Conodont faunas across the mid-Carboniferous boundary from the Barcaliente Formation at La Lastra (Palentian Zone, Cantabrian Mountains, northwest Spain); geological setting, sedimentological characters and faunal descriptions

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Two different tectono-stratigraphic domains are recognised in the Cantabrian Mountains, Asturian-Leonese (Cantabrian Zone) and Palentian (Palentian Zone). The area under investigation belongs to the southern part of the Palentian Domain and attention is focused on the Upper Viséan to lowermost Bashkirian limestones at the village of La Lastra in northern Palencia. A new geological map of the Palentian Zone is accompanied by a more detailed map centred on La Lastra. The Barcaliente Limestone Formation (Serpukhovian to lowermost Bashkirian) occurs in the overturned limb of a recumbent anticline which constitutes the head of a south-verging major thrust unit, the Carrionas Thrust Sheet (Palentian Zone). It shows here a shallowing trend in the Serpukhovian. After a transgressive phase near the mid-Carboniferous boundary, the lower Bashkirian again shows shallowing culminating in a palaeokarst at the base of the overlying Perapertú Formation. The conodont faunas present a continuous succession across the Mississippian-Pennsylvanian boundary, most similar to the ones found at Aksu (Hissar Range, Uzbekistan).

Contents

Introduction and overall geological setting (RHW & CFWP)

The present paper forms part of an ongoing project to examine in depth the stratigraphy and structure of the Palentian Domain in northern Palencia, in the southeastern

part of the Cantabrian Mountains, northwest Spain (Wagner & Winkler Prins, research in progress). A major south-verging structure, the Carrionas Thrust Sheet, with about 4,000 m of upper Silurian to Lower Moscovian (Pennsylvanian) strata, is involved. The head of this thrust sheet, a recumbent anticline, occurs in a narrow strip which contains a condensed development of the Barcaliente Limestone Formation (60 m as against up to 250 m elsewhere in the Cantabrian Mountains). This is the second paper in a series of systematic studies on Carboniferous conodont faunas from the Palentian Domain, in this case involving Viséan, Serpukhovian and lowermost Bashkirian strata in a continuous succession of limestones (Genicera and Barcaliente formations) exposed at the village of La Lastra (Figs. 1, 2). The first paper (Nemyrovska, 2005) dealt with Late Viséan-Early Serpukhovian conodont faunas from a locality in the Carrión river valley, north of the village of Triollo, corresponding to a different part of the Carrionas Thrust Sheet, which has been emplaced across the head of the thrust sheet at La Lastra, with a significant amount of tectonic shortening. Indeed, it shows a rather different development of Mississippian and lower Pennsylvanian limestones (Wagner and Winkler Prins, research in progress).

Two different, major tectono-stratigraphic areas are recognised in the Palaeozoic of the Cantabrian Mountains: the Cantabrian Zone of Lotze (1945) and the Palentian Zone of Martínez-García (1981). Within the Cantabrian Zone two main areas may be distinguished: a relatively small one in the Sierra del Brezo of northern Palencia which is continued westwards in the Esla Nappe and the adjacent region of northeastern León; and a large area embracing a large part of northern León, most of the Asturias and southwestern Cantabria, including the Picos de Europa. The Palentian Zone is mainly characterised by an uninterrupted, relatively thin Devonian succession and major compressional tectonic deformation in Early Moscovian (Late Langsettian) times. Thrust movements were south-directed. The Sierra del Brezo-Esla Nappe area shows north-directed thrusting which has also been dated as Late Langsettian. On the contrary, the first compressional tectonic movements in most of the Cantabrian Zone, including the Picos de Europa, are Late Moscovian, mid-Asturian, in age. Both the Sierra del Brezo-Esla Nappe area and the larger area of the Cantabrian
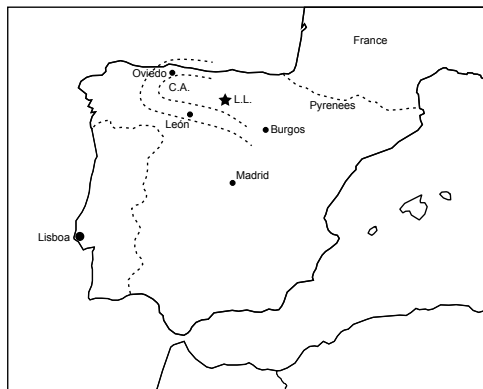
Fig. 1. General position of the Cantabric-Asturian arcuate fold belt (C.A.) in the Iberian Peninsula. Asterisk shows the location of La Lastra village (L.L.).

Fig. 2. General geological map of the southeastern part of the Cantabric-Asturian arcuate foldbelt, showing the total area of the Palentian Domain (Zone) delimited by the Carrionas Thrust Front (and Ruesga Fault) to the south and the Picos Thrust Fault to the north. Uppermost Pennsylvanian, Permian and Mesozoic strata are shown together as post-tectonic, unconformable cover to the northeast, east and south. La Lastra village (LL) is situated in the lower centre, SL is Peña Santa Lucía and LF is the León fault Complex.
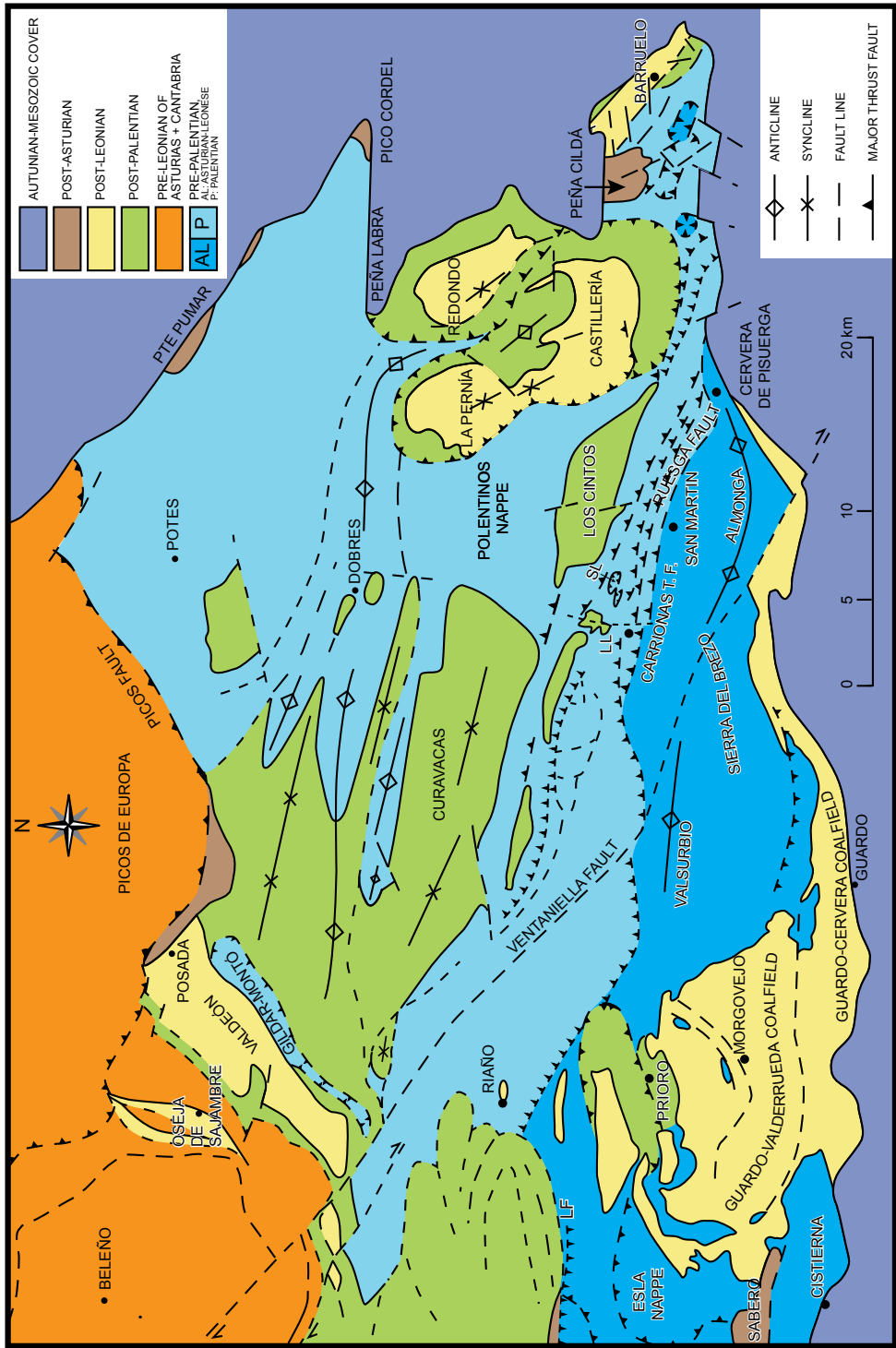
Fig. 3. Detailed geological map of the area around La Lastra. Scale 1:25,000; for legend, see opposite.

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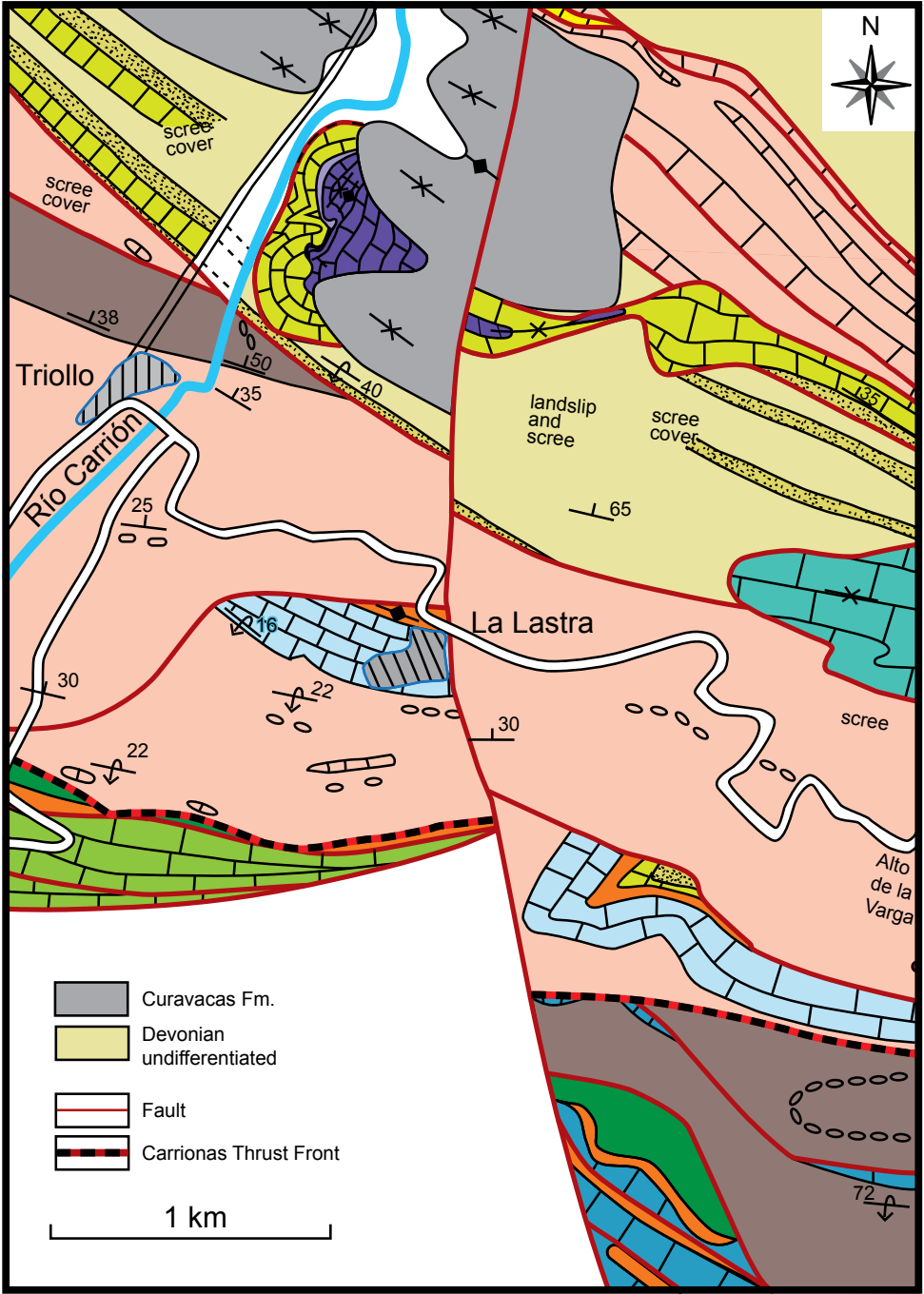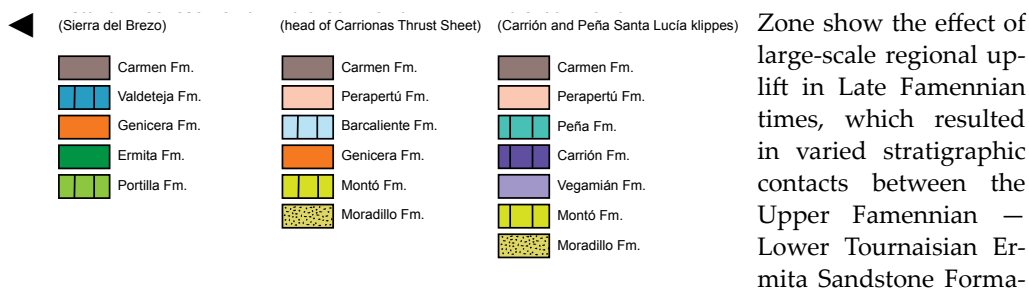| (Sierra del Brezo)	(head of Carrionas Thrust Sheet)	(Carrión and Peña Santa Lucía klippes)
Carmen Fm.	Carmen Fm.	Carmen Fm.
Valdeteja Fm.	Perapertú Fm.	Perapertú Fm.
Genicera Fm.	Barcaliente Fm.	Peña Fm.
Ermita Fm.	Genicera Fm.	Carrión Fm.
Portilla Fm.	Montó Fm.	Vegamián Fm.
	Moradillo Fm.	Montó Fm.
		Moradillo Fm.

Zone show the effect of large-scale regional uplift in Late Famennian times, which resulted in varied stratigraphic contacts between the Upper Famennian — Lower Tournaisian Ermita Sandstone Formation, and underlying Devonian, Silurian and Ordovician strata. It is quite apparent that the arcuate shape of the entire Sierra del Brezo to Picos de Europa (via northern León and central Asturias), leading to opposed vergencies, is a result of high-level compressional tectonic deformation and that a more linear configuration existed previously, with Late Famennian uplift being centred in the east (present day Picos de Europa). Basement is exposed nowhere and the compressional tectonic structures, thrust slices and small nappes, producing the progressively tightening arcuate fold belt, are only indirectly linked to the basement from which they are separated by large scale decollement planes. The exact role of the underlying basement is not determined, but must have involved substantial vertical movements, possibly in conjunction with strike-slip. Geophysical investigations have only confirmed the more or less independent role of basement and sedimentary cover rocks, tens of thousands of metres thick (Pérez-Estaún *et al.*, 1988, 1994).

Tectonic shortening is most severe where the Cantabric-Asturian arcuate fold belt (Fig. 1) has tightened most completely, with the strikes turning around in 180°, with opposed vergencies. This happened in the southern part of the Cantabrian Mountains (Fig. 2) and is the most complicated part of the Palaeozoic structures.

Recent research by RHW and CFWP has focused on the intricate structure of the southern part of the Palentian Zone where it is in fault contact with the Cantabrian Zone in the Sierra del Brezo. North-verging thrust slices of the Sierra del Brezo, in sedimentary rocks of Asturian-Leonese facies, are overthrust by Palentian rocks of largely the same ages, but showing marked differences in facies and stratigraphic development which denote different palaeogeographic positions. These differences were most apparent for the Devonian, as was recognised by the distinction between the Asturian-Leonese and Palentian domains by Brouwer (1964). The fault line separating these two domains was interpreted as a basement fracture, the so-called León Line by de Sitter (1965), as a strike-slip fault by Heward & Reading (1980), and a major overthrust from south to north by Frankenfeld (1984) and Martínez-García (2006). More detailed mapping by the present writers has shown that the line of separation is indeed a massive overthrust, but south-directed, this being the exact opposite to the direction advocated by Frankenfeld who relied on a published map (Savage *in* Savage & Boschma, 1980) which proved rather inaccurate. Recent mapping allowed the recognition of the anticlinal head of a 4 km thick thrust sheet, presumably occupying the entire Palentian Domain in northern Palencia and southern Cantabria (Carrionas Thrust Sheet as mentioned in Wagner, 2009). Decollement planes within this thrust sheet moved different parts of the *c.* 4,000 m thick succession of uppermost Silurian, Devonian, Mississippian and Lower Pennsylvanian strata (up to and including Lower Moscovian) on top of one
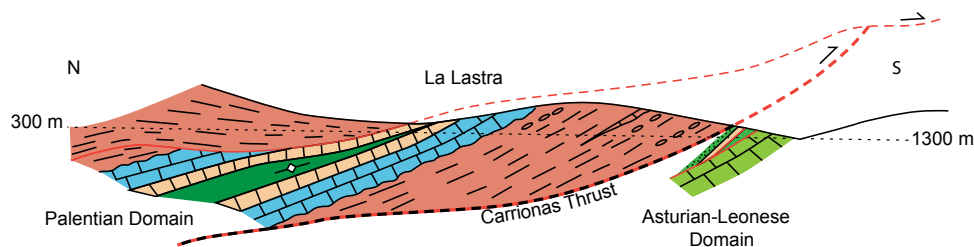
Fig. 4. Cross section at La Lastra showing the recumbent anticline at the head of the Carrionas Thrust Sheet and the shear plane developed in Perapertú shales in the normal flank of this anticline, provoking a shallow thrust sheet by which part of the normal flank moved across the overturned flank and beyond, covering the Carrionas Thrust Front. Direction of thrusting: southwards. For legend, see Figure 3.

another, always with south-directed thrust movements. The Carrionas Thrust Front is well-exposed between south of the village of La Lastra and north of that of San Martín de los Herreros (Fig. 2). West of La Lastra a shallow dipping thrust in the normal flank of the anticlinal head moves southwards to override the Carrionas Thrust Front (Fig. 3), whilst east of San Martín a steeply dipping fault, the Ruesga Fault of Kanis (1956), interferes with the shallowly dipping Carrionas Thrust Front, continuing its trace eastwards (Kullmann *et al.*, 2007).

Substantial shortening is associated with the Carrionas Thrust Front. This is apparent, most clearly, in the presence of the Serpukhovian-lowermost Bashkirian Barcaliente Limestone (60 m thick) at La Lastra village and in outcrops at several kilometres southeast and east of La Lastra, after tectonic displacement by a steeply dipping north-south fault (Figs 3, 4). The same Barcaliente Limestone is largely (almost entirely) eliminated by local uplift of Bashkirian age in the northernmost thrust slices of the Sierra del Brezo (representing a different palaeogeographic area). On the other hand, at La Lastra, the Barcaliente Limestone is overlain, disconformably, by uppermost Bashkirian-Lower Moscovian mudstones of the Perapertú Formation. An erosional contact with hollows of up to 5 m depth (washed-out palaeokarst?) separates these two formations, thus showing substantial uplift leading to the loss of almost the entire Bashkirian record. This is in marked contrast with the northern part of the Sierra del Brezo, where the Bashkirian-age Valdeteja Limestone Formation is found intercalated between basal Barcaliente (or top Genicera Formation where the pre-Valdeteja uplift removed the Barcaliente Formation altogether) and a Lower Moscovian turbidite succession (Carmen Formation). The Valdeteja Limestone of the Sierra del Brezo has been dated as mid-Bashkirian Tashastinsky Horizon in its top part (Villa *in* Wagner & Winkler Prins, 2000, p. 396). These differences (see Fig. 5) suffice to show that the Carrionas Thrust Front marks the contact between two rather different palaeogeographic areas, in addition to the opposed vergencies at this very important tectonic contact, arguably the most important one in the Cantabrian Mountains.

