

Published in *Rivista Italiana di Paleontologia e Stratigrafia*, 112 (1), 3-22.

**THE MID-CARBONIFEROUS BOUNDARY IN NORTHERN SPAIN:
DIFFICULTIES FOR CORRELATION OF THE GLOBAL
STRATOTYPE SECTION AND POINT**

JAVIER SANZ-LÓPEZ¹, SILVIA BLANCO-FERRERA², SUSANA GARCÍA-LÓPEZ² &
LUIS CARLOS SÁNCHEZ DE POSADA²

1 Facultade de Ciencias da Educación. Campus de Elviña s/n. 15071 A Coruña-Spain. E-mail:
jasanz@udc.es

2 Departamento Geología, Universidad Oviedo, Arias de Velasco s/n, 33005, Oviedo-Spain.
E-mails: silvia.blanco@geol.uniovi.es, sgarcia@geol.uniovi.es, lposada@geol.uniovi.es

Key-words: Stratigraphy, correlation, conodonts, Mississippian/Pennsylvanian, Cantabrian Mountains, Pyrenees.

Abstract. The stratigraphy of latest Arnsbergian to early Chokierian (Serpukhovian/Bashkirian) is described for the Barcaliente Formation in the Cantabrian Mountains. The conodont content has been studied at the Millaró section, where the appearance of *Declinognathodus noduliferus* Ellison & Graves, in the lower metres of the Barcaliente Formation is confirmed, and the location of the Mississippian/Pennsylvanian boundary is discussed. The new subspecies *D. noduliferus berneseae* is described and other records are also studied from the Pyrenean Azkarate section. First occurrences of *Declinognathodus* species are discussed from different basins, and a sequence of first appearances is applied for world-wide correlation. The lowest occurrence of *D. inaequalis* at the Mid-Carboniferous boundary GSSP is preferred as the primary correlation marker, because *D. noduliferus* s.l. includes several different taxa. *Gnathodus* and *Lochriea* species persist above the base of the Pennsylvanian and disappear in the Chokierian (early Bashkirian), as described elsewhere.

Introduction

The Mid-Carboniferous boundary, as recognized in recent years in many parts of the world, applied a pragmatic chronostratigraphic criterion: The first finding of *Declinognathodus noduliferus* Ellison & Graves, 1941 sensu lato [including to *D. noduliferus noduliferus*, *D. n. inaequalis* (Higgins, 1975), *D. n. lateralis* (Higgins & Bouckaert, 1968), and *D. n. japonicus* (Igo & Koike, 1964)]. However, the primary correlation criterion entails a

temporal event derived from the phylogenetic evolution of a conodont, i.e., the first appearance of *Declinognathodus noduliferus* s.l., in its evolutionary sequence from *Gnathodus girtyi simplex* Dunn, 1965. The strict application of this success was only possible in the North American Carboniferous. The Mid-Carboniferous boundary is defined in the Global Stratotype Section and Point (GSSP) precisely in a middle level of the bed of sample 61B, at the Arrow Canyon section (southwestern United States, Lane et al. 1999). As declared by Remane et al. (1996), an occurrence of the primary marker in another section does not automatically determine the position of the correlated boundary. In spite of difficulties in determining whether one is dealing with homotaxial sequences of biotic events in a given section, many fossil occurrences distributed near the boundary make it possible to discuss world-wide correlation. Discussions on chronostratigraphy involve not only systematic palaeontology, but also geologic or biotic data, such as sedimentary processes, palaeoecology, and palaeobiogeography. Boundaries of chronostratigraphic units are first defined at levels with the best potential for global correlation; subsequently, further knowledge of correlative horizons should be undertaken. Given the fact that the publication of a significant amount of data is essential for the correct application and discussion of temporal events, it is unfortunate that the publication of basic data is not a priority nowadays.

In the present paper we attempt to determine the position of the Mid-Carboniferous boundary in Northern Spain. In the Cantabrian Mountains, Higgins (1962, pl. 3, fig. 27) reported *Declinognathodus noduliferus* together with *Gnathodus* and *Lochriea* species at the top of the “Griotte” limestone (= Alba Formation of Comte 1959) at the Getino locality (Fig. 1). This unit underlies the Barcaliente Formation (Wagner et al. 1971). Pennsylvanian beds with *D. noduliferus* were recognized in the middle of the Barcaliente Formation at several sections by Menéndez-Álvarez (1991), within 116 to 150 m above the base of the formation. García-López & Sanz-López (2002b) placed the Mid-Carboniferous boundary a few metres

above the base of the Barcaliente Formation at the Millaró section (Fig. 1). Unfortunately, this position was based on only a single sample where *D. noduliferus* occurred. Consequently, a new and detailed sampling of older Barcaliente beds is necessary in order to confidently discuss the basal boundary of the Pennsylvanian in the Cantabrian Mountains.

In the Pyrenees, the first *Declinognathodus* were collected in the lower seven to fifteen metres of a unit equivalent to the Barcaliente Formation, the Iraty Formation (see Perret 1985, 1993). Our conodont records from the Cantabrian Mountains and the Pyrenees, and discussions about current data, reveal some difficulties regarding the location of the Mid-Carboniferous boundary in Spain. These results may also provide a basis for comparison with the possibilities and difficulties for an accurate correlation of the established GSSP for the Mid-Carboniferous boundary in other localities.

Stratigraphic setting

The Mid-Carboniferous boundary is located in rock units comprising black laminated limestones in the North Iberian Peninsula, specifically, the Barcaliente Formation in the Cantabrian Zone and the Iraty Formation (Perret 1993) in the Pyrenees (Fig. 1). Reuther (1982) and Perret (1993) have reported age and facies correlations between the two units, which were deposited in a common Carboniferous foreland area, the current Ebro Basin.

The Barcaliente Formation consists of 110-420 m of black laminated lime-mudstones to wackestones with abundant organic matter. It was deposited in the passive marginal area of a fore-deep basin located south of the Cantabrian Zone (Fig. 2) and filled by Variscan synorogenic siliciclastic deposits of the Cuevas Formation of Boschma & van Staaldin (1968). The Barcaliente platform is thought to have been formed by carbonate turbidites in a

deep slope setting passing upwards to bioturbated limestones with stromatolite development (Reuther 1977). To the east and north, the restricted shallow-water platform (Eichmüller & Seibert 1984) was prone to evaporite precipitation (González Lastra 1978). Laterally, a prograding wedge of carbonates of the Barcaliente platform, or “middle limestone”, divides the Cuevas Formation into a lower and upper member (Fig. 2).

The Barcaliente Formation overlies basinal shales of the Olaja Member (Wagner et al. 1971) or condensed nodular limestones and shales of the Millaró Beds (Sanz-López et al. 2004), both in the upper part of the Alba Formation. The base of the Barcaliente Formation is placed just above a marker-bed at the Millaró and Valporquero localities, comprising grey, cross-laminated, argillaceous limestone (Fig. 3) with small ammonoids in its base. Upwards, black lime mudstones have even-laminations, cross-laminations and some channel fillings. A scarce fauna of ostracods, textularinid foraminifera, gastropods, bryozoans, and deep-water brachiopods decreases in abundance upwards, while the problematical algae *Globochaete* prevails in bed MILL-13D. *Palaeotextularia* sp. is particularly abundant at the base of formation, in sample MILL-13A but rare in MILL-13B. Above these strata, the fauna in the wackestone of bed MILL-13F is more diverse and abundant, then progressively decreases in variety and amount upwards in the overlying mudstone layers.

Conodonts from the lower part of the Barcaliente Formation (Fig. 1) have also been studied from the Figares (samples 218 and 219, Brime et al. 2001) and Bandujo localities (sample 345 from Brime et al. 2001), the Cares River (sample CPE-14 of Blanco-Ferrera et al. 2005), and the Río Ponga section (samples J-283 and J-285 from the Menéndez-Álvarez collection, University of Oviedo). Conodonts from the upper part of the Barcaliente Formation were recorded in the Las Caldas, Las Xanas and Dosango localities (samples 201, 253 and 264 from Brime et al. 2001, respectively).

According to Delvolvé et al. (1993), the Pyrenean Iraty Formation was deposited in a storm-dominated offshore ramp. The Iraty Formation directly overlies nodular limestones of the Aspe-Brousset Formation in many sections of the Aragonese Pyrenees (Perret 1993), and it lies over the Arga Formation (Wirth 1967; Pilger 1973) in the Azkarate quarry (Basque Pyrenees, Navarre, Fig. 1). At this locality, the Arga Formation comprises a maximum thickness of 46 m of shales and some limestone beds. The Iraty Formation is dolomitized and reaches 320 m in thickness. The lower 26 m of the Iraty Formation in the Azkarate quarry corresponds to the Ochaverri Member of Pilger (1973), where marls and black and grey shales intercalate beds of nodular, argillaceous and laminated dolomitized mudstones (Fig. 4). Carbonates are grouped in thickening-upward meter-scale cycles. Some crinoidal grain-classified carbonates with carbonate clasts occur and slumping beds are included in one of the upper cycles. Mudstones, mostly dolomitized, directly underlie the Asturreta Member of Pilger (1973), where carbonate beds increase in thickness.

The Ochaverri Member is interpreted as different pulses of the prograding carbonate ramp sequence onto slope, slope-toe and basinal facies of the Arga Formation. Slope deposits are so classified due to the presence of grain-classified carbonates and slumping episodes.

New conodont records and chronostratigraphy

The Olaja Member and Millaró Beds contain Arnsbergian ammonoids and conodonts (Kullmann 1962; Wagner-Gentis 1963; Wagner et al. 1971; García-López & Sanz-López 2002a, b). Conodont faunas from the lowermost Barcaliente Formation show a decrease in abundance compared to underlying beds. They are dominated by *Gnathodus bilineatus* subsp. A Ji & Ziegler, 1993, with rare elements of *G. postbilineatus* Nigmatganov & Nemirovskaya,

1992, *G. b. bilineatus* (Roundy, 1926), *G. bilineatus* subsp. C García-López & Sanz-López, 2002b, *G. b. cf. bollandensis* Higgins & Bouckaert, 1968, and several species of the genus *Lochriea* (Fig. 3). Menéndez-Álvarez (1991) determined an Arnsbergian age based on the occurrence of *G. bollandensis* (Higgins & Bouckaert, 1968), but our concept of this taxon is more limited and we propose attributing the conodont associations to the *G. bilineatus* subsp. A local Zone. Rare elements attributed to *G. postbilineatus* can be correlated with the latest Serpukhovian of South Tien Shan (Nemirovskaya & Nigmatganov 1994) and the Donets Basin (Nemyrovska 1999), where the *G. postbilineatus* Zone was defined. *G. postbilineatus* occurs with ammonoids correlated with the late Arnsbergian E_{2c}1 ammonoid subzone in the Donets Basin (Nemyrovska 1999). Varker (1994) and Riley et al. (1994) also illustrated it in the E_{2c}3 and E_{2c}4 ammonoid subzones at Stonehead Beck, England. Conversely, it occurs almost simultaneously with the first appearance of the ammonoid *Isohomoceras*, close to the Bashkirian base in the Tien Shan (Nigmatganov & Nemirovskaya 1992). Nemirovskaya & Nigmatganov (1994) indicated findings of *G. postbilineatus* in other collections from Western Europe (Rheinische Schieferbirge and Pyrenees). Conodont elements reported by Conrad et al. (1980) that we identify as *G. bilineatus* subsp. C come from the Hassi-Taïbine Gypsum in the Reggan Basin (Central Sahara). As a matter of fact, they were collected in the *Titanaria africana* horizon and below it, in beds considered as latest Arnsbergian (Manger et al. 1985) or earliest Bashkirian (Lys 1985) in the Béchar Basin (Algeria).

The first elements of *Declinognathodus*, *Declinognathodus noduliferus berneseae* n. subsp. (Pl. 1, figs 9-11), appear in the wackestone bed of sample MILL-13F at the Millaró section (Fig. 3). Menéndez-Álvarez (1991) used the first appearance of species of *Declinognathodus* as the base for his *noduliferus-lateralis* Zone and for the base of the Chokierian in the Cantabrian Mountains. We consider *D. n. berneseae* to be integrated in the concept of *Declinognathodus noduliferus* s.l., the index species for the base of the

Pennsylvanian (Lane et al. 1999). Hence, the Mid-Carboniferous boundary should be located between 2.5 and 2.8 m above the base of the Barcaliente Formation.

