

## FUSULINOIDEANS FROM THE PUENTELLÉS FORMATION (UPPER CARBONIFEROUS, NW SPAIN): DISCUSSION ON PHYLOGENY, PALEOECOLOGY AND PALEOBIOGEOGRAPHY

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**Abstract.** The Cantabrian Zone is the only area in Western Europe that contains marine successions of Kasimovian and Gzhelian (Late Carboniferous, late Pennsylvanian) age. These successions yield fusulinoideans that are presently the subject of an in depth-study by members of a IUGS SCCS working group intending to find stratigraphic markers for the subdivision of the Carboniferous System.

The youngest fusulinoidean faunas of the Cantabrian Zone are recorded in the Puentellés Formation, a succession of calcareous strata consisting of two members. The lower member is made up of reworked and re-sedimented carbonates, which form shallow turbidite deposits showing frequent lateral changes of facies, whereas the upper member corresponds to autochthonous limestones, mainly consisting of dark mudstones, skeletal wackestones and thick-bedded boundstones. Generally speaking, the lower member is late Kasimovian in age while the upper one is early Gzhelian. However, there are also a few successions of late Kasimovian age that show sedimentary facies similar to those of the upper member.

The fusulinoidean assemblages from the lower member are dominated by elongated species of the genus *Ferganites*, which sometimes occur with *Schubertella* and *Staffella* species. *Rauserites*, *Tumefactus*, *Jigulites*, *Quasifusulina*, as well as certain *Ferganites* species showing obese shell, mainly appear in strata belonging to the upper member.

Detailed analyses of the fusulinoideans from the Cantabrian Zone have allowed several questions related to their paleoecology, biostratigraphy, and paleobiogeography to be ascertained. First, it has been shown that the *Ferganites* accumulated in the strata of the lower member could have lived in near-shore and high-energy environments. The presence of some relevant forms (e. g. *Rauserites* cf. *rossicus*, and *Jigulites* sp.) allow a correlation between the Cantabrian successions and the standard stratigraphic units of the Russian Platform. Moreover, the composition of the fusulinoidean assemblages clearly shows the biogeographic affinities of the Cantabrian Zone with the Carnic Alps and the Central Asian regions. On the contrary, these assemblages differ greatly from those in other western Eurasian areas, such as the Russian Platform and the Donets Basin, suggesting that these areas were not well-connected with the Paleo-Tethys.

Some observations give rise to relevant questions on more general aspects dealing with the latest Carboniferous fusulinoideans while yielding, at the same time, preliminary data for solving them. This is the case of the phrenotheca, an inner partition existing in some fusulinoidean shells whose functional role is still uncertain. The abundance in the Cantabrian Zone strata of *Tumefactus* specimens showing phrenotheca provides information for reconstructing its geometry as well as enabling speculation on its likely function.

Another problematic aspect concerns the origin and distribution of the genus *Triticites*. It is noteworthy that this genus seems to be absent from both the Cantabrian Zone and most Eurasian areas, bringing up the question of whether the American and the Eurasian *Triticites* really had a common ancestor. The possibilities involved are discussed here.

**Riassunto.** La Zona Cantabrica è la sola in Europa occidentale che contenga successioni marine dello Kasimoviano e Gzheliano (Carbonifero sommitale). Queste successioni contengono fusulinoidi che sono attualmente in studio da parte di un gruppo di lavoro della Sottocommissione per la stratigrafia del Carbonifero del IUGS, onde ottenere indicatori stratigrafici per le suddivisioni del Sistema Carbonifero. Le faune a fusulinoidi più recenti della Zona Cantabrica sono rinvenute nella Formazione Puentellés, una successione di strati calcarei in cui sono distinti due membri. Il membro inferiore è costituito da carbonati rimaneggiati e risedimentati, che forma depositi torbiditici di limitata profondità con frequenti variazioni laterali di facies, mentre il membro superiore corrisponde a calcari autoctoni, soprattutto calcilutiti scure, wackestone particellari e boundstone ben stratificati. In senso generale, il membro inferiore è del Kasimoviano superiore, mentre il membro superiore è dello Gzheliano inferiore. Tuttavia, vi sono anche alcune successioni del Kasimoviano superiore che mostrano facies sedimentarie simili a quelle del membro superiore.

Le associazioni a fusulinoidea del membro inferiore sono dominate da specie allungate del genere *Ferganites*, che talvolta è associato con specie di *Schubertella* e *Staffella*. *Rauserites*, *Tumefactus*, *Jigulites*, *Quasifusulina*, così come alcune specie di *Ferganites* con conchiglia obesa, compaiono soprattutto in strati del membro superiore.

L'analisi dettagliata dei fusulinoidea della Zona Cantabrica ha permesso di verificare diversi problemi concernenti la loro paleoecologia, biostratigrafia e paleobiogeografia. Si è dimostrato che *Ferganites*, di cui si hanno importanti accumuli nel membro inferiore, dovrebbe

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essere vissuto in ambiente di alta energia, in prossimità della riva. La presenza di alcune forme significative come *Rausevites* cf. *rossicus* e *Figulites* sp., consente una correlazione tra la successione cantabrica, Alpi Carniche e regioni dell'Asia centrale. Invece queste successioni differiscono sostanzialmente da quelle di altre aree dell'Eurasia occidentale, come la Piattaforma Russa e il Bacino del Donets, indicando che queste ultime avevano scarse connessioni con la Paleo-Tetide.

Alcune osservazioni hanno posto quesiti di carattere generale sui fusulinoidea del Carbonifero terminale, suggerendo anche qualche indicazione per risolverli.

Ne è un esempio la frenoteca, una partizione interna che si trova in alcuni fusulinoidea e la cui funzione è ancora incerta. L'abbondanza nella Zona Cantabrica di esemplari di *Tumefactus* con frenoteca, fornisce informazioni per ricostruirne la geometria e avanzare ipotesi sulla sua funzione.

Un altro aspetto problematico è rappresentato dalla origine e distribuzione del genere *Triticites*. Questo genere sembra assente sia nella zona Cantabrica che nella maggior parte delle regioni euroasiatiche, sollevando il quesito se i *Triticites* americani e euroasiatici abbiano un progenitore comune.

## Introduction

During late Kasimovian and early Gzhelian times, the Cantabrian Zone (NW Spain) (Fig. 1 A) was situated in the western end of the Paleo-Tethys, an area that records the youngest marine sedimentation of the Carboniferous of the westernmost area of Europe.

Among the variety of sedimentary settings recorded, the Cantabrian Zone (Lotze 1945) includes shallow carbonate platform deposits, a type of environment that typically contains fusulinoideans. This group of larger foraminifera bears great interest for various reasons connected not only to the clarification of the regional geology, but also to the ascertaining of some paleoecological aspects as well as to establishing long distance correlation and biogeographic relationships. In spite of the wide scope of interests involved here, only recently have detailed studies on this final part of the Carboniferous succession commenced and, in fact, most of the latest Carboniferous fusulinoideans in the region have been discovered in the last few years.

