig. 5) or *Lacunarites* (Pl. 3, fig. 3), or spines, as in some *Progonambonites* (Öpik 1934, pl. 24, fig. 5) and *Estlandia*. It has, however, not been possible to verify the record of the presence of occasional rugae in *Raunites* in any specimen seen by us. The radial ribs are commonly described as hollow; this is a term which needs some clarification.

All ribs are initially 'hollow' in that they represent the external expression of ridge-like undulations of the mantle edge which housed setae along the internal concave surfaces. Along the internal edge of the valves the marginal crenulations reflect the ribs and intercostal spaces, with the setae located in the follicular embayments of Williams and Wright (1963). In most brachiopods these marginal crenulations fade away from the margin as they become concealed by continued secondary shell deposition and, as the shell grows, the modification of this inner surface by differential secretion below the mantle canals and areas of muscle insertion.

However, the term 'hollow ribs' is usually understood to indicate the presence of holes along the length of ribs which are not related to the punctae (endopunctation) and from which they are defined as differing by not passing through the shell to the inner surface, hence the term exopunctation. Although there is a variety of form in external pitting, the larger, forwardly directed, shallow-angled aditicules (Wright 1981, p. 472), which are the most obvious kind of perforations associated with 'hollow ribs', do in fact pass through the entire shell but normally only at or near

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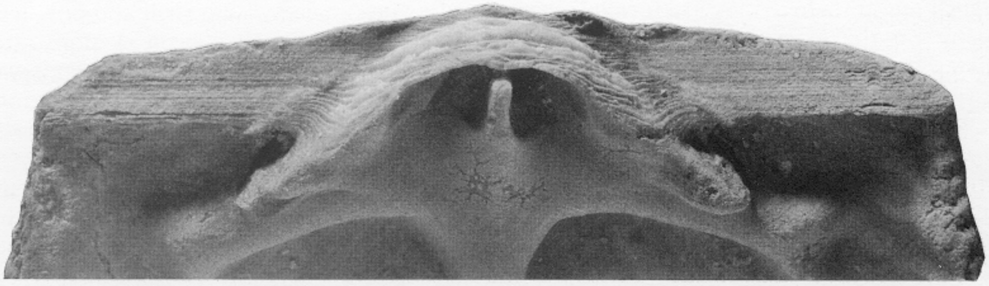
EXPLANATION OF PLATE 5

Figs 1–4. *Clitambonites schmidti* (Pahlen); NHM BB68553; N Estonia; Ordovician, ?Kukruse Stage (CII). 1, detail of chilidium and interarea of dorsal valve; × 6; 2, dorsal valve interior; × 1·5; 3, dorsal valve exterior; × 1·5; 4, oblique view of exterior, showing detail of ornamentation; × 10.

Fig. 5. *Raunites venusta* (Öpik); Vassilkovo, Ingria, Russia; Ordovician (Arenig), Volkov Stage (BII); figure from Öpik 1934, pl. 25, fig. 1*b*, showing nature of ribbing and concentric corrugated fila; × 5.

Fig. 6. *Clitambonites schmidti* (Pahlen) *epigonus* Öpik; Aluvere, Estonia; Ordovician (Lower Caradoc), Johvi Stage (DI); figure from Öpik 1934, pl. 8, fig. 1, showing strongly developed concentric fila and imbrications; × 6.

