Lower Devonian Delthyridoidea (Brachiopoda, Delthyridina) of the Cantabrian Mountains (N Spain)

by Jenaro L. GARCÍA-ALCALDE


Abstract

In the Cantabrian Mountains (N. Spain) spiriferids are the most diversified Lower Devonian brachiopod group (50 species of a total of 212 known articulate brachiopod species). But despite this fact less than a quarter of the spiriferid species have been adequately described in recent times. This paper focuses on Lower Devonian Delthyridoidea of the Cantabrian Mountains (N. Spain) that occur not only in the classical, well-known Asturian-Leonian region but also in the relatively remote and unknown Palentian region, in the eastern part of the Cantabrian Mountain between Palencia, León, and Santander provinces. Six species (three new) are described belonging to five genera (two new). Bultynckia n.gen. with Spirifer rojasi de Verneuil as type-species is proposed as a new generic taxon of the Subfamily Paraspiriferinae based on the characteristic sinus ribbing. The meaning, composition and family assignment into the Cyrtinopsidae of the Subfamily Kozlowskiellininae are discussed. Boucotiellina n.gen. with Spirifer esquerraï de Verneuil as type-species is included in Kozlowskiellininae. This new genus is characterized by the extreme sharpness of the radial ornamentation, faintly capillate, spinose micro-ornamentation developed on growth microfilae, well-developed dental plates and a very low, short, median ventral septum.

Key-words: Brachiopoda, Delthyridoidea, Lower Devonian, Cantabrian Mountains.

Résumé

Dans les Montagnes Cantabriques (Espagne du Nord), les spirifériades sont les brachiopodes les plus diversifiés du Dévonien Inférieur (50 espèces sur un total de 212 espèces connues de brachiopodes articulés). Neanmoins, moins d'un quart des espèces ont été décrites d'une façon appropriée. Ce travail est concentré sur les Delthyridoidea du Dévonien Inférieur qui se trouvent dans la région Asturie-Leonie bien connue et aussi dans la région Palentienne (partie orientale des Montagnes Cantabriques, entre les provinces de Palencia, León et Santander), relativement éloignée et peu connue. Six espèces (dont trois nouvelles), appartenant à cinq genres (dont deux nouveaux), sont décrites. Bul¬tynckia n.gen., avec Spirifer rojasi de Verneuil comme espèce-type, est proposé comme nouveau genre de la Sous-Famille Paraspiriferinae, en se basant sur le plissement caractéristique du sinus ventral. La signifi¬cation, composition et désignation familiale des Cyrtinopsidae de la Sous-Famille Kozlowskiellininae sont discutées. Boucotiellina n.gen., avec Spirifer esquerraï de Verneuil, comme espèce-type, est placé dans Kozlowskiellininae. Ce nouveau genre est caractérisé par le profil très aigu des éléments macro-ornementaux radiaux, par une micro-orne¬mentation faiblement capillaire, épineuse, développée sur les micro¬filae de croissance, les plaques dentales bien développées et le septum moyen ventral très bas et court.

Mots-clés: Brachiopodes, Delthyridoidea, Dévonien Inférieur, Mont¬agne Cantabriques

Introduction

The present work is the second of a series of three focused on Lower Devonian spiriferids of the Cantabrian Mountains (N. Spain) that were conceived and developed by the author during a stay at Oregon State University (OSU) under the direction of Arthur J. Boucot.

The geological relevance of spiriferids that justifies the choice of this research topic was underlined in the first of the papers referred to above on Lower Devonian Spinelloidea and Cyrtospiriferoidea (GARCÍA-ALCALDE, accepted in Géobios, 2004 but not yet published). In short, spiriferids are one of the most important Lower Devonian brachiopod groups in regard to their stratigraphical potential (BRICE et al., 2000); moreover, they are the most diversified Lower Devonian Cantabrian brachiopods (ca. 25%: 50 spiriferid species of a total of 212 known articulate brachiopod species, after partial lists in GARCÍA-ALCALDE 1995, 1996, 2001a, b). Last but not least, despite the facts above, the spiriferids are badly in need of a complete taxonomic revision, because only a small fraction of them (less than fourth of the known species) have adequately been described in recent times.

Most of the Lower Devonian spiriferid species discussed by the author were introduced by the French workers E. de Verneuil, A. d’Archiac and D. & P. Oehlert (DE VERNEUIL & D’ARCHIAC 1845; DE VERNEUIL IN PRADO & DE VERNEUIL 1850; OEHLERT & OEHLERT, 1901). In particular in this paper the taxonomic status of Spirifer Rojasi DE VERNEUIL, 1850, Spirifer Boulei OEHLELT & OEHLERT, 1901, and Spirifer Esquerraï DE VERNEUIL, 1850, are revised.

However, many spiriferid species were unknown to the classical authors referred to above and to most later researchers that worked in the well-known provinces of...
Asturias and León. I refer to the Palentian Domain Devonian forms. The Palentian region and their faunas remained unstudied by brachiopod specialists virtually until the important Binnekamp (1965) monograph, because of remoteness and difficult approach. The Palentian Domain is a predominantly Silurian-Devonian allochthonous unit in the eastern Cantabrian Mountains, outcrops on the border between the provinces of Palencia, León, and Santander (northern Spain) (Text-fig 1) that constituted the deeper part of the Cantabrian Devonian continental shelf (García-Alcalde et al., 2002). Marked differences in facies and faunas occur between the offshore Palentian Domain and the near-shore Asturian-Leonian Domain. Very few common brachiopod species occur in both domains. In recent years I have focused on the Palentian Devonian facies and faunas and on its very complex geology. Some palaeontological fruits of this work have already been published (GARCÍA-ALCALDE, 1998, 1999, 2003) and in the present paper two new spiriferid forms of that region are described and figured: Howellella (Howellella) corallina n.sp. and Hysterolites blodgetti n.sp.

The DPO specimens studied here are housed in the collection of the Department of Geology (Paleontology), University of Oviedo (Spain).

The following abbreviations are used in the text: L = Length, w = width, t = thickness of the measured specimens; Nc = number of ribs on the flank; wsen = width of the ventral sinus at the commissure.

Palaeontology

Suborder Delthyridina Ivanova, 1972
Superfamily Delthyridioidea Phillips, 1841
Family Delthyrididae Phillips, 1841 (sensu Bizzarro & Léspérance, 1994)
Subfamily Howellellinae Johnson & Hou in Carter et al., 1994
Genus Howellella Kozlowski, 1946
Subgenus Howellella (Howellella) Kozlowski, 1946

Howellella (Howellella) corallina nov.sp.
Plate 1, Figures 1-13; Text-figures 1, 2, 5, 6; Table I

Derivatio nominis
Named after the level where the species first occurs, because it matches the first stage of the Cantabrian Devonian reefal development, characterized by the formation of small tabulate and branched rugose patch-reefs frequently in life position.

Material
1017 mainly well-preserved specimens. Holotype DPO 31714 (Pl. 1, Figs. 1-4), 38 paratypes, DPO 32388-33422, 36847-36848 and 37796 (sectioned, Text-fig 6), and 188 specimens more, DPO 32206-32387, from the locus and stratum typicum. 38 specimens DPO 36805-36832, 36834-36836 and 36840-36846 from other levels of the locus typicus. 557 specimens, DPO 36051-36607 (DPO 36811, Pl. 1, Figs. 2-7; DPO 36579, Pl. 1, Figs. 8-10; DPO 36595, Pl. 1, Figs. 11-13) from the Lebanon Quarry (Cervera de Pisuerga, province of Palencia, N. Spain), Lebanon Fm., levels α-320, α-334 and α-336/337, Lower Pragian. 101 specimens, DPO 36608-36710, from the north side of the Váñes Lake, track to Polentinos Village, Lebanon Fm., level α-122, Lower Pragian. 94 specimens DPO 36711-36804, from other section W. of Lebanon, point 5, Lebanon Fm., Lower Pragian.

