A new protorichthofenioid brachiopod (Productida) from the Upper Carboniferous of the Urals, Russia

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SYNOPSIS. A new genus from the mid Upper Carboniferous of the southern Urals, Russia, is described and interpreted as a surprising, aspinose early form of the Richthofenioidea. An undescribed *Proteguliferina*? from the Upper Carboniferous of northern Spain and two previously described Permian Russian species are possibly congeneric, but thereafter the stock probably died out. The new genus *Zalvera* contains the new species *Z. sibaica*, specimens from Spain and the two described Permian species.

INTRODUCTION

In 1982 Dr S. S. Lazarev, of the Palaeontological Insitute, Moscow, led an expedition to the southern Urals where brachiopods were collected and passed to me for comment and description. The brachiopods include seven taxa which can be assigned to productid families with little difficulty. However, most specimens belong to a distinctive species which initially was difficult to identify, even at phylum level. It now seems clear that these subconical, thin-shelled specimens also belong within the Productida, although they display bizarre characteristics.

Material

The material was all collected from a dense, finely-grained buff-coloured limestone within the Kordailovskaya Formation (probably equivalent to the Verejan Horizon in the Moscow area) dated as late Bashkirian to Lower Moscovian (mid Upper Carboniferous) and occurring at the Sibay stream, on the left bank of the Ural River, 6 km up-stream from Pokrovka, in the southern Urals, Russia. The fragments containing brachiopods amount to about 40 in total, several being multi-parts and counterparts of larger pieces that have been broken down to between 20 and 50mm in greatest dimension. Some pieces include more than one brachiopod specimen.

From the total of 40 fragments, about half contain the unusual subconical species. Of the rest:

1. Four contain a species reaching about 15mm in length, with fine spines, densely covering the ventral valve only, but with dorsal valve dimples, and having a low lateral profile. Superficially the species resembles *Stipulina* (Fig. 1).
2. Eleven contain a *Thomasella*-like species, but differ in the absence of rugae over the spinose body region and in having a relatively more strongly ribbed and flanged trail (Figs 2 and 3).
3. Two contain small (*ca.* 7mm wide) specimens more like *Thomasella* than the above in that they are distinctly rugose up to the start of the flange (Fig. 4a, b).

4. One part and counterpart contains a strongly rugose species (only *ca.* 9mm wide) resembling a small plicatiferid, but with a widely flanged and ribbed trail (Fig. 5).
5. There are two incomplete specimens of a rugose and less clearly ribbed (reticulate) species with spines near the umbo and on the ventral exterior which resembles *Pectenoproductus proprius* Likharev, a species reported from the Lower Permian of the Caucasus. Muir-Wood & Cooper (1960) were unsure as to whether this genus was a pectinid mollusc, but the presence of spines on these two specimens confirms their affinity with the Productidina (Fig. 7).
6. There is one incomplete ventral exterior, seen also in section, of a deep bodied, small, rounded species apparently lacking rugae or ribs, but with relatively stout spines, which somewhat resembles a Lower Carboniferous leiproductid, such as genus *Magnumbonella* Carter (Fig. 7).
7. Two specimens like the conical shells described below have variably developed radial ribs, starting within 5 mm of the apex and with a low profile. The cone apex seems to have some attachment spines and others are arranged widely on the cone. The species resembles *Planispina armata* (Girty) from the mid Carboniferous of the USA (Fig. 8).
8. There are, in addition, two pieces of a strongly ribbed rhynchonellid and a section through a probable reticulariacean.

These identifiable productids may prove to be new taxa. However, this paper deals only with the more common (ie. in the collection at hand) subconical species. Of these 25 fragments, 21 are of the subconical valve while four include separate parts of what is clearly a different valve and is interpreted as the second valve of the same species.
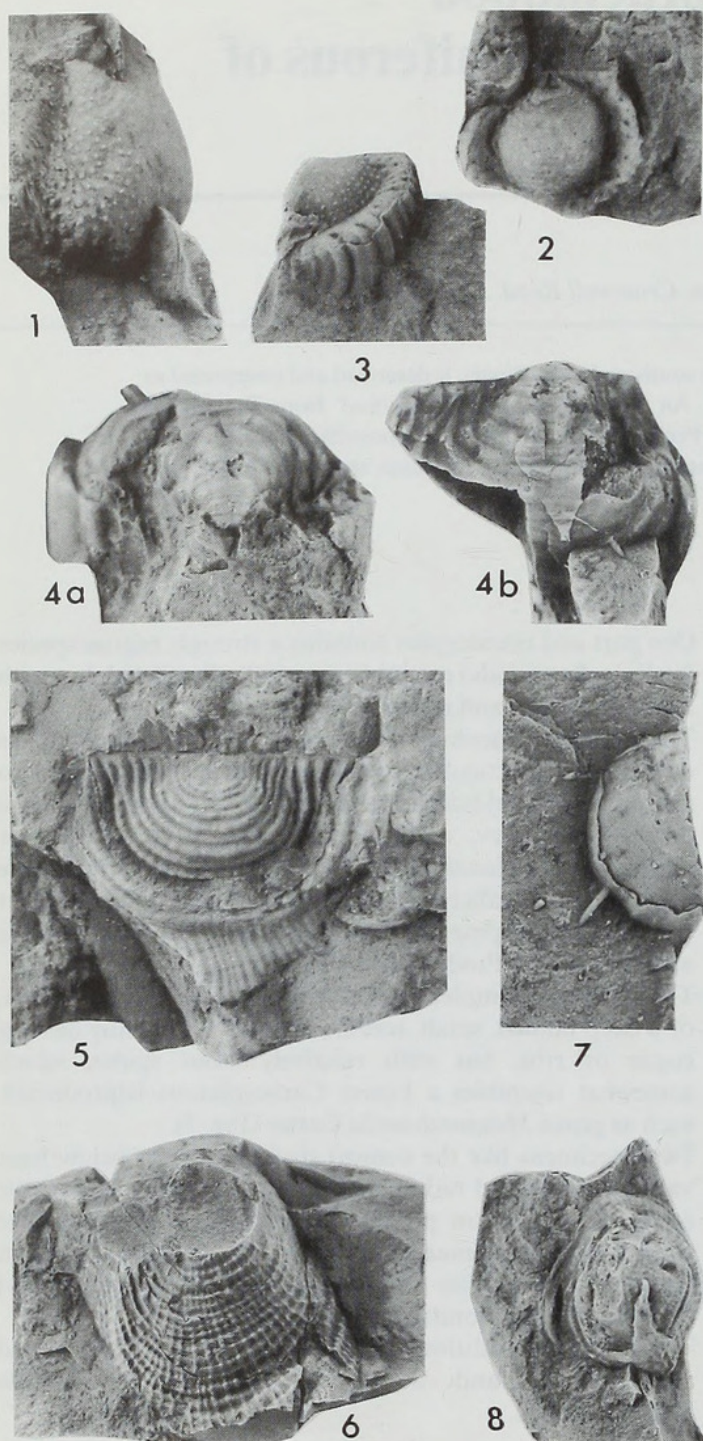
Fig. 1   *Stipulina*-like species, ventral valve exterior, BD9673, ×4.

