

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

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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 Kozlowskiellinae are discussed. *Boucotiellina* n.gen. with *Spirifer ezquerrai* de Verneuil as type-species is included in Kozlowskiellinae. 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 spiriféridés sont les brachiopodes les plus diversifiés du Dévonien Inférieur (50 espèces sur un total de 212 espèces connues de brachiopodes articulés). Néanmoins, 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 Asturo-Léonienne bien connue et aussi dans la région Palentienne (partie orientale des Montagnes Cantabriques, entre les provinces de Palencia, Léon et Santander), relativement éloignée et peu connue. Six espèces (dont trois nouvelles), appartenant à cinq genres (dont deux nouveaux), sont décrites. *Bultynckia* 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 signification, composition et désignation familiale des Cyrtinopsidae de la Sous-Famille Kozlowskiellinae sont discutées. *Boucotiellina* n.gen., avec *Spirifer ezquerrai* de Verneuil, comme espèce-type, est placé dans Kozlowskiellinae. Ce nouveau genre est caractérisé par le profil très

aigu des éléments macro-ornementaux radiaux, par une micro-ornementation 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, Montagnes 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* OEHLERT & OEHLERT, 1901, and *Spirifer Ezquerrai* 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, outcropping 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, w, t = Length, width, and 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 Delthyridoidea PHILLIPS, 1841

Family Delthyrididae PHILLIPS, 1841 (*sensu* BIZZARRO & LESPÉRANCE, 1999)

Subfamily Howellellinae JOHNSON & HOU *in* CARTER *et al.*, 1994

Genus *Howellella* KOZŁOWSKI, 1946

Subgenus *Howellella (Howellella)* KOZŁOWSKI, 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 rugosan 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 32200-32387, 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 36564, Pl. 1, Figs. 5-7; DPO 36579, Pl. 1, Figs. 8-10; DPO 36595, Pl. 1, Figs. 11-13) from the

Lebanza Quarry (Cervera de Pisuerga, province of Palencia, N. Spain), Lebanza Fm., levels α -302, α -334 and α -336/337, Lower Pragian. 101 specimens, DPO 36608-36710, from the north side of the Vañes Lake, track to Polentinos Village, Lebanza Fm., level α -122, Lower Pragian. 94 specimens DPO 36711-36804, from other section W. of Lebanza, point 5, Lebanza Fm., Lower Pragian.

LOCUS AND STRATUM TYPICUM

600 m WSW of the Lebanza Village (San Salvador de Cantamudá, Cervera de Pisuerga, Province of Palencia, N. Spain). "Las Cabañinas" section. Lebanza 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, apsacline 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 deltidial plates normal to the area surface, sometimes fused below the ventral beak forming a small, convex deltidium; 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, deflected postero-

Stratigraphical column for A and B areas
For C area, see Fig.2

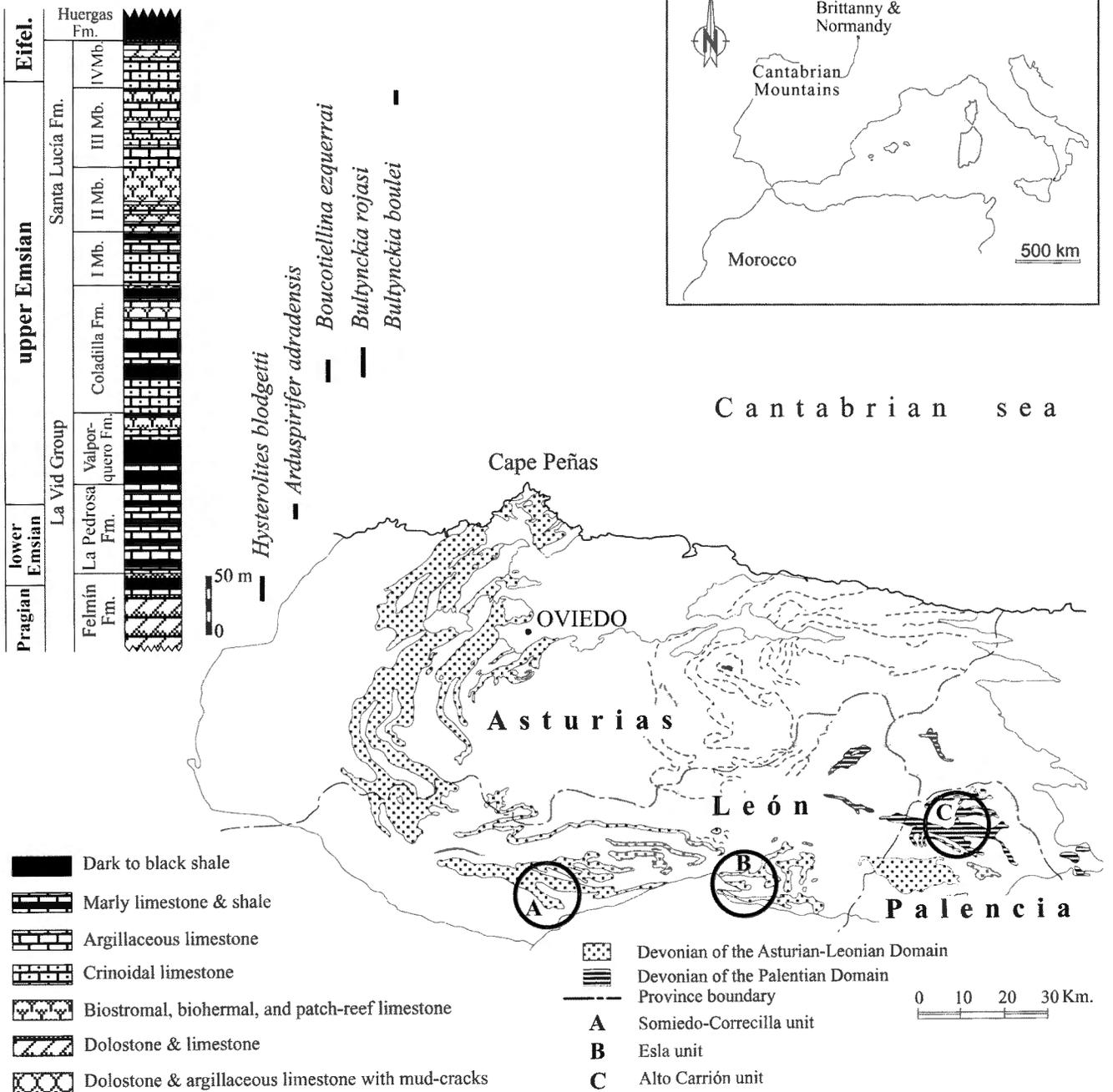


Fig. 1 — Geographical situation of the studied region and stratigraphical situation of the species found in the Bernesga River and Colle areas. Eifel. = Eifelian.

laterally (Pl. 1, Figs. 5, 8), starting at the apices of valves, with sub-angular, narrower interspaces; the ribs close to the palintropes are obsolescent.

Scarce, strong, irregularly distributed growth lamellae, clustered at the front of shell, crossed by subdued concentric filiae. Marginal, spinose, microcostulate microornamentation; 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

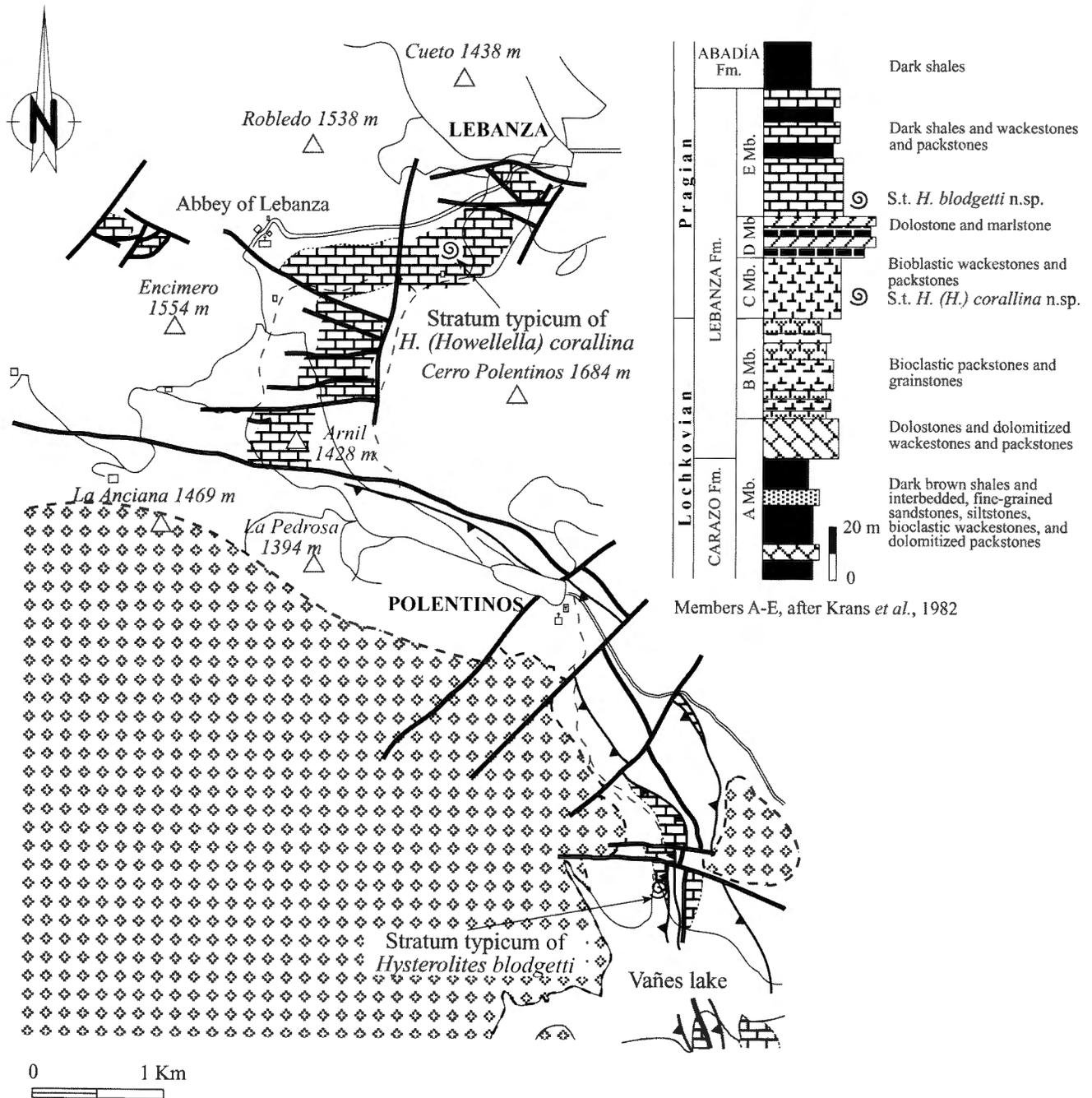


Fig. 2 — Simplified geological map of the Polentinos anticline area (Province of Palencia) and geographical and stratigraphical situation of the stratotypes of *Howellella (Howellella) corallina* n.sp. and *Hysterolites blodgetti* n.sp. S.t. = Stratum typicum.