Locus and stratum typicum
600 m WSW of the Lebanon Village (San Salvador de Cantamudá, Cervera de Pisuerga, Province of Palencia, N. Spain). “Las Cabaninas” section. Lebanon Fm, C Mb level M-LEB-33B/34. Lower Pragian. Faunal Interval 5 (García-Alcalde, 1996) (Text-figs. 1-2).

Diagnosis
Small, slightly transverse (average of L/w = 0,82) H. (Howellella), with numerous lateral ribs (average: 6 to 8; maximum: 10); high, convex dorsal fold; relatively large ventral sinus (average: 28% of the maximum shell width); low, concave, ventral interarea with strongly incurved beak.

Description
Small-sized (average length: 6,2 mm; average width: 13,1 mm) (Text-fig. 5, Table I), brachythyrid, slightly transverse (average L 82% of w), ventribiconvex, not too inflated (average t 73% of L) shell of rhomboidal outline, with very rounded cardinal extremities and maximum width at mid-length.

Differentiated (differently ornamented palintrope and ventral interarea, sensu Krans, 1969, separated by sharp interareal edges) cardinal ventral area. Relatively low, apsacinal to catacline, very concave, longitudinal- and transversally striated ventral interarea much larger than palintrope. Palintrope vaguely delimited laterally by rounded edges showing the same ornamentation (spine-fringed growth lines and filae) as the rest of the shell (Pl. 1, Figs. 3, 10). Wide delthyrium up to 1/4 to 1/5 of the hinge width, bounded by strong deltoidal plates normal to the area surface, sometimes fused below the ventral beak forming a small, convex deltium; well-developed ventral umbo with strongly curved beak sometimes projecting on the hinge line. Anacline to orthocline dorsal area much lower than the ventral area; open notothyrium; small dorsal umbo with curved dorsal beak.

Wide, relatively shallow ventral sinus; flat, concave, sometimes sub-angular bottom, starting at the valve apex, bounded laterally by radial ribs similar to the next ones; in frontal view, the sinus bounding costae occur anteriorly in a lower level than the next pair of costae (Pl. 1, Figs. 2, 7). High, convex to slightly anteriorly flattened dorsal fold, bounded by intercostal spaces similar to the next ones. Uniplicate frontal commissure (Pl. 1, Figs. 2, 7). Relatively low, arched to rounded trapezoidal, anterodorsally oriented tongue. Slightly ventrally oriented lateral commissures in lateral and frontal views.

Six to eight (average: 81% of the measured specimens) (maximum: 10; minimum: 5), simple, rounded, relatively high and narrow costae on each slope, reflected postero-
laterally (Pl. 1, Figs. 5, 8), starting at the apices of valves, with sub-angular, narrower interspaces; the ribs close to the palintrope are obsolescent.

Scarce, strong, irregularly distributed growth lamellae, clustered at the front of shell, crossed by subdued concentric flae. Marginal, spinose, microcostulate micro-ornamentation; fine, sub-radial capillae with regular, elongated, slightly pustulose spine bases (14 to 16/mm at the ventral sinus and dorsal fold, near the anterior margin) fringing the lamellae edges.

Juvenile shells tend to be as long as large, with very rounded cardinal extremities (Pl. 1, Figs. 11, 12) and ventral beak less curved than in adults; in these specimens the radial elements (including the ventral sinus and the dorsal fold) are weaker than in adults. The smaller shells (ca. 3 mm of length) have numerous lateral costae
(5 to 7) and coarser micro-ornamentation than larger specimens.

Strong, long, extra-sinal (usually between the 1st and 2nd pair of costae) dental plates. Well-developed lateral apical cavities. Ventro-medially directed dental bases supporting narrow, strong cardinal teeth; faintly dorsally convergent ventral adminicula. Strong, apical shell callus; relatively strong median myophragm extending forwards to the anterior margin of the muscle field (Text-fig 6).

Well-developed cardinal process, with ctenophoridium provided by 10-12 high, vertical platelets of divergent bases and convergent summits supported by short but well-developed crural plates. Minute, free, dorsal apical cavities. Dorso-medially directed crural bases projecting anterior of the cardinal process with distal ends curved
Fig. 3 — Geological map of the Adrados-Colle area (Province of León). Situation of the stratotypes of *Arduspirifer adradensis* n.sp. (1), and *Bultynckia rojasi* and *Boucotiellina ezquerrai* (2). Situation of the outcrop where the Leonian population of *Hysterolites blodgetti* n.sp. occurs. Fm. = Formation; Up. = Upper.
**UNCONFORMABLE CARBONIFEROUS (STEPHANIAN)**

**LOWER TO MIDDLE CARBONIFEROUS**

- Upper Devonian sandstones
- Portilla Fm.
- Huergas Fm.
- Santa Lucía Fm.
- La Vid Group

**CAMBRIAN-LOWERMOST DEVONIAN**

----- Normal contact
----- Unconformable contact
Fault
Thrust fault
Road
Village
Peak
- Stratotype of *Bultynckia boulei*

Fig. 4 — Geological map of the Bernesga Valley area (Province of León) and situation of the stratotype of *Bultynckia boulei*. Fm. = Formation.

Fig. 5 — *Howellella (Howellella) corallina* n.sp. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

Discussion

As stated by Gourvennec (1989) and other authors, the great number of species assigned to *Howellella* probably means that this genus is an all-embracing taxon embracing several different subgenera or even genera calling for a careful revision in order to discriminate the relation-
ships among the included species-groups. In this way, Carls (1985) and Carls et al. (1993) proposed two new subgenera, H. (Hysterohowellella) and H. (Iberohowellella), the former characterized by its tendency to develop acuminate cardinal extremities, flattened and medially excavated dorsal fold and numerous lateral costae. The latter comprises large-sized, Hysterolites-like forms with micro-ornamentation similar to Vandercammenina. Howellella (H.) corallina nov.sp. has numerous radial ribs as in H. (Hysterohowellella). However, H. (Howellella) corallina nov.sp. is a small-sized, brachythyrid, slightly transverse form, with very rounded cardinal extremities. Its maximum width is situated well anterior to the hinge-line, has a wide ventral sinus, convex to anteriorly flattened, unfurrowed dorsal fold, and low, very concave ventral cardinal area. These last characters occur usually in primitive H. (Howellella) where the new species has now been included. The Cantabrian species differs from other H. (Howellella) forms because of its greater number of radial ribs.

Howellella minora Rzhonsnitskaya (in Alekseeva, 1967) whose size, profile, outline and internal structure are close to the H. (H.) corallina has fewer radial ribs that are also lower and rounder with narrower interspaces.

Fig. 6 — Howellella (Howellella) corallina n.sp. Paratype DPO 37796. Serial sections. Distances measured to the ventral apex. Black bar represents 1 mm.
Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Ne = Number of ribs.

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Howellella (Howellella) corallina n.sp.

Subfamily Hysterolitinae Termier & Termier, 1949
Genus Hysterolites Schlotheim, 1820

Hysterolites blodgetti nov.sp.
Plate 1, Figures 23-27; Plate 2, Figures 1-15; Plate 3, Figures 1-5; Text-figures. 1, 2, 7, 8; Table I

v.1996 - Hysterolites n.sp. A - García-Alcalde, fig. 2.

