Brachiopods from the Valdeteja Formation (Pennsylvanian; Cantabrian Mountains, NW Spain)

María Luisa Martínez Chacón, Oviedo and Cor F. Winkler Prins, Leiden

With 6 figures and 4 tables

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Abstract: After a short introduction on the lower Pennsylvanian (Bashkirian to lowermost Moscovian) Valdeteja Formation in its stratigraphical context, an overview of its brachiopod faunas is presented and their palaeoecological and palaeogeographic importance discussed. Two new genera of the Strophalosiidina, showing adaptations to a reef environment, are described. The genus *Ovetina* (type species *O. truyolsi* gen. et sp. nov.) is an aulostegid with a well developed ventral flange. *Miroproductus* (type species *M. posadai* gen. et sp. nov.) is an early richthofenoid, probably derived from an aulostegid such as *Institina* MUIR-WOOD & COOPER, 1960.

Key words: Brachiopods, Strophalosiidina, Valdeteja Formation, palaeoecology, upper Bashkirian, Cantabrian Mountains, Spain.

1. Introduction

The Valdeteja Formation was originally described by WINKLER PRINS (1968) as the Valdeteja Member of the Escapa Formation and later elevated to the rank of formation by WAGNER et al. (1971). It forms the upper part of what used to be known as the “caliza de montaña” (e.g., EZQUERRA DEL BAYO 1844) or “calcaires des cañons” (e.g., BARROIS 1882), the former being a direct translation of the British Mountain Limestone which is of an older, Mississippian, age.

The Valdeteja Formation consists mainly of light gray, massively bedded limestone, often bioclastic, with some marly beds (EICHMÜLLER 1985). The formation is locally rich in macrofaunas, especially brachiopods (WINKLER PRINS 1971). It varies considerably in thickness: from a few metres to some 800 m and crops out in steeply dipping thrust slices

over a large part of the Asturo-Leonese realm, especially in the Sobia-Bodón, Aramo, Picos de Europa and Sierra del Brezo areas (Fig. 1), as well as in the Revilla Nappe in northern Palencia (see WAGNER & WINKLER PRINS 2000). The Valdeteja Formation (Fig. 2) has been dated, mainly on fusulinids, as Bashkirian-lower Moscovian (VILLA 1982; VILLA et al. 2001).

Underlying the Valdeteja Formation is the Barcaliente Formation (originally described as the Vegacervera Member; see WAGNER et al. 1971), consisting of black, fetid, laminated limestone which is poor in fossils. Occasional conodonts indicate an early Bashkirian age for its upper part, the lower part clearly being of Serpukhovian age (MÉNDEZ & MENÉNDEZ ÁLVAREZ 1985, SANZ-LÓPEZ et al. 2006). The uppermost part of the Barcaliente Formation is characterised by collapse breccias with blocks up to cubic

Fig. 1. Geological map showing the main geological structures (after PÉREZ-ESTAÚN et al. 1988), and the principal faunal localities of the Valdeteja Formation (asterisks). From W to E: Entrago, Latores, Cármenes and Valdeteja.

metre size, the Porma Breccia of REUTHER (1977), as can be clearly seen in the Barcaliente type section (WINKLER PRINS 1971: pl. 1, fig. 2).

The carbonate platform of the Valdeteja Formation formed an external rim around a basin, where the mud sedimentation did not keep up with subsidence (the Ricacabiello Formation, see MARTÍNEZ CHACÓN et al. 1985). Overlying and partly replacing the Valdeteja Formation is the San Emiliano Formation (Fig. 2) of BROUWER & VAN GINKEL (1964), a succession of mudstone with intercalated limestones and sandstones (see also BOWMAN 1982, 1985; CARBALLEIRA et al. 1985; FERNÁNDEZ 1993; VAN GINKEL & VILLA 1996).

2. Faunas and floras

After the (semi-)pelagic faunas of the Mississippian (e.g. MARTÍNEZ CHACÓN & WINKLER PRINS 1993; AMLER & WINKLER PRINS, 1999; SÁNCHEZ DE POSADA et al. 2001), the Pennsylvanian starts with rich benthic faunas of the Valdeteja Formation. Most fossil groups are represented, but many have only been poorly studied (see Table 1) and some are rare, such as the cephalopods (mainly orthocones), rostroconchs, porifera, trilobites and identifiable echinoderms (crinoid ossicles are locally abundant). By far the most com-

mon and best studied fossils are the brachiopods, but these too are in need of a revision. The brachiopod study started with the locality of Latores (see MARTÍNEZ CHACÓN & WINKLER PRINS 2007, 2008) and is continued and extended to other areas by us (MARTÍNEZ CHACÓN & WINKLER PRINS 2006).

3. Comments on the brachiopod faunas

The study of the fossils, and particularly the brachiopods, is hampered by their occurrence in massive and re-crystallised limestone, making extraction of the fossils extremely difficult. The shells are often decorticated and the internal structures can usually only be observed in the apical parts (see MARTÍNEZ CHACÓN & WINKLER PRINS 2006). Although isolated specimens are not uncommon, only levels with rich faunas (forming lenticles), such as those at Latores (DELÉPINE & LLOPIS LLADO 1956; MARTÍNEZ CHACÓN 1979; MARTÍNEZ CHACÓN & WINKLER PRINS 2007), Cármenes and Valdeteja (WINKLER PRINS 1968, 1971), proved useful for a detailed study, since one needs a sufficient number of specimens for identification of the taxa present. Even so, identifications are often insecure and the material proved sometimes insufficient to describe a new species or genus. The

Fig. 2. Stratigraphic columns of the type sections of the San Emiliano Formation (after VAN GINKEL & VILLA 1996: Fig. 3) and the Valdeteja Formation (after VILLA et al. 2001: fig. 2). B.F. = Barcaliente Formation; S.E.F. = San Emiliano Formation.