(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

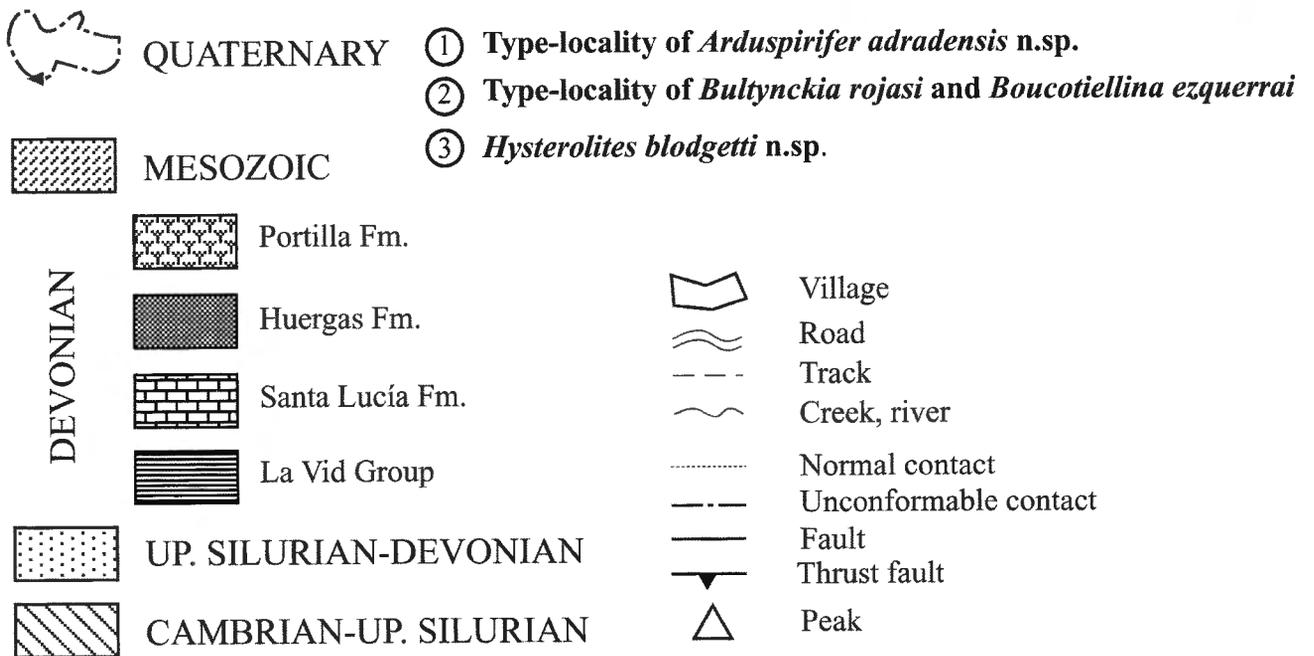
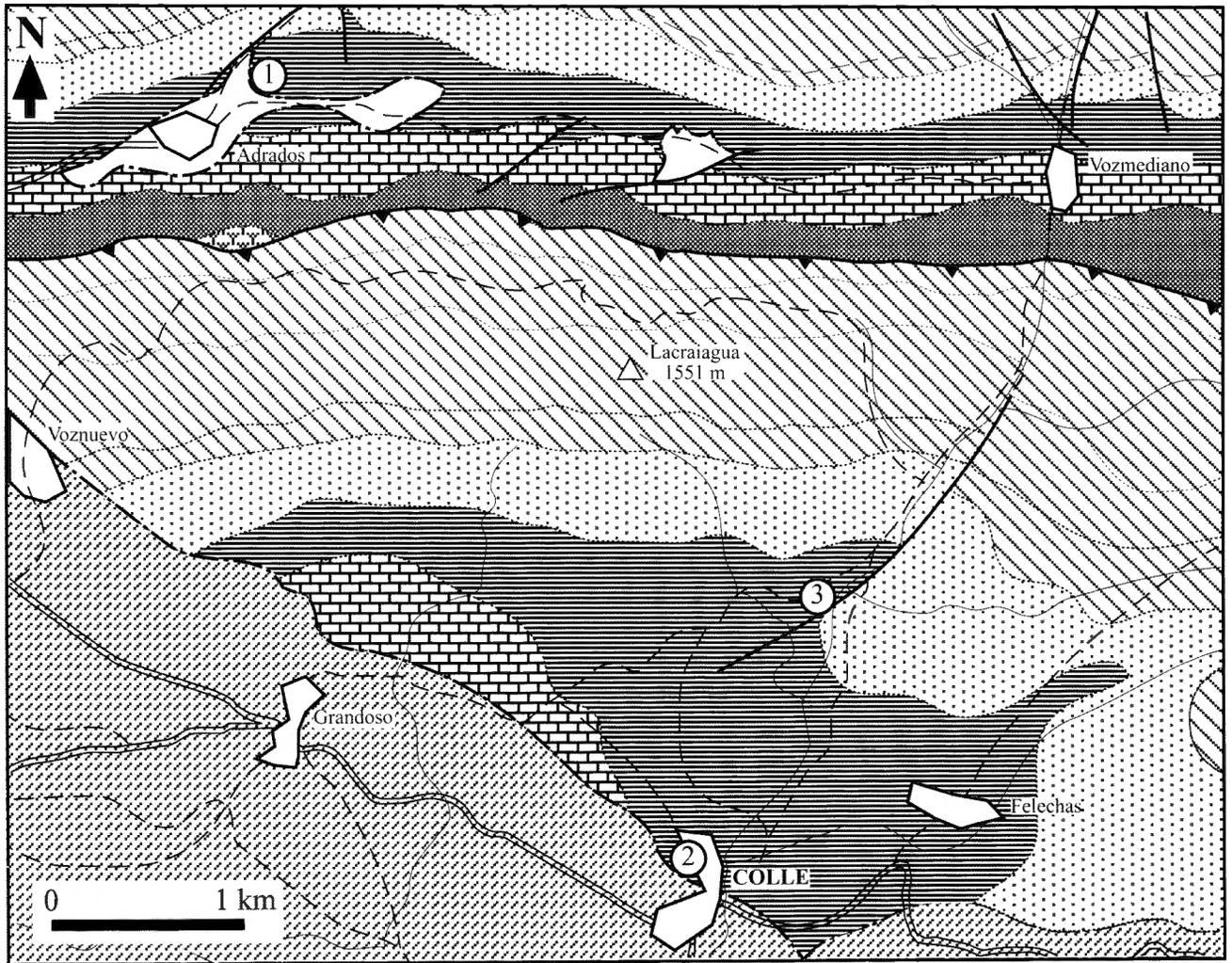
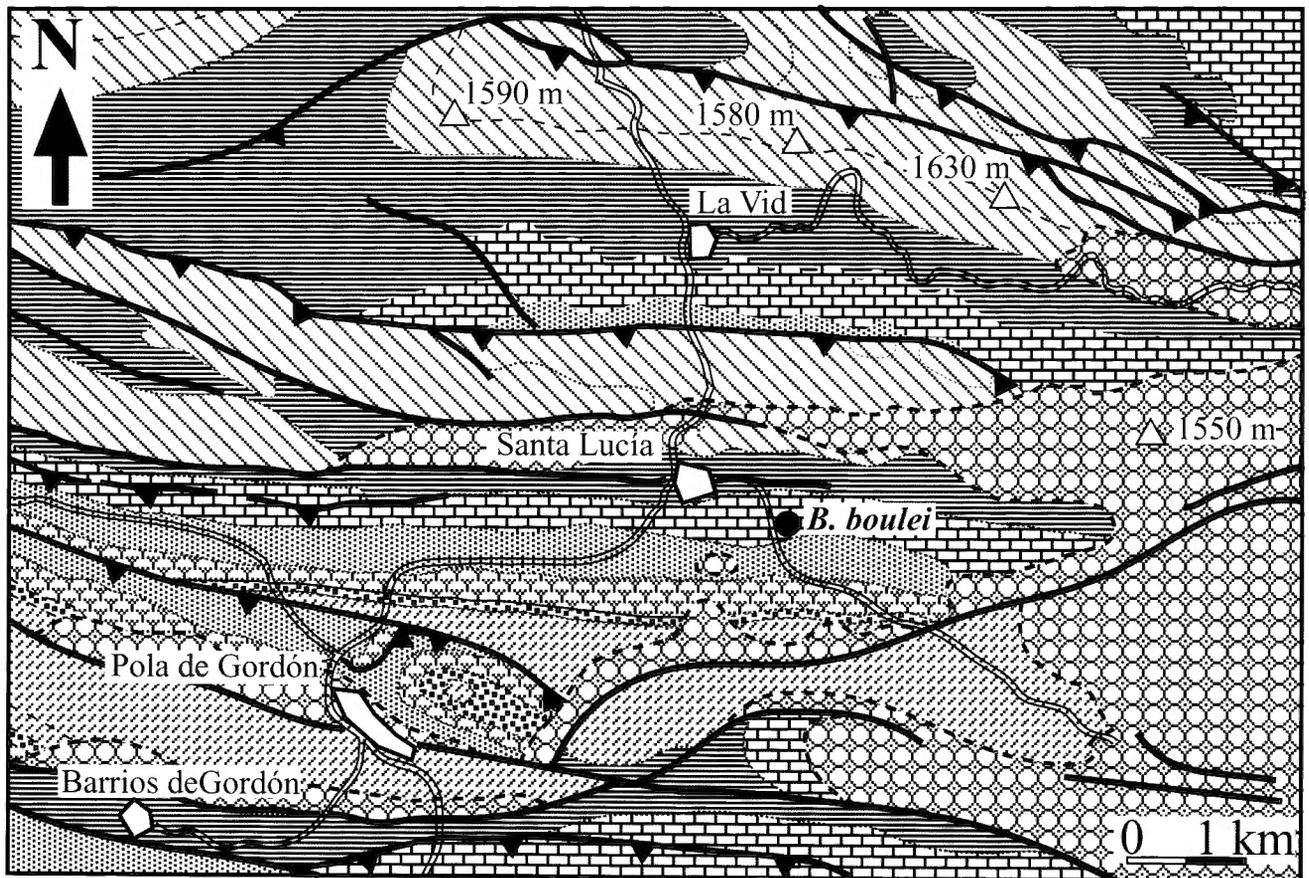


Fig. 3 — Geological map of the Adrados-Colle area (Province of León). Situation of the stratotypes of *Arduspirifer adradensis* n.sp. (1), and *Bultynckia rojasi* and *Boucotiellina ezquerrai* (2). Situation of the outcrop where the Leonian population of *Hysterolites blodgetti* n.sp. occurs. Fm. = Formation; Up. = Upper.



UNCONFORMABLE CARBONIFEROUS (STEPHANIAN)

LOWER TO MIDDLE CARBONIFEROUS

DEVONIAN

- 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.

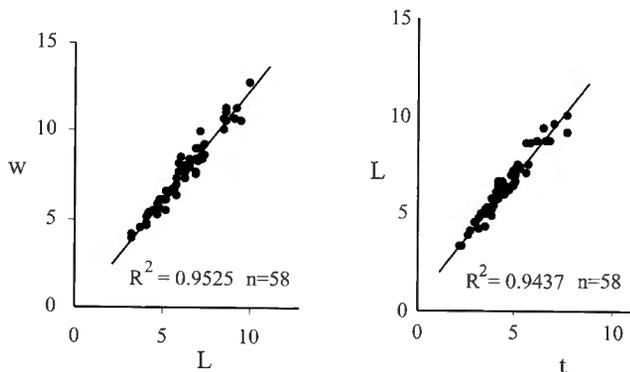


Fig. 5 — *Howellella (Howellella) corallina* n.sp. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

one to another. Narrow, shallow dental sockets, situated high off the shell floor; relatively high inner socket ridges, fitting in narrow furrows developed at the cardinal teeth bases (Text-fig 6).

Thin shell walls so that the external ornamentation is partially reflected in the interior of valves.

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-

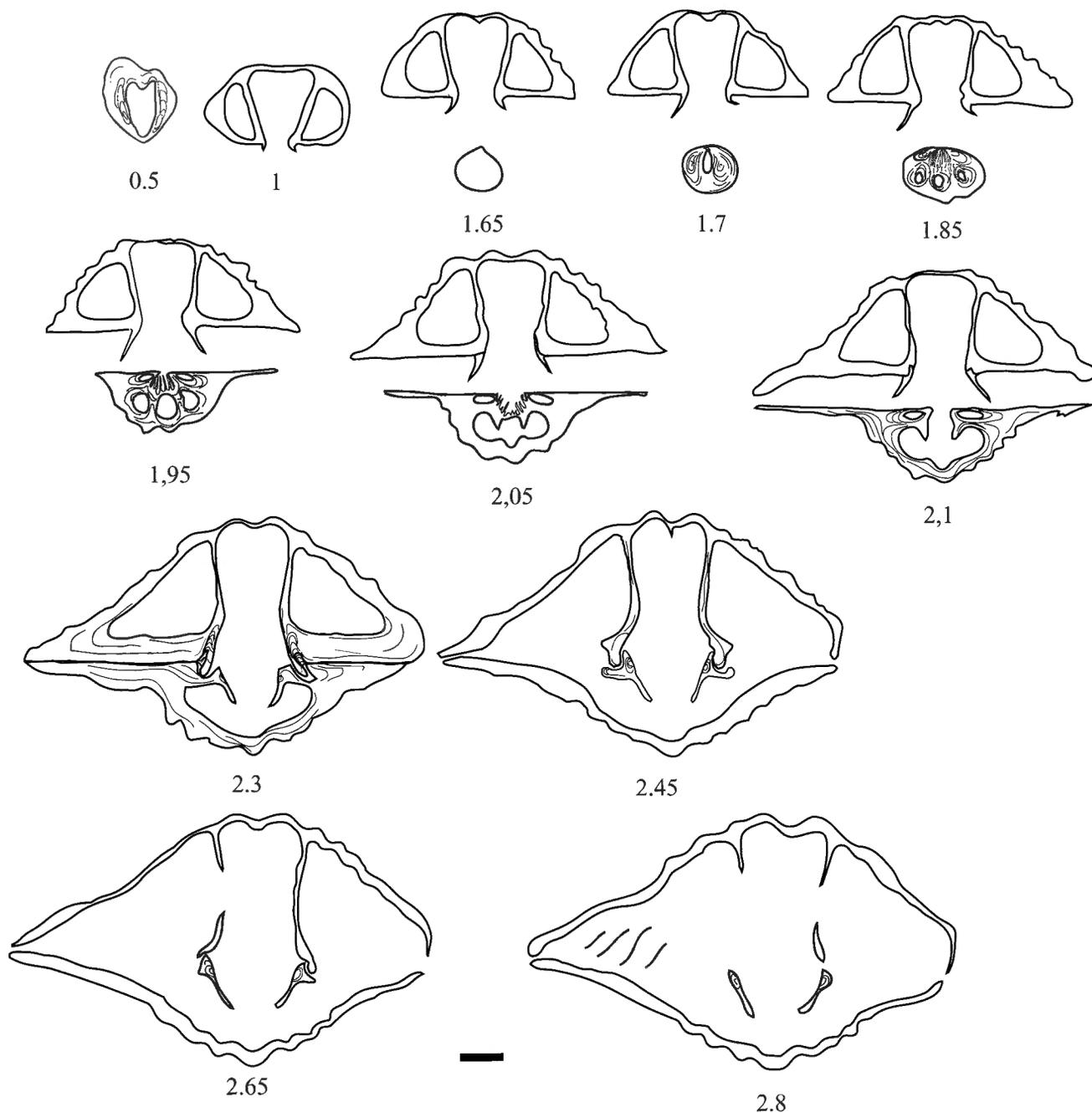


Fig. 6 — *Howellella (Howellella) corallina* n.sp. Paratype DPO 37796. Serial sections. Distances measured to the ventral apex. Black bar represents 1 mm.