Sample 219, from bioturbated grey limestones at Figares, contains a small element of *D. n. bernesgae* (Pl. 1, fig. 8) together with *Lochriea nodosa* (Bischoff, 1957), *L. commutata* (Branson & Mehl, 1941), *L. mononodosa* (Rhodes et al., 1969), *G. b. bilineatus*, *G. bilineatus* cf. *bollandensis*, *G. b.* subsp. A, and *G. postbilineatus*. A similar association (*G. b. bilineatus*, *G. bilineatus* cf. *bollandensis*, and *Gnathodus bilineatus* subsp. A) from black limestones of the Barcaliente Formation at Bandujo (sample 345) contains *Declinognathodus praenoduliferus* Nigmatdganov & Nemirovskaya, 1992 (Pl. 1, fig. 7); consequently, it can be correlated with the *D. praenoduliferus* Zone of Nigmatdganov & Nemirovskaya (1992) from Central Asia.

Younger beds of black laminated limestones at Figares (sample 218) provided *D. inaequalis* (Pl. 1, figs 1-2), *D. n. noduliferus*, *D. japonicus* (Pl. 1, fig. 5), and a small element of *Idiognathoides sinuatus* Harris & Hollingsworth, 1933 (Pl. 2, fig. 13), but lacked elements of *Gnathodus* or *Lochriea*. Other samples from the upper part of the Barcaliente Formation yielded *D. lateralis* at Las Xanas (Pl. 2, figs 15-16), *D. lateralis* with *D. n. noduliferus* at Las Caldas (Pl. 1, figs 3-4; Pl. 2, fig. 14), and *Idiognathoides sinuatus* at Dosango (sample 264).

Menéndez-Álvarez (1991) recorded species of the genera *Gnathodus* and *Lochriea* from the lower half of the Barcaliente Formation (90-110 m above the base) and from the lower member and lower part of the middle member of the Cuevas Formation. He recovered *Declinognathodus inaequalis*, *D. noduliferus*, *D. lateralis*, just above *D. japonicus*, without Mississippian genera, 116 to 150 m above the base of the Barcaliente Formation at several Cantabrian localities. We consider these associations to be from levels higher than the earliest Chokierian and sometimes probably Alportian in age.

The upper part of the Barcaliente Formation (Fig. 2) yielded conodonts that can be correlated with the *sinuatus* Zone (Kinderscoutian, Bashkirian) after Menéndez-Álvarez (1991, Barcaliente section). Wagner et al. (1971) documented Kinderscoutian plant remains from the middle member of the Cuevas Formation. On the basis of cephalopod and spore remains, a Kinderscoutian age is also accepted for siliciclastic beds of the upper member of the Cuevas Formation, which overlies the Barcaliente Formation (Wagner et al. 1971; Kullmann 1979).

In the Pyrenees, a few elements of *D. n. bernesgae* were recovered from the lower beds of the Ochaverri Member of the Iraty Formation at the Azkarate quarry (Fig. 4). The Ochaverri Member contains associations dominated by *Gnathodus* and *Lochriea* elements, where *G. bilineatus* subsp. A, *G. b. bollandensis* (Pl. 2, figs 3-8), and *G. postbilineatus* (Pl. 2, figs 9-12) are important forms.

An early Bashkirian (Pennsylvanian) age is usually assigned to the lower seven to fifteen metres of the Iraty Formation from in the Pyrenees based on the presence of *Declinognathodus* (see Perret 1985, 1993) in the *D. noduliferus* Zone. *Gnathodus* and *Lochriea* are reported from the lower part of the latter zone (Perret & Weyant 1994) and locally with *Idiognathoides* (in a probably reworked association).

A lower location of the Mid-Carboniferous boundary at the Azkarate quarry, with respect to other Pyrenean localities, could be explained by a lateral replacement between the Iraty Formation and the upper part of the Arga Shales. Delépine et al. (1929) determined the presence of Arnsbergian ammonoids *Eumorphoceras bisulcatum* Girty, 1909, *Nuculoceras nuculum* Bisat, 1924, and *Prolecanites quinquelobus* Kittl, 1905 in shales below the Iraty Formation at Lauribar Valley.

Systematic palaeontology

Described specimens are housed in the Department of Geology (Palaeontology section), University of Oviedo, Spain, abbreviated DPO.

Family Gnathodontidae Sweet, 1988

Genus *Gnathodus* Pander, 1856

Type species: *Gnathodus bilineatus* (Roundy, 1926), emend. Lane & Ziegler, 1984

***Gnathodus bilineatus bollandensis* Higgins & Bouckaert, 1968**

Plate 2, Figs 3-8

1968 *Gnathodus bilineatus bollandensis* Higgins & Bouckaert, pl. 2, figs 10 and 13; pl. 3, figs 5-7 (only).

1975 *Gnathodus bilineatus bollandensis* - Higgins, pl. 11, figs 5, 8-9 (only).

1979 *Gnathodus bilineatus bollandensis* - Nemirovskaya in Aisenverg et al., pl. 6, figs 13-14.

1980 *Gnathodus bilineatus bollandensis* - Conrad, Lys & Weyant, text-pl. 1, figs 9-10.

1987 *Gnathodus bilineatus bollandensis* - Riley et al., pl. 2, figs 7-8 (only).

1996 *Gnathodus bollandensis* - Skompski, pl. 6, figs 3 and 7 (only).

2001 *Gnathodus bilineatus bollandensis* - Kulagina et al., pl. 6, figs 12-13.

Examined material. 22 Pa elements from samples NA-7 (DPO 15154), NA-8 (DPO 15111-DPO 15115, DPO 15155), NA-9 (DPO 15156) and NA-24 (DPO 15117, DPO 15157) at the Azkarate quarry, Pyrenees.

Remarks. Since *G. b. bollandensis* covers a wide morphological range, studies of large collections will be necessary to clarify the status of this taxon. The original material from

Higgins & Bouckaert (1968) includes several different morphs. The holotype and some elements of Higgins & Bouckaert (1968, pl. 2, figs 10, 13; pl. 3, figs 5-7) show a deep trough between the inner parapet and the carina. The inner parapet is high, composed of a row of nodes that does not reach the posterior end of the carina. The outer platform is narrow and ornamented by few low nodes near the carina or in the outer anterior part. Higgins later (1975, pl. 11, figs 5, 8-9) illustrated this same morphology in samples from England. It seems to be a variation of *G. bilineatus schmidti* sensu Meischner (1971, fig. 2) nomen nudum. Meischner (1971, fig. 3) published drafts of elements from different Arnsbergian localities in Germany, where the adcarinal trough is long in older elements, but reduced to $\frac{3}{4}$ and finally to $\frac{1}{2}$ of the inner platform length in younger elements.

Apparently, the original material of *G. b. bollandensis* includes other forms apart from the holotype. Higgins & Bouckaert (1968, pl. 3, fig. 4) and Higgins (1975, pl. 11, figs 10-14) illustrated elements with an inner parapet composed of transverse ridges, ending close to the posterior tip of the carina in mature elements, with a narrow outer cup bearing low nodes homogenously arranged.

Some elements from the Azkarate quarry (Fig. 4) assigned to *G. b. bollandensis* (samples NA-8, NA-9, NA-24) show a deep adcarinal trough and an outer platform that is either smooth or has only a few nodes (Pl. 2, figs 3-4). However, other more ornamented elements are included in *G. b. cf. bollandensis*, with shallow, narrow adcarinal troughs and nodes arranged in concentric rows on the outer platforms (Pl. 2, figs 1-2). Certain elements of *G. b. bollandensis* display a ridge located in the anterior outer platform that is at right angles to the carina, and located in the anterior outer platform (Pl. 2, fig. 6), similar to one in an element of *G. b. schmidti* sensu Meischner (1971).

Some elements of *G. b. bollandensis* from sample NA-8 present a deep adcarinal trough and a reduced platform (Pl. 2, fig. 7), but the parapet reaches the end of the carina (Pl. 2, fig. 8)

and the trough only extends to the posterior platform up to transverse ridges (Pl. 2, fig. 5). Occasional elements have a sub-quadrate outer platform, while others are triangular. Both types may have low nodes, sometimes arranged in concentric rows or with ridges at right angles to the carina. Similar elements were illustrated by Nemirovskaya & Nigmadganov (1993, pl. 2, fig. 1) from Serpukhovian slope to basinal settings of the South Fergana (Central Asia) and the Protvinsky Horizon of the Donets Basin (Eastern Europe, Nemirovskaya in Aisenverg et al. 1979, pl. 6, figs 13-14).

Gnathodus postbilineatus Nigmadganov & Nemirovskaya, 1992

Plate 2, Figs 9-12

1974 *Gnathodus bilineatus* cf. *bollandensis* - Austin, Conil, Groessens & Pirlet, pl. 1, fig. 16 (only).

1974 *Gnathodus bilineatus bilineatus* - Austin, Conil, Groessens & Pirlet, pl. 1, fig. 25 (only).

1987 *Gnathodus bilineatus bollandensis* - Riley et al., pl. 2, fig. 12 (only).

1992 *Gnathodus postbilineatus* Nigmadganov & Nemirovskaya, p. 262-263, pl. 1, figs 7-12; pl. 2, figs. 1-5.

1993 *Gnathodus postbilineatus* - Nemirovskaya & Nigmadganov, pl. 2, fig. 7.

1996 *Gnathodus bollandensis* - Skompski, pl. 6, figs 2, 9 and 13 (only).

Examined material. 16 elements from samples NA-7 (DPO 15154), NA-8 (DPO 15109, DPO 15124, DPO 15155), NA-9 (DPO 15156) and NA-24 (DPO 15108, DPO 15125, DPO 15157), Iraty Formation at the Azkarate quarry, Pyrenees. 6 elements from samples MILL-13A (DPO 15056), MILL-13E (DPO 15063), MILL-13F (DPO 15100), 219 (DPO

15159), J-283 and J-285 from the Menéndez-Álvarez collection, Barcaliente Formation, Cantabrian Mountains.

Remarks. Elements assigned to *G. postbilineatus* have teeth fused with the inner parapet at the posterior part of the carina. The parapet is separated from the carina by a very narrow, shallow adcarinal trough at the anterior part of the inner platform. The outer platform is small and nodes are more abundant than in the original material from Central Asia (Nigmadganov & Nemirovskaya 1992). This kind of ornamentation is also present in the Cantabrian element from sample J-283.

Some elements from samples NA-8, NA-9 and NA-24 are assigned to *G. postbilineatus* because they have a posterior transverse ridge joining the posterior carina and the inner parapet. However, they have a long trough between the carina and the inner parapet. Nemirovskaya & Nigmadganov (1993, pl. 2, fig. 7) included and illustrated an element from South Fergana (Central Asia) identical to those we found. On the other hand, the deep anterior adcarinal trough makes them similar to the “Ruhruterweg” morph of *G. b. schmidti* of Meischner (1971, fig. 3) nomen nudum, although the latter has varied ornamentation on the outer platform.

Family Idiognathodontidae Harris & Hollingsworth, 1933

Genus *Declinognathodus* Dunn, 1966

Type species: *Cavusgnathus nodulifera* Ellison & Graves, 1941

Remarks. Dunn (1966) defined the genus *Declinognathodus* based on the position of the medial carina declined to the outer side of the platform and the presence of a node or

nodes on the outer platform before the bend of the blade. Dunn (1970) interpreted that *Gnathodus girtyi simplex* gave rise to *Declinognathodus*, pointing to the slightly sinuous outline of the carina in some elements of *G. g. simplex*, where it may bend gently outwards and have one or two nodes on the outer platform. Later, elements considered transitional with *Declinognathodus* were documented by different authors (Lane et al. 1985, 1999). *Declinognathodus* has a more pronounced declination and a more developed median longitudinal trough than *G. girtyi simplex*. Koike (1967) considered *G. g. simplex* in the range of variability of *Declinognathodus noduliferus*, and accepted its derivation from *G. girtyi* Hass, 1953, including *Declinognathodus* in *Gnathodus* stock. Dunn (1970) expanded the concept of *Declinognathodus* for the forms with a medial longitudinal trough and a long, slightly declined, medial carina as *D. lateralis*. However, Grayson et al. (1990) suggested that Pb elements prove the derivation of *Declinognathodus* from *G. bilineatus* and not from *G. girtyi* stock. In accordance with this notion, *Declinognathodus praenoduliferus* would be derived from *G. postbilineatus* after Nigmatganov & Nemirovskaya (1992), although transitional elements were not illustrated. They suggested that *D. praenoduliferus* originated when the junction of the blade with the platform moved to the mid-line, and the rest of the platform was covered with continuous transverse ridges.