Figs 2, 3   Two views of a non-rugose *Thomasella*-like species. **2**, exfoliated dorsal valve interior and the flanged and geniculated trail, BD9677. **3**, oblique view of a complete specimen viewed anterolaterally showing the strongly ribbed trail, BD9676b, ×3.

Fig. 4   Two views of cf. *Thomasella* showing the posterior rugae, flanged trail and ventral spines, BD9673(0), ×5.

Fig. 5   A Plicatiferinid showing the exfoliated dorsal valve interior, BD9674, ×4.

Fig. 6   *Pectenoproductus* ventral valve exterior, BD9675, ×2.

Fig. 7   The incomplete leioproductine ventral valve, BD9688(1), ×3.

Fig. 8   Cf. *Planispina* sp. viewed almost apically, BD9688(0), ×1.5.

METHODS

The shell material on most specimens is thin, somewhat laminar in appearance and takes the buff colour of the matrix. In order to establish the nature of this shell, slivers from two specimens were studied by qualitative energy dispersive x-ray microanalysis using scanning electron microscopy in the Department of Mineralogy, The Natural History Museum, London. The results show a strong dominance of calcium, with no magnesium or phosphorus present (Fig. 9). The mineralogy indicates dominance of calcium carbonate (lacking magnesium) and the lack of phosphate precludes the presence of apatite. The shell is not calcophosphatic so articulate brachiopods could have been the animals which secreted this shell material.

It seemed unlikely that more material would become available, so it was important to preserve what we had. For this reason only two specimens were sectioned in an attempt to determine what internal structures were present. However, some internal details could also be seen on broken surfaces which cut across specimens while the rock was being broken, as well as on naturally weathered surfaces cutting across the partial interiors of two specimens.

Careful examination of all specimens under a binocular microscope, commonly making drawings using a Wild drawing arm, gradually allowed the recognition of some consistent features on several specimens, which provided a form of orientation. The recognition of the same structures in different views and sections has allowed a general picture of the morphology of these specimens to be built up.

Portions of shell from near the apex and the distal regions of the cone, and from the supposed dorsal valve have been studied uncoated in the environmental chamber of an ISI ABT55 scanning electron microscope and coated using a S2500 Hitachi machine, both in The Natural History Museum.
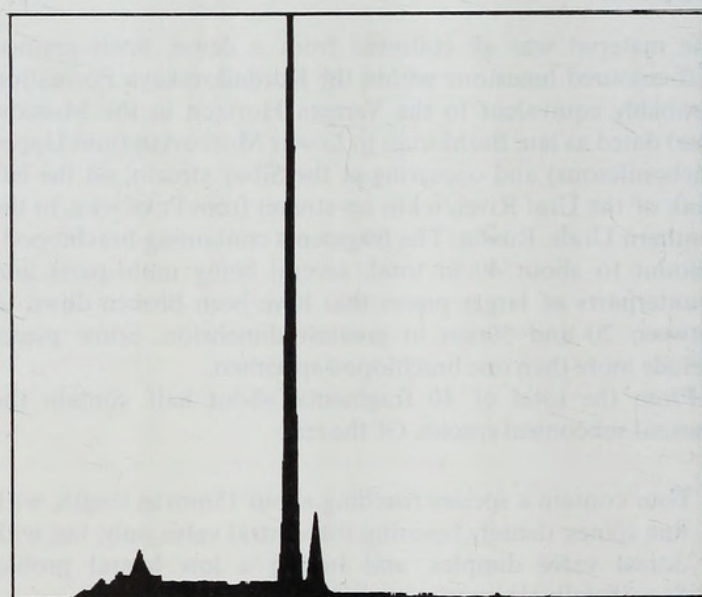

Fig. 9   Plot from qualitative energy dispersive X-Ray microanalysis of non-coated fragments using scanning electron microscopy. The plot displays a major calcium peak (plus a secondary peak to its right), but no phosphorus and only minor amounts of elements with lower atomic weights, to the left.

SYSTEMATIC DESCRIPTIONS

The material described here is housed in the BMNH collections of The Natural History Museum, London. Specimens are uniquely recognised by BD registration numbers.

Order **PRODUCTIDA** Waagen,1883
Suborder **STROPHALOSIIDINA** Schuchert, 1913

DIAGNOSIS. Productida retaining ventral interareas and, commonly, toothed articulation.

Superfamily **RICHTHOFENIOIDEA** Waagen, 1885

DIAGNOSIS. Ventral valve conical or sphenoidal, dorsal valve recessed below the ventral margins. Normally attached by cicatrix and/or spines.

Family **ZALVERIDAE** nov.

DIAGNOSIS. Richthofenioids lacking external body spines, with shallow body cavities and short subparallel ventral ridges associated with a near apical chamber involved in the articulation of the valves; marginal ventral valve protective structures absent.

COMMENTS. Currently only the one genus is known. The family differs from the Richthofeniidae most clearly in its lack of external spines and attachment to the substrate. Although *Collumatus* Cooper & Grant, 1969, lacks spines this Permian genus is attached to the substrate by concentric sheets of shell surrounding the base of the ventral valve.

Genus *ZALVERA* nov.

DIAGNOSIS. Zalveridae retaining small juvenile ventral valve at apex and with strong brachial impressions.

ETYMOLOGY. Anagram of the letters of the name Lazarev.

TYPE SPECIES. *Zalvera sibaica* sp. nov.

DISCUSSION. As well as the type species, the genus may usefully accommodate the specimens described by Tschernyschev (1902) as *Teguliferina(?) uralica* and by Likharev, (1932) as *Keyserlingina caucasica*. Unfortunately, little is known of the internal morphology of these species so this assignment is uncertain. Likharev (1931, 1932) specifically noted the absence of internal dorsal valves, wondering if they ever existed. Externally both these species seem to fit better here than in *Prorichthofenia*, which is a true teguliferinine with external spines. In addition, two specimens referred to as *Proteguliferina*? by Winkler Prins in Sanchez de Posada *et al*. (1993) belong in *Zalvera*. See further discussion under the species description.