Derivatio nominis
Named after Robert Blodgett, formerly of the Oregon State University in Corvallis (US) now of the U.S. Geological Survey, Anchorage, Alaska, admired friend who combines vast palaeontological skills and exceptional humanity and heartiness.

Material
Holotype DPO 30309 (Pl. 2, Figs. 1-4) and 51 paratypes DPO 30310-30329 (DPO 30325, figured in Pl. 1, Figs. 23-27; DPO 30326, Pl. 2, Figs. 10-11; DPO 30327, Pl. 2, Figs. 12-13; DPO 30328, Pl. 2, Figs. 14-15), 31862-31892 (DPO 31867 sectioned, Text-fig 8; DPO 31869, figured in Pl. 2, Figs. 5-9) from the locus and stratum typicum. 80 variably preserved specimens, DPO 30409-30486, 31860-31861, from Arauz Creek, Cortés Valley (north Palencia, Spain), top of Lebanon Fm., bed M-AR-51/52, Pragian. 33 badly preserved specimens, DPO 31893-31922, from Los Payos Hill, south Abadia de Lebanon (Province of Palencia), top of Lebanon Fm., bed α-151, Pragian. 2 well-preserved specimens, DPO 31923-31924 from the Lebanon Quarry (Palencia), top of Lebanon Fm., bed M-LEB-47, Pragian. 103 decorticated specimens, DPO 126403-126505 (DPO 126504, Pl. 3, Figs. 1-5), from NE Colle (Sabero, Province of León, Spain), top of the Felmin Fm., levels 4-5, Pragian-Emsian boundary.

Locus and stratum typicum
Northern side of Varies Lake, SE of the village of Polentinos (Cervera de Pisuerga, Palencia, N. Spain), Lebanza Fm., E Mb., bed a-107, Pragian. Faunal interval 6 (García-Alcalde, 1996) (Text-figs. 1-2).

Diagnosis
Slightly transverse, megathyrid, alate Hysterolites with 7-10 strong, sub-angular costae in each slope, proximally flattened ventral sinus becoming sub-angular anteriorly, strong, frilly growth lamellae, faintly excavated ventral muscle field; small crural plates.

Description
Medium-sized, ventribiconvex, relatively inflated (average: t 75% of L) (Text-fig 7, Tab. I) with maximum thickness at mid-length, of irregular pentagonal outline with the anterior of the shell constituting the shorter side of the pentagon. Brachythryrid, as long as wide, juvenile shells (L <10 mm) with rounded cardinal extremities, to megathyrid, transverse (average: L less than 75% of w, in shells 4-7 mm long or greater) shells, with small ears in late juvenile and adult growth stages (Pl. 2, Figs. 1-9).

Rather low, apsacline, curved, transversal- and longitudinally striated ventral cardinal area, with sharp lateral edges. Small, longer than wide delthyrium (up to 1/5 to 1/7 of the hinge width), with well-developed tooth ridges supporting fine, separate deltidial plates. Strong, prominent ventral umbo with projecting curved beak concealing the delthyrium apex. Faintly anacrine, transversally and longitudinally striated dorsal area, up to 7 times lower than ventral area; low and wide, uncovered notothyrium; well-developed dorsal umbo with a curved, dorsal beak concealing the apex of notothyrium.

Well-delimited, relatively narrow (average: less than 30% of maximum width), rather deep, ventral sinus, beginning at the valve apex. Flattened sinus of trapezoidal section in juvenile stages becoming angular in adults. Relatively low, narrow, faintly convex to flattened, even, medially anteriorly furrowed, dorsal fold. Uniplicate anterior commissure. Short, trapezoidal, postero-dorsally directed tongue. In anterior and posterior views the shell...
Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Nc = Number of ribs.

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Frilly, irregularly spaced, growth lamellae mainly clustered near the anterior region. There are, however, other shell zones where growth lamellae concentrate, i.e. at the growth stage where the shell changes from equidimensional to transverse, and at the growth stage where the transverse shell changes from brachythyrid to megathyrid. Marginal, simple, microspinose micro-ornamentation (Pl. 1, Figs. 23, 27). Slender, sub-radial capillae developed by intercalation, diverging anteriorly at an acute angle from the bottom of costal interspaces and ventral sinus to the summits of costae. Fine, elongated, regularly spaced spine bases (15-20 at the anterior sinus margin), of variable size.

Fig. 7 — Hysterolites blodgetti n.sp. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.
Genus Arduspirifer Mittmeyer, 1972

Arduspirifer adradensis nov.sp.

Plate 1, Figures 14-22; Text-figures 1, 3, 9, 10; Table I

H. dolosus Gourvennec, 1989, from the Pragian of Brittany (France) is smaller and more transverse, with shallower and sharper sinus, a smaller number of lateral costae, fainter growth lamellae and an unexcavated ventral muscle field.

H. gandli Carls, 1986, from the Pragian of Aragón (Spain) has a stronger median fold, deeper and more rounded ventral sinus, more lateral costae (10 per flank, average), higher ventral interarea, and a much more curved ventral beak covering the hinge.

H.? walliseri Jahnke & Slupik, 1993, from the Upper Pragian of the lower part of the Arauz Fm. in the Lezna Peak (Palencia, N. Spain) is larger and more transverse, with no cardinal ears, flatter ventral sinus, regularly spaced growth lamellae, more lateral costae (average: 10-12 per flank), shorter dental plates, small, excavated ventral muscle field, and almost completely filled apical cavities.

The muscle field and shell thickening of apical cavities in H. blodgetti nov.sp., H. venus, and H.? walliseri indicate these forms are close to the transition between the genera Hysterolites and Arduspirifer. In fact, recently Jansen (2001) has tentatively included H.? walliseri in Arduspirifer.

Genus Arduspirifer Mittmeyer, 1972

Arduspirifer adradensis nov.sp.

Plate 1, Figures 14-22; Text-figures 1, 3, 9, 10; Table I

1938 - Spirifer chama Eichwald; Comte, p. 24(62), pl. 2, fig. 1.

Derivatio nominis

Named after the locus typicus of the species, Adrados, in the Province of León.

Material

266 variably preserved specimens. Holotype DPO 31974 (Pl. 1, Figs. 14-17), 59 Paratypes DPO 31975-32033 (DPO 31983, Pl. 1, Figs. 19-21; DPO 31995, Pl. 1, Fig. 18; DPO 31996, Pl. 1, Fig. 22; DPO 32012, sectioned, Text-fig. 10), and other 149 badly preserved specimens, DPO 32034-32182, from the locus and stratum typicum. 49 specimens DPO 31925-31973 from the locus typicus but at a younger level than the typicum, La Vid Group, La Pedrosa Fm., level 1-64, Lower Emsian.

8 specimens DPO 31184-31190 and 32183 from different Lower Emsian levels of the La Pedrosa Fm. at Abelgas (Province of León). Faunal intervals 9-10 (García-Alcalde, 1996)

Locus and stratum typicum

Adrados (Bolar, Province of Leon, north Spain). La Vid Group, La Pedrosa Fm., level I-63, Faunal Interval 9, Upper part of the Lower Emsian (Text-fig. 1) (Text-figs. 1, 3).
Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Nc = Number of ribs.

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**Arduspirifer adradensis** n.sp.