Within the Palentian Zone, the various decollement thrusts produced a succession of thrust slices and quite spectacular nappe structures (indeed, the first to be described as such in the Cantabrian Mountains; Wagner, 1955, 1971) (Wagner and Winkler Prins, research in progress). A small nappe structure at *c.* 1 km north of La Lastra village, in Peña Santa Lucía (Fig. 2), shows a more shallow-water limestone (Peña

Formation) in substitution of the deeper water Barcaliente Formation at La Lastra. Both are Serpukhovian to earliest Bashkirian in age. In another thrust unit underlying the Peña Santa Lucía klippe occurs the Carrión Limestone Formation (Viséan-lowermost Serpukhovian) described by Nemyrovska (2005). The sedimentary facies represented by the Carrión Limestone is rather different (albeit also in condensed facies) as the Genicera Nodular Limestone Formation at La Lastra and in thrust slices further north. It clearly represents an allochthonous occurrence (klippe) derived from an area at some distance to the north in the Palentian Zone. It is obviously of interest to study these various different limestone occurrences in some detail, so as to fit them in a wider context.

Both the Palentian and Cantabrian zones in the southeastern part of the Palaeozoic outcrops in the Cantabrian Mountains also contain totally unconformable, post-tectonic deposits (post-Palentian earth movements) of latest Langsettian, Duckmantian, Bolsovian and early Asturian ages (Fig. 2). These are clearly later than the Carrionas Thrust Sheet and the pseudo-anticlinal structure of the Sierra del Brezo.
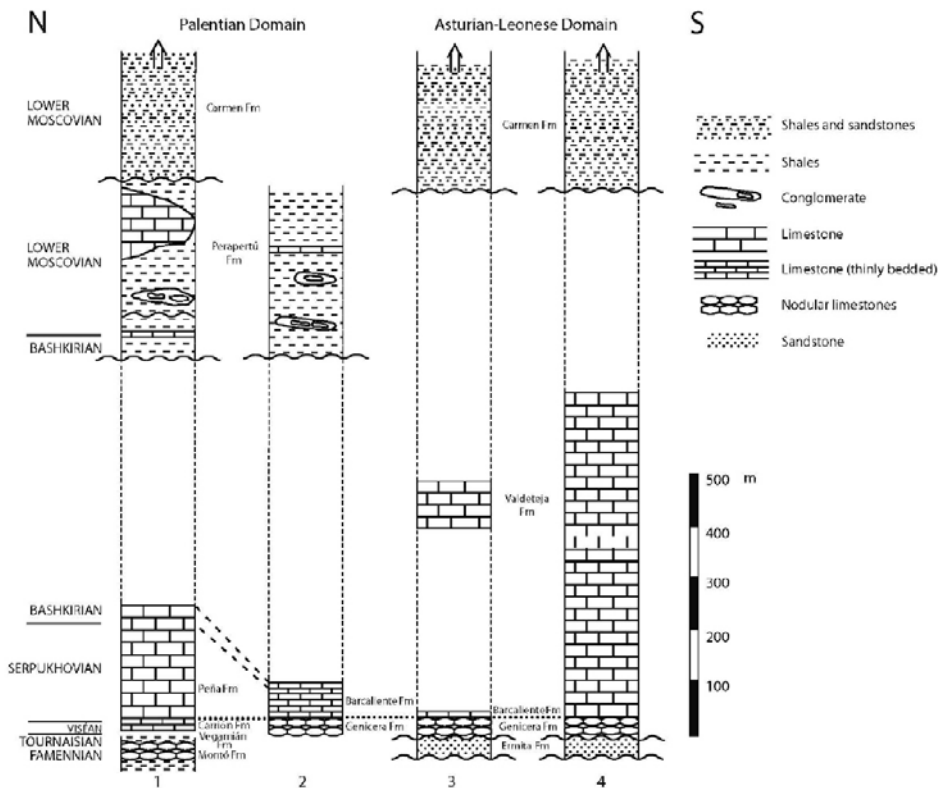

Fig. 5. Stratigraphic columns showing the Carboniferous (up to and including Lower Moscovian) successions in four different parts of northwestern Palencia.
(1) Peña Santa Lucía Klippe near Santibañez de Resoba and Carrión nappe structure.
(2) Head of the Carrionas Thrust Sheet at La Lastra.
(3) Sierra del Brezo (northern flank).
(4) Sierra del Brezo (southern flank).

This post-Palentian succession is overlain in turn by upper Asturian, Cantabrian and lower Barruelian strata (Fig. 2). The contact with lower Asturian strata is pseudo-conformable in La Pernía, with only movements of uplift in between. A full history related to west-northwest and eastern basin margins has been described by Wagner & Winkler Prins (1985) and a mid-Cantabrian expansion of this basin in the direction of Posada de Valdeón (León Province) has been argued by Wagner & Martínez-García (1998).

Westwards, in northeastern Leon, a low-angle unconformity separates Bolsovian and lower Asturian deposits near Prioro (van Loon, 1972) from lower Cantabrian valley fill deposits at neighbouring Tejerina (Fig. 2). Further westwards and northwestwards as well as to the north, a conformable succession of Lower Palaeozoic to lower Asturian strata suffered compressional tectonic deformation in mid-Asturian times. Subsequent strata were laid down with high-angle unconformity.

Another high-angle unconformity underlies post-Asturian (upper Barruelian, Saberian, Stephanian B) deposits found in tectonic outliers all over the Cantabrian Mountains. These represent a coastal basin, with mainly non-marine coal-measures in the west and almost fully marine strata in the Picos de Europa. Several ouliers of the post-Asturian basin are shown in Figure 2 (Sabero, Peña Cildá, Pico Cordal, Puente Pumar, Remoña). These are the latest deposits to participate in the Cantabric-Asturian arcuate fold belt and reflect a progressively tighter arcuate structure.

The entire arcuate fold belt, characterised by high-level thrusting with decollement at several different stratigraphic levels, is overlain with total unconformity by highest Pennsylvanian (Autunian), Permian and Mesozoic strata which belong to the Basque-Cantabrian Basin. Its western basin margin is located a little east of Cervera de Pisuerga (Fig. 2) where Triassic and Jurassic strata feather-edge and are onlapped by Cretaceous siliciclastics followed by limestones which continue westwards along the southern flank of the Cantabrian Mountains.

At La Lastra, the anticlinal head of the Carrionas Thrust Sheet is exposed in Viséan limestones of the Genicera Formation. The village itself is built on thinly bedded limestones of the Barcaliente Formation exposed in the overturned flank of the anticlinal structure (Figs. 3, 4) which is isoclinal and sheared in the anticlinal core. The normal flank of this anticlinal structure contains a shallowly dipping thrust plane on which mudstones of the (Lower Moscovian) Perapertú Formation were moved across the (Serpukhovian-lowermost Bashkirian) Barcaliente Limestone Formation. About 500 m west of La Lastra the Perapertú mudstones of the normal flank were moved progressively across successive formations of the overturned flank so as to eliminate the Carrionas Thrust Front in outcrop at 450 m south of the village of Triollo (Fig. 3). South of Triollo the Perapertú mudstones of the normal flank outcrop as a shallowly dipping, undulate minor thrust sheet, with the underlying rocks of the Sierra del Brezo occurring in some of the anticlinal cores.

All strata are cut by igneous dykes which occur more or less haphazardly and which are regarded as post-arcuate fold belt. The general assumption is that these are of Autunian age.

Barcaliente Formation (CFWP & RHW)

The classical 'Caliza de Montaña' (an unfortunate translation of the (now) obsolete British term 'Mountain Limestone' by Ezquerra del Bayo, 1844) was subdivided by
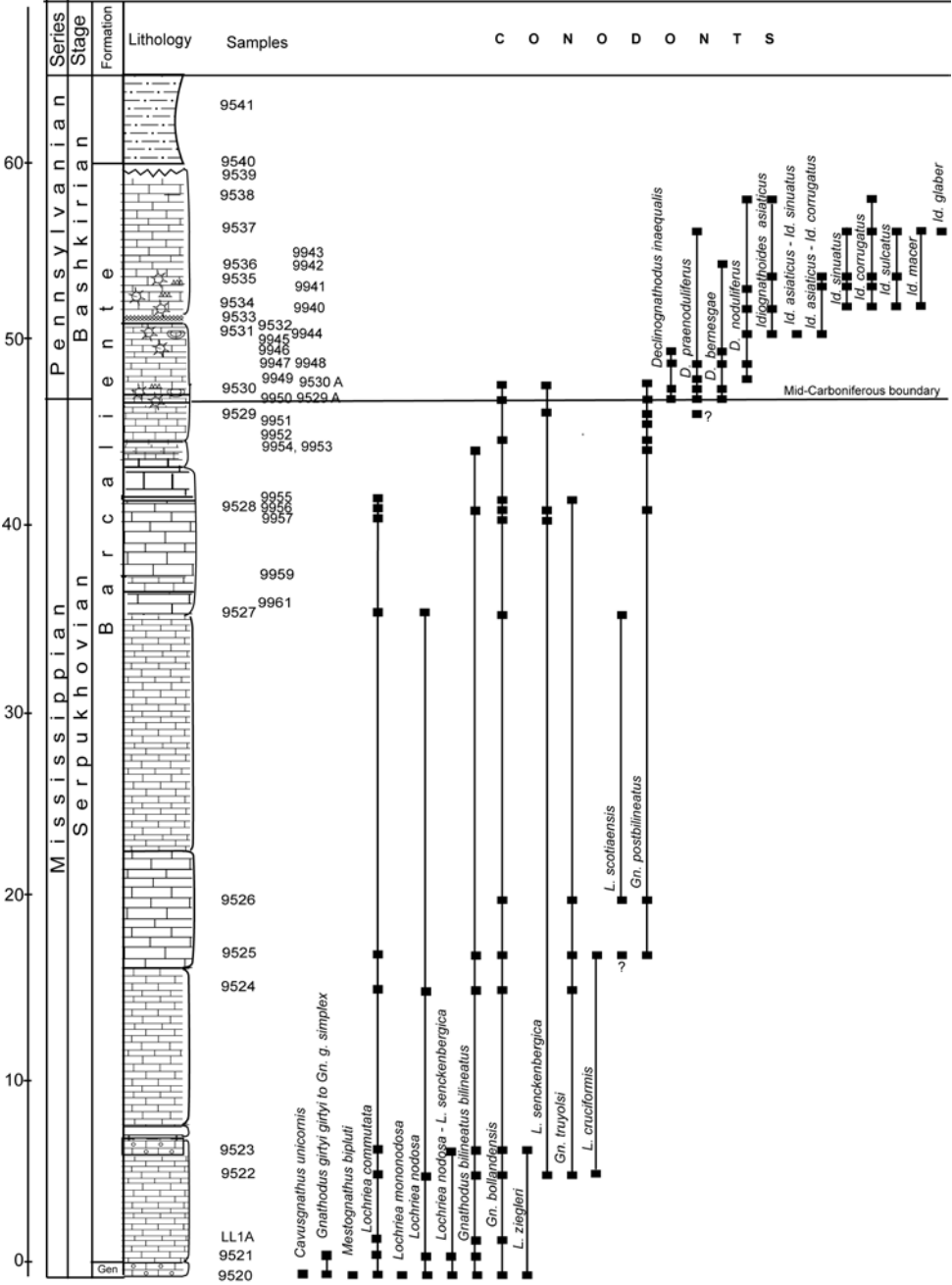
Fig. 6. Lithological column and distribution chart of conodont species in the La Lastra section (modified after Nemyrovska *et al*., 2008, fig. 7).

Table 1ᵃ. Distribution of the conodonts in the La Lastra section; for the sample numbers, see Figure 6.

Conodonts \ Samples	LL7	9520	LL7A	LL1A +9521	9522	9523	LL8	LL1B	9524	9525	9526	LL1C	9527	9961	9959	9957	9956	9528	9955	9954	9953	9952
Cavusgnathus unicornis	1																					
Gnathodus girtyi girtyi - Gn. g. simplex	3																					
Mestognathus bipluti	1	72	3																			
Gn. bilineatus		168	3 juv. 4 juv.	6	1			4 juv. 4 ?	1							1				1		1
Gn. bollandensis		25	2 juv.?	8	3			1	1		1		2			1	3	4	2	1	1	1
Gn. truyolsi		20		2	1			1										1				
Lochriea commutata	2	124	!?	7	3			3 juv. 2	1		2?		2		2	2		1 cf. 1				
L. mononodosa/L. monocostata					1																	
L. nodosa	2	48	3	1			2															
L. scotiaensis										1?	1	1 fragment	2?									
L. ziegleri		3	?				1 mono?			1												
L. cruciformis			1	1						1												
L. nodosa - L. senckenbergica	1		1																			1
N. singularis							3															
L. senckenbergica				1	1										1	1		1				
Gn. postbilineatus				1	2						1				1	1	1	1	3	1		3
Declinognathodus praenoduliferus																						
Decl. bernesgae																						
Decl. inaequalis																						
Decl. noduliferus																						
Idiognathoides asiaticus																						
Id. asiaticus - Id. sinuatus																						
Id. asiaticus - Id. corrugatus																						
Id. sinuatus																						
Id. corrugatus																						
Id. sulcatus																						
Id. macer																						
Neolochriea glaber																						
Ozarkodina spp. (see Pl. 1: 11; Pl. 2: 18)		6												1	1							
Ligonodina spp.														1	1							
Lonchodina spp.		6																				
Synprioniodina spp.		7																				
Subbryanthodus sp.		2							3													
Neoprioniodus singularis																1					1	
Hindeodella sp.	1	7	1	1					1						1							
Total	**10**	**488**	**7**	**27**	**11**			**10**	**10**	**7**	**4**	**1**	**6**	**2**	**3**	**7**	**6**	**6**	**4**	**3**	**3**	**5**

Table 1b. Distribution of the conodonts in the La Lastra section; for the sample numbers, see Figure 6.

Conodonts \ Samples	9951	9529	9950	9530	9949	9948	9946	9531b	9531c	9944	9532	9534	9940	9941	9535	9942	9537	9538	9539	9542	Total
Cavusgnathus unicornis																					1
Gnathodus girtyi girtyi - Gn. g.simplex																					3
Mestognathus bipluti																					76
Gn. bilineatus																					194
Gn. bollandensis		1																			55
Gn. truyolsi																					5
Lochriea commutata																					155
L. mononodosa/L. monocostata																					21
L. nodosa																					57
L. scotiaensis																					4
L. ziegleri																					3
L. cruciformis																					2
L. nodosa - L. senckenbergica																					2
N. singularis																					5
L. senckenbergica	4	1	1	1																	7
Gn. postbilineatus		9	1																		27
Declinognathodus praenoduliferus		1 cf.	1	1	2												1			4	15
Decl. bernesgae			5	5		3	3		1												13
Decl. inaequalis			1	1		1	1														4
Decl. noduliferus					2	21	1			1			1	1				1			28
Idiognathoides asiaticus									2				1		6			2	3		14
Id. asiaticus - Id. sinuatus								1												2	3
Id. asiaticus - Id. corrugatus								1							4				5		11
Id. sinuatus												6 juv.		1	2		2				11
Id. corrugatus												7		3	4		3	2	4		23
Id. sulcatus												1			2		5				8
Id. macer												2					12				14
Neolochriea glaber																	2				2
Ozarkodina spp. (see Pl. 1: 11; Pl. 2: 18)																	5				13
Ligonodina spp.																	2				4
Lonchodina spp.																					6
Synprioniodina spp.																	3				10
Subbryanthodus sp.																					2
Neoprioniodus singularis																					5
Hindeodella sp.	1									1						1			1	1	18
Total	5	12	5	7	4	30	5	3	3	2	0	16	2	6	20	1	35	5	10	9	800

Winkler Prins (1968, p. 49) into a lower Vegacervera Micrite Member and an upper Valdeteja Biosparite Member in northern León. The former was subsequently renamed and redefined as the Barcaliente Formation (Wagner *et al.*, 1971, p. 632), because the type section of the Vegacervera Member proved unsuitable. A description of the Barcaliente type section in northern León (along the Barcaliente stream emptying into the Curueño river) can be found in Winkler Prins (1971). The Barcaliente Formation consists largely of dark grey, micritic, thinly bedded and partly laminated limestones, which have been interpreted as distal turbidites in a euxinic basin (that is, the allodapic limestones of Reuther, 1977, p. 50). Depth must have been below wave base, but need not have been more than 50 m. Macrofossils are rare, although uncommon brachiopods occur as well as small and unidentifiable goniatites, and crinoids. Conodont faunas are common, but not abundant. Radiolarians occur locally. The thickness of the Barcaliente Formation is quite variable, but up to 250 m are recorded most commonly in northern León (e.g., in the Barcaliente type section in the Curueño Valley). This is in marked contrast with the 60 m of Barcaliente Formation at La Lastra in northern Palencia (Fig. 6), representing the same stratigraphic interval (Serpukhovian and lowermost Bashkirian).

The contact with the underlying Genicera (= Alba) Formation (see Wagner *et al.*, 1971) is always a gradual one. Where the dark grey Barcaliente Limestone interfingers with and follows upon the nodular to wavy-bedded, light grey limestones of the Canalón Member representing the upper part of the Genicera Formation in northern León (due to a better oxygen supply after an euxinic episode), this interval is called the San Adrián Member (Reuther, 1977) and is here attributed to the basal part of the overlying Barcaliente Formation. The highest part of the Genicera Formation commonly belongs to the *Eumorphoceras* 2 Zone as determined by its goniatite fauna (Kullmann, 1962; Wagner-Gentis, 1963). This is low in the Serpukhovian (lower Namurian). Although most of the Barcaliente Formation in the Asturian-Leonese Domain (Cantabrian Zone) corresponds to the Serpukhovian, its highest part has been dated on conodonts as earliest Bashkirian (Sanz-López *et al.*, 2004, 2006). The southernmost exposures in northern León show the interfingering of Barcaliente Limestone with siliciclastic turbidites of the Olleros Formation, representing the edge of a carbonate platform where it borders on a turbiditic basin (Wagner *et al.*, 1971, p. 639). The full succession of siliciclastics, with the wedges of Barcaliente Limestone included, was described as the Cuevas Formation by Boschma & van Staalduinen (1968, p. 225).

In the Asturian-Leonese Domain (Cantabrian Zone), the Barcaliente Formation is overlain by either the light grey limestones of the Valdeteja Formation (Winkler Prins, 1971; Villa *et al.*, 2001) or a thin, manganese-rich limestone followed by purplish shales of the Ricacabiello Formation (Martínez Chacón *et al.*, 1985), both with rich faunal assemblages of quite different composition and facies connotations. Brachiopods of the Valdeteja Formation indicate well-aerated, shallow-water conditions, whilst those of the Ricacabiello Formation typically represent a stillwater fauna (compare Martínez Chacón & Winkler Prins, 1993). The upper part of the Barcaliente Formation contains common authigenic quartz crystals and calcified gypsum crystals; also, collapse breccias have been seen with blocks of up to 1 m^3 or more (Winkler Prins, 1971, pl. 1, fig. 2). These characters were interpreted by González Lastra (1978) as indicative of hypersaline conditions in an intertidal to subtidal lagoon.

