



ADAPTATIONS TO HARD SUBSTRATES IN PENNSYLVANIAN PRODUCTIDES (BRACHIOPODA) FROM THE CANTABRIAN MOUNTAINS (NORTH-WEST SPAIN)

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Abstract: The Pennsylvanian deposits with carbonate platforms and reef structures from the Cantabrian Mountains are briefly described. The main portion of this paper is dedicated to the discussion of the adaptations of the Productidina from these Pennsylvanian formations of the Cantabrian Mountains to their life on hard substrates, comparing them with similar forms found elsewhere, notably in the Mississippian of north-

west Europe and the Permian of Texas. In the systematic part, an indeterminate Plicatiferini is described as well as a new genus, *Bruntonoconcha*, and the new species *Limbifera bruntoni*, *Parmephrix candemuelensis* and *Bruntonoconcha celadensis*.

Key words: Productides, Brachiopoda, reef, Pennsylvanian, Cantabrian Mountains, Spain.

THE revision of the brachiopod faunas from the Valdeteja Formation by the present authors (Martínez Chacón and Winkler Prins 2007, 2008, 2009; Winkler Prins 2007) and the analysis of the brachiopods from the lower part of the Cuera Limestones (Martínez Chacón and Bahamonde 2008) made it clear that these Early Pennsylvanian faunas filled the gap between the Mississippian reef faunas from north-western Europe (Wolfenden 1958; Mundy and Brunton 1985; Brunton and Mundy 1988, 1993) and those of the Permian from North America (Cooper and Grant 1969, 1972–1977). This paper highlights the special adaptations of the Pennsylvanian Productidina from the Cantabrian Mountains, not just those from the Valdeteja Formation, with regard to life in a reef environment, especially on hard substrates. It should, however, be noted that the upper Pennsylvanian brachiopod faunas of the Cantabrian Mountains have so far only been listed and partly figured (e.g. Martínez Chacón and Winkler Prins 1985a; Wagner and Winkler Prins 1979, table 3, 1985, table 5; Wagner *et al.* 2002, fig. 9; Sánchez de Posada *et al.* 1993, 2002) and not been revised, apart from those of the upper part of the Cuera Limestones (Martínez Chacón 1990, 1991).

In recent years, a large number of publications dealing with ancient reefs have been published. Particularly interesting is the book ‘Phanerozoic reef patterns’, edited by Kiessling *et al.* (2002), which summarizes the knowledge of Early Cambrian to Late Neogene reefs. We use here

‘reefs’ in the broad sense of Flügel and Kiessling (2002, p. 3): ‘laterally confined biogenic structures, developed by the growth or activity of sessile benthic organisms and exhibiting topographic relief and (inferred) rigidity.’

During the Palaeozoic, reef building reached a peak in the Silurian–Middle Devonian, diminished in the Famennian – Early Tournaisian, increased again with a new peak in the Late Viséan, after which it fell again during the Serpukhovian and Bashkirian, reaching a new acme in the Permian (Kiessling *et al.* 2002).

Pennsylvanian reefs are mainly constructed by calcareous algae, sponges, bryozoans and calcimicrobes. The Cantabrian Mountains provide an exceptional example of platform-to-basin carbonate facies and reef mound development (Webb 2002; Wahlman 2002).

It is not considered opportune to give here an introduction to the geology and general Carboniferous stratigraphy of the Cantabrian Mountains, as we have done before (e.g. Winkler Prins 2007). The reader is referred instead to papers such as Sánchez de la Torre *et al.* (1983), Pérez-Estaún *et al.* (1988, 1994), Aller *et al.* (2002), Sánchez de Posada *et al.* (2002) and Keller *et al.* (2006). Syn-sedimentary tectonics and delta shifting (see van de Graaff 1971) make the Pennsylvanian succession a highly complicated one, which is not yet fully understood. Basically, the basins are filled with shallowing upward cycles, ideally from turbidites through shallow marine and paralic deposits to coals and conglomerates (Wagner and Winkler Prins

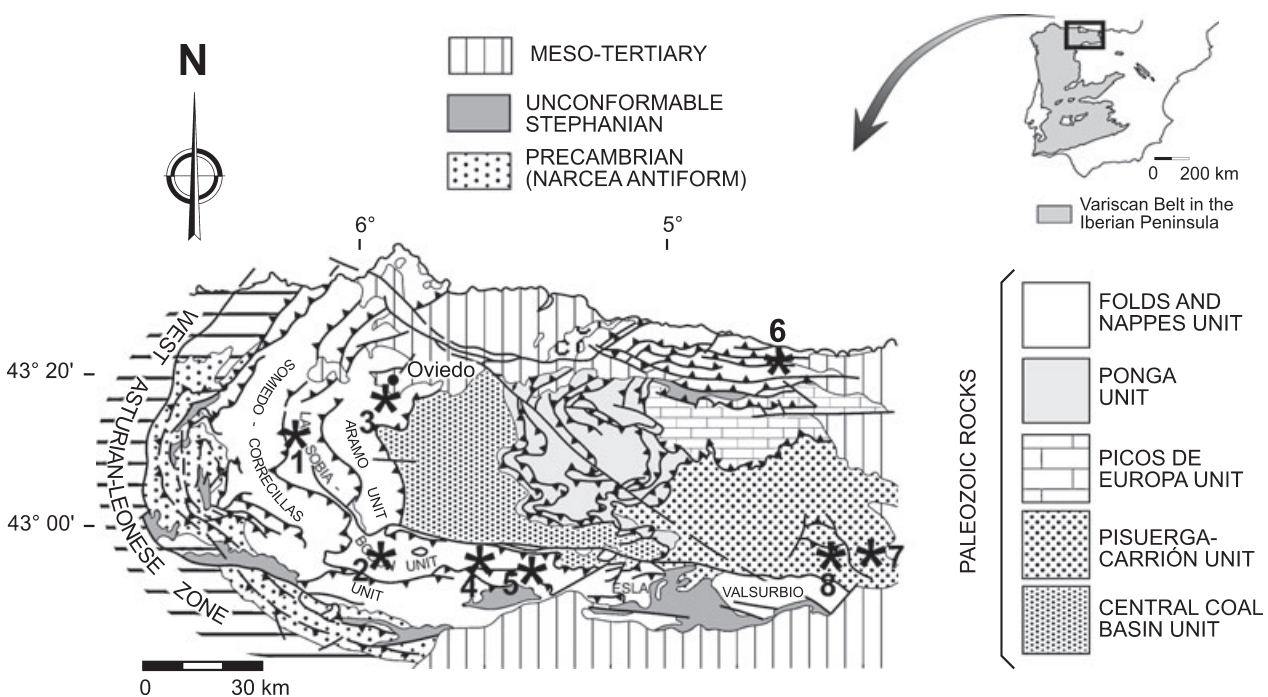
2002). A map with the major tectonic elements is used to show the localities mentioned in the text (Text-fig. 1); the formations with brachiopod faunas of reef affinity are considered below and placed in the Pennsylvanian chronostratigraphic scheme in Text-figure 2. The distribution in the different formations of the species mentioned in this paper can be seen on Table 1. Some species of Strophalosiida (*Hontorialosia uniplicata* Martínez Chacón, 1979, *Ovetina truyolsi* Martínez Chacón and Winkler Prins, 2009, *Plicatiferina sinecosta* (Martínez Chacón, 1979) and *Miropoductus posadai* Martínez Chacón and Winkler Prins, 2009) are illustrated in Text-figures 3 and 4. Moreover, at the end of the paper, a new genus, three new species and an indeterminate Plicatiferini are described and illustrated in Text-figures 5 to 8.

PENNSYLVANIAN CARBONATE PLATFORMS AND REEFS FROM THE CANTABRIAN MOUNTAINS

Valdeteja Formation

In the major part of the Cantabrian Mountains, the Asturian–Leonese Domain, a carbonate platform, was developed in Early Pennsylvanian times, which gradually withdrew to the north-east, to the present-day Picos de Europa.

Initially, a c. 250-m-thick succession of dark grey micritic, laminated, poorly fossiliferous limestones of the Barcaliente Formation (see Wagner *et al.* 1971) was deposited in an euxinic basin, starting in the Serpukhovian and ending in the Early Bashkirian (as dated by conodonts; Sanz-López *et al.* 2006; Nemyrovska *et al.* 2008) with collapse breccias (see Winkler Prins 1971, pl. 1, fig. 2) and calcite pseudomorphs of quartz and gypsum crystals, suggesting a hypersaline, intertidal environment (González Lastra 1978). It is followed by a thick succession of light grey biosparitic limestones deposited on a shallow, subsiding carbonate platform, the Valdeteja Formation (originally described as the Valdeteja Biosparite Member of the Escapa Formation, see Winkler Prins 1968, p. 49), which locally contains rich faunas dominated by brachiopods (e.g. Winkler Prins 1971; Martínez Chacón and Winkler Prins 2007, 2009). The Valdeteja Formation is highly variable in thickness (up to 700 m) and may reach the basal Moscovian (Villa *et al.* 2001). As mentioned in the Introduction, the revision of the rich brachiopod faunas triggered our interest in reef-related brachiopods. New forms from the Valdeteja Formation at Latores (Text-fig. 1) described in this paper are *Limbifera bruntoni* and Plicatiferini gen. et sp. indet. Other interesting forms recently described are an aulostegoid, *Ovetina truyolsi* Martínez Chacón and Winkler Prins, 2009, and an Early richthofenioid, *Miropoductus posadai* Martínez Chacón and Winkler Prins, 2009.