The Cantabrian Zone was subdivided into several structural units by Julivert (1971) (Fig. 1 A), who introduced them mainly on the basis of their distinct stratigraphic characteristics. Roughly speaking, the more to the east a particular unit is situated, the younger the Carboniferous deposits at the top of its Carboniferous succession. Marine strata of late Kasimovian and early Gzhelian age occur only in the Picos de Europa Unit, which corresponds to the northeasternmost part of the Cantabrian Zone. These late Kasimovian and early Gzhelian deposits bearing fusulinoideans correspond to the Puentellés Formation, a calcareous lithostratigraphic unit cropping out in the northern part of the Picos de Europa Unit, within a narrow belt that has been called Gamonedo-Cabrales area (Fig. 1 B). The Puentellés Formation is overlain by a mainly terrigenous turbidite succession (Cavandi For-

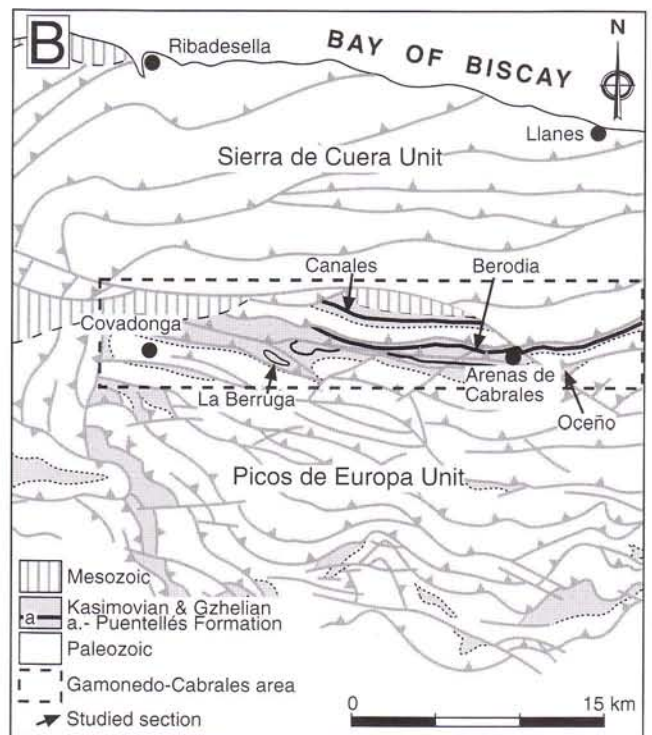
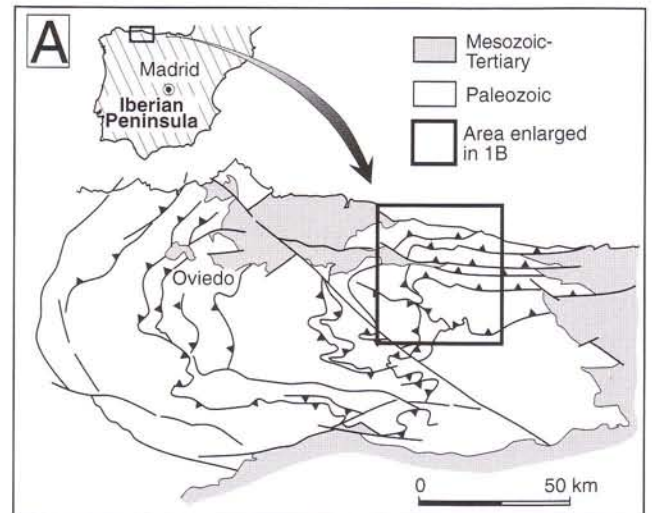


Fig. 1 - A: Sketch of the Cantabrian Zone. B: Geological sketch of the eastern Cantabrian Zone (modified from Marquinez 1989) and location of the area studied.

mation) of presumably Gzhelian age. Apart from some specimens recovered from boulders of older age included within olistolithic megaturbidites, the Cavandi Formation has not yielded fusulinoideans.

The analysis of the fusulinoidean assemblages of the Puentellés Formation may provide clues for understanding the lateral changes and paleogeographic distribution of this formation through the sedimentary basin, as well as on other topics concerning systematics, evolution and biogeography of the Late Carboniferous (Pennsylvanian) fusulinoideans.

