



Original article

Pennsylvanian brachiopod, fish and conodont faunas from the Caliza Masiva (San Emiliano Formation) at the Mina Profunda area, Cantabrian Zone, NW Spain

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ABSTRACT

A rock sample obtained from the Caliza Masiva of the San Emiliano Formation (Bashkirian–early Moscovian) in the Mina Profunda area (NE Villamanín) of the Bodón Nappe (Cantabrian Zone, NW Spain) has yielded numerous brachiopods and fish remains not frequently represented in the fossil record. The brachiopod assemblage comprises 13 taxa and is characterized by phosphatic (*Langella*, *Orbiculoidea*) as well as exceptionally preserved silicified calcitic elements (a small chonetid, *Composita*, *Crurithyris*, *Lambdarina*, and two minute terebratulids) as the main faunal components. Of special importance is the record of the microbrachiopod *Lambdarina winklerprinsi* nov. sp., which reduces the large Viséan–Upper Permian gap in the stratigraphic record of this genus. Conodont elements recovered from the same insoluble residue are indicative of the upper Bashkirian *Idiognathoides sulcatus parvus* Zone. The accompanying fish remains consist of chondrichthyan teeth and scales, an acanthodian scale and osteichthyan tooth-bearing bones, isolated teeth and isolated scales, representing the first Pennsylvanian ichthyoliths analyzed from the Cantabrian Zone. The limestone beds with selective silicification in the San Emiliano Formation provide an exceptional opportunity to improve our knowledge on the patterns of life diversity over geological time.

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1. Introduction

The San Emiliano Formation (Brouwer and van Ginkel, 1964) is a stratigraphic unit of the Bodón and Aramo nappes (*sensu* Alonso et al., 2009), which belong to the Cantabrian Zone, the most external zone of the Iberian Massif in NW Spain (Fig. 1). The San Emiliano Fm. is widely recognized due to its rich Bashkirian–early Moscovian fossiliferous content (van Ginkel, 1965; Sánchez de Posada et al., 1996; van Ginkel and Villa, 1996; Fig. 1). It consists of ca. 1800 m of alternating siliciclastic and carbonate rocks that according to their relative proportions in the type area were grouped into three members, namely the Pinos, La Majúa and Candemuela members from bottom to top (Bowman, 1982). This subdivision is applied elsewhere, with the exception of the study area, where the Pinos Mb., the Caliza Masiva (Moore et al., 1971) and the Villamanín beds (Truyols Santonja and Sánchez de Posada, 1983) have been distinguished in the formation (Fernández, 1993). Brachiopods are the most abundant macrofossils in this formation, especially in the La Majúa Mb., from which

45 different brachiopod species have been described (Martínez Chacón and Winkler Prins, 1985).

In the course of a recent stratigraphic and structural study in the Mina Profunda area (Cármenes, NE Villamanín), the Caliza Masiva was sampled for conodonts, for biostratigraphic and palaeothermometric purposes. After acid etching, the various samples were mostly devoid of fossils with the exception of one from the upper part of the unit. This sample yielded a unique microbrachiopod fauna, exceptionally preserved due to the silicification of its shells, a process that is not frequently reported in Carboniferous deposits (Schubert et al., 1997), especially those of the Pennsylvanian. For this reason, the study of the Pennsylvanian microbrachiopods dealt with in this paper sheds some light on the knowledge of a group of rather peculiar Pennsylvanian fossils.

Among these microbrachiopods, the presence of *Lambdarina winklerprinsi* nov. sp. must be emphasized. The stratigraphic distribution of *Lambdarina* is somewhat strange, probably reflecting biases in the fossil record related to the difficulties of finding and extracting these minute calcareous fossils with their shells preserved. Specimens of this genus have mostly been discovered accidentally, collected as silicified remnants from insoluble residues obtained during micropalaeontological procedures. Exceptionally, Muszer (2014) de-

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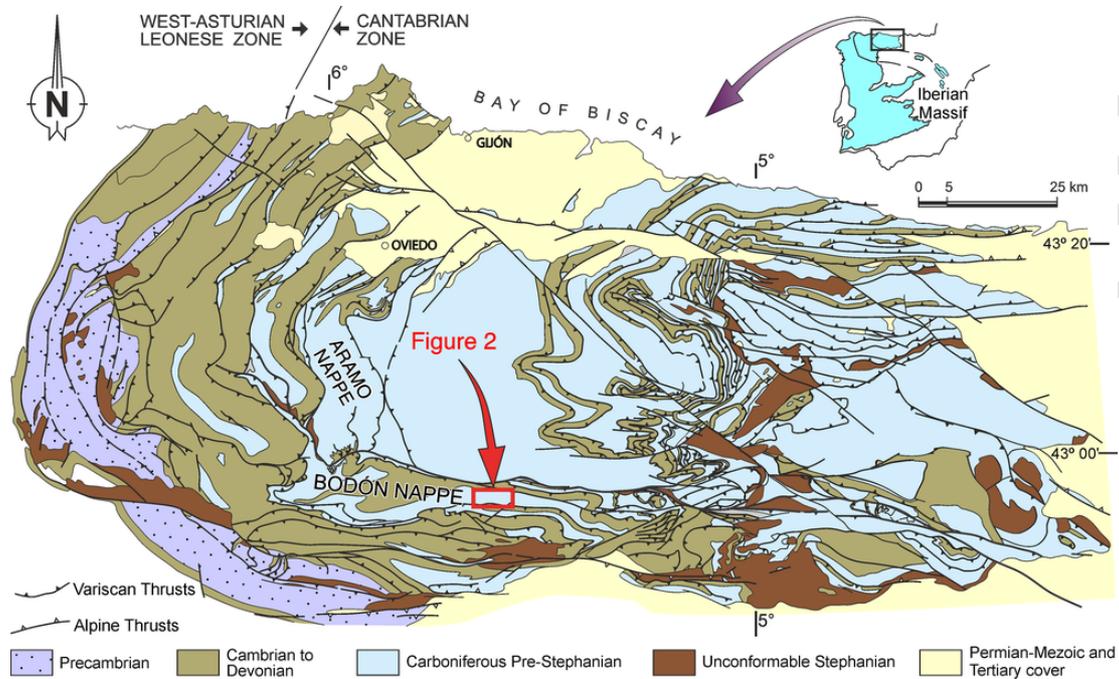


Fig. 1. Schematic geological map of the Cantabrian Zone with location of the study area (adapted from Alonso et al., 2015).

scribed *L. jugowiensis* (upper Viséan, Sudetes) from numerous non-silicified specimens at different growth stages, recovered by thermal fragmentation of limestones aided with sodium sulphate (Glauber's salt). Seven of the eight species of *Lambdarina* known to date are restricted to the Tournaisian–Viséan interval, and the eighth species comes from rocks as young as Late Permian. The new species described below, *L. winklerprinsi*, is late Bashkirian in age; it contributes to the filling of the late Viséan–Late Permian gap in the fossil record of the genus.

The brachiopod assemblage from Mina Profunda comprises 13 different taxa, including phosphatic (*Langella*, *Orbiculoidea*) and calcitic shells (a small chonetid, *Lambdarina winklerprinsi* nov. sp., *Composita*, *Crurithyris*, and two minute terebratulids) as the most conspicuous elements. Conversely, conodont elements are scarce in the sample, being represented by the cosmopolitan subspecies *Idiognathoides sulcatus parvus* Higgins et Bouckaert, which confirms a late Bashkirian age for the sampled interval. In addition, reports of fish remains as part of the associated fauna are frequent in microfossil collections from the Cantabrian Mountains, yet they have not been analyzed in detail so far. In the present contribution, the ichthyoliths from Mina Profunda are analyzed, providing further constraints on the biodiversity and palaeogeographic distribution of the early Pennsylvanian marine faunas from the Cantabrian Mountains.

2. Geological setting

The study area, to the NE of Villamanin (Fig. 2(A)), belongs to the southern branch of the Bodón Nappe. There, the San Emiliano Fm. contains a prominent calcareous unit, the Caliza Masiva of Moore et al. (1971), which forms a several km-long and up to some 330 m-thick carbonate body, sandwiched between the underlying shales with turbidites and carbonate breccias of the Pinos Mb. (previously referred to as the Villanueva beds by Bowman, 1982), and the overlying shales with limestones, sandstones and rare coals of the Villamanin beds.

In the recent study of the Mina Profunda area, the Caliza Masiva was found to exhibit a wide range of facies, from carbonate breccias, calcilithites and calciturbidites, to massive microbial micrites containing *Donezella* and skeletal limestones (cf. also Riding, 1979). These deposits are suggestive of sedimentation in moderately deep-basin to slope, platform-margin to slope, and shallow-shelf settings, respectively. They are arranged into tens-of-metre-thick cycles bound by minor unconformities. The Caliza Masiva has been ultimately dated as upper Bashkirian based on its fusulinid content (van Ginkel and Villa, 1996; van Ginkel, 2014), whereas spores point to a Langsetian (West-phalian A) age (Villa et al., 1988).

Contrary to other faunal elements, conodonts are uncommon in the San Emiliano Fm. The scarce findings, reported by Méndez Fernández (1990), consist of a few elements of *Idiognathoides parvus*, *I. macer* (Wirth), and *I. corrugatus* (Harris et Hollingsworth) from successive limestone beds at Fresnedo (Bodón Nappe, to the north of the type area of the formation), and *Idiognathoides* sp., *I. attenuatus* Harris et Hollingsworth and *Spreptognathodus* sp. from the type area of the formation.

3. Material and methods

Several beds of the Caliza Masiva in the Mina Profunda area were sampled for microfossils. Samples, sized 2–3 kg each, were digested in buffered acetic acid following the standard conodont laboratory procedures (Stone, 1987). Only one sample from the upper part of the Caliza Masiva, ca. 40 m below the top of the unit, was productive (Fig. 2(B)), which led to further intensive resampling. The sampled interval consists of cm- to dm-thick tabular beds of skeletal and lithoclastic pack- to grainstones, amalgamated or interleaved with dark-grey shales to marlstones. Beds display graded and/or parallel laminated divisions and their tops are sharp to gradational with the overlying shales/marlstones. Bioturbation is also scarce. Although field relationships are not clear, the studied beds sharply overlie an interval of massive (microbial?) limestones and pass laterally into similar massive limestones.

