Early Serpukhovian conodonts from the Guadiato Area (Córdoba, Spain)

Conodontos del Serpujoviense inferior del Área del Guadiato (Córdoba, España)

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Abstract: The conodont assemblages of three stratigraphic sections from lower Serpukhovian rocks of the Guadiato Area (southwestern Spain) are composed of fifteen taxa, included in nine genera. Many of them are identified in open nomenclature due to the poor preservation of the specimens, of which most of them are fragmented, the presence of juvenile specimens, and the current controversy in the recognition of some multielement apparatuses. Generally, the faunas are not highly diversified and there is a low abundance of specimens in the horizons that yield conodonts. The assemblages include: *Cavusgnathus navicula, Cavusgnathus* cf. *navicula, Gnathodus girtyi*, of which two subspecies were identified, *Gnathodus girtyi girtyi* and *Gnathodus girtyi meischneri*, *Hindeodontoides*? sp., *Hindeodus cristula, Idioprioniodus healdi, Idioprioniodus* spp., *Kladognathus macrodentata*?, *Kladognathus tenuis-complectens, Lochriea*? sp., *Mestognathus bipluti, Synclydognathus geminus, Synclydognathus* spp. and many unidentifiable fragments. **Key words**: Taxonomy, Conodonts, Biostratigraphy, Serpukhovian, Sierra Morena, Spain.

Resumen: Se describen las asociaciones de conodontos de tres secciones estratigráficas de materiales del Serpujoviense inferior en el Área del Guadiato (Suroeste de España). Se han identificado quince taxones pertenecientes a nueve géneros, muchos en nomenclatura abierta debido a varios factores tales como, la preservación de los especímenes, de los cuales, la mayoría están fragmentados, la presencia de especímenes juveniles, y a la controversia existente en el reconocimiento de los aparatos multielementales. En general, las faunas no son muy diversas y la abundancia de ejemplares es baja. Las asociaciones incluyen: *Cavusgnathus navicula, Cavusgnathus cf. navicula, Gnathodus girtyi*, del que se identificaron dos subespecies, *Gnathodus girtyi girtyi y Gnathodus girtyi meischneri, Hindeodontoides*? sp., *Hindeodus cristula, Idioprioniodus healdi, Idioprioniodus* spp., *Kladognathus macrodentata*?, *Kladognathus tenuis-complectens, Lochriea*? sp., *Mestognathus bipluti, Synclydognathus geminus, Synclydognathus* spp. y elementos no identificados.

Palabras clave: Taxonomía, Conodontos, Estratigrafía, Serpujoviense, Sierra Morena, España.

INTRODUCTION

The studied stratigraphic sections are situated in the Guadiato Area (*sensu* CóZAR & RODRÍGUEZ, 1999a), within Sierra Morena (Fig. 1). These sections are located in the 880 and 901 Spanish Geological Sheets (MAGNA series, 1:50.000), Espiel and Villaviciosa de Córdoba respectively, situated in the Province of Córdoba, SW Spain. The most important towns in the

area are Espiel and Belmez, within the region crossed by the Guadiato River (Fig. 1).

The Guadiato Area shows a narrow, elongate strip of Carboniferous rocks trending WNW-ESE, within which are several belts of Mississippian (Viséan and Serpukhovian) rocks, parallel to each other and separated by faults (Fig. 1). CóZAR (1998) and CóZAR & RODRÍGUEZ (1999a, b) distinguished three tectonosedimentary belts of marine Mississippian rocks in the

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Figure 1.- Geographical and geological setting of the Guadiato Area in Sierra Morena SW Spain and location of studied stratigraphic sections. 1: San Antonio, 2: La Cornuda, 3: Via Crucis (modified from Cózar, 1998).

Figura 1.– Situación geográfica y marco geológico del Área del Guadiato dentro de Sierra Morena SW de España y localización de las secciones estratigráficas estudiadas. 1: San Antonio, 2: La Cornuda, 3: Via Crucis (modificada de CózAR, 1998).

Guadiato Area: the Fresnedoso Unit, equivalent to the 'Detritic Unit in culm facies' of APALATEGUI *et al.* (1985a, b); and the Sierra del Castillo and San Antonio-La Juliana units, both equivalent to the 'Detritic-carbonatic Unit' of APALATEGUI *et al.* (1985a, b).

The San Antonio-La Juliana Unit is generally composed of interbedded terrigenous and carbonate rocks, mostly marine in origin but becoming non-marine deltaic rocks towards the top of the succession (i.e. top of the Lavadero de la Mina section, Cózar & RODRÍGUEZ, 2004). The age attributed to these rocks is early Serpukhovian (Cózar, 2003, 2005), in which, upper Viséan as well as lower Serpukhovian carbonate olistolites are embedded (Cózar, 1998; Cózar & RODRÍGUEZ, 2004). This unit is one of the rare exposures of Serpukhovian marine carbonates located in the southwest of the Iberian Peninsula.

The Serpukhovian strata along the Guadiato Valley are bounded by upper Viséan rocks towards the southwest and by Duckmantian-Langsettian rocks to the northeast (Fig. 1). Outcrops are separated by faults due to significant post-Mississippian tectonics (WAGNER, 1999, 2004). However, the sedimentation of the San Antonio-La Juliana unit was also influenced by a syn-tectonic regime, which results in well-defined half-graben faulted blocks, with distinct sedimentary environments in close stratigraphic proximity as well as the occurrence of large olistolites (CózAR & RODRÍGUEZ, 2004).

Previous studies on Carboniferous conodonts from the Iberian Peninsula are related to its northern part,



Figure 2.- La Cornuda, San Antonio and Via Crucis stratigraphic sections (modified from CózAR, 1998). Note that all the studied levels for conodonts are numbered.

Figura 2.– Columnas estratigráficas de las secciones de La Cornuda, San Antonio y Via Crucis (modificada de CóZAR, 1998). Se han marcado todos los niveles que se han estudiado para el análisis de conodontos. predominantly to the Cantabrian Mountains (Adrichem Boogaert, 1965, 1967; Belka & Korn, 1994; BLANCO-FERRERA et al., 2005; BOOGAARD, 1983, 1992; GARCÍA-LÓPEZ & SANZ-LÓPEZ, 2002; HIGGINS, 1962, 1974; HIGGINS & WAGNER-GENTIS, 1982; Méndez & Menéndez-Álvarez, 1985; Park, 1983) and the Pyrenees (MARKS & WENSINK, 1970; PERRET, 1993; PERRET & WEYANT, 1994; SANZ-LÓPEZ, 1995; WIRTH, 1967; ZIEGLER, 1959), where deep-water conodont faunas have been recognized, dominated by gnathodids and lochrieids (HIGGINS, 1981). However, studies concerning Carboniferous rocks from the southern part of the Iberian Peninsula are scarce (BOOGAARD, 1963; BOOGAARD & SCHERMEHORN, 1975; HIGGINS, 1974; ROBARDET et al., 1986; BERMÚDEZ-ROCHAS et al., 2004).

This paper is the first detailed contribution to the knowledge of conodont assemblages from Serpukhovian rocks of Sierra Morena (southwestern Spain). The objectives of this research are (i) to document the multielement species recovered from the San Antonio, La Cornuda and Via Crucis sections; (ii) to undertake the biostratigraphic dating of the sections using conodonts; (iii) to compare the biostratigraphic ranges and the zonal schemes established using conodonts elsewhere in Europe and North America with those from the Guadiato Area; and (iv) to highlight particular ecological features of our faunas, compared to the faunas recorded from the Cantabrian Zone, Pyrenees, British Isles, Ireland and Poland.

METHODOLOGY AND RESULTS

The studied sections are (Figs. 1, 2): (i) San Antonio Section (geographic coordinates 5°8'20"W-38°14'N), which was measured and sampled along the La Juliana Stream, close to the San Antonio coal mine; (ii) La Cornuda Section (5°6'30"W-38°12'40"N), which was named after a farm house located around 400 m east of the section; and (iii) the Via Crucis Section (5°1'35"W-38°11'40"N), measured beside the track running from Espiel Town to the Estrella Hermitage (CóZAR, 1998).

Conodont elements have been recovered and studied following the traditional methods for the study of this fossil group. In total, 30 samples of approximately two to four kilograms were physical and chemically treated, with a 10% formic acid solution, from each carbonate horizon of the stratigraphic sections. Subsequently, specimens were picked out using an optical microscope and photographed by Scanning Electron Microscope (SEM) for detailed taxonomic analysis.

Only thirteen samples were productive for conodonts (Fig. 2), from which only three samples yielded high values (VCR/7 yielded 83 elements, VCR/10, 69 elements and VCR/11, 40 elements), whereas the other productive samples had very low values that range from 1 to 20 (Table 1). The Via Crucis section has been the most productive section for the recovery of conodont elements, and within this section, unit 7 has given the highest yields from the total of samples. Location of the sampled horizons is shown in figure 2.

Although some specimens are well-preserved, most of the material recovered consists of fragmented elements, which prevents their species and generic identification. It is also necessary to highlight the low diversity recorded, because only fifteen taxa ascribed to nine genera could be identified of the 302 elements recovered.

STRATIGRAPHIC SETTING

The San Antonio, La Cornuda and Via Crucis sections have been previously studied in a unpublished Ph.D. research project by CózAR (1998), involving the analysis of foraminifera, and biostratigraphical and sedimentological features, where precise thicknesses of the units and detailed descriptions of the sections are documented. The rugose coral assemblages in San Antonio and La Cornuda sections were studied in two unpublished M.Sc. research projects by RAMÍREZ-VIU (1994) and GÓMEZ-HERGUEDAS (2003), respectively. The main sedimentological and palaeontological data were published in CózAR & RODRÍGUEZ (1999b, 2004), CóZAR (2003, 2005) and CózAR *et al.* (2003).

The San Antonio section contains mostly shales, marls and siltstones interbedded with sandy limestones, nodular limestones and polymictic conglomerates. There is a 7 m rounded block of brecciated limestones embedded in the shales of unit 1 (Fig. 2). The second unit (50 m thick), is mostly composed of marlstones and siltstones, interbedded with thin intervals of nodular and sandy limestones (productive samples SA/2-1, SA/2-3). Higher in the succession, there is a 16 m thick interval, unit 3 (Fig. 2), which contains interbedded sandy limestones (sample SA/3-2) and shales. Limestone horizons show individual decimetric bed thickness, with an irregular base and top, and a high terrigenous content. In the upper part of the section, the unit 4 is composed of a 64 m thick shaly interval, although more marly intervals are observed. In the middle part of this unit, a calcareous breccia with erosive and channelized base is recorded (sample SA/4-1), which contains two levels of boulders and cobbles and a gigantoproductoid brachiopod concentration band at the base. In the uppermost part of the unit sandy limestone horizons are recorded with cross-lamination and erosive bases.

The section was interpreted as being sedimented in the proximal submarine slope with debris flow (unit 1), and turbidite deposits (limestone beds in units 2 and 3), that pass up to shallower water conditions in the outer platform to inner shelf at the top of the section (Cózar *et al.*, 2003; Cózar & RODRÍGUEZ, 2004; Cózar, 2005).

Most of the La Cornuda section is composed of siltstones separated by isolated carbonates (Fig. 2). The lower 150 m (units 1-3) are characterized by interbedded conglomerates and limestones. In between, 150 m and 356 m (units 4-9), there are more common limestone horizons, e.g. thinly-bedded limestones, brecciated limestones, and calcareous breccias (base of unit 9). Higher in the section (unit 10), there is a 100 m siltstone interval followed by 50 m (unit 11), where locally covered, shales, limestones, sandstones and polymictic conglomerates crop out.

The La Cornuda section was interpreted to be sedimented in a mixed siliciclastic/carbonate shallow-water platform. Shoal, tempestite, lagoonal and deltaic facies were recognized in this subtidal muddy platform, and in the upper part, intertidal channels were interpreted (CóZAR & RODRÍGUEZ, 2004; CóZAR, 2005).

The lower part of the Via Crucis section (109 m thick in total) contains sandstones and polymictic conglomerates (units 1-3), of individual metric to decimetric beds, except for the basal horizon (unit 0), which is a bioclastic grainstone (Fig. 2). Carbonate beds in higher levels occur as partly massive limestones, unit 5, with a high percentage of siliciclastic material (sample VCR/5), followed by nodular limestones composed of interbedded sandstones and limestones (unit 6, sample VCR/6a). Above, interbedded siltstones, shales, and limestones occur (units 7, 8 and 9). In unit 7, bioclastic limestones (sample VCR/7) are partly sandy and reddish in colour, containing black pebbles. Unit 9 contains sandstones (sample VCR/9). Unit 10 is composed of shales and siltstones with interbedded dolomites and sandy limestones (sample VCR/10), and unit 11 is characterized by nodular limestones (sample VCR/11). Units 13 and 14 are also predominantly composed of siltstones and sandstones (samples VCR/13, 14) with carbonate cement.