PLATE 5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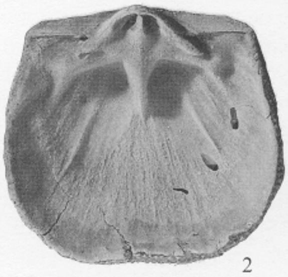
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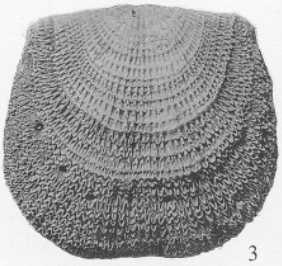
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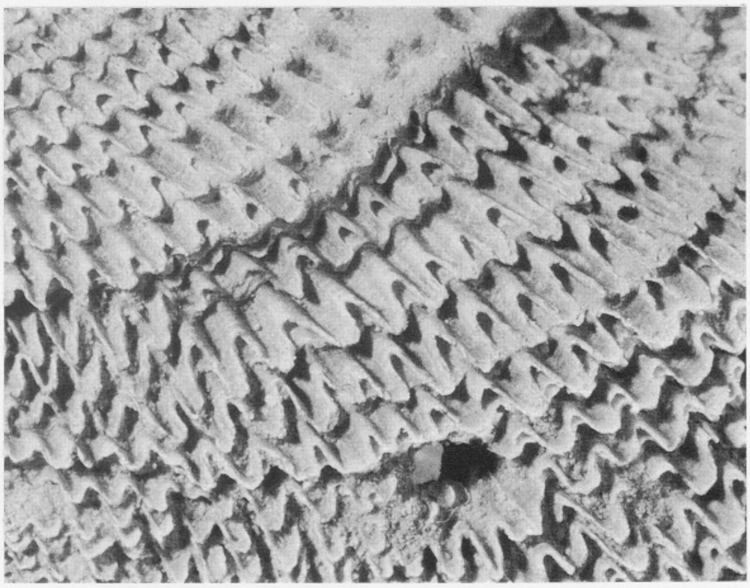
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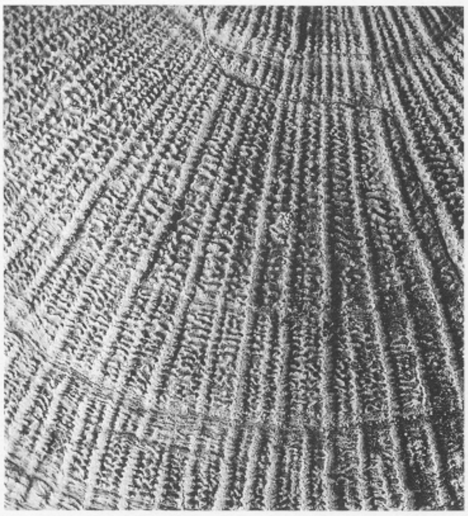
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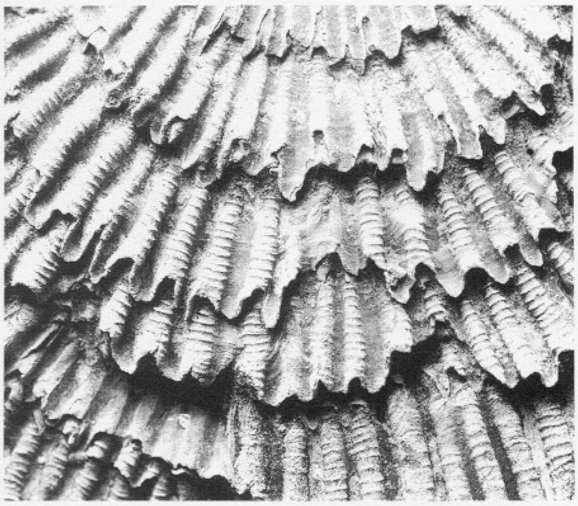
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WRIGHT and RUBEL, *Clitambonites*, *Raunites* to the shell margin where they are formed; thereafter they are sealed within shell and only have an expression on the external surface. The origin of these aditicules has been demonstrated in *Doleroides* and particularly *Rhipidomella* where the presumed setal-bearing follicular embayments can be observed in various degrees of incorporation into the shell (Wright 1981, p. 466), so that in life the setae would have become sealed into the shell as it grew, with a new seta arising along the line of the re-developing rib.

Aditicules are not uncommon in the clitambonitidines, and in fact have already been figured as such on the exterior of *Kullervo lacunata* (Wright 1981, pl. 66, fig. 8). A well preserved dorsal valve of *Kullervo panderi* collected by Professor Jaanusson (from the lowermost Kukruse Stage (CII) at Kohtla-Järve) and a ventral valve of the same species collected by Professor Rõõmusoks (from the Kukruse Stage (CII) at Küttejõu) are figured here (Pl. 1, figs 1–6). Both show even more convincingly than the silicified *Rhipidomella* the relationship between the deep follicular embayments and the external apertures of the aditicules, with some aditicules unusual in maintaining contact with the mantle through a tube-like perforation well to the posterior of the shell margin. This evidence, if any were needed, confirms the previous conviction (Wright 1981) that it is difficult to postulate any other realistic function for aditicules other than the accommodation of setal bristles within the shell surface; any speculation must start with the potential functions of these incorporated bristles. It is noteworthy that both the ventral and the dorsal valves of *Kullervo* show a similar scattering of the aditicules; this is in marked contrast to *Doleroides* and *Rhipidomella*, in which the arrangement differs on the two valves (Wright 1981).