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 ex-

tremities. 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 minima 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.

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.

Specimen	L	w	t	L/w	t/L	wsen/w	Nc
Holotype DPO 31714	9.1	10.7	7.7	0.85	0.85	0.36	9
Paratype DPO 32388	8.7	10.5	6.8	0.83	0.78	0.26	7
Paratype DPO 32391	9.5	10.5	7.1	0.90	0.75	0.28	8
Paratype DPO 32394	7.2	8.9	5.2	0.81	0.72	0.28	8
Paratype DPO 32396	7.3	8.4	5.3	0.87	0.73	0.30	7
Paratype DPO 32399	6.3	7.7	4.5	0.82	0.71	0.26	6
Paratype DPO 32403	5.9	7.3	4.4	0.81	0.74	0.27	7
Paratype DPO 32404	6	7.6	4.2	0.79	0.70	0.30	7
Paratype DPO 32405	6.4	7.6	4.5	0.84	0.70	0.30	9
DPO 36573	7.4	8.6	5.7	0.86	0.77	0.29	8
DPO 36574	7	8.4	5	0.83	0.71	0.28	7
DPO 36579	6.6	7.9	4.4	0.83	0.67	0.30	7
DPO 36581	6.4	7.9	4.5	0.81	0.70	0.26	8
DPO 36583	6.3	7.9	4.3	0.80	0.68	0.26	8
DPO 36597	4.5	5.4	3	0.83	0.67	0.28	6
DPO 36602	4.2	5.1	3.2	0.82	0.76	0.29	7
DPO 36689	7.4	9.2	5.2	0.80	0.70	0.27	8
DPO 36693	6.3	7.2	4.2	0.87	0.67	0.29	7
DPO 36709	3.8	4.5	2.6	0.84	0.68	0.29	6
DPO 36795	5.9	6.9	4.1	0.85	0.69	0.30	8
DPO 36796	5.7	6.6	4.2	0.86	0.74	0.26	8
DPO 36803	3.3	3.9	2.2	0.85	0.67	0.26	6

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 Lebanza Fm., bed M-AR-51/52, Pragian. 33 badly preserved specimens, DPO 31893-31922, from Los Payos Hill, south Abadía de Lebanza (Province of Palencia), top of Lebanza Fm., bed α -151, Pragian. 2 well-preserved specimens, DPO 31923-31924 from the Lebanza Quarry (Palencia), top of Lebanza 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 Vañes Lake, SE of the village of Polentinos (Cervera de Pisuerga, Palencia, N. Spain), Lebanza Fm., E Mb., bed α -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. Brachythyrid, 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 anacline, 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.

Specimen	L	w	t	L/w	t/L	wsen/w	Nc
Holotype DPO 30309	14.4	21.1	11.4	0.68	0.79	0.27	10
Paratype DPO 30310	16.3	21.7	12.2	0.75	0.75	0.28	12
Paratype DPO 30317	13.7	16.6	10	0.82	0.73	0.29	9
Paratype DPO 30319	11.6	17.1	9	0.68	0.77	0.27	9
Paratype DPO 30321	12.1	16	8.8	0.76	0.73	0.30	9
Paratype DPO 30322	10.8	15.2	8.2	0.71	0.76	0.28	8
Paratype DPO 31862	15.7	19.7	12	0.80	0.76	0.29	10
Paratype DPO 31864	15.9	20.5	12.1	0.77	0.76	0.26	10
Paratype DPO 31867	15.4	19.6	11	0.78	0.71	0.32	8
Paratype DPO 31868	13.7	17.9	10.4	0.71	0.76	0.26	9
Paratype DPO 31869	13.8	18.4	10.3	0.75	0.75	0.30	8
Paratype DPO 31870	14.2	20.5	10.2	0.69	0.72	0.24	9
Paratype DPO 31879	12	15.5	9.6	0.77	0.80	0.33	8
Paratype DPO 31881	10.8	15.4	8.5	0.70	0.79	0.29	9
Paratype DPO 31882	11	15.6	8.3	0.70	0.75	0.28	10
Paratype DPO 31890	7.5	10	5.3	0.75	0.71	0.30	8
DPO 30410	16.2	21.3	13.2	0.76	0.81	0.28	9
DPO 30412	13	18	10.7	0.72	0.82	0.29	9
DPO 126404	15.2	22.8	12	0.67	0.79	0.31	9
DPO 126409	17.3	24	13.4	0.72	0.77	0.30	9
DPO 126415	15.7	22	11.1	0.71	0.71	0.29	9
DPO 126417	18.2	26.2	13.4	0.69	0.74	0.30	8
DPO 126421	16.4	22.4	11.7	0.73	0.71	0.25	9

Hysterolites blodgettii n.sp.

flanks are faintly and regularly convex, but the dorsal ones flatten and even become concave near the cardinal extremities so that the lateral commissures appear there as curved dorsally (Pl. 2, Figs. 3, 8, 9).

Seven to ten (90% of the measured specimens) (maximum: 12; minimum: 6), simple, strong, sub-angular, postero-laterally deflected (Pl. 2, Fig. 2) ribs in each flank with similar interspaces. About half of the ribs begin at the shell apices but the others develop along the posterior margins. Subdued external costae sometimes visible only as faint crenulations along the lateral commissures. Relatively frequent costal asymmetries represented by the occurrence of at least a supplementary rib on one of the flanks. The sinus bounding ribs and the fold bounding furrows are similar to adjacent ones. Some specimens show one bifurcating or intercalary ribs, although this

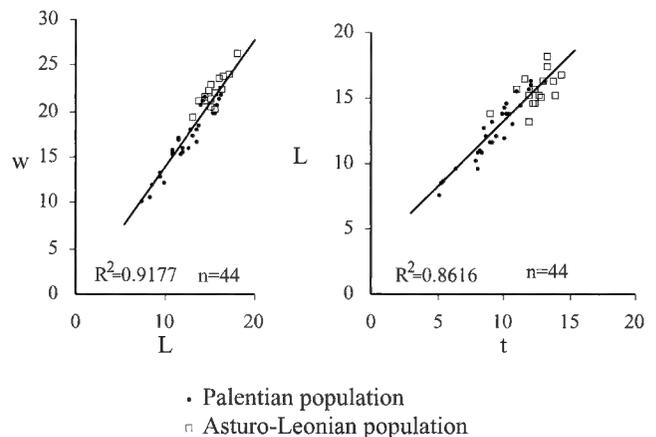
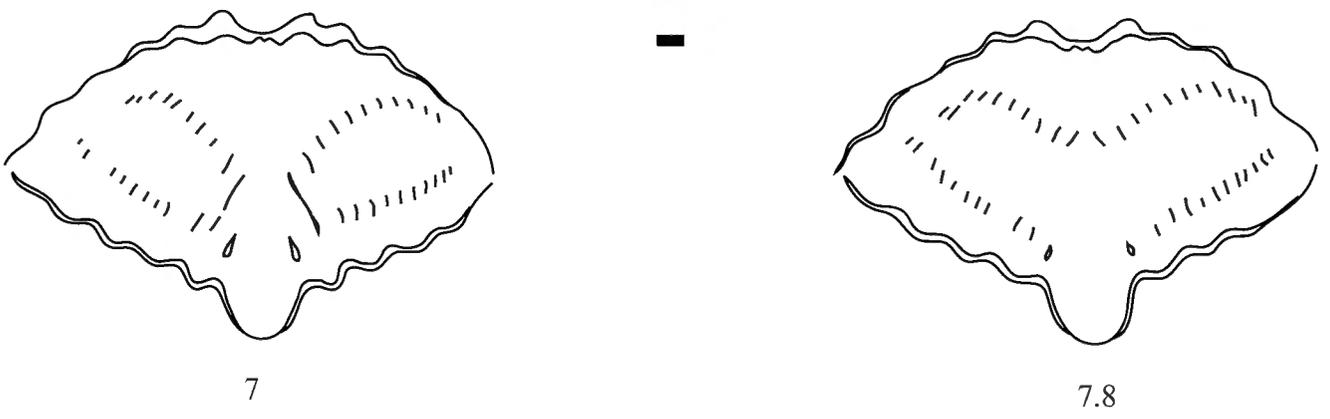
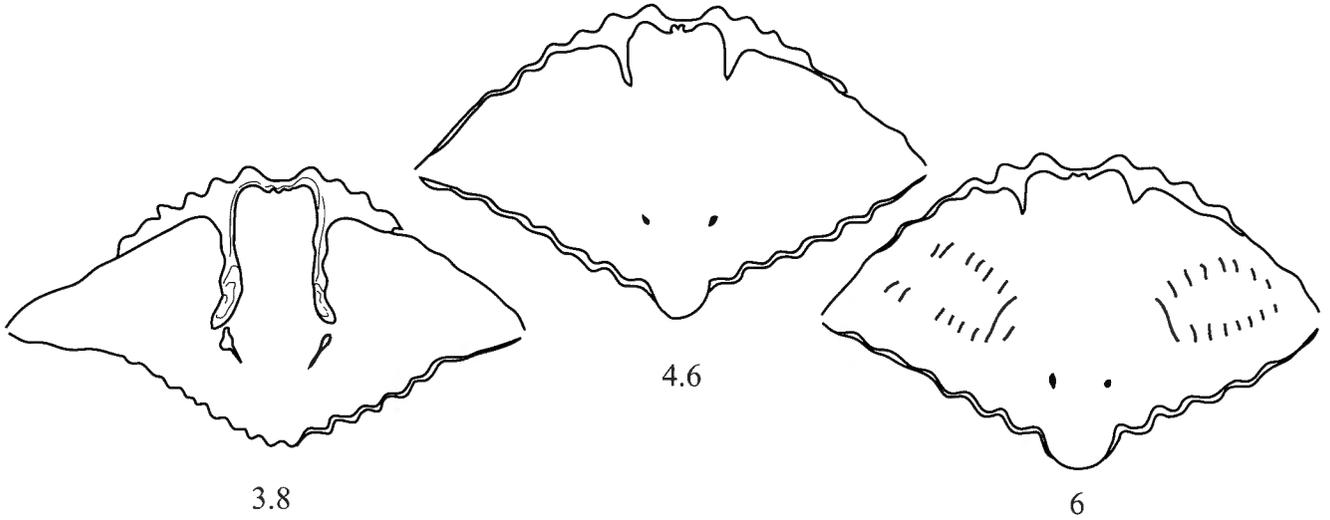
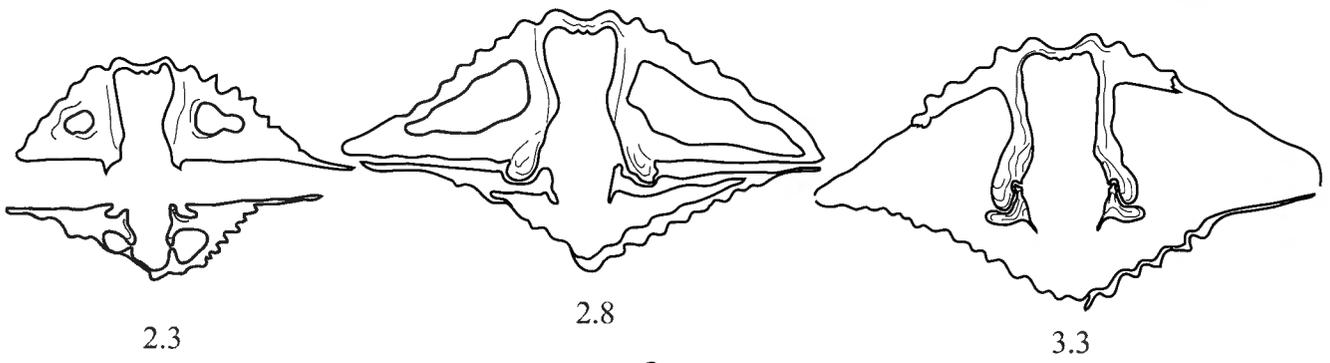
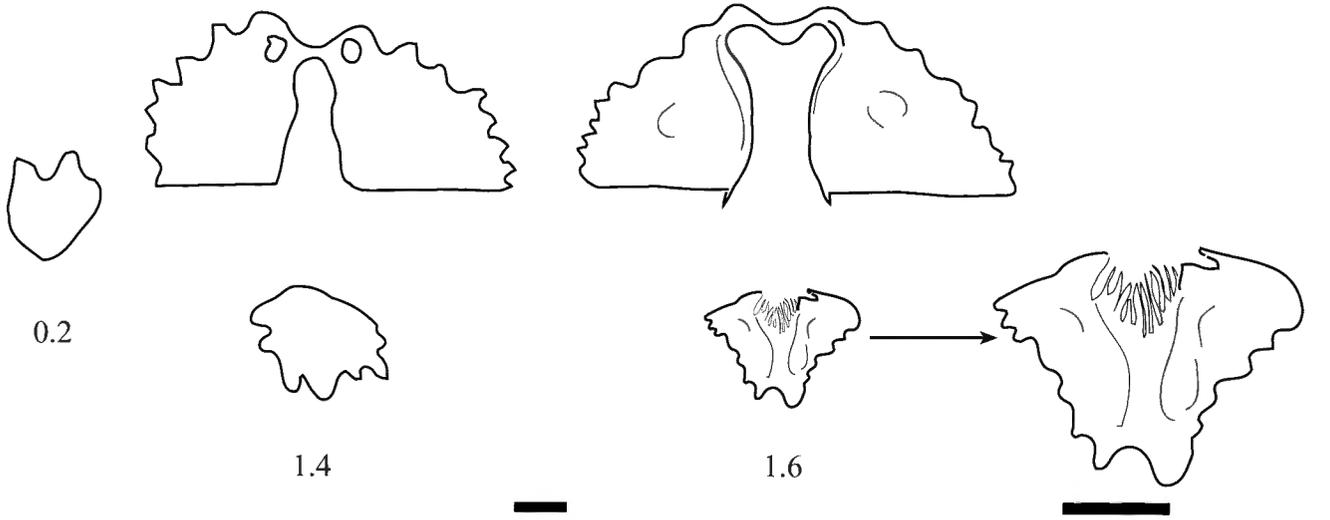