The Barcaliente Formation is widespread and generally well developed throughout the Asturian-Leonese Domain (Cantabrian Zone). It is notably absent, or represented only by its lowermost part in the most northerly part of the Sierra del Brezo (northern flank of the Almonga-Valsurbio pseudo-anticline), where pre-Valdeteja (Bashkirian) uplift has produced an erosional contact in the local area. A structural outlier of the Genicera, Valdeteja, and Carmen formations, all with erosional contacts, occurs as part of the Revilla Nappe near Barruelo de Santullán (Higgins & Wagner-Gentis, 1982; Wagner & Winkler Prins, 2000, fig. 6). This tectonic outlier of the Asturian-Leonese Domain was thrust northwards across strata of the Palentian Domain after the south-verging Carrionas Thrust Sheet was already emplaced. This outlier shows the total absence, as a result of uplift, of the Barcaliente Formation and must have been derived from an area palaeogeographically close to the northern part of the Sierra del Brezo.

In contrast, a complete development of the Barcaliente Limestone Formation occurs in the overturned flank of the recumbent anticline at the head of the Carrionas Thrust Sheet (Palentian Domain) at La Lastra. A full section measured at this village (Fig. 6), shows 60 m of thinly bedded, bluish-grey limestones of the Barcaliente Formation, which are in gradual transition with reddish and light grey nodular limestones of the underlying (modified) Genicera Formation (Nemyrovska *et al.*, 2008).

Whereas the first deposits of the Barcaliente Formation in northern León (Asturian-Leonese Domain) are late Arnsbergian (compare Wagner *et al.*, 1971), a slightly earlier (Serpukhovian) age is suggested by conodont faunas (Fig. 6; Table 1) in the basal part of this formation at La Lastra (Palentian Domain). The Barcaliente Formation at La Lastra

Fig. 7. Typical Barcaliente Formation limestone at La Lastra, near the mid-Carboniferous boundary. Note the thin igneous sill (brownish layer at head of the 400 mm long hammer), which is at 4 m above the mid-Carboniferous boundary.

shows an internal lamination which is not always apparent in hand specimens (Fig. 7). This formation reaches into the lowermost Bashkirian near its top. The overlying Perapertú Formation (mostly Lower Moscovian, but also including, most likely, the highest Bashkirian; Kullmann *et al*., 2007) rests on an erosion surface at La Lastra. It is assumed that this represents a washed-out palaeokarst. A large period of uplift is involved, occupying most of Bashkirian times.

Goniatites and ostracodes were found in thin sections of the Barcaliente Formation at La Lastra studied by P. Cózar (pers. comm. to RHW, April 2000), who noted the absence of benthic elements. An account of the sedimentary facies involved is given below. Conodonts studied by T.I.N. (Fig. 6; Table 1) show the Genicera-Barcaliente formational boundary at La Lastra to coincide approximately with the Viséan/ Serpukhovian stage boundary, a position lower than that recorded in the Asturian-Leonese Domain, where this boundary lies within the Serpukhovian (compare Higgins & Wagner-Gentis, 1982; Belka & Korn, 1994). A very early Bashkirian conodont fauna was recovered from 45 m above the base of the Barcaliente Formation at La Lastra, at 10 to 15 m below the irregular erosional surface which marks the contact with the overlying mudstones of the Perapertú Formation. Nemyrovska (*in* Nemyrovska *et al*., 2008) observed that the composition of this lowermost Bashkirian fauna is similar to that found in beds immediately above the mid-Carboniferous boundary in Central Asia. At Santa Olaja de la Varga in northern León, *c*. 250 m of Barcaliente Limestone are found in apparent conformity by shales from which Kullmann (1979, p. 40) recorded R_1 (Kinderscoutian) goniatites not far from the base. It is emphasised that, whereas the Bashkirian level in La Lastra is reached at 45 m above the base of the Barcaliente Formation, this same level occurs at *c*. 100 to 150 m above the base in the thicker development of Barcaliente Limestone in northern León. However, this is not always the case. Lower Bashkirian conodonts have been recorded from 7 m above the base of the Barcaliente Formation in the Millaró section (in another part of northern León - García-López & Sanz-López, 2002, pp. 182, 184; see also Sanz-López *et al*., 2006, p. 7). (Note that the scale of the Millaró section in papers by Sanz-López *et al*., 2004, fig. 2, and 2007, fig. 2, is incorrect and should be divided by 10; the scale in Sanz López *et al*., 2006, fig. 3 is correct.) It has been noted already that different degrees of condensed facies are represented in different parts of the Cantabrian Mountains. The condensed facies, in evidence at La Lastra, might well be the norm for the entire southern strip of the Palentian Domain.

A different facies development at the same stratigraphic level is recorded in the Peña Santa Lucía klippe, a tectonic unit occurring at only about 1 km north of La Lastra, but which contains strata likely to have been laid down much further north and transported southwards over what seems have been tens of kilometres. In the Peña Santa Lucía klippe, the Barcaliente Formation is replaced by *c*. 250 m of partly bioclastic, more shallow-water limestones (the Flachwasser-Kalke of Boll, 1985). These are to be described as a new nominal formation (Wagner & Winkler Prins, research in progress). The presence of Barcaliente Formation in the southernmost part of the Palentian Zone and its absence at only a short distance to the north suggests that the Palentian Zone in its most southerly part was connected somehow to the Cantabrian Zone, although its condensed development indicates that a ridge of slower subsidence than elsewhere was involved. The conclusion that the Palentian and Cantabrian zones were somehow connected has important palaeogeographic implications.

The fact that the Barcaliente Formation at La Lastra represents the full time interval recorded for this formation elsewhere suggests that the uplift involved with the erosional (palaeokarst?) surface on top of this formation did not result in a substantial removal of strata, but represents mainly a hiatus of deposition. Perhaps, the slow subsidence associated with a relatively thin development of Barcaliente Formation at La Lastra was a prelude to widespread uplift, involving a substantial area. Could it be that the corresponding uplift was related to the very shallow conditions suggested by the evaporitic, inter-subtidal(?) deposition of limestones at the top of the Barcaliente Formation as reported by González Lastra (1978)? The Porma Breccia Member (Reuther, 1977) at the top of the Barcaliente Formation in its type section (Winkler Prins, 1971, pl. 1, fig. 2) seems to fit the same interpretation. The Brezo Breccia (Reuther, 1977), occurring as lenses in basal Valdeteja Limestone Formation in the Sierra del Brezo (Asturian-Leonese Domain of the Cantabrian Zone), has different connotations, viz. the reworked angular clasts of a palaeokarst breccia of Barcaliente Formation origin which became incorporated in the later, post-uplift marine limestone deposits.

Sedimentological characteristics of the Barcaliente Formation (IM)

The carbonates of the Barcaliente Formation at La Lastra contain a range of lithofacies including dark grey, thin- to thick-laminated to strongly bioturbated mudstones and wackestones, and peloidal wackestones and packstones, some of which exhibit clotted mud and peloidal fabrics characteristic of microbial binding and mediation of carbonate mud. Four samples from ~0.3 to 1.5 m below the mid-Carboniferous boundary (see Figs. 6 and 8 for their stratigraphic distribution relative to the boundary) consist of dark laminated calcisiltites, which exhibit increased bioturbation and an abundance of silt-sized, bioclastic material upsection towards the boundary, thus suggesting a shallowing period. All samples contain sparse, low diversity fossil assemblages. The lowest sample (9520), from the top of the Genicera Formation, is a medium brown, slightly peloidal mudstone/wackestone with extensive bioturbation (Ichnofabric Index II 4; Droser & Bottjer, 1986). Biotic components include a thin smooth-walled ostracode, calcified sponge spicules and sparse (1 to 3 %) spherical voids filled with calcite cement of ~50 to 200 μm grain size. These calcite-filled moulds lack external micritic envelopes typical of fossil calcispheres (phytoplanktic resting cysts) and probably represent dissolved radiolarians (Munnecke & Servais, 2008). Overlying samples of the Barcaliente Formation (9521, 9964, and LL5) are dark brown to grey, laminated limestones with a sparse and low diversity fossil assemblage consisting of rare crinoid ossicles and inferred moulds of radiolarians (<1 to 2 %). Laminae are best preserved in the lowermost of these three samples (9521) and occur as graded couplets of fine-grained, silt-size peloidal micrite (referred to as calcisiltites) overlain by carbonate mud. The sample closest to the mid-Carboniferous boundary (LL5 at 1.5 m below), a peloidal wackestone, exhibits the most extensive bioturbation (II 4), contains fewer moulds of radiolarians, is predominantly peloidal and has only a subordinate amount of silt-sized bioclastic material. Bioclasts in sample LL5 cannot be identified given the extent of replacement and dissolution.

The carbonate lithofacies from well below the Serpukhovian-Bashkirian boundary are interpreted as recording an overall shallowing trend. The predominance below the boundary of dark limestones dominated by mm- to cm-scale mudstone and laminated calcisiltite couplets, some exhibiting grading, combined with a lack of early

Fig. 8. Detail of Barcaliente section (see Fig. 6) and conodont distribution across the Serpukhovian/Bashkirian boundary at La Lastra.

cementation leading to extensive stylolitization indicates that these carbonates (samples 9521, 9964, and LL5) were deposited as distal calcareous turbidites well below fair-weather wave-base (FWWB) (Hemleben & Reuther, 1980; Wagner *et al*., 1971). Their moderate to extensive bioturbation further suggests that most were deposited between storm wave-base (SWB) and FWWB. The lack of photozoan bioclasts or abiotic grains (ooids, coated grains) in conjunction with sparse, low diversity heterozoan faunas also suggest they formed, most likely, below the euphotic zone (or locally within the oligophotic zone) (Burchette & Wright, 1992; Merino-Tomé *et al*., 2009). The euphotic zone in modern depositional environments may extend down to 40 or 50 m, but can, of course, be limited to much shallower depths by high turbidity as a result of terrigenous clastic influx and/or high nutrient input (Pomar, 2001; Wilson & Vecsei, 2005). The increase in bioturbation and peloid abundance along with a decrease in spherical moulds, interpreted as dissolved radiolarians, indicates an overall shallowing of the depositional environment on a carbonate platform which still remained well below FWWB in the latest Serpukhovian. The first notable occurrence of bioclastic material in the stratigraphically highest sample (LL5) 1.5 m below the mid-Carboniferous boundary supports this.

Four samples taken close to the Serpukhovian-Bashkirian boundary (from 0.5 m below, at and immediately above; see Fig. 8) exhibit a reverse stratigraphic trend in lithofacies defined by a decrease in extent of bioturbation (from II 3 to rare discrete burrows) concomitant with an increase in preservation of mm- to cm-scale lamination. This trend is accompanied by a decrease in lamination thickness, abundance of peloids and radiolarian moulds. The 'boundary' carbonate (9950) exhibits the finest (mm-scale) laminae that are weakly graded and organic-rich; discrete burrows are rare. The immediately overlying carbonate (LL2) preserves weak, mm-scale lamination, and contains the most organic

residue (kerogen along stylolites) of all examined samples and a marked increase in radiolarian moulds (up to 10 to 15 %), sufficient to be classified as a radiolarian wackestone. The carbonates most proximal to the boundary (9950 and LL2) are also the finest grained and purest carbonate mudstones (i.e., dominantly micrite with little clumped or peloidal mud). Therefore, the La Lastra carbonates straddling the Serpukhovian-Bashkirian boundary have formed in deeper water overall or in less well oxygenated environments (euxinic) than the Serpukhovian carbonates below. The preservation of mm- to cm-scale, graded calcisiltite-mud couplets in all but the stratigraphically lowest sample (LL4) indicates that the boundary interval carbonates formed D-E layers of Bouma sequences in the distal reaches of turbidite fans, well below FWWB and, perhaps, for the finer-laminated (mm-scale) and least bioturbated, organic-rich carbonates, well below SWB. This indicates that turbidity currents can transport shallow-water carbonate silts to outer ramp environments below SWB where the oxidation of organic matter within the sediments is limited by the lack of wave pumping. Storm wave-base in carbonate depositional environments can range from 30 to 60 m based on modern analogues (e.g., Logan *et al.*, 1969, 1970; Purser & Evans, 1973), and varies with the configuration of the platform and basin, typically being deeper in foreland basins than epicontinental seaways. The apparent large amount of non-degraded organic matter in the boundary carbonates (samples 9950 and LL2) could record high rates of primary production favoured by an elevated availability of nutrients in addition to high allochthonous sedimentation rates. Thus, the temporal trend toward the boundary of increasing preservation of laminae and organic content, along with loss of peloids and heterozoan bioclasts (but increasing content of inferred radiolarians), is interpreted to record a deepening trend in the terminal Serpukhovian with maximum water depths and/or the most euxinic conditions reached during deposition of mid-Carboniferous boundary carbonates (samples 9950 and LL2).

The carbonates of the lowermost Bashkirian, uppermost Barcaliente Formation, as represented by six samples (Fig. 8), are similar in lithofacies to those at the mid-Carboniferous boundary and immediately underlying carbonates, with the exception of the introduction of peloidal wackestones with micritic bindstones. Moreover, the lowermost, dark laminated carbonates in this set differ from similar carbonates lower in the section in that they contain larger amounts of silt-size bioclastic material. Rare ostracodes and variable amounts of radiolarian moulds (up to 7 to 10 % in sample 9535; Fig. 8) occur within these carbonates. Within 5-10 m above the mid-Carboniferous boundary, moderately (II2) to extensively (II4) bioturbated dark laminated (mm- to cm-scale) calcisiltites with lenses of silt-size bioclastic material (samples 9940, 9941 and 9935) pass upwards into the shallowest carbonates of the entire suite of samples studied — peloidal wackestones/packstones with clotted micrite and geopetal silt-filled vugs. Sample 9943, a peloidal wackestone, is lighter in colour, exhibits moderate cementation, and is composed of peloids of irregular shape and diverse sizes as well as patches of clotted micrite. Micritic envelopes around calcite-cemented spherical voids are associated with the clotted, wavy micrite. Carbonates (samples LL1 and 9539), stratigraphically higher than sample 9943 (at 79.5 m), mark a return to very dark calcisiltites that are moderately to extensively bioturbated. Biotic components are limited to rare ostracodes, sparse to common moulds of radiolarians (up to 10 %) and very few bioclastic grains. A slight shallowing trend may be identified between samples LL1 and overlying sample 9539, based on an increase in bioturbation and decrease in radiolarian moulds.

The carbonate lithofacies above the Serpukhovian-Bashkirian boundary thus record an overall shallowing in the Bashkirian to minimum inferred water depths at ~12 m above the boundary followed by a moderate deepening and possible slight shallowing in the highest part of the Barcaliente Formation. The shallowing to minimum water depths in the earliest Bashkirian are inferred from the abundance of peloids, clotted micrite and geopetal carbonate silt within primary vugs in the clotted micrite in the carbonates ~12 m above the boundary. Peloids of irregular shape and variable size are interpreted as micrite precipitated in microbial biofilms. Micritic envelopes around calcite-cemented spherical voids associated with clotted micrite and peloids could be carbonate encrustations around coccoidal cyanobacterial cells. This facies is interpreted to have formed in a warm, moderate to low-energy and shallow water environment, perhaps a shallow lagoonal or restricted inner platform depositional area. The calcisiltite-mud couplets with silt-size bioclastic lenses within the dark laminated carbonates in this interval are interpreted as more proximal storm deposits or turbidites than their equivalent Serpukhovian facies; this is further supported by the greater extent of bioturbation in this suite of carbonates. The moderate deepening in the upper part of the Barcaliente Formation is inferred from a return to darker, fine-grained limestones with radiolarians and sparse bioclastic material.

In summary, the carbonates of the studied interval of the Barcaliente Formation at La Lastra village were deposited predominantly in a relatively deep-water setting well below FWWB and, at times, probably below SWB. This interpretation is based on the predominance of laminated calcisiltites and mm- to cm-scale calcisiltite-mud couplets, apparent high organic carbon contents, lack of early cementation, and a sparse and low diversity assemblage with radiolarian moulds as the most abundant biotic component. Carbonates deposited within the regular influence of storm and fair-weather waves and currents are typically lighter in colour and exhibit greater syndepositional marine cementation than is observed in the Barcaliente Formation. This is because pumping of seawater into sediments leads to oxidation of organic matter and syndepositional or very early burial cementation. The one exception is the peloidal wackestone from ~12 m above the mid-Carboniferous boundary with evidence of microbial flocculation, binding and possibly mediation of carbonate mud (micrite) from which minimum water-depths were inferred. The afore-mentioned descriptions of a suite of carbonates and their inferred depositional environments indicate an overall shallowing trend in the late Serpukhovian followed by moderate deepening with maximum water depths reached proximal to the Serpukhovian-Bashkirian boundary. On the other hand, the lower Bashkirian was characterised by a shallowing trend to within 5 to 7 m of the erosional top of the Barcaliente Formation and a subsequent return to moderately deep, followed by slightly shallower, conditions just below the erosional top of the formation.

Conodonts (TIN)

The entire Barcaliente Formation in the La Lastra section was sampled for conodonts (Fig. 6; Table 1), as well as the highest part of the underlying Genicera Formation. Fifty samples were collected, each about 1 to 3 kg. These were dissolved in formic acid and processed with sodium polytungstate for separation. Almost every sample contained conodonts, but the yield was low. In some samples radiolarians are more abun-

dant than conodonts. A high yield, latest Viséan-earliest Serpukhovian conodont assemblage was obtained from sample 9520 in the highest part of the underlying Genicera Formation. Lower Serpukhovian samples of the Barcaliente Formation contain from 5 to 15 specimens per sample on average, and the Upper Serpukhovian ones fewer than ten. Samples from the upper part of the Barcaliente Formation (dated as Early Bashkirian) were more productive with 20 to 30 specimens in some cases. Pa elements are the most abundant ramiform elements, such as Sb element of *Idioprioniodus* sp. (see Pl. 1, fig. 10) and *Lonchodina* sp. (see Pl. 3, fig. 15); others are rare and broken. In general, the conodonts are very small and delicate; some samples contain only juveniles. Their CAI is from 4 to 5.

Almost all the known conodont genera and species characteristic of the Serpukhovian and the lowermost Bashkirian are represented. These belong to the *Gnathodus bilineatus* group including *Gn. bilineatus* (Roundy), *Gn. bollandensis* Higgins & Bouckaert, *Gn. truyolsi* Sanz-López *et al*. and *Gn. postbilineatus* Nigmadganov & Nemirovskaya. *Lochriea* is represented by simple species such as *L. commutata* (Branson & Mehl) (see Pl. 2, figs. 1, 7, 9-11, 14, 15, 17) and *L. scotiaensis* (Globensky, 1967) (see Pl. 1, fig. 7); ornamented taxa like *L. monocostata* Pazukhin & Nemirovskaya (Pl. 2, figs. 2, 6, 8) and rare *L. nodosa* (Bischoff) (Pl. 2, fig. 13); and strongly ornamented species such as *L. ziegleri* Nemirovskaya *et al*., *L. senckenbergica* Nemirovskaya *et al*. and *L. cruciformis* (Clarke) (Pl. 2, figs. 3-5, 12, 16).