Zalvera sibaica sp. nov.   Figs 10–24

TYPE SPECIMEN. Holotype, BD9653, from the Kordailovskaya Formation of late Bashkirian to early Moscovian, mid Upper Carboniferous age, 6km up-stream from Pokrovka, Ural River in the southern Urals, Russia (Figs 20a–c).
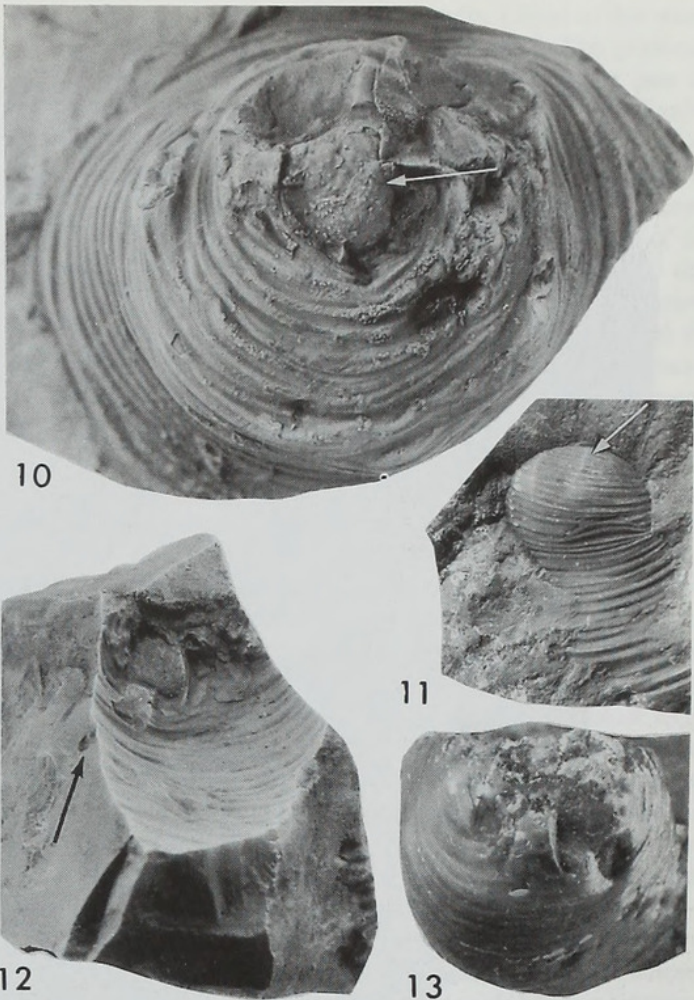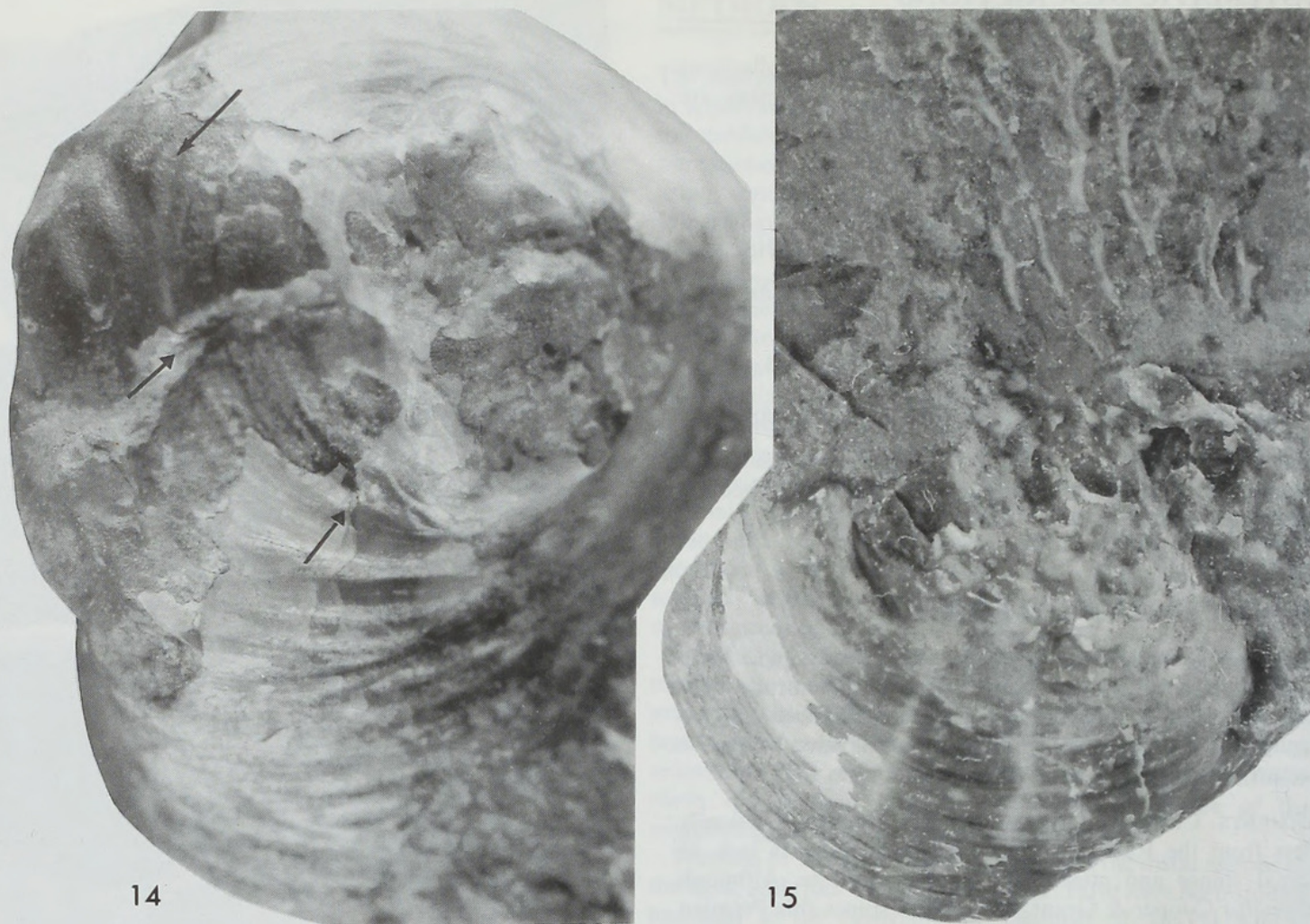

Figs 10–13 *Zalvera sibaica* gen. et sp. nov. from late Bashkirian to early Moscovian rocks in the southern Urals, Russia. **10**, apical view of a slightly crushed specimen including the small regular looking initial growth stages of the ventral valve (arrow). The umbo is to the left. BD9671, ×3. **11**, side view of a specimen showing the inferred subparallel ridges as white lines on the shell (arrow) and rounded apex. BD9669, ×1.5. **12**, part external mould of a specimen viewed towards the apex, in which parts of the subparallel ridges are visible. The rock surface to the left cuts a nodose outgrowth (arrow), BD9661a, ×2. **13**, apical view of a specimen associated with the external mould of figure 12 showing partially exposed subparallel ridges, BD9661b, ×2.