**Diagnosis**

Large, transverse to alate *Arduspirifer*, with 6 to 9 strong, sub-angular costae on each flank, separated by sub-angular and larger interspaces; numerous, regularly spaced growth lamellae; narrow ventral sinus with flattened bottom; no delthyrial plate; relatively excavated ventral muscle field bounded laterally by the dental plates; more or less developed apical cavities in part filled by secondary shell; strong cardinal process; no crural plates.

**Description**

Large, transverse to alate, *Arduspirifer*, with 6 to 9 strong, sub-angular costae on each flank, separated by sub-angular and larger interspaces; numerous, regularly spaced growth lamellae; narrow ventral sinus with flattened bottom; no delthyrial plate; relatively excavated ventral muscle field bounded laterally by the dental plates; more or less developed apical cavities in part filled by secondary shell; strong cardinal process; no crural plates.

Large, transverse to very transverse (L 60% of w in average; sometimes L reaches 50% of w or even less, because most specimens have the cardinal extremities broken), alate, megathyrid, not inflated (average: t up to 75% of L) shell (Text-fig. 9; Tab. I), with maximum thickness in the posterior half of length. Biconvex juvenile and clearly ventribiconvex adult shells.

Low, concave, apsacline to orthocline (Pl. 1, Figs. 15, 17), transversally and longitudinally striated ventral cardinal area bounded by sharp lateral edges. Subdued, longitudinal striae more developed near the delthyrium. Equilateral, triangular delthyrium, 8-11 times shorter than the hinge width; tooth ridges supporting strong deltial plates sometimes fused below the ventral beak forming a convex deltium with a circular, mesothyroid foramen. Faint ventral umbo with an erect to strongly curved beak projecting onto the dorsal umbo, concealing in part the delthyrial area (Pl. 1, Fig. 17). Anacline to orthocline dorsal area, ca. 7 times lower than ventral area and with similar longitudinal and transversal striation; open notothyrium. Small dorsal umbo with a curved beak concealing the notothyrium.

Deep, narrow (less than 25% of the maximum width), trapezoidal, ventral sinus with a flattened to rounded bottom starting at the valve apex, well delimited by radial costae similar to the adjacent ones, although sometimes they are situated anteriorly at a slightly lower height than the adjacent costae. Some specimens develop a subdued median sinus costa near the frontal commissure. Narrow, relatively low, sub-angular to rounded dorsal fold, bounded by furrows similar to others. Uniplicate anterior commissure. Lateral commissure faintly directed dorsally. Short, trapezoidal to parabolic, anterodorsal- to dorsally directed tongue.

Six to nine (85% of measured specimens) (maximum: 10; minimum: 5), simple, strong, narrow, sub-angular lateral costae with interspaces of similar or slightly larger width. Half of costae start at the shell apices, whereas other costae develop along thickenings parallel to the posterior margins (Pl. 1, Fig. 15). In some specimens, one or two subdued costae near the cardinal extremities bifurcate. Quite frequently there are one or two additional costae on one of the sides, and the development of the radial elements on both flanks can differ considerably (Pl. 1, Fig. 19).

Strong, frilly, regularly spaced growth lamellae clustered and more developed in two different shell regions,
Lower Devonian Delthyridoidea Spain
i.e. at the transition between juvenile and adult growth stages and at the shell anterior, mainly at the transition between adult and gerontic growth stages (Pl. 1, Fig. 19).

Subdued to obsolescent, sub-radial, capillate, spinose micro-ornamentation with numerous (20-23 by ram at the anterior part of sinus), long, narrow, variably-sized spine bases fringing the growth lines, that project anteriorly at an acute angle from the valve surface.

Short, extra-sinal (below the 2nd pair of radial ribs) dental plates with distal ends curving slightly towards each other. Massive, large and rather long cardinal teeth. Well-developed apical callus forming a high, striated, faintly concave apical platform with striae converging anteriorly, supporting the median pedicle muscle field (Pl. 1, Fig. 18, Text-fig. 10). Ventral lateral apical cavities partially to completely filled by secondary shell, mainly in adult specimens. Short, excavated, ventral muscle field of irregular rhombic outline with anterior sides shorter than posteriories, laterally bounded by the dental plates (Pl. 1, Fig. 18); long, narrow, lanceolate adductor scars bisected by an acute, low myophragm starting at the base of the apical callus, and placed in a higher level than the adductor scars; triangular, large, radially striated adductor scars bounding the adductor scarlets laterally and anteriorly. Genital markings represented by small, deep, circular pits clustered at the postero-lateral sides of the muscle field including the distal margins of the apical cavities.

Strong and very high notothyrial platform supporting a robust, occasionally triated cardinal process (Pl. 1, Fig. 22; Text-fig. 10), the median lobe higher than the lateral; ctenophoridium constituted by up to 40 fine, vertical, radially distributed platelets. Neither crural plates nor apical cavities. Deep, triangular, partially posterior and laterally covered dental sockets, bounded by strong, high, inner socket ridges (Text-fig. 10). The distal end of the inner socket ridges fit in cavities excavated at the base of the cardinal teeth to form a complementary interlocking device (Text-fig. 10). Excavated adductor muscle field situated below the dorsal fold bisected by a narrow and low myophragm starting at the base of the notothyrial platform. Long, slender crura uniting with the primary lamellae of the spiralium at the commissural plane. Neither jugal processes, nor jugum. Spiral cones with up to 10, circular, spinose (Text-fig. 10) whorls.

ONTGENEY

Three growth stages can be recognized, either by direct observation of different-aged individuals or by the observation of consecutive shell outlines marked by the growth lamellae in single, well-preserved specimens. In the first, juvenile stage (L<4 mm) the shell is very low, biconvex and almost equidimensional. In the second, late juvenile stage (L up to 15 mm) the shell maintains its minimal biconvex lateral profile but becomes strongly transverse and alate. In the third, adult stage (L>15 mm) the shell becomes equidimensional, but it becomes thicker so that older shells are less transverse and thicker than juveniles. Sometimes the lateral slopes develop asymme-
can bifurcate anteriorly one or more times to develop even parietal ribs on the sinus walls. Along the sinus a very wide, low, flat, sometimes branched anteriorly, median costa occurs. Numerous, imbricating, regularly spaced growth lamellae. Capillate, marginal microspinose micro-ornamentation, with spines projecting anteriorly to form strong angles with the shell surface, at least near the commissure. Relatively long, thin, extra-sinal dental plates. Deltidial plates normal to the ventral area, sometimes forming a small deltidium below the ventral beak. Well-developed ctenophoridium. Short, stout, crural plates.

**Discussion**

Several entirely ribbed delthyridid genera are known, most of them with branched or furrowed ribs on the flanks (Fimbrispirifer, Struveina, Multispirifer, and the new genus Bultynckia). To date Vandercammenina Boucot, 1975 is the only genus of the family with unbranched flank ribbing.

All the species included in the new genus have the characteristic sinus ribbing described above but until now the internal dorsal structure of Fimbrispirifer? cf. *F. boulei* is unknown. The sinus ribbing of *Spirifer daleidensis* Steiningera, 1853, type-species of Struveina Boucot, 1975, is close to *Bultynckia* but in the German species all lateral costae bifurcate or divide even more.

*Bultynckia rojasi* (de Verneuil, 1850)
Plate 4, Figures 7-15; Text-figures 1, 3, 11, 12; Table I

v* 1850 *Spirifer Rojasi*, n.sp. - de Verneuil, p. 178, pl. 4, fig. 4.
v. 1938 *Spirifer rojasi* Verneuil - Comte, p. 31(69), pl. 3, fig. 2-3.
1965 *Fimbrispirifer rojasi* (de Verneuil) - Krans, 1965, p. 105, pl. 9, fig. 3.
v. 1996 *Fimbrispirifer? rojasi* - García-Alcalde, Fig. 2.