The earliest Pennsylvanian conodonts are represented by the *Declinognathodus noduliferus* group, including its earliest members such as *D. praenoduliferu*s Nigmadganov & Nemirovskaya and *D. bernesgae* Sanz-López *et al*. These have ridged, not yet nodular, margins. *Declinognathodus inaequalis* Higgins and *D. noduliferus* (Ellison & Graves) *sensu stricto* also occur. *Idiognathoides* includes several Early Bashkirian species such as *Id. sinuatus* Harris & Hollingsworth (Pl. 3, fig. 5), *Id. sulcatus sulcatus* Higgins & Bouckaert, *Id. macer* (Wirth) and its earliest deep water species, *Idiognathoides asiaticus* Nigmadganov & Nemirovskaya. *Neolochriea glaber* (Wirth) was also found in the La Lastra section.

The conodont assemblage of the uppermost part of the Genicera Formation (sample 9520) contains abundant *Gn. bilineatus bilineatus* (more than 160 specimens) and *Gn. bollandensis* (about 25 specimens), as well as numerous Late Viséan-Early Serpukhovian species of *Lochriea*, such as *L. commutata, L. nodosa* and *L. mononodosa*. In this paper we do not differentiate *L. mononodosa* and *L. monocostata* Pazukhin & Nemirovskaya *in* Kulagina *et al*.,1992. Most of the specimens referred herein to *L. mononodosa* have a ridge on the cup, but not a node, which is the main feature to distinguish it from *L. monocostata*, as well as *L. nodosa* from *L. costata*. A number of transitional forms between the above-mentioned species was found, which made the identification more difficult. A discussion on the taxonomy of these species and all the ornamented species of *Lochriea*, including transitional forms between *L. ziegleri* and *L. cruciformis*, is in progress. The first small *L. ziegleri* was also found at this level as well as a number of accompanying ramiform elements (Fig. 6; Table 1).

Slightly below sample 9520, the conodont assemblage is different. Single specimens of *Mestognathus bipluti* Higgins (Pl. 1, fig. 14) and *Cavusgnathus unicornis* Youngquist & Miller have been found. These are considered to be shallow water species. Three specimens correspond to *Gnathodus girtyi* Hass, 1953 *sensu lato*, in transition with *Gn. girtyi simplex* Dunn, 1966, as described from the Triollo section (Nemyrovska, 2005, p. 37). One specimen of *Lochriea* shows the trend to *L. senckenbergica*.

The La Lastra conodonts are generally small. It is, therefore, difficult to say whether the FAD of the advanced, strongly ornamented *Lochriea* species, such as *L. ziegleri* and *L. senckenbergica*, are already at the level of the highest samples of the Genicera Formation. Although sculpture is not yet well developed, these strongly ornamented forms of *Lochriea* are suggestive of the advanced species. They cannot be referred to *L. nodosa*, which has simple nodes (even large ones) in the central parts of each side of the platform.

The same conodont assemblage continues upwards throughout the Barcaliente Formation with the addition of *L. senckenbergica*, *L. cruciformis* and intermediate forms, as well as advanced species of the *Gn. bilineatus* group, such as *Gnathodus postbilineatus* and *Gn. truyolsi*. The highest Serpukhovian samples (in the middle of the Barcaliente Formation at La Lastra) yielded only poor conodont assemblages, both in variety and the number of specimens. These consist of *Lochriea commutata*, *L. senckenbergica*, *Gnathodus bilineatus bilineatus*, *Gn. bollandensis*, *Gn. truyolsi* and *Gn. postbilineatus*.

The Serpukhovian part of the Barcaliente Formation is generally dominated by the *Gnathodus bilineatus* group of species, although *Lochriea* species are rather common as well. The first conodonts of the early Pennsylvanian *Declinognathodus noduliferus* group occur in the deepest water part of the section (sample 9950; see above).

A single specimen of *Declinognathodus praenoduliferus*, two specimens of *D. bernesgae* and one juvenile *D. inaequalis* were found in sample 9950. The first *D. noduliferus noduliferus* was recorded a little higher up section (sample 9949). Additional sampling in between samples 9529 and 9530, viz. one slightly below sample 9950 and another a little higher up, are shown in Figure 8 as samples 9529A and 9530A, respectively. Both yielded single specimens of *Gnathodus bollandensis* and *Gn. postbilineatus*, as well as one *L. senckenbergica* and *Neoprioniodus singularis* (M element of *Lochriea* species). Such an overlap between latest Mississippian conodonts and the first Bashkirian ones has also been recorded from deep-water sections in the Tienshan (Nigmadganov & Nemirovskaya, 1992a, b; Nemirovskaya & Nigmadganov, 1994); also from different localities in the Cantabrian Mountains and in the Pyrenees (Sanz-López *et al.*, 2006). In the Donets Basin, Ukraine, single specimens of *Gn. postbilineatus*, *L. commutata* and *L. ziegleri* were also found above the FAD of *Declinognathodus*, but in those shallow-water settings they might be reworked.

Species of *Idiognathoides* join the conodonts of the *D. noduliferus* group higher up in the La Lastra section. The FAD of *Id. asiaticus* was recorded from *c*. 5 m above the FAD of the first *Declinognathodus*, that is, about 5 m above the base of the Bashkirian. The entry of *Id. asiaticus* was recorded within the lower half of the *Homoceras* Ammonoid Zone in the Tienshan.

Even higher up in the section the conodont yield increased (e.g., sample 9533 above a small sill, *c*. 6 m above the mid-Carboniferous boundary) with the appearance of the *Idiognathoides* species: *Id. sinuatus* (including *Id. corrugatus*; see Pl. 3, figs. 17, 19), *Id. sulcatus sulcatus* (Pl. 3, figs. 2, 6) and *Id. macer* (Pl. 3, figs. 3, 4, 12, 18). Still higher, *Neolochriea glaber* (Pl. 3, fig. 9) occurs. The latter two species have been found in samples with more abundant conodonts than occur below.

A few carbonate lenses in the overlying mudstones of the unconformable Perapertú Formation were sampled for conodonts, but these only yielded fragments of unidentifiable ramiform elements. In the upper part of this thick mudstone succession, in limestone clasts of a debris flow conglomerate, reworked *D. praenoduliferus* occurs

(see Pl. 4, figs 1-3, 5, 9-11, 15, 18, 20), almost identical to the holotype, and to specimens from the basal beds of the *Homoceras* Ammonoid Zone of the Aksu section, Tienshan (Nigmadganov & Nemirovskaya, 1992a, b). Another limestone clast contains also *D. praenoduliferus*, *D. noduliferus* and *Id. asiaticus*; a third clast yielded Devonian conodonts of the genus *Icriodus* as well as some Mississippian conodonts. These obviously do not date the Perapertú Formation, but represent reworked strata of earlier ages.

The distribution of conodonts throughout the La Lastra section confirms the previously expressed point of view on the derivation of the genus *Declinognathodus* from *Gnathodus bilineatus* (see Nemirovskaya & Nigmadganov, 1994, fig. 7). In spite of the fact that specimens with characters intermediate between those of *Gn. girtyi* Hass *sensu lato* and *Gn. girtyi simplex* Dunn occurred in the lower part of the section (highest Genicera Formation), *Gn. girtyi simplex* itself was not found here. It was not found in the other European sections, either. The mid-Carboniferous boundary beds contain *Gn. postbilineatus*, a possible ancestor of *D. noduliferus*, and conodonts of the *D. noduliferus* group of species.

Conodont zonation (TIN)

Although only the mid-Carboniferous boundary interval was sampled in detail (Fig. 8) and the conodont yield is generally low in the La Lastra section (Fig. 6; Table 1), a number of biozones were distinguished.

Lochriea ziegleri Zone — This covers the interval between samples 9520 and 9522, the latter including *Ozarkodina* sp. (Pl. 1, fig. 11; Pl. 2, fig. 18). Its lower boundary cannot be defined exactly since the lowest sample collected already contains the index-species. However, it may be assumed that the lower boundary is quite close since the specimens of *L. ziegleri* do not yet possess the strongly developed ornamentation characteristic for this species, and also because of the number of transitional forms between *L. nodosa* and strongly ornamented forms. But the location of rows of large nodes or elevations with nodes close to the posterior margins of the platform shows that these specimens are within the range of variation of *L. ziegleri*. On the other hand, the occurrence of *Gn. bollandensis* in this interval (mostly juveniles) suggests that this part of the section is younger than Early Serpukhovian. The upper boundary is marked by the first occurrence of *Gn. truyolsi*, a Late Serpukhovian species characteristic of deep-water environments. Characteristic species of the *L. ziegleri* Zone are *Gn. bilineatus*, *Gn. bollandensis*(?), *L. commutata*, *L. nodosa*, *L. ziegleri*, and transitional forms between *L. nodosa* and *L. senckenbergica*. The occurrence of *Gn. bollandensis* in the assemblage corresponding to this zone is apparently anomalous, but the assemblage is a small one and represented, on the whole, by juveniles, which makes it difficult to distinguish *Gn. bilineatus* from *Gn. bollandensis*. The basal bed of the section includes the shallower water species *Cavusgnathus unicornis*, *Mestognathus bipluti*, and forms transitional between *Gn. girtyi sensu lato* and *Gn. girtyi simplex*. Above sample 9520 these forms no longer occur.

Gnathodus truyolsi Zone — The lower boundary of this zone is defined by the FAD of *Gn. truyolsi* (sample 9522); its upper boundary coincides with the FAD of *Gn. postbilineatus*. The zone spans the interval between samples 9522 and 9525. Characteristic species

are *Gn. bilineatus, Gn. bollandensis, Gn. truyolsi, L. commutata, L. nodosa, L. cruciformis* and *L. ziegleri*. Unfortunately, no link is known between *Gn. truyolsi* and the latest Mississippian species of *Gnathodus*, namely *Gn. postbilineatus*. It is possible that *Gn. truyolsi* was derived from *Gn. kiensis* Pazukhin or *Gn. cantabricus*. *Gnathodus postbilineatus* originated either from *Gn. bilineatus* or *Gn. bollandensis*. The relationships between the *Gn. truyolsi* and *Gn. postbilineatus* zones need to be studied anew.

Gnathodus postbilineatus Zone — The lower boundary of this zone is defined by the first appearance of *Gn. postbilineatus* (sample 9525); its upper boundary coincides with the mid-Carboniferous boundary marked by the entry of *D. praenoduliferus*, the earliest Pennsylvanian conodont species. The zone spans the interval between samples 9525 and 9529. Apart from the zonal index, it contains essentially the same conodonts as in the previous zone except for *L. ziegleri* and *L. cruciformis*, which do not range beyond the *Gn. truyolsi* Zone in the La Lastra section. The species characterising the *Gn. postbilineatus* Zone are *Gn. bilineatus, Gn. bollandensis, Gn. truyolsi, Lochriea commutata* and *L. senckenbergica*.

Declinognathodus praenoduliferus Zone — Three Early Pennsylvanian conodont species were found in sample 9950. These are *Declinognathodus praenoduliferus, D. inaequalis* and *D. bernesgae*. *Declinognathodus inaequalis* shows the trend to *D. noduliferus*, which has its first occurrence in sample 9949. It is likely that the interval between samples 9950 and 9949 (see Fig. 8) should still be assigned to the *D. praenoduliferus* Zone. In this zone, single specimens of *D. praenoduliferus* and *D. inaequalis* have been found, as well as several specimens of *D. bernesgae, Gn. postbilineatus* and *L. senckenbergica*. The lower boundary of the *Declinognathodus praenoduliferus* Zone is defined by the entry of the earliest Pennsylvanian conodonts *D. praenoduliferus* and *D. bernesgae*.

Declinognathodus noduliferus Zone — Its lower boundary is defined by the first appearance of *D. noduliferus* and the upper boundary coincides with the entry of *Idiognathoides asiaticus*. This zone spans the interval between samples 9949 and 9944. The characteristic species are *D. noduliferus, D. praenoduliferus, D. inaequalis* and *D. bernesgae*.

Idiognathoides asiaticus Zone — Its lower boundary is defined by the first appearance of *Id. asiaticus* and its upper boundary by the first occurrence of *Id. sinuatus*. The zone is characterised by *Id. asiaticus*, and transitional forms between this species and *Id. corrugatus* and *Id. sinuatus*.

Idiognathoides sinuatus Zone — Its lower boundary is marked by the entry of the most widespread Bashkirian species of the genus *Idiognathoides*, that is, *Id. sinuatus* (left and right-sided elements) as well as *Id. sulcatus* (sample 9534). This zone spans the interval between the samples 9534 and 9539. Its upper boundary is unclear. Characteristic species are *Id. sinuatus, Id. sulcatus* and *Id. macer*. The right-sided *Id. sinuatus*, that is, *Id. corrugatus*, is most abundant. Single specimens of *Neolochriea glaber* and *N.* cf. *nagatoensis* Mizuno (Pl. 1, fig. 8) occur. The *Declinognathodus* group of species as well as *Id. asiaticus* are still present.

Correlations (TIN)

The La Lastra section is readily correlated with other parts of Eurasia since the majority of the conodont species found here are the same or almost the same as elsewhere. The same is true of the general distribution pattern. The La Lastra conodont succession is more difficult to compare with that found in North America since some stratigraphically important taxa, such as the ornamented species of *Lochriea* and *Gnathodus postbilineatus*, are apparently absent from the North American record (although one specimen resembling *Lochriea ziegleri* has been found in the Barnett Shale Formation by D. Boardman, pers. comm., summer 2008). Likewise, some American genera and species have not been found in Eurasian sections (e.g., *Gnathodus girtyi simplex* and most of the species of *Rhachistognathus*). However, there are sufficient species in common to enable correlation.

The three conodont zones recognised in the Serpukhovian part of the Barcaliente Formation, that is, the *L. ziegleri*, *Gn. truyolsi* and *Gn. postbilineatus* zones, allow correlation with other Serpukhovian conodont successions in Eurasia. Since *Gn. truyolsi* has not been documented so far from shallow-water sections, that zone can only be equated approximately with that of *Gn. bollandensis*. However, this can only be accepted provisionally because *Gn. bollandensis* has been encountered at La Lastra below the entry of *Gn. truyolsi*.

It is recalled that the conodonts from La Lastra are very small and mainly represent juveniles, making it difficult to distinguish *Gn. bilineatus bilineatus* from *Gn. bollandensis*. The most reliable correlation is with the Aksu section in Central Asia where *Gn. truyolsi* occurs (it was erroneously assigned to *Gn. bollandensis* by Nigmadganov & Nemirovskaya, 1992a, b; compare the description of *Gn. truyolsi* in the present paper).

The most apparent correlatable horizon is the mid-Carboniferous boundary which represents an important stage in the evolution of Carboniferous conodonts. The changeover between Mississippian and Pennsylvanian conodont faunas is clearly apparent in the La Lastra section. Conodonts of the genera *Gnathodus* and *Lochriea* disappear at the level where the first representatives of the genera *Declinognathodus* and *Idiognathoides* are encountered. As stated above, the first deep-water succession across the mid-Carboniferous boundary has been documented from the Aksu section in the Tienshan, which provides the most complete conodont sequence across the mid-Carboniferous boundary and is a key section for correlation, since it also contains numerous ammonoids. The highest Mississippian conodont zone, the *Gnathodus postbilineatus* Zone, was established in the Aksu section (Nemirovskaya & Nigmadganov, 1994). The index-species of this zone has also been recorded from Stonehead Beck, England (Riley *et al.*, 1987; Varker, 1994), as well as from the Donets Basin, Ukraine (Nemirovskaya & Nigmadganov, 1994), south Tienshan, Uzbekistan (Nigmadganov & Nemirovskaya, 1992a, b; Nemirovskaya & Nigmadganov, 1994), the southern Urals, Russia (Pazukhin *in* Kulagina *et al.*, 1992), the Cantabrian Mountains and Pyrenees in northern Spain, as well as in southern France (Sanz-López *et al.*, 2006, 2007). The lowermost Pennsylvanian *Declinognathodus praenoduliferus* Zone was also first defined in the Aksu section (Nemirovskaya & Nigmadganov, 1994). Later, the zonal index was also encountered in the south Urals (Pazukhin *in* Kulagina *et al.*, 2000, 2001) and the Cantabrian Mountains (Sanz-López *et al.*, 2006; Nemyrovska *et al.*, 2008).

The joint occurrence of the latest Mississippian conodonts with the earliest Pennsylvanian ones, as observed in the Aksu section, was also recorded from other Eurasian areas. At Aksu the Mississippian species of *Gnathodus* and *Lochriea* cross the mid-Carboniferous boundary to join the first Pennsylvanian species. These Mississippian elements disappear later at the height of their abundance. In the La Lastra section the Mississippian conodonts, which are still found a little above the mid-Carboniferous boundary, are only represented by single specimens.

The four lower Pennsylvanian conodont zones of the La Lastra section may be correlated with the three zones distinguished in the Aksu section. Indeed, the conodont succession is virtually the same in the two different areas, with the exception of the earlier occurrence of *Id. asiaticus* at La Lastra. In the Aksu section *Id. asiaticus* occurs together with the other species of *Idiognathoides*. This earlier occurrence of *Id. asiaticus* might support speculation on the origin of *Id. sinuatus* as having been derived from *Id. asiaticus* (Pl. 3, fig. 7). All four earliest Pennsylvanian conodont zones at La Lastra are supposed to coincide with the lowermost Pennsylvanian *Homoceras* Ammonoid Zone, to judge by the record from Aksu where goniatites occur (Nikolaeva, 1994; Nemirovskaya & Nigmadganov, 1994). In shallower water areas, the representatives of the genus *Idiognathoides* appear later, viz. at the beginning of the *Reticuloceras* Ammonoid Zone (Higgins, 1975; Nemirovskaya, 1974, 1999; Nemirovskaya & Nigmadganov, 1994). Since the La Lastra section apparently represents relatively deep water (like the Aksu section), it seems reasonable to assume that the lowermost Bashkirian limestones of the Barcaliente Formation above the mid-Carboniferous boundary should correspond in time to the *Homoceras* Ammonoid Zone. The uppermost beds of the Barcaliente Formation at La Lastra are of shallower facies (see above), so it is not surprising to find *Neolochriea glaber* (not found in the Aksu section) together with the more common *Idiognathoides* species in the highest conodont-bearing samples of the Barcaliente Formation.

So far, we only know of two areas with deep-water conodonts across the mid-Carboniferous boundary, viz. south Tienshan and the Cantabrian Mountains. However, mid-Carboniferous boundary conodonts indicating relatively deep water also occur in some sections in the Pyrenees and Graz (Styria, Austria), as well as in the south Urals which, on the whole, represent shallower facies. These sections contain the first representatives of the *Declinognathodus noduliferus* group with ridged margins; not yet the nodular ones characteristic of relatively shallow water. It is supposed that the forms with ridged margins gave rise to the nodular forms. This would mean that the Tienshan and Cantabrian deep-water sections across the mid-Carboniferous boundary contain the most complete conodont successions, and are, therefore, the key sections for correlation.