Table 1. List of fossil groups occurring in the Valdeteja Formation and authors who studied them.

Algae, Cyanobacteria and Problematica: RÁCZ (1964), RÁCZ & GERMS in WINKLER PRINS (1968), EICHMÜLLER (1985).

Fusulinidae: VILLA (1982, 1989, 1995), EICHMÜLLER (1985), VILLA et al. (2001).

Conodonts: TRUYOLS et al. (1984), MÉNDEZ & MENÉNDEZ ÁLVAREZ (1985), VAN DEN BOOGAARD & BLESS (1985).

Ostracoda: BLESS & SÁNCHEZ DE POSADA (1973), SÁNCHEZ DE POSADA (1976), BECKER (1982).

Trilobita: GANDL, in MARTÍNEZ CHACÓN (1979), GANDL (1987).

Porifera: GARCÍA-BELLIDO CAPDEVILA (2002).

Anthozoa: DE GROOT, in WAGNER (1963), DE GROOT, in WINKLER PRINS (1968, 1971), RODRÍGUEZ (1984), BOLL (1985), EICHMÜLLER (1985).

Crinoidea, Echinoidea: not yet studied.

Cephalopoda: WAGNER GENTIS, in MARTÍNEZ CHACÓN (1979). *)

Bivalvia: DELÉPINE & LLOPIS LLADO (1956).

Gastropoda: DELÉPINE & LLOPIS LLADO (1956).

Rostroconcha: BABIN et al. (1999).

Bryozoa: ERNST & WINKLER PRINS (2006, 2008).

Brachiopoda: DELÉPINE (1943), DELÉPINE & LLOPIS LLADO (1956), WINKLER PRINS (1968, 1971, 2007), TRUYOLS et al. (1984), WINKLER PRINS, in EICHMÜLLER (1985), MARTÍNEZ CHACÓN (1977a, 1977b, 1979), MARTÍNEZ CHACÓN & WINKLER PRINS (2006, 2007, 2008).

*) The specimen from Cármenes identified by WAGNER-GENTIS (in MOORE et al. 1971, pl. 6) as *Branneroceras branneri* and now considered to be a *Diaboloceras?* sp. (J. KULLMANN, pers. comm. 2.8.2006) comes from deposits lying disconformably (with a palaeokarst) upon the Valdeteja Formation, as one of us (C.F.W.P.) found out in July 2006.

richest levels are in the upper part of the formation of late Bashkirian to possibly earliest Moscovian age: Latores (the richest and most varied fauna) and Entrago in Asturias, and Valdeteja (with a succession of fossil horizons of different composition; see WINKLER PRINS 1971) and Cármenes in León; a fauna from San Emiliano is somewhat older, of early Bashkirian age (VAN GINKEL & VILLA 1996).

The rich and varied brachiopod faunas of the Valdeteja Formation are summarised in Table 2. The general aspect of the fauna as a whole is rather similar to that of the Viséan limestone faunas from northern Europe (Kohlenkalk, Mountain Limestone; see WOLFENDEN 1958; BRUNTON 1984), although on closer inspection many forms proved different (cf. MARTÍNEZ CHACÓN & WINKLER PRINS 2007: table 1),

corroborating the younger (essentially Bashkirian) age suggested by WINKLER PRINS (1968) and proven on fusulinids (see VILLA et al. 2001). The close resemblance with the brachiopod fauna from the Hare Fiord Formation (Ellesmere Island, Arctic Canada; see CARTER & POLETAEV 1998) supports the age identification, as do the Bashkirian elements known from the Donnbass (see Table 3). The large number of productides is remarkable, although well known for the Carboniferous-Permian seas, called “Productus” seas by SARYTCHEVA & SOKOLSKAYA (1959, 1960: 350). It will be no surprise that there is a great affinity of the brachiopod faunas of the Valdeteja Formation with those from the Cuera Limestones (28 genera in common, Table 3; see MARTÍNEZ CHACÓN & BAHAMONDE 2008), given the reefoid character of

Table 2. List of brachiopod species found in the Valdeteja Formation listed by locality.