The Via Crucis section was interpreted to be sedimented in a submarine slope, and with a characteristic shallowing-upward sequence to the upper part of the section, within a muddy subtidal setting. This shallowing sequence is marked at the base by a sponge spicule bed in unit 5, debris-flows deposits in unit 6, background sedimentation with common turbidites in unit 7, and in the upper part of the section, shallow-water sediments (units 13-14), rich in siliciclastics, deposited in offshore tidal flats with tidal ripples (CóZAR & RODRÍGUEZ, 2004; CÓZAR, 2005).

SYSTEMATIC PALAEONTOLOGY

Suprageneric classification (orders, families and genera) follows SWEET (1988), except for the phylum, being assigned to the Chordata, according to ALDRIDGE *et al.* (1986), SMITH (1990) and PURNELL (1993). In table 1, the total numeric distribution of conodont taxa recovered from the productive levels of the San Antonio, La Cornuda and Via Crucis sections is documented.

All the recovered material is housed in the Department of Palaeontology, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid.

Phylum Chordata BATESON, 1886 Class Conodonta PANDER, 1856 Order Prioniodinida Sweet, 1988 Family Prioniodinidae BASSLER, 1925

Genus Idioprioniodus GUNNEL, 1933

Type species: Idioprioniodus typus GUNNEL, 1933

Idioprioniodus healdi (ROUNDY, 1926) (Pl. 1, fig. 1)

	Locality	San Antonio (SA)										Via Crucis (VCR)													La Cornuda (COR)						
Taxa and type of elements	Sample	1A1	1A2	1A3	2-1	2-2	2-3	3-1	3-2	4-1	4-2	0	1	6	б	5	6a	6b	7	6	10	11	13	14	1	3	5	7	6	11	[ota]
	Microfacies	Fst	Wst	Fst	Pst	Rst	Pst-Wst	Pst	Pst	Fst-Rst	Gst	Gst	Sst	G	Sst	Wst	W_{Sl}	Wst	Wst	Gst-Pst	Wst-Pst	Wst-Pst	Sil-Sst	Sds	Gst-Pst	Gst-Pst	Pst-Wst	Gst	Pst	Pst-Gst	
Idioprioniodus healdi Pb																			1												1
Idioprioniodus spp. Sa							1					•				•			:						·						1
Sb? S K. macrodentata? Pa-Pb K. tenuis-complectens Pa-Pb M		•			•	•	÷	•	•	•	•	•	•		•	•	•	•	1	•	÷		•	•	·		•	•	·	•	1
						•	1	•	•	•	•	•		•	•	•		•	•	•	1	2	•	·	·			•	•		2
			•		·	•	•	•	•	•	•	•	•	•	•	·	•	·	4	•	2	2	•	·	·	•		•	•	•	6
				÷	÷	÷	÷	÷		÷	÷	Ċ	÷	÷	÷	i	3		1	÷	ĩ	÷	÷		1.		÷	÷	÷		6
Sa																			1												1
Sb																			1						.						1
Sc												•							2		1	1			·						4
Lochriea? sp. S		•										•				1	1				÷				·			:		•	1
Gnathodus girtyi Pa M					•	•			•	·	•	•	•	•	•	•	1	•	3	·	5	3	•	•	·			1	·	•	13
					•	•		•	•	•	•	•	•	•	•	•	3	•	3	•	2	i	•	•	·				•	•	0
G girtvi girtvi Pa			•	•	•	•	•	•	•	•	•	•	•	•	•	i	3	·	9	•	8	2	•	·	·	•	•	•	•	•	23
G. girtvi meischneri Pa										÷				÷		1	2		4		2	3	÷								12
Hindeodus cristula Pa																1			2			1	1		.			1			6
Hindeodontoides? sp. Pa										1															.						1
Synclydognathus geminus Pa																						1			· ·						1
Synclydognathus spp. Pa		· ·			:		1					•				·	1	·	1	·					·			·	·		1
S Cavusgnathus navicula Pa					1	·	1	•	·	·	·	•	•	•	·	·	1	·	1	÷		3	·	·	· ·			•	·		7
		•	•		·	•		·	·	·	•	•	•	•	·	·	1	·	2	1	•		•	·	·	•		•	·		3
	P D M				•	•		•	•	i	•	•	•	•	•	•	•	•	2	1	2	•	•	·	· ·		•	•	•		6
Cavusenathus	cf. navicula Pa					:				i	:	:			:	:		:	1	1	-		1	:				i	:		5
Mestogna	thus bipluti Pa									i	÷	Ċ	÷	÷											11						1
Identified eleme	ents	•			1		3		0	4						5	14		40	4	26	17	2	0				3			119
Unidentified elements					13		17		7	9						5	5		43	5	43	23	6	1	.			6			183
Total					14		20		7	13						10	19		83	9	69	40	8	1	.			9			302
Kg. per sample		1.7	2.1	2.4	2.5	1.8	2.8	1.6	2.3	2.9	2.2	1.9	2.5	2.3	2.7	3.1	4.2	3.1	4.8	3.8	3.6	3.5	3.2	3.4	3.2	2.5	2.7	2.6	2.5	2.8	

Table 1.– Taxa, element-type and number of conodont elements identified in each level of the San Antonio, Via Crucis and La Cornuda sections. Levels with barren samples are marked with a dot. Microfacies of each level are also documented (Wst: Wackestone; Pst: Packstone; Gst: Grainstone; Fst: Floatstone; Rst: Rudstone; Sil: Siltstone; Sst: Sandstone; G: Gravelstone). See Fig. 2 for location of the levels.

Tabla 1.– Taxones, tipos de elementos y número de elementos conodontales identificados en cada uno de los niveles de las secciones estratigráficas de San Antonio, La Cornuda y Via Crucis. Los niveles con muestras no productivas se han marcado con un punto. Las microfacies de cada nivel también están señaladas (Wst: Wackestone; Pst: Packstone; Gst: Grainstone; Fst: Floatstone; Rst: Rudstone; Sil: Siltstone; Sst: Sandstone; G: Gravelstone). Ver la localización de los niveles en la Fig. 2.

Selected synonymy:

*1926 Prioniodus healdi ROUNDY, p. 10, pl. 4, fig. 5a-b.

- 1995 *Idioprioniodus? healdi* (ROUNDY); CHAUFFE & NICHOLS, pp. 889-892, pl. 1, figs. 2-3.
- 1995 Vicarious elements of *Idioprioniodus*? *claviger* and *Idioprioniodus*? *healdi* (ROUNDY); CHAUFFE & NICHOLS, p. 892, pl. 1, figs. 5-10, 12.
- 1999 Idioprioniodus healdi (ROUNDY); SOMERVILLE, p. 178-185, pl. 5, figs. 1-13.
- 1999 *Idioprioniodus healdi* (ROUNDY); SOMERVILLE & SOMERVILLE, pl. 1, figs. 13-18.

Material: 1 Pb element in VCR/7.

Description: The specimen is a ramiform bipennate Pb element that has two processes separated at a high angle, a short posterior one with a rounded posterobasal margin and an elongate laterally compressed anterior process. The element presents an elongate cusp with acute lateral margins that is curved above the base to straighten then to the tip. On the anterior bar a single denticle is preserved, while on the posterior there are two. The anterior denticle presents a flexure similar to that of the cusp and curves posteriorly. The apex of the cusp and denticles is acute. A wide and rounded basal cavity is observed which continues in the processes as a narrow groove that reaches to the border of the posterior process, but ends abruptly at the basal margin of the denticle of the anterior process. There is a flexure of the basal cavity that produces a smooth keel on the upper surface of the basal

cavity that continues longitudinally along the basal part of the cusp.

Remarks: This element has been assigned to *Idioprioniodus healdi* (ROUNDY, 1926) owing to the occurrence of several morphological characters similar to those observed in the specimens illustrated by SOMERVILLE (1999): (1) wide and rounded basal cavity; (2) the base of the anterior process is laterally compressed, wide, and curved downwards; (3) cusp laterally compressed, curved towards the posterior process and with smooth lateral keels running along its length; (4) at least, two discrete denticles on the posterior process; (5) the denticle closest to the cusp is markedly separated from the latter.

NORBY (1976) proposed the reconstruction of the multielement apparatus of I. healdi on the basis of eight natural assemblages. Other reconstructions for this genus are those by MERRIL & MERRIL (1974), STONE & GERAGHTY (1994) and that in CHAUFFE & NICHOLS (1995). NORBY (1976), whose work was posteriorly followed by SOMERVILLE (1999), defined a similar element as our illustrated Pb element (Pl. 1, fig. 1). However, CHAUFFE & NICHOLS (1995) considered this element as a Sc element that is vicariously shared between I.? healdi and I.? claviger, and differentiated both species by other elements which they considered as the Pb elements of the species, ponderosiform and geniculate respectively. Furthermore, the former authors also considered questionable the assignment of both species to the genus Idioprioniodus because the elemental composition of both species differs from that of the type species, Idioprioniodus cornutus which these authors considered the senior synonym of *I. typus*.

Idioprioniodus spp. (Pl. 1, figs. 2, 3)

Material: Highly fragmented material, which consists of 1 Sb? element in VCR/7, 1 juvenile Sa element in SA/2-3, and two unidentifiable S elements one in VCR/10 and in SA/2-3.

Description: Sa element (Pl. 1, fig. 3). This juvenile specimen is a ramiform alate element which lacks the two lateral processes due to fragmentation. These lateral processes show rounded transverse sections. It presents a cusp with two longitudinal keels at its lateral margins and an oval transverse section, and a small semicircular basal cavity at the base of the cusp and between the two lateral processes. The apex of the cusp is fractured.

The Sb element (Pl. 1, fig 2) is a ramiform bipennate element characterized by a large cusp with an oval transverse section and a broad semicircular basal cavity. The posterior process is fragmented.

Remarks: Owing to the fragmentation of the elements, and because the Sa specimen is a juvenile, no morphological characters which allow an unquestionable determination at a species category can be proposed. However, (1) the presence of the rounded basal cavity, (2) the laterally compressed cusp and with lateral keels or acute lateral margins, and (3) the general morphology, allows us to assign the specimens to the genus *Idioprioniodus*.

Genus Kladognathus REXROAD, 1958

Type species: Cladognathus prima REXROAD, 1957

Kladognathus macrodentata? (HIGGINS, 1961) cf. SOMERVILLE & SOMERVILLE, 1999 (Pl. 1, figs. 4-5)

Selected synonymy:

- 1996 *Kladognathus* apparent ecophenotypic variant of *K. tenuis* REXROAD & MERRILL, text-fig. 4, figs. 1-7.
- 1996 *Kladognathus tenuis* (BRANSON & MEHL) emend. REXROAD; SKOMPSKI, pp. 208-209, pl. 4, fig. 7 [*non* figs. 1-6, 8-11].
- 1999 Kladognathus macrodentata (HIGGINS); SOMERVILLE, p. 195-197, pl. 7, figs. 2-8.
- 1999 *Kladognathus macrodentata*? (HIGGINS); SOMERVILLE & SOMERVILLE, pl. 1, fig. 25.

Material: The material consists of fragments of 1 Pa-Pb element from VCR/10 and 2 Pa-Pb elements from VCR/11.

Description: Ramiform bipennate elements which have laterally compressed processes and a concave basal margin. The denticles present an acute apex, are laterally compressed and curve posteriorly. Between the highest denticles, one or two smaller denticles are observed. There is a shallow and narrow aboral groove along the basal margin of the processes.

Remarks: REXROAD & MERRIL (1996) pointed out the morphological similarities between the elements of

an ecophenotypic variant form of *Kladognathus tenuis* and the classical acknowledged elements of *K. macro-dentata*, the ecophenotypic form being characterized by thin and blade-like processes and laterally compressed denticles.

SOMERVILLE (1999), on the basis of the study by REXROAD & MERRIL (1996), considered this variant as a different species from *K. tenuis* and included it in the multielemental apparatus of *K. macrodentata*. In addition, SOMERVILLE & SOMERVILLE (1999), illustrated part of the previous elements as *K. macrodentata*?, but no criteria for this differentiation was mentioned. Our specimens are similar to those of *K. macrodentata*?, the name used here. Nevertheless, the precise taxonomic status of this species of *Kladognathus* remains to be elucidated.