The mid-Carboniferous boundary at La Lastra is defined by the first occurrence of *Declinognathodus praenoduliferus, D. bernesgae* and *D. noduliferus inaequalis* (*D. inaequalis*). This occurs at the level of sample 9950. The first *D. noduliferus noduliferus* (*D. noduliferus s.l.*) was recorded in sample 9949, a little higher in the section. As to the correlation of the mid-Carboniferous boundary horizon of the La Lastra section with that of the type section (Arrow Canyon) there is no problem; the level of sample 9950 can be correlated with sample 61B, at the mid-Carboniferous boundary at Arrow Canyon. Sample 61B contains *D. noduliferus* (Brenckle *et al.*, 1997, pl. 1, fig. 2), which is quite similar to *D. noduliferus inaequalis* although I regard it to show the trend from *Gn. girtyi simplex* to *D. noduliferus*. It is noted that the form illustrated by Brenckle *et al.* (1997, pl. 1, fig. 3) from

sample 62 looks like *D. noduliferus inaequalis*. Sample 61B also contains transitional forms between *Gn. girtyi simplex* and *D. noduliferus sensu lato*. The *D. noduliferus inaequalis* from La Lastra (Pl. 4, figs. 7, 8, 13, 14) is similar to the first American forms of *D. noduliferus* (Brenckle *et al.*, 1997, pl. 1, figs. 2, 3), thus allowing correlation. In the Aksu section the mid-Carboniferous boundary is more difficult to correlate with that defined at Arrow Canyon. The first declinognathodids in Aksu are *D. praenoduliferus* and *D. bernesgae*, which have not been found at Arrow Canyon. If there were no problem with the origin of *D. noduliferus* (different in North America and Eurasia) it might be assumed that the first *D. praenoduliferus* and *D. bernesgae* would occur in the interval between the samples 61 and 61B. However, since *Gn. postbilineatus* and *Gn. bilineatus* do not occur at Arrow Canyon this seems unlikely. That is why Nemirovskaya & Nigmadganov (1994) proposed to position the mid-Carboniferous boundary at the FAD of the earliest known declinognathodids, that is, *D. praenoduliferus* or *D. bernesgae*. Where the conodont faunas are sufficiently representative, the first appearances of the earliest declinognathodids are closely spaced. This means that the mid-Carboniferous boundary level could be marked by just *D. noduliferus sensu lato*. Although not very precise, it is a reasonable approximation, similar to tracing this boundary worldwide by just *D. noduliferus sensu stricto*.

Systematic palaeontology (TIN)

Genus *Declinognathodus* Dunn, 1966

Type species — *Gnathodus noduliferus* Ellison & Graves, 1941, by original designation.

Declinognathodus noduliferus (Ellison & Graves, 1941) *sensu lato*
Pl. 4, figs. 7, 8, 12-14, 19, 21, 22-24.

1941   *Cavusgnathus nodulifera*, Ellison & Graves, p. 4, pl. 3, fig. 4 [*non* fig. 6 = *D. lateralis*].
1970   *Declinognathodus noduliferus*; Dunn, p. 330, pl. 62, figs.1, 2, text-fig. 90.
1974   *Idiognathoides noduliferus*; Lane & Straka, p. 85, pl. 35, figs. 5, 12 [only].
1975   *Declinognathodus noduliferus noduliferus*; Higgins, p. 54, pl. 14, figs. 15, 16.
1975   *Declinognathodus noduliferus inaequalis*; Higgins, p. 53, pl. 12, figs. 1-7, 12, pl. 14, figs. 11-13, pl. 15, figs. 10, 14.
1975   *Declinognathodus noduliferus japonicus*; Higgins, p. 54, p. 14, figs. 7-10
1978   *Declinognathodus noduliferus*; Nemirovskaya *in* Kozitskaya *et al.*, p. 30, pl. 15, figs.7, 9, 10 [*non* 11-14 = *Decl. marginodosus*].
1980   *Declinognathodus noduliferus noduliferus*; Metcalfe, p. 306, pl. 38, figs. 16, 18.
1980   *Declinognathodus noduliferus japonicus*; Metcalfe, p. 306, pl. 38, figs. 14, 17.
1981   *Declinognathodus noduliferus inaequalis*; Méndez & Menéndez-Álvarez, pl. 1, fig. 1.
1981   *Declinognathodus noduliferus noduliferus*; Méndez & Menéndez-Álvarez, pl.1, fig. 2.
1983   *Declinognathodus noduliferus inaequalis*; Nemirovskaya, pl. 1, fig. 27.
1983   *Declinognathodus noduliferus noduliferus*; Nemirovskaya, pl.1, fig. 28.
1983   *Declinognathodus noduliferus*; Park, p. 63, pl. 5, figs. 1-3.
1983   *Declinognathodus lateralis*; Park, p. 60, fig. 5 [= *Decl. inaequalis* (only)].
1987   *Declinognathodus noduliferus noduliferus*; Nemirovskaya, pl. 16, figs. 7, 9, 11, 20, 21.
1987   *Declinognathodus noduliferus inaequalis*; Nemirovskaya, pl. 1, figs. 6, 13, 14, 19.
1989   *Declinognathodus noduliferus noduliferus*; Wang & Higgins, p. 276, pl. 2, figs. 5-9.
1989   *Declinognathodus noduliferus inaequalis*: Wang & Higgins, p. 276, pl. 13, figs. 5, 12.

1990   *"Declinognathodus" noduliferus*; Grayson *et al.*, p. 363, pl. 1, figs. 21, 22.
1990   *Declinognathodus noduliferus inaequalis*; Nemirovskaya *et al.*, pl. 4, figs. 3-18, 20-22, 24-28.
1992   *Declinognathodus noduliferus*; Pazukhin *in* Kulagina *et al.*, pl. 30, figs. 2-4, 7-10.
1992   *Declinognathodus inaequalis*; Pazukhin *in* Kulagina *et al.*, pl. 30, figs. 5, 6, 11.
1992   *Declinognathodus japonicus*; Pazukhin *in* Kulagina *et al.*, pl. 30, fig. 12 [*non cet*.].
1992b *Declinognathodus noduliferus*; Nigmadganov & Nemirovskaya, pl. 3, figs. 6-14, 16-17 [*non* figs. 3-5,
         15 = transitional forms between *D. praenoduliferus* and *D. noduliferus,* i.e., *D. bernesgae*?].
1993   *Declinognathodus noduliferus*; Nemirovskaya & Alekseev, pl. 3, figs. 4, 12.
1994   *Declinognathodus noduliferus*; Nemirovskaya & Alekseev, pl. 1, figs. 2-4, 7.
1996   *Declinognathodus noduliferus noduliferus*; Krumhardt *et al.,* p. 37, 38, pl. 3, figs. 9-14 [only].
1996   *Declinognathodus noduliferus japonicus*; Krumhardt *et al.,* p. 36, 37, pl. 3, figs. 1-9, 19-22.
1997   *Declinognathodus noduliferus*; Mizuno, p. 250, pl. 12, figs. 6-8.
1997   *Declinognathodus inaequalis*; Mizuno, p. 248, pl. 12, figs. 1-5.
1999   *Declinognathodus noduliferus s.l.*; Nemyrovska, p. 55, pl. 1, figs. 7, 9, 12; pl. 2, figs. 1, 3, 4, 6, 10.
1999   *Declinognathodus noduliferus inaequalis*; Nemyrovska, pl. 1, figs. 7, 9, 12.
1999   *Declinognathodus noduliferus noduliferus*; Nemyrovska, pl. 2, figs. 3, 6, 10.
1999   *Declinognathodus noduliferus japonicus*; Nemyrovska, pl. 2, figs. 1, 4.
2000   *Declinognathodus noduliferus*; Kulagina *et al.*, pl. 2, figs. 8, 10.
2000   *Declinognathodus inaequalis*; Kulagina *et al.*, pl. 2, figs. 4-6 [*non* 14 = *D. lateralis*].
2000   *Declinognathodus japonicus*; Kulagina *et al.*, pl. 2, figs. 11, 12, 22.
2002   *Declinognathodus noduliferus inaequalis*; Pazukhin *et al.,* pl. 1, fig. 12.
2003   *Declinognathodus noduliferus noduliferus*; Wang & Qi, pl. 2, fig. 3.
2003   *Declinognathodus noduliferus japonicus*; Wang & Qi, pl. 2, fig. 9.
2006   *Declinognathodus noduliferus noduliferus*; Sanz-López *et al.*, pl. 1, figs. 3, 4.
2006   *Declinognathodus inaequalis*; Sanz-López *et al.*, pl. 1, figs. 1, 2.

Diagnosis — Platform elongate, narrow and oval in shape, with pointed posterior end. Nodular carina inclines to the outer parapet and merges with the latter at a rather long distance from the posterior end. Nodular parapets parallel. Shallow median groove deep, becoming wider posteriorly behind the slope of carina to the outer parapet.

Remarks — Higgins (1975) distinguished three subspecies within *Declinognathodus noduliferus* based on the distance between the point of junction of carina with the outer parapet and the posterior end of the element. *Declinognathodus noduliferus inaequalis* (Higgins, 1975) was regarded as the oldest. It has the longest carina, which merges with the parapet behind the middle of the platform or close to the posterior end of this element. The next subspecies, *D. noduliferus noduliferus* (Ellison & Graves, 1941), appearing a little later, is characterised by a shorter carina that slopes and merges with the parapet in the middle of the platform or even closer to the anterior end of the platform. The third, youngest subspecies, *D. noduliferus japonicus* (Igo & Koike, 1964), possesses a very short carina and a strongly reduced outer parapet, up to one node at the anterior end of the platform. In the distribution chart and Plate 3 of the present paper, the subspecies are recorded separately. Sanz-López *et al*. (2006) established a new subspecies of *D. noduliferus*, *D. noduliferus bernesgae*, intermediate between *D. praenoduliferus* and *D. noduliferus*. It differs from *D. noduliferus sensu lato* by the depth and shape of the median trough, and the ornamentation of parapets. These characters are sufficiently distinctive to regard it as a discrete species of *Declinognathodus*, rather than a subspecies of *D. noduliferus*.

Declinognathodus noduliferus sensu lato differs from *D. praenoduliferus* Nigmadganov & Nemirovskaya, 1992b, by the presence of a groove between the nodular parapets. The platform of *D. praenoduliferus* is covered by transverse ridges and a groove is absent. Only a split may occur at the anterior part of the platform. *Declinognathodus noduliferus sensu lato* differs from *D. lateralis* (Higgins & Bouckaert, 1968) by the fusion of the carina with the nodular outer parapet and continuation of this structure as a parapet to the posterior end of the element. It differs from *D. marginodosus* Grayson by the fusion of carina with the parapet and by more closely spaced nodes on the parapets. *Declinognathodus noduliferus sensu lato* differs from *D. donetzianus* Nemirovskaya, 1990, by its smooth outer side of the platform, not ornamented by additional nodes.

Range — Bashkirian of Eastern Europe, Urals and Central Asia; Namurian of Western Europe; Lower Pennsylvanian (Morrowan) of North America; Kodani Formation of Japan; Weiningian of China.

Occurrence — Samples 9950 through 9538; upper part of the Barcaliente Formation (lower Bashkirian) at La Lastra.

Material — Thirty-six specimens *(Declinognathodus. noduliferus inaequalis* - 8 specimens: RGM 416 106 ; *D. n. noduliferus* — 28 specimens; RGM 416 097-416 105, 599 234/1, 599 255/1, 599 262/1, 599 263/1, 599 266/1, 599 269/1-2/, 599 270/1-7, 599 271/1-13).

Declinognathodus praenoduliferus **Nigmadganov & Nemirovskaya, 1992a**
Pl. 4, figs. 1-3, 5, 9-11, 15, 18, 20.

1992a *Declinognathodus praenoduliferus* Morphotype 1; Nigmadganov & Nemirovskaya, p. 53, pl. 7, figs. 1, 2.
1992a *Declinognathodus praenoduliferus* Morphotype 2; Nigmadganov & Nemirovskaya, p. 53, pl. 7, figs. 3-6, 8, 9 [*non* 7 = *D. bernesgae*].
1992b *Declinognathodus praenoduliferus* Nigmadganov & Nemirovskaya, p. 262, pl. 2, figs. 6-9, 11-13 [*non* 10, 14 = *D. bernesgae*]; pl. 3, figs. 1, 2.
2000   *Declinognathodus praenoduliferus*; Pazukhin *in* Kulagina *et al.*, pl. 2, figs. 1, 2 [*non* fig. 3 = *D. lateralis*].
2006   *Declinognathodus praenoduliferus*; Sanz-López *et al.*, pl. 1, fig. 7.

Diagnosis — Platform covered by transverse ridges. Short carina almost straight or laterally sloping to the outer side of the element. Median groove absent, only a very short, shallow trough or groove is developed between short carina and inner parapet in the most anterior part of the platform.

Description — The platform of the P1 element is long and narrow, pointed at the posterior end. Short carina can be straight or sloping laterally to the outer side of the element. A short and narrow, shallow trough or groove separates short carina from a poorly developed inner parapet at the most anterior part of the platform (Pl. 4, figs. 1, 3). Inner parapet is better developed than the outer one and consists of two fused nodules or three ridges, or two nodules and one ridge. The outer parapet is reduced to one or (less commonly) two distinct nodes or has a longitudinal bulge instead of the

node. It is separated from the carina by a shallow, short trough. Some specimens show a small, indistinct node or bulge instead of the outer parapet (Pl. 4, fig. 2). In this case, the carina joins the first transverse ridge onto the platform perpendicularly. The whole platform is covered posteriorly by continuous, coarse and widely spaced transverse ridges. These are straight and continuous or, uncommonly, depressed by a continuation of a narrow notch at the anterior part of the platform and look slightly sinuous. In this case the outer part of the platform along the axis is slightly higher than the inner part. In lateral view the upper surface of the platform is slightly convex and gently sloping posteriorly. The basal cavity is deep, wide and almost symmetrical.

Discussion — Originally, two morphotypes were distinguished within *Declinognathodus praenoduliferus*. Morphotype 1 (Nigmadganov & Nemirovskaya, 1992a, pl. 7, figs. 1, 2) was characterised by a narrower platform covered, almost completely, by transverse ridges. A short, generally straight carina joins the first transverse ridge of the outer parapet at a right angle. A narrow, short trough separates the carina from a short, slightly uplifted inner parapet. There is no node (or just an indistinct one) at the anterior part of the outer side of the platform. Morphotype 2 (Nigmadganov & Nemirovskaya, 1992a, pl. 7, figs. 3-9) has a slightly wider platform where the carina slopes to the outer side, avoiding one or two nodes on the outer side of the anterior part of the platform. The outer, transversely-ridged part may be slightly uplifted along the axis of the element. Transverse ridges are sometimes interrupted in the anterior part of the platform, coming down into a narrow median trough, which may be slightly longer and wider than that of Morphotype 1.

Later, after additional sampling of the succession in the Tienshan and re-study of the conodonts, both morphotypes were regarded as intraspecific varieties and not described separately (Nigmadganov & Nemirovskaya, 1992b). However, we now agree with Sanz-López *et al.* (2006), who established the new subspecies *Declinognathodus noduliferus bernesgae*. We regard it as very similar to our Morphotype 2, and consider it to be a transitional form between *D. praenoduliferus* and *D. noduliferus* worthy of species rank.

Remarks — *Declinognathodus praenoduliferus* may be distinguished within the *Declinognathodus* group, consisting of *D. noduliferus sensu lato*, *D. marginodosus* and *D. donetzianus,* by its transversely-ridged platform and the lack of a long, deep medial trough. All other species of *Declinognathodus* are characterised by a nodular parapet (or parapets) with a deep medial trough in between. *Declinognathodus praenoduliferus* differs from the similar *D. bernesgae* Sanz-López *et al.,* 2006, by the same characters. *Declinognathodus bernesgae* has a long medial trough and only the most posterior part of the platform is covered by 1-4 continuous transverse ridges. *Declinognathodus praenoduliferus* differs from *D. lateralis* by the absence of a median groove (trough) between the parapets and by the touching or merging of the carinal nodes with the ridges on the outer parapet of *D. lateralis*.

The specimens from the first Bashkirian samples (9950, 9530, 9946, 9948) are similar to those from the deep-water Aksu section (Nigmadganov & Nemirovskaya, 1992b; Nemirovskaya & Nigmadganov, 1994, pl. 2, fig. 7). Two specimens (Pl. 4, figs. 1, 2), resembling the holotype from the Aksu section, were found in samples 9542B and 9542C

from limestone clasts in a conglomerate lens of the Perapertú Formation, which overlies the Barcaliente Formation disconformably.

Range — Lowermost Bashkirian (early *Homoceras* Ammonoid Zone) of south Tienshan (Uzbekistan), the Urals (Russia) and the Cantabrian Mountains (Spain).

Occurrence — Samples 9529(?), 9950, L-8, LL-8A, 9530, 9949, 9948, Barcaliente Formation (lowermost Bashkirian) at La Lastra.

Material — Fifteen specimens (RGM 382 823, 416 083-416 091, 599 253/1, 599 259/1, 599 270/8-10).

Declinognathodus bernesgae **Sanz-López, Blanco-Ferrera, García-López & Sánchez de Posada, 2006**
Pl. 3, figs. 11, 13, 14; Pl. 4, figs. 4, 16, 17, 25, 26.

1992a   *Declinognathodus praenoduliferus* Morphotype 2 Nigmadganov & Nemirovskaya, p. 53, pl. 7, figs. 7, 9.
1992b   *Declinognathodus praenoduliferus*; Nigmadganov & Nemirovskaya, p. 262, pl. 2, figs. 10, 12, 13; pl. 3, fig. 2 [only].
1992b   *Declinognathodus noduliferus s.l.*; Nigmadganov & Nemirovskaya, pl. 3, figs. 14, 15, 17 [only].
1992b   *Idiognathoides asiaticus*; Nigmadganov & Nemirovska, pl. 4, fig. 8 [only].
1997   *Declinognathodus noduliferus*; Mizuno & Ueno, pl. 1, figs. 10, 11.
1997   *Declinognathodus japonicus*; Mizuno & Ueno, pl. 1, figs. 12, 13.
1997   *Declinognathodus japonicus*; Mizuno, p. 249, pl. 12, figs. 9-12.
2006   *Declinognathodus noduliferus bernesgae*; Sanz-López *et al.*, p. 10,11, pl. 1, figs. 8-13, 15-18 [*non* fig. 14 = *D. noduliferus s.l.*].

Diagnosis — P1 element with transversely ridged margins to the platform and a short carina sloping to the outer side of the platform, one or two nodes on its anterior-outer part and a shallow medial trough. Up to four transverse ridges cover the posterior end of the platform.

Description — The margins of P1 elements are covered by transverse ridges. Short carina slopes to the outer side. One or two nodes are located on the anterior-outer part of the platform side. The central groove is shallow (deeper in the juveniles) and disappears in the posterior part of the platform, where up to four short, transverse ridges occur.

Remarks — *Declinognathodus bernesgae* occupies an intermediate position between *D. praenoduliferus* and *D. noduliferus* (see above). *Declinognathodus bernesgae* has mostly ridged parapets as in *D. praenoduliferus*, but not the nodular ones, as occur in the *D. noduliferus* group. *Declinognathodus bernesgae* has a shallow median groove disappearing in the posterior part of the platform. *Declinognathodus praenoduliferus* does not have a median groove, sometimes only just a notch in the anterior part, whereas *D. noduliferus* has a deep groove between the parapets. *Declinognathodus bernesgae* displays the development of a medial trough by its deepening and widening. This was probably followed

later by the transformation of transverse ridges into rows of nodes on both sides of the platform and, thus, into a formation of nodular parapets (or one parapet and carina) as in *D. noduliferus sensu lato.*

Range — Lowermost Bashkirian (the Barcaliente Formation and the lower part of the Iraty Formation, basal part of the *D. noduliferus* Zone) of the Cantabrian Mountains (Spain) and the Pyrenees (France), respectively. Basal part of the Bashkirian (the Suffinskaya Formation, *D. praenoduliferus* Zone of the Hissar Range, south Tienshan, Uzbekistan). Lowermost Pennsylvanian (*D. noduliferus* Zone) of southwestern Japan (Hina Limestone Group).