Grayson et al. (1990), among others, also included Pa elements with a straight medial carina, but with a large node on the anterior-outer platform in *Declinognathodus* (forms of the *D. japonicus* stock). We think that diagnostic characters could be the node or nodes located before the bend of the carina, the declined carina, and the short medial anterior carina, but not the length of the medial trough. The current concept of the genus includes some old species where the medial longitudinal trough is short and also modern taxa where the anterior carina is straight.

Declinognathodus noduliferus noduliferus (Ellison & Graves, 1941)

Plate 1, Figs 3, 4

1941 *Cavusgnathus nodulifera* Ellison and Graves, p. 4-5, pl. 3, fig. 4 (only).

Examined material. Two Pa elements (DPO 15134-15135) from sample 201, Barcaliente Formation.

Remarks. *Declinognathodus noduliferus* exhibits variations that were grouped into different subspecies. Higgins (1975) explained that subspecies form a transitional series characterized by the reduction of nodes in the outer-lateral platform. However, while some authors considered *Declinognathodus lateralis* as a different species, others included it in the variability of *D. noduliferus* (Grayson et al. 1990). Accordingly, Krumhardt et al. (1996) suspected that some of the elements of *D. lateralis* were ecophenotypic variations and/or gerontic specimens of *D. noduliferus*. Other debated taxa are *D. n. inaequalis* and *D. n. japonicus*. Mizuno (1997) interpreted the subspecies as independent species because of their different forms and stratigraphic appearances, which are convincing arguments in our opinion.

Declinognathodus noduliferus berneseae n. subsp.

Plate 1, Figs 8-18

1962 *Cavusgnathus nodulifera* - Higgins, pl. 3, fig. 27.

1992 *Declinognathodus praenoduliferus* Nigmatganov & Nemirovskaya, p. 262-263, pl. 2, figs 10-14; pl. 3, figs 1 and 2 (only).

- 1992 *Declinognathodus noduliferus* s.l. - Nigmadganov & Nemirovskaya, pl. 3, figs 3, 7, 9 and 13? (only).
- 1992 *Idiognathoides asiaticus* - Nigmadganov & Nemirovskaya, pl. 4, figs 8, 10 (only).
- 1996 *Gnathodus girtyi* subspp. transitional to *Declinognathodus* spp. – Krumhardt et al., p. 42, pl. 2, figs 29, 30.
- 1996 *Declinognathodus noduliferus japonicus* – Krumhardt et al., p. 36-37, pl. 3, figs. 1-3 ?, figs 4-8 (only).
- 2001 *Declinognathodus praenoduliferus* - Kulagina et al., pl. 7, figs. 22, 23 (only).
- 2002b *Declinognathodus noduliferus* - García-López & Sanz-López, pl. 5, fig. 5.

Origin of the name. After the Bernesga valley, where the subspecies was collected.

Type specimens. Holotype is the Pa element DPO 15086. The paratypes are elements labelled DPO 15064, DPO 15087 and 15120.

Type horizon. Bed of sample MILL-13F.

Type locality. Millaró section, Province of León.

Examined material. 16 Pa elements from samples MILL-13F (DPO 15.064, DPO15086-15087, DPO 15102), MILL-13G (DPO 15066, DPO 15120), MILL14 (DPO 15067, DPO 15088) at the Millaró section, and sample 219 (DPO 15103), Barcaliente Formation. 7 elements from samples NA-7 (DPO 15104) and NA-8 (DPO 15110, DPO15121-DPO 15123, DPO 15155), Azkarate quarry, Iraty Formation.

Diagnosis. Pa element of *D. noduliferus* with one or, less frequently, two nodes on the anterior-outer side of the platform, carina deflected to the outer side in both left and right elements. Some transverse ridges (1-4) cross the posterior part of the platform, ending the medial trough.

Description. The elements have margins ornamented by transverse nodes. Large elements (samples MILL-13F and NA-8) show two ornamented parapets with ridges. The nodes or ridges are neighbours and form continuous margins, where the ornamentation is

normal to the carina. The carina is deflected in both the left and right elements. The central groove is shallow and disappears in the posterior platform, where short transverse ridges occur. All elements have one or two nodes (Pl. 1, Fig. 13) near the anterior margin of the outer lobe. The basal cavity is wide and asymmetric.

A small element from sample 219 has a slight projection on the anterior-outer node (Pl. 1, Fig. 8). Small elements have a deep, long middle trough (Pl. 1, Figs 9 and 14), but it is always crossed by transverse posterior ridges.

Remarks. The type material of *D. noduliferus* includes the holotype together with *D. lateralis* (Ellison & Graves 1941, pl. 3, figs. 4 and 6, respectively). Elements such as those from the original description show regularly spaced alternating nodes, a little more separated than in our elements. The outer parapet is composed of one or more nodes, usually three in the holotype. The longitudinal trough continues along the length of the platform and, consequently, it seems to be a derived character in relation to *D. n. berneseae*. In our opinion, the Cantabrian specimens correspond to a new subspecies, since they differ somewhat from the type material of *D. noduliferus*. They have one node (occasionally two), while two or normally three nodes are typical of *D. n. noduliferus*. The posterior platform of *D. n. berneseae* is crossed by transverse ridges and the medial trough is short, while it is long and deeper with rare transverse ridges in *D. n. noduliferus*. The elements of *D. noduliferus* illustrated by Mizuno (1997, figs 12.6, 12.8) from the Hina Limestone show four transverse posterior ridges, but the outer-anterior platform bears up to three nodes with characteristics intermediate between the two subspecies. These elements may indicate a transition between the new Cantabrian subspecies and *D. n. noduliferus*, although we cannot verify it with certainty.

Some elements named *D. noduliferus* s.l. by Nigmadganov & Nemirovskaya (1992, pl. 3, figs 3, 7, 9, 13?) from the Aksu section (Central Asia) are included in *D. n. bernesgae*. They have a deflected carina and one nodule in the anterior platform. Other mature elements with two or more nodes could be attributed to *D. n. noduliferus* (see Nigmadganov & Nemirovskaya 1992, pl. 3, figs 4-7).

A part of the elements illustrated as *D. praenoduliferus* by Nigmadganov & Nemirovskaya (1992, pl. 2, figs 10-14; pl. 3, figs 1-2) and by Kulagina et al. (2001, pl. 7, figs 22-23) are included within the variability of *D. n. bernesgae*. As a matter of fact, elements with a short, laterally declined carina that is adjacent to an anterior trough and has a node on the outer-anterior platform are identical to four elements collected from our sample NA-8 (Pyrenees). In contrast, the holotype and other elements of *D. praenoduliferus* described by Nigmadganov & Nemirovskaya (1992, pl. 2, figs 6-9) and Kulagina et al. (2001, pl. 7, figs 24-25) show a shorter anterior trough than *D. n. bernesgae* and a slightly declined or straight anterior carina. Therefore, the platform shows well-developed transverse ridges. Furthermore, the anterior-outer node is attached to the carina with a bridge or connection and is not clearly separated from it. Only one Cantabrian element is assigned to *D. praenoduliferus* (Pl. 1, Fig. 7, Bandujo locality). In accordance with Nigmadganov & Nemirovskaya (1992), *D. noduliferus* derived from *D. praenoduliferus* in Asian deep-water environments through the deepening of the medial trough, the declination of the median carina to the outer margin and the development of parapets. Apparently, old populations of *D. noduliferus* (a morphology here termed *D. n. bernesgae*) evolved from *D. praenoduliferus*, or an ancestral taxon, through the development of a more asymmetrical, slender platform with many posterior transverse ridges and one outer node separated from the carina.

Older elements of *Idiognathoides asiaticus* Nigmadganov & Nemirovskaya (1992, pl. 4, figs 8, 10), with one node on the anterior outer platform and a short anterior trough (1/3 of the

platform length), are also similar to *D. n. berneseae*. Typical elements of *I. asiaticus* described by these authors have no node development and a shorter trough, with a long, narrow, high platform, almost completely crossed by convex, widely spaced ridges, which is a diagnostic character of this species.

Gnathodus g. simplex, transitional to *Declinognathodus n. japonicus* sensu Krumhardt et al. (1996, pl. 2, fig. 30), and the older elements included in *D. n. japonicus* by Krumhardt et al. (1996, pl. 3, figs 4-8) from the lower member of the Wahoo Limestone (Alaska), with one node isolated on the outer platform, a deflected carina, continuous and transverse posterior ridges, are considered to fall within the variation range of *D. n. berneseae*. Posterior transverse ridges are poorly defined in *D. n. japonicus* from younger samples (Krumhardt et al. 1996, pl. 3, figs 1-3), where a central groove is marked.

Illustrated elements from the upper member of the Wahoo Limestone with discrete and rounded nodes, relatively even-noded margins and an undeflected carina are considered as another taxon (Krumhardt et al. 1996, pl. 3, figs 19-22), probably *D. japonicus*. It is characterised by the presence of one or two nodes on the outer-anterior platform, occasionally one large node, but usually including elements with an even-noded margin and carina or a straight carina, and other elements with a deflected carina and continuous medial trough.

Elements of *Gnathodus girtyi simplex* (Dunn 1965, pl. 140, figs 2-3, holotype) from the Bird Spring Formation have a shorter platform than *D. n. berneseae*, and a wider, flared anterior-inner parapet. Both are similar in having two rows of nodes joining in the posterior part on transverse ridges, a medial trough only entirely developed in the anterior platform, and the presence of one or two nodes on the outer-anterior parapet (a single, nearly imperceptible, node in some small elements). *D. n. berneseae* has a more slender platform than *G. g. simplex*, with numerous ridges and nodes, where the declination of the carina is located in the anterior half of the platform. Elements of *G. g. simplex* from Tynan (1980, p. 1303, pl. 1, figs

5-7) have a similar morphology, but a shorter platform, a lower number of ridges and a more flared anterior-inner platform than elements from Dunn (1965) and *D. n. berneseae*.

G. g. simplex (Dunn 1965, pl. 140, fig. 12) has a similar morphology to *D. n. berneseae*, although the platform is shorter. It shows posterior ridges, but two rows of nodes are clearly differentiated from the carina and the anterior outer row is composed of three nodes. This element is similar to the *Gnathodus girtyi simplex*-*D. noduliferus* transitional morphotype of Titus et al. (1997, pl. 1, fig. 4) from the South Syncline Ridge. However, the occasional occurrence and unknown variations of this type hamper a detailed discussion about probable transitions between *Gnathodus girtyi simplex* and *D. noduliferus*. This element has a deep anterior trough and a posterior transverse ridge, as does *D. n. berneseae*, but the two anterior-outer nodes are strongly developed as a ridge. Titus & Manger (2001) explained that elements from the same sample exhibit a carina morphology that anticipates *D. noduliferus*, and considered them to be included in the latter taxa only “if a strict typological approach is applied to the platform elements”.

Elements considered by Brenckle et al. (1997, pl. 1, figs 5-7) as transitional forms between *G. girtyi simplex*-*D. noduliferus* have similarities with *G. defectus* Dunn, 1966, because both have extended posterior carinas with irregular transverse ridges and a short inner parapet. *G. defectus* Dunn (1966, pl. 158, figs 1, 5) has a shorter parapet with strong, high nodes and an unornamented outer platform. Dunn (1970) included in *G. defectus* elements with an inner parapet comprising several nodes and a simple posterior carina, such as elements from Krumhardt et al. (1996, p. 40, pl. 2, figs. 23-24, 31-33; pl. 4, fig. 26) or the *D. noduliferus* morphotype after Titus et al. (1997, pl. 1, fig. 5). This morphology is apparently different from that of *G. defectus* sensu Brenckle et al. (1997, pl. 1, fig. 20), which probably derived from *G. girtyi simplex*, but without ornamentation and with increasing asymmetry of the platform.

