

# Co-existence of interarea and palintrope: contribution of a new pentameride brachiopod from the Upper Ordovician of Sweden

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**ABSTRACT:** A new genus of pentameride brachiopod, *Costilammulella*, described herein from the middle Ashgill of Sweden, is particularly interesting in that the ventral valve possesses both an interarea and a palintrope. Brachiopods normally have one or the other, but both structures do occur amongst the pentamerides, e.g. in *Clorinda*, *Anastrophia* and *Brevilammulella*. The presence of these structures in three separate pentameride families indicates the persistence of the more primitive condition of an interarea whilst the more advanced palintrope is becoming established. *Costilammulella* is interpreted as a restricted side line of the main development of the more widely occurring *Brevilammulella*, which survived the end-Ordovician event and may have shared its ancestry with the ubiquitous *Clorinda*.

**KEY WORDS:** Ashgill, Boda Limestone, hinge development, Mariannaellinae



The carbonate mudmounds of the Upper Ordovician Boda and Kullberg limestones of the Siljan Ring in Dalarna, central Sweden, have long been known to possess rich shelly faunas both in the mudmounds and in the surrounding flank facies. The mounds are predominantly of grey limestones, and commonly contain substantial accumulations ('nests') of illaenid trilobites and of relatively large brachiopods such as *Cryptothyrella* (Jaanusson 1982), typically stained brown by the oil which has accumulated therein. The flank facies, of red and green mudstones alternating with bioclastic limestones which thin away from the mounds, typically contain smaller brachiopods such as *Epitomyonia* (Wright 1968b) and *Ptychopleurella* (Wright 1982) indicating deeper water regimes.

The new pentameride material belongs to the mudmound facies, with all known specimens in the Riksmuseum collections derived from the Boda Limestone of Solberga quarry, in all about 60 shells. It is surprising that, in view of the large number of Boda Limestone mudmounds exposed in the Siljan district, specimens have only been located in this single quarry. This would not be unique however, as *Grammoplecia* is another genus which is known from only one quarry (Kallholn), where it is relatively abundant (Wright & Jaanusson 1993, p. 107). It is of course quite possible that both forms may turn up in other Boda mounds; but not so far.

## 1. A ventral interarea and a palintrope

The new pentameride, named below as *Costilammulella*, is of interest in that it has both an interarea and a palintrope on the ventral valve. The presence of both ventral and dorsal interareas has been considered recently by Jin *et al.* (2006) and Rong *et al.* (2007) although not with regard to the ventral interarea and its relationship to the palintrope, a topic which is considered herein. Among the articulated brachiopods it is assumed that they will have one or the other type of cardinal

area (Williams & Rowell 1965), i.e., like *Orthis*, *Strophomena* or *Spirifer* with a straight hinge line and sharply defined interareas (strophic hinge), or like *Terebratula* and *Rhynchonella* with a curved hinge line and curved palintropes limited by an arcuate umbonal ridge (non-strophic or astrophic hinge).

However, examination of other pentamerides shows that the new genus is not unique in having both types of cardinal areas present, but the combination would not appear to characterise brachiopods outside this order, notwithstanding the fact that strophic genera do occur in essentially astrophic groups, e.g. *Megathiris* and *Argyrotheca* in the terebratulides and various problematic stocks like *Tropidoleptus*, the placing of which is still uncertain.

The parastrophinid *Anastrophia* was described by Carlson (2002, p. 955) as having a hinge line which is 'astrophic, less commonly strophic'. Examination of a small sample in the Leicester University collections (ADW) shows a well-defined if narrow ventral interarea, lateral to which is a smooth concave palintrope. In one specimen of *A. verneuli*, the interarea was three-fifths as wide as the palintrope, although commonly the strong ribbed ornament made the umbonal ridge hard to decipher. It may well be that weak development of the interarea accounts for the Carlson definition.

Again, the combined presence of both palintropes and interareas was seen in the Leicester University collection of *Clorinda globosa*. Although the specimens had rather etched shell surfaces, two specimens were sufficiently well preserved to show short ventral interareas (opposite to very short dorsal interareas) just over half as wide as the curved palintropes and about two-fifths as wide as the valve.