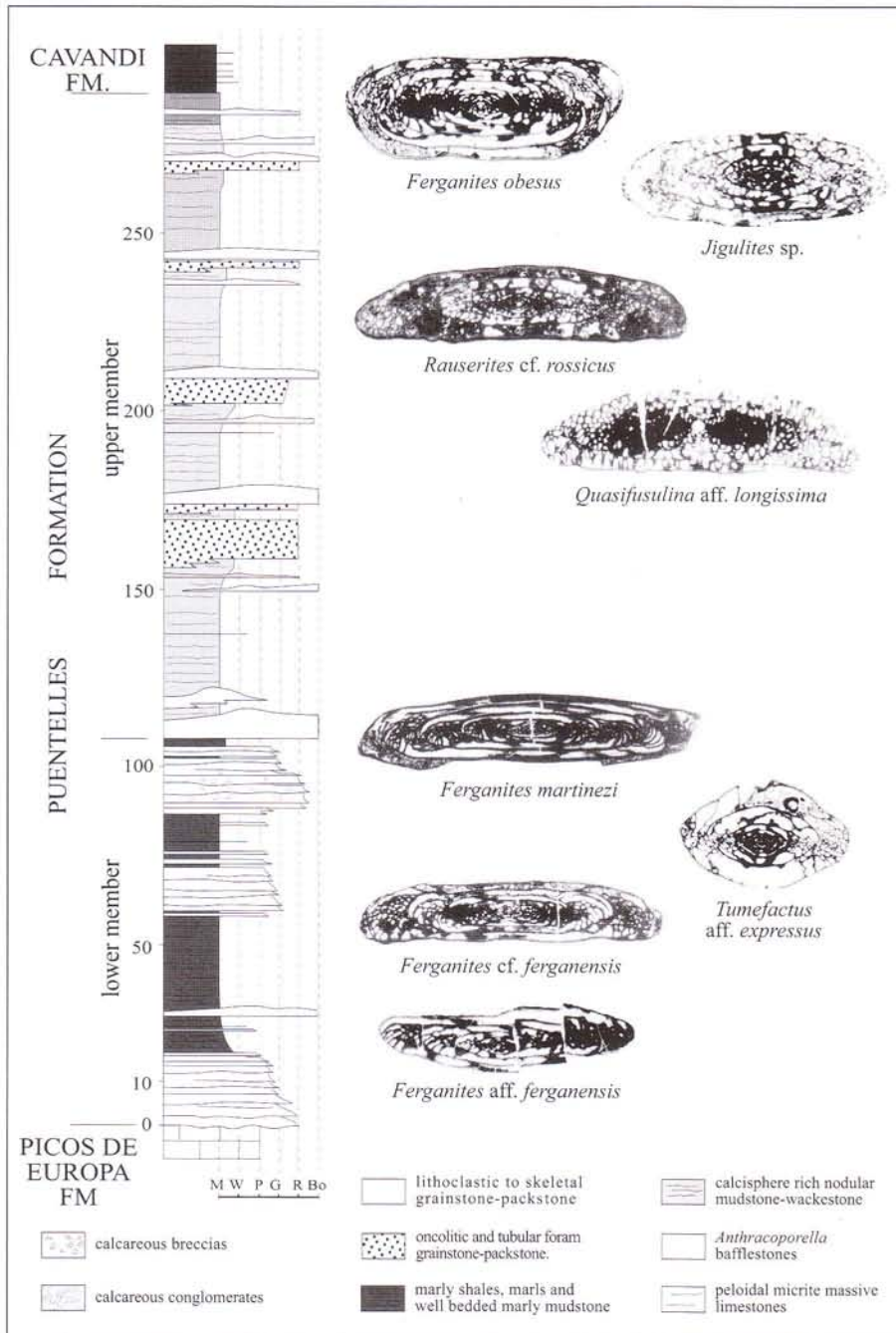


Fig. 2 - Idealized stratigraphic succession and characteristic fusulinoideans of the Puentellés Formation from northern and western Gamonedo-Cabrales area. (M: mudstone; W: wackestone; P: packstone; G: grainstone; Cg: conglomerate; Bo: boundstone).

### The uppermost Carboniferous from NW Spain

The Picos de Europa Unit (eastern part of the Cantabrian Zone) is characterized by the existence of rather complete Carboniferous successions that include extensive carbonate platforms with steep margins (shelves) of Serpukhovian up to early Kasimovian age [see Bahamonde et al. (1997, 2000) for a sedimentological analysis]. The stratigraphic units overlying the carbonate platforms correspond to the synorogenic, mainly clastic, deposits of the Gamonedo-Cabrales area. These clastic units (uppermost Moscovian-lower Kasimovian), which outcrop in small areas and show strong lateral changes of facies, totally buried the previous platforms. Subsequently, during late Kasimovian and early Gzhelian times, a new episode of

calcareous sedimentation, corresponding to the deposition of the Puentellés Formation, took place throughout the whole area.

The Puentellés Formation was introduced by Martínez-García (1981) for upper Carboniferous strata that had been previously dated as late Kasimovian by van Ginkel (1971). More recent investigations showed that the top of the formation can reach, at least locally, an early Gzhelian age (Villa & van Ginkel 1999; Villa & Ueno 2002). A preliminary sedimentological study of the Puentellés Formation was carried out by Truyols et al. (1984), who analyzed the section close to the village of Puentellés. More comprehensive research has been recently carried out by Merino-Tomé (2001) and Villa & Bahamonde (2001).

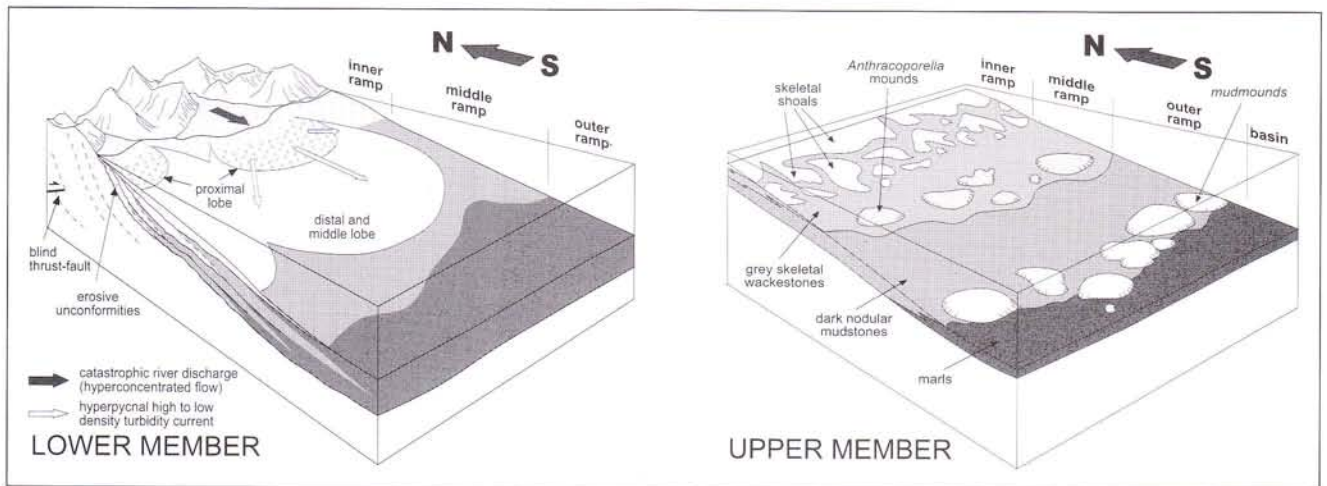


Fig. 3 - Sedimentary models proposed for the lower and upper members of the Puentellés Formation.

### The Puentellés Formation

**Stratigraphy.** The Puentellés Formation is a calcareous succession up to 250-325 m thick. In the northern part of the Gamonedo-Cabrales area, this unit is disconformably overlying the Picos de Europa Formation (Moscovian), while in the south-western part it is conformably resting on Kasimovian (upper Khamovnicheskian-lower Drogomilovian) strata; the latter are deltaic and fan-deltaic terrigenous deposits mainly consisting of sandstones, conglomerates and shales with some coal-seams.

According to Merino-Tomé (2001), two stratigraphic members can be differentiated in the Puentellés Formation (Fig. 2). The lower member (20-160 m thick) is composed of reworked and resedimented carbonates (calcareous conglomerates and breccias, pebbly calcareous sandstones, and graded lithoclastic to skeletal grainstones to packstones), and of in situ deposits such as bioturbated skeletal mud- to wackestones, marls, and few algal (phylloids and dasycladaceans) bafflestone intercalations. A cyclic stacking pattern, consisting of fining upward sequences, limited by erosive unconformities in the most proximal basin sectors, is characteristic of this unit.

The upper member varies in thickness from 150 to 225 m (data from the northern thrust units of the Gamonedo-Cabrales area). It is composed of dark nodular calcispheres, rich mud- to wackestones, thick bedded algal bafflestones, skeletal pack- to grainstones, and massive beds of peloidal or clotted micrite with large voids filled by marine cement (mud mounds) that locally form decametric shallowing upward cycles. These deposits become, southwards, marls, marly shales, and shales included in the Cavandi Formation.

**Facies model.** The Puentellés Formation records the sedimentation in a carbonate ramp developed in a tectonically controlled marine basin with limited water circulation. During the deposition of the lower member,

the basin received an important clastic supply from nearby hinterland domains (located to the north), which were being uplifted as a result of deformation linked to the Variscan orogeny. The hinterland and near-shore derived material was transported basinwards by hyperconcentrated and turbiditic currents (Mulder & Syvitski 1995) generated at river mouths from catastrophic flooding dominated river-delta and fan-delta systems (in the sense of Mutti et al. 1996), to which the ramp was connected. The huge amount of calcareous sediment thus accumulated formed shelfal lobes in the proximal sectors of the carbonate ramp (Fig. 3) (Merino-Tomé 2001; Bahamonde, in Villa & Bahamonde 2001).