***Declinognathodus japonicus* (Igo & Koike, 1964)**

Plate 1, Figs 5, 6

Examined material. Two Pa elements from samples 218 (DPO 15132) and 253 (DPO 15139), Barcaliente Formation, Cantabrian Mountains.

Remarks. Different forms, probably species, are included in this taxon, all of them characterised by the presence of one or two isolated nodes above the outer-anterior platform and appearing in middle to late Bashkirian beds. One of our elements (Pl. 1, Fig. 5) has a narrow medial trough and a deflected outer row of nodes, similar to elements termed “*Idiognathoides* aff. *I. nodulifera*” (Lane 1967). Another element shows a carina without sharp deflection and a narrow platform akin to elements of *D. japonicus* from Krumhardt et al. (1996, pl. 3, figs 19, 20) or Mizuno (1997, fig. 12.11).

The holotype of “*Streptognathodus japonicus*” Igo & Koike (1964) is a sinistral element that has an even-noded margin and carina, and two nodes on the anterior-outer platform. It appears in beds with *Streptognathodus expansus* Igo & Koike, 1964, and the ammonoid *Gastrioceras* from the Omi Limestone. Similar late Bashkirian sinistral elements, with an anterior deflection of the carina and nodular margins, were named *D. nevadensis* Dunn (1965, pl. 158, figs 4-8). Kinderscoutian “*Idiognathoides* aff. *I. nodulifera*” (Lane 1967, pl. 123, figs. 9-11, 13) includes similar dextral elements, with nodes slightly separated from the marginal outer row, an undeflected carina, and a narrow platform for the sinistral element (Lane 1967, pl. 123, fig. 17).

Elements from the Belgium Alportian, included in “*D. n. japonicus*” (Higgins & Bouckaert 1968, pl. 4, fig. 1), have nodular ornamentation above the margins, a straight,

undeflected carina, and a continuous trough, and are clearly distinguished from *D. n. berneseae*. A Marsdenian element (Higgins & Bouckaert 1968, pl. 4, fig. 4) has ornamentation on the margins and a large node on the outer parapet. They are similar to England elements of Higgins (1975, pl. 14, figs. 7-10) and Higgins (1985, pl. 6.3, fig. 9), which were termed *Declinognathodus* sp. B by Grayson et al. (1990).

A few elements of *D. japonicus* illustrated by Lane et al. (1985) from the Mid-Carboniferous boundary stratotype, the Arrow Canyon section, show only a single node on the outer platform (Lane et al. 1985, fig. 7), but have poor ornamentation compared to the Cantabrian *D. n. berneseae*. Another species from the “*japonicus*” morphology is *D. marginodosus* Grayson, 1984, which has a straight carina, nodular ornamentation in the platform and a single or several nodes on the outer-anterior platform.

World-wide conodont sequences near the Mid-Carboniferous boundary

D. noduliferus s.l. was chosen at the 10th International Congress of Carboniferous Stratigraphy and Geology (1983, Madrid) as a world-wide index for the Mid-Carboniferous boundary. At that time, *D. noduliferus* s.l. included a group of forms or subspecies such as *Declinognathodus n. noduliferus*, *D. n. inaequalis*, *D. n. lateralis*, and *D. n. japonicus*. Although some authors subsequently separated those forms into discrete species of *Declinognathodus*, *D. noduliferus* s.l. was nonetheless retained as a guide for the recognition of the Mid-Carboniferous boundary. The *D. noduliferus* complex seems to indicate a synchronous evolutionary event at different localities. This boundary definition, close to that of a genozone, though practical, is not appropriate from our point of view.

On the other hand, the Mid-Carboniferous boundary, as it was defined, coincides with the first appearance of *D. noduliferus* s.l. after its evolutionary sequence from *Gnathodus girtyi simplex*. During recent years, certain authors have supported the origin of *D. noduliferus* from the *G. bilineatus* clade, based on the Pb elements of both apparatuses (Grayson et al. 1990), or on its derivation from the Pa element of *G. postbilineatus* through *D. praenoduliferus* (Nigmatganov & Nemirovskaya 1992). In any case, the probable evolutionary sequence from *Gnathodus girtyi simplex* to *Declinognathodus noduliferus* is only supported by the North American sections. It raised hypotheses such as that presented by Nemirovskaya & Nigmatganov (1994), where two possible homeomorphs of *D. noduliferus* were proposed. One of them most probably derived from *G. g. simplex* in shallow-water settings of North America and the one derived from *G. postbilineatus* in deep-water environments of Central Asia.

The current uncertainty about the origin of *D. noduliferus* is only part of the problem in the definition of the Mid-Carboniferous boundary. Another question is whether different taxa included in *D. noduliferus* s.l., plus *D. praenoduliferus* and *D. n. berneseae*, are recorded at different levels (time planes) in diverse basins. A succession of entries was described in England (Higgins 1975), and other successions were used to divide the *D. noduliferus* Zone into subzones from the Donets Basin and South Urals, or to differentiate two different zones from Japan (Mizuno 1997). Below, we discuss and try to clarify different times of appearance of taxa in the early development of *Declinognathodus*.

The sequence of entries of the different taxa (Fig. 5) can be used as horizons for correlation, although we have not verified whether the sequence is homotaxial. Elements of *D. noduliferus* s.l. from sample 61B at the Mid-Carboniferous GSSP (the Arrow Canyon section) are *D. inaequalis*. This conclusion is based on illustrated elements from Brenckle et al. (1997, pl.1, figs 2-4), and their determination as *D. n. inaequalis* in the list of species (p.

159). It can be confirmed if we see the tab. 1 of Lane et al. (1999). *D. n. noduliferus* and *D. n. japonicus* (together with *D. n. inaequalis*) entry above (in sample 62), if we continue the reading of the reported taxa from this section. Consequently, the first occurrence of *D. inaequalis* coincides with the Mid-Carboniferous GSSP, and could be considered a principal correlative event for global correlation.

Several zones (Fig. 5) based on conodonts from shallow-water facies were distinguished below the first appearance of *D. inaequalis* in the Mid-continent and western United States (*naviculus*, *unicornis*, *G. g. simplex*, and *R. muricatus*; see Lane et al. 1999). Fauna from this Mid-continent province (after Higgins 1981) are dominated by cavusgnathids, adetognathids, rachistognathodids, and gnathodids, such as *G. g. simplex* and *G. defectus*. Contemporaneous fauna from the Eurasian province of Higgins (1981) are dominated by *Lochriea* and other *Gnathodus* species, although shallow-water dweller species, such as *Adetognathus unicornis* (Rexroad & Burton, 1961) and *Rachistognathus muricatus* (Dunn, 1965) are found in the North African craton (Conrad et al. 1980; Weyant & Massa 1985; Weyant 1985). Occasionally, some species are found in other basins, such as *Cavusgnathus naviculus* (Hinde, 1900) and *Cavusgnathus unicornis* Youngquist & Miller, 1949 in England (Higgins 1975), *A. unicornis* and *C. unicornis* in Belgium (Austin et al. 1974; Varker & Austin 1975), and *A. unicornis* from the North Caspian Syncline and Donets Basin (Nemyrovska 1999).

The *G. postbilineatus* Zone was defined in deep-water settings from Central Asia (Nigmadganov & Nemyrovskaya 1992) and recognized in shallower environments of the Donets Basin. In the latter area, it is located above the disappearance of *A. unicornis* and can probably be correlated with the North American upper *R. muricatus* Zone of Baesemann & Lane (1985). The base of the Spanish local deep-water *G. bilineatus* subsp. A Zone is probably older than the base of the *G. postbilineatus* Zone.

Mizuno (1997) used the entries of *D. inaequalis* and *D. noduliferus* to define his *D. inaequalis*-*G. bilineatus* Zone from the Hina Limestone in Japan. The lower boundary could be correlated with the North American *D. noduliferus*-*R. primus* Zone of Baesemann & Lane (1985) and the GSSP at Arrow Canyon. Furthermore, *D. n. noduliferus* appears with *D. inaequalis* and together with elements of *D. n. japonicus* above the Mid-Carboniferous boundary (bed 62 of Brenckle et al. 1997). *D. inaequalis* also occurs below *D. noduliferus* in the Donets Basin where Nemyrovska (1999) defined the *D. n. inaequalis* and *D. n. noduliferus* subzones of the *D. noduliferus* s.l. Zone. In North England, *D. inaequalis* could appear later than earliest Chokierian beds (Varker et al. 1990), as several authors have reported a sedimentary gap in the sequence. Furthermore, *D. inaequalis* was coeval with *Neognathodus* elements and occurred above the first entry of *Rachistognathus minutus* (Higgins & Bouckaert, 1968) in the Chokierian *D. noduliferus* Zone (Higgins 1975, 1985). The sedimentary gap may be small, taking into account the fact that the entry of *D. noduliferus* takes place just above *D. inaequalis* in the England Chokierian.

In the South Urals, *D. inaequalis* first occurs, together with *D. noduliferus*, in the *D. noduliferus*-*G. b. bollandensis* Subzone of Kulagina et al. (1992), or the Early *D. noduliferus* Subzone of Kulagina et al. (2001). In support of these findings indicating a younger than Mid-Carboniferous age for these first occurrences, Groves et al. (1999) detected an erosive unconformity around the Mid-Carboniferous boundary in the Askyn River section, South Urals, later confirmed by isotope studies (Brand & Bruckschen 2002).

Close to the first occurrence of *D. n. noduliferus*, *D. lateralis* is often recorded in England, in H1a Chokierian strata (Riley et al. 1987; Varker 1994). The two species appear together in the Donets Basin (Nemyrovska 1999), but not in the South Urals, where Kulagina et al. (1992) differentiated the *D. noduliferus*-*D. lateralis* Zone with the entry of *D. lateralis*. The first declinognathodids appear almost synchronously in North Africa (Manger et al.

1985). These authors documented *Adetognathus lautus* (Gunnell, 1933) as the first species, after which *D. noduliferus*, together with *D. lateralis* and homoceratid ammonoids, appears in the Béchar Basin. According to Weyant & Massa (1985), the latter two taxa are also the first declinognathodids found in Lybia. However, the Mid-Carboniferous boundary could be located below the *Titanaria africana* horizon based on foraminifera findings (Lys 1985), and below the occurrence of *R. muricatus*.

D. japonicus occurs before the usual entry of *Idiognathoides* and *Neognathodus symmetricus* (Lane, 1967) in the Kinderscoutian of the Arrow Canyon section (Bed 62, Lane et al. 1999) and Donets Basin (Nemyrovska 1999). In addition, *D. japonicus* appears in beds from the English Alportian (Higgins 1975, 1985), in the uppermost part of the *D. noduliferus* Zone in Japan (Mizuno 1997), in the upper part of the *D. noduliferus* Zone in the Chokierian of the South Urals (Kulagina et al. 2001), and in the Chokierian (H_1b , *H. beyrichianum* ammonoid Zone) of Ireland (Austin 1972) and Belgium (Higgins & Bouckaert 1968).

According to various authors, species of *Gnathodus*, *Cavusgnathus*, and *Lochriea* disappeared during the Mid-Carboniferous global extinction episode, where an abrupt biotic turnover is documented (Saunders & Ramsbottom 1986; Nemirovskaya & Nigmadganov 1994; Walliser 1996), including an ammonoid change at super-family level (Kullmann & Nikolaeva 2002). Walliser (1996) described this faunal turnover as a relatively rapid transition but not as an abrupt change in all affected fossil groups. The Mississippian/Pennsylvanian boundary is located at a sequence boundary indicated by a regional unconformity of considerable magnitude on cratonic regions, such as the North American Mid-continent (Manger & Sutherland 1992), Central-Eastern Appalachian Basin, South Urals, and North African basins (Lemosquet & Pareyn 1985). The boundary interval coincides with an interpreted major eustatic fall (Saunders & Ramsbottom 1986) between the Arnsbergian and the Kinderscoutian. In the Arrow Canyon section, the unconformity is

correlated with a minor sequence boundary in the *noduliferus-primus* Zone (Lane et al. 1999), above the GSSP for the Mid-Carboniferous boundary and the entry of *D. n. noduliferus*. *Gnathodus girtyi simplex*, *G. defectus*, and related forms persist above the unconformity up to sample 77, in the early Chokierian (Fig. 5). Brenckle et al. (1977) differentiated the lower subzone of the *noduliferus-primus* Zone in North America, which is characterised by the upper occurrences of *G. girtyi simplex* and *G. cf. G. bollandensis*. However, the few records of American *Gnathodus* in the early Pennsylvanian are generally interpreted as re-deposited elements (Krumhardt et al. 1996).

