The influence of terrestrial run off on marine biotic communities: An example from a thrust-top carbonate ramp (Upper Pennsylvanian foreland basin, Picos de Europa, NW Spain)

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High-diversity marine biotic communities characterize the lower Kasimovian (Upper Pennsylvanian) carbonates of the Las Llacerias Formation in the Ándara Massif (Picos de Europa Province, Cantabrian Mountains, Spain). The carbonates accumulated on a small thrust-top ramp system. Within the shallow, low-energy and euphotic realms, biotic communities were characterized by abundant photozoans (calcareous algae and cyanobacteria) and heterozoans including filter and suspension feeders (calcareous and siliceous sponges, bryozoans, brachiopods, crinoids), diverse other metazoans (rugose solitary and colonial corals, tabulate corals, bivalves, gastropods and echinoids), benthic foraminifers including very abundant small incrusting "tubiforms" and conspicuous swarms of cement-filled spheres (calcispheres or *Penella*). Small-sized buildups of chaetetid sponges, syringoporids, branching rugose corals, *Anthracoporella* and phylloid algae commonly developed in these shallow-water environments. Meanwhile, mud mounds formed at greater water depths, mostly below the lower limit of the phothic zone. The occurrence of such diverse biotic communities and the grain composition of the shallow-water deposits, not recorded in the platform-top successions of the antecedent Bashkirian–Moscovian carbonate shelf (Valdeteja and Picos de Europa formations) are interpreted as linked to increased nutrient levels (mesotrophic to mildly eutrophic conditions) in the actual sea-surface water. The nutrients are inferred to have resulted from land-derived fluxes from the rivers draining the adjacent growing Variscan Orogenic chain. Nutrients were subsequently transported into the narrowed marine shallowing foreland basin located in the eastern side of Pangea, within the palaeoequatorial humid belt. Comparison to the Pennsylvanian Auernig Group in the Carnic Alps allows the discrimination between the influence of land-derived versus upwelling-derived nutrients, providing a useful tool in the interpretation of biotic assemblages in the fossil rock record.

1. Introduction

Environmental factors, primarily water depth, light, temperature, salinity, oxygen level and nutrient supply, control the composition of carbonate rocks, as has been demonstrated in numerous studies during the last decades (Chave, 1967; Lees and Buller, 1972; Lees, 1975; Birkeland, 1977; Hallock, 1987; Carannante et al., 1988; Hallock, 1988; Hallock et al., 1988; Nelson, 1988; Carannante et al., 1997; Hallock,

2001; Mutti and Hallock, 2003; Vecsei, 2003; Halfar et al., 2004; Pomar et al., 2004; Wilson and Vecsei, 2005; Halfar et al., 2006). The biotic associations and non-biogenic composition of carbonate rocks thus represent good proxies for the reconstruction of environmental parameters (James, 1997; Hallock, 2001; Mutti and Hallock, 2003; Pomar et al., 2004; Schlager, 2005).

Current models aiming at classifying and interpreting carbonate rocks therefore are based, among the most important criteria, on the biotic and non-biogenic grains. However, if using a single parameter, the interpretation may be biased by the fact that some physical parameters are closely linked and, thus, difficult to dissociate in the rock record. For example, nutrient supply and temperature may leave similar records in biogenic composition (Mutti and Hallock, 2003; Pomar et al., 2004; Halfar et al., 2006). Also, palaeoceanographic factors may influence the composition of carbonates and, possibly, lead to strange-appearing cases (Lavoie, 1995; Lukasik et al., 2000;