But for the most part shells have one or the other. At one extreme *Stricklandia* has a wide straight hingeline with a well-developed interarea, whilst at the other *Kirkidium* has a curved palintrope lateral to the delthyrium with no interarea; the defining umbonal ridge is weak, and indeed the palintrope

is most simply differentiated from the main shell by the lack of radial ornament.

The posterior of the ventral valve of *Costilammulella* gen. nov. shows an open delthyrium set in a well-defined, posteriorly curved but variably narrow interarea, from the ends of which the straight hinge continues laterally before the commissure develops a rounded, obtuse angled curve at the cardinal margins. In addition, on either side of the beak a low ridge (beak ridge) curves laterally to define a posteriorly facing concave surface (palintrope), the definition of which fades laterally, so that in most cases it is difficult to define where it meets the posterior commissure. In four shells with complete measurements, the interarea was one-sixth as wide as the shell, the palintrope ranged between one-third and approaching one-half, and the hinge-line three-fifths, of the shell width; and in five shells the mean width of the palintrope was two-thirds of the hinge width.

Why should specimens show both types of area on the same shell? The answer may be that during the Ashgill this stock was undergoing a change from the more primitive condition of having an interarea into what is widely taken as the more advanced development of a palintrope. In *Costilammulella*, *Anastrophia* and *Clorinda* then, are representatives of three different pentameride families (Virgianidae, Parastrophinidae and Clorindidae) – and no doubt there are others – which independently show an interarea still persisting whilst the palintrope is becoming established.

A form which we believe is close to *Costilammulella* is Amsden's genus *Brevilammulella* (1974). Having discussed at some length the terms palintrope, interarea and cardinal area for his genus, he concluded that it appeared to have 'a small palintrope' (Amsden 1974, p. 63). The specimens of his figures (pl. 2, figs. 1a, 1b) he described as having an indistinct interarea, and a narrow, flat interarea respectively, but he made no mention of the additional presence of a palintrope. However, his figures 1b and 2a do appear to have umbonal ridges defining palintropes.

Most pentamerides have deltidodont teeth, although according to Carlson & Boucot (2002, p. 925) there are exceptions. A replacement of interarea by palintrope, i.e. strophic by astrophic, would seem to be a precondition for the development of cyrtomatodont teeth. But this is not necessarily so, as the strophic shells cited above like *Tropidoleptus* have cyrtomatodont teeth and strophic hinges, although the latter could be a secondary development. As Jaanusson (1971) pointed out, cyrtomatodont teeth grow by resorption as well as deposition of calcite, a phenomenon which has long been apparent to permit the development of complex lophophore supports but was also demonstrated for the punctate orthide *Dicoelosia* (Wright 1968a, p. 273).

In connection with a revision of two virgianid brachiopods, a preliminary survey of interarea development in the pentameroids was outlined by Jin *et al.* (2006), who noted that while some genera have both ventral and dorsal interareas, others with a rounded ventral palintrope may still possess a well-defined dorsal interarea. They suggested that a comprehensive study is necessary to ascertain which stocks do possess such dorsal interareas, that are often only visible on disarticulated shells, and a feature which is true also of the triplesiidines (Wright 1971). The present study suggests that with the presence of two types of ventral area in some stocks, the story may well be even more intriguing.

## 2. Systematic palaeontology

Family Virgianidae Boucot & Amsden, 1963

Subfamily Mariannaellinae Sapelnikov & Rukavishnikova, 1975

Genus *Costilammulella* Wright & Rong, gen. nov.