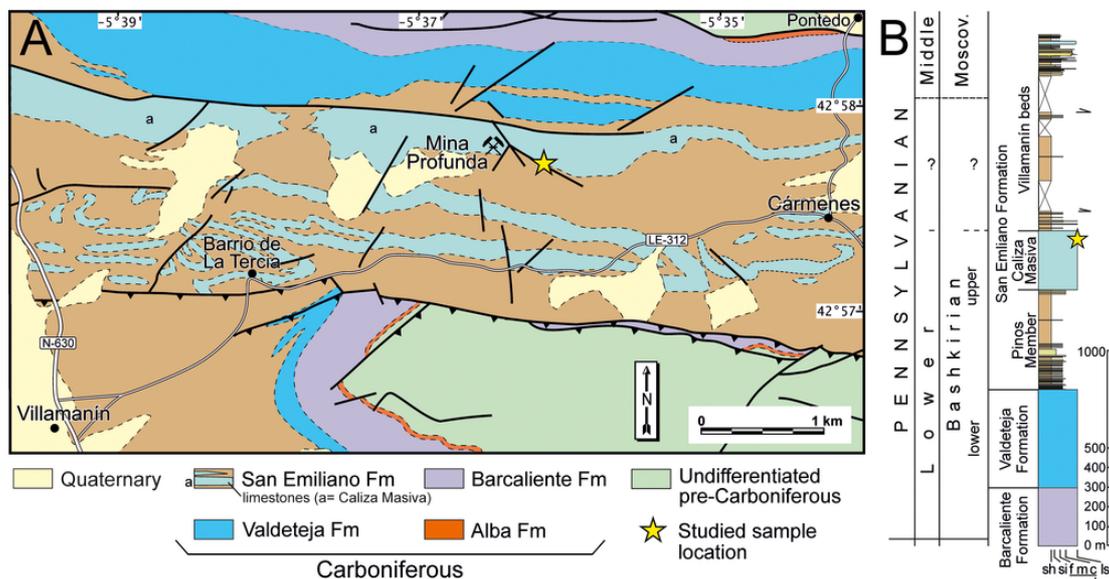


Fig. 2. A. Geological map of the Mina Profunda area (modified from Alonso et al., 1989). B. Simplified stratigraphic column of the San Emiliano Formation in the study area (adapted from Fernández, 1990), with the location of the studied sample.

Under the microscope, grains comprise mainly crinoid, bryozoan and brachiopod fragments. Sponge spicules are abundant in laminae whereas foraminifers and calcispheres are rare (Fig. 3). Micritic intraclasts and lithoclasts, and peloids are also common. Scattered quartz grains and ooids may be found. Grains are moderately to well sorted, and display a variable, often marked, parallel-to-bedding alignment and/or grading. Laterally, other beds with fish fragments are made of calcilithites with microbial micrite lithoclasts and intraclasts, sand to gravel in size, accompanied by large skeletal fragments of the same types described above, plus bivalves and gastropods.

After digesting ca. 18 kg of limestone from these beds, brachiopods, conodonts, and ichthyoliths were recovered. The brachiopod assemblage from the Mina Profunda area is diverse, represented

by 13 taxa. It is composed of phosphatic brachiopods (*Langella*, *Orbiculoidea*) as well as silicified calcitic brachiopods. The phosphatic brachiopods and most of the calcitic brachiopods have very small sizes even at adult stages (Caenanopliinae indet., *Lambdarina*, *Composita*, *Crurithyris*, Terebratulidina indet.). The brachiopod assemblage also includes some fragmented medium-sized specimens (*Maemia*, *Alexenia*, *Anthracospirifer*, *Anthracothyrina*, *Spiriferellina*). The conodont elements, despite being scarce, provide further biostratigraphic constraints. Images of the microfossils were obtained with a Zeiss AxioCam 506 camera attached to an Axio Scope.A1 petrographic microscope (Departamento de Geología, Universidad de Oviedo). Image stacking was conducted with Zerene Stacker and Adobe Photoshop.

The ichthyoliths represent a low diversity chondrichthyan and osteichthyan fauna mostly comprising isolated teeth and scales. Most of the specimens are highly fractured. The less damaged were studied under the light microscope, and imaged at the NHMUK using a Jeol JSM-IT500 Scanning Electron Microscope with an acceleration voltage of 15 kv at a pressure of 40 Pa.

All specimens are housed in the Departamento de Geología, Universidad de Oviedo (prefix DGO). They are preserved on microscope slides and some ichthyoliths on SEM stubs.

4. Brachiopod silicification

The silicification of the brachiopods from Mina Profunda is usually incomplete, diminishing its preservation potential. In particular, all of the shells of *Lambdarina winklerprinsi* nov. sp. from the studied collection lack their posterior extremity. Moreover, the fidelity of the replacement is rather variable, with some specimens presenting gross beekite rings and siliceous grains agglutinated onto the specimen. The shell microstructure is usually not preserved, although the perforations of punctae of the terebratulids and *Spiriferellina*, and the fine hollow spines of the latter genus are preserved.

According to Butt and Briggs (2011), beekite rings are formed in conditions of limited or sporadic silica supply. This circumstance is also probably reflected by the incomplete silicification of the present specimens. As to the silica source, although no detailed study has

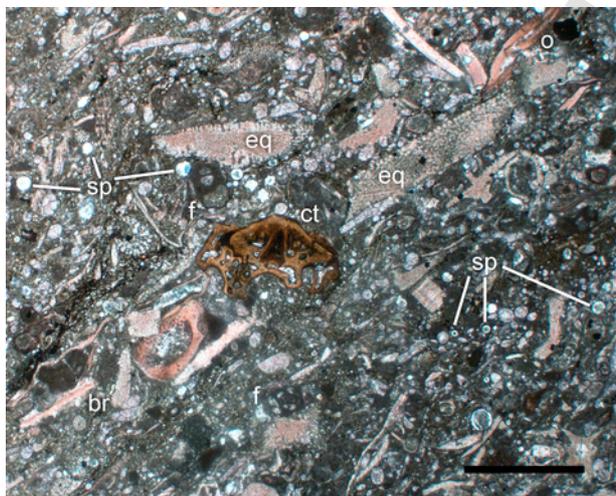


Fig. 3. Photomicrograph showing the texture of the sampled limestone, consisting of a skeletal and peloidal, intraclast-bearing packstone to grainstone. Notice the alternation of moderately to poorly sorted laminae containing sand- to gravel-size skeletal fragments and peloids (dark micritic rounded grains) with better sorted fine-sand-grade laminae mainly formed of sponge spicules and calcispheres. Key: ct, chondrichthyan tooth; eq, equinoderm, mostly crinoids; sp, sponge spicules; br, brachiopods; f, forams; o, ostracods. Scale bar: 1 mm.

been carried out, neither a biogenic origin from sponge spicules nor an input from the hydrothermal fluids responsible for the dolomitization and ore mineralization in the Mina Profunda area can be discarded.

5. Systematic palaeontology

5.1. Brachiopods

Phylum Brachiopoda Duméril, 1805

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer et Popov, 1996

Class Lingulata Gorjansky et Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus *Langella* Mendes, 1961

Type species: *Lingula imbituensis* de Oliveira, 1930.

Langella? sp.

Fig. 4(A-C)