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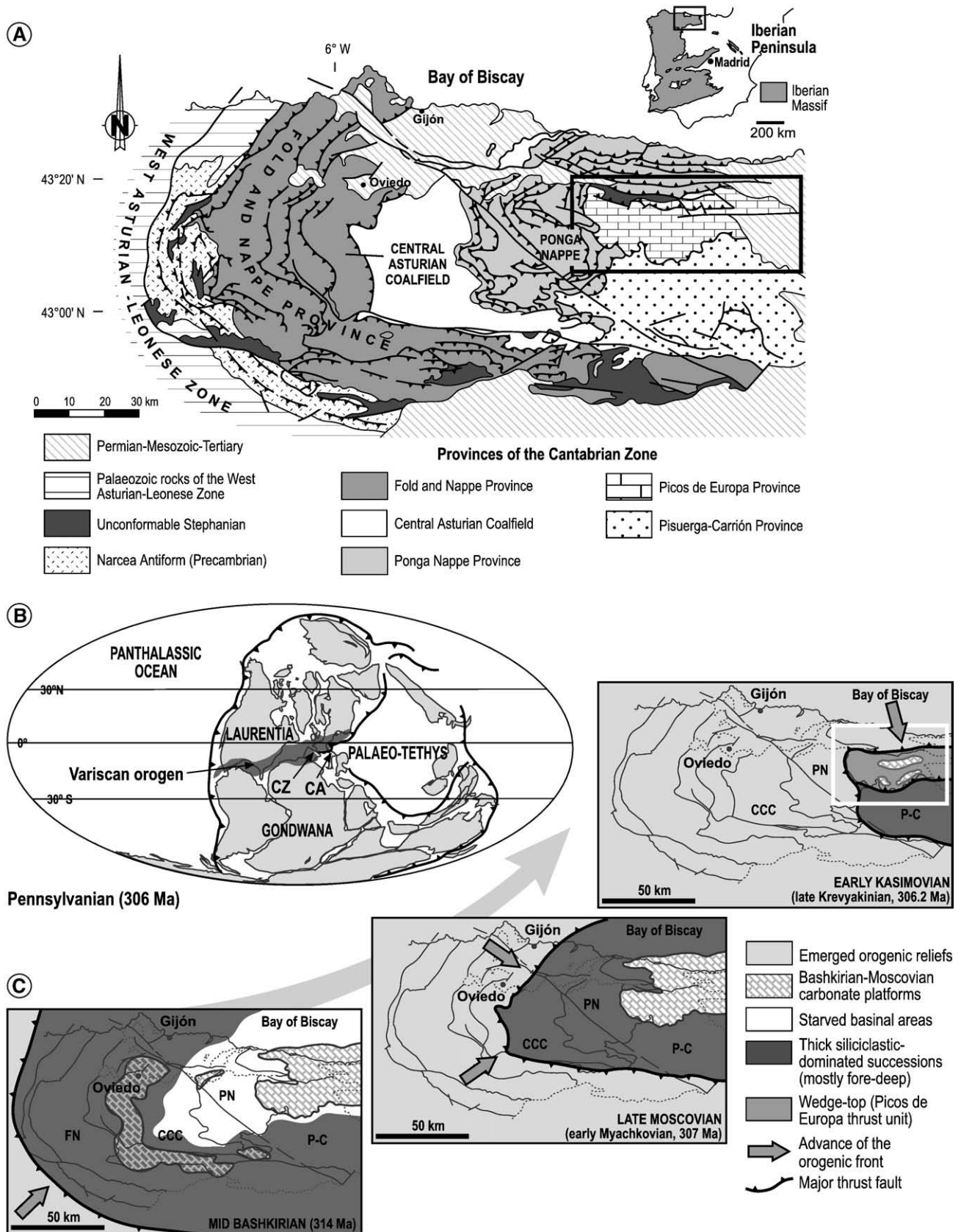
Fig. 1. A) Geological map of Cantabrian Zone showing Picos de Europa Province in boxed area (based on Julivert, 1971; Pérez-Estaún et al., 1988). B) Palaeogeographic map of Pangea during Pennsylvanian time with location of the Cantabrian Zone foreland basin (CZ) and Carnic Alps (CA). Dark grey indicates the location of Variscan orogen. Modified from Golonka et al. (1994). C) Synthetic palaeogeographic maps of Cantabrian Zone during mid-Bashkirian to late Krevyakinian. Note that maps are based on present-day geometry of Cantabrian Zone and, thus, the significant tectonic shortening (nearly 50%) in E–W and N–S direction resulting from Variscan thrusting is not considered.
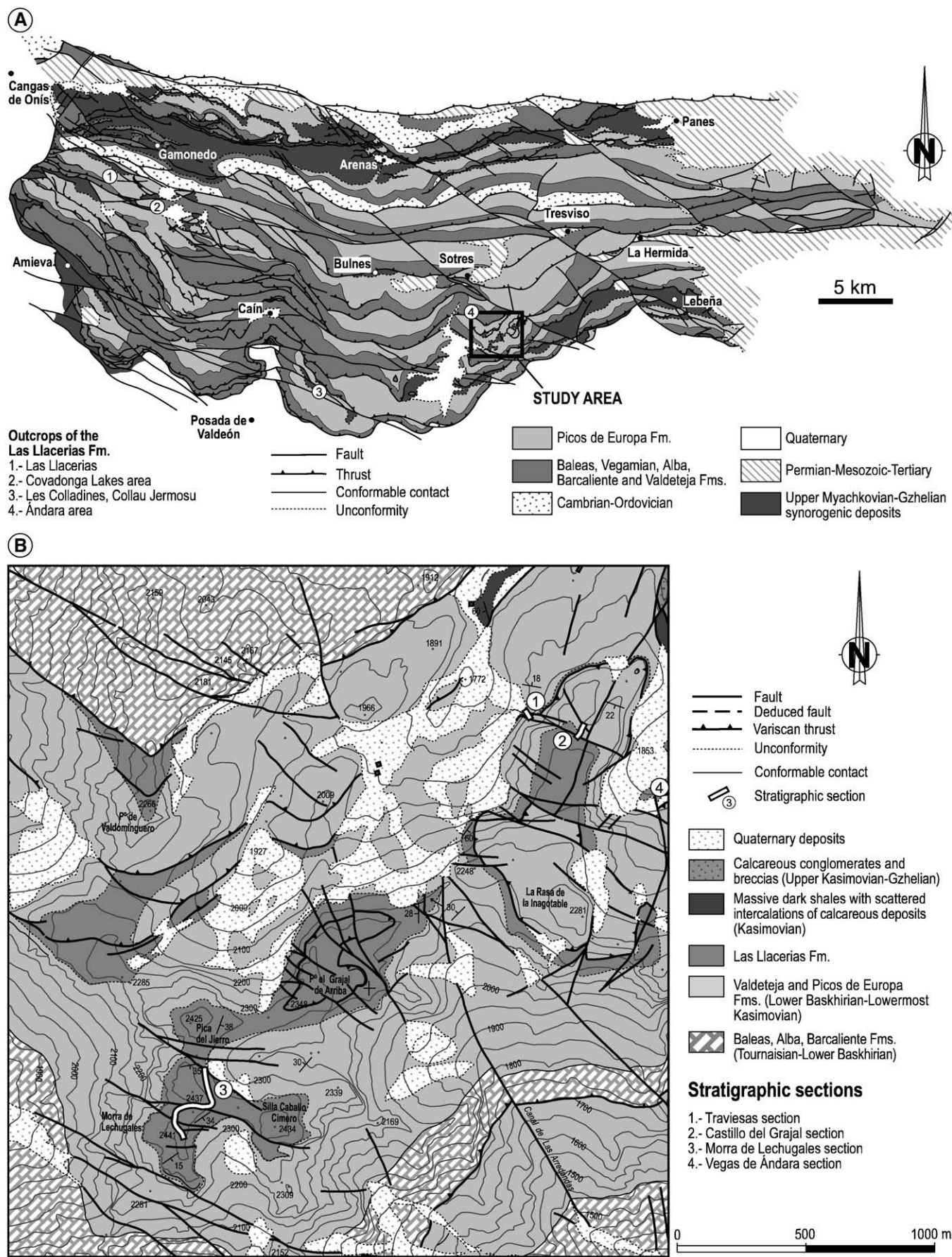
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Fig. 2. A) Synthetic geological map of Picos de Europa Province with location of study area (modified from Marquínez, 1989). B) Detailed geological map of Ándara area showing location of stratigraphic sections of Las Llacerias Formation included in Fig. 4.