Kladognathus tenuis-complectens sensu SOMERVILLE & SOMERVILLE, 1999 (Pl. 1, figs. 6-17)

Selected synonymy:

- * 1941a Prioniodus scitulus BRANSON & MEHL, p. 173, pl. 5, figs. 5-6.
- * 1941a Ligonodina tenuis BRANSON & MEHL, p. 170, pl. 5, figs. 13-14.
- * 1941b *Ligonodina levis* BRANSON & MEHL, p. 185, pl. 6, fig. 10.
- * 1958 Hibbardella milleri REXROAD, p. 18, pl. 2, figs. 13-16.
- * 1960 ? *Ligonodina complectens* CLARKE, p. 9, pl. 1, figs. 14-15.
- 1961 Hibbardella milleri REXROAD; REXROAD & BURTON, p. 1153, pl. 140, figs. 3-4.
- 1961 *Neoprioniodus scitulus* (BRANSON & MEHL); REXROAD & BURTON, p. 1155, pl. 140, figs. 15-17.
- 1961 Ligonodina n. sp.? REXROAD & BURTON, pp. 1154-1155, pl. 141, figs. 2-4.
- 1961 *Ligonodina hamata* REXROAD; REXROAD & BURTON, p. 1154, pl. 141, figs. 5-6.
- 1961 Ligonodina levis BRANSON & MEHL; REXROAD & BURTON, p. 1154, pl. 141, figs. 7-8.
- 1964 *Hibbardella milleri* REXROAD; REXROAD & FURNISH, p. 671, pl. 111, fig. 17.
- 1964 Neoprioniodus peracutus (HINDE); REXROAD & FURNISH, p. 674, pl. 111, fig. 25.
- 1964 Magnilaterella robusta REXROAD & COLLINSON; REXROAD & FURNISH, p. 673, pl. 111, figs. 27-31.
- 1964 Lambdagnathus fragilidens REXROAD; REXROAD & FURNISH, p. 672, pl. 111, fig. 35.

- 1964 Neoprioniodus scitulus (BRANSON & MEHL); REXROAD & FURNISH, p. 674, pl. 111, figs. 36-37.
- 1964 Ligonodina levis BRANSON & MEHL; REXROAD & FURNISH, p. 672, pl. 111, fig. 38.
- 1964 *Ligonodina* sp.; REXROAD & FURNISH, pp. 673, pl. 111, fig. 39.
- 1964 Ligonodina tenuis BRANSON & MEHL; REXROAD & FURNISH, pp. 672- 673, pl. 111, fig. 40.
- 1967 Neoprioniodus peracutus (HINDE); GLOBENSKY, p. 443, pl. 55, figs. 18, 25.
- 1967 *Neoprioniodus scitulus* (BRANSON & MEHL); GLOBENSKY, pp. 443-444, pl. 55, figs. 22, 26.
- 1967 *Ligonodina tenuis* BRANSON & MEHL; GLOBENSKY, p. 442, pl. 56, figs. 13, 14.
- 1967 Ligonodina levis BRANSON & MEHL; GLOBENSKY, p. 442, pl. 56, fig. 16.
- 1969 Magnilaterella contraria Rhodes, Austin & Druce, p. 147, pl. 23, figs. 8, 18.
- 1982 Ligonodina? sp.; BELKA, pl. 2, fig.5.
- 1982 Ligonodina levis BRANSON & MEHL; BELKA, pl. 2, fig. 6.
- 1982 Neprioniodus peracutus (HINDE); BELKA, pl. 2, fig. 9.
- 1985 Magnilaterella sp.; WEYANT & MASSA, pl. 3, figs. 13-15.
- 1985 Hibbardella sp.; WEYANT & MASSA, pl. 3, fig. 16.
- 1985 Neoprioniodus peracutus (HINDE); WEYANT & MASSA, pl. 3, figs. 17-18.
- 1985 *Ligonodina levis* BRANSON & MEHL; WEYANT & MASSA, pl. 3, figs. 19-21.
- 1986 Kladognathus n. sp. MAPES & REXROAD, pl. 2, figs. 1-15.
- 1990 ? Kladognathus complectens (CLARKE); REXROAD & HOROWITZ, pp. 506- 507, pl. 3, figs. 1-11.
- 1990 Kladognathus tenuis (BRANSON & MEHL); REXROAD & HOROWITZ, pp. 505-506, pl. 3, figs. 12-30, 33.
- 1990 shared elements between *K. tenuis* and ? *K. complectens* REXROAD & HOROWITZ, p. 507, pl. 3, figs. 31-32.
- 1991 *Kladognathus* aff. *levis* (BRANSON & MEHL); STONE, pp. 43-45, pl. 5, figs. 3-4, 6, 9-10, 13.
- 1996 Kladognathus tenuis (BRANSON & MEHL); REXROAD & MERRIL; text-fig. 5, figs. 1-8, 10-12.
- 1996 Kladognathus tenuis? (BRANSON & MEHL); REXROAD & MERRIL; text-fig. 5, figs. 9, 14.
- 1996 Kladognathus tenuis (BRANSON & MEHL); SKOMPSKI, pp. 208-209, pl. 4, figs. 1-6, 8-11 [non fig. 7].
- 1996 *Kladognathus* spp. indet.; KRUMHARDT, HARRIS & WATTS, pp. 45-46 , pl. 5, figs. 1-10
- 1999 Kladognathus tenuis/complectens (BRANSON & MEHL), emend. REXROAD; SOMERVILLE, pp. 187-191, pl. 6, figs. 1-15.
- 1999 shared ramiform elements *Kladognathus tenuis/complectens* (BRANSON & MEHL), *Kladognathus macrodentata* HIGGINS; SOMERVILLE, pp. 191-195, pl. 7, figs. 9-17.
- 1999 *Kladognathus tenuis/complectens* (BRANSON & MEHL), emend. REXROAD; SOMERVILLE & SOMERVILLE, pl. 1, figs. 27-31.

Material: The material is moderately fragmented and composed of 18 elements; 1 M element in VCR/5, 3 M elements in VCR/6A, 4 Pa-Pb, 1 M, 1 Sa, 1 Sb and 2 Sc elements in VCR/7, 2 Pa-Pb, 1 M and 1 Sc elements in VCR/10 and 1 Sc element in VCR/11.

Description:

Pa-Pb elements (Pl. 1, figs. 6-11): The specimens recovered are fragments of Pa-Pb processes. These ramiform bipennate elements present laterally compressed processes. The basal margin of the processes is concave and may present a narrow groove. The denticles are curved posteriorly, and an alternation of smaller denticles between larger ones may be observed in some elements.

Another type of Pa-Pb elements are those represented in Plate 1, figures 10-11, which correspond to the central part of a magnilaterellan element. They are characterized by a large cusp flanked by the smaller and slender denticles of the processes. There is an oval basal cavity right beneath the cusp.

M elements (Pl. 1, figs. 12-14): These ramiform dolobrate elements are characterized by a large cusp, a well-developed anticusp, and a denticulated posterior process. The posterior margin of the anticusp is convex. The elongated posterior process curves progressively downwards to the posterior part of the element. The denticles, although fused, are well differentiated, and in the specimens VCR/6a-13 and VCR/6a-12 (Pl. 1, figs. 12 and 14 respectively) curve posteriorly, whereas in VCR/7-30 are straight (Pl. 1, fig. 13). A narrow, elongated basal cavity is situated beneath the first denticle at the basal margin of the process.

Sa element (Pl. 1, figs. 15a, 15b). It is a ramiform alate element with two lateral and one posterior denticulated processes. Each lateral process is situated at a 90° angle with respect to the posterior process, and both of them curve downwards. The processes are compressed and have an oval transverse section. A large, laterally compressed cusp is observed, in which, its posterior margin is acute. Only the base of the denticles is present due to fragmentation, but at least 3 to 4 denticle bases can be recognized in the left lateral process and 2 in the right lateral process, although both processes are also fragmented. Beneath the cusp, there is a small basal cavity that continues within the posterior process as a narrow groove.

Sb element (Pl. 1, fig. 16): The specimen is a ramiform bipennate element with a broken posterior process that bears two small rounded denticles and a lateral process that curves inwards and downwards, in which at least, two rounded denticles are observed. The second denticle of the lateral process seems to be larger than the first one, being the former inclined to the outer part of the element. A wide large rounded cusp is present between the processes which is slightly curved to the posterior part. The basal cavity is semi-circular and is situated beneath the cusp. In the processes, a narrow groove is observed at their aboral margin.

Sc element (Pl. 1, fig. 17): The specimen is a ramiform bipennate element that has a broken posterior process and a short inner and downflexed anterolateral process. The anterolateral process has discrete rounded and delicate denticles that are straight or curve to the outer part of the element and posteriorly. The central denticle is the highest and presents a bulky insertion to the process. The cusp is markedly wider and larger than the denticles and curves posteriorly. The semi-circular basal cavity is situated immediately beneath the cusp and continues within the processes as a narrow groove.

Remarks: REXROAD & HOROWITZ (1990) reconstructed the apparatuses of *Kladognathus tenuis* and ?K. complectens, which basically, as noted by SKOMPSKI (1996), can be distinguished by the S elements [Ligonodina complectens CLARKE, in ?K. complectens (CLARKE, 1960), and Ligonodina tenuis (Sc, morphotype α) as well as *Ligonodina levis* (Sc, morphotype β) in *K. tenuis*; the latter species is also characterized by Magnilaterella robusta (Pa-Pb)]. However, SKOMPSKI (1996) also noted that some of the S and M elements can be vicariously shared, and thus, he alternatively proposed the P elements (i.e. Magnilaterella) for distinguishing them. Nevertheless, PURNELL (1993) had previously documented that in the midgut of a specimen of Typhloesus wellsi, a metazoan of the Bear Gulch Member (Montana, U.S.A.), a complete and well-preserved apparatus of Kladognathus was recorded, in which the P positions were occupied by nonplatform Magnilaterella elements.

SOMERVILLE & SOMERVILLE (1999) were not able to distinguish which *Magnilaterella* elements were biologically associated in their assemblages, and thus, they determined all their specimens as *K. tenuis/complectens*. In the Guadiato Area, the assemblages show a similar problem and, in addition, the number of specimens recovered is scarce. Consequently the same criterion is adopted here.

Medina-Varea et al.

Order Ozarkodinida DZIK, 1976 Family Spathognathodontidae HASS, 1959

Genus Lochriea Scott, 1942

Type species: *Spathognathodus commutatus* BRANSON & MEHL, 1941c

Lochriea? sp. (Pl. 2, figs. 1a,1b)

Material: An S element in VCR/5.

Description: The specimen corresponds to a ramiform bipennate element with a denticulated anterior process at a high angle with respect to the posterior process. The latter is flattened, has its distal part fragmented and bears denticles of two sizes, the highest ones being as large as the cusp. The highest denticles are not present in the posterior process until the middle part, and they are characterized by a slight flexure to the anterior part which produces a concavity in the anterior margin of the denticles and a convexity in the posterior margin. However, the denticles are generally inclined to the posterior part of the element. These same features are observed in the cusp, but in this case it straightens near the apex. The anterior process has a concave inner part and a convex outer part. The denticles of the anterior process are straight or slightly curved to the outer part and smaller than the cusp. A small basal cavity is situated beneath the cusp.

Remarks: The S element is characterized by having both processes with a wide base and the denticles, although posteriorly curved, show a concavity in its anterior margin and a convexity in its posterior margin. The specimen is rather similar to the *Lochriea* S elements illustrated in REXROAD & HOROWITZ (1990) and SOMERVILLE & SOMERVILLE (1999), although not exactly the same, and thus, the specimen is questionably attributed to the genus. The previous features permit to distinguish them from the S element of the genera *Kladognathus* and *Gnathodus*, in that the base of the processes is slender and that, although the denticles do also incline posteriorly, the anterior margin is convex and the posterior is concave.

Family Gnathodontidae SWEET, 1988

Genus Gnathodus PANDER, 1856

Type species: Polygnathus bilineatus ROUNDY, 1926

PLATE 1

Figs. 2,3.- Idioprioniodus spp. 2. VCR/7-28, Sb? element, inner view, 3. SA/2-3-1, Sa element, inner view.

Figs. 4-5.- Kladognathus macrodentata? (HIGGINS, 1961) cf. SOMERVILLE & SOMERVILLE (1999). Pa-Pb elements. 4. VCR/11-2, inner view, 5. VCR/11-15, inner view.