Occurrence —Samples 9950(?), 9530, 9948, LL 8A, 9946 and LL8/84 (9536), upper part of the Barcaliente Limestone Formation (lowermost Bashkirian) at La Lastra.

Material —Thirteen specimens (RGM 416 092-416 094, 599 231/1, 599 232/1-3, 599 267/1).

Genus *Gnathodus* Pander, 1856

Type species — *Gnathodus bilineatus* (Roundy, 1926), by subsequent designation (Lane & Ziegler, 1984).

Gnathodus bollandensis Higgins & Bouckaert, 1968
Pl. 1, fig. 5; Pl. 4, fig. 6.

1968   *Gnathodus bilineatus bollandensis*; Higgins & Bouckaert, p. 29, pl. 2, figs. 10-13; pl. 3, figs. 4-8, 10.
1992a *Gnathodus bilineatus bollandensis*; Nigmadganov & Nemirovskaya, p. 57, pl. 1, figs. 2, 4 [*non* fig. 1 = *Gn. truyolsi*].
1996   *Gnathodus bollandensis*; Skompski, pp.197, 198, pl. 6, figs. 1-7, 10-13 [*non* figs. 8, 9 = *Gn. postbilineatus*].
1999   *Gnathodus bilineatus bollandensis*; Nemyrovska, p. 58, pl. 1, fig. 8.
2006   *Gnathodus bilineatus bollandensis*; Sanz-López *et al.*, p. 8 pl. 2, figs. 3-8.
2009   *Gnathodus bilineatus bollandensis*; Pazukhin *in* Nikolaeva *et al.*, pl. 3, fig. 7.

Description — P1 element has a high asymmetrical platform. Long ridged inner parapet is well developed; shorter than the carina, it may sometimes reach the posterior end of the element. Nodular carina is long; in our specimens it is simple, not expanded. The expanded outer platform is mostly rounded; very seldomly it has an irregularly triangular or subquadrate shape. A narrow groove between the carina and parapet is moderately shallow; it extends along the whole length of the platform becoming shallower posteriorly.

Remarks — In spite of a wide range of morphological variation within *Gnathodus bollandensis*, one must agree with Skompski (1996) that the dissimilarities with *Gn. bilineatus bilineatus* are essential enough to treat *Gn. bollandensis* as a separate species (Nigmadganov & Nemirovskaya, 1992a). *Gnathodus bollandensis* differs from its possible ancestor, *Gn. bilineatus bilineatus*, by a less expanded and less ornamented outer

cup (either smooth or weakly ornamented), and by the absence of a row of nodes close or parallel to the posterior third of the outer side of the carina. It differs from its possible descendant, *Gn. postbilineatus* Nigmadganov & Nemirovskaya, 1992a, by a more expanded and less ornamented outer cup, and by a long groove between parapet and carina, which extends to the posterior end of the element. There is no fusion of parapet and carina at the posterior end as in *Gn. postbilineatus*.

Range — Serpukhovian of Europe and Asia.

Occurrence — Samples 9520, LL1A (9521), 9522-9526, 9527, 9957, 9528, 9955, 9952, 9530A; uppermost part of the Genicera Formation and lower part of the Barcaliente Formation at La Lastra.

Material — Fifty-five specimens (RGM 383 670, 416 057, 416 096, 599 209/1-25, 599 211/1-4, 599 213/1-4, 599 214/1-3, 599 215/1, 599 219/1, 599 221/1, 599 225/1-2, 599 228/1-4, 599 230/1, 599 277/1, 599 280/1-2, 599 281/1, 599 282/1-3).

Gnathodus girtyi Hass, 1953 *sensu lato* transition to *Gn. girtyi simplex* Dunn, 1966
Pl. 1, fig. 12.

2005   *Gnathodus girtyi s.l.* transition to *Gn. girtyi simplex*; Nemyrovska, p. 37, pl. 7, figs. 16-20.

Remarks — P1 elements with an elongated platform, which is widest anteriorly and pointed posteriorly. There are two unequal parapets that do not reach the posterior end of the element and a sloping nodular carina; its posterior half is considerably expanded. A well-developed, ridged inner parapet takes two-thirds of the platform length. The outer parapet consists of several nodes, which are shifted posteriorly from the anterior margin. Although resembling *Gn. girtyi simplex*, it differs by possessing a larger number of nodes on the outer parapet (*Gn. girtyi simplex* has just one node). These forms are identical to those from the Lower Serpukhovian (*Lochriea ziegleri* Zone) of the Triollo section, Palencia. Our forms resemble the specimens from Arrow Canyon (Nevada) assigned to *Gn. girty simplex* and which are transitional to *Gn. defectus* Dunn (Brenckle *et al.*, 1997), but differ by the length of its inner parapet.

Range — Lower Serpukhovian of the Cantabrian Mountains (Triollo and La Lastra sections).

Occurrence — Sample LL7 (9520); uppermost part of the Genicera Formation (lowermost Serpukhovian) at La Lastra.

Material — Three specimens (RGM 416 062).

Gnathodus postbilineatus Nigmadganov & Nemirovskaya, 1992a
Pl. 1, figs. 3, 4, 6, 9, 13.

1987   *Gnathodus bilineatus bollandensis*; Riley *et al.*, pl. 2, fig. 12 [only].
1990   *Gnathodus bilineatus bollandensis*; Nemirovskaya *et al.*, pl. 2, figs. 1, 7(?).

1992   *Gnathodus* spp. 2; Pazukhin *in* Kulagina *et al.*, pl. 27, fig. 11.
1992   *Gnathodus* spp. 3; Pazukhin *in* Kulagina *et al.*, pl. 27, fig. 13.
1992a   *Gnathodus postbilineatus*; Nigmadganov & Nemirovskaya, p. 54, pl. 8, figs. 2-7.
1992b   *Gnathodus postbilineatus*; Nigmadganov & Nemirovskaya, p. 262, pl. 1, figs. 7-12; pl. 2, figs. 1-5.
1993   *Gnathodus postbilineatus*; Nemirovskaya & Nigmadganov, pl. 2, fig. 7.
1999   *Gnathodus postbilineatus*; Nemyrovska, p. 58, pl. 1, fig. 5.
2006   *Gnathodus postbilineatus*; Sanz-López *et al.,* p. 8, pl. 2, figs. 11, 12 [only].
2007   *Gnathodus postbilineatus*; Sanz-López *et al.,* pl. 1, fig. 12.
2008   *Gnathodus postbilineatus*; Perret-Mirouse *in* Kullmann *et al.,* pl. 10, fig. 23.

Remarks — Only a few specimens from La Lastra are assigned to *Gnathodus post-bilineatus*, showing the fused posterior part of carina and parapet. The others have a deep trough between the carina and the parapet in the anterior half of the platform, and a very shallow trough filled with transverse ridges on the posterior half. The outer platform is oval, rather narrow and weakly ornamented by irregular nodes or rows of nodes.

Range — *Gnathodus postbilineatus* Zone (uppermost Serpukhovian) of the Tienshan in Uzbekistan, and the Donets Basin, Ukraine. It was reported from the highest Arns-bergian in England (Riley *et al.*, 1987; Varker *et al.*, 1990; Varker, 1994). It was found in Germany (collection of D. Meischner from the Rheinisches Schiefergebirge); also in the Barcaliente Formation (uppermost Serpukhovian) of the Cantabrian Mountains as well as in the Arga and Iraty formations (Serpukhovian and lower Bashkirian) of the Pyr-enees (Spain and France; Sanz-López *et al.*, 2006, 2007; Kullmann *et al.*, 2008).

Occurrence — Samples 9525, 9526, 9956, 9528, 9954, 9953, 9951, 9529, 9529A, 9530A; lower part of the Barcaliente Formation (Serpukhovian) at La Lastra.

Material — Twenty-seven specimens (RGM 416 052-416 056, 599 214/2, 599 218/1, 599 221/1, 599 226/1, 599 229/8, 599 276/1, 599 277/3, 599 278/1, 599 279/3, 599 281/1).

Gnathodus truyolsi Sanz-López, Blanco-Ferrera, Sánchez de Posada & García-López, 2007
Pl. 1, figs. 1, 2.

1992b   *Gnathodus bilineatus bollandensis*; Nigmadganov & Nemirovskaya, pl. 1, fig. 1.
1994   *Gnathodus bilineatus bollandensis*; Nemirovskaya & Nigmadganov, pl. 1, fig. 7 [only].
2007   *Gnathodus truyolsi*; Sanz-López *et al.*, pp. 896, 897, pl. 2, figs. 9-21.
2008   *Gnathodus* ex gr. *bilineatus*; Perret-Mirouse *in* Kullmann *et al.*, pl. 10, figs. 16, 20, 24.

Description — P1 element of the *Gnathodus bilineatus* group with well-developed in-ner parapet oblique to the carina in the posterior part of the platform. The ridged inner parapet is parallel to the carina in the anterior half, and turns distally to come down as a ramp posteriorly. The lengths of the straight and sloping parts of the inner parapet vary; the sloping part may be shorter than the straight part. Several nodes or several rows of small nodes are located between the carina and the inner parapet in the most posterior part of the platform. Nodular carina is slightly sloping. The outer platform is expanded, mainly subquadrate. It is ornamented by subconcentric rows of small nodes.

Remarks — *Gnathodus truyolsi* differs from the other Serpukhovian species of the *Gn. bilineatus* group mostly by the shape of its inner parapet. In the other species of this group the length of the parapet is found to vary; it is mostly straight. The older species of the *Gn. bilineatus* group, such as *Gn. bilineatus remus* Meischner & Nemyrovska, 1999, and *Gn. cantabricus* Belka & Lehmann, 1998, have also a slightly sloping inner parapet, which is much shorter and not as well developed as in *Gn. truyolsi*. The same difference exists also between *Gn. truyolsi* and *Gn. kiensis* Pazukhin *in* Kulagina *et al.*, 1992. The inner parapet of *Gn. kiensis* is not only less developed and shorter, but also lower than that in *Gn. truyolsi*. The adcarinal trough is much deeper in *Gn. truyolsi* than in *Gn. cantabricus* and in *Gn. kiensis*. *Gnathodus truyolsi* is a more advanced member of the *bilineatus* group than all three older species mentioned above. I agree with Sanz-López that the development of a short, distally turned inner parapet may be interpreted as an evolutionary convergence of the above-mentioned pelagic taxa, which have not been found so far in shallower water sections.

Range — Serpukhovian and lowermost Bashkirian of the Hissar Range (South Tienshan, Uzbekistan), Cantabrian Mountains and the Pyrenees in France and Spain.

Occurrence — Samples 9522, 9524, 9526 and 9955 from the lower part of the Barcaliente Limestone Formation (Serpukhovian) at La Lastra.

Material — Five specimens (RGM 416 050-416 051, 599 211/5, 599 217/1, 599 221/2, 599 280/3).

Idiognathoides Harris & Hollingsworth, 1933

Type species — *Idiognathoides sinuatus* Harris & Hollingsworth, 1933, by original designation.

Idiognathoides asiaticus Nigmadganov & Nemirovskaya, 1992a
Pl. 3, figs. 1, 7, 10, 16, 20, 21.

1992a *Idiognathoides asiaticus*; Nigmadganov & Nemirovskaya, p. 55, pl. 8, figs. 8-11.
1992b *Idiognathoides asiaticus*; Nigmadganov & Nemirovskaya, p. 263, pl. 4, figs. 6, 9, 11-15 [*non* figs. 8, 10 = *D. bernesgae*].
2000   *Idiognathoides asiaticus*; Pazukhin *in* Kulagina *et al.*, pl. 2, figs. 16, 17 [*non cet.*].
2002   *Idiognathoides asiaticus*; Pazukhin *et al.*, pl. 2, figs. 17, 18 [*non cet.*].

Remarks — Left- and right-sided P1 elements with long and narrow platform covered by widely spaced transverse ridges. Very short trough (sulcus) is present. *Idiognathoides asiaticus* differs from the other idiognathodids by having a platform almost completely ornamented by widely spaced coarse transverse ridges. It differs from *Id. corrugatus* (Pl. 3, figs. 17, 19) and *Id. sinuatus* (Pl. 3, fig. 5) by having only a very short shallow trough (sulcus) at the most anterior part of the platform.

Range — Lowermost Bashkirian of the Tienshan (Uzbekistan), south Urals (Russia) and Cantabrian Mountains (Spain).

Occurrence — Samples 9531c, 9940, 9535, 9538 from the upper part of the Barcaliente Formation (lower Bashkirian) at La Lastra.

Material — Sixteen specimens, three of them from sample 9542, a limestone clast from a conglomerate in the Perapertú Formation (RGM 416 107-416 112, 599 242/1-5, 599 255/2, 599 257/1-3, 599 263/2).

Idiognathoides macer **(Wirth, 1967)**
Pl. 3, figs. 3, 4, 12, 18.

1967   *Gnathodus macer*; Wirth, p. 14, 15, figs. 11a-d; pl. 20, figs. 6-10.
1971   *Idiognathoides macer*; Lane *et al.*, pl. 1, figs. 3, 4.
1975   *Idiognathoides macer*; Higgins, p. 49, pl. 10, fig. 10 [*non* figs. 14, 15 = *I. sulcatus*]; pl. 13, fig. 17; pl. 16, fig. 8.
1985   *Idiognathoides macer*; Méndez & Menéndez-Álvarez, p. 78, text-fig. 6.

Remarks — P1 element of *Idiognathoides* with a deep groove between two parapets of equal length. The groove extends to the posterior end. The platform is pointed posteriorly. Outer parapet nodular and the anterior part of inner parapet transversely ridged; its posterior part consists of isolated nodes. Transversely ridged anterior part of the inner parapet is usually shorter than the nodular posterior part. *Idiognathoides macer* is very similar to *Id. sulcatus sulcatus* Higgins & Bouckaert, 1968, but differs from the latter by the ridged anterior part of the inner parapet.

Range — Lowermost Pennsylvanian of the western Pyrenees and the Cantabrian Mountains (Spain). (Although *Idiognathoides macer* in Méndez & Menéndez-Álvarez, 1985, has not been illustrated, I have seen the specimens and confirm the identification.) *Reticuloceras* to *Gastrioceras* Ammonoid Zones of northern England.

Occurrence — Samples 9534 and 9537, upper part of the Barcaliente Formation (lower Bashkirian) at La Lastra.

Material — Fourteen specimens (RGM 416 115-416 118, 599 239/1-2, 599 253/2-9).

Idiognathoides sulcatus sulcatus **Higgins & Bouckaert, 1968**
Pl. 3, figs. 2, 6.

1968   *Idiognathoides sulcata*; Higgins & Bouckaert, p. 41, pl. 41, figs. 6, 7.
1975   *Idiognathoides sulcatus sulcatus*; Higgins, p. 56, pl. 13, figs. 11, 12, 16; pl. 15, fig. 15.
1996   *Idiognathoides sulcatus*; Skompski, p. 206, pl. 9, fig. 8.
1999   *Idiognathoides sulcatus sulcatus*; Nemyrovska, pp. 72, 73, pl. 3, figs. 1, 5, 7, 12, 15, 17.

Remarks — P1 elements with two straight, nodular parapets of equal length and height, extending to the posterior end of the platform. Platform is pointed posteriorly. Rather deep narrow groove occurs between the parapets. *Idiognathoides sulcatus sulcatus* differs from *Idiognathoides sulcatus parvus* by having straight parapets of equal length (whereas *Id. sulcatus parvus* has the inner parapet much shorter than the outer one).

Idiognathoides sulcatus sulcatus differs from *Id. sinuatus* by having nodular parapets of equal height whilst *Id. sinuatus* inner parapet is ridged and lower than the outer one. *Idiognathoides sulcatus sulcatus* differs from the very similar *Id. macer* by having the inner parapet covered in nodules, whereas the anterior part of the inner parapet of *Id. macer* is always ridged.

Range — Lower Bashkirian of Europe and Asia.

Occurrence — Samples 9534, 9535 and 9537; upper part of the Barcaliente Formation (lower Bashkirian) at La Lastra.

Material — Eight specimens (RGM 416 113, 416 114, 599 239/2, 599 245/1-2, 599 248/1-3).

Genus *Lochriea* Scott, 1942

Type species — *Spathognathodus commutatus* Branson & Mehl, 1941 (P1 element); *Lochriea montanaensis* Scott, 1942 (M element).

Lochriea ziegleri Nemirovskaya, Perret & Meischner, 1994
Pl. 2, figs. 3, 5, 16.

1994   *Lochriea ziegleri* Nemirovskaya *et al.*, 1994, pp. 312, 313, pl. 1, figs. 1-4, 6, 7, 11, 12; pl. 2, figs. 2, 11.
1995   *Lochriea ziegleri*; Skompski *et al.*, pl. 3, figs. 5, 7-9, 11, 12; pl. 2, figs. 7, 10; pl. 3, figs. 2, 4, 5, 11, 12, 14; pl. 4, figs. 6, 7, 9, 13, 15.
1996   *Lochriea ziegleri*; Skompski, pl. 3, figs. 2, 3.
1999   *Lochriea ziegleri*; Nemyrovska, p. 76, pl. 1, fig. 6.
2005   *Lochriea ziegleri*; Nemyrovska, p. 45, pl. 8, figs. 11, 14, 16.
2005   *Lochriea ziegleri*; Qi & Wang, pl. 1, figs. 14, 15, 17, 18.
2008   *Lochriea ziegleri*; Kullmann *et al.*, pl. 8, figs. 2, 6, 8.
2009   *Lochriea ziegleri*; Nikolaeva *et al.*, pl. 3, fig. 6 [*non cet.*].

Remarks — P1 elements of this species are ornamented by rows of large, discrete nodes located on thick ridge-like elevations on both sides of the cup close to its posterior margin. This distinguishes it from the other strongly ornamented *Lochriea* species (see below). Among the few examples found in the La Lastra section, only one broken specimen has rather well-developed ridges consisting of fused nodes. These ridges are located very close to the posterior margins of the platform (Pl. 2, fig. 5). The other specimens are transitional between *L. nodosa* (Bischoff, 1957) and *L. ziegleri* (Pl. 2, fig. 3). RGM 416 077 (Pl. 2, fig. 16) has weakly developed ridges close to the posterior margin of the platform and, therefore, cannot be regarded as a transitional form between *L. nodosa* and *L. ziegleri*, as nodes of the former are located usually in the middle of the platform sides (see Pl. 2, fig. 13). It is considered here to be a juvenile of *L. ziegleri*.

Range — Serpukhovian of Eurasia; uppermost Viséan through Serpukhovian of the Rheinisches Schiefergebirge, Germany.

Occurrence — Sample 9520, uppermost part of the Genicera Formation (lowermost Serpukhovian) at La Lastra.

Material — Four specimens (RGM 416 075- 416077, 599 214/1).

Lochriea senckenbergica **Nemirovskaya, Perret & Meischner, 1994**
Pl. 2, fig. 12.