TEXT-FIG. 1. Structural map of the Cantabrian Zone (after Pérez-Estaún *et al.* 1988) with the relevant fossil localities indicated. 1: Teverga area; 2: San Emiliano area; 3: Latores; 4: Cármenes; 5: Valdeteja; 6: Sierra del Cuera; 7: Celada de Robledo; 8: San Salvador de Cantamuda.

TEXT-FIG. 2. Stratigraphical sketch of the Carboniferous formations of the Cantabrian Mountains mentioned in this paper. Numbers refer to the localities of Text-figure 1.

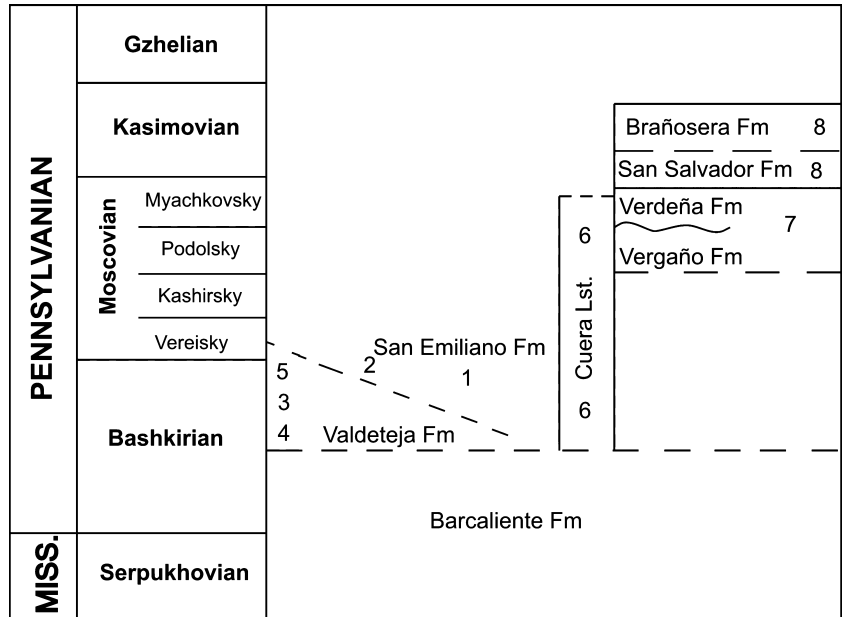


TABLE 1. Distribution of the species mentioned in this paper in the different formations.

Productidina	A	B	C	D	E	F
<i>Alitaria frechi</i> (Paeckelmann, 1931)	X					
<i>Rugivestis</i> sp.	X					
<i>Plicatiferini</i> gen. et sp. indet.	X					
<i>Limbifera bruntoni</i> sp. nov.	X	X				
<i>Productus concinnus</i> Sowerby, 1821	X					
<i>Admoskovia</i> cf. <i>aljutovensis</i> Lazarev, 2000	X	X				
<i>Kutorginella</i> cf. <i>stepanovi</i> (Lapina, 1957)	X	X				
<i>Fluctuaria undata</i> (Defrance, 1826)	X					
<i>Institiferini</i> gen. et sp. indet.		X				
<i>Hontorialosia uniplicata</i> Martínez Chacón, 1979		X				
<i>Parmephrix candemuelensis</i> sp. nov.			X			
<i>Plicatiferina sinecosta</i> (Martínez Chacón, 1979)	X	X	X			
<i>Rugicostella?</i> sp.		X				
<i>Ovetina truyolsi</i> Martínez Chacón and Winkler Prins, 2009	X					
<i>Bruntonoconcha celadensis</i> sp. nov.				X	X	
<i>Mioproductus posadai</i> Martínez Chacón and Winkler Prins, 2009	X					
<i>Zalvera</i> sp.				X		
<i>Eolyttonia</i> sp.						X

A, Valdeteja Fm.; B, Cuera Lst.; C, San Emiliano Fm.; D, Vergaño Fm.; E, Verdeña Fm.; F, Brañosera Fm.

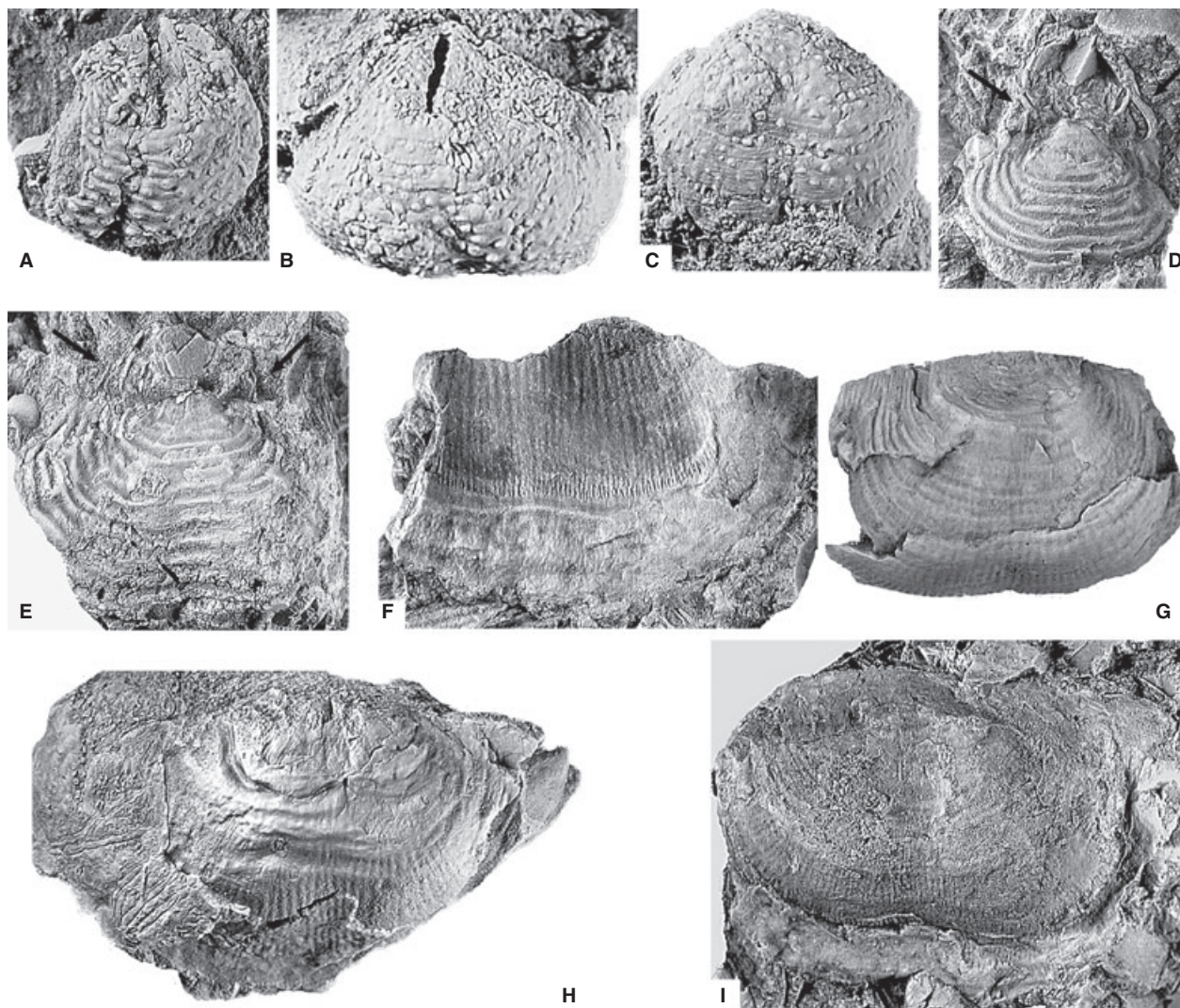
San Emiliano Formation

A basin gradually replaced the carbonate platform of the Valdeteja Formation, and in the west, a thick succession (c. 1800 m) of siliciclastics with occasional limestones, the San Emiliano Formation of Brouwer and van Ginkel (1964), was deposited during the Late Bashkirian and Early Moscovian (Carralreira *et al.* 1985; van Ginkel and Villa 1996). The limestones occur in its middle (La Majúa) member and are dominated by algal mounds, but locally a carbonate platform with a rich brachiopod fauna was developed (wackestone facies of Bowman 1985, fig.