Serpukhovian genera (*Gnathodus* and *Lochriea*) are found together with lower records of *D. lateralis* (late Chokierian) in the Donets Basin (Nemyrovska 1999), Malaysia (Igo & Koike 1968; Metcalfe 1980) and, locally, in the Southern Urals (Kulagina et al. 2001), where they are associated with *Idiognathoides* and *D. lateralis* in the *Homoceras* Zone (late H1b). *Gnathodus b. bollandensis* is found together with *D. japonicus* in the Chokierian (early H_{1b1}) of Belgium (Higgins & Bouckaert 1968), and *Gnathodus postbilineatus* is just at the entry of *D. japonicus* in the Donets Basin (Kalmius section, Nemyrovska 1999). Serpukhovian genera are in the *noduliferus-bollandensis* assemblage Zone (Bashkirian) from the Lali section (Guangxi) according to Ji & Ziegler (1993), and from the Luosu section (Guizhou) in South China according to Wang et al. (1987, in Mizuno 1997). They are also found in Pennsylvanian shallow-water limestones in west Libya (Weyant & Massa 1985) and Japan (Koike 1967, Mizuno 1997). Another Central Asian record of Serpukhovian genera in Pennsylvanian rocks is found at the Aksu section (Nigmadganov & Nemirovskaya 1992), where younger forms of *Gnathodus* (early Chokierian) coexisted with *Declinognathodus*, and the earliest entry of *Idiognathoides*.

Consequently, *Gnathodus* and *Lochriea* species are found in association with Chokierian conodonts and ammonoids in different basins, and they were not extinct at the

base of the Pennsylvanian. This survival is widely described for the Palaeo-Tethys Ocean and the Eurasian province of Higgins (1981), not only from deep-water but also in shallow-water facies; i.e., the Pyrenees, Southern Urals, Tien Shan, South China, Malaysia and Japan. The conodont turnover occurs later than the abrupt ammonoid change, particularly in deep-water sequences such as the relevant sections from Tien Shan of Nigmatganov & Nemirovskaya (1992).

Nemirovskaya & Nigmatganov (1994) reported several turnover episodes in the Mid-Carboniferous conodont fauna from Central Asian deep-water environments. They have reported a stepped period of re-organization of conodont assemblages, including a radiation of *Declinognathodus* and *Idiognathoides* just before the extinction of *Gnathodus* and *Lochriea* during the H1 Chokierian. Consequently, the Mid-Carboniferous extinction event is younger than the position of the Mid-Carboniferous boundary, and should therefore be locally evaluated.

Mid-Carboniferous boundary in Northern Spain

Menéndez-Álvarez (1991) defined the base of his *noduliferus-lateralis* Zone, and the base of the Chokierian in the Cantabrian Zone, based on the first appearance of all species of *Declinognathodus*. The first appearance of *Declinognathodus* taxa occurs in the lower metres of the Barcaliente Formation, although an accurate correlation with the Mid-Carboniferous GSSP is still difficult. The entry of *Declinognathodus* corresponds to a level where the relative abundance of conodonts increased sevenfold with respect to adjacent levels, and in mixed gnathodid-declinognathodid biofacies at the Millaró section, which probably corresponds to a more oxygenated or ventilated horizon. At the Alba/Barcaliente formations

boundary, a significant decrease in conodont abundance is evident, reflecting a change towards a poorly oxygenated environment with restricted water circulation (González Lastra 1978), and an increase in the rate of sedimentation.

The time of origin of *D. n. bernesgae* is still not known, although it probably occurred within the Central Asian *D. praenoduliferus* Zone in the early Chokierian, but a correlation with the North American zonal scheme is not clear, in particular with the GSSP for the Mid-Carboniferous boundary, as *D. n. bernesgae* apparently has its first appearance close to the boundary. In America, the entry of *D. noduliferus* “*japonicus*” (a form that we include in *D. n. bernesgae*) was used to establish the boundary at the Wahoo Limestone by Krumhardt et al. (1996) in the Northeast Brooks Range (Alaska). Later, Harris et al. (1997) described the entry of *D. inaequalis* at same level as *D. noduliferus* “*japonicus*” and below the occurrences of *D. n. noduliferus* and *D. lateralis*, in somewhat deeper-water, open-marine conditions than those considered for the sequence studied by Krumhardt et al. (1996). Consequently, different facies could control the presence of both taxa.

D. n. bernesgae could eventually appear earlier than *D. inaequalis*. In this case, *G. postbilineatus* and the succeeding *D. praenoduliferus* (and elements herein considered as *D. n. bernesgae*) were collected below *D. noduliferus* s.l. in the sense of Nigmatganov & Nemirovskaya (1992), within the range of the lowest homoceratid records at the Aksu section. The lowest homoceratid occurrence in the South Syncline Ridge section (North America) was interpreted as being in the latest Mississippian (in the Upper *R. muricatus* Zone of Titus et al. 1997); hence, Titus & Manger (2001) concluded a correlation between the Mississippian Upper *R. muricatus* conodont Zone with the earliest part of the European Chokierian Stage. Furthermore, Kullmann & Nikolaeva (2002) considered the lower record of the American ammonoid to be in a younger level than the first world-wide homoceratid occurrence. Unfortunately, scarce episodic conodonts were collected with ammonoids in this American

sequence. The first occurrence of *Declinognathodus* (i.e., *D. noduliferus* morphotype or “*G. g. simplex-D. noduliferus* transitional complex”) with problematic taxonomic status is still older than the homoceratid occurrence, in the Lower *R. muricatus* Zone sensu Titus et al. (1997). Consequently, the probable appearance of *D. n. berneseae* before *D. inaequalis* seems to be confirmed, and the entry of *D. inaequalis* in the GSSP could occur after the lowest homoceratids. Thus, the Mid-Carboniferous boundary in the Cantabrian Zone can be correlated with beds overlying the appearance of *D. n. berneseae*. It could therefore lie below the known entrance of *D. inaequalis*, because it appears together with other declinognathodid species, which we suspect appeared later than *D. inaequalis*, without *Gnathodus* and *Lochriea* associated species.

In a similar way, *D. n. berneseae* appears at the base of the Iraty Formation in the Pyrenean Azkarate quarry section. The low ratio of *Declinognathodus* compared to other genera from this section could be interpreted in relation to an environmental control by slope facies of a carbonate ramp, where *Declinognathodus* only occurs in re-deposited beds. Perret (1993) and Perret & Weyant (1994) used the first appearance of *Declinognathodus* for the recognition of the base of their *D. noduliferus* Zone in the Pyrenees. It occurred in the lower ten metres of the Iraty Formation in several sections (Perret 1985, 1993).

Gnathodus and *Lochriea* species did not disappear with the entry of declinognathodids in the Pyrenees and the Cantabrian Mountains. In the latter area, local extinctions of these genera could be related to the prograding marginal Barcaliente limestones towards the turbiditic fore-deep trough in the studied sections (Fig. 2). The dominant *Declinognathodus* biofacies in the upper Barcaliente Formation occurs in a shallower environment than that of the lower Barcaliente Formation, where *Gnathodus* and *Lochriea* species persisted. Consequently, the extinction is diachronous and linked to facies control, although it did occur during the Chokierian (as in other areas of the Palaeo-Tethys).

The arrival of *Idiognathoides* species to the Cantabrian Zone occurred later than the appearance of deeper-water genera from Central Asia (Nemirovskaya & Nigmatganov 1994). The genus appeared in the early Chokierian of the South Urals (Kulagina et al. 2001) and subsequently expanded, probably arriving in the European and North American basins during the Kinderscoutian. The entry of *Idiognathoides* species in the Cantabrian Zone can be reasonably related with retrograding marginal carbonates of the Barcaliente platform and the extension, in the foreland, of the area with siliciclastic sedimentation throughout the Kinderscoutian (Fig. 2). Davis & Webster (1985) differentiated a *Declinognathodus/Idiognathoides* biofacies deposited in a moderately shallow, open-marine environment. They indicated the possibility of a nearer-shore location for *Declinognathodus* than for *Idiognathoides*, but the hypothesis requires additional studies to be verified.

Conclusions

The conodont *Declinognathodus noduliferus berneseae*, related to *D. praenoduliferus* and *D. n. noduliferus*, appears between 2.5 and 2.8 m above the base of the Barcaliente Formation at the Millaró section (Cantabrian Zone). Furthermore, it appears at the base of the Ochaverri Member of the Iraty Formation in the Azkarate quarry (Pyrenees). We discuss some elements included in the new subspecies from Alaska and Asia, although new studies on early *Declinognathodus* are necessary. The first Spanish records of *Declinognathodus* species can be correlated with the Mississippian/Pennsylvanian boundary; however, correlative horizons may be located a few metres above, at the currently unknown earliest appearance of *D. inaequalis*. This appearance took place before the extinction of *Gnathodus* species and the

entrance of *D. n. noduliferus* or *D. lateralis*, as can be deduced from the correlation of different biotic horizons around the world.

The entry of *Declinognathodus* is not preceded by an extinction of Early Carboniferous *Gnathodus* and *Lochriea* taxa at the Mid-Carboniferous boundary. In the Cantabrian Zone, all genera coexisted during the sedimentation of the lower part of the carbonate Barcaliente Formation in the passive margin of the Variscan foreland basin, while a fore-deep basin was filling quickly. Supposedly Mississippian taxa survived there during the early Chokierian until the carbonate platform prograded towards the fore-deep basin.

According to our knowledge, the principal correlative event at the Mid-Carboniferous boundary GSSP is the lowest occurrence of *D. inaequalis*. We think that it is a more accurate and preferable correlation marker than the selected lowest occurrence of *D. noduliferus* s.l. Furthermore, the application of a sequence of appearances of different *Declinognathodus* taxa provides a biostratigraphic framework for the correlation between different basins. It should be refined and used in conjunction with other methods for correlation.

Acknowledgements. We are indebted to the Magnesitas de Navarra S.A. company, which promoted the study of the Azkarate quarry through a special project with the IGME. We are grateful to the Department of Geology at the University of Oviedo, which allowed us to study conodonts from the Menéndez-Álvarez collection. We would also like to thank María Belén López for the SEM service at the University of A Coruña. We also thank Guillermo L. Albanesi for reading the type-script and for many helpful suggestions about the English, and Christine Laurin for revising the English text. The paper profited from the critical reviews of the manuscript provided by Marie-France Perret and James E. Barrick. This work was

sponsored by Spanish projects BTE2003-01609 and BTE2003-01012, which were funded by the “Ministerio de Ciencia and Fondo Europeo de Desarrollo Regional” (FEDER).

REFERENCES

- Aisenverg D.R., Brazhnikova N.E., Vassilyuk N.P., Reitlinger E.A., Fomina E.V. & Einor O.L. (1979) - The Serpukhovian Stage of the Lower Carboniferous of the USSR. In: Wagner R.H., Higgins A.C. & Meyer S.V. (eds.)- The Carboniferous of the U.S.S.R. *Yorkshire Geol. Soc., Occas. Publ. 4*: 43-59, Leeds.
- Alonso J.L., Suárez Rodríguez A., Rodríguez Fernández L.R., Farias P., Villegas F., Marquínez J., Menéndez Duarte R.A., Jiménez M., Barba P., Gallastegui G., Paniagua A., Heredia N., Martínez Álvarez A., Torres Alonso M. & Galán L. (1991) - Mapa Geológico de España Escala 1:50.000 La Pola de Gordón (103) 2ª serie, 1ª edición. V. of 138 pp. Inst. Tecnol. Geom. Esp., Madrid.
- Austin R.L. (1972) - Problems of conodont taxonomy with special reference to Upper Carboniferous forms. *Geol. et Palaeont.*, SB1: 115-126, Marburg.
- Austin R., Conil R., Groessens E. & Pirlet H. (1974) - Étude biostratigraphique de l'Encrinite de Tramaka. *Bull. Soc. belge Géol.*, 83: 113-129, Bruxelles.
- Baeseman, J.F. & Lane H.R. (1985) - Taxonomy and evolution of the genus *Rachistognathus* Dunn (Conodonts; Late Mississippian to Early Middle Pennsylvanian). *Cour. Forsch.-Inst. Senckenberg*, 74: 93-136, Frankfurt am Main.
- Blanco-Ferrera S., García-López S. & Sanz-López J. (2005) - Conodontos carboníferos de la sección del río Cares (Unidad de Picos de Europa, Zona Cantábrica, NO de España). *Geobios*, 38: 17-27, Lyon.