Between the clastic input phases, the autochthonous carbonate production was renewed and skeletal mud- to wackestones, marls, and algal bafflestones were deposited, overlaying the lobe deposits. The observed cyclic stacking patterns were probably produced by alternating periods of tectonic uplift (accompanied by tilting and generation of erosive unconformities in the most proximal basin areas) and denudation.

Once the clastic supply ended, the carbonate sedimentation spread throughout the whole basin. This is the type of sedimentation recorded in the upper member (Fig. 3). The shallowest ramp areas (inner ramp) were characterized by the development of bioclastic shoals with small *Anthracoporella* colonies. In deeper zones, corresponding to the middle ramp, these dasycladacean algae locally formed meter scale mounds, whereas in more distal sectors (outer ramp) mud mounds thrived.

In tectonic units situated in the southernmost part of the Gamonedo-Cabrales area, limestones of the upper member laterally become marlstones, marly shales, and shales, which record the transition to basinal environments. On the other hand, a latest Kasimovian (late Drogomilovian)-early Gzhelian transgressive trend caused the carbonate production to be progressively constrained to northern (proximal) areas. As a result of these later-

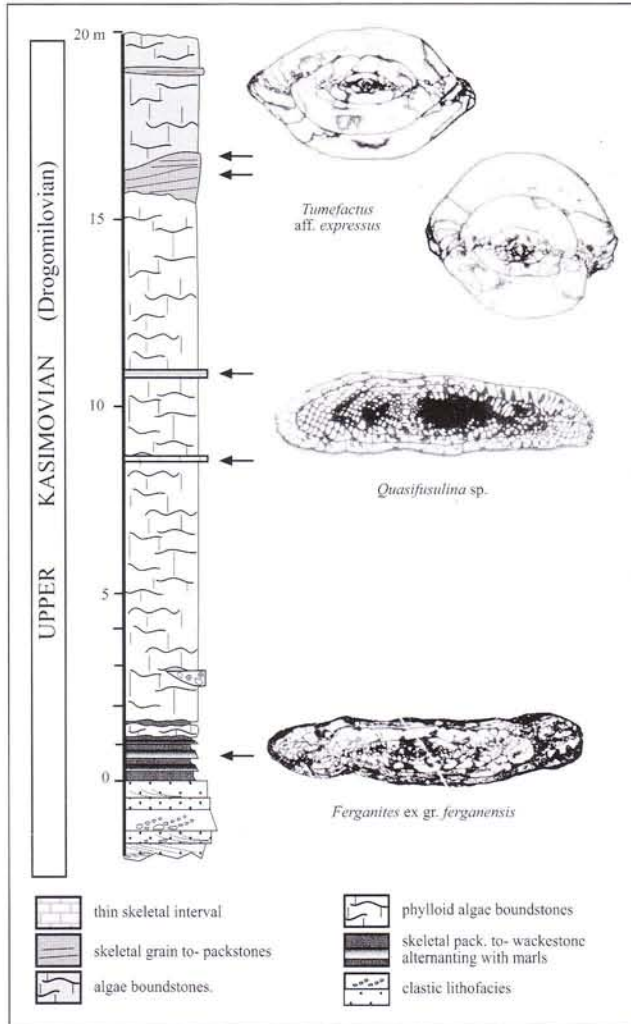


Fig. 4 - Stratigraphic succession and characteristic fusulinoideans of the Puentellés Formation at the La Berruga section.

al and vertical changes from carbonate to marly or shaly sedimentation, the boundary between the Puentellés Formation and the overlying Cavandi Formation appears diachronous through the Gamonedo-Cabrales area.

**The La Berruga succession.** A few sections (located in the southern part of the area studied) show strata that cannot be easily assigned to either of the two members observed in the northern part of the Gamonedo-Cabrales area.

This is the case of the La Berruga section (Fig. 4), in which the Puentellés Formation is very thin (only 20 m thick against more than 250 m in northern units) and consists mainly of nodular dasycladaceans and phylloid algae boundstones. Although these facies are similar to those typical of the upper member, the fusulinoideans recovered indicate that the La Berruga section is late Kasimovian in age and, thus, La Berruga succession is coeval with the lower member strata outcropping in northern sections.

The biostratigraphic data gained from the fusulinoideans collected in this section, along with the facies model and paleogeographic context pictured above for the Puentellés Formation, have led us to interpretate the La Berruga succession as autochthonous deposits accumulated in inter-lobe areas situated within the middle ramp.

### Fusulinoideans from the Puentellés Formation

#### Summary of the generic characteristics

Apart from some small fusulinoideans (such as *Schubertella* and *Staffella*), so far the uppermost Kasimovian and lowermost Gzhelian strata of the Puentellés Formation have yielded fusulinoidean species belonging to the genera *Montiparus*, *Rauserites*, *Jigulites*, *Tumefactus*, questionable *Triticites*, *Ferganites* and *Quasifusulina*. A remarkable fact is that fusulinoideans do not occur uniformly along the two members recognized in this formation.

In general, the lower one is dominated by the presence of *Ferganites* species whereas the upper one contains much more varied assemblages.

- *Montiparus*. A globose *Montiparus* species, closely related to typical *Montiparus* from the Russian Platform, such as *M. ex gr. paramontiparus* (Rozovskaya, 1950), has been found in one single locality of the Puentellés Formation (Oceño section), in strata of late Kasimovian age belonging to the lower member. However, the most representative *Montiparus*, frequently found in the Puentellés Formation, are *Montiparus* species belonging to a lineage leading from *Montiparus* to *Rauserites*. They are transitional forms inbetween these two genera which show an elongated shell and irregular septal folding. Their closest relatives seem to be forms such as *Montiparus varians* and *Rauserites alaicus*, described by Bensch (1972) in Central Asian areas. These Cantabrian species are also similar to forms reported by Forke (in Villa et al. 2002) from the Carnic Alps. It is noteworthy that so far these elongated *Montiparus* have only been found in the sedimentary facies typically represented in the upper member strata.

- *Rauserites*. Apart from the *Montiparus-Rauserites* transitional forms mentioned above, the upper part of the Puentellés Formation has yielded other *Rauserites* species occurring in lower Gzhelian strata. The most relevant species are *Rauserites cf. erraticus* (Rozovskaya, 1952) from the Asiego section (Villa & van Ginkel 1999) and *Rauserites cf. rossicus* (Schellwien, 1908) from the Cavandi section (Villa & Ueno 2002). These two forms are interesting because they are closely related (if not identical) to species described from the Russian Platform and, therefore, they allow correlation with the Russian chronostratigraphy. Moreover, *Rauserites rossicus* is widely distributed all over Eurasia and is considered to be typical of lower Gzhelian strata.

– *Jigulites*. So far this genus has been found in a single locality (Asiego section, Villa & van Ginkel 1999). However, its presence is very relevant because it allows comparisons with species from the Russian Platform and the Urals. The Cantabrian species resembles forms belonging to the *Jigulites formosus* (Rozovskaya, 1950) group, and, especially, a species from the southern Urals described by Davydov (in Davydov & Popov 1986).