**Material**

124 variably preserved specimens DPO 34818-34941 (DPO 34818, figured in Pl. 4, Figs. 7-11; DPO 34823, Pl. 4, Figs. 12-14; DPO 34828, Pl. 4, Fig. 15; DPO 34875 sectioned, Text-fig. 12), from Colle (Sabero, Province of León, N. Spain) (Text-figs. 1, 3) at different levels in the upper part of the La Vid Group, Coladilla Fm., Upper Emsian. Faunal intervals 11-12 (GARCÍA-ALCALDE, 1996).

**Locus and Stratum Typicum**

The locus typicus of the species is Colle, a small village, near Sabero (Province of León, N. Spain) (Text-fig. 3). However, until now no stratum typicum has precisely been defined. Here, bed 29 in the measured section (published in GARCÍA-ALCALDE, 1998) at the northern slope of the hill where the church of the village occurs, corresponding to the lower half of the Coladilla Formation (Upper Emsian) is proposed as stratum typicum of *Bultynckia rojasi*.

**Diagnosis**

Small, brachythrytid *Bultynckia* with rounded cardinal angles. Subdued, simple or exceptionally branched median sinus rib, starting relatively far from the valve apex. The sinus bounding ribs bifurcate one or two times giving way to weak parietal secondary ribs at the sinus walls. Variably sized, elongated spine bases fringing the growth lines. Short, stout, sub-parallel crural plates.

**Description**

Small, ventribiconvex, non inflated (average: t up to 64% of L), rhomboidal, transverse (average: L 80% of w) shell (Text-fig. 10, Tab. I) with very rounded cardinal extremities (average: hinge 65-70% shorter than maximum width); maximum width between the first third and mid-length; maximum height at the umbonal region.

Rather high, curved, strongly apsaccline to catacline, transverse and longitudinally striated cardinal ventral area with well-defined, rounded interarea margins (Pl. 4, Fig. 9); the longitudinal striae define costellae that unite forward in coarser elements resulting anteriorly in small denticles along the hinge; in some specimens a narrow palintrope also occurs. Wide delthyrium up to 1/3 of the hinge width; strong deltidial plates, normal to the area surface, sometimes forming a small deltidial cover below the beak; well-developed umbo with a strong, sub-erect to erect beak, slightly projecting above the interarea. Almost flat, orthoclinal dorsal interarea, 7-10 times lower than ventral, with marked transversal striae; large, open nothothyrium; faint umbo and dorsal beak.

Entirely costate shell. Relatively narrow (up to 30% of maximum width), shallow, poorly delimited ventral sinus, starting at the valve apex; flat bottom occupied from near the beak (2-3 mm from the valve apex) by a wide, very low elevation (Pl. 4, Fig. 12), tending to bifurcate anteriorly in the more convex specimens; the sinus-bounding costae are proximally slightly stronger than the next ones but distally lose relative importance occurring even at a lower level than the other costae near the anterior margin in anterior view; the sinus-bounding ridges bifurcate usually one or two times anteriorly, giving way to faint parietal elements at the sinus walls.

![Fig. 11 — Bultynckia rojasi. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.](image-url)
Flattened to slightly medially depressed dorsal fold, divided at most by two pairs of faint radial furrows, defining wide, very low, rounded plicae (Pl. 4, Fig. 13, 14); the fold-bounding furrows are proximally stronger than the others but become distally of similar importance to their neighbours. Uniplicate to faintly sulciplicate anterior commissure; low, trapezoidal, antero-dorsally directed tongue (Pl. 4, Fig. 11); ventrally arched, lateral commissures indented by the radial ribs (Pl. 4, Fig. 8).

Seven to ten (90% of the measured specimens) (maximum: 10; minimum: 6) simple (exceptionally bifurcating), narrow and relatively low, rounded to sub-angular, slightly deflected postero-laterally (Pl. 4, Fig. 7, 10), radial costae in each slope, separated by interspaces of the latéral costae bifurcate or are more divided. Some relatively well preserved broken spines occur in the matrix; they are short, square in section and with a fine delthyridid-like (GOURVENNE UN, 1987) furrow on the upper side.

Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Ne = Number of ribs.

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Discussion

Bultynckia rojasi resembles the smaller Vandercammenina species, as V. sollei CARLS, 1986 and V. gaugeri CARLS, 1986 in the small number of sinus costae. However, the sinus costae in Vandercammenina are similar to the lateral ribs, the number of lateral costae is greater than in Bultynckia and the ventral sinus is well delimited by simple costae. On the other hand, Vandercammenina gaugeri has a much more developed ventral interarea, and in V. sollei the dental plates are sub-parallel with distal ends strongly curved to one another.

Vandercammen & Krans (1964) cited the occurrence both of a median longitudinal slit along the microspines and of a small delthyrid plate. None of these characters have been observed in the material at hand of Bultynckia rojasi.

B. boulei (OEHLERT & OEHLERT, 1901) and B.? cf. boulei GOURVENNE UN, 1989 are larger, with more lateral and sinus ribs. Moreover in the latter species most of the lateral costae bifurcate or are more divided.
**Bultynckia boulei** (OEHLERT & OEHLERT, 1901)
Plate 4, Figures 1-6; Text-figures 1, 4; Table I

* 1901 *Spirifer Boulei*, nov.sp - OEHLERT & OEHLERT, p. 233, pl. 6, fig. 1.

non 1989 *Fimbrispirifer* ? *cf.* *F. boulei* (OEHLERT, 1901) - GOURVENNEC, p. 182, pl. 19, fig. 9-11, text-fig. 103.

v. 1996 "*Fimbrispirifer*" *boulei* - GARCÍA-ALCALDE, Fig. 2.

**MATERIAL**
13 variably preserved specimens from several localities of the Province of Leon (north Spain), Santa Lucia Fm., latest Emsian. DPO 32840 from Quejo (Pola de Somiedo), DPO 32841-32842 (Pl. 4, Fig. 1-4) from Argovejo (Crémenes), DPO 32843-328445, from El Millar (La Pola de Gordón), DPO 32846-32851 (DPO 32850, Pl. 4, Fig. 6) from the type-locality in Santa Lucia (La Pola de Gordón) and DPO 36049, from Aviados (Boñar). Faunal interval 16 (GARCÍA-ALCALDE, 1996) (Text-fig. 1, 4).

Fig. 12 — *Bultynckia rojasi*. Serial sections of a broken and decorticated specimen, topotype DPO 34875. Distances measured to the ventral apex. Black bars represent 1 mm.
Locus and stratum typicum

The locus typicus occurs to the ESE of Santa Lucia Village (La Pola de Gordón, Province of León, N. Spain), along El Puerto Creek, in the Santa Lucia-Amézola road (Text-fig. 4). However, until now no stratum typicum was precisely defined. Here, bed SL-55/56 in the measured section (published in García-Alcalde et al., 1979) at the III Member of the Santa Lucia Formation (uppermost Emsian) is proposed as stratum typicum of Bultynckia boulei.

Diagnosis

Medium to large, entirely costate shell. Very low and wide, anteriorly bifurcated or even more divided, median sinus costa very differentiatively from the lateral costae. The sinus-bounding ridges and even the next lateral pair usually bifurcate in large specimens. Small, sub-parallel crural plates.

Description

Medium to large (Tab. I), ventribiconvex, relatively inflated, rhomboidal, transverse shell with maximum width at the hinge or slightly before and maximum thickness at mid-length.