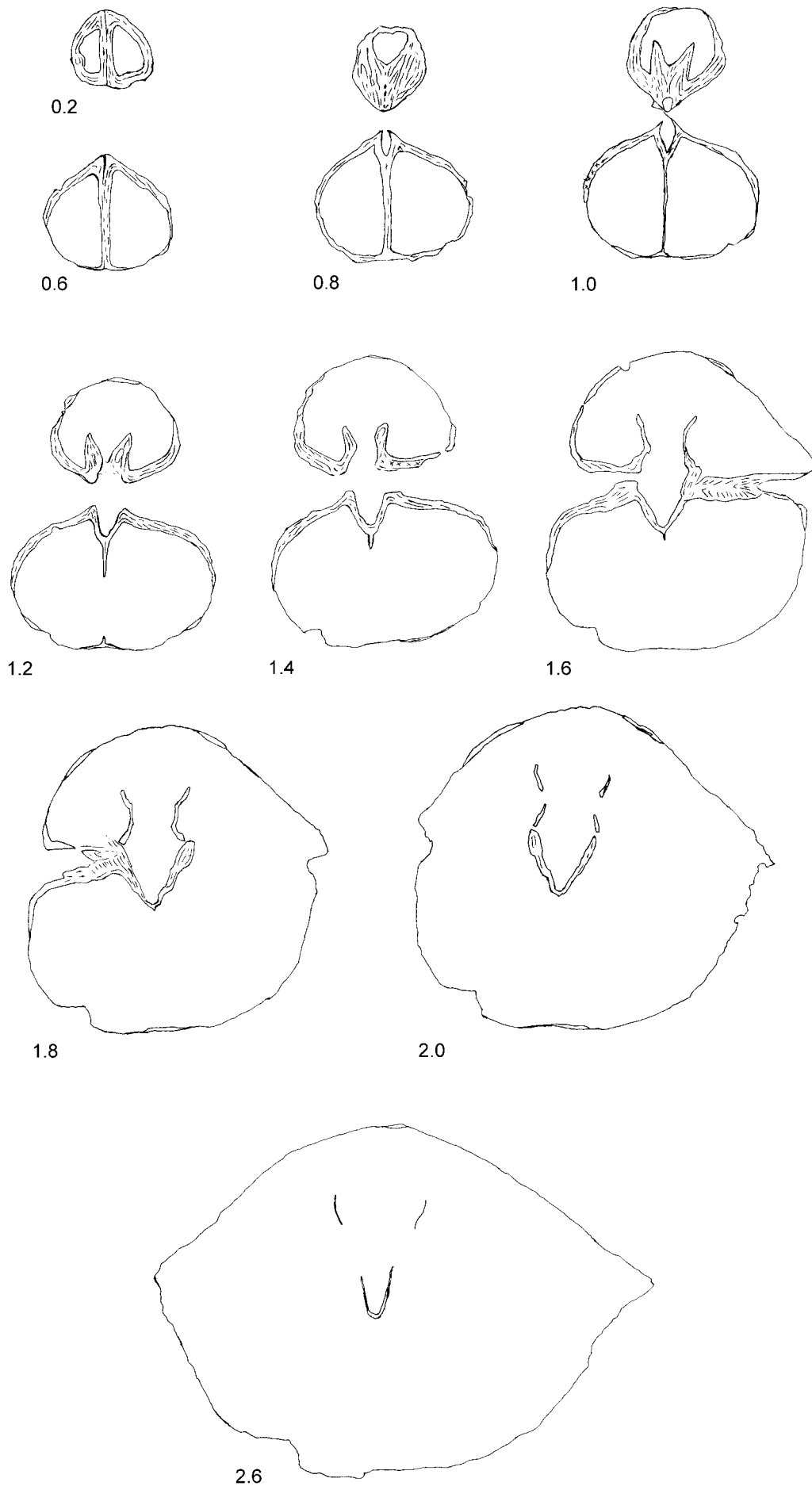
**Derivation of name.** Latin 'costa', rib, and 'lammulella' small plate, referring to the short inner plates, and expressing some affinity to the existing genus *Brevilammulella*.