Aditicules have not been observed in all clitambonitidines. Indeed, the absence of hollow ribs is used as a generic character in *Apomatella*; but occasional aditicules occur sporadically in many genera such as *Pahlenella*, *Raunites*, *Vellamo* and even *Lacunarites* (Pl. 3, fig. 7), a form which is more obviously characterized by strong intercostal pitting. In strongly imbricate stocks like *Ladogiella* and *Clitambonites* the aditicules occur largely in concentric rows associated with the anterior edges of the imbrications, while the extreme development is represented by *Estlandia*. A ventral exterior of *Ladogiella imbricata* is figured in Plate 3, figure 8. The young stages of this well preserved shell show 13 initial costae with very fine concentric filose growth lines (20 per mm) and only two weak imbrications prior to a well marked imbrication at 2·0 mm by which stage there are 27 ribs, the additional costellae apparently all arising by branching. This pattern is essentially repeated to the next well-marked imbricate growth stage at 3·8 mm (47 ribs here, with additional costellae arising on the downslope side of existing ribs). At the weak imbrications the ribs simply step down, as at any accentuated growth line, with, for the most part, little space at the crest of a rib for the incorporation of a seta as a bristle within the shell. Continued growth resulted in increasingly strong imbrications developing at about every half mm; when forward growth stopped temporarily at an imbrication, the valve would have had a scalloped margin, with the crests of the ribs marking embayments. Renewed growth along the line of the ribs produced a flat floor, partly arched over by the sides of the ribs along the embayments to give a cave-like effect, before the rib again developed at about half the length of the invagination. This morphology indicates that a seta could have projected from such a site, but the fact that other ribs appear to have developed very tightly against the rib of the previous imbrication, and commonly so along particular imbrications, indicates that any such incorporated setae would not have been uniformly developed across the shell, although potential setal sites increase in number in the later imbrications. The scalloped margins in life would not have been as exaggerated as they now appear. Where the shell is well preserved, the concentric fila can be traced down off the rib and across the intercostal spaces where they advance modestly, and postero-laterally such fila correspond with the shell edge of the time. But where the scalloping is well displayed, although the fila at the front of the rib crest can be traced, again advancing slightly, across the intercostal space, the fila parallel to them along the sides of the ribs terminate abruptly against the outside edge (as illustrated for *Clitambonites* in Pl. 5, fig. 4), i.e. they do not follow the line of the embayment. Whilst it is possible that the shell was resorbed medianly, it seems more probable that, protruding away from the surface, the fragile edge of the imbrication was simply abraded.

In *Clitambonites* the imbrications are more exaggerated (Öpik 1934, pl. 8, fig. 1, reproduced here as Pl. 5, fig. 6). The radial ornament consists of costellae, which arose by intercalation or branching, that show clear, sharp-crested concentric fila with a density of about 5 per mm. The shell growth is interrupted by a small number of strongly defined imbrications, typically *c.* 2·5 mm apart, which reflect marked pauses in anterior growth. Öpik's figure shows ribs with the crests withdrawn from the margin of the earliest imbrication shown, sometimes with a clear 'cave' proximally. But these are not widely present, and the appearance of these ribs would appear to result again from abrasion of the crests of the ribs along the edge of the imbrication, a view supported by the variably frayed margins of the other imbrications as well as the pattern of the concentric fila crossing the rib without any inflexion that would correspond to an invagination along the rib crest. In the specimen of *C. schmidti* (Pl. 5, fig. 4) the margin of the imbrication has a modest scalloping compared with that of the rib and intercostal groove. Again the fila along the advancing edges of the rib are truncated and suggest abrasion of the rib crest. At the same time, the revealed forward-pointing apertures (aditicules) strongly suggest an array of setae incorporated all along the imbrication.