Fig. 7 — *Hysterolites blodgettii* n.sp. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

anomaly seems usually related to repaired shell damage.

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.

Long, high, extra-sinal (between the 1st and 2nd pair of lateral costae) dental plates. Strong, normal to valve bottom dental adnacula with bases proximally divergent to distally curved one to another, laterally bound the muscle field (Pl. 2, Figs. 10-15, Text-fig. 8). Short dental bases converge ventrally. There is no delthyrial plate, but faint, medially cleft, apical shell callus forms a high platform at the level of the distal ends of dental bases; sometimes the median cleft develops proximally, whereas distally a faint rounded ridge occurs; at the callus base a small, depressed secondary shell material occurs; a low, fine, median myophragm extends from this secondary thickening to the adductor muscle field, bisecting the adductor scars (Pl. 1, Figs. 11, 13, 15, Text-fig. 8). Faintly excavated, triangular, elongated muscle field with rounded anterior angles growing slightly before the distal ends of dental plates; very narrow, lanceolate, adductor scars differentiated in two different muscle fields, the posterior scars being more ornamented and higher than the anterior one. Triangular diductor scars, divided into two bundles by curved, angular depressions, extending between the dental plates and the adductor scars, bounding laterally the adductor field and extending slightly before it; diductor muscle field crossed by two bundles of fine, curved striae encircling the adductor muscle field; the striae of the posterior group are turned lateral- and



postero-laterally and the anterior group anterolateral- and anteriorly (Pl. 1, Figs. 10-15).

Well-developed lateral apical cavities that in adults become partially filled by secondary shell (Text-fig. 8). Genital markings, represented by minute pits, developed at both sides of the muscle field.

High notothyrial platform supporting an undifferentiated ctenophoridium with numerous (up to 12-14), radially extended, vertical platelets. Small crural plates sometimes extended slightly anterior to the notothyrial platform, delimiting minute lateral cavities partially filled by secondary shell (Text-fig. 8). Large, shallow, denticulate dental sockets detached well above the bottom of valve, bounded by well-developed inner socket ridges. The inner socket ridges fit in cavities situated below the cardinal teeth to form a complementary interlocking device (Text-fig. 8). Deeply excavated, long adductor muscle field, developed below the dorsal fold and bisected by a long (more than half of length), narrow, high and sharp myophragm.

The external radial ornamentation is clearly reflected in the shell interior, even along the muscle field (Pl. 1, Figs. 10-15, Text-fig. 8).

Slender crura uniting to latero-ventrally directed spiral cones with up to 11 rather circular whorls. Neither jugal processes nor jugum (Text-fig. 8).

DISCUSSION

The occurrence of specimens with the typical high hystero-litine notothyrial shelf, general morphology and macro- and micro-ornamentation allows the assignment of our species to *Hystero-lites*. The faint excavation of the ventral muscle field, development of dental plates and more or less free apical cavities in the ventral valve separates *H. blodgetti* nov.sp. from the very similar genus *Arduspirifer*.

The Colle specimens (Asturo-Leonian Domain, Cantabrian Mountains) of *H. blodgetti* n.sp. are slightly larger than the Lebanza specimens (Palentian Domain, Cantabrian Mountains) (Text-fig. 7). Likewise the median dorsal fold and ventral sinus of Colle specimens are a little more developed in height and width, respectively, than in Lebanza specimens (Pl. 3, Figs. 1-5). Anyway, the lateral profile, proportions, micro-ornamentation, number of ribs and internal structures are very close in both populations so that the differences could be interpreted as corresponding to populations palaeogeographically differentiated of the same species.

Hystero-lites venus (D'ORBIGNY, 1850), from the Pragian of the Armorican Massif (France) is a similar form but differs from *H. blodgetti* in the more transverse outline, deeper and flatter ventral sinus, smaller ventral beak and straight, not deflected, radial ribs.

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 *Hystero-lites* 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 I-64, Lower Emsian. 8 specimens DPO 31184-31190 and 32183 from different Lower Emsian levels of the La Pedrosa Fm. at Abelgas (Province of Leon). Faunal intervals 9-10 (GARCÍA-ALCALDE, 1996)

LOCUS AND STRATUM TYPICUM

Adrados (Boñar, 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).



Fig. 8 — *Hystero-lites blodgetti* n.sp. Paratype DPO 31867. Serial sections. Distances measured to the ventral apex. Black bars represent 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. Nc=Number of ribs.

Specimen	L	w	t	L/w	t/L	wsen/w	Nc
Holotype DPO 31974	18.8	30.4	16.5	0.62	0.88	0.28	10
Paratype DPO 31975	20.9	33	16.1	0.63	0.77	0.26	9
Paratype DPO 31982	10.4	17.4	7	0.60	0.67	0.20	7
Paratype DPO 31984	5	7.6	3.6	0.66	0.72	0.24	7
Paratype DPO 32000	16.5	26	13.5	0.63	0.82	0.26	7
Paratype DPO 32007	16.2	26.6	13.2	0.61	0.81	0.27	8
Paratype DPO 32008	13	23	10.2	0.56	0.78	0.25	8
Paratype DPO 32010	12.1	21.4	9	0.56	0.74	0.26	8
Paratype DPO 32011	14.6	23.8	11.2	0.61	0.77	0.21	9
Paratype DPO 32016	11.6	17.7	9.4	0.65	0.81	0.20	7
Paratype DPO 32022	10.7	17	8	0.61	0.75	0.20	7
Paratype DPO 32029	8.6	14.7	7	0.58	0.81	0.22	6

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 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 deltidial plates sometimes fused below the ventral beak forming a

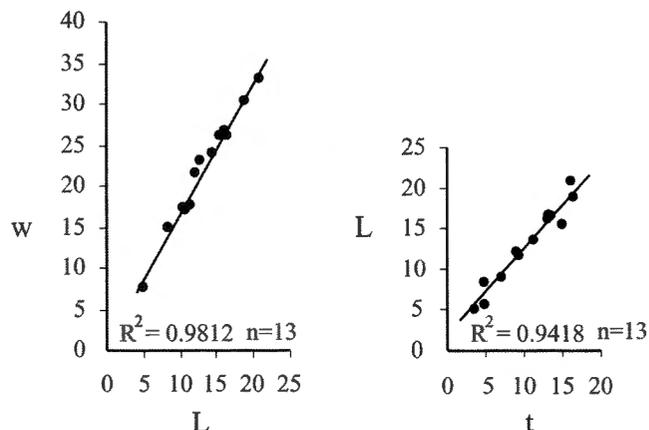


Fig. 9 — *Arduspirifer adradensis* n.sp. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

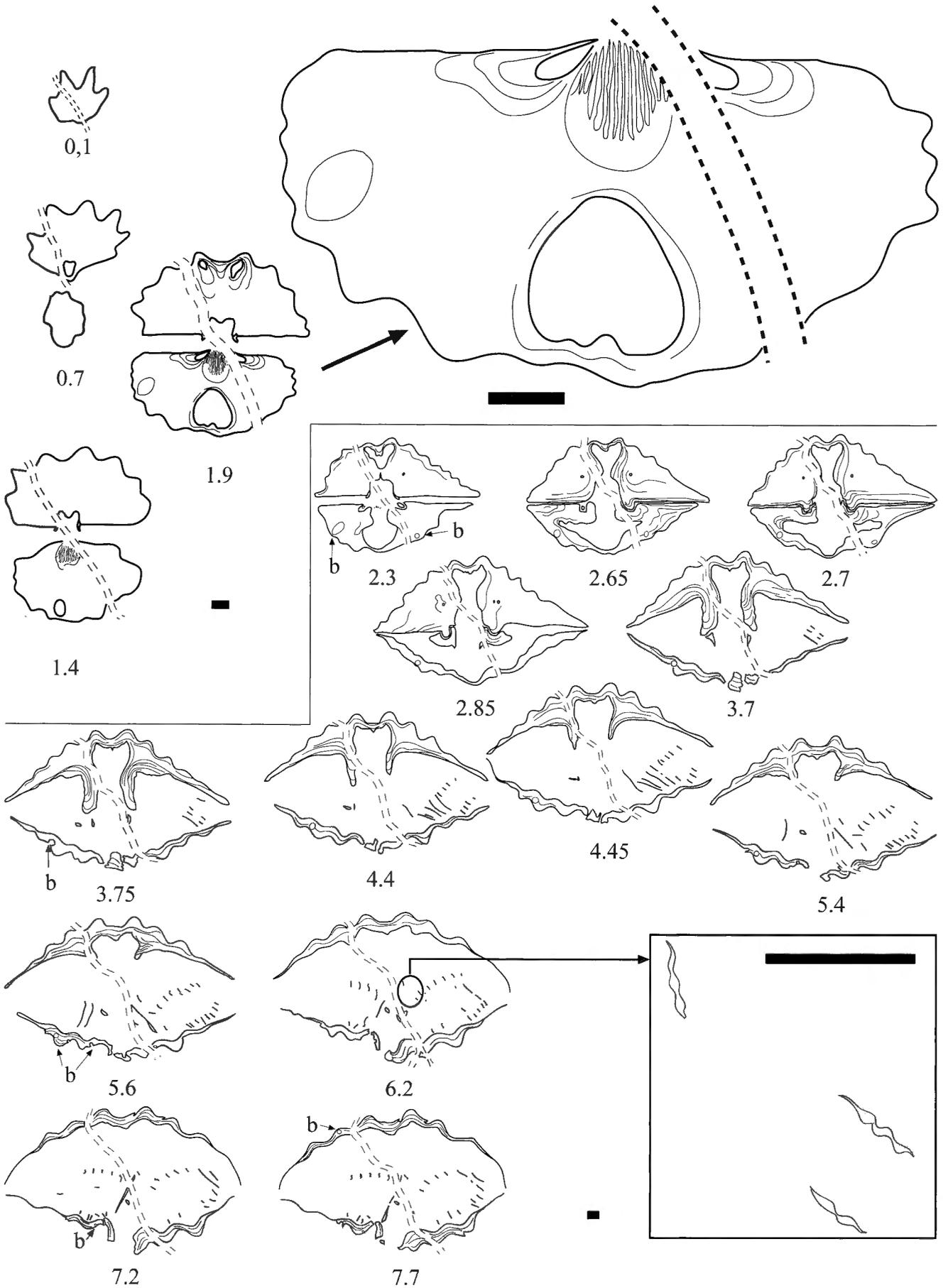
convex deltidium with a circular, mesothyrid foramen. Faint ventral umbo with an erect to strongly curved beak projecting onto the dorsal umbo, concealing in part the delthyrial area (Pl. 1, Fig. 17). Anacline to orthocline dorsal area, ca. 7 times lower than ventral area and with similar longitudinal 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,

Fig. 10 — *Arduspirifer adradensis* n.sp. Serial sections of a broken specimen, Paratype DPO 32012. Distances measured to the ventral apex. See the spinose character of the spiral cone whorls at the enlarged 6.2 mm section. b = burrows. Black bars represent 1 mm.