– *Tumefactus*. *Tumefactus* species occur in both the lower and the upper members of the Puentellés Formation. One of the species [*Tumefactus* aff. *expressus* (Anosova, in Bensch 1969)] may rarely occur in the lower member. So far, it has been found in the Oceño section, in lower member strata of late Kasimovian age. The same species also occurs in large numbers in contemporaneous strata exposed at La Berruga section, but in facies displaying characteristics typical of the upper member. A more advanced *Tumefactus* species has been described at the top of the formation (lower Gzhelian) in the Cavandi section (Villa & Ueno 2002). It is relevant to mention that all the *Tumefactus* species so far recorded come from Central Asia, Carnic Alps, and Cantabrian Mountains. Some aspects related to the taxonomy of this genus and to the morphology of its shell are further discussed below.

– *Triticites*. Only a few fusulinoideans from the Cantabrian Zone are assigned nowadays to *Triticites* and all of them are, in fact, questionably *Triticites*. With regard to the Puentellés Formation, only two forms have been found in lower Gzhelian strata. One of them is *Triticites*? aff. *acutus* Dunbar & Condra, 1927 from the Asiego section (Villa & van Ginkel 1999), which is probably a *Rauserites* related form, and the other is *Tr.*? aff. *gusanicus* Bensch, 1972 from the Cavandi Section (Villa & Ueno 2002), which, according to the systematics by Rauscher-Chernousova et al. (1996), could belong to a *Schwageriniformis* species. Some additional comments on the phylogeny and geographic origin of *Triticites* are discussed in the next chapter.

– *Ferganites*. This is the most abundant fusulinoidean genus in uppermost Kasimovian/lower Gzhelian strata of the Cantabrian Zone. In the lower member of the Puentellés Formation (upper Kasimovian), it usually occurs in large numbers forming monospecific assemblages of species belonging to the *Ferganites ferganensis* (Miklukho-Maklay 1950) species group. In the upper member (lower Gzhelian), *Ferganites* is represented by species belonging to the *Ferganites obesus* Villa & Ueno, 2002 group. The latter group seems to be restricted to the Cantabrian Zone.

– *Quasifusulina*. *Quasifusulina* species occur in upper Kasimovian and lower Gzhelian assemblages. Gzhelian specimens belong to either *Quasifusulina longissima* (von Möller, 1878) or to a related species. *Quasifusulina longissima* is a long-ranging species that has been reported from many Eurasian areas in strata from the uppermost Carboniferous up to the lower Permian.

## Discussion on several fusulinoidean problems

Certain features of the Cantabrian fusulinoideans, including their composition and occurrence, give rise to several other questions bearing a more general interest.

### Some questions concerning *Tumefactus*

**Taxonomic position.** The genus *Tumefactus* has been recently introduced by Leven & Davydov (2001). Its morphology, characterized by a globose shell, an extremely rapid expansion of the outer volutions, and the presence of a distinct phrenotheca, gives *Tumefactus* species a “Permian” appearance, since they are roughly similar to *Pseudoschwagerina* and other Permian genera. The first species of this type described in the literature were originally assigned to the genus *Triticites* (e. g. *Triticites expressus* Anosova in Bensch 1969), but are now included in *Tumefactus*.

Villa & Ueno (2002) discussed the systematic position of *Tumefactus* proposed by Leven & Davydov (2001). According to these last authors, *Tumefactus* is a subgenus of *Schwageriniformis*, a genus which, in turn, had been created by Bensch (in Rauscher-Chernousova et al. 1996) to include *Triticites schwageriniformis* Rauscher-Chernousova, 1938 species group. Villa & Ueno (2002) consider *Tumefactus* to be neither closely related to *Triticites* nor to *Schwageriniformis*, since *Tumefactus* species have a distinct phrenotheca which is absent from the others. Therefore, they agree with Leven & Davydov to consider *Tumefactus* species to make up a separate taxon, but being a genus in itself.

**Discussion on morphology.** One of the species found in the Puentellés Formation (La Berruga and Oceño sections) is close to the *Tumefactus expressus* Anosova (in Bensch, 1969). Nevertheless, our species differs from the Central Asian one in several features, especially in that the Cantabrian species shows an extremely high intraspecific variability in shell shape, development of juvenile volutions, and type of chomata.

The phrenotheca of *Tumefactus* also deserves an additional comment. From what is observed in the specimens available, the function of phrenotheca in *Tumefactus* could be reducing the chamber space potentially occupied by cytoplasm, since in these forms chamber volume had experienced a remarkable growth.

The observation of different types of test sections (Fig. 5) provides a general picture of the phrenotheca geometry. As was postulated by Hasegawa (1964), within chambers phrenotheca formed a sort of small cave-like chamberlet or “inner chamber”. According to our observations, each inner chamber consists of a more or less irregular tube whose diameter decreases towards the polar ends and which opens in its central part allowing communication between two adjacent chamberlets. Apparently,

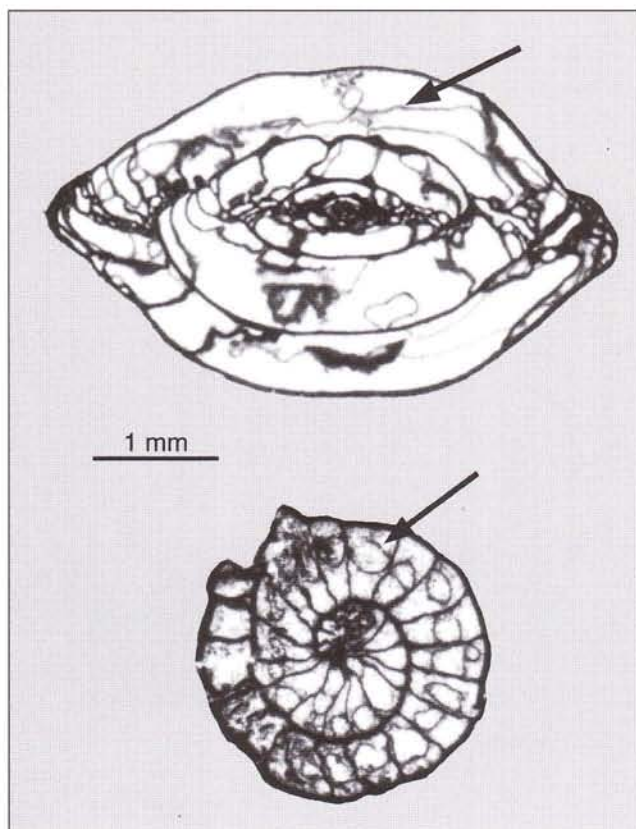


Fig. 5 - Specimens of *Tumefactus* aff. *expressus* from the La Berruga section showing phrenotheca (arrows). Note the circular profiles of the phrenotheca in the parallel section.

towards the central part of the chamber, the lower part of the tube merges with the chamber floor and then, the phrenotheca appears only in the upper part of the chamber. On the contrary, close to the polar ends of the shell the tube width decreases and the inner chamber is completely separated from both the chamber bottom and roof. Therefore, when observed in parallel sections, phrenotheca is seen as forming circular profiles (Fig. 5).

Anyway, the phrenothechal geometry in *Tumefactus* still leaves some relevant questions open: to what type of life was this morphology adaptive? What kind of matter, or substance, filled up the remaining chamber space?