DIAGNOSIS. *Zalvera* with irregular rounded dorsal outline and apex profile, rugae relatively prominent.

ETYMOLOGY. Species named from the Sibay stream, where the specimens were found.

MATERIAL. All specimens of *Z. sibaica* are from the one locality in the southern Urals (BMNH BD9653 (the holotype), BD9654-9672). A few other fragments occur with specimens of other species.

DESCRIPTION. In one specimen (BD9671) the earliest growth stage of the subconical valve resembles a tiny (*ca.* 5mm diameter) productid valve (Fig. 10). This consists of a subtriangular, gently convex valve exterior, which appears to be covered by closely spaced, but fine spine bases. There is, therefore, a question as to the reliability of this small valve being part of the species. The specimen was cut medianly and appears to show continuous shell between the small spinose valve, its thick-shelled gutter-like surround and the remaining

Figs 14, 15 *Zalvera sibaica* gen. et sp. nov. from late Bashkirian to early Moscovian rocks in the southern Urals, Russia. 14, oblique apical view of a partially exfoliated specimen showing the fine internal tuberculation on the internal mould (arrow) and positions of the subparallel ridges (arrows), BD9664, ×7. 15, apical view of a specimen with a xenomorphic apex associated with a bryozoan and showing the subparallel ridge positions, BD9663, ×5.

thin-shelled cone. A small apical spinose valve was also noted by Tschernyschev (1902) in his original description of *Tegulifera(?) uralica*. The material has been checked recently by Dr Lazarev (personal communication) who confirmed its presence, so for now it is accepted as part of *Z. sibaica*. Most of the material consists of broken parts of a subconical to subcylindrical structure with a flattened, weakly rounded, 'base' (Fig. 11), extending directly from the initial tiny spinose valve. The cone expanded rapidly to about 15mm in diameter and then expanded gradually to as much as 25mm in diameter. The preserved length is variable, but no specimen exceeds 25mm; some are much more squat in shape. The exteriors are smooth apart from irregularly developed rugae (Fig. 11) and very rare non-hollow, nodose outgrowths on the subcylindrical area (Fig. 12). Growth lines are commonly visible. The shell material is thin except for restricted areas in which there are internal ridges or blunt, rounded endospines. A few specimens display two layers of thin shell in the rugose cone region, each separated by a narrow (less than 1mm) layer of sediment. The place from which the inner, younger, shell layer originated can be found rarely, but indicates that these lamellose layers were growth structures resulting from a mobile mantle epithelium.

On the weakly rounded 'bases', beyond the small initial spinose valve, the shell material appears to be finely pseudopunctate, with small tubercles on internal surfaces (Fig.

14). Breakage and shell exfoliation is common in this area, with the result that complete undamaged exteriors are rare. However, this does allow recognition of some structures from the outside. Most obvious is a pair of plates or ridges (Figs 11, 13), about 2 to 3mm apart distally, diverging slightly from within about 1mm to between 5 and 10mm from the apex, and extending to or beyond the growth stage at which the cone expansion slowed to give a more subcylindrical profile. The presence of drusy crystals between these plates indicates an original cavity in that region. Similar crystals are commonly present apically and externally to these plates in specimens from which the base of the subconical valve appears to have been broken. More complete specimens show signs of shell growth distortion over this basal area; in one example a fenestellid bryozoan is adpressed to the surface (Fig. 15).

The cutting of two relatively complete subconical valves failed to reveal a second valve within the cone, although one specimen has a platform-like 2.8mm extension into the 'internal' space originating about 5mm from the apex. This specimen was cut between the pair of subparallel plates, allowing reference to a position in the shell, and these plates are probably connected, thus forming a chamber. More information about interiors was obtained from broken sections through three specimens, one of which is additionally weathered and displays parts of a flat, thin structure lying near the base of the cone, which can be
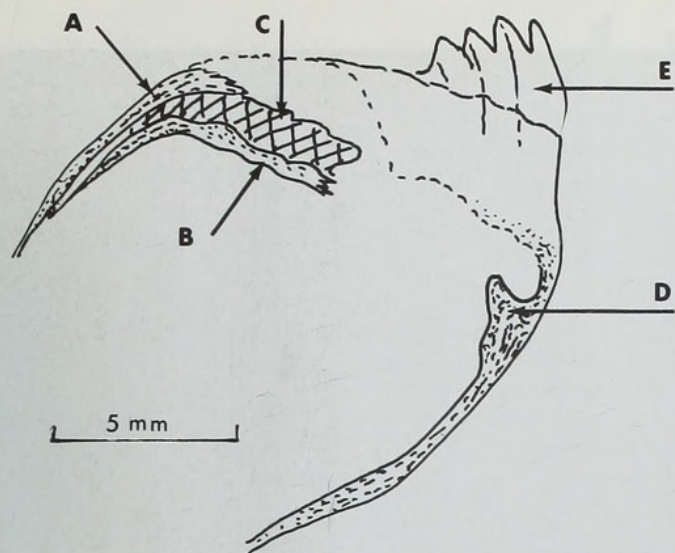
Fig. 16 Drawing of a natural section through a specimen with its apex uppermost and in which part of a dorsal valve is preserved (B). A = ventral valve; C = crystaline cavity infilling; D = part of the ventral valve internal articulatory structure; E = external mould of rugae near the apex. From specimen BD9663(2).

interpreted as a second valve (Fig. 16). The available specimens all display a consistent relationship between the conical valve and internal plate-like structures, indicating that the latter are remnants of a second valve in their positions of articulation, or the support structures for a second valve.