Figs. 6-15.– *Kladognathus tenuis-complectens* cf. SOMERVILLE & SOMERVILLE (1999). 6. VCR/7-40, Pa-Pb element, a. inner view, b. outer view, 7. VCR/7-39, Pa-Pb element, inner view, 8. VCR/7-15, Pa-Pb element, inner view, 9. VCR/7-41, Pa-Pb element, a. inner view, b. outer view, 10. VCR/10-29, Pa-Pb element, inner view, 11. VCR/7-46, Pa-Pb element, posterior-lateral view, 12. VCR/6a-13, M element, lateral view, 13. VCR/7-30, M element, lateral view, 14. VCR/6a-12, M element, lateral view, 15. VCR/7-42, Sa element, a. inner view, b. inner-lateral view, 16. VCR/7-36, Sb element, inner view, 17. VCR/10-11, Sc element, inner view.

Fig. 18.- Gnathodus girtyi HASS, 1953. VCR/10-1, M element, inner view.

LÁMINA 1

Fig. 1.- Idioprioniodus healdi (ROUNDY, 1926). VCR/7-20, elemento Pb, vista lateral-interna.

Figs. 2, 3.- Idioprioniodus spp. 2. VCR/7-28, elemento Sb?, vista interna. 3. SA/ 2-3-1, elemento Sa, vista interna.

(Escala gráfica= $100 \ \mu m$)

Fig. 1.- Idioprioniodus healdi (ROUNDY, 1926). VCR/7-20, Pb element, inner-lateral view.

⁽Scale bar= 100 µm).

Figs. 4-5.- Kladognathus macrodentata? (HIGGINS, 1961) cf. SOMERVILLE & SOMERVILLE (1999). Elementos Pa-Pb. 4. VCR/11-2, vista interna, 5. VCR/11-15, vista interna.

Figs. 6-15.- Kladognathus tenuis-complectens cf. SOMERVILLE & SOMERVILLE (1999) 6. VCR/7-40, elemento Pa-Pb, a. vista interna, b. vista externa, 7. VCR/7-39, elemento Pa-Pb, vista interna, 8. VCR/7-15, elemento Pa-Pb, vista interna, 9. VCR/7-41, elemento Pa-Pb, a. vista interna, b. vista externa, 10. VCR/10-29, elemento Pa-Pb, vista interna, 11. VCR/7-46, elemento Pa-Pb, vista lateral-posterior, 12. VCR/6a-13, elemento M, vista lateral, 13. VCR/7-30, elemento M, vista lateral, 14. VCR/6a-12, elemento M, vista lateral, 15. VCR/7-42, elemento Sa, a. vista interna, b. vista lateral-interna, 16. VCR/7-36, elemento Sb, vista interna, 17. VCR/10-11, elemento Sc, vista interna. Fig. 18.- Gnathodus girtyi HASS, 1953. VCR/10-11, elemento M, vista interna.

PLATE I / LÁMINA I



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Gnathodus girtyi HASS, 1953 (Pl. 1, fig. 18, Pl. 2, figs. 11-14)

Selected synonymy:

*1953 Gnathodus girtyi HASS, p. 80, pl. 14, figs. 22-24.

1999 *Gnathodus* sp. ramiform elements; SOMERVILLE, pl. 3, figs. 1-20.

Material: The material consists of fragments and relatively well preserved elements, comprising 23 elements: 1 Pa and 3 S elements in VCR/6A, 3 Pa and 3 S elements in VCR/7, 5 Pa, 1 M and 2 S elements in VCR/10, 3 Pa and 1 S elements in VCR/11 and 1 Pa element in COR/7. Description:

Pa elements: The specimens are pectiniform carminiscaphate elements and present the principal characteristics of the species *Gnathodus girtyi*, such as a large free blade composed of several discrete denticles and an asymmetric platform in which two parapets are developed to a different degree. The inner parapet is higher and usually more developed than the outer one, and of a similar height as the carina to which both parapets are subparallel. The carina consists of a series of nodes in a longitudinal arrangement that can be completely or partially fused. These elements show a broad cup-like basal cavity with two distinct flarings, the outer one being usually more developed than the inner one.

The specimen VCR/11-12 (Pl. 2, fig. 11) is characterized by two similarly developed parapets as narrow ridges parallel to the carina, which is axial and robust in its anterior part. The sole ornamentation present is a series of transverse ridges and grooves at the posterior part of the platform, produced by the fusion of the nodes of the carina and parapets. The outer flaring of the basal cavity in upper/oral view, presents a medial development whereas the inner one has an anterior disposition.

The specimen VCR/10-34 (Pl. 2, fig. 12) is characterized by a well developed carina and a conspicuously high inner parapet. The specimen has the typical transverse ridges at the inner parapet and nodes arranged longitudinal to the platform at the outer parapet. The anterior part of the platform is curved downwards. An important character is the disposition of the flarings of the basal cavity in upper/oral view, extending in the outer one from the anterior part of the platform to the posterior margin, whereas the inner one is very narrow and restricted medially. *M* element: The specimen (Pl. 1, fig. 18) corresponds to a ramiform dolobrate M element that is characterized by a long posterior process and by a cusp and an anticusp and a fragmented anterior process. The cusp is slightly larger than the highest denticles of the posterior process, and has acute lateral margins. In the posterior process, smaller and larger denticles alternate. The cusp and the denticles show acute apexes

S elements: The VCR/6a-5 (Pl. 2, fig. 13) specimen is a ramiform bipennate element and is characterized by a large denticulated posterior process and a short, denticulated anterior process curved downwards. Both processes are situated at a 90° angle to each other. The bar-like posterior process presents a longitudinal groove at the base of the denticles. The denticles of this process incline posteriorly, are fused at their base and are of two sizes, alternating between the smaller ones and larger ones. The cusp is situated at the anterior part of the posterior process and it is higher and wider than the denticles of the anterior and posterior process. The denticles of the anterior process are large and straight. The narrow basal cavity is situated in the basal margin at the junction of the two processes.

In the specimen VCR/6a-8 (Pl. 2, fig. 14) only the posterior process is present and the smaller denticles are completely fused between each other and to the higher ones.

Remarks: The Pa elements recovered show the typical characters of *Gnathodus girtyi* HASS, such as an asymmetric platform differentiated into parapets, that reach the posterior margin of the platform, a wide basal cavity and a carina that runs longitudinally to the platform. No diagnostic features for a subspecies determination are recognized.

In the case of the S elements, they are considered as vicariously shared between the different species of *Gnathodus*. However, *Gnathodus girtyi* is the only species occurring in our sections, and thus, the recovered S elements are assigned to this species.

Gnathodus girtyi girtyi HASS, 1953 (Pl. 2, figs. 2-6)

Selected synonymy:

* 1953 Gnathodus girtyi HASS, p. 80, pl. 14, figs. 22-24.

1974 *Gnathodus girtyi* HASS; MATTHEWS & THOMAS, pl. 51, figs. 16-17, 28-31.

- 1982 *Gnathodus girtyi girtyi* HASS; BELKA, pl. 1, figs. 2-7, pl. 2, figs. 3, 7.
- 1982 Gnathodus girtyi girtyi HASS; HIGGINS & WAGNER-GENTIS, p. 334, pl. 34, fig. 9.
- 1982 Gnathodus girtyi HASS; VON BITTER & PLINT-GEBERL, p. 200, pl. 6, fig. 5 [non fig. 7].
- 1985 Gnathodus girtyi girtyi HASS; BELKA, pl. 4, figs. 4, 9.
- 1985 Gnathodus girtyi girtyi HASS; VARKER & SEVASTOPULO, p. 202, pl. 5.6, figs. 1-2.
- 1985 Gnathodus girtyi girtyi HASS; HIGGINS, p. 220, pl. 6.2, fig. 2.
- 1993 Gnathodus girtyi girtyi HASS; PERRET, p. 334, pl. CV, figs. 32, 36.
- 1996 Gnathodus girtyi girtyi HASS; SKOMPSKI, pp. 198-199, pl. 1, figs. 8-9.
- 1996 Gnathodus girtyi girtyi HASS; KRUMHARDT, HARRIS & WATTS, pp. 40- 41, pl. 2, figs. 20-22, 29.
- 1999 Gnathodus girtyi (HASS); SOMERVILLE, pl. 2, figs. 4-7.
- 1999 *Gnathodus girtyi* (HASS); SOMERVILLE & SOMERVILLE, pl. 1, fig. 10.
- 2002 Gnathodus girtyi girtyi HASS; GARCÍA-LÓPEZ & SANZ-LÓPEZ, pl. 4, fig. 15.

Material: The material is generally well preserved, and 23 Pa elements have been recovered in VCR/5 (1), VCR/6A (3), VCR/7 (9), VCR/10 (8) and VCR/11 (2).

Description: The specimens recovered (Pl. 2, figs. 2-6) correspond to pectiniform carminiscaphate Pa elements, that are characterized by a large free blade and an asymmetric platform with two robust, well developed parapets. The height of the free blade decreases from its anterior part to its insertion within the platform and bears rounded, discrete denticles. The parapets are subparallel to the central carina, which slightly curves to the inner part of the element. Both parapets reach the posterior margin, although the outer parapet begins slightly posteriorly than the inner one. The inner parapet is as high as the carina, and both higher than the outer parapet. The maximum width of the outer parapet is in the anterior part whereas the inner parapet has a similar development along its entire extension. Both parapets can be transversely ridged in their anterior part although this feature is more common in the inner one than in the outer one, which usually bears nodes subparallel to its margin and the carina. The inner parapet presents nodes at its posterior part that, together with those of the carina and the outer parapet, can be fused developing transverse ridges at the posterior part of the platform. The carina is composed of nodes that can be discrete or fused. These elements are characterized by a broad cup-like basal cavity with a narrow groove that runs longitudinally to it and that continues within the basal margin of the free blade. The inner flaring of the basal cavity has a longitudinal development, beginning at the anterior part of the platform, whereas, the outer flaring is restricted anteriorly and medially.

Remarks: The study of SKOMPSKI (1996) is adopted here for the determination of this subspecies, in which, the author characterized it by having two well-developed parapets, mostly the inner one, and by a more posterior beginning of the outer parapet with respect to the inner one. Both parapets reach the posterior margin of the platform and they develop ridges and nodes.

Gnathodus girtyi meischneri Austin & Husri, 1974 (Pl. 2, figs. 7-10)

Selected synonymy:

- *1974 Gnathodus girtyi meischneri AUSTIN & HUSRI, pp. 53-54, pl. 2, figs. 1-3, 6, pl. 9, fig. 3.
- 1982 Gnathodus girtyi meischneri Austin & Husri; Belka, pl. 1, fig. 1, pl. 2, fig. 4.
- 1993 Gnathodus girtyi meischneri AUSTIN & HUSRI; PERRET, p. 334, pl. CV, figs. 28, 35.
- 1996 *Gnathodus girtyi meischneri* AUSTIN & HUSRI; SKOMPSKI, pp. 199-200, pl. 1, figs. 4-7, pl. 2, figs. 1, 2.

Material: The elements are generally well preserved, comprising 12 Pa elements; 1 in VCR/5, 2 in VCR/6A, 4 in VCR/7, 2 in VCR/10, and 3 in VCR/11.

Description: Pa pectiniform carminiscaphate elements are characterized by a large free blade with rounded and discrete denticles and an asymmetric platform composed of two parapets developed to a different degree. The outer parapet is developed as a narrow ridge subparallel to the carina and begins more posteriorly than the inner one. The former can be restricted in some cases to the anterior-medial part of the platform. The inner parapet can be of the same height as the carina and both are higher than the outer parapet. This different development of the parapets produces a more slender and delicate element morphology than in *G. girtyi girtyi*, whose Pa elements are more robust. Transverse ridges are observed in the inner parapet, whereas the outer one usually does not present ornamentation, but in some specimens small and delicate nodes are observed (Pl. 2, fig. 8a). The specimens have a central carina of different size consisting of a row of nodes that can be completely or partially fused. An adcarinal groove occurs between the carina and each parapet. The basal cavity is developed as a broad cup but to a lesser degree than in *G. girtyi girtyi*. The inner flaring of the basal cavity is usually restricted anteriorly in upper/oral view, whereas the outer one develops at the anterior-medial part of the platform.