Because of the delicate nature of lamellose structures and the possibility that damage has occurred during extraction from the matrix, a ventral valve of *C. schmidti* with adherent matrix was embedded in resin and sectioned longitudinally (Text-fig. 5). This shows the extended nature of the imbricated rib beyond the underlying step, which must make it prone to breakage. Internal to a rib there is a groove, interpreted as being the site of a seta. This groove swells at the proximal end into a slender bulb, so that the overall shape corresponds to that of a setal follicle in an extant brachiopod. The younger shell below an imbrication shows the pronounced step before the shell advanced again, just as in shells manually freed from their matrix; but what has not been observed in such shells are the small lamellose extensions on this step, which indicate a series of anteriorly directed growth layers which built up the shell thickness before the shell finally advanced to form the succeeding imbrication.

TEXT-FIG. 5. Longitudinal section through a ventral valve of *Clitambonites schmidti* (Pahlen) with the exterior embedded in matrix (stippled) to show a series of surface imbrications (i) underlain by a setal groove terminating proximally in a bulb (b) interpreted as containing a setal follicle. The succeeding step (s) shows fine laminae, not preserved in matrix-free shells, representing minor oscillations in the mantle edge before the growth of the succeeding imbrication. RMS Br92111; Kukruse Stage (CII); Kohtla, Estonia; × 10.

The ornament of *Estlandia* (Pl. 2, fig. 5) appears to be peculiar to this genus. The costellae arise largely by intercalation on this dorsal valve, and the regular, straightish concentric fila of the intercostal spaces (*c.* 8 per mm) cut back across the ribs, where their topographic development varies. Some cross the ribs simply as strong fila; with growth, an increasing number become lamellose with the posterior side curving away from the valve surface to form an arch over a pit, the attitude of which varies from being directed anteriorly to almost perpendicular to the surface.

When developed evenly over the whole length of a rib such lamellae strongly resemble the overlapping hip tiles along roof angles but with pits between; other lamellae which are directed upwards away from the shell surface may have the sides joined beneath to form a hollow spine in the manner of *Spinorthis* (Wright 1964). The arched pits and hollow spines of these tubulose ribs are all interpreted as aditicules each of which contained a seta embedded in the shell. Around the internal margin, outside the subperipheral rim, deep follicular embayments with pits or, posterolaterally, just single pits, remain as evidence of the connection of the aditicule to the internal valve margin.