Brachiopoda	Latores	Enrago	Valdeteja	Cármenes
<i>Caenanoplia</i> ? sp.	X			X
<i>Rugosochonetes</i> sp.	X	X		
<i>Plicochonetes</i> ? sp.	X			X
<i>Productina pectinoides</i> (Phillips, 1836)	X			
<i>Alitaria frechi</i> (Paeckelmann, 1931)	X		X	
<i>Rugivestis</i> ? sp.	X			X
<i>Quasiavonia</i> cf. <i>aculeata</i> (Sowerby, 1814)	X		X	
<i>Krotovia granulosa</i> (Phillips, 1836)			X	X
<i>Breileenia</i> ? sp.	X	X	X	X
<i>Incisiidae</i> gen. et sp. nov.			X	
<i>Limbifera</i> ? sp. nov.	X			
<i>Maemia archboldi</i> Martínez Chacón & Winkler Prins, 2008	X	X	X	X
<i>Duarte</i> sp.	X	X	X	
<i>Inflatia</i> sp.	X		X	
<i>Productus carbonarius</i> de Koninck, 1842			X	
<i>Productus concinnus</i> Sowerby, 1821	X	X	X	X
<i>Hystriulina</i> sp.	X	X	X	X
<i>Eomarginifera praecursor</i> (Muir-Wood, 1928)	X	X	X	X
<i>Alexenia</i> ? sp.	X	X	X	
<i>Pugilis</i> ? sp.	X			
<i>Bicarteria</i> ? sp.	X		X	X
<i>Latispinifera</i> cf. <i>chaykensis</i> Lazarev, 2000	X		X	
<i>Latispinifera</i> aff. <i>ivanovi</i> (Lapina, 1957)	X	X	X	X
<i>Admoskovia</i> cf. <i>aljutovensis</i> Lazarev, 2000		X		
<i>Buxtonia</i> ? sp.	X			
<i>Kochiproductus</i> ? sp.	X			X
<i>Echinaria</i> cf. <i>knighti</i> (Dunbar & Condra, 1932)	X	X	X	
<i>Echinoconchella</i> ? <i>elegans</i> (M'Coy, 1844)	X	X	X	X
<i>Echinoconchella</i> ? <i>venusta</i> (Thomas, 1914)	X			
<i>Pustula</i> ? sp.			X	
<i>Balakhonia</i> ? <i>continentalis</i> (Tornquist, 1895)			X	X
<i>Fluctuaria undata</i> (Defrance, 1826)		X		X
<i>Fluctuaria</i> sp.	X		X	
<i>Marginovatia</i> ? sp.	X	X	X	X
<i>Liraria</i> ? sp.	X			
<i>Ovatia</i> cf. <i>laevicosta</i> (White, 1861)	X	X	X	
<i>Plicatiferina sinecosta</i> (Martínez Chacón, 1979)	X		X	X
<i>Miropductus posadai</i> gen. et sp. nov.	X	X		
<i>Retroplexus</i> ? sp.	X			
<i>Ovetina tuyolsi</i> gen. et sp. nov.	X			
<i>Meekella</i> sp.	X	X	X	
<i>Meekella</i> ? ex gr. <i>gigantea</i> Stuckenberg, 1905	X	X		
<i>Schuchertella</i> sp.	X		X	
<i>Streptorhynchus</i> ? cf. <i>subpelargonatus</i> sensu Demanet, 1934	X			
<i>Rhipidomela michelini</i> (Léveillé, 1835)	X		X	X
<i>Orthotichia</i> ? sp.	X	X		X
<i>Pugnax</i> aff. <i>acuminatus</i> (Sowerby, 1822)	X			X
<i>Pugnoides rosae</i> Martínez Chacón, 1979		X		
<i>Callaiapsida alcaldei</i> (Martínez Chacón, 1977)	X	X		X
<i>Psilocamara</i> sp.	X			
<i>Lambdarina</i> ? sp.			X	
<i>Rhynchopora nikitini</i> (Tschernyschew, 1885)	X			
<i>Rhynchopora</i> sp.	X			
<i>Trasgu minor</i> Martínez Chacón, 1979	X	X		
<i>Yanishewskiella globosa</i> Martínez Chacón, 1979		X	X	

Table 2 cont.

Rhynchonellida indet. A	X				
Rhynchonellida indet. B	X				
Cleiothyridina sp.	X	X			
Cardiothyris sp. nov.		X			
Athyrididina indet.	X	X			
Hustedia sp.	X				
Crurithyris cf. urei (Fleming, 1828)	X	X	X	X	
Tiramnia aff. walteri Carter & Poletaev, 1998	X	X			X
Donispirifer? sp.		X			
Anthracospirifer cf. solenensis Poletaev, 2001	X	X			
Anthracothyris? sp.	X		X	X	
Alphachoristites (Prochoristites)? sp.	X		X		
Parachoristites sp.	X				
Gypospirifer sp.	X				
"Neospirifer" ex gr. dunbari King, 1933		X	X	X	
Cantabriella sp.	X				X
Brachythyris? sp.	X				
Meristorygma sp.	X		X		
Kitakamithyris? sp.	X				
Phricodothyris ovata (Chao, 1929)	X	X	X	X	
Punctospirifer? sp.	X				
Altiplecus sp.					X
Crenispirifer sp.		X	X		
Spiriferellinidae indet.	X				
Girtyella llopisi Martínez Chacón & Winkler Prins, 2008	X	X	?	?	
Dielasmella? delepinei M. Ch. & W. P., 2008	X	X			X
Gillediinae gen.et sp. nov.		X			
Terebratulida indet. A		X			
Terebratulida indet. B		X			
	84	66	38	37	30

these limestones and the fact that the brachiopods are from levels of the same age (late Bashkirian-early Moscovian). There is also a strong similarity with the brachiopods from the San Emiliano Formation (23 genera in common, Table 3), which however lack the specialised forms characteristic of a reefoid environment.

4. Palaeoecological remarks

The brachiopods of the Valdeteja Formation are characteristic of shallow water faunas of a well oxygenated, warm sea with wave action and in particular for the carbonate platforms with reefoid structures (we use "reefs" in the broad sense of FLÜGEL & KIESSLING 2002: "laterally confined biogenic structures, developed by the growth or activity of sessile benthic organisms and exhibiting topographic relief and [inferred] rigidity.") in contrast to the Mississippian semi-pelagic "quiet-water" faunas (see for example MARTÍNEZ CHACÓN & WINKLER PRINS 1993; SÁNCHEZ DE POSADA et al. 2001). The bottom was stable enough

to support a varied fauna and flora. Many forms characteristic for a reefoid environment, similar to those from the Viséan (e.g., MUNDY & BRUNTON 1986; BRUNTON & MUNDY 1986, 1988; BRUNTON et al. 1994) and Permian (GRANT 1971; COOPER & GRANT 1975) are found especially among the strophalosiidines. The productides of this suborder normally were fixed to the substrate by cementation of the ventral valve or by rhizoid spines.