16). The brachiopod faunas from the Teverga and San Emiliano areas (Text-fig. 1; for locality details see Winkler Prins 1968 and Martínez Chacón 1979) were summarized by Martínez Chacón and Winkler Prins (1985b). An unnamed species assigned to *Heteralosia* is here re-described as *Parmephrix candemuelensis* sp. nov.

Cuera Limestones

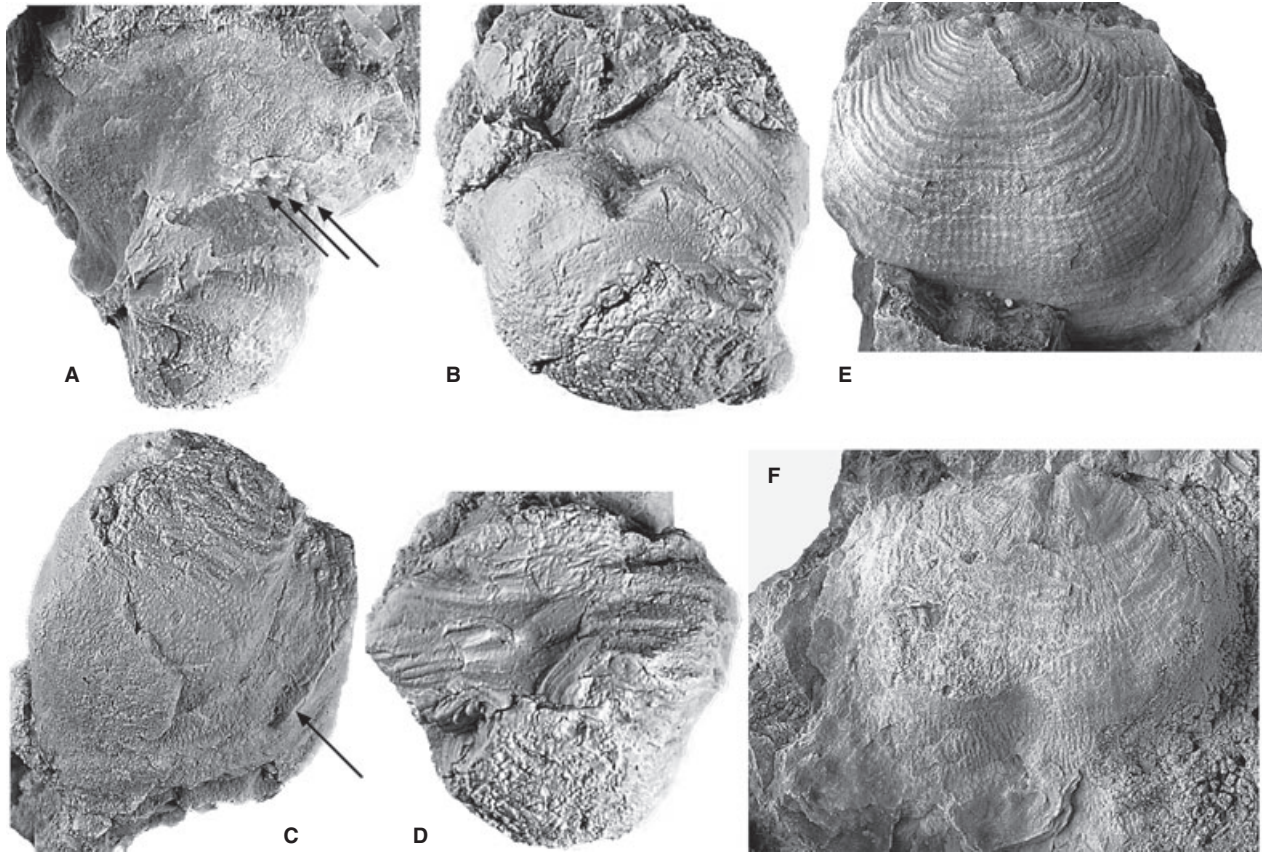
More to the north-east (Text-fig. 1), the carbonate platform continued high into the Moscovian (Myachkovsky



TEXT-FIG. 3. A–C, *Hontorialosia uniplicata* Martínez Chacón, 1979, upper Moscovian, Cuera Limestones, Hontoria (Llanes, Asturias). A, DPO 8765, ventral valve showing the large and broken cicatrix surrounded by vermiform spines, $\times 5$. B, C, DPO 8766, ventral valve, with cicatrix and vermiform spines, $\times 5$, and anterior view with regular spines, $\times 4$. D, E, *Plicatiferina sinecosta* (Martínez Chacón, 1979), upper Bashkirian, Valdeteja Fm, Latores (Oviedo), ventral valves, DPO 8850–8851, showing the clasp spines (arrows) attached to a crinoid stem, $\times 3$. F–I, *Ovetina truyolsi* Martínez Chacón and Winkler Prins, 2009, upper Bashkirian, Valdeteja Fm, Latores (Oviedo); all $\times 2$. F, DPO 38836, internal view of an incomplete ventral valve showing the gutter. G, DPO 38833, ventral view of the holotype showing the large cicatrix. H, DPO 39487, decorticated ventral valve with posterior part of ventral internal mould, showing large spines on left side. I, DPO 38835, dorsal external mould and gutter.

and an up to 1500-m-thick limestone succession was deposited, including reef limestones, microbial boundstones with calcareous algae, brachiopods and bryozoans and voids filled with botryoidal and radiaxial fibrous cement (Bahamonde *et al.* 2004; Martínez Chacón and Bahamonde 2008). The succession consists of two formations, the Valdeteja and the Picos de Europa formations, which, because of continuous sedimentation, were not distinguished in the north-east part of the Ponga Unit (Text-fig. 1). The succession has been informally termed the Cuera Limestones

(*Calizas del Cuera*) by Navarro *et al.* (1986). Brachiopods and their morphological adaptations to hard substrates from the upper Bashkirian–lower Moscovian beds in the Sierra del Cuera were described by Martínez Chacón and Bahamonde (2008). The type material of the new species *Limbfifera bruntoni* comes from these limestones, at a horizon near the Bashkirian/Moscovian boundary, at some 190 m of palaeowater depth. Moscovian brachiopods from the Asturian coast have been known for a long time (e.g. Barrois 1882; Martínez Chacón 1990, 1991).



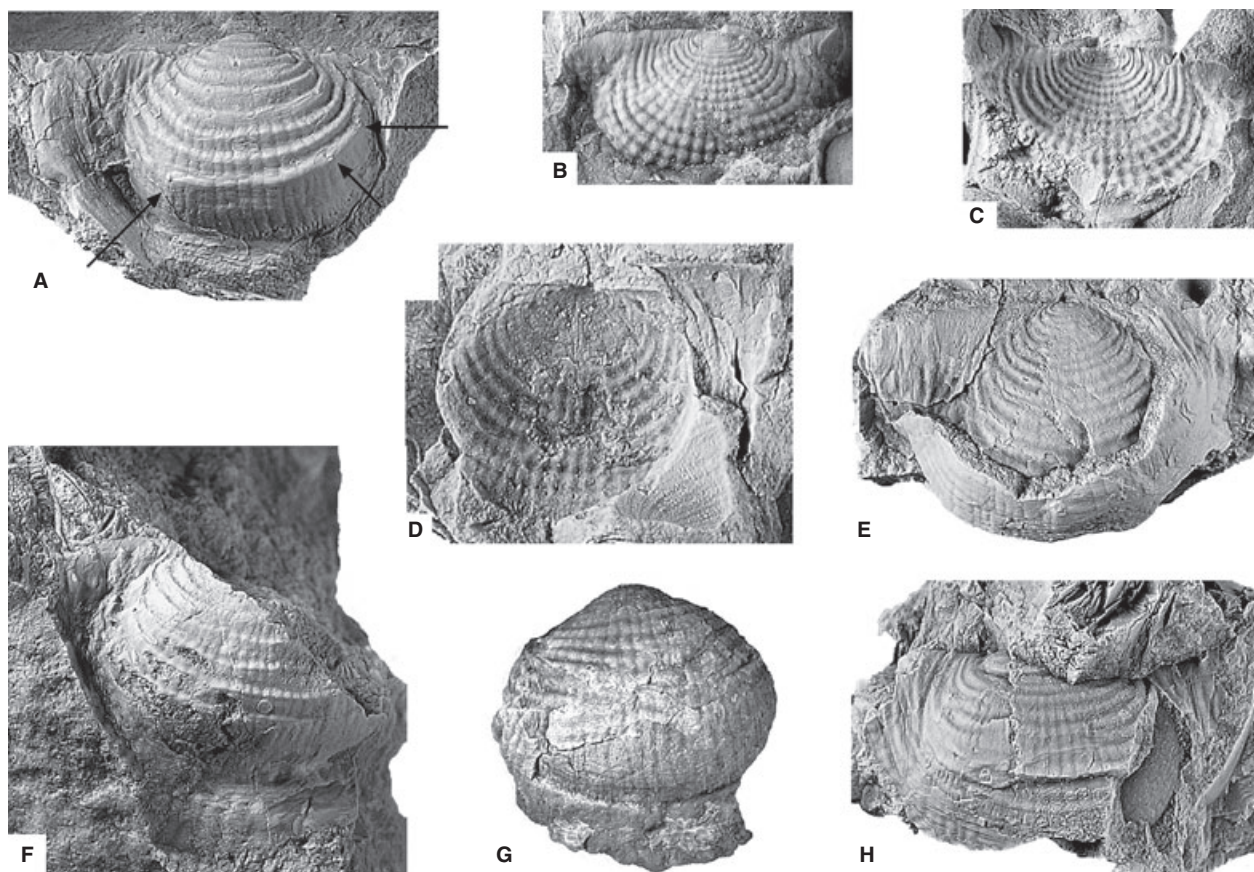
TEXT-FIG. 4. A–D, *Miroproductus posadai* Martínez Chacón and Winkler Prins, 2009, upper Bashkirian, Valdeteja Fm, Latores; all $\times 3$. A, DPO 9440, holotype, lateral view of a partly decorticated specimen showing the mould of three protective endospines (arrows). B–D, DPO 38842, two lateral (both sides) and posterior views showing cicatrix, posterior spine bases, shell filling the region above the hinge (D) and line of junction between aulostegoid and richthofenioid stages (especially in C, arrow). E, F, Plicatiferini gen. et sp. indet., upper Bashkirian, Valdeteja Fm, Latores; $\times 1$. E, RGM 290617, ventral view showing the gutter. F, RGM 290805, ventral exterior with part of ventral internal mould.