Dunbar & Skinner (1937) suggested that the phrenothecha may have been formed within the chambers at the top of the protoplasm when the organism partly withdrew from the shell. Thompson (1948), who introduced the term phrenothecha, pointed out that these partitions are most commonly present in highly inflated and loosely coiled specimens in which the cell would not have filled the complete shell permanently. He proposed that adverse conditions could have made the cell size decrease and that the phrenothecha would have acted as a protective covering around vital parts of the cell. However, as this last author remarks, there are other fusulinoideans with very inflated shells that do not have phrenothecha.

According to Severin & Lipps (1989), *Alveolinella quoyi*, a large living fusiform foraminifer, can only fill an average of 39% of its chamber space with protoplasm. They suggested that the chamber space containing no organic substances could be filled with gas, leading to a lower overall density of the test and making it easier for the organism to move. This is a possibility to be taken into account for the *Tumefactus* shell, in which the part of the chamber surrounding the inner tube could be occupied by gas, with the phrenothecha representing an effective separation between gas and protoplasm. The presence of gas, together with the globose and expanded shell, suggest that these benthonic forams possess a certain level of buoyancy. This would not mean that the *Tumefactus* tests were able to float but simply that their low density allowed these foraminifera to live as epibionts on organisms such as algae, on which a low weight was a necessary requirement.

Unfortunately, the question about which was the particular habitat of *Tumefactus* cannot be solved by the sedimentological analysis of the La Berruga sequence that has yielded these specimens (Fig. 3). Although *Tumefactus* occurs commonly, we must presume that the tests were accumulated after the organisms died, since these strata are skeletal limestones corresponding to shoal deposits (interbedded in algal build-ups barren of fusulinoideans). Obviously, all the components in the skeletal limestones, including *Tumefactus* shells, have experienced transport to some extent and, therefore, the particular habitat of these inflated forms, as well as the precise functional role of the phrenothecha, remain obscure.

### The origin of *Triticites*

*Triticites* was mentioned in Eurasia as early as in the 1930's (e. g. Chen 1934; Rauzer-Chernousova et al. 1936). Since that time, many *Triticites* species from Eurasian Carboniferous areas, such as the Russian Platform, Urals, Central Asia, and China, have been described. However, it was soon realized that remarkable differences existed among those species and so several genera were separated from what was formerly considered to make up a single genus. *Montiparus*, *Rauserites*, *Jigulites*, *Ferganites*, *Schwageriniformis*, *Kushanella*, *Tumefactus*..., and so on, currently include species plexus formerly assigned to *Triticites*. In view of this situation, one may wonder if *Triticites* ever existed in Eurasia or if it was restricted only to the American continent.

According to the phylogeny of the early schwagerinids established by various authors, *Triticites* is generally envisioned to derive from a Eurasian ancestor. This may be seen in the phylogenetic schemes proposed by Rozovskaya (1975), Davydov (1990), Remizova (1994), and van Ginkel & Villa (1999), represented in the three schemes of Fig. 6a. All of them consider *Triticites* as deriving from mid-Kasimovian forms either assigned to *Obsoletes* (schemes I and II), or to *Protriticites* of "*Obsoletes*

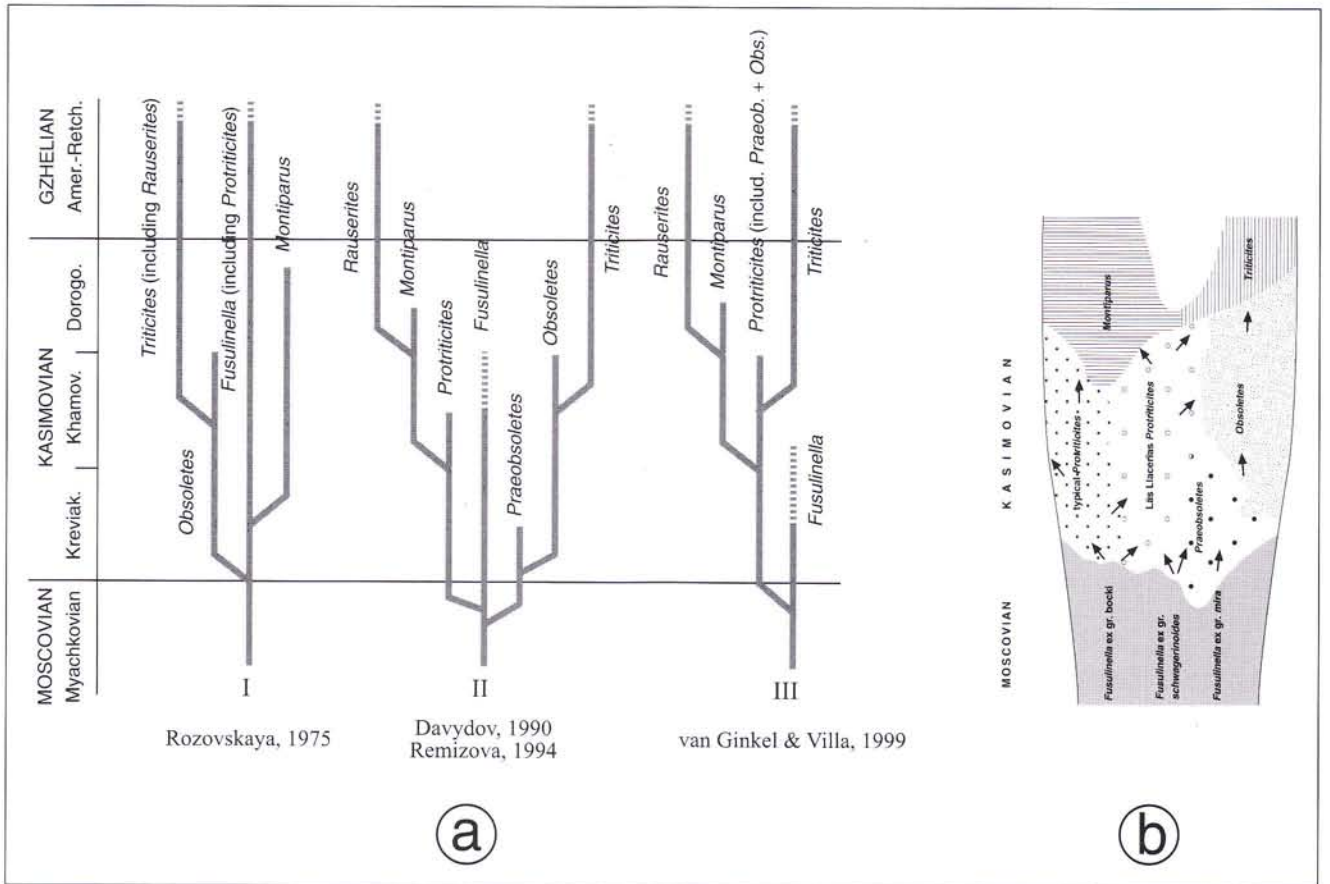


Fig. 6 - a: Phylogeny of early schwagerinids after several authors. b: Scheme by van Ginkel & Villa (1999) illustrating the idea of *Protriticitites* (including *Obsoletes*) as composed of several species groups that evolved to produce *Montiparus* and *Triticites*.

type" (scheme III), the latter group being *Protriticitites* species that show weak or nearly absent tectorial deposits.