Four strophalosiidine species are present in the Valdeteja Formation, belonging to different superfamilies of this suborder. The strophalosioid *Plicatiferina sinecosta* (MARTÍNEZ CHACÓN, 1979) (Fig. 3.1-3.2) is one of the most abundant species from Latores, occurring also at Valdeteja and other localities in the Cantabrian Mountains of the same age. The genus is also known from the Pennsylvanian of the Urals and its prolongation, reaching into the Canadian Arctic. Two species, each represented only by a few specimens, were assigned to the aulostegoid subfamily Institellinae; both are considered typical of a reef community and are compared with species from the

Table 3. List of brachiopod genera found in the Valdeteja Formation compared with other formations in the Cantabrian Mountains and with other areas in order to show their palaeogeographic distribution.

genus	Valdeteja	Cuera	San Em	Hare Fi	Vis. NW E	Alps	Donnb	Urals	Spitsb	Texas P.
<i>Caenanoplia</i>	x									
<i>Rugosochonetes</i>	X		X		X	X	X	X		
<i>Plicochonetes</i>	x				X					
<i>Productina</i>	X				X		X	X		
<i>Alitaria</i>	X	x	X		X					
<i>Rugivestis</i>	X			X				X		X
<i>Quasiavonia</i>	X		x		X	x				
<i>Krotovia</i>	X	X	X	X	X	X	X	X	X	
<i>Breileenia</i>	x				X		X			
<i>Incisiinae gen. nov.</i>	X		X				x			
<i>Limbifera</i>	x	X			X					
<i>Maemia</i>	X	X		X				X		
<i>Duartea</i>	X							x	x	
<i>Admoskovia</i>	x	X					X			
<i>Bicarteria</i>	x	x	x						X	
<i>Latispinifera</i>	X		x						X	
<i>Inflatia</i>	X	X			X					
<i>Productus</i>	X		x		X		X	X		
<i>Hystriculina</i>	X	X	X	x		x	X	X	x	X
<i>Eomarginifera</i>	X		X	X	X					
<i>Alexenia</i>	x	x				x		X		
<i>Pugilis</i>	x				X					
<i>Buxtonia</i>	x				X		X	X	X	
<i>Kochiproductus</i>	x				X			X		X
<i>Echinaria</i>	X	X		x				X	x	X
<i>Echinoconchella</i>	X				X				X	
<i>Pustula</i>	x				X		X			
<i>Fluctuaria</i>	X	X		X	X		X	X		
<i>Marginovatia</i>	x									
<i>Ovatia</i>	X		X		X			X	X	
<i>Balakhonia</i>	X							x		
<i>Liraria</i>	x	X		X						X
<i>Plicatiferina</i>	X	X	X	X				X		
<i>Retroplexus</i>	x				X					
<i>Ovetina</i>	X									
<i>Mioproductus</i>	X									
<i>Meekella</i>	X							X	X	
<i>Schuchertella</i>	X	X			X		X			x
<i>Streptorhynchus</i>	X				X	X		X	X	x
<i>Rhipidomella</i>	X	X	X	X	X	x		X	X	X
<i>Orthotichia</i>	X	X	X	X				X	X	X
<i>Pugnax</i>	X	x			X		X			
<i>Pugnoides</i>	X									
<i>Callaiapsida</i>	X	X	X					X	X	
<i>Psilocamara</i>	X									X
<i>Yanishewskiella</i>	X					x		X		
<i>Lambdarina</i>	x				X					
<i>Rhynchopora</i>	X	x		X		x		X	X	X
<i>Trasgu</i>	X									
<i>Cleiothyridina</i>	X	X	X		X	x	X	X	X	X
<i>Cardiothyris</i>	X									
<i>Hustedia</i>	X	X	X	X	X	X		X	X	X
<i>Crurithyris</i>	X	X	X	X	X	X		X	X	X
<i>Tirannia</i>	X	X	x	X				X		
<i>Donispirifer</i>	x	X		X			X	X		

Table 3 cont.

<i>Anthracospirifer</i>	X	X	X	X		X	X			
<i>Anthracothyrina</i>	x	X	X	x	x		X			
<i>Alphachoristites (Prochoristites)</i>	X	X	X				X	X		
<i>Parachoristites</i>	X	X	x	X			X	X		
" <i>Neospirifer</i> "	x		X			x	x	x		
<i>Gypospirifer</i>	X	X		x						
<i>Cantabriella</i>	X	X	X	X		x				
<i>Brachythyris</i>	x	x		X	X	x		X		
<i>Meristorygma</i>	X	X		X						
<i>Kitakamithyris</i>	x							X		
<i>Phricodothyris</i>	X	X	X	X	X		X	X		X
<i>Crenispirifer</i>	x									X
<i>Punctospirifer</i>	x				X			X	X	
<i>Girtyella</i>	X				X					
<i>Gilleidae</i> gen. nov.	X									
<i>Dielasmella</i>	x									

upper Viséan of NW Europe. One of them, *Retroplexus* sp., is included in a genus known from the last-mentioned area and age; the other is new and the type species of a new genus (*Ovetina truyolsi* gen. et sp. nov.). The forth species is very interesting because it is the second richthofenioid known from the Cantabrian Mountains: *Miroproductus posadai* gen. et sp. nov. *Miroproductus* is, together with the North American *Ardmosteges*, one of the earliest representatives of this coral-like superfamily. The only other richthofenioid, *Zalvera* sp., was described from a Moscovian limestone in the eastern part of the Cantabrian Mountains by BRUNTON (1996).