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 mm 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 posteriors, 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 diductor scars; triangular, large, radially striated diductor scars bounding the adductor scars 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 trilobed 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 spirallium at the commissural plane. Neither jugal processes, nor jugum. Spiral cones with up to 10, circular, spinose (Text-fig. 10) whorls.

ONTOGENY

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-

trically, so that the shell can develop an acuminate long flank on one side and a mucronate, short flank on the other side (Pl. 1, Figs. 19, 20).

DISCUSSION

The profile, shell outline, ornamentation and occurrence of a very well developed notothyrial shelf allow the assignment of *A. adradensis* nov.sp. to the Hysterolitinae. The inclusion in *Arduspirifer* is based on the micro-ornamentation, development of the apical callus and the relatively low number of lateral costae. Late juvenile or early epebic specimens are very transverse, matching the alate outline of *Euryspirifer* species; however the last genus comprises forms with numerous radial ribs, usually with one or more well-developed sinus costae, very sharp, angular dorsal fold, more excavated ventral muscle field, and shorter dental plates included usually in secondary shell entirely obliterating the lateral apical cavities.

Arduspirifer extensus (SOLLE, 1953), from the Emsian of the Rheinische Schiefergebirge and Armorican Massif comprises forms as transverse as *A. adradensis* nov.sp., but this character occurs along the entire shell growth and not only in some developmental stages as in the younger species. Moreover *A. extensus* has a delthyrial plate, a triangular, strongly excavated ventral muscle field, short crural plates, a less developed cardinal process, and moreover it is larger, with a narrower, concave ventral sinus, a smaller ventral beak, and a greater number of lateral ribs with narrower inter-costal spaces.

Subfamily Paraspiriferinae PITRAT, 1965

Genus *Bultynckia* nov.gen.

TYPE-SPECIES: *Spirifer Rojasi* DE VERNEUIL, 1850.

DERIVATIO NOMINIS

Genus dedicated to Pierre Bultynck, of the Royal Belgian Institute of Natural Sciences, as a deserved homage to his vast and creative work on Devonian conodont biostratigraphy.

INCLUDED SPECIES

The type-species, *Spirifer Boulei* OEHLERT & OEHLERT, 1901, and *Fimbrispirifer* ? cf. *F. boulei* GOURVENNEC, 1989.

AGE, STRATIGRAPHIC, AND GEOGRAPHIC DISTRIBUTION

Both the type-species and *B. boulei* (OEHLERT & OEHLERT 1901) occur in the Province of Leon (Cantabrian Mountains, N. Spain). The former is abundant in La Vid Group, Coladilla Fm., Upper Emsian, and the latter occurs in the upper part of the Santa Lucia Fm., uppermost Emsian. *Fimbrispirifer* ? cf. *F. boulei* GOURVENNEC, 1989 occurs in the Upper Pragian to Lower Emsian of the Montguyon Fm., in the Sarthe and Mayenne (Armorican Massif, France).

DIAGNOSIS

Entirely ribbed, brachythyrid forms. Simple, radial ribs, excepting the 1st to 3rd pairs closer to ventral sinus that

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-sinial 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 to now the internal dorsal structure of *Fimbrispirifer*? cf. *F. boulei* is unknown. The sinus ribbing of *Spirifer daleidensis* STEININGER, 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.
 v. 1964 *Fimbrispirifer rojasi* (VERNEUIL, 1850) - VANDERCAMMEN & KRANS, p. 24.
 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, brachythyrid *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 apsacline 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, orthocline dorsal interarea, 7-10 times lower than ventral, with marked transversal striae; large, open notothyrium; 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.

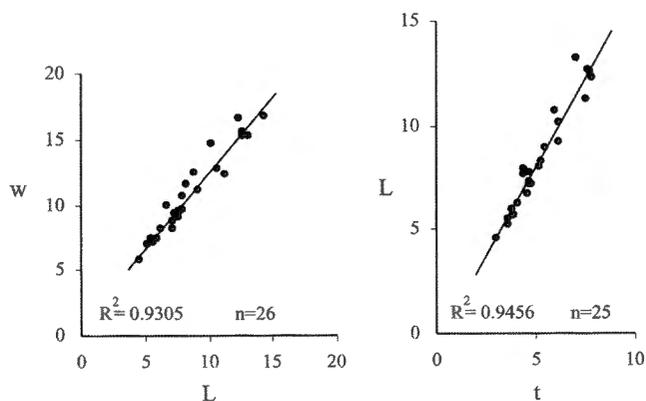


Fig. 11 — *Bultynckia rojasi*. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

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 sulcinate 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 similar or slightly larger; the two or three distal pairs of costae, close to the palintropes are obsolescent.

Numerous, close, regularly spaced, imbricate growth lamellae (Pl. 4, Figs. 12-14). Marginal, microspinose micro-ornamentation (Pl. 4, Figs. 12-15) with elongated

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.

Specimen	L	w	t	L/w	t/L	wsen/w	Nc
DPO 34821	9.2	11.1	6.2	0.83	0.67	0.31	7
DPO 34822	7.2	8.7	4.8	0.83	0.67	0.30	9
DPO 34823	7.3	9.3	4.7	0.78	0.64	0.28	8
DPO 34824	6.2	8.1	4.1	0.76	0.66	0.31	8
DPO 34825	5.5	7.4	3.6	0.74	0.65	0.26	6
DPO 34827	4.6	5.8	3	0.79	0.65	0.22	7
DPO 34833	12.3	16.6	7.8	0.74	0.63	0.31	9
DPO 34835	12.6	15.2	7.7	0.83	0.61	0.28	10
DPO 34841	12.7	15.6	7.6	0.81	0.60	0.33	10
DPO 34845	8.9	12.4	5.5	0.72	0.62	0.33	9
DPO 34846	8.3	11.6	5.3	0.71	0.64	0.26	9
DPO 34848	7.9	10.6	4.4	0.74	0.56	0.29	8
DPO 34852	8	9.6	5.2	0.83	0.65	0.24	10
DPO 34855	7.7	9.5	4.7	0.81	0.61	0.28	8
DPO 34858	7.6	9	4.4	0.84	0.58	0.32	10
DPO 34861	7.7	9.4	4.6	0.82	0.60	0.23	8
DPO 34864	5.7	7.1	3.9	0.80	0.68	0.29	7
DPO 34865	6	7.4	3.8	0.81	0.63	0.24	8
DPO 34866	5.2	7	3.6	0.74	0.69	0.23	8
DPO 34939	7.2	8.2	4.7	0.88	0.65	0.30	7

Bultynckia rojasi n.gen.

spine bases of different sizes; smaller and greater spine bases sometimes alternate along the growth lines; in other specimens the smaller spine bases group in 2-3 element series among the greater bases; 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 the radial ribs. Usually the spine bases show cuneiform, very fine, anterior prolongations, narrowing distally, suggesting that the spines projected anteriorly from the valve surface at angles close to 90° or greater. There are 25-35 spine bases in 3 mm near the anterior margin. Some relatively well preserved broken spines occur in the matrix; they are short, quadrangular in section and with a fine delthyridid-like (GOURVENNEC, 1987) furrow on the upper side.

Long, slender, extra-sinal dental plates (between the 2nd and 3rd pair of lateral costae). Strong, normal to valve bottom dental adminicula with bases diverging anteriorly. Short dental bases supporting slender cardinal teeth. Strong proximally to faint distally median ventral myophragm reaching anteriorly to the level of the distal end of the dental adminicula (Text-fig. 12).

Dorsal, apical, centrally depressed massif of secondary shell supporting the cardinal process; well-developed, undifferentiated ctenophoridium composed of up to 25 fine, vertical platelets. Crural bases developed on discrete outer hinge plates almost parallel to the commissural plane, supported by short but strong, sub-parallel crural plates. Well-developed, free, lateral apical cavities. The inner socket ridges fit in cavities excavated at the bases of the cardinal teeth to form a complementary interlocking device (Text-fig. 12).

Minute crura joining to postero-dorsally directed primary lamellae of the brachidium. Laterally directed spiral cones composed by 9 rather circular whorls entirely filling the internal shell cavity. Neither jugal processes nor jugum (Text-fig. 12).

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 delthyrial 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* GOURVENNEC, 1989 are larger, with more lateral and sinus ribs. Moreover in the latter species most of the lateral costae bifurcate or are more divided.

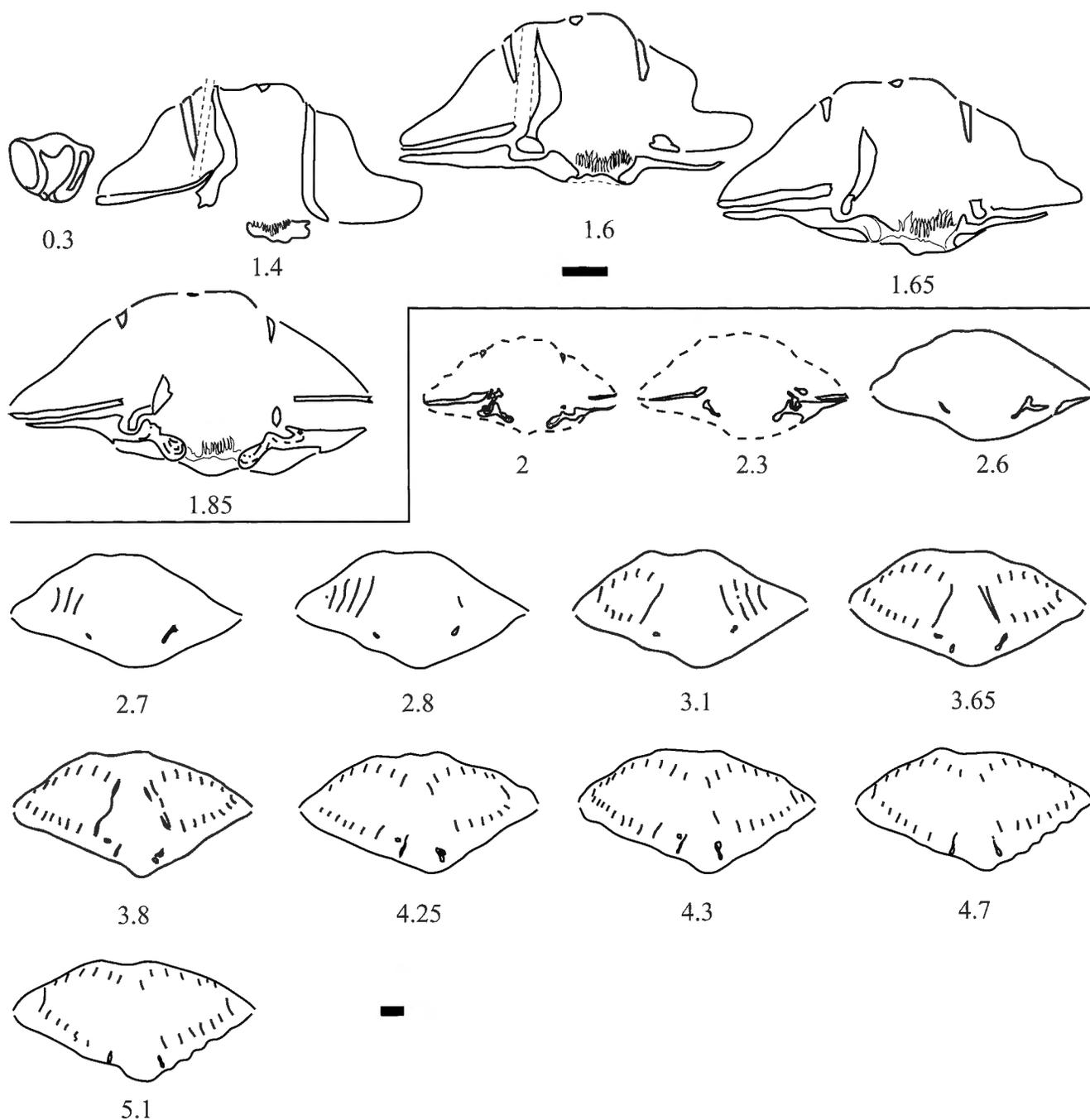


Fig. 12 — *Bultynckia rojasi*. Serial sections of a broken and decorticated specimen, topotype DPO 34875. Distances measured to the ventral apex. Black bars represent 1 mm.