Four different-looking specimens in the collection are taken as being conspecific. These are fragments of nearly complete, oval-shaped valves, 12 to 15mm wide, and are interpreted as interior surfaces, one of which has a counterpart. Their size and general outline would allow them to have fitted into the more apical region of the conical valves. One edge, seemingly parallel to the maximum width, shows a slight median flattening and is taken as being posterior. The most obvious feature is a pair of weak, crescent-shaped ridges (Fig. 17a, b), which bound shallow depressions, follow close to the edges of the valve and originate from posteromedian positions on each side of a low broad median ridge. Surfaces on either side of the crescent-shaped ridges are finely endospinose (Fig. 18). Posteriorly, close to the straighter sector of the margin, is a pair of shallow pits, between which is the posterior end of the wide median ridge. Posteromedially, a transverse ridge is situated just anterior to the posterior flattened sector. This expands widely anterior to the median ridge, leaving a T-shaped pair of lateral protuberances, 2mm wide (Fig. 19). The lateral and anterior margins of these valves are of thin shell substance, which display growth lines, and seem to be reflexed away from the internal surface, resembling a valve trail.

SHELL STRUCTURE. Scanning electron microscopy of shell sections (Figs 22, 23) and fractured fragments (Fig. 24) show the shell to be composed of somewhat recrystallised laminae, probably originally made up of thin laths. Macroscopic examination revealed rather fine pseudopunctation, especially in the apical regions of the ventral and dorsal valves (Fig. 18), and thus confined mostly to the body region. The conical trail, beyond the body cavity, has fewer internal tubercles (Fig. 22) indicating a reduction in the pseudopunctation.

INTERPRETATION. The scant and poorly preserved characters available indicate a subconical valve, which is interpreted as

ventral, within which lies a dorsal valve close to the apex of the shell, resulting in a very shallow body cavity. Distal to this was a relatively long subcylindrical skirt of thin shell. The posterior transvere ridge in the dorsal valve articulated with a pair of grooves associated with the subparallel plates in the ventral valve (Fig. 21). Additionally, the dorsal valve bent dorsally around its lateral and anterior margins forming a short trail against the longer internal surface of the ventral valve (Figs 19, 21). There is no direct evidence for the dorsal trail being as long as that of the ventral valve, but it is possible that there was an extremely thin layer of dorsal shell supporting the mantle in this trail region. On the other hand, a long dorsal trail might have hindered the opening of the shell, performed by contraction of diductor muscles attached to the poorly differentiated cardinal process situated between the ventral articulatory ridges. A short dorsal trail would have left the internal mantle epithelium of the ventral valve open to the sea and vulnerable. Cowan (1970) suggested similar exposed epithelia in lyttonioids, and similarly exposed epithelia occurs in other Productida, including teguliferinids. However, the evidence for this in the present material is insufficient to allow further discussion.

The internal morphology of the few dorsal valves available indicates a standard anatomy in which the lophophore was probably a schizolophe, strung from brachial ridges close to the edges of the body cavity (Fig. 17). Dorsal adductor muscles were attached posteromedianly, anterior to the articulation ridge and between the median ridge and posterior ends of the brachial ridges. Diductor muscles were probably attached at a small posteromedian boss, which hardly deserves the term cardinal process.

Externally, the ventral apical region is somewhat distorted on some specimens, which might indicate that initial growth closely followed the substrate. However, the apparent lack of external body spines, which might have been used to fix specimens, and the variable nature of this 'basal' deformation seems to indicate that specimens were not cemented or closely adpressed to a hard substrate, but occurred on, or partially buried in, a relatively soft substrate. Unfortunately, field observations are lacking on both the orientation of specimens in the rock and on the nature of adjacent lithologies. Drusy fillings in body cavity regions could have developed whichever way up the specimens were entombed in the sediment, provided both valves were preserved and the shell was closed. However, the rare specimens showing these features invariably have drusy crystals within the body cavity, not dorsal to the dorsal valve, indicative of an apex down position in life. The rock appears not to include potential hard substrates, other than the fossils themselves, although algae could have caused surfaces to become firm.

Although probably not fixed to a hard substrate, these specimens appear to have resembled richthofenioids lacking adult spines, and lived in areas of soft, fine sediment. If they sat, rather cup-like, with their bases buried in sediment, the ventral trails would have raised the inhalent areas well above the sediment surface. To have achieved this position with only a thin-shelled ventral valve and no anchoring structures indicates that the environment was probably one of quiet water and fine-grained sedimentation.

DISCUSSION. Specimens somewhat resembling this material were described by Tschernyschev (1902) from Lower Permian, Asselian, rocks on the river Yuresan, also in the Urals, Russia, as *Tegulifera (?) uralica*. One specimen figured by Tschernyschev (1902, fig. 85, pl. 60, fig. 14) has a small triangular, regular-looking productid valve at its apex like that on *Z. sibaica*
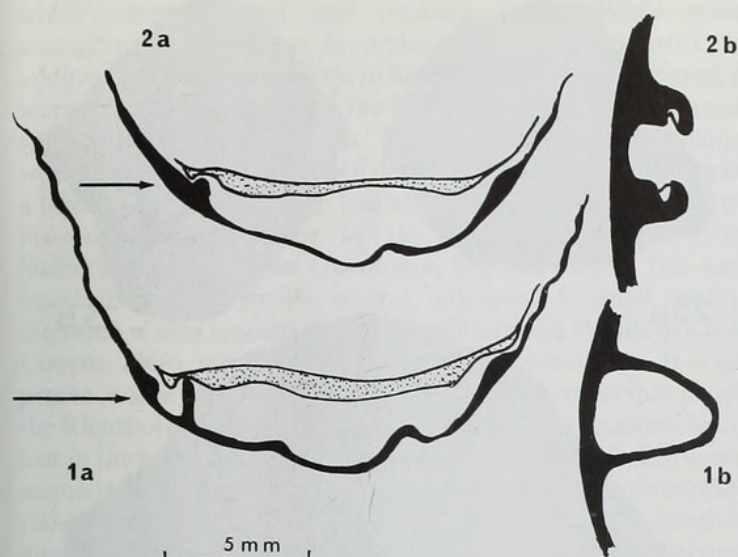
17a