Well-developed, catacline to strongly apsacline, curved, transversally and longitudinally striated ventral cardinal area (Pl. 4, Fig. 2, 5); the longitudinal striae define slender costules that unite two or three abreast anteriorly becoming progressively thicker resulting in minute denticles along the hinge. Very wide delthyrium up to 1/3 of the hinge width; strong, discrete, deltidial plates. Well-developed ventral umbo with an erect to curved beak that projects slightly on the cardinal area (Pl. 4, Fig. 2). Orthocline, transverse and longitudinally extended platelets and small, sub-parallel radial ribs. The morphology of the spine bases allow one to suppose that the spines formed at a high angle, close to 90° with the shell surface; some broken spines that occur in the matrix of specimens, are massive, relatively long (ca. 2-4 mm), with a rounded section lacking a longitudinal "delthyrid" (Gourvennec, 1987) furrow.

Relatively wide, shallow ventral sinus, starting at the valve apex. In the bottom sinus a wide, very low, median costa starting at the valve apex occurs; the median costa bifurcates or even further divides anteriorly in similarly very low and flattened radial elements (Pl. 4, Fig. 1, 6). The sinus-bounding ribs are proximally similar to the others but occupy anteriorly a lower level than the neighbours in anterior view so that the sinus is badly defined in that region; the sinus-bounding ridges and sometimes the next 1st and 2nd pairs of lateral ribs bifurcate anteriorly one or two times, the former originating as parietal elements at the sinus walls that exceptionally bifurcate in turn in older specimens.

Convex to flattened dorsal fold starting at the valve apex longitudinally furrowed reproducing the divisions of the sinus costae (Pl. 4, Figs. 4, 6).

Uniplicate anterior commissure; trapezoidal, anterodorsally directed tongue (Pl. 4, Fig. 2); faintly arched, lateral commissures ventrally oriented in anterior and lateral views (Pl. 4, Figs. 2, 4). In anterior and posterior views the valve slopes are faint and regularly convex forming acute angles at the lateral commissures (Pl. 4, Figs. 4-5)

Eleven to fourteen (maximum 16-17 at the margin of shell if bifurcated elements are counted) rounded to sub-angular, relatively high costae in each slope, with interspaces similar. Lateral ribs simple in young individuals but in adults to gerontic shells the two or three first pairs close to the sinus and fold bifurcate one or two times near the commissure (Pl. 4, Figs. 1, 3)

Numerous, close, imbricate, regularly spaced growth lamellae fringed by strong, elongated spine bases, of similar size (Pl. 4, Fig. 6); the spine bases are aligned along the successive growth lines forming sub-radial series opening anteriorly at relatively high angles from the bottom of the inter-costal spaces to the summits of radial ribs. The morphology of the spine bases allow one to suppose that the spines formed at a high angle, close to 90° with the shell surface; some broken spines that occur in the matrix of specimens, are massive, relatively long (ca. 2-4 mm), with a rounded section lacking a longitudinal "delthyrid" (Gourvennec, 1987) furrow.

Relatively short, extra-sinal (between the 2nd and 3rd pair of lateral costae) dental plates visible in eroded specimens. No delthyritic plate. In the dorsal valve a well-developed echinophoridium provided with numerous, longitudinally extended platelets and small, sub-parallel crural plates occur.

Discussion

The type of the species, figured by Oehlert & Oehlert (1901, pl. 6, fig. 1) has anteriorly bifurcating sinus-bounding costae. This feature also occurs in the larger Cantabrian specimens perhaps indicating an evolutionary trend from simple costate delthyridid shells as in Vandercammenina to taxa with different kinds of bifurcated lateral costae as in Bultynckia, Fimbрисpirifer, Struveina or Multispiifer.

The differences between F.? cf. boulei Gourvennec, 1989 and Spirifer boulei Oehlert & Oehlert, 1901 have been described by Gourvennec (1989). In the Cantabrian specimens assigned to B. boulei the maximum number of lateral costae (including bifurcated elements) at the anterior margin of shell is not greater than 16-17, the two or three pairs of costae closer to the ventral sinus and dorsal fold only bifurcate rather anteriorly, and there are a maximum of 7 to 9 costae in the sinus. On the other hand S. boulei has rounded to sub-angular lateral ribs whereas in F.? cf. boulei they are flattened. All these characters separate both species, otherwise closely related.

Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Nc = Number of ribs.

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Bultynckia boulei
The form identified by Comte (1938, pl. 3, fig. 5) as *Spirifer cf. parcefurcatus* shows bifurcating elements along the entire shell and possibly belongs to *Struveina Boucot*, 1975

Family Cyrtinopsidae Weidekind, 1926

Subfamily Kozlowskiellininae Boucot, 1957

Remarks

The classification of *Cyrtinopsis* Scupin, 1896, *Kozlowskiella Boucot*, 1957 (nom. nov. pro *Kozlowskiella Boucot*, 1957) and related forms has been a difficult matter. *Cyrtinopsis* was considered, long ago, so unique as to represent a subfamily, the Cyrtinop-sinae Weidekind (in Salomon, 1926) or a family, the Cyrtinopsidae (Boucot, 1957a) (although see Havlícek, 1959). On the other hand, Boucot (1957b) stated that *Kozlowskiellina, Megakozlowskiella Boucot*, 1957b (first proposed as a *Kozlowskiella* subgenus), and *Hedecnina Boucot*, 1957 (= *Boucotinskia Brunton & Cocks*, 1967; cf. Brunton & Cocks 1967, Krans, 1973) would form another consistent, well-differentiated subfamily group (although see Ivanova, 1972). Krans (1969, 1971) revised *Kozlowskiellina* (including the *Megakozlowskiella* species) and *Cyrtinopsis* and concluded (Krans, 1971) that both genera must be grouped into the same subfamily, choosing for it the name Cyrtinopsidae (following incorrect family name usage) and *Hedecnina Boucot*, 1957 (= *Boucotinskia Brunton & Cocks*, 1967). And, later on, after a revision of the genus *Boucotinskia*, joined it to the same subfamily (Krans, 1973). Other authors (Lenz, 1972; Chatterton, 1973; Perry, 1984) discussed the relationships among *Cyrtinopsis, Megakozlowskiella* and *Plicocyrtina Havlícek*, 1956, and considered they are very close. The essential of Krans's conclusion was agreed to by Carter et al. (1994). In their spiriferid classification these authors accepted the Family Cyrtinopsidae as constituted by the separte Subfamily Cyrtinopsinae (with *Cyrtinopsis, Kozlowskiellina, Megakozlowskiella* and *Plicocyrtina* and the aseptate Subfamily Araspiriferinae Johnson in Carter et al., 1994) (with *Araspirifer Havlícek*, 1987 and *Boucotinskia*).

More recently, Bizzarro & Lespérance (1999) disqua-lified the above authors referring to Boucot's original thought, slightly modified. According to the former authors, *Cyrtinopsis* would be the sole genus of the Subfamily Cyrtinopsinae, whereas the Subfamily Kozlowskiellininae, would embrace *Kozlowskiellina, Megakozlowskiella, Araspirifer, Boucotinskia* and *Plicocyrtina*. On the other hand, both subfamily taxa and five more, would constitute the Family Deltthyrididae according to their own revised concept (Bizzarro & LESPÉRANCE, 1999, p. 1059, Fig. 3).