Remarks: Our specimens are similar to those illustrated in SKOMPSKI (1996), who interpreted *Gnathodus girtyi meischneri* as having an outer parapet smaller and lower than the inner one, and that is usually developed as a small and narrow ridge, parallel to the carina. The outer parapet can be restricted to the middle and anterior part of the platform owing to its marked posterior beginning, and may develop nodes as ornamentation. The inner parapet is as high as the carina, having transversal ridges.

Family Anchignathodontidae CLARK, 1972

Genus Hindeodus REXROAD & FURNISH, 1964

Type species: *Trichonodella imperfecta* REXROAD, 1957

Hindeodus cristula (YOUNGQUIST & MILLER, 1949) (Pl. 2, figs. 15-18)

Selected synonymy:

- *1949 Spathognathodus cristula YOUNGQUIST & MILLER, p. 621, pl. 101, figs. 1-3.
- 1961 Spathognathodus cristula YOUNGQUIST & MILLER; REXROAD & BURTON, pp. 1156, pl. 141, fig. 9.
- 1964 Spathognathodus cristula YOUNGQUIST & MILLER; REXROAD & FURNISH, p. 674, pl. 111, fig. 15.
- 1967 Spathognathodus cristula YOUNGQUIST & MILLER; GLOBENSKY, p. 447, pl. 57, figs. 15-16.
- 1982 Hindeodus cristulus (REXROAD); VON BITTER & PLINT-GEBERL, p. 200, pl. 4, figs. 15-19, pl. 5, fig. 12, pl. 7, fig. 21.
- 1985 *Hindeodus*? cf. *cristulus* (YOUNGQUIST & MILLER); VARKER & SEVASTOPULO, p. 194, pl. 5.2, fig. 20.
- 1987 Hindeodus cristula (YOUNGQUIST & MILLER); VON BITTER & PLINT, pp. 358-359, pl. 2, fig. 9, pl. 3, figs. 11, 15-16.
- 1990 *Hindeodus cristula* (YOUNGQUIST & MILLER); REXROAD & HOROWITZ, pp. 502-504, pl. 1, figs. 21-42.
- 1991 *Hindeodus cristula* (YOUNGQUIST & MILLER); STONE, pp. 12-13, pl. 1, figs. 1-2, 5, 8.
- 1996 *Hindeodus cristulus* (YOUNGQUIST & MILLER); SKOMPSKI, pl. 5, fig. 15.
- 1999 *Hindeodus cristula* (Youngquist & Miller); Somerville, pl. 4, figs. 6-14.
- 1999 *Hindeodus cristula* (YOUNGQUIST & MILLER); SOMERVILLE & SOMERVILLE, pl. 1, figs. 4-6.

PLATE 2

Figs. 7-10.- Gnathodus girtyi meischneri AUSTIN & HUSRI, 1974. Pa elements. 7. VCR/11-9, a. inner-lateral view, b. upper view, 8. VCR/10-8, a. upper view, b. lower view, 9. VCR/11-30, upper view, 10. VCR/7-47, upper view.

Figs. 11-14.– *Gnathodus girtyi* HASS, 1953. 11. VCR/11-12, Pa element, upper view, 12. VCR/10-34, Pa element, upper view, 13. VCR/6a-5, S element, inner view, 14. VCR/6a-8, S element, inner view.

Figs. 15-18.– *Hindeodus cristula* (YOUNGQUIST & MILLER, 1949). Pa elements. 15. VCR/7-9, lateral view, 16. VCR/7-17, lateral view, 17. COR/7-2, lateral view, 18. VCR/11-22, lateral view.

LAMINA 2

Fig. 1.- Lochriea? sp. VCR/5-1, elemento S, a. vista interna, b. vista externa.

Figs. 2-6.- Gnathodus girtyi girtyi HASS, 1953. Elementos Pa. 2.- VCR/10-10, a. vista superior, b. vista inferior, 3. VCR/6a-9, vista superior, 4. VCR/7-8, vista superior, 5. VCR/6a-2, vista superior, 6. VCR/11-7, vista lateral-externa.

Figs. 7-10.- Gnathodus girtyi meischneri AUSTIN & HUSRI, 1974. Elementos Pa. 7. VCR/11-9, a. vista lateral-interna, b. vista superior, 8. VCR/10-8, a. vista superior, b. vista inferior, 9. VCR/11-30, vista superior, 10. VCR/7-47, vista superior.

Figs. 11-14.– Gnathodus girtyi HASS, 1953. 11. VCR/11-12, elemento Pa, vista superior, 12. VCR/10-34, elemento Pa, vista superior, 13. VCR/6a-5, elemento S, vista interna, 14. VCR/6a-8, elemento S, vista interna.

Figs. 15-18.– Hindeodus cristula (YOUNGQUIST & MILLER, 1949). Elementos Pa. 15. VCR/7-9, vista lateral, 16. VCR/7-17, vista lateral, 17. COR/7-2, vista lateral, 18. VCR/11-22, vista lateral.

(Escala gráfica= 100 µm)

Fig. 1.- Lochriea? sp. VCR/5-1, S element, a. inner view, b. outer view.

Figs. 2-6.- Gnathodus girtyi girtyi HASS, 1953. Pa elements. 2. VCR/10-10, a. upper view, b. lower view, 3. VCR/6a-9, upper view, 4. VCR/7-8, upper view, 5. VCR/6a-2, upper view, 6. VCR/11-7, outer-lateral view.

⁽Scale bar= 100 μ m) LÁMINA 2



PLATE II / LÁMINA II

Material: Six well preserved Pa elements recovered in VCR/5 (1), VCR/7 (2), VCR/11 (1), VCR/13 (1) and COR/7 (1).

Description: Only Pa elements have been recovered. These elements are characterized by a robust triangular cusp in lateral view, situated in the most anterior part of the blade. The cusp is higher and wider than the denticles. These decrease and are more inclined to the posterior margin of the element. The denticles are fused throughout most of their length although their apexes tend to be discrete. The posterior margin of the element is rounded to slightly acute. The specimens present a wide, subsymmetric basal cavity that extends from immediately after the cusp to the posterior basal margin, occupying more than two-thirds of the basal margin of the element.

Remarks: The specimens have been ascribed to this species due to the presence of an elongated basal cavity, that begins posteriorly to the cusp and that ends in the posterior edge of the blade, and a robust triangular cusp in an anterior position within the blade.

Family Anchignathodontidae? CLARK, 1972

SWEET (1988) described, as representative of this family, a seximembrate conodont apparatus, which is characterized by the spathognathodontiform Pa carminiscaphate elements, including in this family most of the form species of spathognathodontids. These form species were transferred to the multielement apparatuses of different species of *Hindeodus*.

Subsequently, REXROAD & MERRIL (1996) and REXROAD & VARKER (1992) described two new genera, *Hindeodontoides* and *Synclydognathus* respectively, but suprageneric classification for them was not established. The Pa elements of both genera are spathognathodontiform, and thus, according to the family diagnosis by SWEET (1988), these genera are questionably assigned to the Family Anchignathodontidae, until the family status is elucidated

Genus Hindeodontoides REXROAD & MERRIL, 1996

Type species: *Spathognathodus spiculus* YOUNGQUIST & MILLER, 1949

Hindeodontoides? sp. (Pl. 3, figs. 1a-1b)

Material: A juvenile Pa element in SA/4-1.

Description: Pa pectiniform carminate element of spathognathodid type. The element is a juvenile characterized by three triangular and fused denticles of similar size at the anterior part of the blade, which are fragmented, and several discrete denticles that slightly incline to the posterior margin of the blade. The basal cavity is wide and large, and extends for the threequarters of the basal margin.

Remarks: NORBY (1976) observed differences in the microstructure of *Spathognathodus spiculus* compared with that in *Hindeodus*. This feature was adopted by REXROAD & MERRIL (1996), who also highlighted the occurrence of different basal cavities, and considered that the elements of *Spathognathodus spiculus* should not be included within the multielemental genus *Hindeodus*, and thus, they proposed a new genus, *Hindeodontoides*.

Our specimen is included in the genus *Hindeodontoides* with a question mark, because it has discrete denticles, of which, the first three are of a similar basal size, which is interpreted as having the entire denticles of a similar size. In addition, the basal cavity is present over the entire basal margin of the blade. These features differentiate this element from the Pa element of *Hindeodus*, which is characterized by a robust cusp in the anterior position and a basal cavity developed from behind the cusp up to the posterior margin of the blade.

Genus Synclydognathus REXROAD & VARKER, 1992

Type species: Prioniodus geminus HINDE, 1900

Synclydognathus geminus (HINDE, 1900) (Pl. 3, fig. 10)

Selected synonymy:

*1900 Polygnathus scitulus HINDE, p. 343, pl. 9, figs. 9, 11.

- 1960 Spathognathodus scitulus (HINDE); CLARKE, p. 21, pl. 3, figs. 12-13.
- 1967 Spathognathodus scitulus (HINDE); GLOBENSKY, p. 447, pl. 56, figs. 7, 17, 21.
- 1980 Spathognathodus scitulus (HINDE); METCALFE, pl. 38, fig. 7.

- 1982 Spathognathodus scitulus (HINDE); HIGGINS & VARKER, pp. 164-165, pl. 19, fig. 14.
- 1982 Spathognathodus scitulus (HINDE); VON BITTER & PLINT-GEBERL, p. 200, pl. 6, figs. 1-3.
- 1985 Spathognathodus scitulus (HINDE); BELKA, pl. 15, fig. 2.
- 1987 *Hindeodus? scitulus* (HINDE); VON BITTER & PLINT, p. 359, pl. 4, fig. 1.
- 1991 *Hindeodus? scitulus* (HINDE); STONE, pp. 13-16, pl. 1, figs. 3, 4, 6, 7.
- 1992 Synclydognathus geminus (HINDE); REXROAD & VARKER, p. 168, text-figs. 1-10.
- 1996 Synclydognathus geminus (HINDE); SKOMPSKI, pp. 210-212, pl. 5, figs. 1-11.
- 1997 Synclydognathus geminus (HINDE); DUMOULIN & HARRIS, text-figs. A-D, M, N.
- 1999 Synclydognathus geminus (HINDE); SOMERVILLE, pl. 10, figs. 1-19.
- 1999 Synclydognathus geminus (HINDE); SOMERVILLE & SOMERVILLE, pl. 1, figs. 7-8.

Material: A single Pa element in VCR/11.

Description: Pa spathognathodontiform element of pectiniform carminate type. It presents a robust cusp at an anterior position and a series of denticles, partially fused at their base, that incline posteriorly. The denticles are of a similar size until the third-quarter of the blade where they markedly reduce their size to the posterior margin. The cusp as well as the denticles are longitudinally striated. The element presents markedly convex and concave upper and basal margins, respectively. The asymmetrical basal cavity is situated beneath the second and fourth denticles.

Remarks: The study of REXROAD & VARKER (1992) is adopted here, who proposed this new genus and reconstructed the multielement apparatus from discrete specimens.

Synclydognathus spp. (Pl. 3, figs. 11-15)

Material: The recovered material is well preserved and consists of 8 elements; 1 S element in VCR/6A, 1 S and 1 Pa elements in VCR/7, 3 S elements in VCR/11, and 2 juvenile S elements, one each in SA/2-1 and SA/2-3.

Description:

Pa element (Pl. 3, fig. 11): Pectiniform carminate element with a robust anterior cusp. The denticles are fused except at their apexes; they are well differentia-

ted along its length and begin near the basal cavity or the basal margin. They are inclined posteriorly with a fan-like arrangement. Its size decreases progressively to the posterior margin. The element presents a subrounded basal cavity beneath the second and third denticles and right after the cusp.

S elements: These specimens are ramiform digyrate to alate elements. The specimen VCR/11-4 (Pl. 3, fig. 12) presents four central well-developed denticles that are triangular in shape and which are inclined to the posterior part of the element. The three central denticles are larger than the anterior one, and all of them are fused at their base. The element shows a concave inner part and convex outer one, and the base of the central part is subrounded and well developed. The posterior process is bar-like, large and oval and presents a series of denticles, smaller than those in the central part, which increase their size posteriorly.

The specimen VCR/11-6 (Pl. 3, fig. 13) is a poorly preserved element, which presents a very well-developed lateral process when compared to the posterior one, which is slender and fragmented in our case. Both processes are disposed in different planes. The cusp is triangular and is slightly inclined to the posterior process. The morphologic characteristics of the denticles are not well observed due to fragmentation and abrasion, but they are readily fused. The first lateral denticle is fused to the cusp. The small basal cavity is situated beneath the cusp, within the basal margin.