17b

18

19

20a

20b

20c
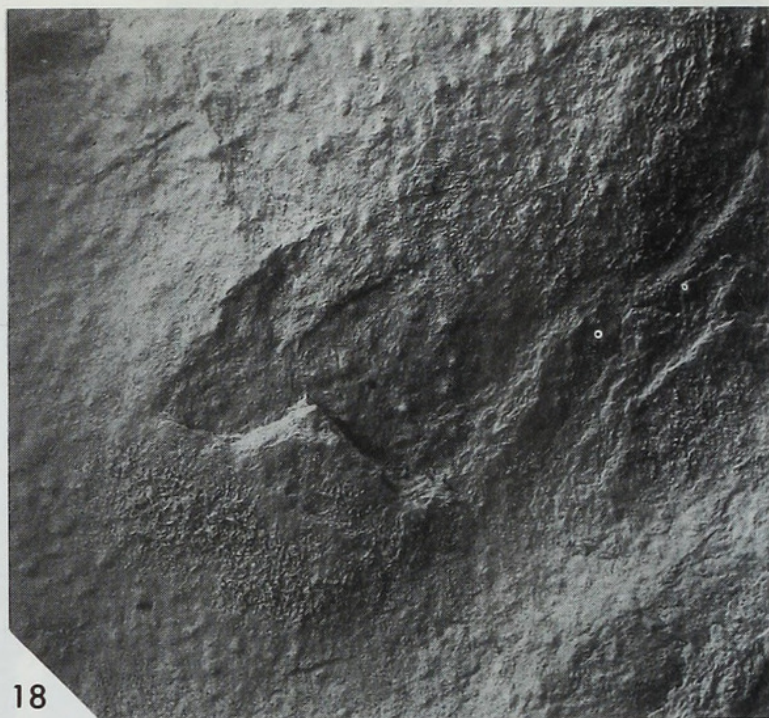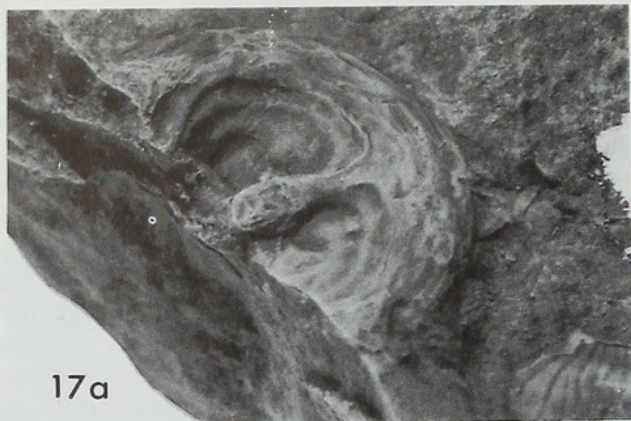
Fig. 21 Reconstruction of the apical area of *Zalvera* in median longitudinal section (1a), between the subparallel ridges, and an apical view of the ventral valve at the arrow position (1b). In 2a the section cuts one of the subparallel ridges in which the articulatory groove is situated (2b). Ventral valve black; dorsal valve stippled.

(BD9671) (Fig. 10). Also, the species seem to be of comparable size and both have similar concentric ornamentation. Dr Lazarev has inspected the Tschernyschev specimen and confirms the similarity.

Another similar-looking species was first described by Likharev in 1931 as *Teguliferina? (Chaoella) caucasica* and again in 1932 as *Keserlingina caucasica*. It came from Permian rocks in the Caucasus, originally described as P_{1b}, but now thought to be of Kazanian, early Upper Permian age. Likharev also recorded related specimens from the Sim river in the southern Urals. Likharev (1932) gives a measure of 9mm for the maximum width, so his specimens are about half the size of the new material. Otherwise the illustrations closely resemble the Carboniferous specimens and one figure (1932, pl. 2, fig. 9b) seems to show similar subparallel marks near the apex. In describing *caucasica* Likharev briefly referred to *uralica*, but other than discussing the apparent small ventral valve at the apex he wrote little to differentiate between the two species.

Thus, somewhat similar specimens to *Z. sibaica* occurred in the Urals at Bashkirian to Moscovian boundary times and again in the Permian. Neither Tschernyschev's *T. uralica* nor Likharev's *K. caucasica* belong in *Teguliferina* or *Keyserlingina*, the latter belonging with the Lyttonioidea on account of its lobate interiors. *Teguliferina* and *Proteguliferina* belong in the Richthofenioidea and are thus more closely related to the new material than is *Keyserlingina*. For instance, *Proteguliferina* displays a weakly concave dorsal valve within a gently convex ventral valve which does not reach the internal margins of the spinose ventral valve. Its ventral marginal epithelium may, therefore, have been exposed.

Girty (1908) described two species, *Tegulifera armata* and *T. kansasensis*, from rocks of late Missourian (mid Kasimovian)

age, from localities in Illinois and Kansas respectively. These species differ in important characters from the new Urals specimens described here. The American specimens are less deeply conical, less rugose, are radially ornamented, and are attached by cementation and external spines, as well as having internal ventral spines. These species were placed by Muir-Wood & Cooper (1960) into *Planispina* Stehli, a genus assigned to the Teguliferininae. The radial ribbing and possible spinose exteriors of two specimens in the Urals collection (Fig. 8) resemble *P. armata* (Girty, 1908, pl. 20, fig. 10).

Sutherland (1989) reported another species, well preserved as silicified specimens, from early Upper Carboniferous (Morrowan [= Bashkirian]) rocks in Oklahoma, USA. This material as yet remains un-named, but is probably closely related to *Teguliferina*, with somewhat similar dorsal valve interiors and similar external rhizoid fixing spines. These Morrowan specimens, therefore, appear to be the earliest known true teguliferinids, and are the earliest known Richthofenioidea.

The material from the Urals is of similar age to that described by Sutherland (1989) but is very different in character, resembling more closely the specimens described by Tschernyschev (1902) and Likharev (1931). The brachiopod relationship of the new Urals material is no longer in doubt and the general form of the shell is highly indicative of a richthofenioid relationship. However, other than in the Permian genus *Collumatus* Cooper & Grant, 1969, from Texas, the richthofenioids have external spines to aid the fixing of specimens to hard substrates, commonly within reef environments, while *Z. sibaica* has no such spines. Apart from this difference, the general architecture of the shell fits with that of richthofenioids; a conical ventral valve with a dorsal valve recessed below its margins, the two valves articulating, not by true ventral teeth and dorsal sockets, but by dorsal protuberances fitting into ventral cavities. In detail the Urals specimens differ from the general richthofenioid pattern: they lack external spines, other than perhaps at the earliest stages in ontogeny when ventral valves show signs of fine spines for about 5mm of growth; the body cavity is shallow, with the dorsal valve deeply recessed below the ventral margin; the dorsal valve has internal structures producing relatively thick shelly ridges, the brachial impressions and wide median ridge; the dorsal valve has short, geniculated, thin-shelled margins extending a short distance up the ventral valve interior; the ventral valve interior has a simple posteromedian structure of subparallel plates acting as supports for the dorsal valve; the ventral valve cone interior has sparcely distributed blunt, well rounded, endospines protruding into the space above the dorsal valve exterior; there is no indication of any complete protection for the opening to the subconical valve margins, as in most true richthofenioids.