**Type species.** *C. valdari* Wright & Rong sp. nov.

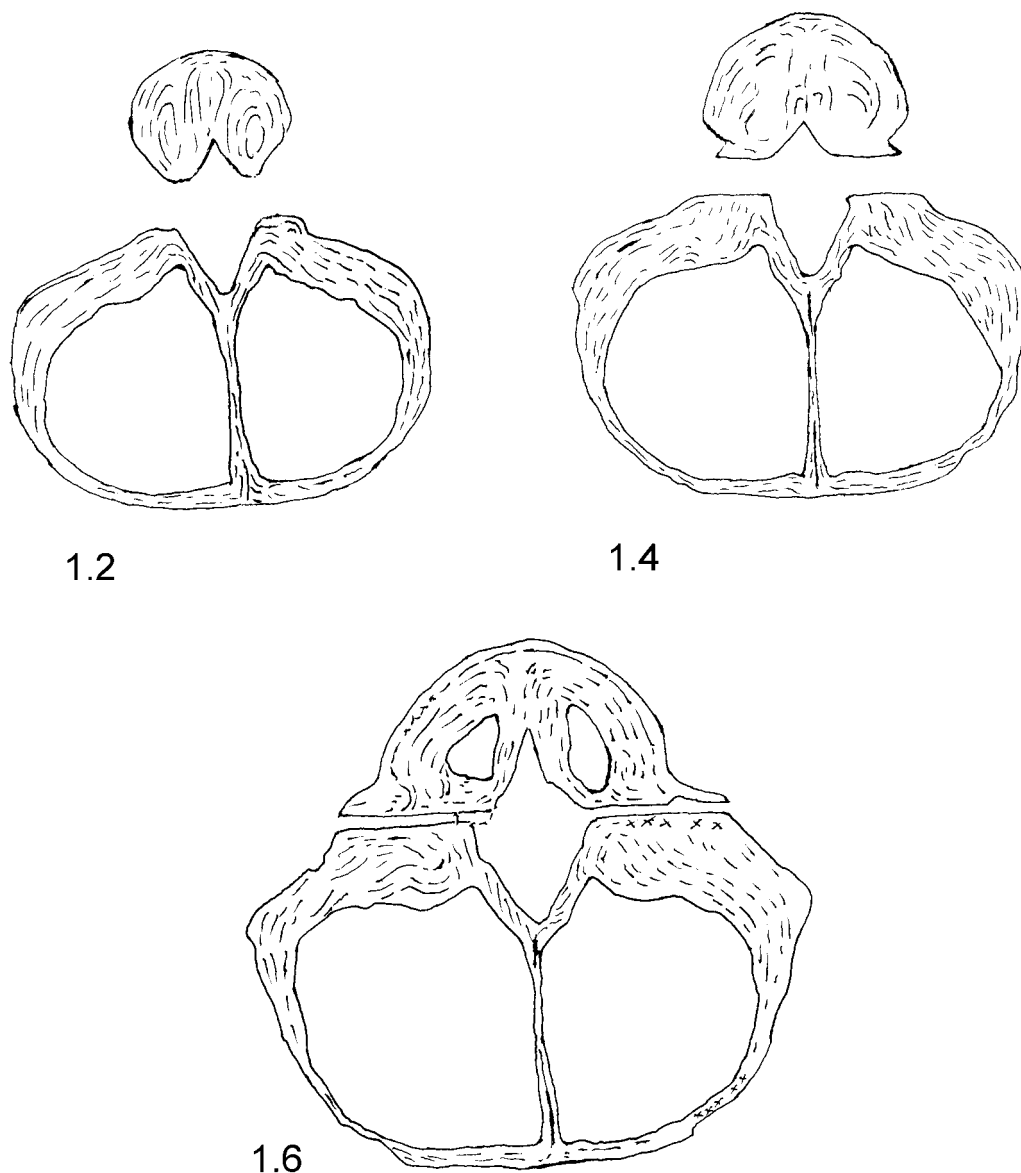
**Diagnosis.** Transverse, slightly ventribiconvex shells with ventral sulcus and dorsal fold; paucicostate, median rib of sulcus rising early; ribs arising lateral to fold and sulcus delayed; both interarea and palintrope developed. Ventral interior with small spondylium duplex, posteriorly supported on median septum. Dorsal interior with very short inner hinge plates; crura and outer hinge plates with waisted profile, crura extending to front of tip of spondylium.