The specimen VCR/7-3 (Pl. 3, fig. 14) is characterized by a robust, triangular cusp flanked by two bar-like processes, disposed in different planes. The denticles of the posterior process are rounded and discrete, whereas those of the lateral process are fused together and are inclined towards the cusp. The element has a small narrow basal cavity situated beneath the cusp that continues within the process as a narrow groove.

Finally, the specimen VCR/6a-4 (Pl. 3, fig. 15) is a ramiform alate element characterized by two denticulated lateral processes arranged in the same plane. The denticles have a rounded transverse section, are fused, and are inclined towards the cusp. The base of the processes is flattened and a smooth groove extends longitudinally at the base of the denticles. The cusp, which is higher and wider than the denticles, has a subtriangular transverse section owing to the development of a smooth ridge at its inner-central part. The element has a small basal cavity right beneath the cusp.

Remarks: The recovered Pa element is included in the genus *Synclydognathus* because the basal cavity is restricted to the central basal margin of the element and the entire element is not as long as that in the genus *Hindeodus*.

This Pa element differs from the Pa elements in *Synclydognathus geminus* because in the former, the denticles begin slightly above the basal cavity and the length of the element is smaller than in *S. geminus*; in addition, in our material, the denticles show a more fan-like arrangement, increasing their curvature from the cusp to the posterior basal margin.

The S elements are recognized as apatognathids, but they are not similar to the S elements of S. geminus sensu REXROAD & VARKER (1992) (Apatognathus? geminus VARKER, 1967, Apatognathus? cuspidata VARKER, 1967, Apatognathus? chaulioda VARKER, 1967. Apatognathus? petila VARKER, 1967. Apatognathus? scalena VARKER, 1967). Particularly, the specimen VCR/6a-4 (Pl. 3, fig. 15) is similar to Apatognathus? porcata (HINDE, 1900) illustrated by GLOBENSKY (1967, Pl. 56, fig. 24). However, REXROAD & VARKER (1992) included the apatognathodids recovered by GLOBENSKY (1967) within the multielement species Synclydognathus libratus (VARKER, 1967), which, as the former authors noted, is distinguished from S. geminus by one of the S elements of their apparatuses, which in former taxonomy are the discrete elements Apatognathus? libratus and Apatognathus? geminus respectively. Although elements of A.? libratus and our specimen are symmetric in inner lateral view, several morphologic differences are recognized between the element Apatognathus? libratus and our specimen, which is similar to the one figured in GLOBENSKY (1967): (i) the length of the processes in A.? libratus is shorter than in our specimen, (ii) the processes in A.? libratus are straight from their beginning in the basal margin right beneath the cusp whereas in our specimen the processes are slightly curved inwardly at their onethird-part, and (iii) the denticles of the processes as well as those in the central part of the element are of similar size in A.? libratus (uniform denticulation as stated by VARKER, 1967) whereas, in our element, a well-developed cusp is differentiated in the anterior and central part of the element, and the denticles of the processes are clearly smaller than the cusp.

The stratigraphic range of *S. geminus* and *S. libratus*, are based respectively on the stratigraphic range of A.? geminus and A.? libratus in the Yoredale Series (northern England) and in the St. Louis and Maxville Limestones (North America) as documented by REXROAD & VARKER (1992). According to this work, A.? libratus, and thus, S. libratus, does not extend further from the Middle Limestone (Yoredale Series) which corresponds to the lower part of the late Brigantian, whereas A.? geminus (= S. geminus) reaches up to the Little Limestone (Yoredale Series) which is Pendleian in age. The Via Crucis section has been assigned to the Pendleian by CóZAR (2003, 2005) using foraminifera and algae, and thus, is certainly questionable the record of A.? libratus (= S. libratus).

The Pa and S elements of *Synclydognathus* recovered in the Guadiato Area, are recovered in a low number from different horizons and sections, and thus at present, no biological association is recognized which permits to assign the specimens to a single species.

Family Cavusgnathidae AUSTIN & RHODES, 1981

Genus Cavusgnathus HARRIS & HOLLINGSWORTH, 1933

Type species: *Cavusgnathus alta* HARRIS & HOLLINGSWORTH, 1933

Cavusgnathus navicula (HINDE, 1900) (Pl. 3, figs. 2-7)

Selected synonymy:

- *1900 Polygnathus navicula HINDE, p. 342, pl. 9, fig. 5.
- 1961 Cavusgnathus navicula (HINDE); REXROAD & BURTON, pp. 1151-1152; pl. 139, figs. 4-13.
- 1985 Cavusgnathus naviculus (HINDE); HIGGINS, p. 218, pl. 6.1, fig. 3.
- 1985 Cavusgnathus navicula (HINDE); WEYANT & MASSA, p. 89, pl. 1, figs. 24-26.
- 1986 Cavusgnathus naviculus (HINDE); MAPES & REXROAD, pl. 1, figs. 25-39.
- 1996 Cavusgnathus naviculus (HINDE); SKOMPSKI, pl. 2, fig. 6.
- 1999 Cavusgnathus naviculus (HINDE); SOMERVILLE, pl. 1, figs. 4-5.
- 1999 non-platform elements of *Cavusgnathus* sp.; SOMERVILLE, pl. 1, figs. 10-13.
- 1999 Cavusgnathus naviculus (HINDE); SOMERVILLE & SOMERVILLE, pl. 1, fig. 1.

Material: Well preserved material consisting of 12 elements; 3 Pa elements (VCR/6A, VCR/7, VCR/9), 3 Pb elements [VCR/7 (2), VCR/9 (1)], and 6 M elements [VCR/7 (2), VCR/9 (1), VCR/10 (2), SA/4-1 (1)].

Description:

Pa elements: Pectiniform carminiscaphate elements characterized by a well-developed platform and a free blade, two-thirds of which are included within the platform. The free blade can be attached to the platform at the central trough (Pl. 3, fig. 2a) or at the outer parapet (Pl. 3, fig. 3a). The denticles are fused and the posterior denticle of the free blade is larger than the other denticles. The element tends to curve to its outer part. In upper/oral view, the inner parapet begins more anteriorly than the outer one. There is a central, shallow trough that runs longitudinally to the platform. The ornamentation of the platform consists of one or two rows of longitudinal nodes at each side of the central trough (Pl. 3, fig. 3a and Pl. 3, fig. 2a, respectively). In the latter case, the nodes can be fused in pairs forming transverse ridges. The nodes closer to the central trough are larger than those closer to the margins of the platform. In VCR/6a-10 (Pl. 3, fig. 3a) the posterior nodes are fused producing a small longitudinal ridge that reaches the posterior margin of the platform. The upper margin of the platform is slightly convex whereas, in lateral view, its lateral parts are concave (Pl. 3, fig. 2c), due to shallow grooves that run longitudinally from the beginning of the inner and outer parapets to the posterior margin of the platform. The wide asymmetrical basal cavity can be subrounded (Pl. 3, fig. 2b) or lanceolate (Pl. 3, fig. 3b) depending on the development of the platform and, in both cases, it reaches the posterior margin of the platform, where it becomes narrower. A longitudinal groove is observed within the central part of the basal cavity.

Pb elements: The specimens recovered are pectiniform angulate elements (Pl. 3, figs. 4, 5). The anterior process and its denticles are more developed than the posterior process and its denticles. The denticles of both processes are partially fused at their base and have acute anterior and posterior margins. The denticles of the anterior process have a triangular shape whereas those of the posterior process show a more longitudinal development, as well as being more slender than the anterior denticles. The cusp is situated between the two processes and is similar in shape to the denticles of the anterior process. It is double the height of the anterior denticles and at least, three times higher than the denticles of the posterior process, as well as wider than the denticles of both processes. It shows acute anterior and posterior margins as the denticles. There is a basal pit situated immediately beneath the cusp and the recessive basal margin is observed in both processes, although it is more marked in the anterior one.

M elements: The specimens are ramiform dolobrate elements characterized by a broad cusp and anticusp at its anterior part and by a denticulated posterior process. The elements can present three smooth grooves: one at the base of the denticles along the posterior process, another close to the basal margin of the posterior process that can continue within the posterior process of the anticusp, and finally, another one that runs along the anterior margin of the cusp and the anticusp. The posterior margin of the cusp is straight, the one of the anticusp is slightly convex or straight, whereas the basal margin of the posterior process is concave. The cusp is more developed than the denticles of the posterior process, which are fused together (Pl. 3, fig. 7) or are discrete (Pl. 3, fig. 6). If they are fused, they are well-differentiated from their bases. The narrow basal cavity is situated at the angle between the anticusp and the posterior process and it continues to some degree within the posterior margin of the anticusp and the basal margin of the posterior process.

Remarks: The Pa element in *Cavusgnathus navicula* does not show a conspicuous development of the posterior denticle within the free blade, which characterizes *C. unicornis*. It also differs by a more developed central trough, extended longitudinally along the platform, and a more rudimentary or absent axial carina than in *C. unicornis*, in which in addition, the carina occurs in a posterior position.

C. navicula differs from *C. regularis* because the latter is characterized by its compact form and its regular denticulation (VARKER & SEVASTOPULO, 1985) whereas *C. navicula* has a more elongated Pa element, the free blade does not extend within the platform as much as in *C. regularis* and the denticulation is less regular, the denticles decreasing in height towards the anterior part of the free blade (HIGGINS, 1985).

Cavusgnathus cf. navicula (HINDE, 1900) (Pl. 3, fig. 8)

Material: Fragmented material composed of 5 Pa elements, one each in VCR/7, VCR/9, VCR/13, SA/4-1 and COR/7.

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Description: The Pa element is a pectiniform carminiscaphate element. The specimen SA/4-1-1 (Pl. 3, fig. 8) corresponds to a platform in which its fixed blade and posterior margin are fragmented. Due to abrasion the morphological characters observed are smoothened, such as the transversal ridges produced by the fusion of nodes, the longitudinal and central shallow trough, and the flarings of the basal cavity, which have an anterior-medial disposition.

Remarks: The elements are assigned to *C*. cf. *navicula* due to their poor preservation, which does not allow an unquestionable determination.

Family Mestognathidae AUSTIN & RHODES, 1981

Genus Mestognathus BISCHOFF, 1957

Type species: Mestognathus beckmanni BISCHOFF, 1957

Mestognathus bipluti HIGGINS, 1961 (Pl. 3, figs. 9a-9b)

Selected synonymy:

*1961 Mestognathus bipluti HIGGINS, p. 216, pl. 10, figs. 1-2, text-fig. 4.

- 1961 Mestognathus dhuensis n. sp. GLOBENSKY, pp. 442-443, pl. 57, figs. 23-24 [non figs. 21, 22].
- 1970 Mestognathus bipluti HIGGINS; MARKS & WENSINK, pp. 266, pl. 1, figs. 7a-b, 8a-b.
- 1985 Mestognathus bipluti HIGGINS; VARKER & SEVASTOPULO, p. 198, pl. 5.4, figs. 17-18.
- 1987 *Mestognathus bipluti* HIGGINS; VON BITTER & PLINT, pp. 357-358, pl. 4, figs. 4-6, 11-12.
- 1993 *Mestognathus* cf. *bipluti* HIGGINS; PERRET, pp. 347-348, pl. CVI, fig. 33.
- 1996 Mestognathus bipluti HIGGINS; SKOMPSKI, pl. 2, figs. 4-5.
- 1999 *Mestognathus bipluti* HIGGINS; SOMERVILLE, pl. 9, figs. 2, 4-5.
- 1999 non-platform elements of *Mestognathus* spp.; SOMERVILLE, pl. 9, figs. 6-16.
- 1999 *Mestognathus bipluti* HIGGINS; SOMERVILLE & SOMERVILLE, pl. 1, fig. 3.

Material: A well preserved Pa element in SA/4-1.

Description: The specimen corresponds to a pectiniform carminiplanate Pa element. It is characterized by a free blade attached to a broad platform. The blade is fragmented anteriorly and it consists of, at least, 5 fused denticles which are well differentiated from its base, with a triangular apex and the posterior denticle being larger than the others. The inner and outer parapets are developed to a different degree, the former beginning more anteriorly than the latter. The inner

PLATE 3

Fig. 1.- Hindeodontoides? sp. SA/4-1-4, Pa element, a. lateral view, b. upper view.

Figs. 2-7.– *Cavusgnathus navicula* (HINDE, 1900). 2. VCR/7-6, Pa element, a. upper view, b. lower view, c. inner-lateral view, 3. VCR/6a-10, Pa element, a. upper view, b. lower view, 4. VCR/7-18, Pb element, inner view, 5. VCR/7-11, Pb element, outer view, 6. VCR/7-14, M element, lateral view, 7. SA/4-1-2, M element, lateral view.