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 Lucía 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 Lucía (La Pola de Gordón) and DPO 36049, from Aviados (Boñar). Faunal interval 16 (GARCÍA-ALCALDE, 1996) (Text-fig. 1, 4).

LOCUS AND STRATUM TYPICUM

The locus typicus occurs to the ESE of Santa Lucía Village (La Pola de Gordón, Province of León, N. Spain), along El Puerto Creek, in the Santa Lucía-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 Lucía 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 differentiated 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 striated dorsal area, much lower than the ventral area; very large, open notothyrium. Small umbo and dorsal beak.

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 ele-

ments 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 delthyrial plate. In the dorsal valve a well-developed ctenophoridium 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*, *Fimbrispirifer*, *Struveina* or *Multispirifer*.

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.

Specimen	L	w	t	L/w	t/L	wsen/w	Nc
DPO 32842	29	37	21.7	0.78	0.75	0.28	16
DPO 32843	15.7	21.8	12.5	0.72	0.80	0.27	11

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 WEDEKIND, 1926

Subfamily Kozłowskiellinae BOUCOT, 1957

REMARKS

The classification of *Cyrtinopsis* SCUPIN, 1896, *Kozłowskiellina* BOUCOT, 1957 (*nom.nov. pro Kozłowskiella* BOUCOT, 1957, *non* PRIBYL, 1953) and related forms has been a difficult matter. *Cyrtinopsis* was considered, long ago, so unique as to represent a subfamily, the Cyrtinopsinae WEDEKIND (in SALOMON, 1926) or a family, the Cyrtinopsidae (BOUCOT, 1957a) (although see HAVLÍČEK, 1959). On the other hand, BOUCOT (1957b) stated that *Kozłowskiellina*, *Megakozłowskiella* BOUCOT, 1957b (first proposed as a *Kozłowskiella* subgenus), and *Hedeina* 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 *Kozłowskiellina* (including the *Megakozłowskiella* 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 by STRUVE, 1965). 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*, *Megakozłowskiella* and *Plicocyrtina* HAVLÍČEK, 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 septate Subfamily Cyrtinopsinae (with *Cyrtinopsis*, *Kozłowskiellina*, *Megakozłowskiella* and *Plicocyrtina*) and the aseptate Subfamily Araspiriferinae JOHNSON (in CARTER *et al.*, 1994) (with *Araspirifer* HAVLÍČEK, 1987 and *Boucotinskia*).

More recently, BIZARRO & LESPÉRANCE (1999) disqualified 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 Kozłowskiellinae, would embrace *Kozłowskiellina*, *Megakozłowskiella*, *Araspirifer*, *Boucotinskia* and *Plicocyrtina*. On the other hand, both subfamily taxa and five more, would constitute the Family Delthyrididae according to their own revised concept (BIZARRO & LESPÉRANCE, 1999, p. 1059, Fig. 3).

Lacking new data on the micro-ornament of the discussed genera, in particular of the Subfamily Kozłowskiellinae *sensu* BIZARRO & 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 *Megakozłowskiella* and *Plicocyrtina*, as characters that closely relate them phylogenetically to *Cyrtinopsis* (and to *Jehlanaria* n.g. included in Cyrtinopsinae by HAVLÍČEK & 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 *Kozłowskiellina*, *Araspirifer*, *Boucotinskia*, and the new genus proposed here, *Boucotiellina* nov.gen., would constitute the Subfamily Kozłowskiellinae (with *Araspiriferinae* as a younger synonym). *Kozłowskiellinae* 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 Kozłowskiellinae, perhaps from *Kozłowskiellina* itself (KRANS, 1971, fig. 10). And more speculatively, *Boucotinskia* shared a common ancestry with *Kozłowskiellina* (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 *Kozłowskiellina* (*K. strawi*) 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 Kozłowskiellinae 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 ezquerrai* DE VERNEUIL, 1850.

DERIVATIO 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 Rañeces Group (Aguión Fm.), in Asturias, Upper Emsian; and much more questionably *Kozłowskiellina acuta* SU, 1976, from the Lower Devonian/Middle Devonian boundary beds, in China.

DIAGNOSIS

Small, megathyrid, sometimes mucronate shells. Undifferentiated cardinal ventral area. Open delthyrium with well-developed tooth ridges. Costate flanks with strong, sharp angular ribs and similar interspaces intersected by imbricate growth lamellae. Smooth, ventral sinus and dorsal fold with an angular section. Faintly capillate, spinose micro-ornamentation developed on the growth micro-filae. Well-developed dental plates. Very low, short, median ventral septum. Simple, rudimentary cardinal process with few but high vertical platelets. Short crural plates.

DISCUSSION

Boucotiellina nov.gen. differs from all the genera of the subfamilies *Kozlowskiellinae* 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 "*Howellevella*" *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 questionably 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 *Kozlowskiella 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 (Ferroñes, Avilés, Province of Asturias), upper part of Rañeces Group (Aguión 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 *Bultynckia rojasi* 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 ($t/L=0,6$ 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).

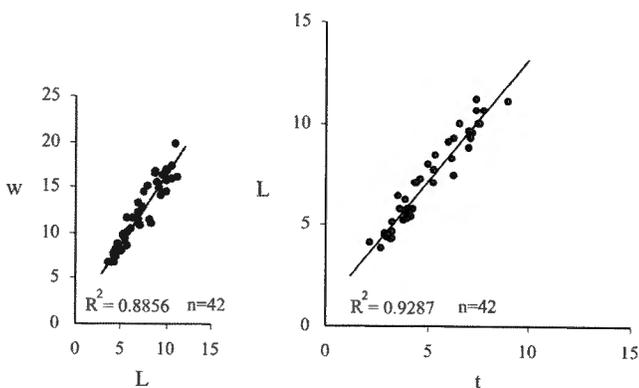


Fig. 13 — *Boucotiellina ezquerrai*. Length/Width (L/w) and Length/Thickness (L/t) dispersion diagrams.

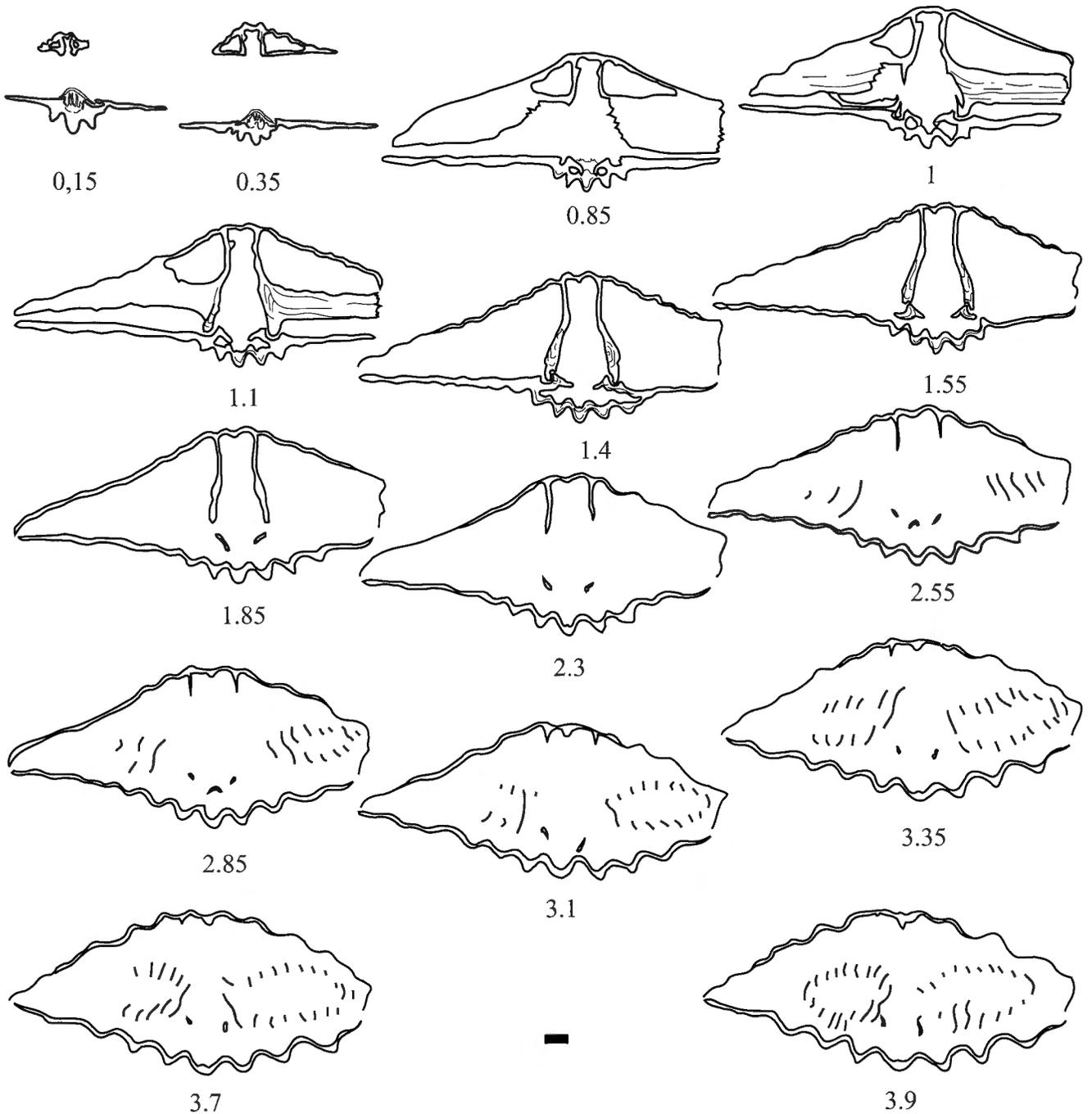


Fig. 14 — *Boucotiellina ezquerrai*. Serial sections of the toptype DPO 34804. Distances measured to the ventral apex. Black bar represents 1 mm.