Lacking new data on the micro-ornament of the discussed genera, in particular of the Subfamily Kozlowskiellininae sensu Bizzarro & LESPÉRANCE, 1999, I feel it more convenient:

1) To consider the extreme development of the ventral septum and the trend to lose the dental plates and to form a spondylium in *Megakozlowskiella* and *Plicocyrtina*, as characters that closely relate them phylogenetically to *Cyrtinopsis* (and to *Jehlanaria* n.g. included in Cyrtinopsinae by Havlícek & VaneK, 1998). All these genera would form a homogeneous unit, the Subfamily Cyrtinopsinae, ranged over two great palaeogeographic domains.

2) The non septate or moderately septate genera with well-developed dental plates *Kozlowskiellina, Araspirifer, Boucotinskia*, and the new genus proposed here, *Boucotiellina nov.gen.*, would constitute the Subfamily Kozlowskiellininae (with Araspiriferinae as a younger synonym). Kozlowskiellininae is, no doubt, a more artificial taxon than Cyrtinopsinae, but a convenient one in our present state of knowledge.

The phylogenetic links among the above subfamilies are not clear, although there are morphologic, stratigraphic and palaeogeographic arguments supporting the conclusion that the Cyrtinopsinae arose from the Kozlowskiellinae, perhaps from *Kozlowskiellina itself* (Krans, 1971, fig. 10). And more speculatively, *Boucotinskia* shared a common ancestry with *Kozlowskiellina* (Krans, 1973, fig. 4). *Araspirifer*, lacking delthyrial cover and ctenophoridium and with micro-ornamentation devoid of capillae and spines, would be the more generalized and primitive form of the group, although it is a Wenlockian species not older than some *Boucotinskia* (B. decemiplicata) or *Kozlowskiellina* (K. strawni) forms. And finally, *Boucotiellina nov.gen.* would represent a new evolutionary trend in the subfamily, developed in another palaeogeographic area, and its rise and relationships are difficult to be perceived.

 provisionally, Cyrtinopsinae and Kozlowskiellininae would be included in the Family Cyrtinopsidae because of the lack or rudimentary development of the ctenophoridium and of the fimbriate micro-ornamentation. The Cyrtinopsidae diagnosis must however be modified to include forms such as *Boucotiellina nov.gen.* with fimbriate micro-ornamentation.

Genus *Boucotiellina* nov.gen.

Type-species: *Spirifer esquerrai de Verneuil*, 1850.

Derivation nominis

Named after Arthur J. Boucot, of the Oregon State University for his large contributions to the knowledge of Silurian and Devonian stratigraphy worldwide and in particular to the spiriferid brachiopods of both periods.

Included species

The type-species, from the upper part of the La Vid Group (Coladilla Fm.), in León, and upper part of Raheces Group (Aguión Fm.), in Asturias, Upper Emsian; and much more questionably *Kozlowskiellina acuta* St. 1976, from the Lower Devonian/Middle Devonian boundary beds, in China.
DIAGNOSIS

DISCUSSION
Boucotiellina nov.gen. differs from all the genera of the subfamilies Kozlowskiellininae and Cyrtinopsinae in the sharpness of its radial ornamentation and lack of a delthyrial cover. Further differences from Kozlowskiellina and Megakozlowskiella are the low ventral septum and undifferentiated cardinal ventral area.

The biconvex lateral profile, septate ventral valve, and lack of delthyrial cover separates Boucotiellina from Boucotinskia. And the occurrence of a ventral septum, comb-like cardinal process and capillate, spinose micro-ornamentation separates the new genus from Araspirifer.

The Arctic Canadian Lower Devonian species "Howlcella‘ smithi JONES & BOUCOT, 1983, resembles the type-species of Boucotiellina, because it has imbricate growth lamellae, few, simple, angular radial elements and crural plates. However the "H.’ smithi micro-ornamentation is faintly capillate with well-developed marginal spines fringing the growth lamellae, and it lacks either a well-developed median septum or myophragm in the ventral valve.

The Chinese species Kozlowskiellina acuta SU, 1976, with very sharp radial elements and well-developed median elevation in the ventral valve interior is only unquestionably included in Boucotiellina due to its short, and inadequate description and obscure original figures.

Boucotiellina ezquerrai (DE VERNEUIL, 1850)
Plate 3, Figures 6-20; Plate 4, Figures 16-19; Text-figures 1, 3, 13-15; Table I

* 1850 Spirifer Ezquerra, n.sp - DE VERNEUIL (in PRADO & DE VERNEUIL), p. 178, pl. 4, fig. 6.
. 1882 Spirifer Ezquerrae - BARROIS, p. 250.
v. 1938 Spirifer ezquerrai VERNEUIL - COMTE, p. 24, pl. 1, fig. 11-12.
. 1964 Kozlowskiellia ezquerrai (E. VERNEUIL, 1850) - VANDERCAMMEN & KRANS, p. 34.
v. 1996 'Kozlowskiellina’ ezquerrai - GARCÍA-ALCALDE, fig. 2.

MATERIAL
More than 500 rather well-preserved specimens. DPO 34335-34817 (DPO 34348, figured in Pl. 3, Figs. 6-9; DPO 34349, Pl. 3, Figs. 17-20; DPO 34499, Pl. 3, Fig. 15; DPO 34500, Pl. 3, Fig. 16; DPO 34804 and 34805 (sectioned, Text-figs 14-15) and 34963-34982 (DPO 34970, Pl. 4, Figs. 16-19) from Colle (Sabero, Province of León), upper part of La Vid Group (Coladilla Fm.), Upper Emsian. DPO 35506-35509 (DPO 35506, Pl. 3, Figs. 10-14 from La Palla (Perrote, Asturias, Province of Asturias), upper part of Raíces Group (Aguin Fm.), Upper Emsian. Faunal intervals 12-13 (GARCÍA-ALCALDE, 1996) (Text-figs. 1, 3)

LOCUS AND STRATUM TYPICUM
The locus typicus of the species is the same as for Byultynckia rojasai in Colle (Sabero, Province of León, N. Spain) (Text-fig. 3). However, no stratum typicum has yet been precisely defined. Here, bed 32 in the measured section (published in GARCÍA-ALCALDE, 1998) at the northern slope of the hill where the church of the village occurs, corresponding to the Coladilla Formation (Upper Emsian) is proposed as stratum typicum of Boucotiellina ezquerrai.

DESCRIPTION
Small, biconvex to faintly ventribiconvex, transverse (average: L 60% of width), megathyrid, non inflated (t/L = 0.6 a 0.8 for the 75% of the 44 measured specimens) (Text-fig. 13, Tab. I), irregularly pentagonal, with the shorter side at the front, shell, with hinge sometimes projecting in short ears; maximum thickness at the umbonal region.

Well-developed, almost flat except at the more or less curved apical end, apsacline, transverse and longitudinally striated ventral area; subdued longitudinal striae visible mainly near the hinge. Sharp interarea sides coinciding with the umbonal slopes (Pl. 3, Figs. 13, 18). Small, sub-erect ventral beak in juvenile specimens, sometimes prominent, erect to curved in adults (Pl. 4, Figs. 17, 19). Narrow, open delthyrium, with well-developed teeth ridges (Pl. 3, Fig. 13).

Curved, anacline to orthocline dorsal interarea, 6-8 times lower than ventral; open notothyrium.