**Affinities.** The biconvex valves, well-developed spondylium and hinge plates clearly indicate the order Pentamerida, and more particularly the suborder Pentameridina. Whilst the vast majority of taxa in this suborder are of post Ordovician age, the oldest known stocks of the superfamily Pentamerioidea occur within the Ashgill, where they appear to be restricted to the family Virgianidae. Typically these are large forms with strongly rostrate shells and lack the marked uniplication seen in *Costilammulella*. However the subfamily Mariannaellinae was erected by Sapelnikov & Rukavishnikova (1975) to accommodate virgianids of small to moderate size and transverse outline with a well developed fold and sulcus, and contains genera like *Brevilammulella* and the bisulcate *Disulcatella*, which not only show some external similarities but also internal similarities to *Costilammulella*. The new genus resembles *Brevilammulella* rather than other virgianids in having a uniplicate shell with the spondylium supported on a septum. Externally *Costilammulella* is more transverse and paucicostate, with the median costa of the sulcus rising early. *Costilammulella* differs internally from *Brevilammulella* in the brachial apparatus firstly in its miniscule inner hinge plate contact with the valve floor. In Figure 2 the hinge plates appear as a continuous structure at 1.6 mm from the ventral umbo (0.6 from the dorsal umbo). In Figure 1, the inner hinge plates have already disappeared by 1.0 mm from the ventral umbo (0.3 from dorsal umbo). Amsden's figures (1974, text-figs. 37, 38) of *Brevilammulella* show the inner hinge plates still to be continuous to the valve floor at 1.2 and 1.7 mm from the dorsal umbo. Secondly, in *Brevilammulella* the outer hinge plates and crura still converge medianly once free from the inner hinge plates (Amsden 1974, figs. 37D, 37E); by contrast the combined plates in *Costilammulella* become arcuate in section, diverging away from the median plane at both ends to give the waisted section of the crura and outer hinge plates (Fig. 1).

Externally, apart from lacking a galeate profile, the shape is not dissimilar to the smooth, uniplicate Silurian pentameroid clorindids like *Clorinda* and *Boucotides* while some, like *Clorindella*, even possess costae. Apart from its less extreme transverse outline, *Clorinda* is the most similar clorindid in external appearance to *Costilammulella*. Internally, although this group has short inner hinge plates, it has a cruralium or widely divergent inner hinge plate bases, unlike *Costilammulella* (Fig. 2), where the inner hinge plates are even shorter and the brachial apparatus lacks the carinae of the clorindids. Regarding this last point, it is worth emphasising that, although the presence of carinae is an important character of the group, they are not present in some stocks, while in others their presence or absence is unproven (Boucot *et al.* 2002). The waisted profile of the hinge plates in *Costilammulella* is like the lyre shaped section, without its basal inner hinge plate part, seen in many clorindids although not *Clorinda* itself.



**Figure 1** Transverse sections taken through conjoined valves of *Costilammulella valdari* gen. et sp. nov., at distances indicated from the ventral umbo (mm). Boda Limestone, Solberga Quarry, Siljan District, Dalarna. RMS. Br108595,  $\times 5$ . Earliest two sections through ventral valve only; remainder with dorsal valve uppermost.



**Figure 2** Sequence of transverse sections taken through conjoined valves of *Costilammulella valdari* gen. et sp. nov., at distances indicated from the ventral umbo (mm), to show inner hinge plates in contact with the valve floor. Boda Limestone, Solberga Quarry, Siljan District, Dalarna. RMS. Br108596,  $\times 5$ . Dorsal valve uppermost.

Externally, as it lacks the ribs of *Costilammulella*, *Brevilammulella* is very similar to *Clorinda* and may well have been confused with the latter in the past, as they occur together in the lowest Llandovery (Rhuddanian) strata in Wales (Temple 1987). But the distinguishing presence of carinae in the *Clorinda* was well demonstrated by Temple (1987, p. 103).

*Costilammulella* is, on the basis of its overall morphology, accordingly considered to be most appropriately placed within the subfamily Mariannaellinae near to but distinct from the more widely occurring *Brevilammulella*. Boucot (1975) suggested that *Brevilammulella* may be the ancestor of *Clorinda*. *Brevilammulella*, known from both sides of the Ordovician-Silurian boundary, clearly survived the end Ordovician mass extinction and as such is one of the very few pentamerids which did survive this extinction event, possibly to evolve subsequently into many other genera. *Costilammulella*, with its ribs already developed by the mid Ashgill, would seem to be a side line of the main development towards the ubiquitous and essentially smooth *Clorinda*.