Vergaño Formation

In Palencia, basin development continued with deposition of siliciclastics and local limestone development, partly of reefoid character. A good example showing delta shifting (van de Graaff 1971) is the Vergaño Formation, which is of Westphalian D (=Asturian; see Wagner *et al.* 2002) or Late Moscovian (Podolsky to Early Myachkovsky) age, dated by land plants and fusulinids, respectively (Wagner *et al.* 1983, fig. 54). From an inlier of the Castillería Limestone (Myachkovsky) perforating Triassic cover, 6.5 km east of Celada de Robledo, Brunton (1996) described a richthofenioid, *Zalvera* sp. (*Teguliferina?* sp. of Wagner and Winkler Prins 1979, table 3). In a limestone lens near a coal mine 1 km east of Celada de Robledo (Text-fig. 1), somewhat below the Sierra Corisa Limestone (also Myachkovsky?), an interesting new aulostegoid, *Bruntonoconcha celadensis* gen. et sp. nov., was found in large numbers, the only brachiopod species present at this locality apart from a large terebratulid.

Verdeña Formation

In a different basin, after the Leonian folding phase (see Wagner and Winkler Prins, 1985), clastic deposits of the Verdeña Formation with a thick limestone (laterally replaced by calcareous mudstones) were laid down unconformably on the Vergaño Formation (see Wagner *et al.* 1983, fig. 55, p. 121). The limestone was originally named the Verdegosa Limestone (Wagner and Varker 1971, p. 579), a name that had already been used by van de Graaff (1971) for a limestone of the Vergaño Formation (see Wagner *et al.* 1977, p. 105). The Verdeña Limestone Formation (including a basal decalcified mudstone) has been dated as Early Cantabrian and corresponds most probably to the Late Myachkovsky. The brachiopod fauna from the basal part of the formation (in mudstone, 30 m below the Verdeña limestone in a trench on Verdegosa Hill, c. 1.5 km east of San Salvador de Cantamuda; Text-fig. 1) has not yet been published but is of special interest because it is the only locality where the new aulostegoid,



TEXT-FIG. 5. *Limbifera bruntoni* sp. nov.; all $\times 3$. A, Holotype, DPO 39488, Bashkirian/Moscovian transitional beds, Cuera Limestones, Sierra del Cuera (Asturias), ventral valve showing gutter, spine bases at the hinge line and posterior to geniculation (some of them marked with arrows). B, C, DPO 39491, type locality, dorsal view of an incomplete and partially decorticated specimen (C), and its external mould with part of dorsal interior (B). D, DPO 39493, upper Bashkirian, Valdeteja Fm, Latores, dorsal view of an incomplete and eroded specimen showing the mould of dorsal interior structures and the ventral interior of an ear with some spine apertures (right side). E, DPO 9445b, same locality, ventral view of a broken specimen with part of dorsal external mould. F, DPO 39489, type locality, ventral view of an incomplete and eroded specimen showing spines at the hinge and spine basis on the ear. G, DPO 39495, upper Bashkirian, Valdeteja Fm, Latores, ventral view of an incomplete specimen. H, DPO 39492, same locality, ventral view showing spines on the ears.

Bruntonoconcha celadensis gen. et sp. nov., was found apart from its type locality.

Brañosera Formation

The Verdeña Formation is followed by a coal-bearing succession, the San Salvador Formation, which in turn is followed by the marine, largely clastic Brañosera Formation with turbidites and carbonate debris flows (Wagner and Winkler Prins 1985). The latter has been dated as Late Cantabrian on floras and as Kasimovian by fusulinids (Wagner and Winkler Prins 1985). The brachiopod faunas from the Brañosera Formation have not been described yet. Of special interest, however, is a specimen of *Eolyttonia* sp. (Martínez Chacón and Winkler Prins 1993, pl. 2, fig. 4), found at the base of the Brañosera Formation, in

a river section (Río Pisuerga) 1.5 km S of San Salvador de Cantamuda (Text-fig. 1). It is the only specimen of a lyttonioid known so far from the Cantabrian Mountains.

CARBONIFEROUS REEF BRACHIOPODS

During the Carboniferous, brachiopods are mostly simple reef dwellers (dweller guild of Fagerstrom 1988), although some (e.g. Rhythofenioida) contribute to the framework (constructor guild of Fagerstrom 1988). Mississippian examples are well known, both from the Tournaisian (Waulsortian reefs) and the Viséan (see Wolfenden 1958; Mundy and Brunton 1985; Brunton and Mundy 1993). Pennsylvanian ones are less common, although some are known from the Urals and the Canadian Arctic (Carter and Poletaev 1998), the examples from the Cantabrian

TABLE 2. Distribution of the genera cited in this paper in other areas.

Genus	Cantab Mts	Vis NW Eu	Hare Fiord	Alps	Urals	Texas
<i>Alitaria</i>	X	X				
<i>Rugivestis</i>	X		X		X	X
<i>Limbifera</i>	X	X				
<i>Productus</i>	X	X			X	
<i>Admoskovia</i>	X				X	
<i>Kutorginella</i>	X				X	
<i>Fluctuaria</i>	X	X	X		X	
<i>Hontorialosia</i>	X					
<i>Parmephrix</i>	X	X				
<i>Plicatiferina</i>	X		X		X	
<i>Rugicostella</i>	X	X				
<i>Ovetina</i>	X					
<i>Bruntonoconcha</i>	X					
<i>Miroproductus</i>	X					
<i>Zalvera</i>	X				X	
<i>Eolyttonia</i>	X			X	X	X
Total	16	6	3	1	8	2

Mountains being therefore important exceptions bridging the gap between Viséan and Permian reef faunas (Winkler Prins 2007; Martínez Chacón and Bahamonde 2008). Table 2 illustrates the distribution in other areas of the genera mentioned in the text. The connection with the Viséan of north-west Europe on the one hand and with the Urals (see Kalashnikov 1980) on the other is obvious, although the connection with the Urals could prove to be more closely if their Pennsylvanian brachiopod faunas (e.g. Tschernyschew 1902) were completely revised. The connection with the Pennsylvanian and Permian of North America is, however, much less obvious than when the complete faunas are considered and the comparison is restricted to the Valdeteja Formation, partly because of the fact that the Ellesmere Island faunas as known so far are restricted to the Bashkirian–Early Moscovian (cf. Winkler Prins 2007). The connection with Central Europe (the Carnic Alps in particular) appears to be practically nonexistent, but this is because of the fact that there were no reef complexes in the Pennsylvanian; they are found only from much younger, Middle Permian, deposits. In contrast, the general Pennsylvanian brachiopod faunas show rather close relationships (see Winkler Prins 2007, p. 231). It should be noted that four genera are endemic.