Strongly plicate shell, with 4-6 (98% of 205 measured specimens) (maximum: 7; minimum: 4) simple, very high, sharp ribs on flanks. One or two of the more external pair of costae are much less developed than the others and originate in front of the thickened posterior margins (Pl. 3, Figs. 17, 19, Pl. 4, Fig. 19).
Well-delimited ventral sinus and dorsal fold, scarcely differentiated from the other radial elements (Pl. 3, Figs. 6-8). Deep, narrow (up to 1/4 to 1/3 of the maximum shell width, in the 72% of 57 measured specimens) (Tab I), very sharp ventral sinus, starting at the apex of valve, usually with an over-excavated bottom forming a narrow longitudinal slit and sometimes developing one pair of subdued furrows along the sinus walls (Pl. 3, Fig. 8, Pl. 4, Fig. 18). Narrow, relatively low, angular dorsal fold starting at the valve apex (Pl. 3, Figs. 7-8), faintly curving to the anterior commissure from the mid-length or anterior third of the length anteriorly in lateral view (Pl. 3, Fig. 14; Pl. 4, Fig. 17). Very short, triangular, anterodorsally to dorsally directed tongue (Pl. 4, Fig. 17).

Very strong, regularly spaced, imbricate growth lamellae (Pl. 3, Figs. 6-7, 10-11, 15, 17, 19; Pl. 4, Fig. 16-19) covered by parallel, concentric, densely crowded microfilae thicker near the growth lines. Sub-radial, very fine, sometimes obsolescent, microcostulate micro-ornamentation (Pl. 3, Figs. 15-16); numerous, minute, spine bases

Fig. 14 — Boucotiellina ezquerrai. Serial sections of the topotype DPO 34804. Distances measured to the ventral apex. Black bar represents 1 mm.
developed at the intersections between the microcostules and the growth lines and microfilae; microspines projecting at an acute angle, less than 90° from the shell surface.

Some specimens develop more or less marked asymmetries, in particular twisting of the ventral beak resulting in an unequal development of the cardinal area sides and different numbers of costae on the flanks, usually one supplementary rib (or two, at maximum) on a slope.

Well-developed, fine, extra-sinal (between the first and second pair of lateral ribs) dental plates, extended further than the hinge region. Low, parallel ventral adamicula with bases diverging slightly anteriorly. Strong, dental bases diverging dorsally. Relatively faint cardinal teeth fitting in dental sockets developed well above the bottom of the valve. Short, low ventral median septum that lacks in appearance of mediotest and usually develops not far from the delthyrial chamber (Text-figs. 14-15).

Very short crural plates defining free, small lateral apical cavities. Crural bases developed along outer cardinal plates extended dorso-medially to sometimes almost join together, forming a sub-horizontal, discrete cardinal plate supporting proximally a small, simple ctenospheridium provided with 7-8 vertical platelets, longitudinally extended. Inner socket ridges fitting in cavities excavated at the bases of the cardinal teeth. Simple jugum developed near the junction among the crura and the primary lamellae of the spiral cones. Laterally directed spiral brachidium with up to 10 whorls in each spine (Text-figs. 14-15).

Very thin shell wall with the radial external elements clearly reflected in the shell cavity. Slender and very low dorsal myophragm bisecting the muscle field (Text-figs. 14-15).

**Discussion**

*Boucotiellina ezquerrai* was included in *Kozlowskiella* (= *Kozlowskiella Boucot, 1958, nov.nom. pro Kozlowskiella Boucot, 1957, non Pribyl, 1953*) by VanderCammen & Krans (1964) but, as previously remarked by de Verneuil (1850), the very sharp profile of sinus, dorsal fold and lateral ribs clearly separate the species from all forms usually included in *Kozlowskiella* and related genera, where the radial elements are usually very rounded. On the other hand, Krans (1969) presented a large and documented revision of *Kozlowskiella* and *Megakozlowskiella* species, with no reference to the Devonian Cantabrian species and he did not reject it from the former genera. According to the serial sections given by Krans (1969, text-fig. 23), the *Megakozlowskiella raricosta* (Conrad, 1842) cardinaulium resembles that of *Boucotiellina ezquerrai*, but the external ornamentation of the former species is completely different with low, wide, very rounded lateral ribs; moreover the dental plates of *M. raricosta* converge to almost unite with a very high and long ventral median septum. In general, *B. ezquerrai* differs from all *Kozlowskiella* and *Megakozlowskiella* species in the undifferentiated ventral cardinal area, open delthyrium, weakly developed ventral...
Table — Measurements of some specimens of the studied species. L, w, t = Length, width, and thickness (in mm). wsen/w = width of the ventral sinus/width of the shell. Nc = Number of ribs.

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Boucotiellina ezquerrai

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Explanation of Plates

PLATE 1

Figs. 1-13 — Howellella (Howellella) corallina n.sp. 1-4: Holotype DPO 31714, ventral, anterior, posterior and lateral views, x3.- 5-7: DPO 36579, ventral, dorsal and anterior views, x3.- 8-10: DPO 36579, ventral, dorsal, and posterior views, x3.- 11-13: DPO 36595, ventral, dorsal and anterior views of a juvenile specimen, x3.

Figs. 14-22 — Arduspirifer adradensis n.sp. 14-17: Holotype DPO 31974, ventral, dorsal, anterior, and lateral views, x3.- 18: Paratype DPO 31995, fragmentary ventral valve, x2.- 19-21: Paratype DPO 31983, ventral, anterior, and lateral views of a markedly asymmetric specimen, x3.- 22: Paratype DPO 31996, fragmentary dorsal valve showing the strong and high notothyrial platform and robust cardinal process, x3.

Figs. 23-27 — Hysterolites blodgetti n.sp. ventral, lateral, anterior views, x3, and enlargement of the fig. 23 to show the microspinose micro-ornamentation, x4.

PLATE 2

Figs. 1-15 — Hysterolites blodgettii n.sp. 1-4: Holotype DPO 30309, ventral, dorsal, anterior, and lateral views, x3.- 5-9: Paratype DPO 31869, ventral, lateral, dorsal, and anterior views, x1.- 10-11: Paratype DPO 30326, ventral valve and latex, x3.- 12-13: Paratype DPO 30327, ventral valve and latex, x3.- 14-15: Paratype DPO 30328, ventral valve and latex, x3.
PLATE 3

Figs. 1-5 — *Hysterolites blodgettii* n.sp. DPO 126504, ventral, lateral, dorsal, anterior, and posterior views, x2.
Figs. 6-20 — *Boucotiellina ezquerrai* (de Verneuil, 1850). 6-9: DPO 34348, ventral, dorsal, anterior, and posterior views, x2.-10-14: DPO 35506, ventral, dorsal, anterior, posterior, and lateral views, x4.-15: DPO 34499, fragmentary ventral valve, micro-ornamentation, x4.-16: DPO 34500, fragmentary dorsal valve, micro-ornamentation, x4.-17-20: DPO 34349, ventral, posterior, dorsal, and anterior views, x2.

PLATE 4

Figs. 1-6 — *Bultynckia boulei* (D. Oehlert & P. Oehlert, 1901). 1-5: DPO 32842, ventral, lateral, dorsal, anterior, and posterior views, x1. See the characteristic sinal ribbing.-6: DPO 32850, dorsal valve, micro-ornamentation, x3.
Figs. 7-15 — *Bultynckia rojasi* (de Verneuil, 1850). 7-11: DPO 34818, ventral, anterior, posterior, dorsal, and lateral views, x1.-12-14: DPO 34823, ventral, dorsal, and anterior views of a juvenile specimen, x3.-15: DPO 34828, fragmentary dorsal valve, micro-ornamentation.
Figs. 16-19 — *Boucotiellina ezquerrai* (de Verneuil, 1850). DPO 34970, ventral, lateral, anterior views, x2, and dorsal view, x3.