Apart from *Brevilammulella thebesensis* (Savage), the type species of Amsden's genus from the Hirnantian of Illinois, that genus has now been recorded widely in rocks ranging in

age from mid Ashgill into Rhuddanian. This includes the middle Ashgill of Chingiz, Kazakhstan (Sapelnikov & Rukavishnikova 1975); the Hirnantian of Kolyma (Rozman 1978; Oradovskaya 1983); ?Hirnantian of Gornyi Altay (Severgina 1978); Hirnantian or Rhuddanian, W Canada (Jin & Chatterton 1997); Hirnantian, Norway (Kiær 1902; St. Joseph 1938); Rhuddanian, Wales (Temple 1987); Hirnantian, Tadzhikistan (Menakova 1984, 1991), although the age of the containing strata is more probably pre-Hirnantian (L. Popov, pers. comm. 2007); Hirnantian, NE Guizhou, SW China (Rong *et al.* 2006); lower Rhuddanian, W Zhejiang and NE Jiangxi, E China (Rong & Zhan 2006); ?Rhuddanian, Shaanxi-Gansu-Ningxia, NW China (Fu 1983). The various species described are typically smooth, but some may develop a few short ribs at the anterior of the shell.

A marianellinid which is also similar to *Costilammulella* is *Viridita* Jin & Copper, 2000 from the later, Lower Rhuddanian Becscie Formation of Anticosti Island. This genus, again with a distinct ventral interarea, is however very variable, ranging from smooth in small shells to costate in larger ones, and with an unstable ventral sulcus and dorsal fold (Jin, pers. comm. 2007).



**Figure 3** *Costilamnulella valdari* gen et. sp. nov. Boda Limestone, Solberga Quarry, Siljan District, Dalarna. Repository: Riksmuseum, Stockholm (RMS): (a)–(e) Ventral, dorsal, lateral, posterior and anterior views of *holotype* (Br108548).  $\times 2$ ; (f)–(j) Lateral, anterior, postero-dorsal, dorsal and ventral views of conjoined valves (Br108549).  $\times 2$ ; (k) Conjoined valves showing delthyrial margins, interareas, beak ridges and palintropes (Br108544).  $\times 4$ ; (l) Dorsal view of conjoined valves showing late costae and lateral exfoliation (Br108563).  $\times 2$ ; (m) postero-dorsal view showing asymmetrical interarea with pitted gonocoel areas in front of ventral palintropes (Br108563).  $\times 2$ ; (n) Partially exfoliated conjoined valves showing interarea, palintrope, impressions of part of pitted gonocoels and spondylial septum in ventral valve (above), and low median ridge with weak surmounting thread and posterior parts of adductor scars in dorsal valve. (Br108586).  $\times 4$ ; (o) Posterior region of broken shell. Ventral valve (below hinge), showing hinge line, interareas, palintropes, with base of spondylium and pitted gonocoel areas in front; dorsal valve (above) with postero-median diductor scars, low median ridge with weak surmounting thread between posterior parts of adductor scars at top of picture. (Br108567).  $\times 6$ ; (p) Ventral valve mould with impression of spondylial septum and vascula media (Br108599).  $\times 4$ .

*Costilamnuella* by contrast externally has a transverse shell, a more strongly defined fold and sulcus, with stronger ribbing which arises earlier. Although *Viridita* is defined (Jin & Copper 2000, p. 32) as subcircular, the rare species *V. becsiensis* (Twenhofel 1928), and now known only from the holotype (Jin & Copper 2000, p. 833) is a transverse species, but differs externally from *Costilamnuella* as the shell shows no ribs other than the median sulcal rib. The interior is clearly unknown, but as it comes from the same Becscie Formation as the more abundant type species (*Camerella lenticularis* Billings, 1866), it is presumed that the brachial structures are similar. Internally, the orientation of the outer hinge plates and crura of *Viridita* (Jin & Copper 2000, text-fig.17) are virtually identical with those of *Brevilamnuella* (Amsden 1974, text-fig. 37), and quite distinct from the waisted arrangement in *Costilamnuella* that occurs in the later *Clorinda*.

Apart from this advanced arrangement in the otherwise primitive virgianid internal structures, another puzzle is that the new genus is morphologically more advanced than the later variable *Viridita*. This again suggests to us that *Costilamnuella* is a side line of the main development towards *Clorinda*.