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 microfiliae thicker near the growth lines. Sub-radial, very fine, sometimes obsolescent, microcostulate micro-ornamentation (Pl. 3, Figs. 15-16); numerous, minute, spine bases

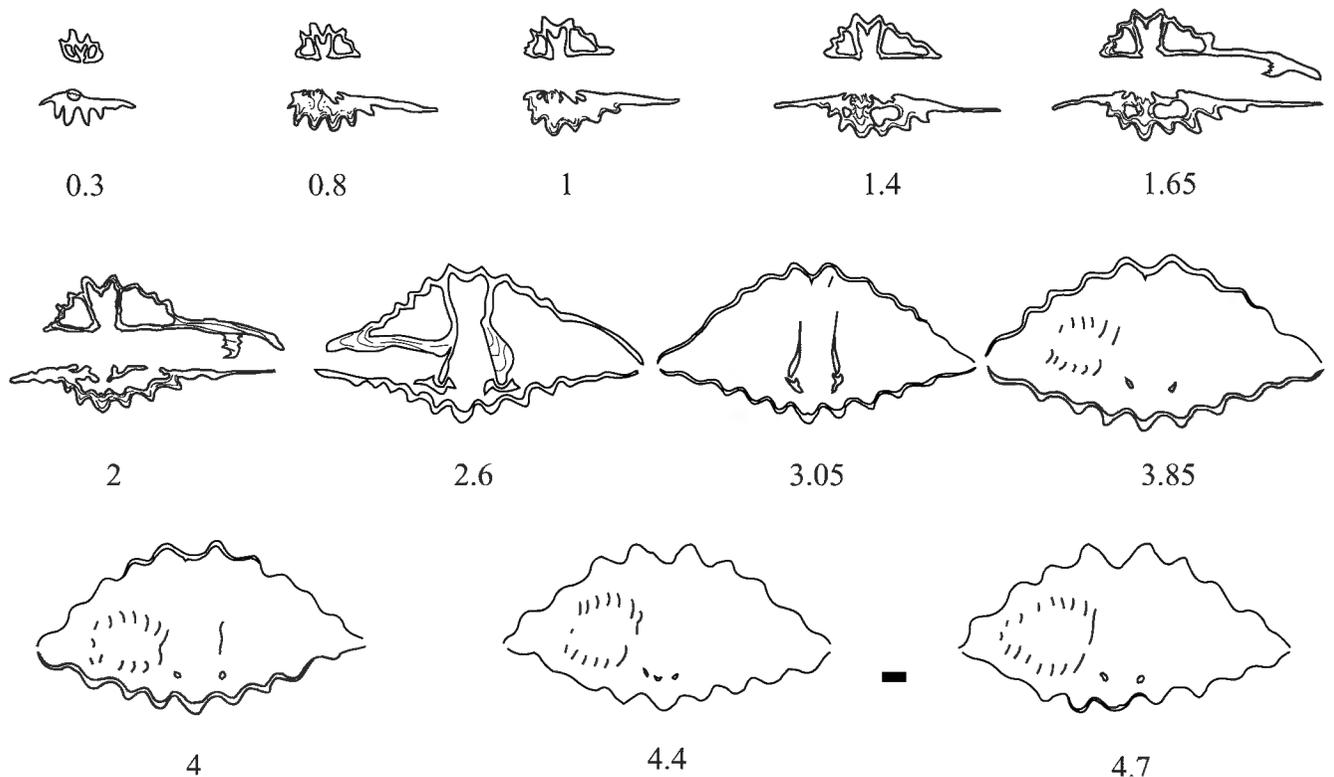


Fig. 15 — *Boucotiellina ezquerrai*. Serial sections of the topotype DPO 34805. Distances measured to the ventral apex. Black bar represents 1 mm.

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 1st and 2nd pair of lateral ribs) dental plates, extended further than the hinge region. Low, parallel ventral adminicula 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 ctenophoridium 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 spire (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 *Kozłowskiella* (= *Kozłowskiellina* BOUCOT, 1958, *nov. nom. pro Kozłowskiella* 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 *Kozłowskiellina* and related genera, where the radial elements are usually very rounded. On the other hand, KRANS (1969) presented a large and documented revision of *Kozłowskiellina* and *Megakozłowskiella* 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 *Megakozłowskiella raricosta* (CONRAD, 1842) cardinalium 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 *Kozłowskiellina* and *Megakozłowskiella* 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.

Specimen	L	w	t	L/w	t/L	wsen	wsen/w
DPO 34336	9.6	16.2	7	0.59	0.73	4	0.25
DPO 34337	10.6	17.2	7.4	0.62	0.70	4.3	0.25
DPO 34346	7.2	10.8	4.7	0.66	0.65	3	0.28
DPO 34350	6.2	10.4	3.9	0.60	0.63	2.7	0.26
DPO 34353	5.8	8.6	4.3	0.67	0.74	2.6	0.30
DPO 34355	5.5	9.4	4	0.58	0.73	2.6	0.28
DPO 34357	4.7	8.8	3.3	0.53	0.70	2.3	0.26
DPO 34359	5.8	10	4	0.58	0.69	2.6	0.26
DPO 34361	5.1	8.2	3.3	0.62	0.65	2.7	0.33
DPO 34362	4.3	7.8	3.2	0.55	0.74	1.9	0.24
DPO 34363	4.3	7.6	3.3	0.56	0.77	2.3	0.30
DPO 34366	4.6	7.4	2.9	0.62	0.63	2.5	0.34
DPO 34370	3.8	6.8	2.7	0.56	0.71	2.1	0.31
DPO 34373	10.6	15.9	7.8	0.67	0.73	4.4	0.28
DPO 34970	10	15.6	6.6	0.64	0.66	4.8	0.31
DPO 34975	9.2	14.8	7.1	0.62	0.77	4.3	0.29
DPO 34976	9.1	15.4	6	0.59	0.66	4.2	0.27
DPO 34978	7.7	14.5	5.3	0.53	0.69	4.1	0.28
DPO 34982	7	13.2	4.5	0.53	0.64	3.4	0.26

Boucotiellina ezquerrai

References

- ALEKSEEVA, R. E., 1967. Brachiopody i Stratigraphiya Niznego Devona Severo-Vostoka SSSR. Akademiya Nauk SSSR, Sibirskoe Otdelenie Institut Geologii i Geofiziki, Izdatelstvo "Nauka", 1-160, (in Russian).
- BARROIS, CH. 1882. Recherches sur les terrains anciens des Asturies et de la Galice. *Mémoires de la Société Géologique du Nord*, **2**(1): 1-630.
- BINNEKAMP, J. G., 1965. Lower Devonian brachiopods and stratigraphy of North Palencia (Cantabrian Mountains, Spain). *Leidse Geologische Mededelingen*, **33**: 1-62.
- BIZZARRO, M. & LESPÉRANCE, P. J., 1999. Systematics of some lower and middle Devonian spiriferid brachiopod from Gaspé with a revision of the Superfamily Delthyridoidea. *Journal of Paleontology*, **73** (6): 1056-1077.
- BOUCOT, A. J., 1957. A Devonian brachiopod, *Cyrtinopsis*, redescribed. *Senckenbergiana lethaea*, **38** (1/2): 37-48.
- BOUCOT, A. J., 1957b. Revision of Some Silurian and Early Devonian Spiriferid Genera and Erection of *Kozlowskiellinae*, New Subfamily. *Senckenbergiana lethaea*, **38** (5/6): 311-334.

median septum, and simple, non bilobed, cardinal process. Furthermore it differs from *Kozlowskiellina* in the occurrence of short ears at the cardinal extremities, greater convexity of the dorsal valve, and free, well-developed ventral apical lateral cavities that occur even in gerontic specimens. If true *kozlowskiellina* genera lack microspines as stated by KRANS (1969, 1971, 1973), this would be another significant difference with the microspinose *B. ezquerrai*.

"*Howellella*" *smithi* JONES & BOUCOT, 1983 differs from *B. ezquerrai* in the greater number of lateral ribs, micro-ornamentation composed of very faint capillae with well-developed marginal spines fringing the growth lines, and lack of either ventral median septum or myophragm.

B. ? acuta (SU, 1976) is a smaller-sized form, with fewer lateral ribs.

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BOUCOT, A. J., 1958. *Kozlowskiellina*, new name for *Kozlowskiella* Boucot, 1957. *Journal of Paleontology*, **32** (5), 1030.

BOUCOT, A. J., 1975. Evolution and extinction rate controls. Developments in Palaeontology and Stratigraphy, Elsevier, 1: 1-427.

BRICE, D., CARLS, P., COCKS, L. R. M., COPPER, P., GARCÍA-ALCALDE, J. L., GODEFROID, J. & RACHEBOEUF, P. R., 2000. Brachiopoda. In: P. BULTYNCK (Editor) Subcommission on Devonian Stratigraphy. Fossil groups important for boundary definition. *Courier Forschungs-Institut Senckenberg*, **220**: 65-86.

BRUNTON, C. H. C., COCKS, L. R. M. & DANCE, S. P., 1967. Brachiopods in the Linnaean Collection. *Proceedings of the Linnaean Society London*, **178** (2): 161-183.

CARLS, P., 1985. *Howellella (Hysterohowellella) knetschi* (Brachiopoda, Spiriferacea) aus dem tiefen Unter-Gedinnium Keltiberiens. *Senckenbergiana lethaea*, **65** (4/6): 297-326.

- CARLS, P., 1986. Neue Arten von *Vandercammenina* und *Hysterolites* (Brachiopoda, Acrospiriferinae; Devon). *Senckenbergiana lethaea*, **67** (1/4): 33-41.
- CARLS, P., MEYN, H. & VESPERMANN, J., 1993. Lebensraum, Entstehung und Nachfahren von *Howellella* (*Iberohowellella*) *hollmanni* n.sp., n.sp. (Spiriferacea; Lochkovium, Unter-Devon). *Senckenbergiana lethaea*, **73** (2): 227-267.
- CARTER, J. L., JOHNSON, J. G. & GOURVENNEC, R. & HOU, H., 1994. A revised classification of the spiriferid brachiopods. *Annals of the Carnegie Museum*, **63** (4): 327-374.
- COMTE, P., 1938. Brachiopodes dévoniens des gisements de Ferroñes (Asturies) et de Sabero (Léon). *Annales de Paléontologie*, **27**: 41-87.
- CONRAD, T. A., 1842. Observations on the Silurian and Devonian systems of the U.S. with descriptions of new organic remains. *Academy of Natural Sciences Philadelphia Journal*, **8**: 228-280.
- CHATTERTON, B. D. E., 1973. Brachiopods of the Murrumbidgee Group, Taemas, New South Wales. *Bulletin of the Department of Minerals & Energy, Bureau of Mineral Resources, Geology & Geophysics*, **137**: 1-146.
- GARCÍA-ALCALDE, J. L., 1995. L'évolution paléogéographique pré-varisque de la Zone Cantabrique septentrionale (Espagne). *Revista Española de Paleontología*, **10**(1): 9-29.
- GARCÍA-ALCALDE, J. L., 1996. El Devónico del dominio Astur-Leonés en la Zona Cantábrica (N de España). *Revista Española de Paleontología*, n.º extraordinario, 58-71.
- GARCÍA-ALCALDE, J. L., 1998. Braquiópodos rinconélidos del Lochkoviense (Devónico Inferior) de la Cordillera Cantábrica (Norte de España). *Geobios*, **31** (6): 767-789.
- GARCÍA-ALCALDE, J. L., 1999. Nuevo género de braquiópodos rinconélidos del Praguense (Devónico Inferior) de la region Cantabro-Celtestibérica (España). *Revista Española de Paleontología*, **14** (2): 247-255.
- GARCÍA-ALCALDE, J. L., 2001a. Paleobiogeographical relationships between North Gondwana and South Baltica: The Ivanothyris fauna (Cantabrian Zone, latest Emsian). *Journal of the Czech Geological Society*, **46** (3-4): 35-44.
- GARCÍA-ALCALDE, J. L., 2001b. Braquiópodos del Emsiense Superior (Intervalos faunísticos 11 a 13) del Dominio Astur-Leonés (Cordillera Cantábrica, N España). In: MELÉNDEZ, G. et al. (eds.), "Los fósiles y la Paleogeografía". *Publicaciones del Seminario de Paleontología de Zaragoza*, **5**: 545-549.
- GARCÍA-ALCALDE, J. L., 2003. *Bimeristina binnekampi* n.g., n.sp., Meristeloideo (Braquiópodo) del Devónico Inferior (Praguense) de España. *Revista Española de Paleontología*, **18** (1): 103-112.
- GARCÍA-ALCALDE, J. L., 2004. Upper Emsian Spinelloidea and Cyrtospiriferoidea (Brachiopoda, Spiriferidina) of the Cantabrian Mountains (N. Spain). Accepted for *Geobios*.
- GARCÍA-ALCALDE, J. L., ARBIZU, M. A., GARCIA-LOPEZ, S. & BENDEZ-BEDIA, I., 1979. Guidebook Field Trip Meeting International Subcommission Devonian Stratigraphy Spain 1979. Servicio Publicaciones Universidad Oviedo:1-41.
- GARCÍA-ALCALDE, J. L., CARLS, P., PARDO ALONSO, M. V., SANZ LÓPEZ, J., SOTO, F., TRUYOLS-MASSONI, M. & VALENZUELA-RÍOS, J. I., 2002. Devonian. In: W. GIBBONS & T. MORENO (Editors), *The Geology of Spain*. The Geological Society of London, 67-91.
- GOURVENNEC, R., 1987. Morphologie des épines chez les brachiopodes Delthyrididae. *Lethaia*, **20**: 21-31.
- GOURVENNEC, R., 1989. Brachiopodes Spiriferida du Dévonien Inférieur du Massif Armoricaín. *Biostratigraphie du Paléozoïque*, **9**: 1-281.
- HAVLÍČEK, V., 1956. The brachiopods of the Branik and Hlubočepý Limestones in the immediate vicinity of Prague. *Sbornik Ustředního ústavu geologického*, **22**: 1-131.
- HAVLÍČEK, V., 1959. Spiriferidae v českém siluru a devonu (Brachiopoda). *Rozpravy ústředního ústavu geologického*, **25**: 1-275, (in Czech).
- HAVLÍČEK, V., 1987. New genera of Silurian brachiopods. *Vestník Ustředního ústavu geologického*, **62** (4): 239-244.
- HAVLÍČEK, V. & VANEK, J., 1998. Pragian brachiopods, trilobites, and principal biofacies in the Prague Basin (Lower Devonian, Bohemia). *Sbornik Geologických věd, Paleontologie*, **34**: 27-109.
- IVANOVA, E. A., 1972. Main features of spiriferid evolution (Brachiopoda) (Translated from Russian to English), *Paleontologicheskii Zhurnal*, **1972** (3): 28-42.
- JAHNKE, H. & SLUPIK, C., 1993. Stromatolithen der oberen Lebanza-Kalke im östlichen Kantabrischen Gebirge (Unter-Devon; N-Spanien). Walliser-Festschrift, *Göttinger Arbeiten Geologie und Paläontologie*, **58**: 51-54.
- JANSEN, U. 2001. Morphologie, Taxonomie und Phylogenie unter-devonischer Brachiopoden aus der Dra-Ebene (Marokko, Prä-Sahara) und dem Rheinischen Schiefergebirge (Deutschland). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Frankfurt am Main*, **554**: 1-389.
- JONES, B. & BOUCOT, A. J., 1983. Spiriferids from the Lower Devonian strata of southwest Ellesmere Island, Arctic Canada. *Journal of Paleontology*, **57** (2): 327-346.
- KOZŁOWSKI, R., 1946. *Howellella*, a new name for *Crispella* Kozłowski, 1929. *Journal of Paleontology*, **20**,3: 295.
- KRANS, T. F., 1965. Etudes morphologiques de quelques spirifères dévoniens de la Chaîne Cantabrique (Espagne). *Leidse Geologische Mededelingen*, **33**: 74-148.
- KRANS, T. F., 1969. Morphological observations on *Kozłowskiellina* (Spiriferida). *Leidse Geologische Mededelingen*, **44**: 265-307.
- KRANS, T. F., 1971. The relation between the genera *Cyrtinopsis* Scupin, 1896 and *Kozłowskiellina* Boucot, 1957. *Leidse Geologische Mededelingen*, **47** (1): 99-113.
- KRANS, T. F., 1973. On the phylogenetic position of the genus *Boucotsinskia* Brunton and Cocks, 1967 (Spiriferida). *Leidse Geologische Mededelingen*, **49** (2): 277-283.
- KRANS, T. F., GUIT, F. A. & OFWEGEN, L. P. van, 1982. Facies patterns in the Lower Devonian carbonates of the Lebanza Formation (Cantabrian Mountains, Province of Palencia, NW Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **163**: 192-230.
- LENZ, A. A., 1972. *Plicocyrtina* and *Plicoplasia* (Brachiopoda) from the Lower Devonian of the northern Canadian Cordillera. *Journal of Paleontology*, **46** (1): 99-103.
- MITTMAYER, H. G., 1972. Delthyrididae und Spinocyrtiidae (Brachiopoda) des tiefsten Ober-Ems im Mosel-Gebiet (Ems-Quarzit, Rheinisches Schiefergebirge). *Mainzer geowissenschaften Mittelrhein*, **1**: 82-121.
- OEHLERT, D. & OEHLERT, P., 1901. Fossiles dévoniens de Santa-Lucia (province de Léon, Espagne) (Deuxième partie). *Bulletin de la Société Géologique de France*, (4), **1** (4): 233-250.
- ORBIGNY, A. D', 1850. Prodrôme de paléontologie stratigraphique universelle, Victor Masson, 1: 1-294.