- Boschma D. & Staalduinen C. J., van (1968) - Mappable units of the Carboniferous in the southern Cantabrian Mountains. *Leidse Geol. Meded.*, 43: 221-232, Leiden.
- Brand U. & Bruckschen P. (2002) - Correlation of the Askyn River section, Southern Urals, Russia, with the Mid-Carboniferous Boundary GSSP, Bird Springs Formation, Arrow Canyon, Nevada, USA: implications for global paleoceanography. *Paleogeogr., Palaeoclim., Palaeoecol.*, 184: 177-193, Amsterdam.
- Brenckle P.L., Baesemann J.F., Lane H.R., West R.R., Webster G.D., Langenheim R.L., Brand U. & Richards B.C. (1997) - Arrow Canyon, the Mid-Carboniferous Boundary Stratotype. In: Brenckle P.L. & Page W.R. (eds.)- Guidebook: Arrow Canyon Range, Nevada. *Cushman Found. for Foram. Res., Spec. Publ.*, 36 Suppl.: 13-32, Washington.
- Brenckle P., Lane H.R., Manger W. & Saunders W.B. (1977) - The Mississippian-Pennsylvanian boundary as an intercontinental biostratigraphic datum. *Newsl. Stratigr.*, 6: 106-116, Stuttgart.
- Brime C., García-López S., Bastida F., Valín M.L., Sanz-López J. & Aller J. (2001) - Transition from diagenesis to metamorphism near the front of the Variscan regional metamorphism (Cantabrian Zone, Northwestern Spain). *J. Geol.*, 109: 363-379, Chicago.
- Comte P. (1959) - Recherches sur les terrains anciens de la Cordillère Cantabrique. *Mem. Inst. Geol. Min. Esp.*, 60: 1-440, Madrid.
- Conrad J., Lys M. & Weyant M. (1980) - Mise en évidence du Carbonifère moyen (Moscovien au Sahara central –Bassin de Reggan- et conséquences paléogéographiques. *Bull. Soc. Géol. Fr.*, 22: 115-124, Paris.
- Davis L.E. & Webster G.D. (1985) - Late Mississippian to Early Pennsylvanian conodont biofacies in central Montana. *Lethaia*, 18: 67-72, Oslo.

- Delépine G., Dubar G. & Laverdière J.W. (1929) - Observations sur quelques gisements du Carbonifère des Pyrénées. *Bull. Soc. Géol. Fr.*, 29: 236-238, Paris.
- Delvolvé J.J., Souquet P., Vachard D., Perret M.F. & Aguirre P. (1993) - Caractérisation d'un bassin d'avant-pays dans le Carbonifère des Pyrénées: faciés, chronologie de la tectonique synsédimentaire. *C. R. Ac. Sc.*, 316: 959-966, Paris.
- Dunn D.L. (1965) - Late Mississippian conodonts from the Bird Spring Formation in Nevada. *Jour. Paleontology*, 39: 1145-1150, Tulsa, Okla.
- Dunn D.L. (1966) - New Pennsylvanian platform conodonts from southwestern United States. *Jour. Paleontology*, 40: 1294-1303, Tulsa, Okla.
- Dunn D.L. (1970) - Middle Carboniferous conodonts from western United States and phylogeny of the platform group. *Jour. Paleontology*, 44: 312-342, Tulsa, Okla.
- Eichmüller K. & Seibert P. (1984) - Faciesentwicklung zwischen Tournai und Westfal im Kantabrischen Gebirge (NW-Spanien). *Z. dt. geol. Ges.*, 135: 165-191, Hannover.
- Ellison S. & Graves R.W. Jr. (1941) - Lower Pennsylvanian (Dimple Limestone) Conodonts of the Marathon Region, Texas. *Missouri Univ. Sch. Mines and Metall. Bull.*, 14: 1-21, Rolla.
- García-López S. & Sanz-López J. (2002a) - The Paleozoic succession and biostratigraphy of the section between Cape Peñas and Cape Torres (Cantabrian coast, NW Spain). In: García-López S. & Bastida F. (eds.)- Palaeozoic Conodonts from Northern Spain. *Inst. Geol. Min. Esp., Cuadernos del Museo Geominero*, 1: 125-162., Madrid.
- García-López S. & Sanz-López J. (2002b) - Devonian to Lower Carboniferous conodont biostratigraphy of the Bernesga Valley section (Cantabrian Zone, NW Spain). In: García-López S. & Bastida F. (eds.)- Palaeozoic Conodonts from Northern Spain. *Inst. Geol. Min. Esp., Cuad. Museo Geom.*, 1:163-205, Madrid.

- Gibshman N.B. & Akhmetshina L.Z. (1990) - Micropaleontologic basis for determination of the Mid-Carboniferous boundary in the North Caspian Syncline, U.S.S.R. *Cour. Forsch.-Inst. Senckenberg*, 130: 273-295, Frankfurt am Main.
- Gonzalez Lastra J. (1978) - Facies salinas en la Caliza de Montaña (Cordillera Cantábrica). *Trab. Geol.*, 10: 249-265, Oviedo.
- Grayson R.C. Jr., Merrill G.K. & Lambert L.L. (1990) - Carboniferous gnathodontid conodont apparatuses: Evidence of a dual origin for Pennsylvanian taxa. *Cour. Forsch.-Inst. Senckenberg*, 118: 353-396, Frankfurt am Main.
- Groves J.R., Nemyrovskaya T.I. & Alekseev A. (1999) - Correlation of the type Bashkirian Stage (Middle Carboniferous, South Urals) with the Morrowan and Atokan series of the Midcontinental and Western United States. *Jour. Paleontology*, 73: 529-539, Tulsa, Okla.
- Harris A.G., Brenckle P.L., Baesemann J.F., Krumhardt A.P. & Gruzlovic P.D. (1997) - Comparison of conodont and calcareous microfossil biostratigraphy and lithostratigraphy of the Lisburne Group (Carboniferous), Sadlerochit Mountains, northeast Brooks Range, Alaska. In: Dumoulin J.A. & Gray J.E. (eds.)- Geologic studies in Alaska by the U.S. Geological Survey, 1995. *U.S. Geol. Surv., Prof. Papers*, 1574: 195-219, Washington.
- Higgins A.C. (1962) - Conodonts from the "Griotte" Limestone of North West Spain. *Not. Com. Inst. Geol. Min. Esp.*, 65: 5-22, Madrid.
- Higgins A.C. (1975) - Conodont zonation of the late Viséan-early Westphalian strata of the south and central Pennines of northern England. *Bull. Geol. Surv. of Great Britain*, 53: 1-127, London.

- Higgins A.C. (1981) - The distribution of conodonts in relation to the paleogeography of late Viséan-Namurian Time. In: Neale J.W. & Brasier M.D. (eds.)- Microfossils from recent and fossil shelf seas. Ellis Horwood Limited: 37-51, Chichester.
- Higgins A.C. (1985) - The Carboniferous system: Part 2-Conodonts of the Silesian subsystem from Great Britain and Ireland. In: Higgins A.C. & Austin R.L. (eds.)- A stratigraphical index of conodonts: 210-217. Ellis Horwood Limited, Chichester.
- Higgins A.C. & Bouckaert J. (1968) - Conodont stratigraphy and paleontology of the Namurian of Belgium. *Mém. Serv. Géol. Belgique*, 10: 1-64, Bruxelles.
- Igo H. & Koike T. (1964) - Carboniferous conodonts from the Omi Limestone, Niigata Prefecture, Central Japan (Studies of Asian conodonts, part I). *Trans. Proc. Palaeont. Soc. Japan*, 53: 179-193, Tokyo.
- Igo H. & Koike T. (1968) - Carboniferous Conodonts from Kuantan, Malaya. Contributions to the Geology and Palaeontology of Southeast Asia, LV. *Geol. Palaeont. Southeast Asia*, 5: 26-30, Tokyo.
- Ji Q. & Ziegler W. (1993) - The Lali Section: an excellent reference section for Upper Devonian in South China *Cour. Forsch.-Inst. Senckenberg*, 157: 1-183, Frankfurt am Main.
- Koike T. (1967) - A Carboniferous succession of conodont faunas from the Atetsu Limestone in southwest Japan (Studies of Asiatic conodonts, Part 6). *Sc. Rep. Tokyo Kyoiku Daigaku Sec. C*, 9: 279-318, Tokyo.
- Krumhardt A.P., Harris A.G. & Watts K.F. (1996) - Lithostratigraphy, Microlithofacies, and Conodont Biostratigraphy and Biofacies of the Wahoo Limestone (Carboniferous), Eastern Sadlerochit Mountains, Northeast Brooks Range, Alaska. *U.S. Geol. Surv., Prof. Papers*, 1568: 1-70, Washington.

- Kulagina E. I., Rumyantseva Z. S., Pazukhin V. N. & Kochetova N. N. (1992) -
Lower/Middle Carboniferous boundary in the South Urals and Central Tien Shan. V.
 of 112 pp. Hayka, Moskva. [in Russian]
- Kulagina E. I., Pazukhin V. N., Kochetova N. M., Sintsyna Z. A., & Kochetova N. N. (2001)
 - The stratotype and key sections of the Bashkirian stage (Carboniferous) in the
 Southern Urals. V. of 139 pp. Gilem, for 2000, Ufa. [in Russian]
- Kullmann J. (1962) - Die Goniatiten der Namur-Stufe (Oberkarbon) im Kantabrischen
 Gebirge, Nordspanien. *Abh. Math. Natur. kl. Akad. Wiss.*, 6: 259-377, Mainz.
- Kullmann J. (1979) - Die “*Reticuloceras-Zeit*” (Oberkarbon) in der entwicklung des
 Kantabrischen Variszikums. *Clausthaler Geol. Abh.*, 30: 34-44, Clausthal-Zellerfeld.
- Kullmann J. & Nikolaeva S.V. (2002) - Mid-Carboniferous boundary and the global lower
 Bashkirian ammonoid biostratigraphy. In: Hills L.V., Henderson C.M. & Bamber
 E.W. (eds.)- Carboniferous and Permian of the World, Calgary 1999. *Can. Soc. Petrol.*
Geol. Mem., 19: 780-795, Calgary.
- Lane H.R. (1967) - Uppermost Mississippian and Lower Pennsylvanian conodonts from the
 type Morrowan region Arkansas. *Jour. Paleontology*, 41: 920-943, Tulsa, Okla.
- Lane H.R., Baesemann J.F., Brenckle P.L. & West R.R. (1985) - Arrow Canyon, Nevada – a
 potential mid-Carboniferous boundary Stratotype. In: Escobedo J.L., Granados L.F.,
 Meléndez B., Pignatelli R., Rey R. & Wagner R.H. (eds.)- Xth I.C.S.G.C. Madrid
 1983, 4. *Int. Geol. Min. Esp.*: 429-439, Madrid.
- Lane H.R., Brenckle P.L., Baesemann J.F. & Richards B. (1999) - The IUGS boundary in the
 middle of the Carboniferous: Arrow Canyon, Nevada, USA. *Episodes*, 22: 272-283,
 Nottingham.
- Lemosquet Y. & Pareyn C. (1985) - Béchar Basin. In: Wagner R.H., Winkler Prins C.F. &
 Granados L.F. (eds.)- The Carboniferous of the World vol. 2, Australia, Indian

- Subcontinent, South Africa, South America and North Africa. *IUGS Publ.*, 20: 306-315, Madrid.
- Lys M. (1985) - Foraminifera of North Africa. Conodonts in North Africa. In: Wagner R.H., Winkler Prins C.F. & Granados L.F. (eds.)- The Carboniferous of the World vol. 2, Australia, Indian Subcontinent, South Africa, South America and North Africa. *IUGS Publ.*, 20: 354-364, Madrid.
- Manger W.L. & Sutherland P.K. (1992) - Analysis of sections presumed to be complete across the Mississippian-Pennsylvanian Boundary, Southern Midcontinent. *Oklahoma Geol. Surv. Circular*, 94: 69-79, Norman, Okla.
- Manger W.L., Weyant M. & Pareyn C. (1985) - Mid-Carboniferous ammonoid biostratigraphy, Bechar Basin, Algeria. *Cour. Forsch.-Inst. Senckenberg*, 74: 181-196, Frankfurt am Main.
- Meischner D. (1971) - Conodonten-Chronologie des Deutschen Karbons. In: Stubblefield J. (ed.)- *Compte Rendu 6e Congress Intern. Strat. Geol. Carbonif. Sheffield 1967*, Volume III: 1169-1180. Publishing Company "Ernest Van Aelst", Maastricht.
- Menéndez-Álvarez J.R. (1991) - Conodontos del Carbonífero Inferior y Medio de la Cordillera Cantábrica. Ph.D. thesis Oviedo Univ., 283 pp. (unpublished).
- Metcalf I. (1980) - Upper Carboniferous conodont faunas of the Panching Limestone, Pahang, West Malaysia. *Palaeontology*, 23: 297-314, London.
- Mizuno Y. (1997) - Conodont faunas across the Mid-Carboniferous boundary in the Hina Limestone, Southwest Japan. *Paleontol. Research*, 1: 237-259, Tokyo.
- Nemirovskaya T.I. & Nigmatganov I. (1993) - Some new conodonts of the Mid-Carboniferous Boundary deposits of Central Asia. *Jb. Geol. Bundesanst.*, 136: 213-221, Wien.