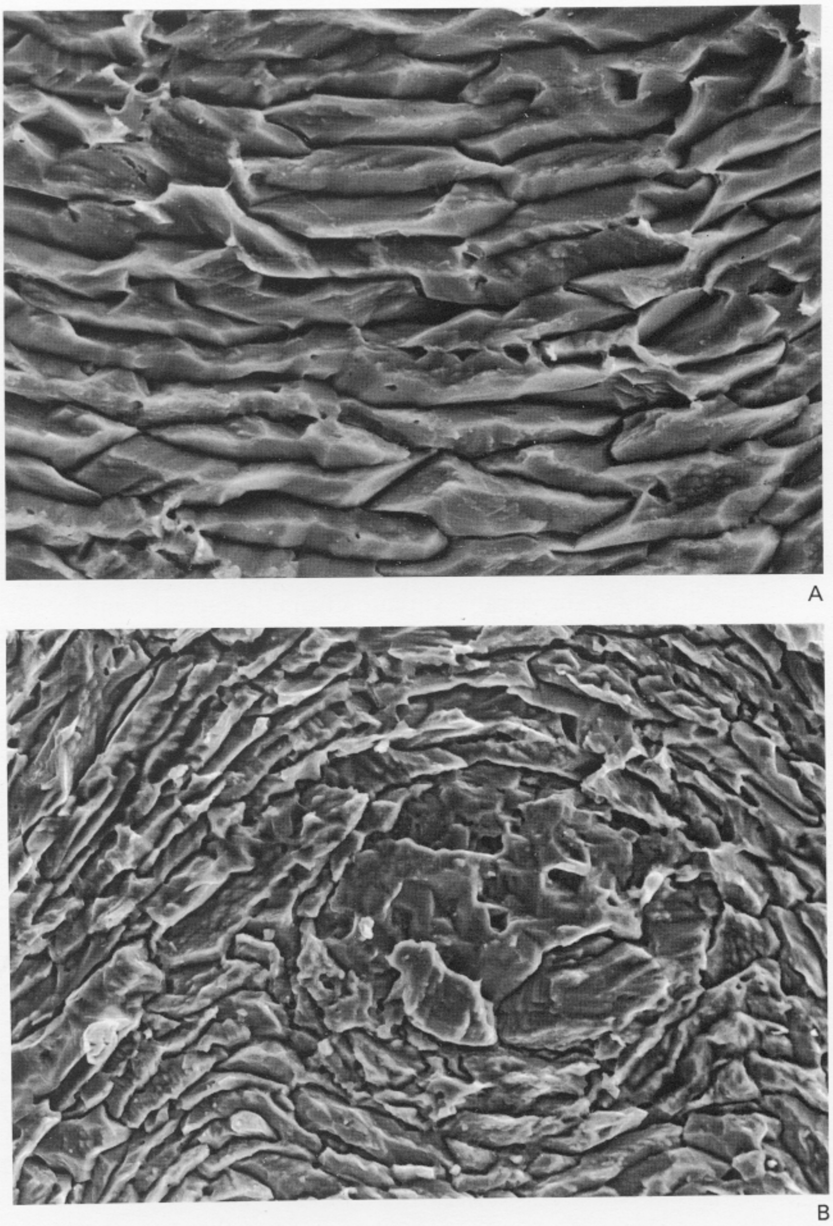
In the Polytoechiidae, *Tritoechia* is a form which shows well developed aditicules along the rib crests. *Acanthotoechia* appears to be unique in this family in developing rows of spines along the ribs peripherally. Their distribution on the differentiated ribs is detailed by Williams and Curry (1985, p. 224) and is characterized by the coarser primary ribs bearing two rows of laterally inclined fine cylindrical spines with the finer intermediary ribs bearing a single row of hollow erect spines. The paired spines are clearly not situated centrally along the rib as are aditicules and, moreover, there is a tendency for those of the single rows to zig-zag, so that their distribution is closely comparable to these features as displayed by arrugiae and not aditicules (Wright 1981, p. 476). A second feature of significance of these pits is their size; the diameter of the largest aperture figured by Williams and Curry (1985, fig. 159*b*) is 0·04 mm; this compares well with the diameter of 0·04 mm for the arrugiae but not with that of 0·18 mm for the aditicules on the *Doleroides* illustrated by Wright (1981, pl. 70, fig. 2). This again supports the interpretation of the *Acanthotoechia* perforations as being comparable to arrugiae and not aditicules.

SHELL SUBSTANCE

The shell substance of the clitambonitidines had been regarded as being impunctate until Öpik (1932) established the presence of pseudopunctae in the shell of stocks such as *Estlandia* and *Kullervo*. Williams (1968, p. 35), in his review of the shell structure of the articulate brachiopods as revealed by transmission electron microscopy, reported the presence of a fibrous secondary layer in *Vellamo*, *Eremotoechia* and *Antigonambonites*. These genera represent the broad spread of the clitambonitidines, covering both impunctate and pseudopunctate stocks. The fibres were well illustrated by Williams for *Vellamo* (1968, pl. 18, fig. 6).

Within the clitambonitidines, it is the Superfamily Gonambonitacea which is characterized by the presence of pseudopunctae. This shell modification is strikingly obvious in most genera ascribed to the superfamily, with the associated granular internal surface being visible at relatively low magnifications, e.g. in *Estlandia* (Pl. 2, fig. 8). The exception to this dense granulation is *Anomalorthis*, which was reported by Ulrich and Cooper (1938, p. 127) as having 'scattered pseudopunctae like those occurring in the Strophomenacea'. The mixture of clitambonitid and orthid characters in these enigmatic shells resulted in Ulrich and Cooper placing the family on balance in the Orthacea. Williams (1965, p. H353) judged it best to assign the stock to the Gonambonitidae.