In a biostratigraphical description of regions in Cantabria, northern Spain, Sanchez de Posada *et al.* (1993) listed '*Proteguliferina*? n. sp.' from 'Kasimovian' rocks. Dr C. F. Winkler Prins has kindly lent me the two specimens from which this reference was made, which he now dates as Moscovian, possibly Podolsky age. They do appear to be congeneric with the new Urals specimens. Specimens (also seen) determined by


Figs 17–20 *Zalvera sibaica* gen. et sp. nov. from late Bashkirian to early Moscovian rocks in the southern Urals, Russia. **17**, part and counterpart of an incomplete dorsal valve showing probable brachial impressions and the median ridge. The valve margins curve away into the rock in 17a, BD9659, ×4. **18**, scanning electron micrograph showing the finely endospinose surface within the dorsal valve brachial impression, BD9659a, ×60. **19**, a rather elongate, deformed and partly exfoliated dorsal valve interior; posterior is to the top, showing the transverse ridge (exfoliated and arrowed), interpreted as the dorsal articulation structure, and one brachial ridge, on the right, BD9670, ×10. **20**, holotype viewed apically and 'anteriorly' (×1.5) and obliquely apically (×5) showing the positions of the subparallel ridges 'posteriorly'. BD9653.
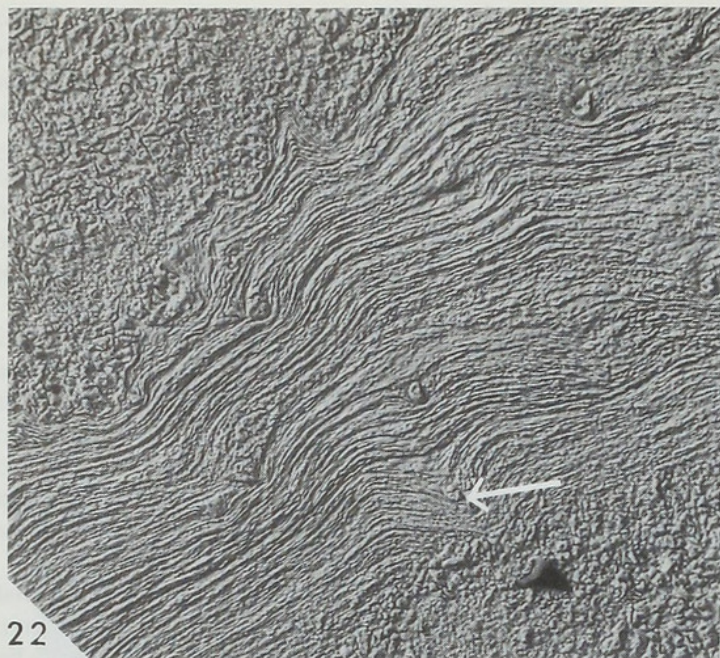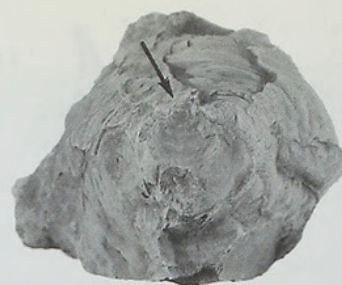
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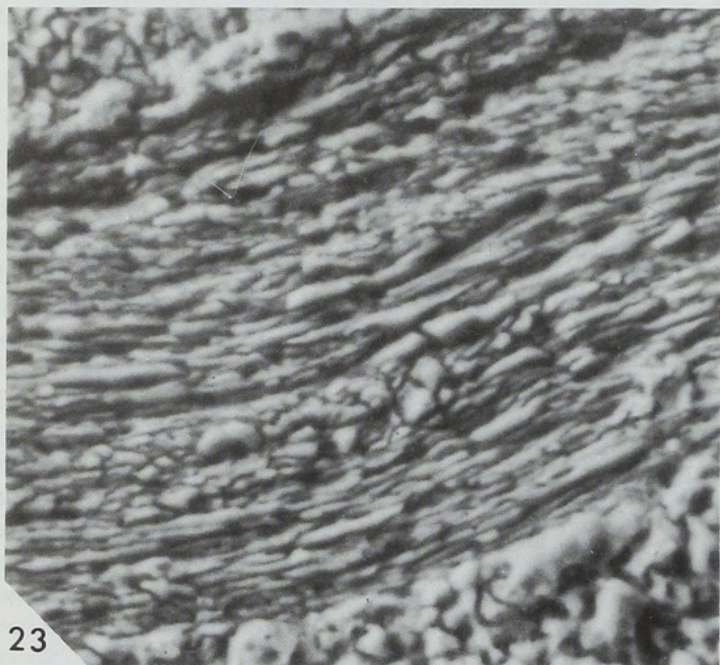
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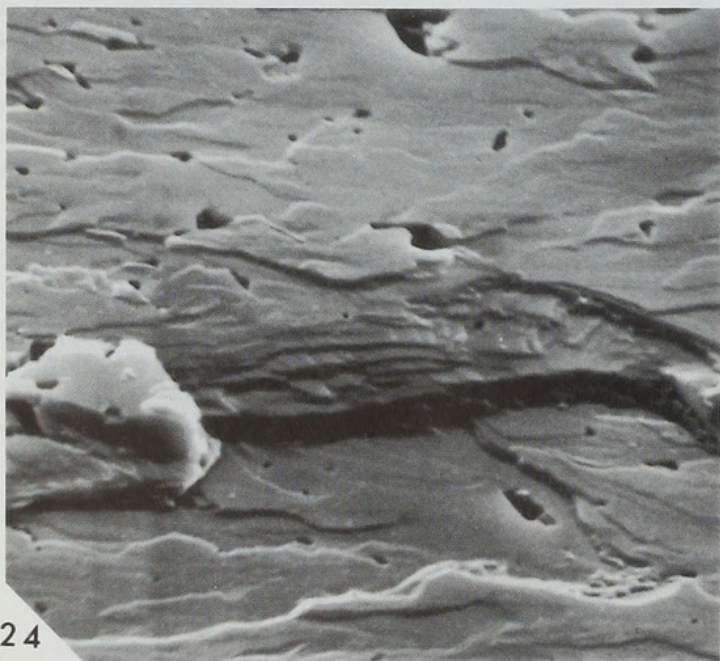
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25a   25b

25c

Fig. 25 *Zalvera* sp. from early Upper Moscovian rocks north of Bran-
cosera, Palencia, Spain. **25a,b,** apical and lateral views of the speci-
men (×1) showing an 'umbonal' region (arrowed). **25c,** an
enlargement (×3) of 25b showing pseudopunctate shell (arrowed)
and the layered nature of the valve, each with thin sediment between.
National Museum of Natural History, Leiden, WAG 77.