- PERRY, D. G., 1984. Brachiopoda and biostratigraphy of the Silurian-Devonian Delorme Formation in the District of Mackenzie, the Yukon. *Royal Ontario Museum of Life Sciences Contributions*, **138**: 1-243.
- PHILLIPS, J., 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the ordnance geological survey of that district. London, Longman, Brown, Green, & Longmans, 1-231.
- PITRAT, C. W., 1965. Spiriferida. In: R. C. MOORE (editor): "Treatise on Invertebrate Paleontology", part H Brachiopoda, Geological Society of America and University of Kansas, 667-728.
- PRADO, C. DE & VERNEUIL, E. DE, 1850. Note géologique sur les terrains de Sabero et de ses environs dans les montagnes de Léon (Espagne) suivie d'une description des fossiles de ces terrains (E. de Verneuil). *Bulletin de la Société Géologique de France*, (2), **7** (2): 137-186.
- PRIBYL, A., 1953. Skorepatci polského stredního devonu (Givetu) z profilu Grzegorzowice-Skaly v horách Svatokrizských. *Sbornik Ústřední Ústav Geologie, odd. paleont.*, **20**: 1-112, (in Czech).
- SCUPIN, H., 1896. Versuch einer Classification der Gattung *Spirifer*. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **2**: 239-248.
- SCHLOTHEIM, E. F., 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier und Pflanzenreichs der Vorwelt erläutert. Gotha, Becker'schen Buchhandlung, 1: 1-378.
- STEININGER, J., 1853. Geognostische Beschreibung der Eifel. Trier, 1-144.
- SOLLE, G., 1953. Die Spiriferen der Gruppe *arduennensis-intermedius* im rheinischen Devon. *Abhandlungen Hessischen Landesamtes für Bodenforschung*, **5**: 1-156.
- STRUVE, W., 1965. Beiträge zur Kenntnis devonischer Brachiopoden, 13: Zur Morphologie, Biochronologie und Phylogenie der mitteleuropäisch-nordafrikanischen *Cyrtinopsis*-Arten (Spiriferacea). *Fortschritte in der Geologie von Rheinland und Westfalen*, **9**: 7-50.
- SU, Y., 1976. Cambrian-Devonian Brachiopoda. *Paleontological Atlas of North China, Nei Mongol* (ed. Geological Bureau Nei Mongol Autonomous Region & Northeast Institute of Geological Sciences), **1**: 159-227, (in Chinese).
- TERMIER, H. & TERMIER, G., 1949. Essai sur l'évolution des Spiriféridés. *Notes et Mémoires, Service géologique, Division des Mines et de la Géologie, Maroc*, **74** (2): 85-112.
- VANDERCAMMEN, A. & KRANS, T. F., 1964. Revision de quelques types de Spiriferidae d'Espagne. *Bulletin de l'Institut des Sciences naturelles de Belgique*, **40** (16): 1-40.
- VERNEUIL, E. DE & ARCHIAC, A. D', 1845. Note sur les fossiles du terrain paléozoïque des Asturies. *Bulletin de la Société Géologique de France*, (2) **2** (2): 458-480.
- WEDEKIND, R. (in SALOMON, W. H.), 1926. Die Devonische Formation. Grundzüge der Geologie, 2, Erdgeschichte, 194-226.
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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.- 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, x1.- 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 blodgetti* 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, and posterior view, x2.- 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 blodgetti* 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 sinial 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.



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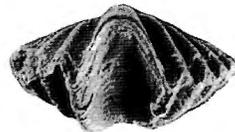
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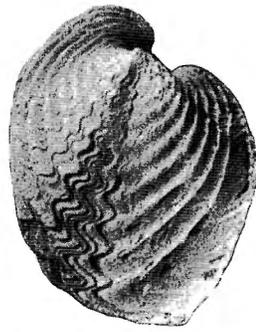
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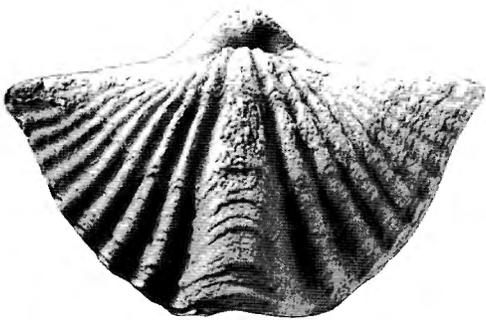
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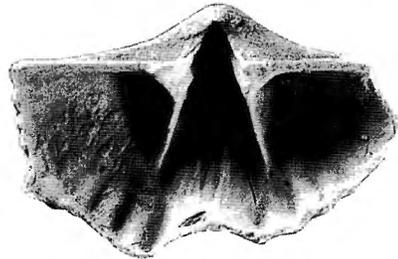
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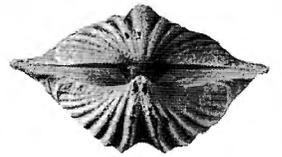
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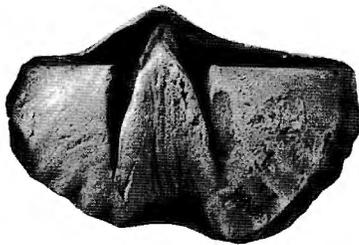
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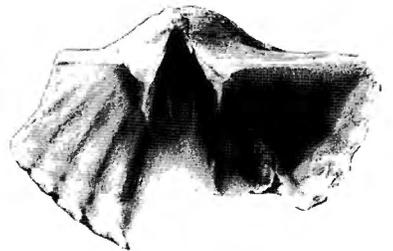
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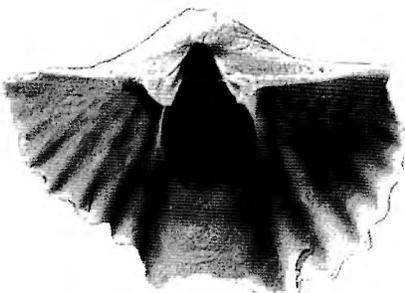
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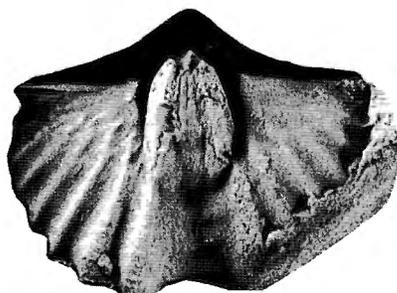
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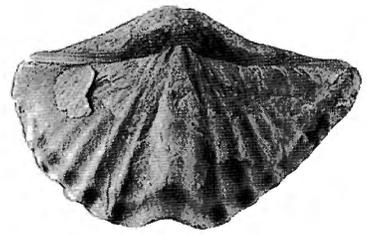
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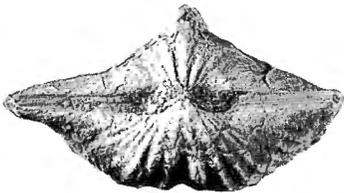
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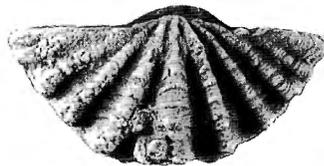
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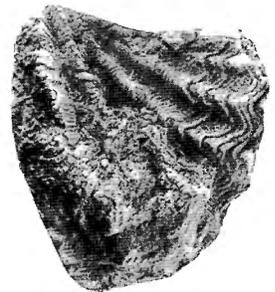
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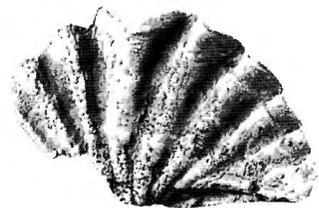
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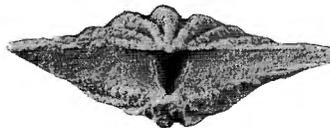
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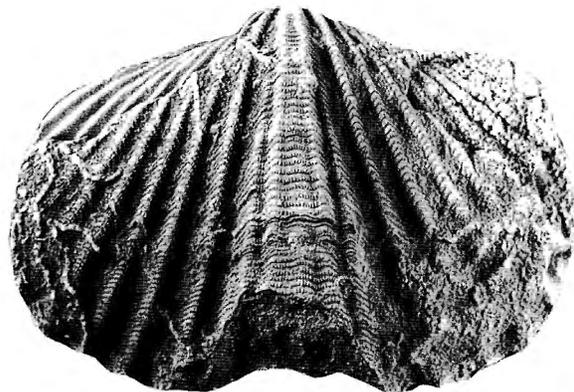
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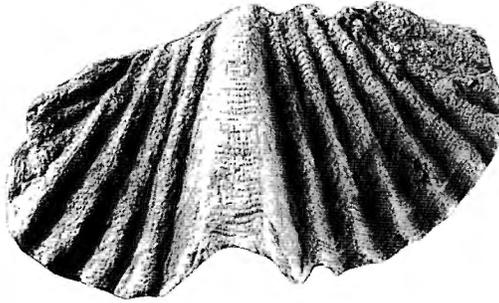
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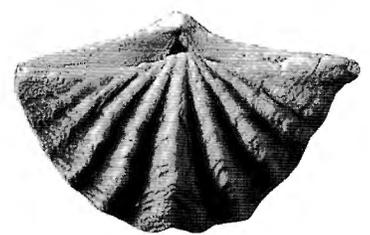
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