PRODUCTIDE ADAPTATIONS WITH REGARD TO THE FIXATION TO HARD SUBSTRATES

During Carboniferous and Permian times, productides underwent a series of morphological changes. Some of

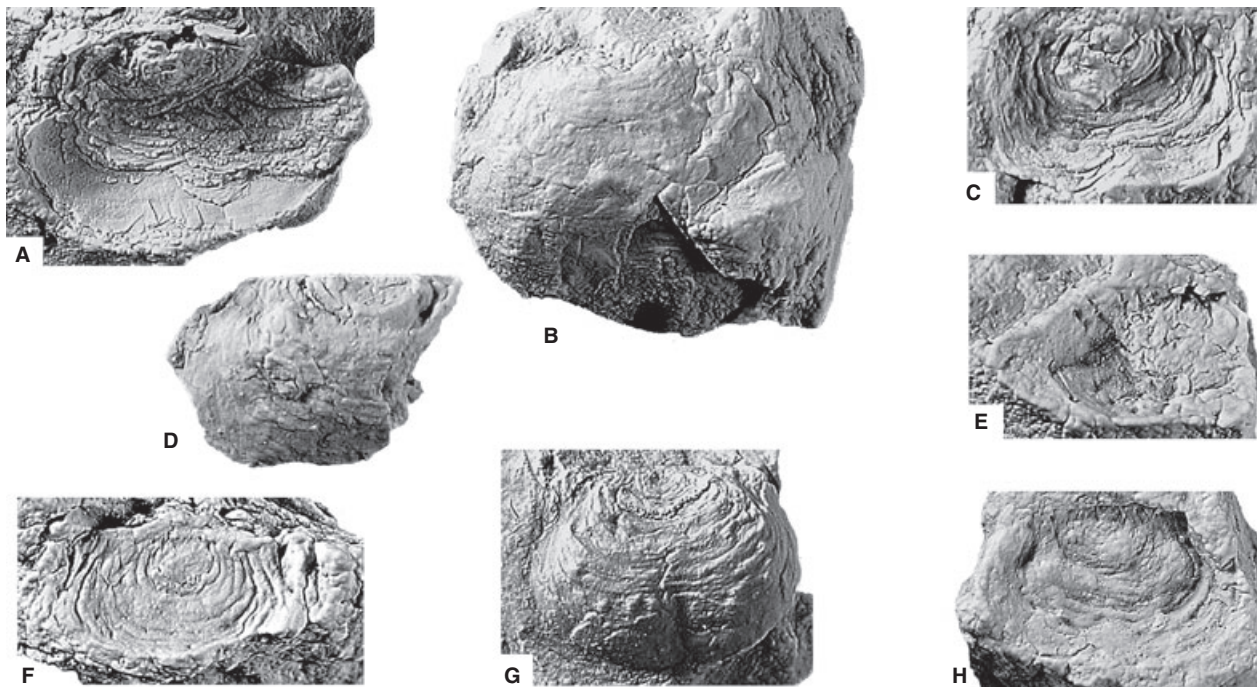
the most marked changes occurred amongst the strophalosiidines, which were adapted to life on hard substrates, commonly reef environments. In the Cantabrian Mountains, we have examples of the three superfamilies included in the suborder, developing some morphological adaptations in response to these habitats: *Hontorialosia uniplicata* Martínez Chacón, 1979, *Parmephrix candemuelensis* sp. nov. and *Plicatiferina sinecosta* (Martínez Chacón, 1979), in the Superfamily Strophalosioidae; *Ovetina truyolsi* Martínez Chacón and Winkler Prins, 2009, *Bruntonoconcha celadensis* gen. and sp. nov. and *Rugicostella?* sp., included in the Superfamily Aulostegoidea; and *Miroproductus posadai* Martínez Chacón and Winkler Prins, 2009 and *Zalvera* sp., the only two Richthofenioidea known from the area. These specialized species are generally represented by a few specimens only; *P. sinecosta* is exceptional in being quite common, and *B. celadensis* is rather abundant but at two localities only, suggesting that it required special conditions.

Cementation by part of the ventral valve is the most common adaptation. This habit left the cicatrix of attachment in the place of cementation. The attachment is reinforced by different types of spines in the ventral valve: (1) clasping spines growing from near the hinge; in some species, the clasping spines formed a complete ring around the attachment object (Text-fig. 3D, E); (2) creeping adherent spines that grew in length until they touched a hard surface and then grew over it attaching to it by cementation. In addition to these spines, some species may have root-like spines positioned more anteriorly assisting in the fixation by entangling the shell with other organisms (Muir-Wood and Cooper 1960; Rudwick 1970; Brunton and Mundy 1988). Large cicatrices are developed in *H. uniplicata*, *P. candemuelensis*, *O. truyolsi* and *B. celadensis* (Text-figs 3A–C, F–I, 6, 8). In all of these species, different kinds of spines have collaborated in the attachment. In *H. uniplicata*, the large cicatrix is surrounded by a tangled mass of vermiform spines (Text-fig. 3A, B). The strong attachment causes gross distortion in the postero-medial region of ventral valve in *P. candemuelensis*; thin spines close to the hinge could probably have collaborated with the attachment (Text-fig. 6B). *Ovetina truyolsi* has a row of thin spines along the hinge and a row of thick rhizoid spines separating the ears that helped to attach the shell (Text-fig. 3H). *Plicatiferina sinecosta* has no clear cicatrix; the attachment is by clasping spines growing near the hinge which, in some specimens, formed a ring around a crinoid stem (Text-fig. 3D, E). *Rugicostella?* sp. also bears attachment spines (Martínez Chacón and Bahamonde 2008, fig. 2L, M). All these taxa have a shallow corpus cavity and most of them have a short trail and are of small size. These characteristics could have facilitated their attachment on the bottom of a reefal environment. In *P. sinecosta*, with no clear cicatrix, its clasping hinge

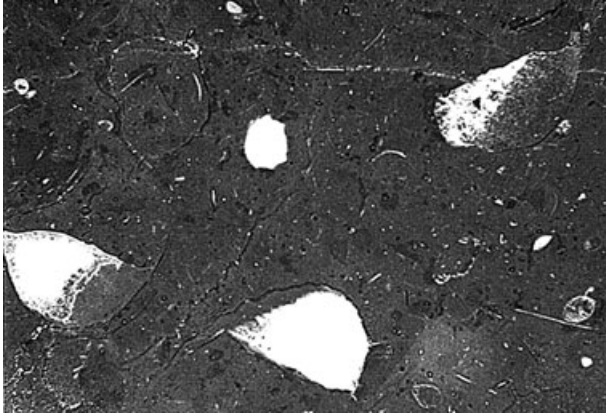
spines seem to have been the principal means of support, in the same way as indicated by Brunton and Mundy (1988) for *Sinuatella sinuata* (de Koninck, 1851). *Ovetina truyolsi* has a shell of medium size, strongly concavo-convex with a shallow corpus cavity and a relatively long trail (12 mm in the specimen on Text-fig. 3H), which rotates anteriorly to produce a well-developed gutter all around the margin. The gutter is large, flaring, flattened but slightly ventrally directed (Text-fig. 3F, I). The relatively big and heavy shell was held on the substrate by a cicatrix and with the help of the thick rhizoid ventral spines (Text-fig. 3G, H). The relatively long trail elevated the anterior commissure and therefore the inhalant current above the sediment surface. As suggested by Brunton and Mundy (1988, p. 74) for their genus *Limbifera*, a gutter may be functionally advantageous while filtering inhalant water, thus providing a better system for removal of heavier particles, allowing the entrance of more water and more space for the lophophore filaments than in a straight trail. *Bruntonoconcha celadensis* was fixed by its large cicatrix to some surface with the additional help of spines. The ventral cicatrix is reflected as a xenomorphic area in the dorsal valve (Text-fig. 8C, E, F); this characteristic shows the strength of the fixation. The genicula-

tion of the shell and the various trails of the dorsal valve were important for an adequate inhalant current.

Richthofenioidea, with their aberrant coral-like form, are typical brachiopods in the Permian reef environments (e.g. Muir-Wood and Cooper 1960; Cooper and Grant 1975). The two Cantabrian species, *M. posadai* and *Zalvera* sp., are fixed by the apex of their conical ventral valve, the attachment being reinforced in the former by rhizoid spines; *Zalvera* Brunton, 1996, lacks spines except in a small apical spinose part. The genera *Miroproductus* Martínez Chacón and Winkler Prins, 2009, and *Zalvera* are among the earliest representatives of this superfamily, which originated in the Late Bashkirian. *Ardmosteges* Sutherland, 1996, comes from the Bashkirian (Morrowan) of Oklahoma. Sutherland (1996) described his genus as having an early aulostegid stage with a ventral interarea, followed by an adult richthofenioid conelike form, highlighting the derivation of the superfamily from the Aulostegidae. *Miroproductus posadai* has also an early aulostegid stage of growth, with ventral interarea, large cicatrix and rhizoid spines, followed by a richthofenioid stage with the lateral margins of the trail fused posteriorly, and finally the process continues with holoperipheral growth producing a short cone (Text-fig. 4A–D). A line



TEXT-FIG. 6. *Parmephrix candemuelensis* sp. nov. All specimens from the San Emiliano Fm, La Majúa Mb, upper Bashkirian; $\times 6$. A, holotype, DPO 8734, south of Candemuela (León), dorsal view showing interareas, teeth and bilobed cardinal process. B, DPO 8733, type locality, ventral valve showing the large cicatrix. C, DPO 8735, type locality, dorsal view. D, DPO 8749, Pinos (León), ventral valve with large cicatrix. E, DPO 8761, Hedrada (Tevega, Asturias), ventral valve, internal view showing teeth, septum and spine apertures. F, DPO 8739, type locality, ventral interior with part of dorsal valve of an incomplete specimen. G, DPO 8751, north-east of Pinos (León), decorticated dorsal interior. H, DPO 8736, type locality, eroded ventral interior showing the distortion caused by the attachment.