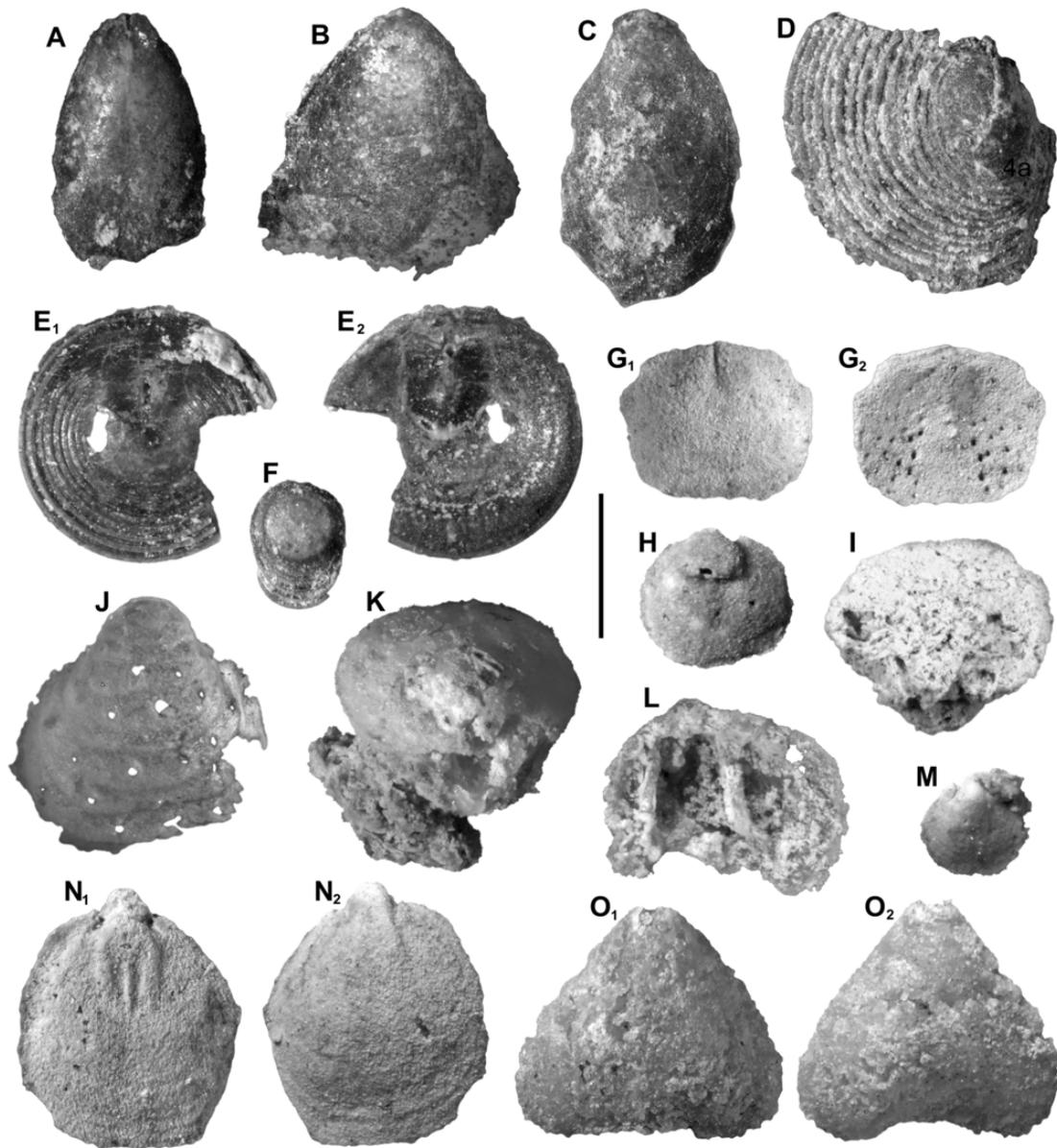


Fig. 4. A–C. *Langella?* sp. A: DGO 25486, ventral valve; B, C: DGO 25487-25488, dorsal valves. D–F. *Orbiculoidea* sp. D: DGO 25491, incomplete ventral valve; E: DGO 25490, incomplete ventral valve in external (E₁) and internal (E₂) views; F: DGO 25492, ventral valve of a juvenile specimen. G. Caenanopliinae gen. et sp. indet., DGO 25494, internal mould in ventral (G₁) and (G₂) dorsal views. H, I, K–M. *Crurithyris* cf. *urei* (Fleming, 1828). H: DGO 25519, internal mould of a ventral valve; I: DGO 25518, internal mould in dorsal view; K: DGO 25517, specimen in dorsal-posterior view, showing the high interarea; L: DGO 25520, posterior part of the interior of a dorsal valve showing the cardinal process and the posterior part of the crura; M: DGO 25524, dorsal internal mould. J. *Maemia* cf. *archboldi* Martínez Chacón et Winkler Prins, 2008, DGO 25496, ventral external view. N. *Composita* sp., DGO 25515, internal mould in dorsal (N₁) and ventral (N₂) views. O. Terebratulidina gen. et sp. indet. 1, DGO 25531, specimen in ventral (O₁) and dorsal (O₂) views. Scale bar: 1 mm.

Material: One ventral valve (DGO 25486), two dorsal valves (DGO 25487–25488) and a valve fragment (DGO 25489).

Measurements (in mm): DGO 25486: L = 1.75, W = 1.03; DGO 25487: Ld = 1.78, W = 1.35; DGO 25488: Ld = 2.03, W = 1.21.

Occurrence: The genus was first described for the Permian of Paraná, Brazil (de Oliveira, 1930). Sun and Baliński (2008) described it from the middle Tournaisian of southern China. The Cantabrian specimens could fill the large temporal gap between both records.

Description: Shell elongated, drop-shaped, and biconvex. Ventral valve with narrow pedicle groove. Dorsal valve with a small, undivided pseudointerarea which results in a rounded, thickened posterior margin. Ornamentation of dense growth lines. Both valves are thin and the internal characters are not impressed.

Remarks: The general external shape of the present material evokes the genera *Langella* or *Barroisella* Hall et Clarke. The preservation of the Cantabrian specimens, with a thin shell which does not show any internal characteristics, prevents us from making a more precise identification. The specimens are assigned, with some doubts, to *Langella* because the shell of this genus seems to be thinner and with internal structures less marked than those of the genus *Barroisella*.

Superfamily Discinoidea Gray, 1840

Family Discinidae Gray, 1840

Genus *Orbiculoidea* d'Orbigny, 1847

Type species: *Orbicula forbesii* Davidson, 1848.

Orbiculoidea sp.

Fig. 4(D–F)

Material: Two incomplete ventral valves, a juvenile ventral valve and ca. 12 valve fragments, mostly ventral, and a few juveniles, DGO 25490–25493.

Occurrence: *Orbiculoidea* is cosmopolitan ranging from Silurian (with doubts from Ordovician) to Permian.

Description: Ventral valve with holoperipheral growth, subcircular in outline, low cone shaped, with subcentral apex; pedicle slit closed anteriorly by listrium; foramen at posterior end of listrium, continued as internal tube to open in front of posterior margin (Fig. 4(E₂)). Larval shell smooth, subcircular, reaching ca. 0.5 mm in length; post-larval shell ornamented with well-developed, high concentric ridges (7 in 0.5 mm). The best preserved specimen is 1.75 mm in length.

Remarks: *Orbiculoidea* is a well-known genus generally represented in Carboniferous fossil localities, though often by only a few specimens. It is known from the San Emiliano Fm. at its type area (*Orbiculoidea* sp.; Carballeira et al., 1985) and from the Villamanín beds, N of Villamanín (unpubl. data). All the above specimens are significantly larger and have an ornamentation finer than those studied in this work. Moreover, the small size and strong concentric ornamentation distinguishes the present material from the other species of the genus.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer et Popov, 1996

Order Productida Sarytcheva et Sokolskaya, 1959

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1862

Family Anopliidae Muir-Wood, 1962

Subfamily Caenanopliinae Archbold, 1980

Caenanopliinae gen. et sp. indet.

Fig. 4(G)

Material: An internal mould of both valves, DGO 25494.

Occurrence: The subfamily Caenanopliinae ranges in age from the Lochkovian (Devonian) to the Kungurian (Permian). *Globosochonetes* is the most common genus of this subfamily in the Car-

boniferous of the Cantabrian Zone. It occurs in several localities of the San Emiliano Fm., including the Moscovian Villamanín beds (Villa et al., 1988).

Description: Shell very small (L = 1.14 mm, W = 1.32 mm, measurements of the only specimen), strongly concavo-convex, subcircular in outline, ears incomplete. Marks of external costae seem to occur in the anterior region of the ventral internal mould. Ventral interior with short and high median septum. Dorsal interior without median septum; with long and high inner socket ridges supporting small cardinal process; antheridia slightly marked and anteriorly divergent at a large angle; without accessory septa; with relatively large endospines arranged in five pairs of radial rows; the endospines closest to the median axis are the largest.

Remarks: The very small size, almost equidimensional shell and the absence of a dorsal median septum suggest that this specimen is a member of the Family Anopliidae. The probable costate exterior points towards the subfamily Caenanopliinae, particularly to the genera *Globosochonetes* Brunton and *Subglobosochonetes* Afanasjeva. These two genera are distinguished on the presence or absence of accessory septa; the Tournaisian *Subglobosochonetes* lacks accessory septa and is the most similar to specimen DGO 25494. The present specimen also resembles the Permian genus *Neotornquistia* Afanasjeva of the subfamily Anopliinae, as a smooth exterior surface cannot be discarded. However, DGO 25494 could be a juvenile form that has not yet developed diagnostic generic characters. These uncertainties prevent us from making a more accurate determination.

Suborder Productidina Waagen, 1883

Superfamily Productoidea Gray, 1840

Family Productellidae Schuchert, 1929

Subfamily Plicatiferinae Muir-Wood et Cooper, 1960

Tribe Semicostellini Nalivkin, 1979

Genus *Maemia* Lazarev in Brunton and Lazarev, 1997

Type species: *Maemia chaykensis* Lazarev, 1997 in Brunton and Lazarev.

Maemia cf. *archboldi* Martínez Chacón et Winkler Prins, 2008

Figs. 4(J), 5(B)

Material: One articulated specimen (DGO 25495) and two isolated ventral valves (DGO 25496–25497).

Occurrence: *M. archboldi* is known from the Pennsylvanian (late Bashkirian–early Moscovian) of the Cantabrian Zone (Martínez Chacón and Winkler Prins, 2008).

Description: Shell small, almost equidimensional (L = 7.1 mm, W = 7.3 mm, Th = 2.95 mm in the articulated specimen), with subcircular outline. Ventral valve strongly convex, with umbo inflated, rounded and extending behind the hinge; ornamentation of irregular concentric rugae slightly lamellose; a row of spines is developed along the hinge and others, relatively large, seemingly straight, are arranged in quincunx. Dorsal valve with lamellae in its anterior part, pits corresponding to the spines of the opposite valve and a few spines thinner than those of the ventral valve.

Remarks: The specimens are very similar to *M. archboldi* by their ventral convexity, ornamentation with concentric, lamellose rugae and large spine bases scattered in quincunx; dorsal valve with a few spines thinner than the ventral ones. Their incomplete preservation prevents us from making a more precise determination. Their very small size and undeveloped trail suggest that they could be juveniles of this species.

The present specimens also resemble *Quasiavonia aculeata* (Sowerby, 1814), a species frequently described or cited from the Carboniferous of the Cantabrian Zone (Winkler Prins, 1968; Martínez Chacón, 1979; Martínez Chacón and Winkler Prins, 1985, 2007), although part of this material has been synonymized with *M. archboldi*

(Martínez Chacón and Winkler Prins, 2008). The main differences between the genera *Quasiavonia* and *Maemia* are the geniculation of both valves, the deeper corpus cavity and the dorsal adductor scars raised with median-curving crests of *Maemia*. None of these characteristics can be observed in the present material. However, the small size, inflated ventral valve and coarse spine bases quincunxially arranged, widely separated from each other, suggest co-specificity with *M. archboldi*, although with some doubts.

Family Productidae Gray, 1840

Subfamily Productinae Gray, 1840

Tribe Spyridiophorini Muir-Wood et Cooper, 1960

Genus *Alexenia* Ivanova in Ivanov, 1935

Type species: *Alexenia reticulata* Ivanova in Ivanov, 1935.

Alexenia? sp.

Fig. 5(D)

Material: A single specimen, very deformed, crushed and incomplete, DGO 25498.

Occurrence: *Alexenia* is a genus known from the late Moscovian to Kasimovian of Eurasia. *Alexenia? delepinei* is known from the late Bashkirian–early Moscovian interval of the Cantabrian Mountains. Amongst other species from the Cantabrian Zone, *A. arbizui* Martínez Chacón, 1979, known from the upper Kashirsky (lower Moscovian) has a dorsal interior typical of *Alexenia*.

Description: Medium-sized shell ($L > 17$ mm, $W > 25.7$ mm), ears large, flat and strongly differentiated, frontal commissure uniplicate. Ventral valve with ears sharply separated from the disc by a deep sulcus and a ridge on the flanks, which carries a row of thick spines with their diameter increasing strongly forward. Ornamentation semireticulate, with rounded costae (7 in 5 mm on the disk) becoming coarse on the trail (5 in 5 mm); the spines are few in number: one row on the ridges on the flanks, one row along the hinge and several scattered over the valve.