The productides of the Suborder Productidina generally were adapted to a soft substrate, but some species from the Valdeteja Formation show also structures considered to be adaptations to reef-dwelling, such as an enlargement and modification of its trail leading to the development of a flange or gutter, as in *Admoskovia* cf. *aljutovensis* LAZAREV, 2000 (Fig. 3.3), a species from the lower Moscovian (Vereyan) of the Moscow region (the genus is also known from

the Cuera Limestone). A gutter is also developed in *Limbifera?* sp. nov. (Fig. 3.4), a rare species better preserved in the Cuera Limestone (MARTÍNEZ CHACÓN & BAHAMONDE 2008: fig. 2B-C). The trail could also extend anteriorly, forming a fold, as in *Rugivestis?* sp. (WINKLER PRINS 2007, fig. 1A-B), probably a new species of a genus known from the Permian of North America and Russia, but also from the upper Bashkirian of Arctic Canada and Alaska (CARTER & POLETAEV 1998; LAZAREV & CARTER 2000). In *Alitaria frechi* (PAECKELMANN, 1931), one of the most abundant species at Latores and Valdeteja, the trail is also extended (Fig. 3.5). The maximal development of the trail is observed in *Productus concinnus* (SOWERBY, 1821) (Fig. 3.6-3.7). On the other hand, some productides, such as the small *Incisiini* gen. et sp. nov., have probably lived sheltered on the platform.

The orthotetides are another group of brachiopods which normally lived cemented to the substrate by the umbo of its pedicle valve. In the Valdeteja Formation, they are represented by four species (Table 2), e.g.,

Fig. 3. 1-2 – *Plicatiferina sinecosta* (MARTÍNEZ CHACÓN, 1979), two specimens, DPO 8850-8851, in ventral view, showing the clasping spines (arrows) attached to a crinoid stem, Latores; 3 – *Admoskovia* cf. *aljutovensis* LAZAREV, 2000, DPO 127807, in ventral view showing the gutter, Entrago; 4 – *Limbifera?* sp. nov., DPO 9445, ventral view of an incomplete specimen, Latores; 5 – *Alitaria frechi* (PAECKELMAN, 1931), DPO 9399, lateral view, Latores; 6-7 – *Productus concinnus* (SOWERBY, 1821) showing the great development of the trail, 6 – DPO 10078, ventral valve, 7 – DPO 10080, mould of dorsal disc, and ventral trail, Entrago; 8 – *Meekella?* ex gr. *gigantea* STUCKENBERG, 1905, DPO 127808, ventral view, Latores; 9 – *Streptorhynchus?* cf. *subpelargonatus* sensu DEMANET, 1934, DPO 127809, Latores; 10 – *Parachoristites* sp. DPO 127810, ventral valve, Latores; 11-12 – *Alphachoristites (Prochoristites)* sp., DPO 127811, ventral valve in ventral and posterior views, Latores. Scale bars = 2 mm.

Fig. 3 (Legend see p. 98)

a large species probably belonging to the genus *Meekella* (*M.*? ex gr. *gigantea* STUCKENBERG, 1905; Fig. 3.8), and *Streptorhynchus*? cf. *subpelargonatus* sensu DEMANET 1934, with a cicatrix and high ventral interarea (Fig. 3.9).

Many other brachiopod genera occurring in the Valdeteja Formation are common in a reef environment but occur also in other deposits, such as the orthids *Rhipidomella* and *Orthotichia*, the rhynchonellids *Callaiapsida* and *Lambdarina*, the latter being a small rhynchonellide, which lived sheltered in the reef (e.g., BRUNTON & CHAMPION 1974; BASSETT & BRYANT 1993: 518), possibly attached to algae or bryozoans. *Rhynchopora* also appears to be characteristic of a reef environment in Pennsylvanian and Permian times. This genus may have been derived from the Viséan genus *Tretorhynchia*. Several species of Athyrididina and the Retziidina *Hustedia* lived on the reefs, but not exclusively so since they were not particularly adapted to them. The same holds true for many representatives of the Spiriferida (*Crurithyris*, *Tiramnia*, *Anthracospirifer*, “*Neospirifer*”, *Gypospirifer*, *Phricodothyris*) and Spiriferinida (*Punctospirifer* and *Crenispirifer*), but some forms were particularly well adapted to agitated water through their relatively large interareas (*Cantabriella*) and large size (*Parachoristites* [Fig. 3.10] and *Alphachoristites* (*Prochoristites*) [Fig. 3.11-3.12]). However, *Cantabriella* and *Alphachoristites* are also found in mudstone. The Terebratulida have no apparent adaptations to life on a reef, other than their pedicle attachment.

5. Palaeobiogeographic connections (Table 3)

The Viséan brachiopods from NW Europe (WOLFENDEN 1958; BRUNTON 1966, 1968, 1984, 1987; BRUNTON & MUNDY 1988; BRUNTON & TILSLEY 1991; BRUNTON et al. 1994; HARPER & JEFFREY 1996) show close similarities at the generic level with the Valdeteja faunas, but for a large part these similarities could be due to the fact that specimens corresponding to new genera were provisionally attributed to Viséan

genera, which show the same adaptations to life on a reef.

The relationship shown by the Pennsylvanian brachiopod faunas of the Cantabrian Mts with those from the Carnic Alps, Karavanke Mts (e.g., RAMOVŠ 1971; WINKLER PRINS 1983; MARTÍNEZ CHACÓN & WINKLER PRINS 1993) and Bükk Mts (GULYÁS-KIS 2004) of Central Europe are less evident for the brachiopods from the Valdeteja Formation, due to their somewhat older age and different environment. The latter plays also a role when comparing the Valdeteja brachiopods with those from the Donbass (Ukraine) and particularly the Moscow Platform (Russia). In the Urals, the carbonate platforms are poorly developed in the Bashkirian and the brachiopod faunas become richer towards the Permian, thus preventing a close comparison.