Winkler Prins (personal communication, September 1993) as
Proteguliferina sp. from Austria are not *Zalvera*, but are more
like an early form of the Permian teguliferinid *Acritosia*.

The two Moscovian specimens from northern Spain resemble
Z. sibaica closely, but appear to differ in having well flattened
apices, suggesting closer attachment to the substrate than seen in
the specimens from the Urals. Both specimens show signs of the
subparallel   internal   ridges,   the   apical   internal
microtuberculation and both have comparable external irregular
rugae. These similarities between the Spanish and Russian
specimens reinforce the concept of widespread marine faunas in
Eurasia during Upper Carboniferous times.

Present   evidence,   therefore,   indicates   two   almost
contemporaneous stocks in the early to mid Upper
Carboniferous, one in North America which evolved into the
Richthofeniidae, the other in Russia which, although considered
as belonging in the Richthofenioidea, was an early
'experimental' stock which lost its spines early in ontogeny and
lived on relatively soft substrates, unlike the American forms

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Figs 22–24 *Zalvera sibaica* gen. et sp. nov. from late Bashkirian to
early Moscovian rocks in the southern Urals, Russia. **22,** a cut and
lightly etched section through a ventral valve just distal to the inter-
nal thickening against which the dorsal valve rested. Apex to the top
right, exterior to the left. Irregularities in the laminae are oblique sec-
tions through pseudopunctae, apparently with taleolae (arrows),
BD9669a, ×160. **23,** same section, closer to the apex, ×1200. **24,** a
fracture flake of shell from a thickened area of a dorsal valve. Signs
of original laths can be seen centrally, BD9670, ×5000.

which were attached and retained spines. While some stratigraphically younger examples of this aspinose stock, in addition to those from northern Spain, may yet be discovered, it seems it did not persist after the Kazanian, when the Caucasian species of Likharev died out. The Permian genus *Collumatus* would appear not to have been derived from this stock, but to be a true richthofenioid which had also lost its spines. A feature of taxonomical importance in the specimens described by Sutherland (1989) from Oklahoma, but not seen in this new material, is the juvenile ventral interarea. A small ventral interarea is also reported in the Teguliferininae (Muir-Wood & Cooper, 1960), which belongs in the Richthofenioidea. It is the presence of interareas in these Carboniferous species that places the Richthofenoidea in the Strophalosiidina, the structure being lost in the more common Permian richthofenioids. In *Zalvera* it seems the earliest growth of the ventral valve was normal for productids, but whether it involved the growth of a juvenile interarea is unknown. If present it might have become incorporated into the later subconical valve growth. In any event, once growth changed, after the initial 4–5mm, from being a small finely spinose subtriangular valve to a rapidly expanding rounded cone with a spineless exterior, shell growth was holoperipheral. In the North American species there was a short period when the ventral interarea grew before the posterolateral mantle margins grew posteromedianly to continue the style of shell secretion seen for the rest of the valve. This left the juvenile interarea preserved, but with a short suture line posteromedianly where the two mantle margins had grown together and fused, allowing the typical teguliferinid cone to grow. In the Urals material this posterior fusion of the mantles occurred earlier in growth so that no interarea has been preserved. This raises the question as to whether *Zalvera* should be assigned to the Strophalosiidina. The alternative is to consider *Zalvera* within the Productidina as a unique aberrant offshoot showing tendencies towards the morphology of the Richthofenioidea. This seems less likely than placing *Zalvera* in the Richthofenioidea and accepting that the interarea never developed in these unusually-shaped brachiopods. It is hoped that more of this material will become available so as to allow more complete preparation and a better insight into the way in which this strange brachiopod grew.

There is no clear evidence for the origin of the Zalveridae, but it is possible to suggest that the ancestral stock was within the Strophalosiidina. The cone development seems to have been from exaggerated, and posteriorly fused, growth of the ventral trail. Within strophalosiidines the Aulostegoidea includes many groups with elaborate trails, and as they lack a toothed articulation and have variably developed interareas, they provide possible ancestors for *Zalvera*.

REFERENCES

Cooper, G. A. & Grant, R. E. 1969. New Permian brachiopods from Texas. *Smithsonian Contributions to Paleobiology*, 1: 1–20

Cowen, R. 1970. Analogies between the Recent bivalve *Tridacna and the fossil brachiopods* Lyttoniacea and Richthofeniacea. *Palaeogeography, Palaeoclimatology and Palaeoecology*, 8: 329–344.

Girty, G. H. 1908. On some new and old species of Carboniferous fossils. *Proceedings of the United States National Museum*, Washington, 34: 281–303, pls 14–21.

Likharev, B. K. 1931. Uber eine problematische Brachiopode aus den unterpermischen Ablagerungen des Nordlichen Kaukasus. *Annuaire des Société Paleontologique de Russie*, Leningrad, 9: 157–161, figs 1–5.

——— 1932. Fauna of the Permian deposits of northern Caucasus, 2 Brachiopoda, Lyttonidae. *Trudy Vsesoyuznogo geologo-razvedchnogo ob'edineniya NKTP [Transactions of the Geological Prospecting Service of USSR]*, Leningrad & Moscow, 215: 55–84 (in Russian), 85–111 (in English), 5pls.

Muir-Wood, H. M. & Cooper, G. A. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Memoirs of the Geological Society of America*, New York, 81: 447pp, 135 pls.

Sanchez de Posada, L. C., Martinez Chacon, M. L., Mendez, C. A., Menendez Alvarez, J. R., Truyols, J. & Villa, E. 1993. El Carbonifero de las regiones de Picos de Europa y Mantuo del Ponga (zona Cantabrica, N de Espana): Fauna y biostratigrafia. *Revista Espanola de Paleontologia*, No. Extraordinario: 87–108.

Schuchert, C. 1913. *Class 2. Brachiopoda, in* Zittel, K. A., *Text book of Palaeontology*, 1: 355–420. London.

Sutherland, P. K. 1989. Possible ancestor to the late Carboniferous/early Permian Teguliferiniid brachiopods in the Middle Carboniferous of Oklahoma, USA. *XIe Congres International de stratigraphie et de géologie du Carbonifère, Beijing 1987, Compte Rendu*, 2: 355–360, pl.1.

Tschernyschev, T. 1902. Die obercarbonischen Brachiopoden des Ural und des Timan. *Memoires du Comite géologique*, St Petersburg, 16 (2): 749pp, 63 pls (in Russian & German).

Waagen, W. H. 1882–1885. Salt Range Fossils, Pt. 4 (2), Brachiopoda. *Palaeontologia Indica, Memoirs of the Geological Survey of India*. Calcutta.