Remarks: Given the conditions of preservation of the specimen, it is impossible to know its original dimensions, even approximately. Its external characteristics suggest the genus *Alexenia*, but we do not know its interior. In the Cantabrian Mountains, the species *Alexenia? delepinei* Martínez Chacón et Winkler Prins, 2015 has been described

from coeval deposits. The latter species differs from the typical *Alexenia* in the arrangement of the dorsal muscle field, placed on the bottom of the valve, bordered medially by parallel ridges lower than those usually found in *Alexenia*. On the basis of this character, Martínez Chacón and Winkler Prins (2015) consider that *Alexenia? delepinei* could belong to a new genus at the base of the Tribe Spyridiophorini or perhaps the earliest representative of *Alexenia*, but which has not yet developed the elevated muscle platforms typical of other species in the genus. As we do not know the dorsal interior of the specimen on hand, we attribute the specimen from Mina Profunda to *Alexenia* with reservations. Moreover, despite the fact that it resembles *A.? delepinei*, its larger size and poor preservation precludes a confident comparison. Therefore, we prefer to leave its classification open.

Order Rhynchonellida Khun, 1949

Superfamily Lambdarinoidea Brunton et Champion, 1974

Family Lambdarinidae Brunton et Champion, 1974

Subfamily Lambdarininae Brunton et Champion, 1974

Genus *Lambdarina* Brunton et Champion, 1974

Type species: *Lambdarina manifoldensis* Brunton et Champion, 1974.

Lambdarina winklerprinsi Martínez Chacón nov. sp.

Fig. 6(A–J)

?1993. *Lambdarina* sp. – Martínez Chacón et Winkler Prins, p. 576, pl. 2, fig. 6.

Derivation of the name: In honour of Dr. Cornelis Winkler Prins (Naturalis Museum, Leiden), colleague and friend, recently passed away (18 April 1939–27 June 2019). He guided MLMCh masterfully in her beginnings in the study of Carboniferous brachiopods. With her grateful memory.

Holotype: shell with its posterior part not preserved, DGO 25506 (Fig. 6(B_{1,2})).

Paratypes: 22 shells also with the posterior part not preserved due to incomplete silicification, one complete internal mould of a juvenile specimen, and 4 incomplete internal moulds, DGO 25499–25505, 25507–25514.

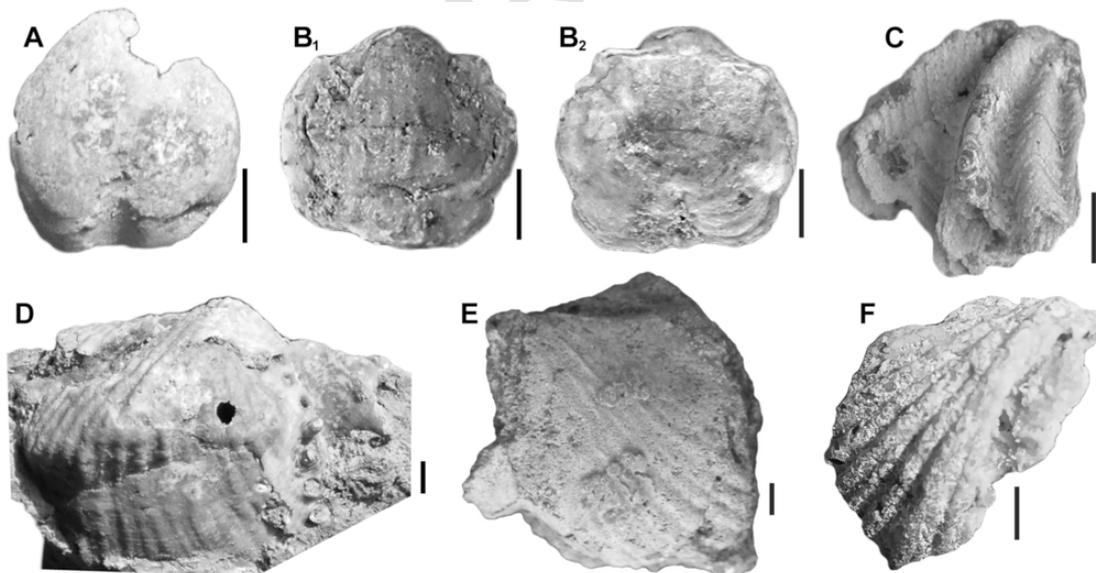


Fig. 5. A. Terebratulidina gen. et sp. indet. 2, DGO 25534, fragment of the anterior part of ventral valve. B. *Maemia* cf. *archboldi* Martínez Chacón et Winkler Prins, 2008, DGO 25495, specimen in ventral (B₁) and dorsal (B₂) views. C. *Spiriferellina* sp., DGO 25530, fragment of ventral valve. D. *Alexenia?* sp., DGO 25498, incomplete specimen in ventral view. E. *Anthracothyrina?* sp., DGO 25529, incomplete ventral internal mould. F. *Anthracospirifer* sp., DGO 25528, fragment of ventral valve. Scale bars: 2 mm.

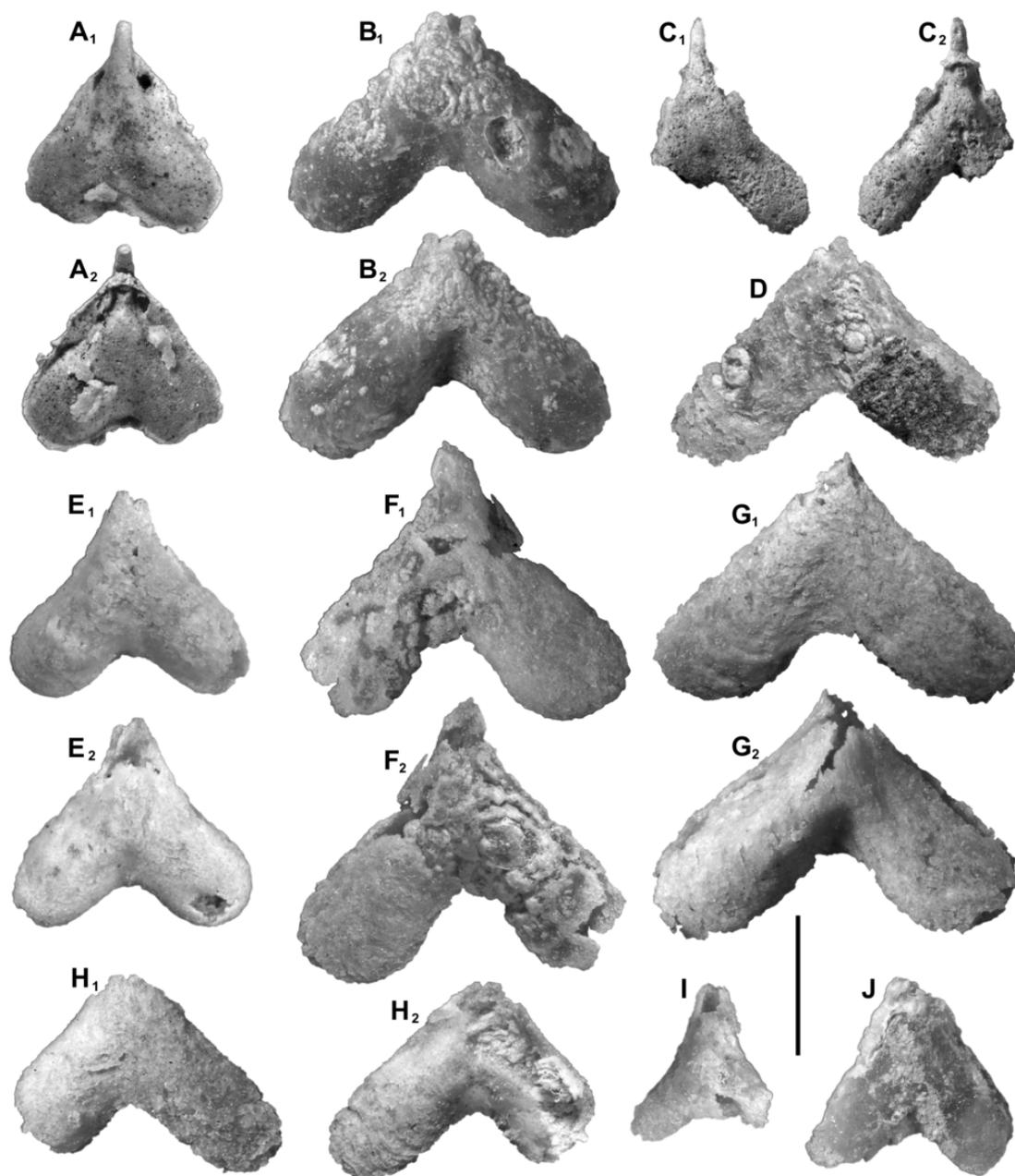


Fig. 6. *Lambdarina winklerprinsi* Martínez Chacón nov. sp. **A.** DGO 25499, internal mould of a juvenile specimen in ventral (A_1) and dorsal (A_2) views. **B.** Holotype, DGO 25506, specimen in ventral (B_1) and dorsal (B_2) views. **C.** DGO 25507, fragmentary internal mould in ventral (C_1) and dorsal (C_2) views. **D.** DGO 25503, ventral valve. **E.** DGO 25501, specimen in ventral (E_1) and dorsal (E_2) views. **F.** DGO 25502, incomplete specimen in ventral (F_1) and dorsal (F_2) views. **G.** DGO 25500, specimen in ventral (G_1) and dorsal (G_2) views. **H.** DGO 25508, specimen with one of its lobes broken in ventral (H_1) and dorsal (H_2) views. **I.** DGO 25505, juvenile specimen in dorsal view. **J.** DGO 25504, juvenile specimen in dorsal view. Scale bar: 1 mm.

Type locality: 370 m to the SW of Mina Profunda ($42^{\circ}57'43''N$, $5^{\circ}36'14''W$), Cármenes (León, NW Spain), San Emiliano Fm., upper part of the Caliza Masiva (after Moore et al., 1971), upper Bashkirian.

Occurrence: As indicated above, the stratigraphic range of *Lambdarina* is middle Tournaisian–Upper Permian. *L. winklerprinsi* nov. sp. was recovered from the upper Bashkirian rocks.

Measurements: See Table 1. Owing to the fact that all the shells are devoid of their apical region, the measured length is less than the actual value.

Diagnosis: *Lambdarina* with wide and quite long lobes, rounded at the end; dorsal valve with deep median sulcus; ventral valve with very weak or absent median sulcus, usually without median ridge. Dental plates long, supporting the teeth on their anterior end; inner socket ridges strong and high, joined to the notothyrial platform.

Description: Small shell (the largest specimen reaches little more than 2.07 mm in length, DGO 25502), approximately equidimensional or slightly transverse in adults, and a little elongated in juveniles, dorsibiconvex, smooth, heart-shaped, bilobate, with lobes starting in the anterior half of the length in larger specimens in which the margins of the lobes are more or less parallel, rounded at the front;

Table 1
Measurements (in mm) of some specimens of *Lambdarina winklerprinsi* nov. sp.