**Preservation.** The overwhelming majority of the Solberga shells are present in the form of conjoined calcite valves, which are commonly exfoliated to a varying degree. This inhibits the collection of data for the origin of ribs, fold and sulcus in particular. The exfoliation of the outermost shell further results in the exposed secondary fibres having the appearance of fine radial costellae, and occasionally reveals a capilla-like thread as on the fold of the *holotype* (Fig. 3b) that is in fact an internal feature, which is seen to disappear under calcite shell in Br108554 and Br108583. Exfoliation does however provide some data on the length of the short ventral spondylial septum and the even shorter bases to the dorsal inner hinge plates, as measured on the shell surfaces as opposed to the true anterior direction, which is best measured from the peel sections. Rare specimens that have lost most of their umbonal calcite reveal partial internal moulds (Br108599 and Br108586), whilst a single interior of the posterior part of a conjoined shell (Br108567) provides the most useful information on the features of the valve floors. Otherwise, information on the interiors is derived from two specimens that were serial sectioned (Figs 1, 2).

*Costilamnuella valdari* sp. nov.  
(Figs 1, 2, 3a–p)

**Derivation of name.** Named in honour of the late Professor Valdar Jaanusson, who drew the senior author's attention to this unusual brachiopod.

**Material.** About 60 specimens, all from the Boda Limestone, Upper Ordovician (middle Ashgill), Solberga Quarry, Siljan District, Dalarna, Sweden. It has not been possible to ascertain the precise correlation within the middle Ashgill. Repository – Riksmuseum, Stockholm (RMS). Holotype Br108548, conjoined valves, L 16.2, W 25.1 (L = length of ventral valve, W = maximum width, in mm). Figured paratypes: conjoined valves Br108549, L 15.4, W 24.9; Br108544, L 11.8, W 19.1; Br108563, L 16.6, W 26.2; damaged shell Br108586 L–W 24.8; broken shell showing interiors of valves Br108567, L–W–.

**Diagnosis.** Transversely elliptical *Costilamnuella*; fold with two costae, sulcus defined by costae with median costa, flank ribs arising later, typically two pairs, but up to five, size diminishing laterally.

**Description.** Transversely elliptical biconvex shells, about two-thirds as long as wide and two-thirds as deep as long. Ventral valve slightly more convex than dorsal; maximum

width at about three-fifths of shell length. Dorsal fold and ventral sulcus well developed, arising at about 3.5 mm and 4 mm from the respective umbones; fold with variable symmetry, typically about one-quarter as high as wide. Ventral valve with convex lateral profile, more deeply so posteriorly; posterior profile evenly convex; beak ridges curve and commonly fade laterally, to define concave palintropes two-thirds as wide as hinge and over one-third as wide as valve; ventral interarea curved, apsacline, about one-quarter as long as wide, only about one-sixth of valve width, and about one-third width of straight hinge, that continues laterally to about two-thirds of shell width before commissure develops rounded, obtuse-angled curve at cardinal angle. Dorsal valve convexity flattening in lateral profile; smooth convexity of posterior profile interrupted by fold. Dorsal interarea flatly curved anacline, about one-half as long as ventral area. Delthyrium and notothyrium open. Rib development of simple, rounded costae invariably with two on fold, and early single median rib in sulcus with defining pair; later ribs variable, those on flanks generally weak and low, with stature diminishing laterally, typically two or three pairs, rarely up to five pairs (Fig. 3l). Concentric ornament of fine growth lines and occasional well marked growth stages.

Ventral interior with spondylium extending anteriorly over one-quarter of valve length, twice as far as median septum; trace of septum on valve floor for up to 4.5 mm on valve surface. Extensive pitted areas of gonocoels postero-laterally; lateral to median septum pair of mantle canals (vascula media) initially flare outwards then continue anterolaterally in front of gonocoels before becoming lost on valve floor.

Dorsal interior with short inner hinge plates attached to shell floor for up to 3 mm on valve surface; united outer hinge plates and crura waisted in section, crura extending further anteriorly to front of spondylium (Figs 1, 2). Alate plates and carinae lacking. Postero-median narrow triangular diductor scar with low ridge extending forwards and fading between pair of well impressed subcircular adductor scars; other lightly impressed scars lateral to diductors and median to gonocoels may be posterior adductors. Shell substance fibrous, impunctate.

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