The thin section of *Anomalorthis oklahomensis* figured by Ulrich and Cooper (1938, pl. 22, fig. 6) has been examined for the present study, and the small dots visible in that figure are certainly the right diameter for pseudopunctae although the usual swirling of the shell about such structures was not seen. A small piece of shell, 3·7 mm wide, was kindly made available from the Ulrich and Cooper Collection by the Smithsonian Institution for examination under SEM. This was cut transverse to the growth direction, etched, coated and the surface examined; then reground, polished and the examination repeated. These examinations established the fibrous nature of the shell (Text-fig. 6A), but only one pseudopuncta was observed in the two operations (Text-fig. 6B). The confirmed scattered and sporadic nature of the pseudopunctae does not match their distribution in the other members of the family. Accordingly, the contribution of the shell substance to its systematic position remains ambiguous. In our opinion, little systematic significance can be placed on the occasional presence of pseudopunctae in *Anomalorthis*, any more than it can on the presence of pseudopunctae in the Triplesiacea, where they also occur only rarely in some species of



TEXT-FIG. 6. Scanning electron micrographs of a tranverse section of a ventral valve fragment of *Anomalorthis oklahomensis* Ulrich and Cooper; USNM 91293; Oil Creek Limestone; Falls Creek, Oklahoma. A, stacked fibres, ×2500; B, pseudopuncta, ×1300. Exterior of shell uppermost.

Ogmoplecia (Wright 1970). Again, the Orthotetidina have long been known to have impunctate shells in the earlier stocks, with pseudopunctae developing only in the later forms. *Anomalorthis* is accordingly here considered probably better placed as an aberrant orthidine.

CONCLUSIONS

1. While a widely distributed clitambonitidine like *Vellamo* is well recognized by its assemblage of characters, when these characters are examined for the whole group of genera currently assigned to the Suborder Clitambonitidina, the variation is such that it is difficult to arrive at a clear-cut diagnosis of a clitambonitidine.

(a) Shell. The secondary shell substance is fibrous, but may be impunctate or pseudopunctate.

(b) Attachment. The means of attachment to the substrate, the pedicle, may have functioned throughout life but in many stocks became atrophied with progressive sealing of the foramen. The delthyrial cover may be entire, partial, or absent altogether. The notothyrial cover may be large and semicircular, with a different growth arrangement to one which is small and triangular; or may only be partial, or absent altogether.

(c) Shell opening. The valve consistently opened about a strophic hinge with a deltidiodont dentition. But the ventral muscles were located on a spondylium which is typically simplex, may be triplex or be merely a pseudospondylium. The dorsal adductor scars may be quadripartite or radially arranged; in either case the anterior pair may or may not be larger, a character which may or may not vary within a genus. The cardinal process, typically a strong ridge separating the diductor scars, may not be developed; while the ancillary ridges appear to reflect differential shell secretion in different individuals rather than to have any taxonomic value.

2. Shape, profile, proportions and ornamentation, useful taxonomically at generic level, can be expected to, and indeed do, show considerable variation from the typical ventribiconvex shells with a moderately long apsacline ventral interarea and, although costellate ribbing is almost universal, the concentric ornament varies from the almost imperceptible to grossly exaggerated frills and imbrications, surface pitting and even spines.

3. The ribs commonly may be perforated by aditicules, numerous or sparse, initially passing through to the inner shell surface and interpreted as the site of setae; rarely by finer and differently disposed arrugiae; or lacking any form of exopunctae.

4. Evidence of the growth of the delthyrial cover, not available to Williams and Rowell (1965, p. H88) when they assumed the structure to be a pseudodeltidium, shows a series of stages of development indicating it to be a deltidium.

5. The recently discovered mantle canals lining the ventral interareas of certain procline clitambonitids, important for their soft tissue implications (Wright 1994), are now recorded for the apsacline *Estlandia*.

6. After re-examination, the aberrant *Anomalorthis*, which lacks many 'typical' morphological features of the clitambonitidines, is here considered rather to be an aberrant orthidine, with little taxonomic weight being ascribed to the presence of scattered and sporadic pseudopunctae.

Repositories. The institutional abbreviations for the repositories of the specimens illustrated in this paper are: IGT, Institute of Geology, Tallinn; NHM, The Natural History Museum, London; QUB, Department of Geology, Queen's University of Belfast; RMS, Riksmuseum, Stockholm; USNM, National Museum of Natural History, Smithsonian Institute, Washington DC.

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A. D. WRIGHT

School of Geosciences
The Queen's University
Belfast BT7 1NN
Northern Ireland

MADIS RUBEL

Geoloogia Instituut
Tartu University
Vanemuise, 46
Tartu EE 2400
Estonia

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