Specimen	Length	Width
DGO 25499	1.49	1.40
DGO 25500	>1.86	2.56
DGO 25501	>1.49	1.68
DGO 25502	>2.07	~2.30
DGO 25503	>1.67	2.31
DGO 25504	>1.43	1.44
DGO 25505	>1.12	~1.12
DGO 25506 ^a	>1.71	2.32
DGO 25508	>1.55	~2.22

^a Holotype.

angle of lobe bifurcation increases with age, ranging from 65° to 98° (this last value in the specimen DGO 25500; Fig. 6(G)). Ventral valve with umbo long and narrow, tube-like, slightly curved dorsally; the rounded and relatively large foramen is situated at the apex of the tube-like umbo (DGO 25499; Fig. 6(A₂)) or slightly displaced in a dorsal direction (DGO 25507; Fig. 6(C₂)); median sulcus very weak or absent, usually without median ridge. Dorsal valve rather shorter than ventral valve, with well-developed and deep median sulcus.

Ventral interior with strong teeth and long dental plates supporting the teeth on their anterior end and not extending anteriorly beyond the teeth. Dorsal interior with deep dental sockets, limited by strong and long inner socket ridges, united to the notothyrial platform; the notothyrial platform is depressed in its ventral side; a small cardinal process seems to be present on its posterior end (Fig. 6(A₂)).

With ontogeny, the specimens show changes in the shell form and in the size of the lobes. Specimens smaller than 1.07 mm in length are not present in the studied collection. The smaller specimens have a triangular outline, are slightly elongated, and the lobes only appear in the anterior end; the dorsal medial sulcus starts to develop. The shell acquires a heart-shaped outline during the process of growth, becoming slightly transverse, and the lobes start a little ahead of half the length of the shell, increasing their divergence. In adult specimens, the typical characteristics for the species are developed: deep dorsal medial sulcus, long lobes that reach a little more than half of the shell length, and a large angle of divergence.

Remarks: So far, eight species have been included in the genus. *L. jugowiensis* Muszer is most similar to *L. winklerprinsi* nov. sp. by its general shape, development of bilobation and absence of a median ridge in the ventral sulcus. However, it differs from the species described here in having a slightly elongated shell and shorter and less separate lobes. Both *L. manifoldensis* and *L. glaphyra* Basset et Bryant also have outlines and bilobations similar to those of *L. winklerprinsi* nov. sp. However, these two species differ from the new one in having the ventral sulcus well developed and with a median ridge. *L. sinensis* Baliński et Sun, *L. babini* Martínez Chacón, and *L. granti* Nazer differ from *L. winklerprinsi* nov. sp. by possessing a less lobate shell; the last two species also have a well-developed ventral sulcus with a median ridge. On the other hand, *L. brownendensis* Morris and *L. iota* Grant are clearly distinguishable by their long, narrow and widely separated lobes.

Lambdarina is a genus essentially known from the Viséan, based on the records of *L. manifoldensis* and *L. brownendensis* (early Viséan, North Staffordshire, England), *L. granti* (upper Viséan, Queensland), *L. jugowiensis* (late Viséan, Sudetes, SW Poland), and *L. babini* (late Viséan, Los Santos de Maimona, Badajoz, SW Spain). Two species are described from the Tournaisian, *L. sinensis* (middle Tournaisian, Guizhou Province, South China), the oldest known to date, and *L. glaphyra* (late Tournaisian, Belgium). A temporal gap of 56 myr separates the former species with *L. iota* (Late Permian, Hy-

dra Island, Greece). *L. winklerprinsi* nov. sp., from the late Bashkirian, partially fills this large gap, being the first species of *Lambdarina* known from the Pennsylvanian.

This is not the first time that the genus *Lambdarina* is mentioned in the late Bashkirian of the Cantabrian Zone. Martínez Chacón and Winkler Prins (1993) cited a single incomplete specimen from the Valdeteja Fm. (Valdeteja, Bodón Nappe, several km to the east of the studied area), as *Lambdarina* sp. The specimen has not been described and the only figure published is insufficient for definitive comments. However, it seems similar to *L. winklerprinsi* nov. sp. in outline, both have the same age and come from nearby locations, although of different formations. For these reasons, we consider, although with doubts, that the specimen from Valdeteja Fm. assigned to *Lambdarina* sp. could belong to *L. winklerprinsi* nov. sp.

The material of *L. winklerprinsi* nov. sp. includes internal moulds of the two joined valves, some of which reveal important details of the interior. This is the first record of internal moulds of representatives of the genus *Lambdarina*.

Order Athyridida Boucot, Johnson et Staton, 1964

Suborder Athyrididina Boucot, Johnson et Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Spirigerellinae Grunt, 1965

Genus *Composita* Brown, 1845

Type species: *Spirifer ambiguus* Sowerby, 1822.

Composita sp.

Fig. 4(N)

Material: 3 internal moulds of both valves and 4 incomplete silicified shells, DGO 25515-25516, DGO 25526-25527.

Occurrence: *Composita* is a cosmopolitan genus ranging from the Upper Devonian to the Upper Permian. In the Cantabrian Zone it has been reported and described from the San Emiliano Fm. (Carballeira et al., 1985) and the Calizas del Cuera (Martínez Chacón, 1990) of upper Bashkirian–upper Moscovian age.

Description: Shell ventribiconvex, subovate or tear-drop shaped, slightly elongated, widest near mid-length, without fold and sulcus, anterior commissure rectimarginate. Shell smooth, with concentric lines of growth marked in the anterior part of the internal mould of both valves.

Ventral interior with dental plates thin and short, very close to the side wall. Between them and extending further forward is the muscle field, depressed at the bottom of the valve, little marked and divided by a low and wide myofragma.

Dorsal interior with cardinal plate short and wide, ventrally concave, projecting backwards and with two small diductor pits; from its anterior part rose the crura. The adductor muscle field is narrow and long; at its posterior end, it is divided by a very short, narrow and low myofragma, followed by a median depression; the two pairs of muscles are practically parallel, the middle pair is elevated above the bottom of the valve and the outermost pair is depressed.

Remarks: By its smooth shell and the internal characteristics observed, the present material seems to belong to the genus *Composita*, but the poor preservation of the specimens prevents attribution to species level.

Order Spiriferida Waagen, 1883

Suborder Spiriferidina Waagen, 1883

Superfamily Ambocoelioidea George, 1931

Family Ambocoeliidae George, 1931

Subfamily Ambocoeliinae George, 1931

Genus *Crurithyris* George, 1931

Type species: *Spirifer urei* Fleming, 1828.

Crurithyris cf. *urei* (Fleming, 1828)

Fig. 4(H, I, K–M)

Material: 20 shells incompletely silicified, 10 internal moulds of two valves and 1 incomplete dorsal valve showing part of the interior, DGO 25517-25525.

Occurrence: *C. urei* is typically known from the Viséan of Great Britain and the Tournaisian-upper Viséan of the Moscow Basin (Brunton, 1984). It has been cited or described from the Tournaisian to the upper Bashkirian of the Cantabrian Zone (Martínez Chacón and Winkler Prins, 1985; Martínez Chacón and Sánchez de Posada, 2018).

Description: Small ventribiconvex shell with hinge line less than width of shell, high apsacline ventral interarea and short catacline dorsal interarea; subcircular outline with width slightly longer than length; both valves with very weak sulci. The larger specimen measures 1.46 mm in length and 1.67 mm in width; the smallest measures 0.53 mm in length and 0.61 mm in width. Ventral interior with dental ridges and without dental plates; muscle scars well impressed, confined to the posterior region and with indistinct adductors and diductors. Dorsal interior with a small, triangular cardinal process raised on a short notothyrial platform in the apex of the inner socket ridges; inner socket ridges strong, elevated; crural bases united to valve floor by short crural plates; crura subparallel, extending forward, they are long but their end cannot be observed because the dorsal valve is broken (Fig. 4(L)).

Remarks: The specimens on hand closely resemble the type species *C. urei* from which they differ slightly because of the less convex ventral valve, the narrower hinge and the less developed median groove of both valves. The present specimens also look like *C. planoconvexa* (Shumard, 1855), from which they are distinguished by their less flattened dorsal valve.

Superfamily Spiriferoidea King, 1846

Family Spiriferidae King, 1846

Subfamily Sergospiriferinae Carter, 1974

Genus *Anthracospirifer* Lane, 1963

Type species: *A. birdspringensis* Lane, 1963.

Anthracospirifer sp.

Fig. 5(F)

Material: A single fragment of ventral valve, DGO 25528.

Occurrence: *Anthracospirifer* is a cosmopolitan genus known throughout the Carboniferous. In the Cantabrian Zone it is known from the upper Bashkirian of the San Emiliano Fm. (Martínez Chacón and Winkler Prins, 1985), and from upper Bashkirian–lower Moscovian strata of the Calizas del Cuera (Martínez Chacón and Bahamonde, 2008).

Description: The specimen presents the ventral interarea denticulated. The ornamentation consists of strong, thick and subangular costae, the grooves that separate them are similar to the costae; the costa that limits the sulcus is thicker than the rest and bifurcates once into the sulcus and twice to the flank; the next costa on the flank bifurcates once towards the middle and towards the side; the next two bifurcate once to the side.

Remarks: The ornamentation of the fragment on hand fits into those of the genus *Anthracospirifer*. However, the poor preservation of the specimen prevents us from making a more precise attribution.

Family Choristitidae Waterhouse, 1968

Subfamily Angiospiriferinae Legrand-Blain, 1985

Genus *Anthracothyryna* Legrand-Blain, 1984

Type species: *Brachythyryna (Anthracothyryna) perextensa* Legrand-Blain, 1984.

Anthracothyryna? sp.

Fig. 5(E)

Material: One incomplete ventral internal mould, DGO 25529.

Occurrence: The genus *Anthracothyryna* is known in the Cantabrian Zone from the upper Bashkirian to the Bashkirian/Moscovian boundary, as is the genus *Anthracospirifer*.

Description: Ventral valve convex, with sulcus wide and relatively deep in its front; interarea denticulate; ornamentation of rounded costae which widened to the front, the 3 costae closest to the sulcus bifurcate, the rest are simple; 4–5 costae are counted in 5 mm at the front of the shell. Vascular impressions ramiform at their beginning. $L > 21.14$ mm, $W = \sim 32$ mm.