1994   *Lochriea senckenbergica*; Nemirovskaya *et al.*, p. 313, pl. 1, fig. 5; pl. 2, figs. 7-10, 12.
1995   *Lochriea senckenbergica*; Skompski *et al.*, pl. 2, figs. 1-3, 6; pl. 3, fig. 13; pl. 4, figs. 8, 10-12.
1996   *Lochriea ziegleri*; Skompski, pl. 3, fig. 1.
1997   *Lochriea nodosa*; Mizuno, pl. 11, fig. 11.
1998   *Lochriea senckenbergica*; Belka & Lehmann, pl. 4, figs. 3-5.
2005   *Lochriea senckenbergica*; Nemyrovska, p. 44, pl. 8, fig. 12
2005   *Lochriea nodosa*; Qi & Wang, pl. 1, figs. 2, 10.
2005   *Lochriea cruciformis*; Qi & Wang, pl. 1, fig. 13 [only].
2008   *Lochriea senckenbergica*; Kullmann *et al.*, fig. 8 (18).

Remarks — *Lochriea senckenbergica* is one of four strongly ornamented, advanced, latest Mississippian species of *Lochriea*. Its P1 element has two large, high nodes or bars located on both sides of the central part of the platform (cup). It differs from the similar *L. ziegleri* by the central position of higher nodes or bars, and from *L. multinodosa* by its ornamentation; the latter has a wide and large platform ornamented by numerous small nodes. *Lochriea cruciformis* (Clarke, 1960) is characterised by thin, straight ridges on both sides of the platform connected to carina, whilst *L. senckenbergica* possesses a larger, nodular ornamentation not connected to the carina (see Pl. 2, fig. 4). However, there are many transitional forms between *L. senckenbergica* and *L. cruciformis* that show isolated ornamentation extending from the carina to the connected ones. Our specimens mostly have isolated big nodes or bars, but some of these have additional nodes between the large node and carina on the outer side, which looks like a junction to the carina (Pl. 2, fig. 12b).

Range — Serpukhovian of Eurasia; uppermost Viséan through Serpukhovian of the Rheinisches Schiefergebirge (Germany).

Occurrence — Samples 9522, 9957, 9956, 9529A, lower part of Barcaliente Formation (Serpukhovian) at La Lastra.

Material — Six specimens (RGM 416 079, 599 212/1, 599 274/1, 599 279/1, 599 281/1, 599 282/1).

Genus *Neolochriea* Mizuno, 1997

Type species — *Neolochriea hisaharui* Mizuno, 1997, by original designation.

Diagnosis — Scaphate pectiniform elements with an oval elongated, mostly smooth platform pointed posteriorly and a long, thick, nodular carina.

Description — The oval or elliptical platform of P1 elements is mostly smooth or bears additional ornamentation such as one or more rows of small weak nodes parallel to the carina. Sometimes, they look like low weak parapets much shorter than the carina. The blade is about half the length of the platform. The carina is ornamented by nodes, which are becoming thicker posteriorly. It is sometimes ornamented by short transverse ridges. The carina extends down to the posterior end of the element. The basal cavity is large.

Remarks — *Neolochriea* Mizuno is similar in shape to *Lochriea* Scott, 1942, its probable ancestor, but differs from the latter by a longer and better-developed platform. Although Mizuno described the platform of *Neolochriea* as mostly smooth, the majority of the illustrated and described species show a linear ornamentation parallel and close to the carina, which sometimes resembles weak parapets. It differs from *Ferganaegnathodu*s Nemirovskaya & Nigmadganov, 1993, by a nodular carina and in having two unequally high parapets (Nemirovskaya & Nigmadganov, 1993). From *Idiognathoides* Harris & Hollingsworth, 1933, it differs by the median junction of the blade to the platform and the absence of a sulcus in the anterior part of the platform. Mizuno (1997) regarded *Neolochriea* as an ancestor of *Lochriea* and a probable descendant of *Idiognathoides*. Even though the apparatus of *Neolochriea* is unknown, the conodonts assigned to this genus cannot be referred to any other known Pennsylvanian genus. Like the representatives of the genus *Ferganaegnathodus*, they are short ranging. They appeared after the mid-Carboniferous extinction event and played their role in the subsequent recovery of conodont faunas.

Range — Lower Bashkirian of Spain, France, Austria, Kyrghyzstan and Japan.

Neolochriea glaber (Wirth, 1967)
Pl. 3, fig. 9.

1967   *Gnathodus glaber*; Wirth, pp. 210, 211, pl. 29, figs. 1-5.
1977   *Gnathodus glaber*; Ebner, pp. 469, 470, pl. 5, figs. 1-3.
1985   *Paragnathodus glaber*; Méndez & Menéndez-Álvarez, p.76, 77, fig. 4.
1993   *Gnathodus glaber*; Perret, pl. 109, figs. 2, 5-7.

Description — P1 elements with oval-triangular shaped platform, pointed at the posterior end. Platform sides flat, slightly swollen. The blade joins the platform in mid-line of the anterior margin of the platform. It transforms into a carina consisting of small low nodes or denticles in its anterior, shortest part (1/4 to 1/6) and becomes expanded posteriorly. This larger, highly expanded part of the carina consists of 5 to 7 big nodes, which appear sometimes as short transverse ridges. In our specimens the carina extends posteriorly beyond the platform sides.

Remarks — *Neolochriea glaber* was originally found in Lower Namurian strata of the western Pyrenees (Spain). Ebner (1977) later described it from the *Declinognathodus-Idiognathoides* fauna of Graz (Austria) and Perret (1993) from the uppermost Serpukhovian through Lower Bashkirian of the French Pyrenees. Méndez & Menéndez-Álvarez (1985) found it in the basal part of Lower Bashkirian strata in the Cantabrian Mountains.

Ebner (1977) regarded *Neolochriea glaber* as having evolved from *L. commutata* (see Pl. 2, figs. 1, 7, 9-11, 14, 15, 17) and noted that it could have given rise to *Idiognathoides*. Some later workers assigned this species to the genus *Idiognathoides*. However, in spite of its resemblance to species of *Idiognathoides* such as *Id. pacificus* Savage & Barkley, 1983, or *Id. planus* Furduj, 1975, it does not have the main generic characters such as the lateral position of junction of the free blade with the platform. So, the generic assignment of *glaber* remained unclear. However, the erection of *Neolochriea* by Mizuno (1997) allows *glaber* to be referred to this genus, by the shape of its P1 element and by the median junction of the free blade to the platform, as well as its expanded carina. Although *Neolochriea glaber* resembles Mizuno's species from the Hina Limestone of Japan (Mizuno, 1997), it differs from *N. hisaharui* Mizuno, *N. hisayoshii* Mizuno and *N. nagatoensis* Mizuno by the absence of the additional row of nodes parallel to the carina, and the shallow sulcus between the existing two rows of nodes. It differs from *N. koikei* Mizuno, 1997, by the absence of well marked transverse ridges covering the platform completely, giving this species a washboard-like appearance. *Neolochriea glaber* resembles *Idiognathoides convexus* and *Id. pacificus* or *Id. planus* by the general appearance of its platform, but differs by the almost median junction of free blade to its platform, and by the absence of a shallow, very short median trough (sulcus) between carina and an indistinct parapet at the most anterior part of the platform.

A specimen (RGM 382 824; Pl. 3, fig. 8) from sample LL8A (between samples 9530 and 9537) is broken and could only be identified as *Neolochriea* cf. *glaber*. Specimen RGM 416 059 (sample 9538; see Pl. 1, fig. 8) resembles juvenile forms of *Neolochriea nagatoensis* Mizuno, 1997.

Range — Lowermost Pennsylvanian: Namurian of the western Pyrenees, the lowermost Bashkirian of the Cantabrian Mountains, Spain (in a collection examined by the present author); the *Homoceras* through lower *Reticuloceras* ammonoid zones or *Declinognathodus-Idiognathoides* conodont fauna of Graz, Austria; lowermost Bashkirian of the Fergana Valley, Kyrghyzstan (unpublished work of the present writer).

Occurrence — Sample 9537, upper part of the Barcaliente Formation (lower Bashkirian) at La Lastra.

Material — Two well preserved specimens (RGM 416 122, 599 250).

Mid-Carboniferous boundary (TIN, RHW & CFWP)

At the VIII International Congress on Carboniferous Stratigraphy and Geology held in Moscow, 1975, it was suggested that the northwest European subdivision of the Carboniferous (into Dinantian and Silesian subsystems) should be replaced by Mississippian and Pennsylvanian, and that the higher subsystem could be subdivided on the Russian model (Bouroz *et al.*, 1977-1978). The Mississippian equated to the Lower Carboniferous as used throughout the former USSR. The Pennsylvanian combined the Middle and Upper Carboniferous of the Russian threefold division. The Pennsylvanian as defined in North America did not seem to have the faunal and floral successions adequate for worldwide correlations. The marine "Middle" and "Upper" Carboniferous

succession in Eastern Europe seemed more adequate with regard to completeness and variety of marine faunas. The problems of correlation and chronostratigraphic subdivision were discussed during the sessions of the IUGS Subcommission on Carboniferous Stratigraphy (SCCS) at Moscow and subsequent venues, one of the most important being the meeting at Leeds in 1981 (Ramsbottom *et al.*, 1982). A major problem was the correct use of the Namurian Stage, defined originally in northwest Europe. In 1974 the Namurian as used in the Soviet Carboniferous Stratigraphic classification was abandoned as being incompatible with the original definition of this term, and the Serpukhovian and Bashkirian stages were adopted with the lower boundary of the latter at the base of the *Reticuloceras* Ammonoid Zone, this being the Lower-Middle Carboniferous boundary in East European usage.

Conodont studies in the Donets Basin, Ukraine, starting with the early 1970s, showed that the main faunal turnover took place earlier, that is, in latest Serpukhovian times (Nemirovskaya, 1974, p. 131, 1978). Indeed, the most important changes in conodont associations occurred close to the base of the *Homoceras* Zone, below the level of the *Reticuloceras* Ammonoid Zone. This seemed to correspond closely to the Mississppian/ Pennsylvanian boundary of North America. The results of these conodont studies were supported by data on other faunal groups, such as ammonoids and foraminifers (Aisenverg *et al.*, 1976).

At the IX International Congress on Carboniferous Stratigraphy and Geology in Washington and Urbana (Illinois), 1979, it was decided to organise a SCCS Field and General Meeting in Leeds, England, where the faunal and floral changes near the mid-Carboniferous boundary would be analysed (Ramsbottom *et al.*, 1982) so as to have the means to decide at which level this boundary should be drawn, and which faunal or/ and floral changes would fit a proper boundary definition. It was also realised that biological changes at the mid-Carboniferous boundary could be related to the beginning of the Permo-Carboniferous Ice Age and that some changes might have come about earlier than others (notably within the land plants).

The mid-Carboniferous boundary, as presently defined (Heckel & Clayton, 2006), divides the Carboniferous into the Mississippian and Pennsylvanian subsystems, which differ both palaeontologically and palaeoclimatologically. The historical names adopted did not imply stratotypes in North America. The early Carboniferous or Mississippian was characterised by rather stable climatic conditions and a relatively high sea level, whilst a more pronounced climatic differentiation and widespread (global) regression was recognised as having taken place at the end of the Mississippian. Sedimentation of the Pennsylvanian could have started at a different age in different parts of continental platforms laid bare by the end-Mississippian regression. It is now generally recognised that this eustatic event would be most noticeable in cratonic areas such as the East European Platform and the North American Midcontinent. A hiatus in sedimentation is often present as well as a change from marine to terrestrial sedimentation. At the same time a strongly reduced taxonomic diversity occurred. It was a time of major extinction of marine invertebrates including the conodonts. Its magnitude varied taxonomically and geographically; that is, about 89 % of conodont species, 80 % of ammonoids, 83 % of corals, 65 % of crinoids, 40-50 % of foraminifers, and about 50 % of brachiopods would have become extinct.

An ad-hoc committee reported on the position of the mid-Carboniferous boundary in biostratigraphic terms (Lane *et al.*, 1985a). Their proposal to use the first entry of *Declinognathodus noduliferus* (Ellison & Graves, 1941) as a suitable marker was approved at the SCCS Meeting held in conjunction with the X International Congress on Carboniferous Stratigraphy and Geology at Madrid in 1983 (Wagner *et al.*, 1985, p. LX). Thus, the mid-Carboniferous boundary was defined by the FAD of *Declinognathodus noduliferus* within the interval transitional between the *Eumorphoceras* and *Homoceras* ammonoid zones. The recovery of the earliest species of the *Declinognathodus noduliferus* group in deep-water sequences, together with all the transitional forms between representatives of the Mississippian genus *Gnathodus* and Pennsylvanian members of the *D. noduliferus* group permits the placement of the mid-Carboniferous boundary at the level of FAD of any species of the *D. noduliferus* group as such. The foraminifera *Globivalvulina moderata*, *Millerella marblensis* and *M. pressa* were chosen as additional markers of this boundary. Candidates for a suitable stratotype were discussed at a SCCS Meeting in Liège, 1992 (Lane, 1993). Several sections with strata deposited in different geological settings were proposed as candidates for the boundary stratotype, viz. the Stonehead Beck section in northern England, the Kalmius section of the Donets Basin (Ukraine), the Aksu section in the Hissar Range (southern Tienshan, Uzbekistan), and Arrow Canyon in Nevada (USA).

Stonehead Beck is a well exposed section of shales with limestone interbeds, with an almost complete ammonoid sequence. However, the facies of the boundary interval were unfavourable for conodonts. Apart from ammonoids, bivalves (near the boundary), spores and pollen, and some conodonts were recorded.

The Kalmius section shows a succession of interbedded shales and limestones, with an almost complete conodont sequence. It also contains many other groups of fossils, important for the correlation. However, a ferruginous zone, 100 mm thick, was found just at the boundary. Since this might represent a stratigraphic gap, this section was rejected.

The Aksu section is the most continuous deep-water succession with the most complete conodont sequence known to extend across the mid-Carboniferous boundary; this section also contains ammonoids. However, this section was also rejected because it did not contain additional fossil groups to the conodonts, ammonoids, deep-water ostracodes, and recrystallised radiolarians; further, access is difficult.

Therefore, it appeared that the only section fulfilling the requirements for a boundary stratotype was that at Arrow Canyon (Lane *et al.*, 1985b). It is a carbonate section with conodonts, foraminifers, brachiopods, *etc*. It contains some minor gaps, as is quite common in carbonate sections, but not at the boundary horizon itself; indeed, the strata on both sides of the boundary lie within the same conodont zone (Lane *et al.*, 1999). It was elected as the mid-Carboniferous boundary stratotype, a decision made at the XI International Congress on Carboniferous Stratigraphy and Geology at Kraków, 1995 (Paproth, 1997, p. 63). Doubts were raised later as to whether this was a wise decision (Barnett & Wright, 2008).

It was noted that the Aksu section was the only one with deep-water faunas. A new mid-Carboniferous conodont assemblage, unique at that time, was discovered and described (Nemyrovskaya & Nigmadganov, 1993). This deep-water section displayed a different conodont distribution pattern across the mid-Carboniferous boundary to that which occurs in shelf sections.

A typical conodont distribution pattern across the mid-Carboniferous boundary in a shallow-water shelf biofacies was documented from the Kalmius section (Donbass) and others, and reads as follows:

(1) Extinction of the Mississippian conodont genera *Gnathodus* and *Lochriea* close to the boundary.

(2) A gradual appearance of new Pennsylvanian genera after the extinction event. This includes the first occurrence of *Declinognathodus*. This taxonomically impoverished fauna characterises the entire interval of the *Homoceras* Ammonoid Zone; only with the *Reticuloceras* transgression another Pennsylvanian genus appears, viz. *Idiognathoides* (Nemyrovskaya, 1978, 1987; Nemyrovskaya & Nigmadganov, 1994). Such a distribution pattern is characteristic for many sections including the deeper-water Stonehead Beck ammonoid-rich section.

The deep-water Aksu section displays a conodont distribution pattern different from the above (Nemirovskaya & Nigmadganov, 1994; Nemyrovska *et al.*, 2008, figs. 3-4). A unique conodont assemblage discovered for the first time at the Aksu deep-water section includes transitional species between the Mississippian and Pennsylvanian conodont faunas. Several new species appeared within the *Declinognathodus noduliferus* group. These display ridged platform margins, not nodular ones like in *Declinognathodus noduliferus sensu stricto*. *Declinognathodus* and *Idiognathoides* appeared almost simultaneously during *Homoceras* times. A large number of conodonts of the genus *Gnathodus* occur here together with the first Pennsylvanian conodonts. Later, *Gnathodus* became extinct quite suddenly (Nigmadganov & Nemyrovskaya, 1992b; Nemirovskaya & Nigmadganov, 1994). The recovery of the earliest species of the *Declinognathodus noduliferus* group in the deep-water sequences, together with all the transitional forms between the representatives of *Gnathodus* and the Pennsylvanian members of the *D. noduliferus* group, permits the placement of the mid-Carboniferous boundary at the level of FAD of any species of the *D. noduliferus* group. The occurrence of transitional species between the Mississippian *Gnathodus bilineatus* group and the Pennsylvanian *D. noduliferus* group led to the assumption that *D. noduliferus* would have originated from *Gn. bilineatus sensu lato*, not from *Gn. girtyi simplex* as several authors had suggested previously, regardless of the fact that *Gn. girtyi simplex* is absent from the Eurasian sections (Nemyrovskaya & Nigmadganov, 1994). The idea that *D. noduliferus* originated from *Gn. bilineatus* (Fig. 8) was expressed by both Grayson *et al.* (1990) and Nemyrovskaya & Nigmadganov (1994). Grayson *et al.* based their conclusion on the hypothetical multi-element apparatuses of these two species. The conodonts from the Aksu section gave support to this idea. The abundant collections of conodonts from the mid-Carboniferous boundary beds in North America contained several of transitional forms between *Gn. girtyi simplex* and *D. noduliferus*. If we are dealing only with P1 elements, as is often the case, especially for the Pennsylvanian conodonts where the ramiform elements are quite rare, it would appear that the American *D. noduliferus* descended from *Gn. girtyi simplex* (Dunn, 1970; Webster, 1969; Lane & Straka, 1974; Lane *et al.*, 1985a, b). The different points of view on the origin of *D. noduliferus* still require additional work on the mid-Carboniferous boundary conodonts. Every new section with conodonts, like the one recorded here from La Lastra, brings additional data useful for solving the problem in hand.

The FAD of *Idiognathoides* as early as the *Homoceras* Zone interval was explained by a biofacies model showing that it would have originated in a deep-water environment

and migrated to shallower waters afterwards, with the *Reticuloceras* transgression. This is why *Idiognathoides* species in platform facies occur only within the *Reticuloceras* Zone (Nemirovskaya & Nigmadganov, 1994).

During the past few decades, other deep-water sections across the mid-Carboniferous boundary were explored in Spain. The conodonts of the Barcaliente Formation of the Cantabrian Mountains and from equivalent strata in the Pyrenees are similar to the deep-water conodonts of the Aksu section. The Spanish conodonts were studied most recently by Sanz-López *et al.* (2006, 2007). Deep water representatives of the *Gnathodus bilineatus* group of species and of the *Declinognathodus noduliferus* group were recorded from the south Urals (Kulagina *et al.*, 2000). The conodonts from these areas show the transition between the latest species of the *Gnathodus bilineatus* group and the earliest *Declinognathodus noduliferus* group. The two different points of view on the origin of *D. noduliferus*, as mentioned above, need additional, more thorough study. The Barcaliente Formation at La Lastra is a case in point (Fig. 8). Its deep-water conodonts are almost identical to those from the Aksu section. First investigated fourteen years ago, the La Lastra section was measured and sampled repeatedly, allowing the results of more complete conodont studies to be presented herein.