The scheme by van Ginkel & Villa (1999) proposed that different *Fusulinella* groups derived to produce *Protriticitites* (Fig. 6b). Note that, according to Simpson (1961), this situation must not be labeled as polyphyletic, since monophyly can be considered "the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank" (Simpson 1961, p. 124). In that same scheme by van Ginkel & Villa (1999), *Protriticitites*, in turn, would be also composed of various species groups (some of them showing "Obsoletes type" features), which were not still sufficiently separated to make up different genera. During mid-Kasimovian times, these *Protriticitites* groups evolved to produce two separate lineages that originated *Montiparus* and *Triticites*.

In any case, in the van Ginkel and Villa's scheme, as well as in the other schemes, *Triticites* is seen to derive from a Eurasian lineage. However, in view of the few Eurasian forms that could nowadays be considered to belong to *Triticites*, one may wonder whether this lineage extended to the North-American Mid-continent and there it gave rise to the numerous species of American *Triticites*. However, a remarkable fact is that, in comparing the type species of this genus, *Triticites secalicus* (Say in James,

1823, emend. Dunbar & Condra, 1927), with the Eurasian *Triticites*, some species from Northern Urals (e.g. *Triticites petschoricus* Rauszer-Chernousova & Belyaev in Rauszer-Chernousova et al. 1936) are found to be very similar to some American *Triticites*.

Another similar species is *Triticites samaricus* Rauszer-Chernousova 1938 (= *Triticites secalicus* var. *samarica*), from the Volga Region. Obviously, these resemblances either could be the result of parallel or convergent evolution in different lineages, or they could evidence that *Triticites* really originated in Eurasia and that the Urals region constituted the corridor for their expansion to North America (Fig. 7).

From the stratigraphic record of the Carboniferous of North America, a remarkable gap between the last *Fusulinella* (which, in case of a local origin of the American species, would be the potential ancestor of *Triticites*, as questionably suggested by Thompson 1948, Fig. 4) and the first occurrence of *Triticites* is evidenced. The last *Fusulinella* are recorded from lower Desmoinesian strata of the North American Mid-continent and the Rocky Mountains, whereas the first *Triticites* species appear in the lower part of the Missourian stage (see Dunbar & Henbest 1942; Douglass 1987; Barrick et al. 1996; Wahlman et al. 1997, among others).



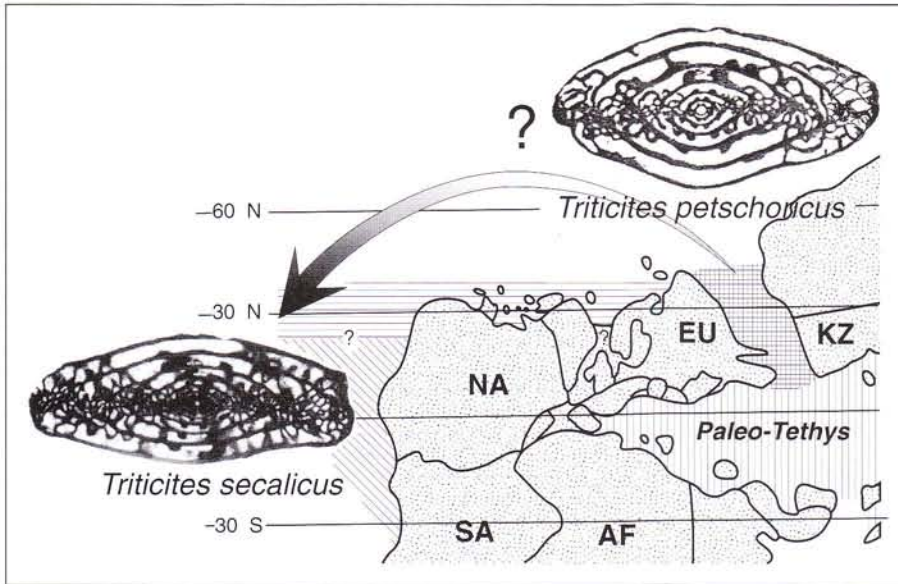


Fig. 7 - Paleogeographic map illustrating a potential way for the dispersal of *Triticites* from Eurasia into the North American Mid-continent (explanation of map as in Fig. 9).

This fact seems to reinforce the likely immigration of the first American *Triticites* from Eurasia.

However, after the discovery of *Protriticites* (Wahlman et al. 1997) in the western part of the USA, it could be alleged that the American *Triticites* evolved from some of the *Protriticites* species found in the Rocky Mountains. Yet, according to the stratigraphic range of these genera shown by Wahlman et al. (1997), an objection, similar to that formulated in the case of *Fusulinella*, may be raised here too: the Rocky Mountains *Protriticites* have been reported to occur in the lower part of the upper Desmoinesian, which still leaves a considerable gap with respect to the first occurrence of *Triticites*.

Moreover, the American *Protriticites* do not seem to have any American potential ancestor: besides the existing gap between the last occurrence of *Fusulinella* and the *Protriticites* occurrences, they resemble Eurasian forms very much. Therefore, it is conceivable that, although during Late Carboniferous (=Pennsylvanian) North America and Eurasia belonged to different and efficiently separate biogeographic provinces, some rare

connections could have allowed faunas to spread out (see Ross 1967, p. 1350).

#### An explanation of the *Ferganites* accumulations

Accumulations of cigar-like fusulinoidean tests occur in strata of different ages and connected to different fusulinoidean genera. One of these cases refers to *Ferganites*, a genus often reported in different parts of the world in large numbers and in sandy facies (Miklukho-Maklay 1950; Davydov 1990; Villa et al. 2002). In these concentrations, *Ferganites* is usually the only large fusulinoidean.

The lower member of the Puentellés Formation contains striking accumulations of *Ferganites* shells of the characteristics mentioned above (Fig. 8). The sedimentological analysis of these beds, coupled with paleogeographical data from the regional geology of the Cantabrian Zone, led Villa and Bahamonde (2001) to relate *Ferganites* accumulations and high-energy deposits. *Ferganites* specimens probably lived in near-shore areas, in stressed environments affected by river discharges producing strong currents and changes in water salinity.



Fig. 8 - *Ferganites* specimens embedded in a calcareous siltstone part of a hummocky cross-stratified bed.