TEXT-FIG. 7. Rock sample with sections through various specimens of *Bruntonoconcha celadensis* gen. et sp. nov., showing trails and spines; $\times 2$; RGM 290675, type locality.

marks the junction of the two growth stages (Text-fig. 4C, arrow). The characteristics of *Miroproductus* corroborate the aulostegoid origin for this superfamily as proposed by Sutherland. The genus *Institina* Muir-Wood and Cooper, 1960, could have been the ancestor for *Miroproductus* because its general shape looks like the initial phase of *Miroproductus*. An aulostegoid ancestry was also suggested for *Zalvera* by Brunton (1996). Specimens from limestones of Late Moscovian (Podolsky) age in the Cantabrian Mountains have been described and figured by Brunton (1996, p. 58, fig. 25) as *Zalvera* sp.

The dorsal valve of *Miroproductus* (as in *Ardmosteges*) is opercular and remains apical throughout growth leaving a vestibule above it, with protective spines in the internal upper part of the ventral valve (Sutherland 1996; Martínez Chacón and Winkler Prins 2009). These two genera probably lived fixed to a hard substrate in reefal environments (in fact, *A. orchamus* Sutherland, 1996, constitutes a patch reef with the virtual exclusion of all other fossils); the conical shape would have raised the inhalant areas well above the bottom, and the thick endospines could have protected the shell aperture preventing the entrance of big and undesirable particles. On the other hand, Brunton (1996) supposed that *Z. sibaica* had lived partially buried in a relatively soft substrate, owing to the lack of external spines and the variable nature of the ventral 'basal' deformation. However, this author pointed out that the Cantabrian *Zalvera* sp. has flattened ventral apices, suggesting closer attachment to the substrate than for *Z. sibaica*.

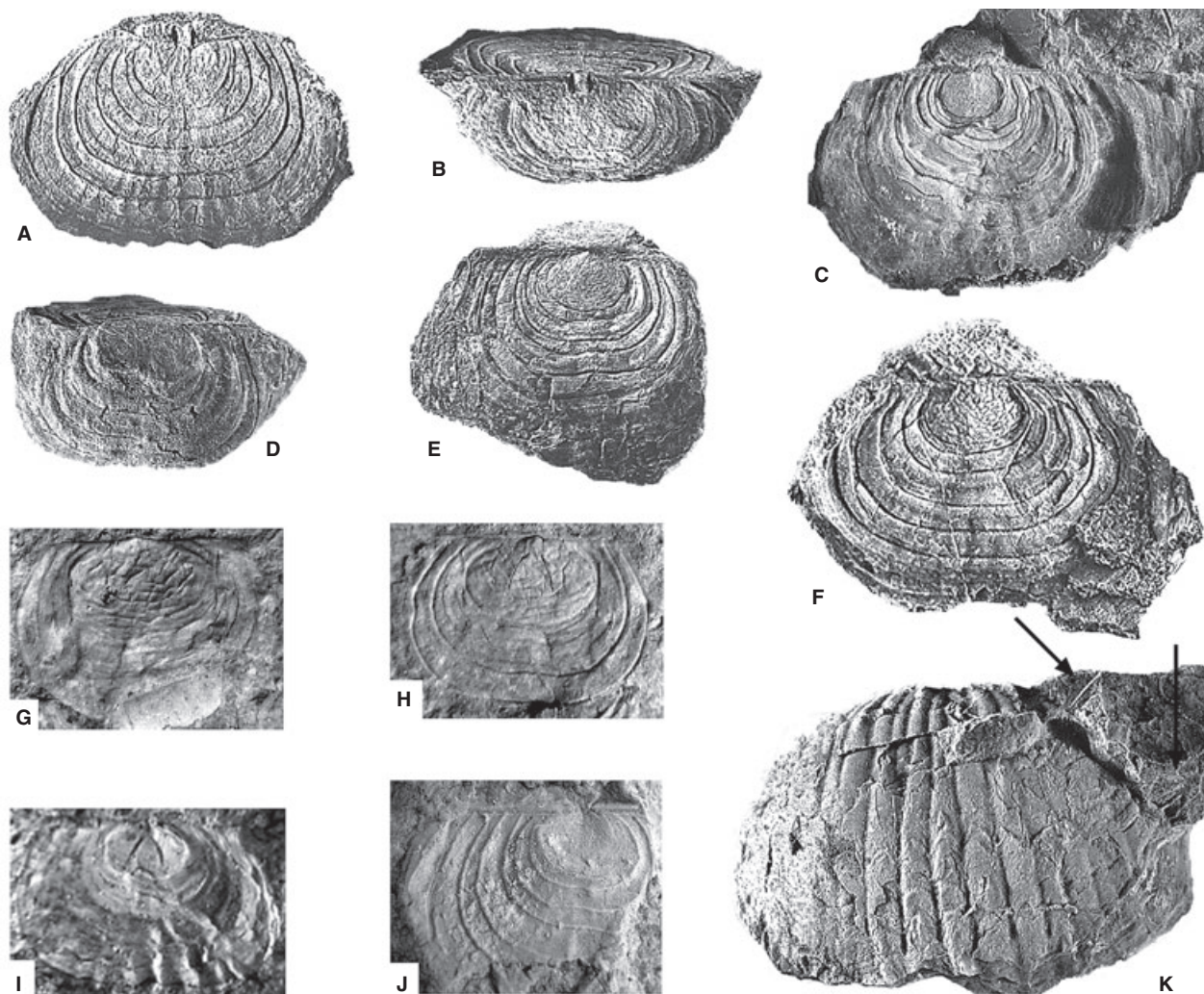
Representatives of the Suborder Lyttoniida are the more unusual brachiopods, generally supposed to have lived attached to some hard substrate. The peculiar dorsal valve, which was probably covered with mantle material, suggests a possible symbiosis with algae (see Cowen 1970). This makes it likely that the lyttoniids (and the richthofenioids as well) lived in shallow (sub)tropical seas

in a reef-like environment. Although the only specimen from the Cantabrian Mountains belonging to the suborder, a dorsal valve of *Eolyttonia* sp. (Martínez Chacón and Winkler Prins 1993, pl. 2, fig. 4), was found in a decalcified mudstone and there is no evidence for a relation to a hard substrate, we suppose it would have lived in the same reef environment as the rest of the lyttoniids and may possibly have drifted in from elsewhere.

Productides of the Suborder Productidina generally were adapted to life in a soft substrate, buried in sediment, in a quasi-infaunal way, with ventral spines probably rooting the shell and keeping it from sinking more than convenient (Rudwick 1970). But some species also show structures considered to be adaptations to reef-dwelling such as an enlargement or modification of its trail, leading to the development of a flange or gutter. *Limbifera bruntoni* sp. nov. has a row of posteriorly directed creeping spines and a short geniculated trail that continues in a gutter (Text-fig. 5A, F). We interpret the species as having lived in the same way as pointed out by Brunton and Mundy (1988, p. 74) for the genus: attached by its spines to a solid object 'and to have been supported more or less in free water even if surrounded by other organisms'. The functionally advantageous character of a gutter against a straight trail was postulated by Brunton and Mundy (1988) as mentioned earlier.

Some other productidines from the formations dealt with in this paper show also modifications of their trails but have no clear mechanisms of attachment. *Institiferini* gen. et sp. indet., from the upper Bashkirian–lower Moscovian Cuera Limestone (Martínez Chacón and Bahamonde, 2008, p. 139, fig. 2A), is a minute shell with numerous very fine spines and trail deflected to form a flange. This small shell could have lived entangled with its spines amongst surrounding organisms, taking advantage of its flanged trail while filtering inhalant water. A similar species from the Late Bashkirian – Early Moscovian of the southern Urals has been identified by Lazarev (1990, pl. 10, figs 7–8) as *Thomasella* sp., and by Brunton (1996, p. 51, figs 2–3) as 'Thomasella-like species'.