Acknowledgements

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Plate 1

Figs. 1, 2. *Gnathodus truyolsi* Sanz-López, Blanco-Ferrera, Sánchez de Posada & García-López, 2007.
Fig. 1. RGM 416 050, sample 9522.
Fig. 2. RGM 416 051, sample 9843.

Figs. 3, 4, 6, 9, 13. *Gnathodus postbilineatus* Nigmadganov & Nemirovskaya, 1992a.
Fig. 3, 6, 9. RGM 416 052, 416 053 and 416 054, respectively, sample 9951. In (6), the posterior end is broken off, but the shallow adcarinal trough and poor ornamentation of the outer platform, as well as the transverse ridge at the posteriormost part of the element, permits assignment to *Gn. postbilineatus*.
Fig. 4. RGM 416 055, sample 9529.
Fig. 13. RGM 416 056, sample 9525.

Fig. 5. *Gnathodus bollandensis* Higgins & Bouckaert, 1968; RGM 416 057, sample 9520.

Fig. 7. *Lochriea scotiaensis* (Globensky, 1967); RGM 416 058, sample 9527.

Fig. 8. *Neolochriea* cf. *nagatoensis* Mizuno, 1997; RGM 416 059, sample 9538, juvenile specimen.

Fig. 10. *Idioprioniodus* sp.; Sb element; RGM 416 060, sample 9522.

Fig. 11. *Ozarkodina* sp; RGM 416 063, sample 9522.

Fig. 12. *Gnathodus girtyi* Hass, 1953 *sensu lato* transitional to *Gn. girtyi simplex* Dunn, 1966; RGM 416 062, sample LL7/84 (equivalent to 9520).

Fig. 14. *Mestognathus bipluti* Higgins, 1961; RGM 416 064, sample 9520.

All specimens are from the La Lastra section, northern Palencia; magnification × 70. Repository: NCB Naturalis, Leiden, The Netherlands.
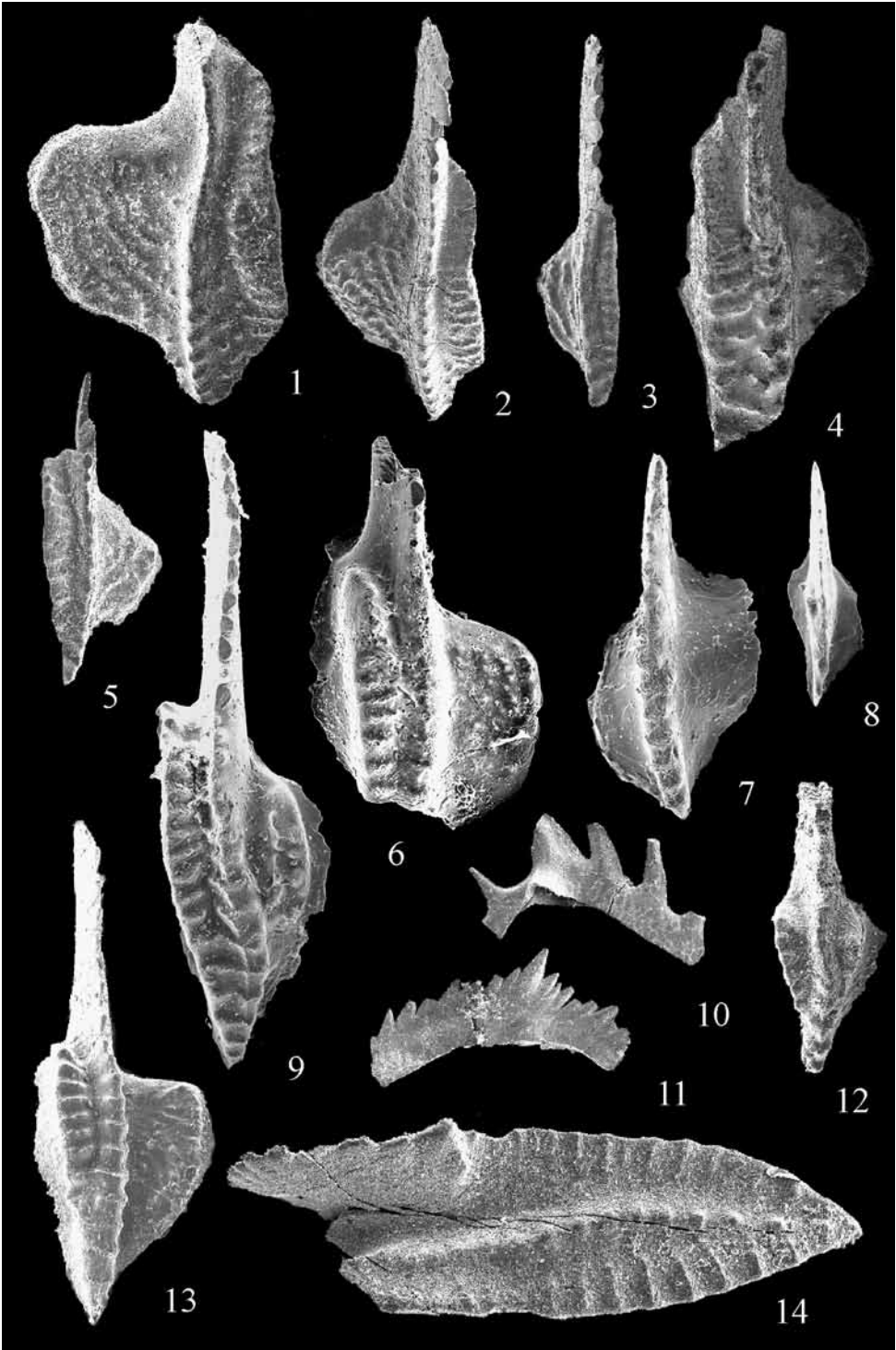
Plate 2

Figs. 1, 7, 9-11, 14, 15, 17. *Lochriea commutata* (Branson & Mehl, 1941).
P1 elements:
Fig. 1. RGM 416 065, oral view, sample 9525.
Figs. 7, 10. RGM 416 066 and 416 067, respectively, oral views, sample 9520.
Fig. 11. RGM 416 068, oral view, sample 9522.
Fig. 15. RGM 416 069, lateral view, sample 9951.

M elements (of *Neoprioniodus singularis* Hass, 1953):
Fig. 9. RGM 416 070, sample 9522.
Fig. 14. RGM 416071, sample 9527.

S element (of *Hindeodella* sp.):
Fig. 17. RGM 416 072, sample 9522.

Figs. 2, 6, 8. *Lochriea monocostata* Pazukhin & Nemirovskaya *in* Kulagina *et al.*, 1992; RGM 416 073, 416 074 and 416 120, respectively, sample 9520.

Figs. 3, 5, 16. *Lochriea ziegleri* Nemirovskaya, Perret & Meischner, 1994; RGM 416 075, 416 076 and 416 077, respectively, juvenile or subadult, sample 9520.

Fig. 4. *Lochriea cruciformis* Clarke, 1960; RGM 416 078, sample 9522.

Figs. 12a, b. *Lochriea senckenbergica* Nemirovskaya, Perret & Meischner, 1994; RGM 416 079, sample 9529A.

Fig. 13. *Lochriea nodosa* (Bischoff, 1957); RGM 416 080, sample 9520.

Fig. 18. *Ozarkodina* sp.; RGM 416 082, sample 9522.

All specimens are from the La Lastra section, northern Palencia; magnification × 70. Repository: NCB Naturalis, Leiden, The Netherlands.
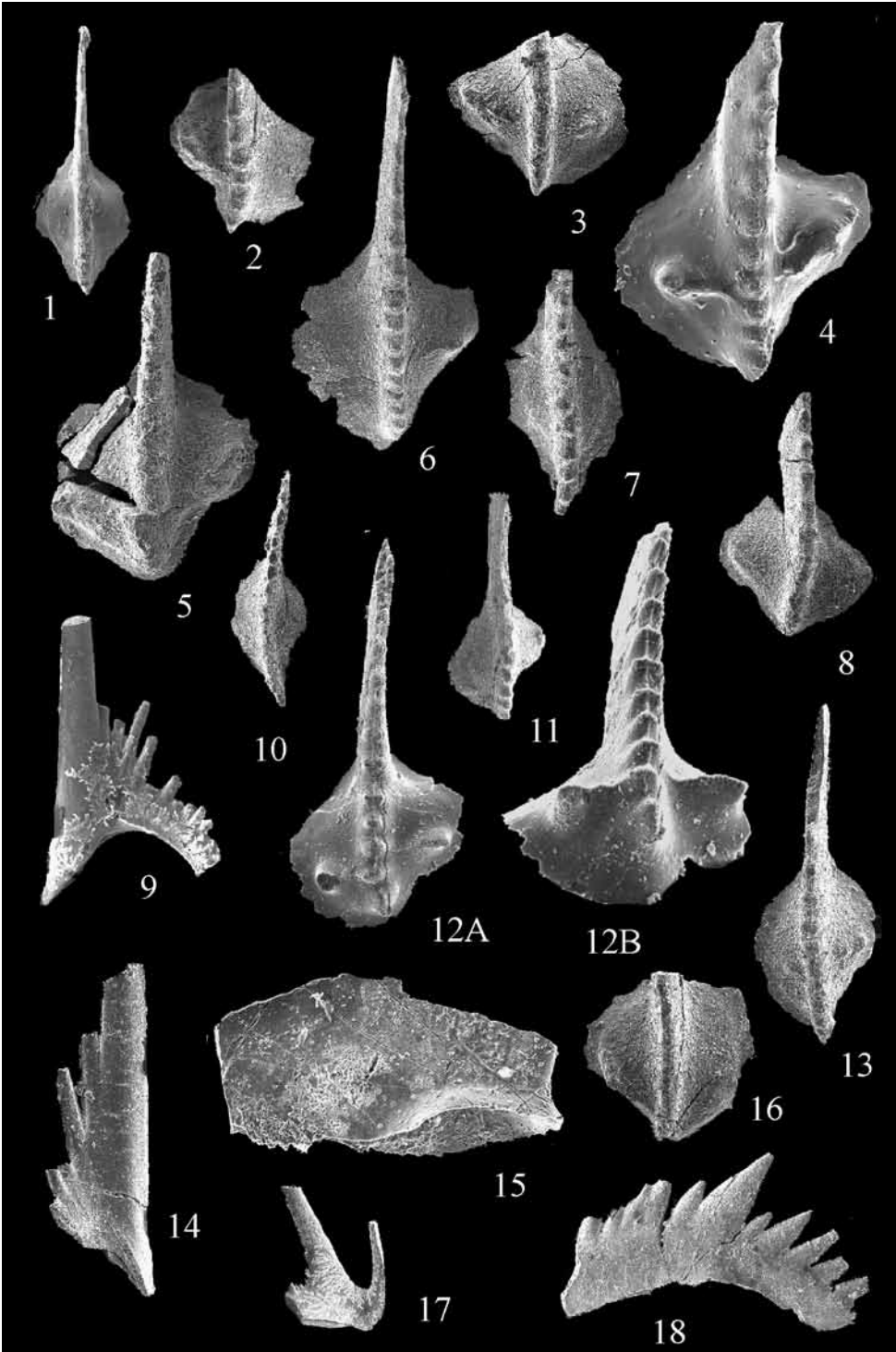
Plate 3

Figs. 1, 7, 10, 16, 20, 21. *Idiognathoides asiaticus* Nigmadganov & Nemirovskaya, 1992a.
Fig. 1. RGM 416 107, sample 9535.
Fig. 7. RGM 416 108, specimen transitional to *Id. sinuatus* Harris & Hollingsworth, 1933, sample 9531B.
Figs. 10, 20. RGM 416 109, 416 111, sample 9531C.
Fig. 16. RGM 416 110, sample 9537.
Fig. 21. RGM 416 112, sample 9534.

Figs. 2, 6. *Idiognathoides sulcatus sulcatus* Higgins & Bouckaert, 1968; RGM 416 113 and 416 114, respectively, sample 9537.

Figs. 3, 4, 12, 18. *Idiognathoides macer* (Wirth, 1967); RGM 416 115, 416 116, 416 117 and 416 118, respectively, sample 9537.

Fig. 5. *Idiognathoides sinuatus* Harris & Hollingsworth, 1933; RGM 416 119, sample 9535.

Fig. 8. *Neolochriea* cf. *glaber* (Wirth, 1967); RGM 382 824, sample LL8A (between samples 9530 and 9537).

Fig. 9. *Neolochriea glaber* (Wirth, 1967); RGM 416 122, sample 9537.

Figs. 11, 13, 14. *Declinognathodus bernesgae* Sanz-López, Blanco-Ferrera, Sánchez de Posada & García-López, 2007
Fig. 11. RGM 416 121, sample 9950.
Fig. 13. RGM 382 823, sample LL8A (between samples 9530 and 9537).
Fig. 14. RGM 384 549, specimen transitional between *D. praenoduliferus* and *D. bernesgae*, sample LL2[1] .

Fig. 15. *Lonchodina* sp.; RGM 416 123, sample 9534.

Figs. 17, 19. *Idiognathoides corrugatus* (Harris & Hollingsworth, 1933).
Fig. 17. RGM 416 124, sample 9537.
Fig. 19. RGM 416 125, sample 9941.

All specimens are from the La Lastra section, northern Palencia; magnification × 70. Repository: NCB Naturalis, Leiden, The Netherlands.
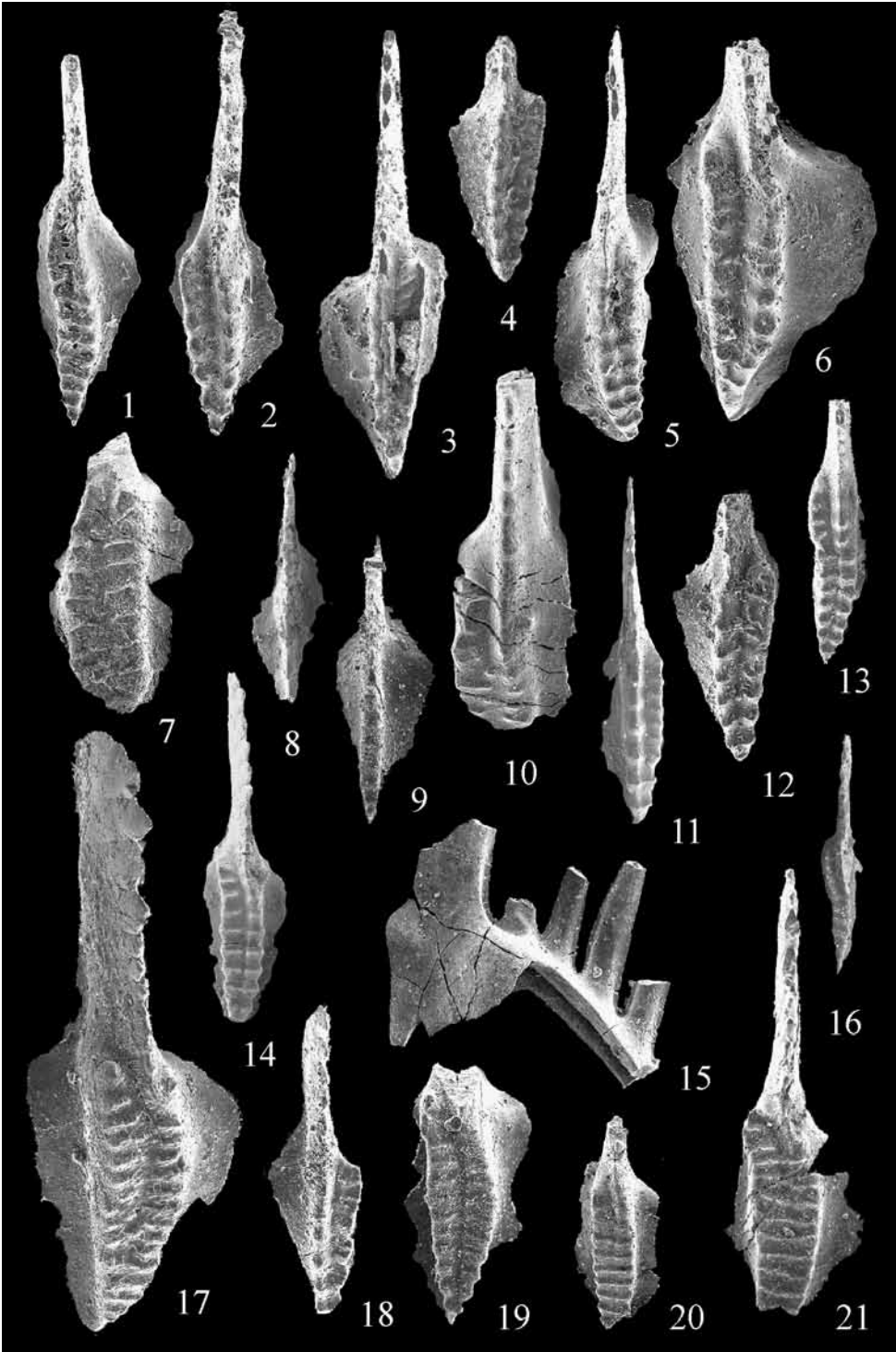
Plate 4

Figs. 1-3, 5, 9-11, 15, 18, 20. *Declinognathodus praenoduliferus* Nigmadganov & Nemirovskaya, 1992a.
Fig. 1. RGM 416 083, sample 9542 C.
Figs. 2, 15. RGM 416 084 and 416 085, respectively, sample 9542 B.
Fig. 3. RGM 416 086, sample 9949.
Fig. 5. RGM 416 087, sample 9950.
Fig. 9. RGM 416 088, sample 9948.
Fig. 10. RGM 416 089, sample 9530.
Fig. 11. RGM 382 823, sample LL-8A (between samples 9530 and 9538).
Fig. 18. RGM 416 090, sample 9946.
Fig. 20. RGM 416 091, sample 9948.

Figs. 4, 16, 17, 25, 26. *Declinognathodus bernesgae* Sanz-López, Blanco-Ferrera, Sánchez de Posada & García-López, 2007.
Figs. 4, 16. RGM 416 092 and RGM 416 093, respectively, sample 9946.
Fig. 17. RGM 382 822, sample LL8/84.
Fig. 25. RGM 416 094, sample 9940.
Fig. 26. RGM 416 095, sample 9530.

Fig. 6. *Gnathodus bollandensis* Higgins & Bouckaert, 1968; juvenile, RGM 416 096, sample 9530A.

Fig. 7, 8, 12-14, 19, 24. *Declinognathodus noduliferus inaequalis* (Higgins, 1975).
Fig. 7. RGM 416 097, sample 9946.
Figs. 8, 14. RGM 416 098 and 416 099, respectively, sample 9530.
Fig. 12. RGM 416 100, sample 9950.
Fig. 13, 19, 24. RGM 416 101, 416 102 and 416 103, respectively, sample 9948.

Figs. 21, 22. *D. noduliferus noduliferus* (Ellison & Graves, 1941)
Fig. 21. RGM 416 104, sample 9537.
Fig. 22. RGM 416 105, sample LL8A (between the samples 9530 and 9537).

Fig. 23. *D. noduliferus inaequalis* (Higgins, 1975) transitional to *D. lateralis* (Higgins & Bouckaert, 1968); RGM 416 106, sample 9948.

All specimens are from the La Lastra section, northern Palencia; magnification × 70. Repository: NCB Naturalis, Leiden, The Netherlands.