The close relationship with the brachiopods from the Hare Fiord Formation of Ellesmere Island (Canadian Arctic) – especially at the generic level, and much more so than with Spitsbergen and Greenland – is explained by the similar age and environment of that formation: upper Bashkirian or lower Moscovian bryozoan reef mounds (CARTER & POLETAEV 1998: 106). Still, it seems very likely that the connection was through the Urals and the Arctic, although a direct connection through a branch of the Iberian-Mid-continent seaway cannot be excluded (see for example ERNST & WINKLER PRINS 2008).

The connections with the Pennsylvanian faunas from the American Midcontinent were rather poor (see WINKLER PRINS 1983), but there are definite links with the Permian reef faunas from Texas (COOPER & GRANT 1972-1977), which could have been through the Canadian Arctic. The presence of several taxa in Texas that may have been derived from NW Europe (cf. MUNDY & BRUNTON 1986) and which have no direct relatives known from the Canadian Arctic (and only partly from the Cantabrian Mts) is puzzling, but the excellent preservation of specimens from Great Britain and Texas with their spines attached make a direct comparison with the less well preserved Hare

Fig. 4. *Ovetina truyolsi* gen. et sp. nov. **1-2** – Holotype, DPO 38833, ventral and dorsal views; **3** – DPO 38834, decorticated dorsal interior with part of dorsal external mould, and gutter; **4** – DPO 38836, internal view of an incomplete ventral valve; **5** – DPO 38835, dorsal external mould and gutter; **6** – DPO 38837, dorsal view of a some decorticated and fragmentary specimen. **7-8** – DPO 39487, ventral view of a decorticated ventral valve with posterior part of ventral internal mould, showing median septum, muscle scars and large spines in left side; and internal view of the posterior part of valve. Scale bars = 2 mm.

Fig. 4 (Legend see p. 100)

Fiord and Spanish material difficult. Furthermore, these specialised forms are rather rare and could have been missed in the less extensively studied areas in Canada and Spain. These differences are in part due to the fact that brachiopods of British Isles and Texas are silicified and so much easier to extract from limestone.

6. Conclusions

The late Bashkirian-early Moscovian subsiding basin with carbonate platform deposits of the Valdeteja Formation in the Cantabrian Mountains was ideal for rich and varied benthonic faunas, especially brachiopods, and has apparently played an important role in providing a niche for the survival of reef-related brachiopod faunas during the Pennsylvanian, bridging the gap between the Mississippian brachiopods from reefoid deposits in northern Europe and the Permian faunas from reefs in the Urals and Texas. Surprisingly, they have their counterpart on Ellesmere Island in the Canadian Arctic, another refuge for these brachiopods during the Bashkirian-Moscovian, although the rare new forms specialised to a reef environment described below are missing there.

7. Systematic palaeontology

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

Order Productida SARYTCHEVA & SOKOLSKAYA, 1959
 Suborder Strophalosiidina WATERHOUSE, 1978
 Superfamily Aulostegoidea MUIR-WOOD & COOPER, 1960
 Family Aulostegidae MUIR-WOOD & COOPER, 1960
 Subfamily Institellinae MUIR-WOOD & COOPER, 1960

Genus *Ovetina* nov.

Type species: *Ovetina truyolsi* gen. et sp. nov.

Etymology: The genus is named after the city of Oviedo (L: *Ovetus*) near which the type species was found.

Diagnosis: Institellinae with a semielliptic outline and weakly developed sulcus, ventral interarea with delthyrium filled by pseudodeltidium and lophidium, rather large cicatrix, ears small; rugose visceral ornamentation, becoming reticulate on the anterior part of corpus, trail costate, gutter well developed all around the margin; row of thin spines along hinge, row of large spines separating the ears and a few spines scattered on ventral visceral area. Dorsal valve concave with weakly developed fold, without interarea; ornamentation similar to that of the ventral valve but without spines; long median septum rising anteriorly from between the muscle scars, cardinal process externally bilobed.

Species included: Type species only.

Comparisons: The genus appears to have derived from *Sinuatella* MUIR-WOOD, 1928, from which it is distinguished by its weakly developed sulcus, large cicatrix, lack of costae on the posterior part, thin spines along the hinge and large spines separating the ears, which appear to be smaller than in *Sinuatella* (cf. BRUNTON & MUNDY 1988: 66 f.).

Ovetina truyolsi gen. et sp. nov.

Fig. 4

2008 Institellinae gen. et sp. indet. – MARTÍNEZ CHACÓN & WINKLER PRINS, p. 195.

Etymology: The species is named after the highly esteemed professor emeritus Jaime TRUYOLS SANTONJA, father of the palaeontological school of Oviedo (see SÁNCHEZ DE POSADA & GARCÍA-ALCALDE 1999).

Type locality and horizon: Latores, 6 km SW of Oviedo (Asturias, N Spain) (Fig. 1); light gray limestone, upper part of the Valdeteja Formation, upper Bashkirian.

Material: Holotype, DPO 38833 (Fig. 4.1-4.2), and other 6 specimens, DPO 38834-38838, 39487, all from the type locality.

Fig. 5. *Miropoductus posadai* gen. et sp. nov. **1-3** – Holotype, DPO 9440, 1: lateral view (the specimen is partly decorticated) showing the wide flange with the mould of three protective endospines, the aulacotermia and the line of junction of the two stages of growth; 2: posterior view (the apical region is broken) showing the section of dorsal valve (arrowed) and the trail without endospines; 3: fragment of ventral interior showing endospines and aulacotermia; **4-5** – DPO 9453, ventral and posterior views; **6-9** – DPO 38839, 6-7: two specimens, *a* on the left hand and *b* on the right hand, in ventral and ventral anterior views showing the ring of spines around the venter; 8: view from the specimen *b* showing the development of an irregular fold; 9: lateral view of specimen *a*; **10-12** – DPO 38841, 10: lateral view showing the flange with protective spines (arrowed); 11: dorsal view of the flange (arrowed the same spines as in 10); 12: posterior view showing the irregular extensions of shell filling the region above the hinge line. All the specimens are from the type locality. Scale bars = 2 mm.