- Fig. 8.- Cavusgnathus cf. navicula (HINDE, 1900). SA/4-1-1, Pa element, upper-lateral view.
- Fig. 9.- Mestognathus bipluti HIGGINS, 1961. SA/4-1-3, Pa element, a. inner-lateral view, b. lower view.

Fig. 10.- Synclydognathus geminus (HINDE, 1900).VCR/11-18, Pa element, lateral view.

Figs. 11-15.– Synclydognathus spp. 11. VCR/7-33, Pa element, lateral view, 12. VCR/11-4, S element, outer view, 13. VCR/11-6, S element, inner view, 14. VCR/7-3, S element, inner view, 15. VCR/6a-4, S element, inner view.

Fig. 1.- Hindeodontoides? sp. SA/4-1-4, elemento Pa, a. vista lateral, b. vista superior.

Figs. 2-7.– Cavusgnathus navicula (HINDE, 1900). 2. VCR/7-6, elemento Pa, a. vista superior, b. vista inferior, c. Vista lateral-interna, 3. VCR/6a-10, elemento Pa, a. vista superior, b. vista inferior, 4. VCR/7-18, elemento Pb, vista interna, 5. VCR/7-11, elemento Pb, vista externa, 6. VCR/7-14, elemento M, vista lateral, 7. SA/4-1-2, elemento M, vista lateral.

Fig. 8.- Cavusgnathus cf. navicula (HINDE, 1900). SA/4-1-1, elemento Pa, vista superior-lateral.

Fig. 9.- Mestognathus bipluti HIGGINS, 1961. SA/4-1-3, elemento Pa, a. vista lateral-interna, b. vista inferior.

Fig. 10.- Synclydognathus geminus (HINDE, 1900). VCR/11-18, elemento Pa, vista lateral.

Figs. 11-15.– Synclydognathus spp. 11. VCR/7-33, elemento Pa, vista lateral, 12. VCR/11-4, elemento S, vista externa, 13. VCR/11-6, elemento S, vista interna, 14. VCR/7-3, elemento S, vista interna, 15. VCR/6a-4, elemento S, vista interna.

(Escala gráfica= 100 µm).

⁽Scale bar= 100 μm). LÁMINA 3

PLATE III / LÁMINA III



parapet is curved outwards at its anterior part and a partly fragmented denticle is still preserved. A carina formed by a row of nodes, partially to completely fused, is developed longitudinally to the platform. The carina begins at the anterior part of the inner platform and it is flanked by an adcarinal groove between the carina and the inner platform, and by a trough between the carina and the free blade that continues within the outer platform as an adcarinal groove. The ornamentation of the inner platform consists of a row of nodes parallel to the inner margin of the platform, which increase in size towards the posterior margin. The outer platform is characterized by a series of transverse ridges that decrease their length towards the posterior margin. The small basal pit is restricted to the anterior part of the basal margin, which continues anteriorly as a narrow groove. The recessive basal margin has a lanceolate shape, narrowing to the posterior margin. The margins of the recessive basal margin are robust, producing at the posterior part a longitudinal pseudo-keel.

Remarks: VARKER & SEVASTOPULO (1985) noted that the main difference between *Mestognathus bipluti* and *M. beckmanni* is the presence in the former of two denticulated parapets. Another important feature to take into consideration is that in *M. beckmanni* the anterior part of the inner parapet and the free blade do not diverge as much as in *M. bipluti*. In addition, PERRET (1993) considered as an important feature, the pseudo-keel present at the posterior basal margin of *M. bipluti*, due to the strengthening of the borders of the recessive basal margin.

BIOSTRATIGRAPHY

The stratigraphic ranges of the most important taxa recovered in our sections are shown in figure 3 and compared to those of ZIEGLER *et al.*, 1974; SANDBERG & GUTSCHICK, 1984; VARKER & SEVASTOPULO, 1985; HIGGINS, 1985; MAPES & REXROAD, 1986; SWEET, 1988; REXROAD & VARKER, 1992; PERRET, 1993; PERRET & WEYANT, 1994; CHAUFFE & NICHOLS, 1995; SKOMPSKI, 1996 and SOMERVILLE, 1999. In addition, some of the authors, e.g. VARKER & SEVASTOPULO (1985), based some of the distribution of the species on previous authors (RHODES *et al.*, 1969; AUSTIN, 1973; METCALFE, 1981; JOHNSTON & HIGGINS, 1981; HIGGINS & VARKER, 1982). SWEET (1988) characterized the range of *Idioprioniodus healdi* from the middle part of the Meramecian (Viséan) to the late Namurian. CHAUFFE & NICHOLS (1995) acknowledged that this species is recorded in North America from the late Osagean (early Viséan) to the late Chesterian (Fig. 3). SOMERVILLE (1999) established its stratigraphical range in the British Isles from the *G. bilineatus* to the *G. b. bollandensis* zones (Asbian to Arnsbergian).

Although HIGGINS (1985) considered the range of Kmacrodentata from the late Brigantian (Gnathodus girtyi collinsoni Zone) to the upper part of the Pendleian, SOMERVILLE (1999) documented that it already occurs in the Early Brigantian (upper part of the G. bilineatus Zone). In the case of K. tenuis/complectens, SKOMPSKI (1996) considered that K. tenuis is a characteristic taxon from the upper part of the Brigantian to the Arnsbergian (Serpukhovian) in England. This author also noted that this species has the same stratigraphical range in the Lublin Basin, from the Lochriea nodosa Zone (Brigantian) to the Gnathodus bollandensis Zone (Arnsbergian). MAPES & REXROAD (1986) recovered specimens of Kladognathus complectens from the Imo Formation, Arkansas, which is late Chesterian in age.

The species Gnathodus girtyi shows a long stratigraphical range [early Viséan to late Namurian, SWEET (1988), or from the Gnathodus bilineatus-Paragnathodus commutatus Zone to the Paragnathodus nodosus-Gnathodus bilineatus Zone, PERRET & WEYANT (1994)]. As a result of this long stratigraphic range, as noted by SKOMPSKI (1996), it is of greater stratigraphical value to identify the specimens at a subspecies category. VARKER & SEVASTOPULO (1985) mentioned the first occurrence of the subspecies G. girtyi girtvi in the British Isles at the base of the Gnathodus bilineatus Zone, (METCALFE, 1981) (Asbian), together with the occurrence of G. bilineatus. However, VARKER & SEVASTOPULO (1985) acknowledged that this subspecies can appear earlier, below the upper boundary of the Lochriea commutata Zone (METCALFE, 1981) (Arundian to early Asbian). HIGGINS (1985) considered its last occurrence at the Gnathodus bilineatus bollandensis Zone (Arnsbergian). SKOMPSKI (1996) recorded specimens of G. girtyi girtyi from upper Viséan rocks (Calcareous complexes A2, A3 and probably A1) up to the G Limestone Band, which was included in the Gnathodus bollandensis Zone.



Figure 3.– Foraminiferal (MAMET, 1974, CONIL *et al.*, 1991) and conodont zonal schemes (British Isles and Ireland: VARKER & SEVASTOPULO, 1985 and HIGGINS, 1985; Poland: BELKA, 1985 and SKOMPSKI, 1996; Pyrenees: PERRET & WEYANT, 1994) and stratigraphic ranges for the conodont species recorded in the Guadiato Area as proposed by different authors (SWEET, 1988; SOMERVILLE, 1999; SKOMPSKI, 1996; VARKER & SEVASTOPULO, 1985; HIGGINS, 1985; PERRET & WEYANT, 1994; REXROAD & VARKER, 1992). *G. = Gnathodus, G. g. = Gnathodus girtyi, P. = Paragnathodus, L. = Lochriea.*

Figura 3.– Biozonas de foraminíferos (MAMET, 1974, CONIL et al., 1991) y conodontos (Islas Británicas e Irlanda: VARKER & SEVASTOPULO, 1985 y HIGGINS, 1985; Polonia: BELKA, 1985 y SKOMPSKI, 1996; Pirineos: PERRET & WEYANT, 1994) y distribuciones estratigráficas de las especies de conodontos registradas en el Área del Guadiato según diversos autores (SWEET, 1988; SOMERVILLE, 1999; SKOMPSKI, 1996; VARKER & SEVASTOPULO, 1985; HIGGINS, 1985; PERRET & WEYANT, 1994; REXROAD & VARKER, 1992). G. = Gnathodus, G. g. = Gnathodus girtyi, P. = Paragnathodus, L. = Lochriea.

PERRET (1993) considered *G. girtyi meischneri* as one of the characteristic taxa from the *Paragnathodus nodosus-Gnathodus bilineatus* Zone. SKOMPSKI (1996) mentioned that in the Lublin Basin this subspecies also occurred in the upper part of the *L. nodosa* Zone, appearing in the A3 Limestone Complex, and extended its stratigraphical range to the *Gnathodus bilineatus bollandensis* Zone, where it is dominant (Fig. 3). The author considered that in Ireland, the first appearance of this subspecies is in the late Viséan, at the *G.* (*=Lochriea*) *nodosus* and *G. girtyi collinsoni* zones, although in the latter, *G. girtyi meischneri* is associated with *G. girtyi soniae*, which in the British Pennine region, is exclusively recorded in lower Namurian rocks.

Hindeodus cristula is a species with a long stratigraphic range. SWEET (1988) recognized it through the Chesterian in North America. *Hindeodus*? cf. cristulus extends from the Courceyan (*Pseudopolygnathus multistriatus* Zone) to the late Brigantian (*G. girtyi collinsoni* Zone), although VARKER & SEVASTOPULO (1985) did not precisely established its upper limit.

REXROAD & VARKER (1992) proposed the genus Synclydognathus, and documented that the stratigraphical range of the species Synclydognathus geminus in the Yoredale Series is early Brigantian (Gayle Limestone) to the lower part of the Namurian (Little Limestone). SKOMPSKI (1996) recorded this species from the Lochriea nodosa Zone (Brigantian) to the G. bollandensis Zone (Serpukhovian, Namurian A). In the British Isles, Spathognathodus scitulus and several species of apatognathids, which belong to the multielement reconstruction of the apparatus of Synclydognathus geminus, have been recognized from Asbian rocks (VARKER & SEVASTOPULO, 1985) to Pendleian rocks, Kladognathus-G. girtyi simplex Zone, (HIGGINS, 1985) from Northern England. In addition, in North America Hindeodus (=Spathognathodus) scitulus is recorded from the Osagean to the middle Chesterian (SWEET, 1988).

Cavusgnathus navicula shows a stratigraphical range from slightly above the base of the *C. naviculus* Zone (middle part of the Chesterian), up to the *Rhachistognathus muricatus* Zone (upper part of the Chesterian) in North America as considered by SWEET (1988). In the British Isles (VARKER & SEVASTOPULO, 1985; HIGGINS, 1985), it is present from the *G. girtyi collinsoni* Zone (latest Brigantian) to the *G. bilineatus bollandensis* Zone (Arnsbergian), whereas in Ireland it has been recorded since the *Gnathodus bilineatus* Zone (SOMERVILLE, 1999; SOMERVILLE & SOMERVILLE, 1999). SKOMPSKI (1996) noted that this species occurs in the Lublin Basin in the upper part of the *L. nodosa* Zone (A3 Limestone band), up to the *G. bollandensis* Zone (Namurian A).

VARKER & SEVASTOPULO (1985) considered that *Mestognathus bipluti* extends from the *L. mononodosa* and *G. girtyi collinsoni* zones, with its last occurrence (HIGGINS, 1985) in the upper boundary of the *Kladognathus-G. girtyi simplex* Zone (Pendleian). In the Lublin Basin *M. bipluti* (SKOMPSKI, 1996), occurs from the *Lochriea nodosa* Zone (late Brigantian) to the *G. bollandensis* Zone (Namurian A). However, JONES & SOMERVILLE (1996) and SOMERVILLE (1999) considered that the incoming of this species in Ireland is in the upper part of the *G. bilineatus* Zone (early Brigantian), much earlier than in Britain or Poland (Fig. 3).