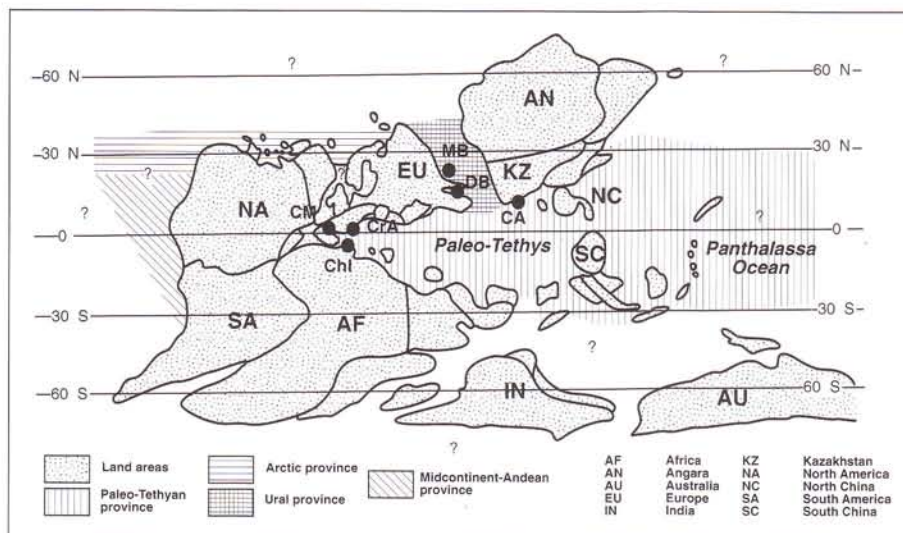


Fig. 9 - Paleogeographic map showing the distribution of fusulinoidean provinces during Late Carboniferous time and location of several relevant areas (taken from Villa et al. 2002, who modified it from Rui and others 1991). CM= Cantabrian Mountains; CrA= Carnic Alps; ChI= Chios Island; CA= Central Asia; MB= Moscow Basin; DB= Donets Basin.

These strong currents could have transported *Ferganites* shells to more distal areas, where they were deposited in beds forming hummocky cross stratification. These would be now the deposits of inner to middle ramp recorded in the lower member of the Puentellés Formation.

As no other large form is present in these beds, it is inferred that the *Ferganites* species constituted essentially the original fusulinoidean biocoenosis. The morphology of their shell (that is, its subcylindrical shape, numerous septa, tight coiling and relatively thick wall) could represent an advantage to endure high energy and sandy environments. On the other hand, the inferred near-shore habitat of the *Ferganites* from the Cantabrian Zone, which was probably very close to river mouths, seems to indicate that species belonging to this genus were able to resist the relatively low salinity conditions created by river supplies of fresh water.

#### Biogeographic affinities and correlation

The fusulinoidean assemblages commented above show closest affinities with those found in Central Asian areas (Tien-Shan, Fergana, and, especially, with Darvaz) and differ greatly from those found in the type-areas of the Kasimovian and Gzhelian stages, especially from the Moscow Basin.

These affinities, already pointed out in Villa et al. (2002) and Villa & Ueno (2002), are evidenced by the presence of Central Asian elements, such as *Ferganites*, *Tumefactus*, and some particular *Rauserites* species. These "Asian" elements indicate that the Cantabrian Zone was part of the western Paleo-Tethys province, a biogeographic division that also included the Carnic Alps (Fig. 9). On the contrary, the Moscow Basin and the Donets Basin seem to have been situated in the Urals province. [Paleobiogeographic provinces according to Ross and Ross (1987) and Rui et al. (1991)].

The paleogeographic affinities of the Cantabrian Zone make it difficult to establish a direct correlation with the chronostratigraphic units of the Russian Platform. Fortunately, although most of the assemblage components are restricted to the Paleo-Tethys, a few of them correspond to more cosmopolitan forms.

As commented above, one of the main links in this correlation is *Rauserites cf. rossicus*, a species closely related, or identical, to the widespread and typically lower Gzhelian fusulinoidean *R. rossicus*. According to this and other fusulinoideans, the upper part of the Puentellés Formation is correlated with the lower Gzhelian of the Russian Platform. We, therefore, consider its lower part to belong to the upper Kasimovian. It is noteworthy that all cosmopolitan elements are of Gzhelian age, so suggesting that an early Gzhelian transgression could have facilitated their dispersion.

Fig. 10 shows the correlation of the Puentellés Formation with the Russian stratigraphic units and with the biozonation established by Leven & Davydov (2001) in Darvaz, Central Asia. The Puentellés Formation can be correlated with the Kalaiukhna Formation (members 5 to 7) studied by these authors.

#### Remarks

From the analysis of the fusulinoideans from the Puentellés Formation, some remarkable facts may be emphasized:

- Most of the upper Kasimovian and lower Gzhelian fusulinoideans of the Cantabrian Zone are closely related to Central Asian forms.
- Two genera (*Ferganites* and *Tumefactus*) have only been found in Paleo-Tethyan areas.
- Late Kasimovian fusulinoideans are either endemic or restricted to Paleo-Tethyan areas.
- On the contrary, Gzhelian assemblages contain more

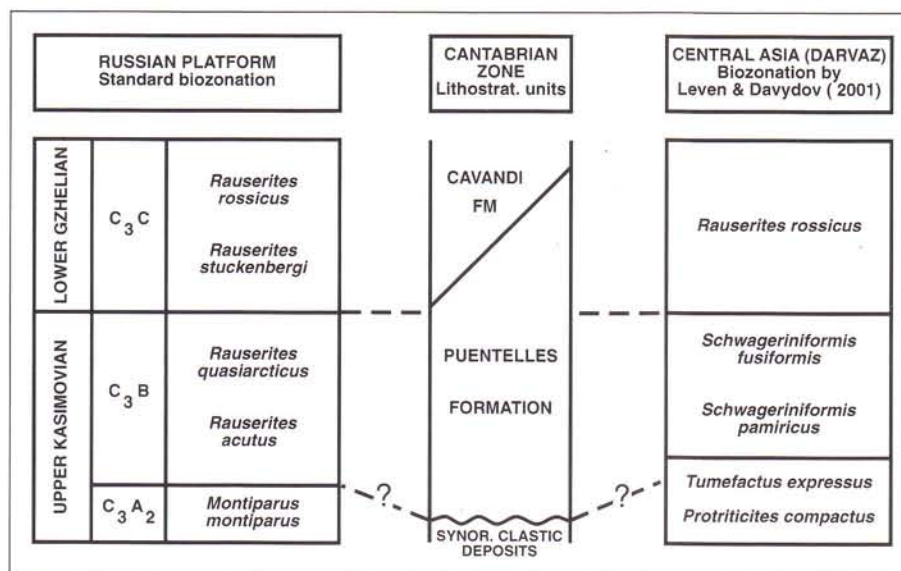


Fig. 10 - Correlation of the Puenteles Formation with the biozonation and stratigraphic units of the Russian Platform and Darvaz.

cosmopolitan elements, perhaps evidencing an early Gzhelian transgression.

- Due to its wide distribution, *Rauserites rossicus* might represent an important stratigraphic marker for long distance correlation.
  - The Gzhelian *Ferganites obesus* species group seems to be restricted to the Cantabrian Zone.
  - Monospecific *Ferganites* assemblages observed in shallow turbidite deposits probably reflect the adaptation of these forms to stressed near-shore environments.
- This study arises other relevant questions that should be further investigated:
- Did *Triticites* exist in Eurasia?

- Who was the ancestor of the American *Triticites*?
- Which was the functional role of the phrenotheca?
- Why was *Tumefactus* so inflated and had its chamber space partitioned?

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