Fig. 5 (Legend see p. 102)

Diagnosis: The genus is monospecific, so the generic diagnosis also applies to the species.

Description: Medium size: the holotype (an incomplete specimen lacking the bordering gutter) is 18.08 mm length and 25.25 mm width; the biggest specimen (DPO 38835, Fig. 4.3) reaches 24.12 mm length and ~36.50 mm width. Outline nearly semielliptic; maximum width at hinge line; strongly concavoconvex with shallow corpus cavity. Ornamentation of both discs by concentric regular rugae (about 5 per 5 mm in front of cicatrix); becoming reticulate on the anterior part of corpus and costate on trails (some 9-10 costae per 5 mm on trail); growth lines on trails may be lamellose. Gutter well developed all around the margin, reaching 6.40 mm in DPO 38836 (Fig. 4.4).

Ventral valve with weakly convex disc, abruptly bending to the trail. A weak median sulcus beginning at the anterior part of corpus and extends to the gutter. Interarea reaching almost 3 mm height; delthyrium filled by pseudodeltidium and lophidium; beak indistinct, not projecting posteriorly; large cicatrix of attachment reaching in the holotype 7 mm length and 10.8 mm width. Row of thin spines along hinge, row of thick rhizoid spines separating the ears and a few fine spines scattered on disc. Muscle scars well developed, separated by a median septum, with adductors and diductors well differentiate; interior surface pustulose, with pustulae forming ribs immediately before the interior of gutter; other internal details unknown.

Dorsal valve concave, with weakly developed fold, without spines. Internal characteristics difficult to observe: cardinal process externally bilobed, long median septum rising anteriorly from between the muscle scars, lateral ridges probably parallel to the hinge; other internal details not observed.

Discussion: For a comparison with *Sinuatella sinuata* (DE KONINCK, 1851) see the generic description. This species was listed by the authors as *Institellinae* gen. et sp. indet. (MARTÍNEZ CHACÓN & WINKLER PRINS 2008).

Superfamily Richthofenioidea WAAGEN, 1885
Family Cyclacanthariidae COOPER & GRANT, 1975
Subfamily Teguliferinae MUIR-WOOD & COOPER,
1960

Genus *Miroproductus* nov.

Type species: *Miroproductus posadai* gen. et sp. nov.

Etymology: The name refers to a "*Productus*" with peculiar (L: *mirus*) characteristics.

Diagnosis: Sphenoid (obliquely conical) ventral valve having an early aulostegid phase with large cicatrix and rhizoid spines, followed with an abrupt vertical bend by a richthofenioid stage with lateral margins of trails fused posteriorly and resting on the upper surface of the vestigial interarea; interior of valve shows a wide flange with protective spines emerging from its internal border at the anterior margin. Opercular dorsal valve apical throughout growth, leaving a vestibule above it.

Species included: Type species only.

Comparisons: *Miroproductus* resembles *Ardmosteges* (admirably described and depicted by SUTHERLAND 1996) in its primitive richthofenioid character with an early aulostegid stage of growth. However, the aulostegid stage is better developed in our genus in detriment of the richthofenioid, which only reaches the last few millimetres of the shell. Moreover, both genera differ in that a wide internal flange bearing protective spines is developed in *Miroproductus*, which also has a larger cicatrix and a ventral cone shorter than that of *Ardmosteges*.

The early growth stages of *Miroproductus* resemble those of the genus *Institina* MUIR-WOOD & COOPER, 1960, especially the illustration of *I. marginalis* (DE KONINCK, 1847) in the new *Treatise* (BRUNTON et al. 2000, fig. 428.1e), which looks to have similar spines and flange, although in our material the growth continues after the development of the flange.

Discussion: SUTHERLAND (1996) proposed that his genus *Ardmosteges* evolved from an aulostegid ancestor, the upper Mississippian genus *Sinuatella* MUIR-WOOD, 1928 being the most likely candidate. *Miroproductus* is also at the base of Richthofenioidea; its characteristics corroborate the aulostegid origin for this superfamily as proposed by Sutherland. It is remarkable that both genera are of a similar (Bashkirian) age. However, the late Viséan genus *Institina* is more likely to be the ancestor of *Miroproductus* rather than *Sinuatella* (since they have the same initial general shape).

Miroproductus posadai gen. et sp. nov.
Figs. 5-6

1979 *Alitaria frechi* (PAECKELMANN, 1931). – MARTÍNEZ CHACÓN, p. 144 (pars).

Fig. 6. *Miroproductus posadai* gen. et sp. nov. **1-4** – DPO 38842, postero-ventral, lateral, posterior and lateral (the other side) views showing cicatrix, posterior spine bases, extensions of shell filling the region above the hinge (3), line of junction between aulostegid and richthofenioid stages, and one irregular lateral fold (1, 4), Latores; **5-7** – DPO 38851, La Manjoya, 5-6: lateral and posterior views; 7: fragmentary ventral interior; **8-10** – DPO 38854, dorsal, dorsal tilted and lateral views of an incomplete juvenile specimen showing the concentric ornamentation, Entrago; **11-13** – DPO 38853, Entrago, 11-12: ventral and dorsal views of a juvenile specimen showing the interarea; 13: dorsal external mould; **14** – RGM 288957, ventral view, Latores. Scale bars = 2 mm.

Fig. 6 (Legend see p. 104)

Table 4. Measurements (in mm) of *Miroproductus posadai* gen. et sp. nov.