Remarks: The genus has been described from many localities exposing the San Emiliano Fm., including the region N of Villamanín, and especially by the species previously described as *Brachythyryna pinica* Martínez Chacón, 1978. The characteristics that can be seen in the present specimen point towards the genus *Anthracothyryna*. The distinctive vascular impressions of this genus are reticulate, but only their beginnings are visible in the studied specimen. For this reason, the attribution to the genus is done with some reservations. The species from Mina Profunda differs from *A. pinica* in its larger number of thinner, bifurcating ribs.

Order Spiriferinida Ivanova, 1972

Suborder Spiriferinidina Ivanova, 1972

Superfamily Pennospiriferinoidea Dagys, 1972

Family Spiriferellinidae Ivanova, 1972

Genus *Spiriferellina* Frederiks, 1924

Type species: *Terebratulites cristatus* von Schlotheim, 1816.

Spiriferellina sp.

Fig. 5(C)

Material: A fragment of a ventral valve, DGO 25530.

Occurrence: *Spiriferellina* is a cosmopolitan genus ranging from the Mississippian to the Upper Permian. In the Cantabrian Zone, the species *S. multispinosa* Martínez Chacón, 1991, is known from the Podolskian (upper Moscovian) beds of the Calizas del Cuera.

Description: The specimen is a very incomplete ventral fragment. Only the sulcus is preserved with the plicae that limit it and one more plica on the left side. Length of the preserved part measures 8.05 mm. Sulcus deep, subangular, smooth and with abrupt walls; sulcus-bounding plicae, coarser than the lateral plicae, all of them, strong, coarse and subangular; micro-ornamentation of imbricate and close growth laminae, 8–9 in 3 mm, wearing very fine, hollow spines. Shell punctate with coarse punctae. Interior unknown.

Remarks: The observed characteristics of the specimen coincide with those of *Spiriferellina* but the fragmentary preservation of the material precludes a specific identification.

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Terebratulidina gen. et sp. indet. 1

Fig. 4(O)

Material: Three articulated specimens more or less complete and 1 internal mould of both valves, DGO 25531–25533.

Description: Shell small (DGO 25531: $L > 1.64$ mm, $W = 1.78$ mm), endopunctate, biconvex, triangular in outline, slightly transverse, with the maximum width located almost in front of the shell, anterior commissure slightly unisulcate. Dorsal valve with a median sulcus that originates towards half the length of the valve and which widens and deepens in the front, trending ventrally. Ventral valve practically smooth, presenting only a very slight median elevation corresponding to the sulcus of the other valve.

Both valves without median septum. Ventral valve with pedicle collar and very short dental plates. Dorsal valve with strong crural plates.

Remarks: The endopunctate nature and the form of the shell suggest that these specimens belong to the Order Terebratulida and the

Suborder Terebratulidina, the only suborder with Palaeozoic representatives. The lack of knowledge of its loop and other details of the dorsal interior prevent us from a more precise diagnosis.

Terebratulidina gen. et sp. indet. 2

Fig. 5(A)

Material: One fragment of the anterior part of a ventral valve, DGO 25534.

Description: Shell endopunctate. The fragment shows a narrow median sulcus with rounded bottom and parallel sides which divides the valve in two wide lateral lobes.

Remarks: The preserved fragment resembles the species *Girtyella llopisi* Martínez Chacón et Winkler Prins, 2008, described from the late Bashkirian of the Valdeteja Fm. at Latores (SW of Oviedo). The poor preservation of the single fragment does not allow a more confident identification.

5.2. Conodonts

Class Conodonta Pander, 1856

Order Ozarkodinida Dzik, 1976

Family Idiognathodontidae Harris et Hollingsworth, 1933

Genus *Idiognathoides* Harris et Hollingsworth, 1933

Type species: *Idiognathoides sinuatus* Harris et Hollingsworth, 1933.

Idiognathoides sulcatus parvus Higgins et Bouckaert, 1968

Fig. 7

1968. *Idiognathoides sulcata parva* subnov. sp. – Higgins et Bouckaert, p. 41, pl. 6, figs. 1–6.

1975. *Idiognathoides sulcatus parvus* Higgins et Bouckaert – Higgins, p. 56, pl. 13, figs. 13, 14, 18, pl. 14, figs. 2, 3.

1990. *Idiognathoides parvus* (Higgins et Bouckaert) – Méndez Fernández, p. 100–101, pl. 9, figs. 15, 16.

1999. *Idiognathoides sulcatus parvus* Higgins et Bouckaert – Nemyrovska, p. 72, pl. 3, figs. 6, 16.

2003. *Idiognathoides sulcata parva* Higgins et Bouckaert – Wang and Qi, pl. 1, figs. 13, 18.

2016. *Idiognathoides sulcatus parvus* Higgins et Bouckaert – Qi et al., fig. 11J.

2017. *Idiognathoides sulcatus parvus* Higgins et Bouckaert – Nemyrovska, pl. 2, fig. 2.

Material: One complete P₁ element and two P₁ fragments (DGO 25535–25537).

Occurrence: The genus *Idiognathoides* characterizes most of the Bashkirian and lower Moscovian rocks of Europe and Asia. *Idiognathoides sulcatus parvus* is an index fossil in South Guizhou of China, where its first record marks the beginning of the homonymous

biozone, and ranges into the overlying *Streptognathodus expansus* Zone (Wang and Qi, 2003; Qi et al., 2016). In the Donets Basin of Ukraine, the FAD of *I. sulcatus parvus* occurs in the *Idiognathodus sinuosus* Zone (Prikamian, upper middle Bashkirian), ranging up to the *Idiognathoides tuberculatus–I. fossatus* Zone (Cheremshankian, middle upper Bashkirian) (Nemyrovska, 2017; Nemyrovska and Hu, 2018). In the Cantabrian Zone, it was previously described from the San Emiliano Fm. at Fresno (a stratigraphic section situated in the Sobia nappe) and from the lower Picos de Europa Fm. at Les Llaceries (Picos de Europa Unit), and referred by Méndez Fernández (1990) to the upper Bashkirian and lower Moscovian, respectively. The records of both ‘*Str.*’ *expansus* and ‘*Str.*’ *suberectus* in the Valdeteja Fm. (Nemyrovska, 2017), which interdigitates with the San Emiliano Fm., conceivably reinforce an early late Bashkirian age for the studied faunal assemblage.

Description: The free blade is straight and of approximately the same length as the platform, and carries 8–10 discrete denticles that slightly decrease in height towards the platform junction. The platform is divided by a narrow groove that separates two noded parapets, the rostral (outer) one is a prolongation of the blade and continues up to the dorsal tip of the element, the caudal (inner) parapet is less developed, being slightly lower in height and tapering posteriorly to the rostral parapet at ca. 3/4 the length of the platform. The basal cavity is deep and occupies the entire length of the element, being narrow in the free blade and expanded under the platform. The basal cavity tip is not apparently centred, but situated below the oral groove. The lower portion of the lateral walls of the element, particularly at the free blade, are slightly flexed inwards.

Remarks: *Idiognathoides sulcatus parvus* differs from *Idiognathoides sulcatus sulcatus* Higgins et Bouckaert by possessing a shorter inner parapet, though as it is difficult to distinguish them in some cases, transitional forms have been adopted. *Idiognathoides postsulcatus* Nemyrovska is also distinguished by its equal length parapets, very convex platform sides, and shallow groove. *Idiognathoides macer* (Wirth) presents ridges in the ventral section of the inner parapet, not nodes as in *I. s. parvus*.

5.3. Vertebrates

Class Chondrichthyes Huxley, 1880

Order Ctenacanthiformes Glikman, 1964

Family indet.

Genus *Glencartius* Ginter et Skompski, 2019

Type species: *Ctenacanthus costellatus* Traquair, 1884.

Glencartius costellatus (Traquair, 1884)

Fig. 8(A, B)

Material: Two incomplete, isolated teeth, DGO 25459 and 25462.

Description: The largest specimen (DGO 25459; Fig. 8(A)) measures 2.0 mm mesiodistally along the labial border and 0.9 mm labiolingually; it has a cladodont organization. The tooth is quite elongate mesiodistally. The cusps have sustained much damage and only their bases are present. A relatively large central cusp is flanked by two pairs of lateral cusplets; the cusp and cusplets are joined at their bases. The central cusp is somewhat compressed labiolingually; the labial face is flattened and the lingual face is strongly convex. The occlusal crest is labially displaced from the cusp centre and forms well developed cutting edges. Moderately strong vertical ridges or cristae ascend the cusp from the cusp base both labially and lingually; the ridges on the labial face of the cusp are stronger and less densely packed than those on the lingual face, and they occasionally show bifurcation basally. The vertical ridges on the mesial and distal parts of the lingual face of the central cusp have curved trajectories as they



Fig. 7. *Idiognathoides sulcatus parvus* Higgins et Bouckaert, 1968, P₁ element, San Emiliano Formation, Mina Profunda, DGO 25535, lateral (A) and oral (B) views. Scale bar: 10 µm.