Other species with modified trails have on the contrary a large size and heavy shells. *Admoscovia* cf. *aljutovensis* Lazarev, 2000 (Martínez Chacón and Winkler Prins 2009, fig. 3.3), and *Plicatiferini* gen. et sp. indet. (Text-fig. 4E) developed a big gutter. *Kutorginella* cf. *stepanovi* (Lapina, 1957) (Martínez Chacón and Bahamonde 2008, fig. 2G, H) has a trail with a median tubiform extension; the maximal development of the trail is observed in *Productus concinnus* Sowerby, 1821 (Martínez Chacón and Winkler Prins 2009, fig. 3.6–3.7). A tubiform trail is also developed in *Fluctuaria undata* (Defrance, 1826) (Winkler Prins 2007, fig. 2.6). In two species of more modest size, *Rugivestis* sp. (Winkler Prins 2007, fig. 2.1) and *Alitaria frechi* (Paeckelmann, 1931) (Martínez Chacón and



TEXT-FIG. 8. *Bruntionoconcha celadensis* gen. et sp. nov. A, B, holotype, RGM 290663, Vergaño Fm, Late Moscovian (Podolsky), east of Celada de Robledo (Palencia), somewhat decorticated specimen, in dorsal view showing traces of dorsal valve interior with muscle ridges, brevisseptum, cardinal process, and cinctures; and in umbonal view showing cicatrix and cinctures; $\times 4$. C, RGM 290666, type locality, dorsal view showing cicatrix, xenomorphic area in dorsal valve, one ear, hinge spines and cinctures; $\times 3$. D, E, RGM 290662, type locality, umbonal view showing cicatrix and cinctures, and dorsal view showing xenomorphic area and cinctures; $\times 4$. F, RGM 290661, type locality, dorsal view showing cicatrix, xenomorphic ornamentation and cinctures; $\times 4$. G, H, RGM 290718A, Verdeña Fm, Late Moscovian (Myachkovsky), east of San Salvador de Cantamuda (Palencia), external and internal moulds of a juvenile dorsal valve showing the muscle ridges; $\times 7$. I, RGM 290721, same locality, dorsal internal mould with muscle ridges; $\times 4$. J, RGM 290670, type locality, incomplete dorsal valve and ventral interarea; $\times 4$. K, RGM 290668, type locality, ventral anterior view showing costae and spines (arrows); $\times 3$.

Winkler Prins 2009, fig. 3.5), the trail is also extended anteriorly, and in *Rugivestis* it forms a fold. It is difficult to speculate on how these species lived, without any scar of attachment and, some of them, even having halteroid spines (e.g. *A. frechi*) considered typical for 'antireef dwellers' by Grant (1971). The modest size of some could have helped them to live in the reef, tangled by their spines. On the other hand, the big and heavy posterior part of the shell of some others may have stabilized them in the substrate by the differential weight of the shell, with the posterior part downwards and the anterior com-

missure away from the substrate, thanks to the very long and elaborated trails. The spines may have taken a rhizoid function helping to stabilize the shell.

SYSTEMATIC PALAEOLOGY

Repository. The specimens are housed in the Geology Department of the University of Oviedo (numbers prefixed by DPO) and the National Museum of Natural History of The Netherlands at Leiden (numbers prefixed by RGM).

Order PRODUCTIDA Waagen, 1883
 Suborder PRODUCTIDINA Waagen, 1883
 Superfamily PRODUCTOIDEA Gray, 1840
 Family PRODUCTELLIDAE Schuchert, in Schuchert and
 LeVene, 1929
 Subfamily PLICATIFERINAE Muir-Wood and Cooper, 1960
 Tribe PLICATIFERINI Muir-Wood and Cooper, 1960

Genus LIMBIFERA Brunton and Mundy, 1988

Type species. *Productus griffithianus* de Koninck, 1847; by original designation.

Remarks. The genus was originally placed in the aulostegoid family Sinuatellidae, but in the Revised Treatise (Brunton *et al.* 2000), it was transferred to the tribe Semicostellini of the productoid subfamily Plicatiferinae. The shallow corpus cavity, lack of marginal ridges and the strong rugae made us transfer the genus to the Tribe Plicatiferini, although the costae are rather well developed.

Limbifera bruntoni sp. nov.
 Text-figure 5

- .2008 *Limbifera?* sp. Martínez Chacón and Bahamonde, p. 139, fig. 2B–C.
 .2009 *Limbifera?* sp. nov. Martínez Chacón and Winkler Prins, p. 8, fig. 3.4.

Derivation of name. The species was named after the renowned brachiopod specialist Dr Howard Brunton of The Natural History Museum (London). His recent passing is an irreparable loss for the brachiopodologists community.

Holotype. Specimen DPO 39488 (Text-fig. 5A).

Type locality and horizon. Sierra del Cuera, section SC8, Cuera Limestones, Bashkirian/Moscovian transitional beds (see Martínez Chacón and Bahamonde 2008, fig. 1).

Material. Holotype and three more specimens from the type locality (DPO 39489–39491) and another five specimens from the Valdeteja Formation at Latores (DPO 9445b, 39492–39495).

Diagnosis. Shell small; corpus cavity narrow; ears large, flat and strongly differentiated; gutter narrow, ventrally geniculated; without median sulcus or fold. Strong rugae on visceral disc, costae weakly developed; spines along hinge and on ventral disc.

Description. Small *Limbifera* with narrow corpus cavity (holotype: L >11.3 mm, W c. 21.4 mm; corpus: L = 9.29 mm, W = 10.17 mm; length of trail posterior to gutter c. 5 mm); semicircular shape with largest width at hinge; gutter narrow.

Ventral valve weakly convex, medianly flattened without sulcus, with short geniculated trail; umbo small, hardly extending beyond the hinge margin; ears flat and strongly differentiated. Visceral disc without ears subpentagonal to subrectangular in shape. Prominent rugae (five rugae in 5 mm on anterior part of corpus) on visceral disc and ears, costae weakly developed (eight costae in 5 mm in central part) forming a distinct reticulation on the anterior part of the visceral disc; they continue in gutter, become more visible on trail and are absent from the ears; row of posteriorly directed spines along hinge, fine near umbo but thick (up to 0.7 mm in diameter) and slightly diverging from hinge near the cardinal extremities; some four additional thick spines form a row posterior to geniculation (three are arrowed in Text-fig. 5A) and another row above the gutter. Internal structures weakly developed, internal surface pustulose. Dorsal valve weakly concave with geniculation, without median fold; prominent rugae, also on trail; costae more prominent than on the ventral valve, producing a distinct reticulation; no spines. Interior of dorsal valve with bilobate cardinal process and long median septum continuing almost to end of visceral disc; muscle scars and brachial ridges poorly developed, the latter directed anteriorly, almost parallel to the lateral margins.

Remarks. Our new species can be easily distinguished from the type species *L. griffithiana* by its smaller size, lack of median sulcus and fold, more prominent rugae and the rows of spines around the visceral disc and above the gutter. Also, the form of the corpus (without gutter and ears) is in our species subpentagonal to subrectangular in shape, whilst in *L. griffithiana*, it is rather triangular to subpentagonal (Brunton and Mundy 1988).

Distribution. Latest Bashkirian to earliest Moscovian (Cuera Limestones and Valdeteja Formation) from the Cantabrian Mountains (north-west Spain).

Plicatiferini gen. et sp. indet.
 Text-figure 4E, F

- .1993 *Institina?* sp. Martínez Chacón and Winkler Prins, p. 578, pl. 2, fig. 2.
 .2007 *Limbifera?* sp. Winkler Prins, p. 224, fig. 2.2.

Material. Two pedicle valve interiors (RGM 290805, 290617) from the Valdeteja Formation at Latores.

Description. Pedicle valve large, subrectangular, wider than long with broad gutter. Ornamentation semireticulate, spines not observed. Interior with short median septum between muscle scars. Brachial valve unknown.

Remarks. The specimens resemble *Ovetina truyolsi* Martínez Chacón and Winkler Prins, 2009, but it is much bigger and lacks an interarea. The semireticulate ornamentation distinguishes our material easily from *Institina*.

The latter is further also distinguished by its triangular visceral disk.

Suborder STROPHALOSIIDINA Waterhouse, 1978
 Superfamily STROPHALOSIOIDEA Schuchert, 1913
 Family CHONOPECTIDAE Muir-Wood and Cooper, 1960

Genus *PARMEPHRIX* Brunton and Mundy, 1994 (*in* Brunton *et al.* 1994)

Type species. *Parmephrix eileenarum* Brunton and Mundy, 1994 (*in* Brunton *et al.* 1994).

Remarks. Brunton and Mundy (1994 *in* Brunton *et al.* 1994) designated their new species *Parmephrix eileeni* as the type species of the genus. The name was changed to *P. eileenarum* by Brunton, Lazarev and Grant (2000 *in* Brunton *et al.* 2000). However, the valid date and authors of the species are those of the original spelling (Article 19.2, ICZN, 4th ed., 1999).

Parmephrix candemuelensis sp. nov.
 Text-figure 6

- .pars 1979 *Heteralosia* sp. Martínez Chacón, p. 117,
 pl. 11.4–11.5.
 .1985b *Heteralosia* sp. Martínez Chacón and Winkler
 Prins, p. 236.

Derivation of name. The species is named after its type locality.

Holotype. Specimen DPO 8734 (Text-fig. 6A).

Type locality and horizon. Locality WP-24, S of Candemuela (León), San Emiliano Formation, La Majúa Member, marly limestone, Late Bashkirian (see Winkler Prins 1968 and Martínez Chacón 1979).

Material. Holotype and other 12 specimens, DPO 8733, 8735–8745, from the type locality; two specimens, DPO 8749–8750, from Pinos (León), locality WP-29; nine specimens, DPO 8751–8755, RGM 290540, RGM 291691–291693, north-east Pinos, locality WP-30; one specimen, DPO 8756, locality T-1, near La Plaza (Teverga, Asturias); two specimens, DPO 8761–8762, B-115, Hedrada (Teverga), San Emiliano Formation, La Majúa Member (see Winkler Prins 1968 and Martínez Chacón 1979).