Number	Length	Width	Hinge width	Height	Surface length
DPO 38853	6.95	8.77	5.72		15.67
DPO 38854	8.89				17.67
Holotype	19.2	20.63		18.16	
DPO 9453	13.96	>14.05		13.38	>24.22
DPO38839b	12.53	14.41	3.98	12.57	19.13
DPO 38839a	12.52	11.63	3.32	10.61	18.4
DPO 38840	12.28	>13.97	5	12.24	~20.21
DPO 38841	16.51	~18.93	6.06	11.53	~27.12
DPO 38851	17.88	18.94	6.33	15.71	28.62
DPO 38852	13.83	14.82	5.1		
DPO 38842	17.65	17.29	5.08	16.04	24.92
DPO 38843	>12.33	>15.41	5.7	>11.51	>22.08
RGM 290597	13.0	13.0	10.4		
RGM 288961	8.0	14.6	14.6	>5	
RGM 288958	9.0	10.6	9.7	>4	

2007 *Institina?* sp. – WINKLER PRINS, pl. 1, fig. 4 (pars, non fig. 5).

2008 *Institina?* sp. – MARTÍNEZ CHACÓN & WINKLER PRINS, p. 195.

Etymology: The species is named after Professor LUIS C. SÁNCHEZ DE POSADA (Department of Geology, Oviedo University), husband of M. L. MARTÍNEZ CHACÓN, who helped a lot collecting the material in the field.

Type locality and horizon: Latores, 6 km SW of Oviedo (Asturias, N Spain) (Fig. 1); light gray limestone, upper part of the Valdeteja Formation, upper Bashkirian.

Material: Holotype, DPO 9440 (Fig. 5.1-5.3), and 23 other specimens, DPO 9434-9435, 9453, 9180B, 38839-38850, and RGM 288957, 288961, 290597 from the type locality; two specimens, DPO 38851-38852, from La Manjoya, a locality close to the type one; and two specimens, DPO 38853-38854 from Entrago (Teverga, Asturias, Fig. 1; this is loc. B129 of MARTÍNEZ CHACÓN 1979). All from the upper part of the Valdeteja Formation, upper Bashkirian.

Diagnosis: The genus is monospecific, so the generic diagnosis also applies to the species.

Description: Ventral valve with interarea well visible in early growth stages; delthyrium closed (it is impossible to discriminate the kind of plate); beak indistinct, not projecting posteriorly. Hinge line relatively narrow; postero-lateral extremities of dorsal valve project laterally and fit in articulation grooves located just anteriorly to the extremities of the ventral interarea (Fig. 6.12). Large, flat cicatrix of attachment reaching some 6 mm in length. A few millimetres in front of this cicatrix, the valve becomes dorsally geniculated; at the same time, the shell began to fill gradually the posterior region above the hinge line by adding shell material posteriorly to the lateral slopes, as far as they became fused on the upper surface of the interarea, at a short distance from the apex, leaving clear vestiges of

this structure. This process continues until the posterior margin equalled the anterior trail; then, growth bands became continuous around the valve for a few millimetres (up to 5.5 mm in DPO 38842, Fig. 6.3). A clear line marks the junction of the two kinds of growth (Figs. 5.1-5.2, 6.1, 6.3). Externally, the growth lines or bands, which are irregular in the posterior region, sometimes give rise to rugae. Patches of rhizoid spines are situated on the posterior part, at both sides of venter; moreover, circular spine bases are situated close to each other forming a ring around the venter, just before the geniculation; on the rest of the cone, scattered spine bases are seen; the posterior part of the venter has thinner spine bases. The ventral valve shows a thickening around its interior (the aulacoterma) on which the dorsal valve rests when the shell is closed (Fig. 5.1, 5.7-5.8, 5.10), so leaving a vestibule above it. At some distance in front of the aulacoterma, a wide flange is developed, all around the valve; the internal border of the flange bears protective spines except, apparently, in the region above the interarea (see the holotype, Fig. 5.2).

Dorsal valve opercular, remaining in its original position throughout growth; exterior only known in juvenile specimens, with even growth lines and no spines; cardinal process extending posteriorly above hinge; other internal details not observed.

Owing to the attachment, the general aspect of the shell is irregular. The ventral cones are oblique in many specimens but they become vertical with growth. Two specimens develop irregular, more or less vertical folds (Figs. 5.8, 6.1, 6.4). In some cases, the upper part of the cone is undulate.

Measurements of some specimens are given in Table 4. They were taken in the same way as SUTHERLAND did (1996, fig. 9).

Discussion: The earliest formed part of the shell, with geniculated dorsal valve, the internal thickening of the aulacoterma and the ring of big spine bases resemble a marginiferid in the sense of the old *Treatise* (MUIR-WOOD 1965). For this reason, the holotype (which was partially

included in the matrix) and other four specimens were previously put in the species *Alitaria frechi*, which is very abundant in the locality of Latores (MARTÍNEZ CHACÓN 1979; MARTÍNEZ CHACÓN & WINKLER PRINS 2007). As stated before, *Miroproductus* also resembles *Institina*; and this species was listed by us as *Institina?* sp. (MARTÍNEZ CHACÓN & WINKLER PRINS 2008; WINKLER PRINS 2007).

The differences between the new species and *Ardmosteges orchamus* SUTHERLAND, 1996, type species of the monospecific genus, are the same as those between *Ardmosteges* and *Miroproductus*.

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Addresses of the authors:

MARTÍNEZ CHACÓN, M. L., Departamento de Geología, Universidad de Oviedo, Arias de Velasco s.n., 33005 Oviedo, Spain;
E-mail: mmchacon@geol.uniovi.es

WINKLER PRINS, C. F., Nationaal Natuurhistorisch Museum, P.O. box 9517, 2300 RA Leiden, The Netherlands;
e-mail: winkler@nnm.nl