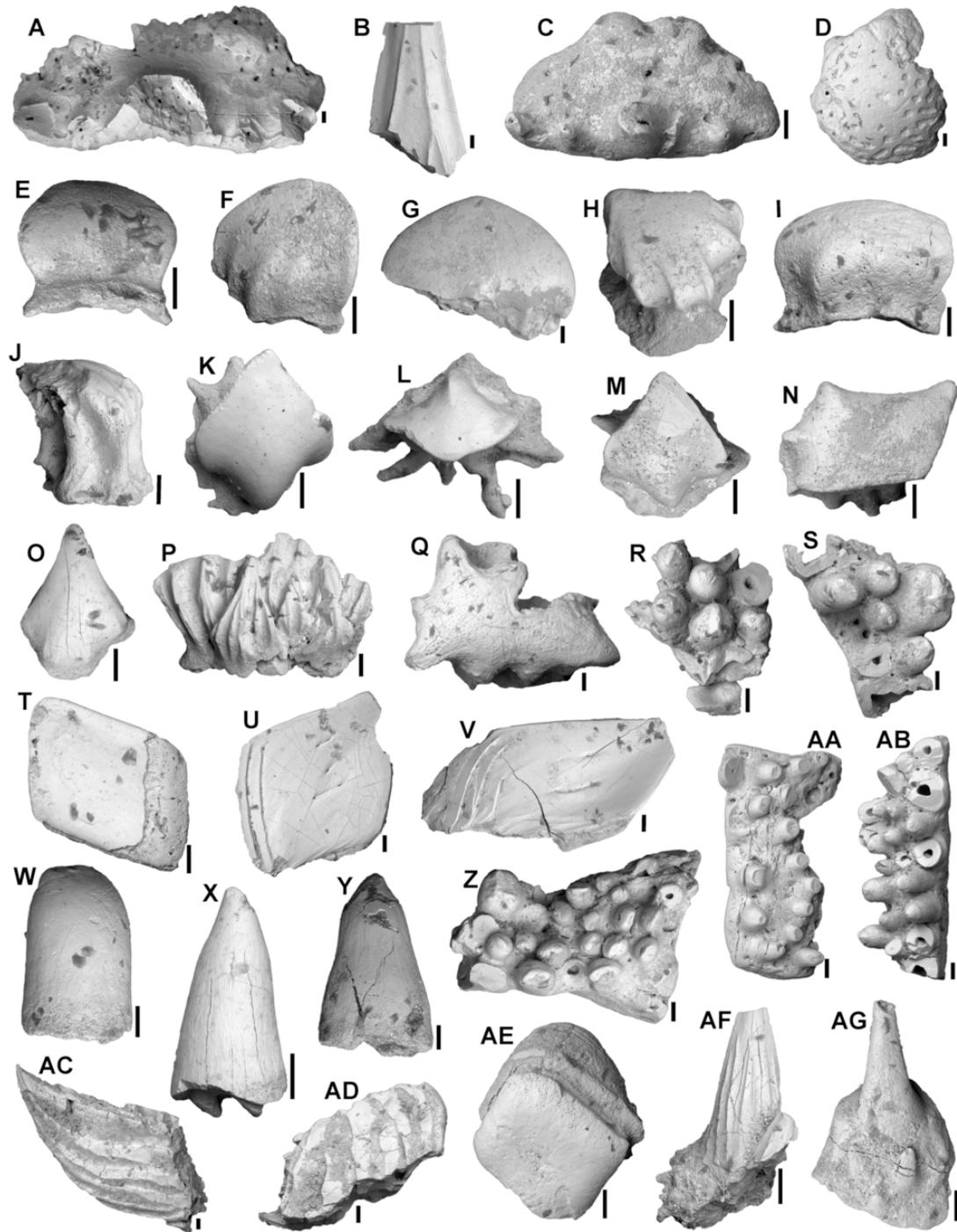


Fig. 8. Ichthyoliths recovered from the Caliza Masiva Member of the San Emiliano Formation (late Bashkirian), in the Mina Profunda area, NW Spain. **A.** *Glencartius costellatus* (Traquair, 1884), DGO 25459, oral view. **B.** Probably *Glencartius costellatus* (Traquair, 1884), DGO 25462, labial view. **C.** *Denaeva* sp., DGO 25458, oral view. **D.** helodont tooth crown, DGO 25454, oral view. **E–O.** Ellasmobranchii indet., placoid scales. **E:** DGO 25463; **F:** DGO 25451; **G:** DGO 25456; **H:** DGO 25457; **I:** DGO 25477; **J:** DGO 25466; **K:** DGO 25467; **L:** DGO 25469; **M:** DGO 25470; **N:** DGO 25478; **O:** DGO 25480. **P.** Ctenacanthiform scale, DGO 25452. **Q.** Chondrichthyan scale, DGO 25464. **R.** Osteichthyan bone with teeth, DGO 25484. **S.** Osteichthyan bone with teeth, DGO 25479. **T.** Osteichthyan scale, DGO 25482. **U.** Osteichthyan scale, DGO 25472. **V.** Osteichthyan scale, DGO 25471. **W.** Isolated osteichthyan tooth, DGO 25485. **X.** Isolated osteichthyan tooth, DGO 25483. **Y.** Isolated osteichthyan tooth, DGO 25465. **Z.** Osteichthyan bone with teeth, DGO 25461. **AA.** Osteichthyan bone with teeth, DGO 25453. **AB.** Osteichthyan bone with teeth, DGO 25460. **AC.** Osteichthyan scale, DGO 25474. **AD.** Osteichthyan scale, DGO 25475. **AE.** Acanthodian scale, DGO 25476. **AF, AG.** Unidentified palaeoniscoid teeth. **AF:** DGO 25473; **AG:** DGO 25468. Scale bars: 100 μ m.

ascend the cusp base. The lateral cusplet bases have similar cross-sectional shapes to that of the central cusp, and similar vertical ridge distribution. The first or intermediate lateral cusplet pair is smaller in size than the second or outermost pair. The tooth base is incomplete,

but the mesial and distal wings extend slightly beyond the bases of the outermost lateral cusplet bases. In occlusal view, the base has two prominent, widely separated orolingual buttons with oval outlines elongated mesiodistally. Vascular foramina penetrate the root tissues

around the bases of the orolingual buttons and in single rows around the labial border of the base, close to the lateral cusplet bases mesial and distal to the central cusp base, and between the orolingual buttons on the lingual shoulder of the base. In labial view, the base of the tooth is very shallow with two basally-projecting basolabial projections, each situated beneath one of the orolingual buttons. The labial margin of the base between these two projections is arched.

DGO 25462 (Fig. 8(B)) is an isolated central cusp fragment which probably also belongs to *Glencartius costellatus*; the 0.8 mm-long fragment is compressed labiolingually, has well-defined cutting edges, and coarse, basally bifurcating vertical ridges on the somewhat flattened labial face.

Remarks: DGO 25459 is most likely a specimen of *Glencartius costellatus* (Traquair), a ctenacanthiform shark of undetermined familial status previously described from the Viséan of Glencartholm, Scotland (Traquair, 1884; Moy-Thomas, 1936; Ginter et al., 2010; Ginter and Skompski, 2019), the Upper Viséan of Ticknall (Derbyshire, UK) and Todowa Grząba (Holy Cross Mountains, Poland) (Ginter et al., 2015), and Upper Viséan (V3a-c) limestones sampled in the Włodawa IG-4 borehole section of the Lublin-Lviv Basin (eastern Poland; Ginter and Skompski, 2019). The Spanish specimen matches well in all respects with the material described and figured by Ginter et al. (2015: p. 915, fig. 9D, E) and Ginter and Skompski (2019: text-fig. 4C-E), although the Viséan material has more lateral cusplet pairs.

Superorder Cladodontomorphi Ginter, Hampe et Duffin, 2010

Order Symmoriiformes Zangerl, 1981

Family Falcatidae Zangerl, 1990

Genus *Denaëa* Pruvost, 1922

Type species: *Denaëa furnieri* Pruvost, 1922.

Denaëa sp.

Fig. 8(C)

Material: one isolated tooth, DGO 25458.

Occurrence: *Denaëa* was originally erected for articulated specimens from the Viséan of Denée, Belgium (Pruvost, 1922), but a number of tooth based species have subsequently been established, giving the genus a range from the Fammenian (Late Devonian) to the Bashkirian (Ginter et al., 2010: p. 66).

Description: DGO 25458 measures 0.9 mm mesiodistally and 0.5 mm labiolingually. The base outline is roughly pentagonal in occlusal and basal views, and the symmetrical crown comprises a central cusp flanked by two pairs of lateral cusplets, each of which is slightly curved lingually in lateral view. In this instance, the central cusp and lateral cusplets have rounded rather than labio-lingually compressed cross sections; their bases are well separated from each other and the cusp axes are mildly divergent apically. The coronal ornament is much reduced compared to that in DGO 25459, comprising only a few indistinct, non-bifurcating vertical ridges ascending the lateral cusplets labially. There is no occlusal crest or cutting edge development. The base is shallow. A weak basolabial projection with a square outline is situated directly beneath the base of the central cusp. The base is relatively deeper than is the case in DGO 25459. The lateral wings are relatively bulbous and deep with rounded lateral margins. A single, very low, weakly developed orolingual button is situated at the labial midpoint of the base and is perforated by a foramen for the main vascular canal on the basolabial margin, and again in the centre of the occlusal surface of the base.

Remarks: The combination of characters in this specimen, especially the shallow base, weak articulation device and delicate cusps with circular cross-section, suggests that it should be allocated to the falcatid symmoriiform shark, *Denaëa* sp. The lack of clearly defined

coronal ornament prevents assignment of the Spanish specimen to any particular species of the genus.

Subclass Subterbranchialia Zangerl, 1979

Superorder Holocephali Bonaparte, 1832–1841

Order Helodontiformes Patterson, 1965

Family Helodontidae Patterson, 1965

Genus *Helodus* Agassiz, 1838

Type species: *Helodus simplex* Agassiz, 1838.

Helodus sp.

Fig. 8(D)

Material: a single isolated tooth fragment, DGO 25454.

Description: Heavily worn, the fragment measures approximately 0.8 mm across its largest dimension and consists of a broken, rather low and tumid cusp from the central part of the crown. The hypermineralised tissue of the crown is clearly visible, but further taxonomically useful morphological details are lacking.

Remarks: *Helodus* is the sole member of the holocephalan Order Helodontiformes. Ranging from Late Devonian to Early Permian and represented by a large number of species, *Helodus* is a fairly common component of marine Carboniferous successions (Stahl, 1999).

Elasmobranchii indet. scales

Fig. 8(E–Q)

Material: numerous isolated scales belonging to several morphotypes, including DGO 25441–25442, 25451, 25456–25457, 25463–25464, 25466–25467, 25469–25470, 25477–25478, 25480.

Morphotype 1: placoid scales

Fig. 8(E–O, Q)

Description: Placoid scales (also known as dermal denticles) are non-growing scales which have a simple crown connected to a basal plate by means of a stalk-like neck. The dermal denticles from the San Emiliano Fm. all have posteriorly-directed crowns with a single cusp. The tip of the cusp may be rounded (e.g., DGO 25451 and 25456; Fig. 8(F, G)) or pointed. In the pointed examples, the cusp may be acutely pointed (DGO 25457 and 25467; Fig. 8(H, K)), very acutely pointed (DGO 25480; Fig. 8(O)), or relatively obtusely pointed (DGO 25468 and 25478; Fig. 8(N)). The crown is usually ornamented by a series of vertical striations which usually arise from the basal plate, ascend the neck and then encroach onto the anterior face of the crown base. The lateral margins of the cusp are often accentuated with lateral ridges (e.g., DGO 25451, 25469, 25470, and 25477; Fig. 8(F, I, L, M)).