Diagnosis. Shell small, ventrally geniculated, outline subrectangular to subtrapezoidal, well-defined ventral and dorsal interareas, large cicatrix, slight ventral sulcus and dorsal fold.

Description. Small *Parmephrix* reaching *c.* 6 mm in length and up to 8 mm in width (holotype: L = 5.6 mm; W = 8 mm),

irregularly concavo-convex, with a shallow corpus cavity, ventrally geniculated with short trail; rounded subrectangular or subtrapezoidal shape, with hinge line commonly narrower than maximum width; anterior commissure slightly uniplicate. Ventral valve with large cicatrix distorting the posterior or postero-medial region of the valve; interarea well developed but short, with narrow triangular delthyrium; trail with a slight median sulcus. Ornamentation of strong, rather irregular rugae, less prominent and more widely placed anteriorly; growth lines well defined; spines thin, a row close to hinge line and scattered over the rugae. Dorsal valve with interarea well developed but narrower than the ventral one, trail close to the other valve, with a slight median fold; rugae less pronounced and more lamellose than those in the ventral valve; no spines. The shell material is thin, so the rugation is distinguishable internally. Ventral interior with small but robust teeth, short and relatively wide septum. Dorsal interior with relatively wide, bilobed cardinal process, the external part of which fits into the open part of the delthyrium (Text-fig. 6A); the cardinal process is supported by short but thick inner socket ridges; adductor muscle scars bean shaped, located posteriorly, and separated by a median septum.

Remarks. These specimens were previously described as *Heteralosia* sp. (Martínez Chacón 1979) based on the presence of interareas in both valves, the ventral valve being fixed by a large cicatrix, and spines developed only ventrally. Nevertheless, the irregular distorted discs, strong rugae and less numerous and finer spines developed in the new species separate it from *Heteralosia* and bring it closer to *Parmephrix*. The differences with the type species are the smaller size, the different shape, with the hinge line narrower than maximum width, and the anterior commissure slightly uniplicate in *Parmephrix candemuelensis* sp. nov.

Distribution. Late Bashkirian, San Emiliano Formation. This species extends the range of the genus, previously known only from the upper Viséan.

Superfamily AULOSTEGOIDEA Muir-Wood and Cooper, 1960
 Family AULOSTEGIDAE Muir-Wood and Cooper, 1960
 Subfamily CHONOSTEGINAE Muir-Wood and Cooper, 1960

Genus *BRUNTONOCONCHA* gen. nov.

Derivation of name. Latin: Brunton's shell, named after the renowned brachiopod specialist Dr Howard Brunton of The Natural History Museum (London).

Type species. *Bruntonoconcha celadensis* gen. et sp. nov.

Species included. Type species only.

Diagnosis. Plano-convex shells with strongly geniculated trail; interareas low; prominent cicatrix, granulose or

smooth, reflected dorsally as xenomorphic ornamentation; visceral disc with prominent cinctures and weak costae anteriorly, trail coarsely costate; spines along hinge, on visceral disc and on trail (obviously not on cicatrix). Dorsal valve with multiple diaphragms and up to three trails, without spines. Interior with prominent, bilobed cardinal process supported by parallel muscle ridges that subsequently diverge at an angle of some 40 degrees; halfway down the thin muscle ridges a weak median septum is developed in between them.

Description. See the description of the type species.

Remarks. The genus was mentioned by one of us (Winkler Prins 1983, p. 73) as a new genus of the group of 'Alexenia' *adhaerescens* (Ivanov, 1935). The latter species is the type of the genus *Lopasnina* Ilkhovskiy, 1990 (in Lazarev 1990, p. 103), which is included in the Productini in the new brachiopod treatise (Brunton *et al.* 2000, p. 469). This attribution seems, however, doubtful because in the original description of the genus (and of the type species), a (small?) cicatrix is mentioned (see also Sarytcheva and Sokolskaya 1952, p. 162 of French translation), which can,

however, not be recognized on the available illustrations and which is not mentioned in the Treatise. *Bruntonoconcha* is clearly distinguished from *Lopasnina* by its large cicatrix, its well-developed cinctures on the visceral disc of both valves, its diverging muscle ridges (in *Lopasnina* they remain parallel; see Ivanova 1951, fig. 2), its rather flat visceral discs and strong geniculation; also no interarea was observed in the ventral valve of *Lopasnina*. *Bruntonoconcha* is included in the Chonosteginae because of its strong geniculation, its cinctures on the visceral disc, its strong costae anteriorly, but differs from most other genera belonging to the subfamily by the lack of complicated structures around the anterior margin. *Diaphragmus* Girty, 1910, which also has multiple diaphragms and trails, lacks a cicatrix and the cinctures and has costae starting at the umbo; also its internal structure is rather different.

Bruntonoconcha celadensis gen. et sp. nov.
Text-figures 7, 8

.1989 'Alexenia' *adhaerescens* (Ivanov, 1935); Winkler Prins, p. B14, fig. 49.

TABLE 3. Measurements in mm of some specimens of *Bruntonoconcha celadensis* gen. et sp. nov.

RGM	Specimen	L	Ltrail	Ldv	W	Wdv	Th	Lmr	Lbs	Costae/5 mm
290715	dvim			6.5		9.9		2.8	2.2	
290716	dvi/em			>3.4		4.5		0.6		
290718A	dvi/em			3.6		5.4		1.0		
290718B	vvi/em	10.0			12.0					5
290719	dvi/em			5.0		7.0		4.6		
290721	dvi/em			6.6		9.5		2.3		6
290661				10.0		15.0				
290662				8.4		10.6		1.8	1.8	
*290663				8.3		12.5			3.0	
290664				12.3		16.4				
290665				12.2		17.1				
290666				12.0	18.4	16.6				
290667	vv		15.5			16.6				
290668	vv	16.3			22.3					
290669	dv + vv			10.8	16.0	15.0				
290670	dv			>7.0	14.0					
290671	dv + vv		5.2		18.8					
290672	dv			9.8		>10.4		3.9	7.0	
290673	dv			8.8	22.2	14.2				
290674	dv			13.6			7.6			
290677	dv					14.4				
290678	vv		15.0	10.7	19.1					
290682	vv (int)	18.0		10.2	21.8	11.0				
290683	vv (int)	15.0		9.2	17.0	11.4				
290684		18.3	8.4	16.5		17.5				

dv, dorsal valve; vv, ventral valve; im, internal mould; em, external mould; int, interior; L, length; W, width; Th, thickness; mr, muscle ridge; bs, brevisseptum.

*Holotype.

Derivation of name. The species is named after the type locality Celada de Robledo.

Holotype. Specimen RGM 290663 (Text-fig. 8A, B).

Type locality and horizon. Limestone lens near mine east of Celada de Robledo (northern Palencia, see Text-fig. 1) in shales of the Vergaño Formation of Late Moscovian (Podolsky Horizon) age (see Text-fig. 2), locality VII of Dr W. J. E. van de Graaff (1971 = WP 485). It should be noted that the fauna in this limestone consists exclusively of specimens of our new species (Text-fig. 7), with the exception of one large terebratulid.

Material. Holotype and abundant topotype material (RGM 290661–290684), most specimens being incomplete, however. Moreover, internal and external moulds in a decalcified mudstone from a trench on Verdegosa Hill 1 km east of San Salvador de Cantamuda, Verdeña Formation, some 30 m below the limestone; Late Myachkovsky (Early Cantabrian) in age (levels Wag. 2754 (RGM 290715), Wag. 2755 (RGM 290716–290720), and Wag. 2756 (RGM 290721)).

Diagnosis. See the Diagnosis of the genus.

Description. Small shells (see Table 3) with distinctive cicatrix *c.* one-third the size of the visceral disc, which is weakly convex, continuing with a strong geniculation in a moderately long trail; interareas low. Cicatrix smooth or granulose, remainder of visceral disc shows prominent cinctures; coarse costae start near the anterior border of the visceral disc and become prominent on the trail; spines along the hinge and scattered on trail. Dorsal valve with a nearly flat visceral disc, showing a xenomorphic area corresponding to the cicatrix of the ventral valve, diaphragms and strongly geniculated trails, which are easily broken off, but up to three may be (partly) preserved; cinctures undulated because of traces of costae, no spines. Interior of ventral valve poorly known, anterior part pseudopunctate. Dorsal valve interior reflects the external ornamentation, has thin parallel muscle ridges supporting the bilobed cardinal process which is at right angles with the valve, the ridges almost immediately diverge at an angle of some 40 degrees; at *c.* 1 mm below the hinge, a thin median septum is weakly developed, extending well beyond the muscle ridges.

Remarks. See the Remarks of the genus.

Distribution. Late Moscovian, Vergaño and Verdeña formations of the Cantabrian Mountains.

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