- Nemirovskaya T.I. & Nigmadganov I. (1994) - The Mid-Carboniferous conodont Event. .
Cour. Forsch.-Inst. Senckenberg, 168: 319-333, Frankfurt am Main.
- Nemyrovska T.I. (1999) - Bashkirian conodonts of the Donets basin, Ukraine. *Scripta Geol.*,
119: 1-115, Leiden.
- Nigmadganov I. & Nemirovskaya T.I. (1992) - Mid-Carboniferous boundary conodonts from
the Gissar Ridge, South Tienshan, Central Asia. *Cour. Forsch.-Inst. Senckenberg*,
154: 253-275, Frankfurt am Main.
- Perret M.-F. (1985) - La limite Mississipien-Pennsylvanien dans les Pyrénées françaises. In:
Escobedo J.L., Granados L.F., Meléndez B., Pignatelli R., Rey R. & Wagner R.H.
(eds.)- Xth I.C.S.G.C. Madrid 1983, vol. 4. *Inst. Geol. Min. Esp.* 350-369, Madrid.
- Perret M.-F. (1993) - Recherches micropaléontologiques et biostratigraphiques (Conodontes-
Foraminifères) dans le Carbonifère Pyréen. *Strata*, 21: 1-597, Toulouse.
- Perret M.-F. & Weyant M. (1994) – Les biozones à conodontes du Carbonifère des Pyrénées.
Comparaisons avec d'autres régions du globe. *Geobios*, 27: 689-715, Villeurbanne.
- Pilger A. (1973) - Die Entwicklung von Oberdevon, Unterkarbon und Namur im Gebiet des
Magnesites von Eugui in den spanischen Westpyrenäen. *N. Jb. Geol. Paläontol. Abh.*,
142: 44-58, Stuttgart.
- Remane J., Bassett M.G., Cowie J.W., Gohrbandt K.H., Lane H.R., Michelsen O. & Wang N.
(1996) - Revised guidelines for the establishment of global chronostratigraphic
standards by the International Commission on Stratigraphy (ICS). *Episodes*, 19: 77-
81, Nottingham.
- Reuther C.-D. (1977) - Das Namur im südlichen Kantabrischen Gebirge (Nordspanien).
Klutenbewegungen und Faziesdifferenzierung im Übergang Geosynklinale-Orogen.
Clausthaler Geol. Abh., 28: 1-122, Clausthal-Zellerfeld.

- Reuther C.-D. (1982) - The Lower Carboniferous facies levelling and the first Upper Carboniferous tectonic events in the Cantabrian Mountains and the Pyrenees (Spain). *N. Jb. Geol. und Paläontol. Abh.*, 163: 244-256, Stuttgart.
- Riley N.J., Varker W.J., Owens B., Higgins A.C. & Ramsbottom W.H.C. (1987) - Stonehead Beck, Cowling, North Yorkshire, England: A British proposal for the mid-Carboniferous boundary stratotype. *Cour. Forsch.-Inst. Senckenberg*, 89: 159-171. , Frankfurt am Main.
- Riley N.J., Claoué-Long J., Higgins A.C., Owens B., Spears A., Taylor L. & Varker W.J. (1994) - Geochronometry and geochemistry of the European Mid-Carboniferous boundary global stratotype proposal, Stonehead Beck, North Yorkshire, UK. *Ann. Soc. Géol. Belgique*, 116: 275-289, Liège.
- Sanz-López J., Blanco-Ferrera S. & Sánchez de Posada L.C. (2004) - Estratigrafía del Serpukhoviense y el Bashkiriense inferior (Carbonífero) en la provincia de Pliegues y Mantos, Zona Cantábrica. *Geotemas*, 6: 131-134, Madrid.
- Saunders W.B. & Ramsbottom W.H.C. (1986) - The mid-Carboniferous eustatic event. *Geology*, 14: 208-212, Washington.
- Skompski S. (1996) - Stratigraphic position and facies significance of the limestone bands in the subsurface Carboniferous succession of the Lublin Upland. *Acta Geol. Polon.*, 46, 171-268, Warszawa.
- Titus A.L. & Manger W.L. (2001) - Mid-carboniferous ammonoid biostratigraphy, southern Nye County, Nevada: implications of the first North American Homoceras. *Jour. Paleontology*, 75: 1-31, Tulsa, Okla.
- Titus A.L., Webster G.D., Manger W.L. & Dewey Ch.P. (1997) - Biostratigraphic analysis of the Mid-Carboniferous boundary at the south Syncline Ridge Section, Nevada Test Site, Nevada, United States. In: Podemski M., Dybova-Jachowicz S., Jaworowski K.,

- Kureczka L. & Wagner R. (eds.)- XIIIth *I.C.C.S.G.* Krakow 1995, Proceedings, 3: 207-214, Krakow.
- Tynan M.C. (1980) - Conodont biostratigraphy of the Mississippian Chainman Formation, Western Millard County, Utah. *Jour. Paleontology*, 54: 1282-1309, Tulsa, Okla.
- Varker W.J. (1994) - Multielement conodont faunas from the proposed Mid-Carboniferous boundary stratotype locality at Stonehead Beck, Cowling, North Yorkshire, England. *Ann. Soc. Géol. Belgique*, 116: 301-321, Liège.
- Varker W.J. & Austin R.L. (1975) – The significance of *Adetognathus unicornis* (Rexroad and Burton) in the Mirk Fell Beds (E2a) of the north England. *J. Earth Sciences*, 8: 399-408, Leeds.
- Varker W.J., Owens B. & Riley N.J. (1990) - Integrated biostratigraphy for the proposed Mid-Carboniferous boundary stratotype, Stone Beck, Cowling, North Yorkshire, England. *Cour. Forsch.-Inst. Senckenberg*, 130: 221-235, Frankfurt am Main.
- Wagner R.H., Winkler Prins C.F. & Riding R.E. (1971) - Lithostratigraphic units of the lower part of the Carboniferous in the northern León, Spain. *Trab. Geol.*, 4: 603-663, Oviedo.
- Wagner-Gentis C.H.T. (1963) - A general account of the Palaeozoic rocks between the rivers Porma and Bernesga (León, NW. Spain). *Bol. Inst. Geol. Min. Esp.*, 74:171-331, Madrid.
- Walliser O.H. (1996) - Global events in the Devonian and Carboniferous. In: Walliser O.H. (ed.)- Global events and event stratigraphy in the Phanerozoic. Springer-Verlag: 225-250, Berlin.
- Weyant M. (1985) - Conodonts in North Africa. In: Wagner R.H., Winkler Prins C.F. & Granados L.F. (eds.)- The Carboniferous of the World vol. 2, Australia, Indian

Subcontinent, South Africa, South America and North Africa. *IUGS Publ.*, 20 : 364-367, Madrid.

Weyant M. & Massa D. (1985) - Conodontes du Carbonifère de Libye occidentale. In: Escobedo J.L., Granados L.F., Meléndez B., Pignatelli R., Rey R. & Wagner R.H. (eds.)- Xth I.C.S.G.C. Madrid 1983, vol. 1. *Inst. Geol. Min. Esp.*: 83-98, Madrid.

Wirth M. (1967) - Zur Gliederung des höheren Paläozoikums (Givet-Namur) im Gebiet des Quinto Real (Westpyreäen) mit Hilfe von Conodonten. *N. Jb. Geol. Paläontol. Abh.*, 127: 179-244, Stuttgart.

Figure Captions

Fig. 1. Geological sketch of the Cantabrian Zone and the western part of the Pyrenees with the location of studied conodont localities.

Fig. 2. Correlation scheme between different composite stratigraphic sections of the Barcaliente Formation at Bernesga Valley (data after Wagner et al. 1971, Reuther 1977, Alonso et al. 1991, and Menéndez-Álvarez 1991). Location is in Fig. 1 and horizontal scale is free. Vertical and horizontal distributions of some conodont genera are outlined.

Fig. 3. Detailed stratigraphic section and conodont content of the Millaró Beds and lowermost part of the Barcaliente Formation at the Millaró section (Cantabrian Zone).

Fig. 4. Detailed stratigraphic section and conodont content of the Ochaverri Member of the Iraty Formation at the normal limb of the anticline cropping out in the Azkarate quarry (Pyrenees).

Fig. 5. Global correlation of first or latest conodont taxa occurrences and zones around the Mid-Carboniferous boundary. Ammonoid genozones and units are depicted as an external control for conodont entries. Note the homotaxial presence of *Declinognathodus* taxa with the exception of *D. n. "japonicus"* (= *D. n. bernesgae*) from North America. Another point noted in the scheme is the first occurrence of *Rachistognathus minutus*, considered diachronic by some authors (Krumhardt et al. 1996; Groves et al. 1999) or used for intercontinental correlations by others (Lane et al. 1999). In our scheme, *R. minutus* appeared in the earliest

Chokierian of the European Variscan Realm and, progressively later, in the Donets Basin, the South Urals and Alaska, to finally arrive in the Mid-continent and western North America at the time of *Reticuloceras*. The migration route over time suggests an explanation for shallow-water dweller species, such as *R. minutus*. For abbreviations: Al. = Alportian, Kin = Kinderscoutian, ext. = extinction.

PLATE 1

Oral views of different Pa elements; graph scale is 200 μ m. 1-2. *Declinognathodus inaequalis* (Higgins, 1975), Barcaliente Formation, small DPO 15130 and medium-sized DPO 15131 elements from sample 218. 3-4. *Declinognathodus noduliferus noduliferus* (Ellison & Graves, 1941), Barcaliente Formation, sample 201 (Las Caldas), immature DPO 15135 and mature DPO 15134 elements. 5-6. *Declinognathodus japonicus* (Igo & Koike, 1964), Barcaliente Formation, element DPO 15132 with a large anterior node from sample 218 (5) and immature element (6), DPO 15139 from sample 253. 7. *Declinognathodus praenoduliferus* Nigmatdaganov & Nemirovskaya, 1992, Barcaliente Formation, DPO 15129 from sample 345. 8-18. *Declinognathodus noduliferus berneseae* n. subsp.; Barcaliente Formation, immature element DPO 15103 with an incipient node from sample 219 (8), immature element DPO 15102 (9), Holotype DPO 15086 (10), mature element DPO 15087 (11) from sample MILL-13F, mature element DPO 15120 (12) from sample MILL-13G, element DPO 15088 (13) with two nodes from sample MILL-14; Iraty Formation, immature element DPO 15104 from sample NA-7 (14), mature elements DPO 15110 (15), DPO 15121 (16), DPO 15122 (17) and DPO 15123 (18) from sample NA-8 where the posterior trough is not developed.