The vertical ridges may be very weak and impersistent (e.g., DGO 25456 and 25463; Fig. 8(E, G)) or, more commonly, much stronger. In some cases, especially those with acutely pointed cusps, there is a single well-developed, rounded ridge located centrally on the anterior border of the cusp (e.g., DGO 25467, 25469, 25470, and 25477; Fig. 8(K, I, L, M)), and occasionally surmounted by a single or even a double sharp crest (DGO 25469 and 25480, respectively; Fig. 8(L, O)). Occasionally, very strong ridges are also developed posteriorly (DGO 25466; Fig. 8(J)). In at least one example, the ridge pattern is quite complex with at least four clearly discernible ridges, each bearing one or even two crests (DGO 25457; Fig. 8(H)). In one instance (DGO 25464; Fig. 8(Q)) the rather flat crown is surrounded by coarse ridges.

The neck may be quite deeply incised and relatively fragile (e.g., DGO 25451 and 25463; Fig. 8(E, F)) or quite thick and robust (e.g., DGO 25457 and 25466; Fig. 8(H, J)).

The basal plate is sometimes quite compact with conservative margins (e.g., DGO 25466 and 25480; Fig. 8(H, O)), while in other instances, it is considerably flared and bears numerous long, thin denticulations, especially posteriorly (e.g., DGO 25469 and 25470; Fig. 8(L, M)).

Morphotype 2: ctenacanthiform scales
Fig. 8(P)

Description: DGO 25452 is an example of a large (0.8 mm wide) ctenacanthiform scale. The crown of the scale comprises at least two rough longitudinal rows of fused cusps, which reflect the growing nature of the scale. The most recently added cusps are situated on the anterior face. Each of these cusps is unicuspid with a lanceolate, sharply pointed outline. The anterior face of each cusp is marked by strong vertical ridges, which ascend the cusp from the base of the neck, terminate just below the cusp apex, and converge and fuse apically. The lateral margins of each cusp are defined by strong vertical ridges. The neck of the scale is only slightly incised, and the base is very compact, not extending significantly beyond the bounds of the coronal area.

These scales compare well with those figured by Ginter and Skompski (2019: text-fig. 6F) for *Glencartius costellatus* from the Upper Viséan limestones in the Włodawa IG-4 borehole, Lublin-Lviv Basin.

Class Acanthodii Owen, 1846
Order Acanthodiformes Berg, 1940
Incertae familiae
Fig. 8(AE)

Material: one isolated scale, DGO 25476.

Description: DGO 25476 is an isolated scale of *Acanthodes* type, measuring ca. 0.5 mm across the widest diameter. Roughly diamond-shaped in surface view, the unornamented outer surface is separated from the robust base by a prominent groove. The outline of the base matches that of the crown, but is slightly larger. The base displays a number of concentric growth lines on the lateral walls and is unevenly thickened with a convex underside.

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Woodward, 1891
Order Palaeonisciformes Jarvik, 1961
Suborder Palaeoniscoidea Nelson, 2006
Undetermined palaeoniscoids
Fig. 8(R-Z, AA-AD, AF, AG)

Material: Osteichthyans are represented in the fauna by tooth-bearing bones, isolated teeth and isolated scales.

Description: As far as can be determined, the isolated teeth and tooth-bearing bones all belong to the same, as yet unidentified taxon. The bone fragments vary in size and shape from 0.7 to 1.5 mm in length, and from roughly triangular (DGO 25479, 25484; Fig. 8(R, S)) to an elongate rectangle (DGO 25454, 25460, 25461; Fig. 8(Z, AB)). The identity of the bone fragments has not been determined. The number of teeth and tooth bases represented on the fragments varies from 6 (DGO 25479, 25480; Fig. 8(S)) to 24 (DGO 25461; Fig. 8(Z)). The teeth are arranged in roughly linear series on the biting surfaces of the bones and each tooth has a circular to slightly oval cross-section. The shafts of the teeth may be smooth (e.g., DGO 25460; Fig. 8(AB)) or ornamented by a series of very fine vertical striations (e.g., DGO 25453; Fig. 8(AA)), and are generally parallel-sided. The occlusal surface is marked by an acrodin pad, which may present a simple central apical cusp, a slightly divided apical cusp (DGO 25460; Fig. 8(AB)), a straight transverse ridge (DGO 25461; Fig. 8(Z)), a somewhat curved transverse ridge (DGO 25461) or a complex star-shaped cusp (DGO 25479; Fig. 8(S)).

These morphologies are matched in general terms by those of the isolated teeth, which may have circular (DGO 25483; Fig. 8(X)) or more oval cross-sections (DGO 25485; Fig. 8(W)) and parallel-sided (DGO 25485; Fig. 8(W)) or tapering shafts (DGO 25465, 25483; Fig. 8(X, Y)).

The scales in the collection vary from regular rhomboidal (DGO 25472; Fig. 8(U)) to more elongate shapes (DGO 25471, 25482; Fig. 8(T, V)). In complete specimens the outer surface of the scale is relatively smooth with a series of short microscopic ridges covering the scale surface and oriented parallel to the diagonal from the upper posterior corner of the scale to the lower anterior corner. Some of these scales are perforated with channels of the lateral line sensory canal (DGO 25471, 25472; Fig. 8(U, V)). A series of oblique folds may be present along the presumed dorsal border of the scale (DGO 25471, 25472; Fig. 8(U, V)), and a series of several prominent ridges may be developed parallel to the presumed posterior border (DGO 25471; Fig. 8(V)). Some fragmentary specimens consist of a series of parallel ridges, which probably represent the partial remains of the posterior borders of former larger scales (DGO 25474, 25475; Fig. 8(AC, AD)).

6. Discussion

The late Bashkirian faunal assemblage from Mina Profunda consists of skeletal parts of benthic organisms (e.g., brachiopods, echinoderms, bryozoans) along with nektonic elements (conodonts, sharks). The brachiopod assemblage fits into the shallow-water faunas of Martínez Chacón and Winkler Prins (1993), characterized by rich associations that lived in well-oxygenated warm waters. The Lingu-loidea genera and the small Chonetidina, typical of the quiet-water faunas of the same authors, occur in the shallow-water faunas as well (Martínez Chacón and Winkler Prins, 1993).

Different life habits have been proposed for the micro-rhynchonellid *Lambdarina*, characterized by a relatively big pedicle foramen with respect to the small-sized shell, leading to the possession of a functional pedicle throughout its lifetime. Brunton and Champion (1974) suggested an epiplanktonic habit with the pedicle attached to plants or animals. It has also been proposed that *Lambdarina* lived in clusters, either in relatively low-energy carbonate environments (Nazer, 1983) or occupying small crevices on a rocky bottom (Morris, 1994). Bassett and Bryant (1993) agree with Grant (1988) in that the foramen size is no guide to pedicle form and function, seeing no reason to favour an attachment to hard substrates or an epiplanktonic mode of life and suggesting that a rhizoid pedicle would permit *L. glaphyra* Bassett et Bryant to colonize low-energy soft bottoms.

The presence of one circular, minute predatory boring per specimen, probably produced by small gastropods, is characteristic of lambdarinids and cardiarinids (Cooper, 1956; Brunton and Champion, 1974; Grant, 1988; Bassett and Bryant, 1993; Morris, 1994; Martínez Chacón, 1997). Remarkably, no clear predatory borings have been observed in the specimens of *L. winklerprinsi* nov. sp., as in *L. granti* Nazer and *L. jugowiensis* Muszer.

Noticeably, apart from broken and disarticulated shells, brachiopods from the Mina Profunda appear as intact specimens, with the shells not filled with sediment. This mode of occurrence suggests that their transport and their burial possibly occurred soon after, or was directly related to their death (Underwood, 1994; Brett, 2003). The facies features of the hosting beds suggest that they were deposited by traction-plus-fallout or fallout sedimentation from relatively dilute gravity flows transporting grains and mud (Middleton and Hampton, 1973; Lowe, 1982). Field relationships suggest that these sediment gravity flows would have been mostly sourced from a nearby shallow-water area and that they transported their load into a low-energy, partially restricted slope-to-basin environment. Thus, it is likely that the gravity flows entrained the living brachiopods from the sea floor and transported them into the deep-water setting where they were deposited as part of the turbidite beds.

Another example of gravity-flow deposits from a deep-water setting containing transported shallow-water fauna, including *Lambdarinids* and associated microbrachiopods, is represented by the middle Tournaisian Muhua Fm. of South China (Baliński, 1999; Ginter and Sun, 2007; Baliński and Sun, 2008).

The palaeobiogeographic connections of the late Bashkirian–early Moscovian Cantabrian brachiopods (Valdeteja, San Emiliano and Calizas del Cuera formations) have been discussed in Martínez Chacón and Winkler Prins (1993, 2009, 2015). The main relationships are with Central Europe, Donbass (Ukraine) and the Moscow Syncline (Russia), in agreement with its palaeogeographical position in the western margin of the Palaeotethys. There are also links with America, apparently established through the Urals and the Arctic. However, as Martínez Chacón and Winkler Prins (2015) have suggested, a connection between the western Palaeotethys and the Panthalassa Ocean through the Iberian-Midcontinent Seaway cannot be excluded, since Vai (2003) and García Bellido and Rodríguez (2005) pointed out that this seaway did not close until Kasimovian times.

The fish and conodont assemblage from Mina Profunda were likely either pelagic or benthopelagic, being widely represented in different regions of the world. Chondrichthyan cladodonts probably hunted close to the sea surface, and thus their remains could occur in very different environments, from shallow- to deep-sea biofacies. The presence of *Helodus* is consistent with a shallow-water environment (Roelofs et al., 2016), following the chondrichthyan biofacies model of Ginter (2000, 2001). Conversely, the cladodont teeth of *Denaea* is associated with basinal carbonate facies in northern Europe (Ginter et al., 2015).

7. Conclusions

The application of micropalaeontological techniques to the upper Bashkirian Caliza Masiva of the San Emiliano Fm. (Cantabrian Zone) recalls how the difficulties to extract the fossils without the appropriate techniques and certain preservation conditions produce biases in the fossil record, distorting the patterns of diversity over time. The studied faunal assemblage is primarily characterized by phosphatic (*Langella* and *Orbiculoidea*) and silicified calcareous articulate microbrachiopods (chonetid, *Lambdarina*, *Composita*, *Crurithyris*, and terebratulids), frequently under-represented due to their low fossilization potential. The exceptional record of the microbrachiopod *Lambdarina winklerprinsi* nov. sp. contributes to filling the very discontinuous Viséan–Late Permian fossil record of this genus. The abundant and diverse fish remains obtained from the same insoluble residues are consistent with a highly efficient marine ecosystem during the sedimentation of the Caliza Masiva. The accompanying conodont elements are scarce, though indicative of a late Bashkirian age (*Idiognathoides sulcatus parvus* Zone) for the faunal assemblage.

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