In the zonal scheme of HIGGINS (1985) for the Silesian (Serpukhovian and younger) in the British Isles and Ireland, the Kladognathus-G. girtyi simplex Zone is restricted to the Pendleian and is characterized by several taxa which occur in previous zones, such as Gnathodus bilineatus bilineatus, Gnathodus girtyi girtyi, G. girtyi intermedius, Lochriea commutata, Lochriea nodosa, L. mononodosa and Kladognathus macrodentata. Its lower boundary is marked by the incoming of G. girtyi simplex and its upper limit by the first appearance of G. bilineatus bollandensis, which is the index taxon of the successive zone, and by the last occurrences of Gnathodus homopunctatus, Kladognathus macrodentata, Neoprioniodus peracutus (included within the multielemental apparatus of Kladognathus tenuis) and of the genus Mestognathus. HIGGINS (1985) acknowledged that in Northern England (Yoredale facies) the conodont assemblages correspond to shallow-water faunas, which are characterized by the presence of several apatognathodids (Apatognathus scalenus, A. cuspidatus and A. petilus, included in the multielement species Synclydognathus geminus) within the otherwise, common Pendleian assemblages. The presence of these species implies a slight difference in the assemblages composition to those to the south of Northern England, which correspond to basinal environments.

The Kladognathus-G. girtyi simplex Zone of HIGGINS (1985) corresponds to the Lochriea cruciformis Zone proposed by SKOMPSKI (1996) for the Lublin Basin, Poland. The lower boundary of the latter is marked by the first appearance of the index taxon, Lochriea cruciformis, and the upper boundary, by the incoming of G. bollandensis, which is the index taxon of the succeeding zone. The L. cruciformis Zone is restricted to the lower and middle part of the Namurian A. It is characterized by numerous species of Lochriea and by several subspecies of G. girtyi, which are present from the previous zone (the L. nodosa Zone), such as L. nodosa, L. mononodosa, L. commutata, G. girtyi girtyi, G. girtyi meischneri and G. bilineatus, and at the upper part of the zone by new appearance of Lochriea species (L. ziegleri, L. senckenbergica) and G. girtyi intermedius. Cavusgnathus navicula, Kladognathus tenuis and Synclydognathus geminus are also recognized.

The Paragnathodus nodosus-Gnathodus bilineatus Zone of PERRET (1993) and PERRET & WEYANT (1994), defined for the Pyrenees, comprises the uppermost Viséan to the Serpukhovian. It is defined by the simultaneous appearance of Paragnathodus nodosus, P. mononodosus and P. cruciformis. P. multinodosus and Mestognathus, the latter is noted by the authors as being a rare species in the Pyrenees and that appears lately there than in other regions, are also recorded in the this zone, but higher in the zone, and their last occurrence being at its upper limit. The characteristic species of this zone, apart from the previously mentioned taxa, are G. girtyi girtyi, G. girtyi intermedius, G. girtyi soniae and G. girtyi meischneri, which are also last recorded at the upper boundary of the zone, and Pseudognathodus homopunctatus and Vogelgnathus *campbelli*, that are present from the previous zone. The Paragnathodus nodosus-G. bilineatus Zone corresponds with the L. mononodosa, G. girtyi collinsoni, Kladognathus-G. girtyi simplex and G. bilineatus bollandensis zones of HIGGINS (1985) and with the L. nodosa, L. cruciformis and G. bollandensis Zones recognized by SKOMPSKI (1996).

In our sections no index taxa of each of the described zones are present (Fig. 3), and none of the San Antonio and La Cornuda sections have produced a sufficient number of recovered specimens. In the case of the Via Crucis section the number of specimens and species is representative enough, and it can be generally ascribed to the *Kladognathus-G. girtyi simplex* Zone of HIGGINS (1985), the L. cruciformis Zone of SKOMPSKI (1996) or to the Pendleian part of the Paragnathodus nodosus-Gnathodus bilineatus Zone of PERRET (1993). In figure 3 is highlighted the concurrent range of the species and subspecies present in our sections, which allowed us to ratify a Pendleian age for Via Crucis section. Unfortunately, the age of the San Antonio and La Cornuda sections cannot be determined with conodonts due to the scarce number of specimens recovered. The studies undertaken by Cózar (1998, 2003, 2005), with foraminifera and calcareous algae, assigned the sections of San Antonio, La Cornuda and Via Crucis to the early Serpukhovian (Pendleian to possibly Arnsbergian in the uppermost beds of the sucession). Moreover, Cózar (1998) recognized two foraminiferal zones of MAMET (1974), Zone 17, which is present throughout most parts of the sections and Zone 18, which is recognized, in some cases, at the top of the sections. The coral assemblages of San Antonio (RAMÍREZ-VIU, 1994) and La Cornuda (GÓMEZ-HERGUEDAS, 2003; GÓMEZ-HERGUEDAS & RODRÍGUEZ, this volume) also suggest a Serpukhovian age by the presence of small lithostrotionids, axophyllids, *Melanophyllum* and mostly endemic aulophyllids.

PALAEOCOLOGICAL REMARKS

The Via Crucis section has the most diverse conodont assemblage from the three sections studied, with a predominance of gnathodids, becoming enriched to the top of the section in kladognathids, cavusgnathids and synclydognathids. As noted by DRUCE (1973), AUSTIN (1976), VON BITTER (1972, 1976) SANDBERG & GUTSCHIK (1984), PLINT & VON BITTER (1986) and BOOGARD (1992), gnathodids were nektobenthic dwellers, with a low tolerance to high or variable salinity that commonly occur in open-shelf deep-water environments. This environment agrees with their record throughout the section. However, the relatively common presence of kladognathids and specially of cavusgnathids and synclydognathids towards the top of the sequence in the Via Crucis section, suggests shallower conditions in the slope up to shelf conditions, which are reached at the top of the section. Cavusgnathus and Synclydognathus inhabited marginal restricted shelf environments characterized by shallow-water nearshore conditions that involved a wide range in salinity and energy (MERRILL, 1973; VON BITTER, 1976; MERRILL & VON BITTER, 1976; REXROAD, 1981; SWEET, 1988; REXROAD & HOROWITZ, 1990; DAVIES et al., 1994). This shallow-water assemblage is also recognized in the San Antonio section (SA/4-1), where elements of Cavusgnathus navicula, Cavusgnathus cf. navicula and Mestognathus bipluti are recorded. VON BITTER et al. (1986) considered the latter taxon as inhabitant of marginal nearshore environments and tolerant to fluctuating salinity and energy conditions. Hindeodontoides? sp., which has also been recorded in SA/4-1-1, shares the same ecological preferences with the former taxa (REXROAD & MERRILL, 1996). The latter group of taxa are the sole components of the conodont assemblage in this bed at San Antonio.

The conodont assemblages recovered from San Antonio and Via Crucis sections support the microfacies analysis and environmental interpretation exposed in Cózar (1998) and Cózar & Rodríguez (2004), in which a slope facies are recognized throughout most of the sequence with a transitional shallowing-upward trend, until shelf environments are reached at their tops. However, the high values recovered of certain taxa, e.g. Kladognathus, Cavusgnathus and Synclydognathus and the occurrence of Mestognathus point out that, although the sedimentation took place in a submarine slope, the environment was not a basinal facies. This is also supported if we compare our conodont assemblages with those from the Cantabrian Mountains and the Pyrenees which are readily distinct. The latter are slightly less diverse than the fauna of shallow-water high-energy and basin environments (HIGGINS, 1981) and are characterized by the dominance of gnathodids, particularly Gnathodus bilineatus, and lochrieids, e.g. L. commutata, L. cruciformis, L. mononodosa and L. multinodosa, taxa that are common in open marine environments with uniform ecological conditions and greater depth of water (HIGGINS, 1981; HIGGINS & WAGNER-GENTIS, 1982). In the Guadiato Area assemblages it is noteworthy the absence of those taxa, but other taxa commonly represented in our assemblages such as G. girtyi and Cavusgnathus, are rare in the Cantabrian Zone and the Pyrenees. During the Mississippian, the Cantabrian Zone was interpreted as a submarine slope with a considerable depth of water, that HIGGINS (1981) interpreted as a pelagic platform, whereas the Pyrenees are characterized by outer platform or slope deposits (PERRET & WEYANT, 1994). These deep-water environments are in both cases in agreement with the deepwater conodont fauna recorded (HIGGINS, 1974; HIGGINS & WAGNER-GENTIS, 1982; PERRET, 1993; PERRET & WEYANT, 1994; GARCÍA-LÓPEZ & SANZ-LÓPEZ, 2002; BLANCO-FERRERA et al., 2005).

Our conodont faunas are more similar to those of the Yoredale Series in northern England (HIGGINS, 1981; HIGGINS,1985), which are characterized by the occurrence of gnathodids (with *G. girtyi* and *G. bilineatus* as dominant taxa), cavusgnathids, *Mestognathus* and, particularly, by *Synclydognathus*, typifying a shallow-water fauna from shelf environments. SOMERVILLE (2005; written communication) noted that the unpublished conodont assemblages recorded by DEAN (1987) from Brigantian and Namurian limestones of the Midland Valley of Scotland are also similar to that recorded in the Guadiato Area. SOMERVILLE (1999) documented that a similar suite of conodonts recorded in the Midland Valley also occurs in Brigantian shelf limestones in Cookstown and Kingscourt (Ireland). This suite is characterized by the occurrence of Idioprioniodus healdi, Cavusgnathus naviculus, Kladognathus tenuis/complectens, Synclydognathus geminus, Gnathodus girtyi and Gnathodus homopunctatus (the so-called "Gnathodus symmutatus" fauna of DEAN. 1987), as well as, Gnathodus bilineatus, Lochriea nodosa, L. commutata, Hindeodus cristula and Vogelgnathus campbelli. Then, the Serpukhovian conodont fauna from the Guadiato Area can be compared with the fauna recorded by SOMERVILLE (1999). Similarities with Polish faunas are also recognized. The Lublin-Lvov area corresponds to a shallow, broad embayment with normal salinity, connected with open sea but at the same time, protected from important sea activity during the Mississippian (SKOMPSKI, 1996). SKOMPSKI (1996) documented that conodonts were recovered solely from carbonate facies of more restricted or brackish environments whereas the shaly facies, which were barren for conodonts, were ascribed to proximal, nearshore areas. As in the Guadiato Area, the conodont assemblages from the Lublin Basin, show a mixed ecological composition where typical offshore taxa like Gnathodus girtvi, Lochriea or Hindeodus (SKOMPSKI, 1996), occur together with taxa that inhabited more nearshore environments with higher energy and variable salinity, such as Cavusgnathus, Mestognathus, and Synclydognathus. SKOMPSKI (1996) also highlighted the abundance of Synclydognathus elements as well as the similarity between the conodont faunas from the Lublin Carboniferous Basin with those from the Yoredale Series.

CONCLUSIONS

Three stratigraphic sections, San Antonio, La Cornuda and Via Crucis, from the Mississippian of the Guadiato Area, southwest Spain, were sampled for conodonts to undertake a detailed analysis with this fossil group. From the 30 samples only thirteen were productive in conodonts, and from these, only three samples yielded high values of abundance and diversity.

Fifteen taxa within nine genera have been descri-

bed. Despite the absence of typical index taxa of the zonal schemes of previous authors, the concurrent range assemblage (Fig. 3) allowed us to ascribe the Via Crucis section to the *Kladognathus-Gnathodus girtyi simplex* Zone of HIGGINS (1985), to the *Lochriea cruciformis* Zone of SKOMPSKI (1996) and to the upper part of the *Paragnathodus nodosus-Gnathodus biline-atus* Zone of PERRET & WEYANT (1994), and to determinate a Pendleian age for the section. This Pendleian age agrees with the foraminiferal zones assigned to the same section (CóZAR, 2003).

The conodont assemblages suggest a proximal slope environment due to the occurrence of a Gnathodus-dominated fauna occurring together with typical nearshore fauna, such as Kladognathus and specially Cavusgnathus. Mestognathus and Synclydognathus. In addition, the vertical variation of the taxa throughout the San Antonio and Via Crucis sections is consistent with the shallowing-upward sequence recognized by Cózar (1998, 2005) and CÓZAR & RODRÍGUEZ (1999b, 2004). The conodont assemblages from the Guadiato Area differ from those from the Cantabrian Zone and the Pyrenees in that the latter are more deep-water assemblages, typically occurring in basin environments. In contrast, a more mixed ecological composition is recorded in the Guadiato Area, with taxa from shallow and deepwater environments and with different tolerances to variable ecological conditions. The Guadiato conodont assemblages of Pendleian age are similar to those recorded from northern England (HIGGINS, 1985), the Scottish Midland Valley (DEAN, 1987), northeastern (SOMERVILLE, 1999; SOMERVILLE Ireland & SOMERVILLE, 1999) and from the Lublin Carboniferous Basin (SKOMPSKI, 1996).

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