PLATE 2

Oral views of different Pa elements; graph scale is 200 μm . 1-2. *Gnathodus bilineatus* cf. *bollandensis* Higgins & Bouckaert, 1968 from the Azkarate quarry, sample NA-8, DPO 15144 and DPO 15116. 3-8. *Gnathodus bilineatus bollandensis* Higgins & Bouckaert, 1968 from the Azkarate quarry, DPO 15117 from sample NA-24 (3), DPO 15111 to DPO 15115 from NA-8 (4-8). 9-12. *Gnathodus postbilineatus* Nigmatganov & Nemirovskaya, 1992 from the Azkarate quarry, DPO 15109 and DPO 15124 from sample NA-8 (9-10), DPO 15108 and DPO 15125 from sample NA-24 (11-12). 13. *Idiognathoides sinuatus* Harris & Hollingsworth, 1933 immature element DPO 15133 from sample 218, Barcaliente Formation. 14-16. *Declinognathodus lateralis* (Higgins & Bouckaert, 1968) from the Barcaliente Formation, DPO 15036 from sample 201 (14), DPO 15037 and DPO15038 from sample 253 (15-16).

Figure 1

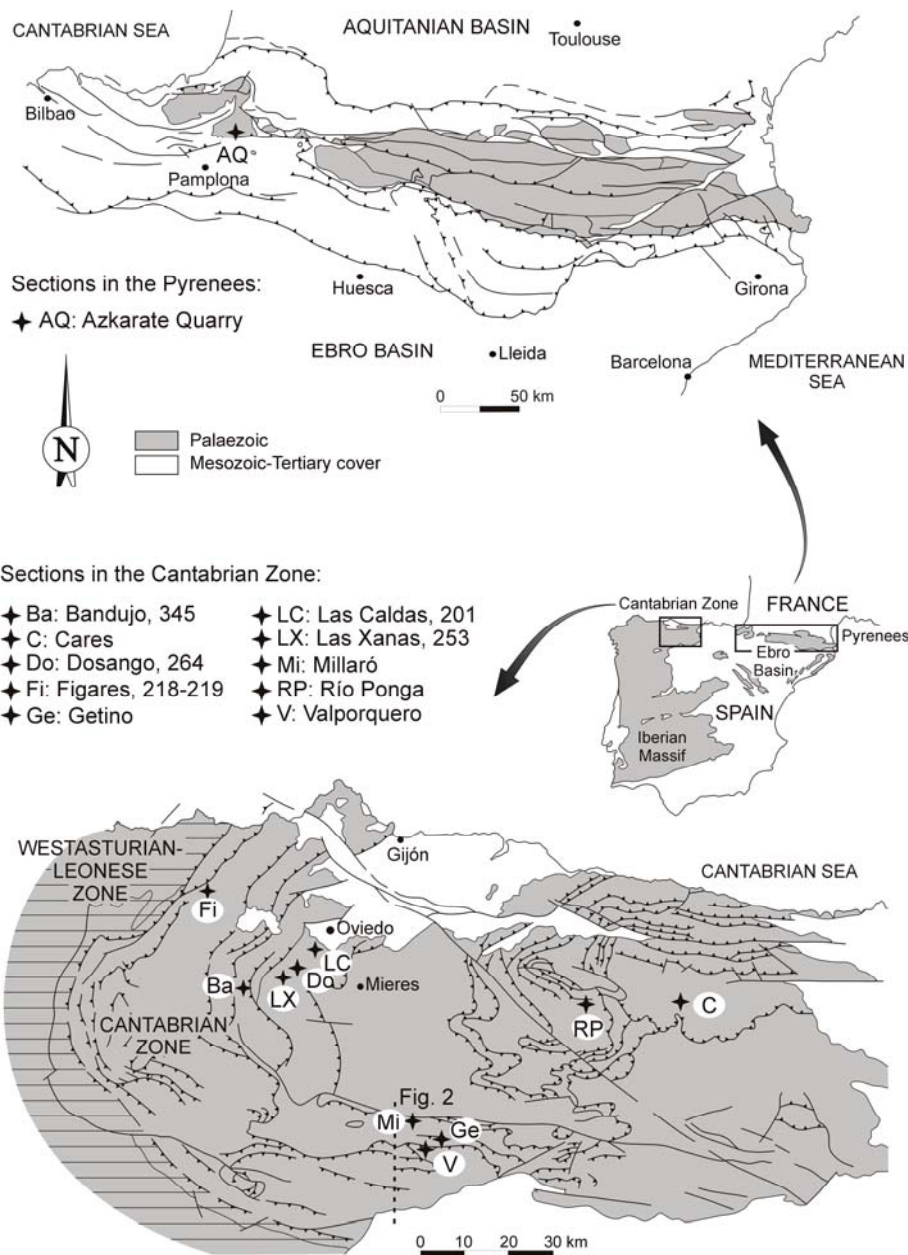


Figure 2

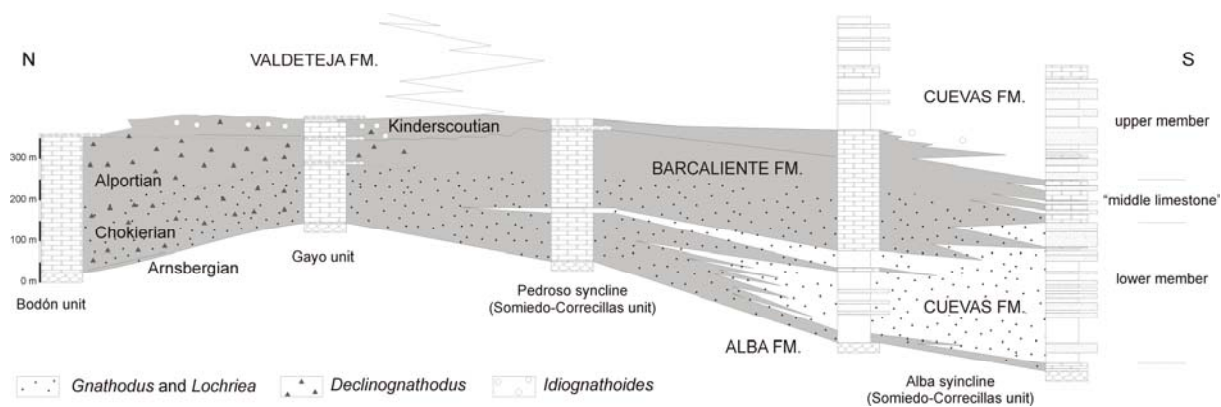


Figure 3

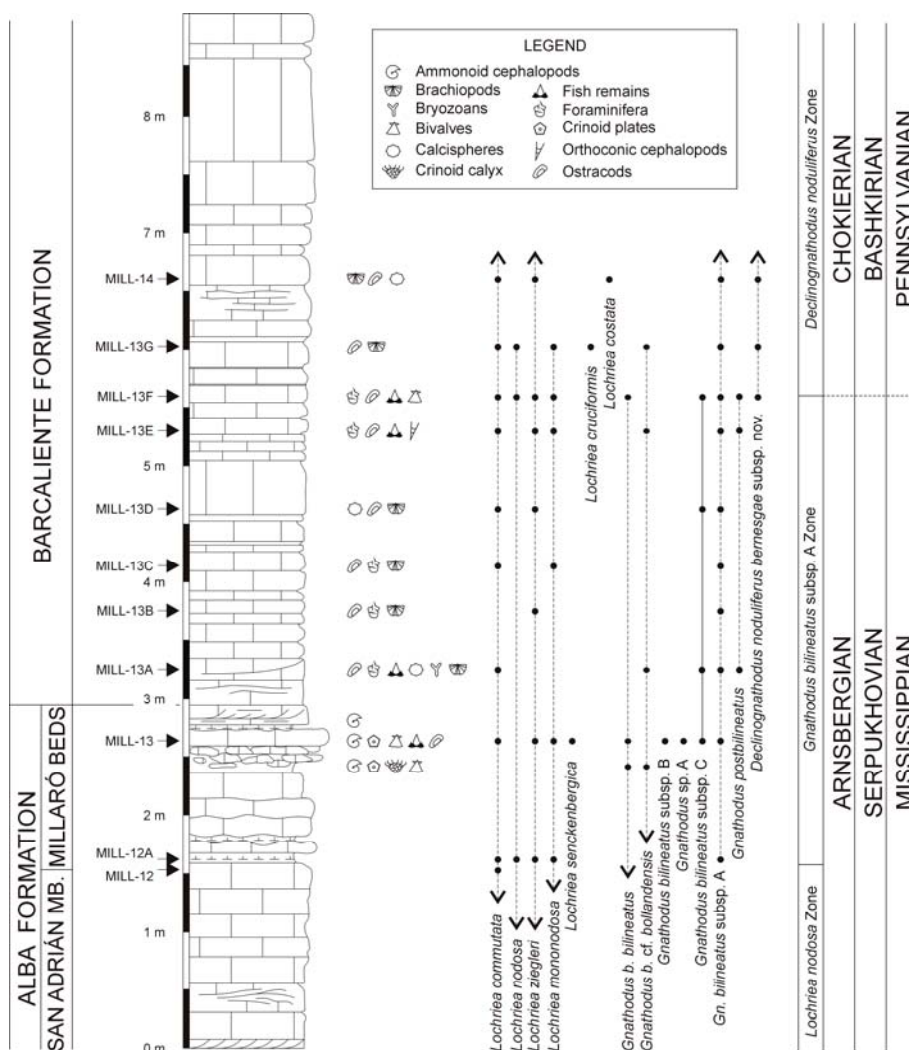


Figure 4

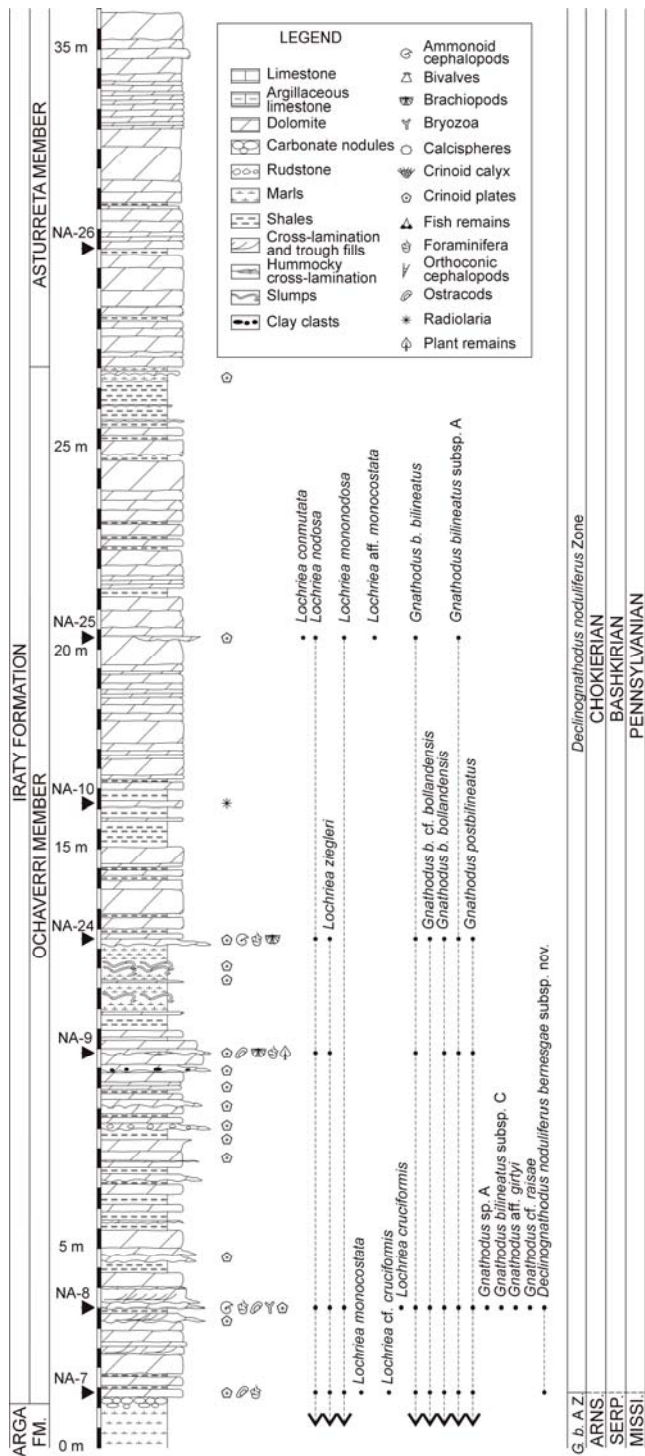


Plate 1



Plate 2