3

Samankassou, 2002; Wilson and Vecsei, 2005; Coffey and Read, 2007). Moreover, nutrients may derive from either upwelling or continental runoff, making the reconstruction questionable if the overall context is not well understood (Coffey and Read, 2007).

The example documented in the present paper demonstrates how knowledge of the overall tectonic context may help in deciphering palaeoecological factors. Highly diverse biotic associations occur within the Kasimovian (late Pennsylvanian) carbonate ramp deposits of Las Llacerias Formation in the Ándara Massif (Picos de Europa, Northern Spain), which unconformably overlies Bashkirian–earliest Kasimovian shelf limestones. The benthic communities that flourished on these ramps were not recorded in the previous carbonate platform. The area lacks evidence of coastal upwelling during deposition in early-mid Kasimovian time. Knowledge of the tectonic setting and the geodynamic reconstruction in an overall biostratigraphically well-constrained context allow recognition of the siliciclastic input related to land-derived runoff as the main driving factor controlling the biotic association encountered. Comparisons are made to distinct intervals in the Pennsylvanian deposits of Carnic Alps (Austria–Italy), where the influence of terrigenous input and upwelling can be discriminated.

2. Geological setting

The Cantabrian Zone (NW part of the Iberian Massif) comprises a thick succession of Palaeozoic rocks mostly deformed by thin-skinned tectonics during the Variscan orogeny (Upper Devonian–Pennsylvanian) (Pérez-Estaún et al., 1988; Fig. 1A). During the Pennsylvanian, the Cantabrian Zone consisted of a marine foreland basin located at an equatorial position on the eastern coast of Pangea (Fig. 1B, C), with a pronounced asymmetric profile (Colmenero et al., 2002). In the distal part of this basin (the Picos de Europa and northern Ponga provinces), a large microbial boundstone-dominated carbonate platform developed (Bahamonde et al., 2000; Bahamonde et al., 2007) from Bashkirian to early Kasimovian times (Fig. 1C). Initially, the carbonate platform prograded into a starved marine basin, which was gradually filled and narrowed due to the sediment input from the orogen and the forward advance of the deformation.

The migration of the orogenic front towards the foreland during the last stages of the Variscan orogeny (late Pennsylvanian) led to the progressive deformation of the carbonate platform. During the Moscovian–Kasimovian transition, the northern domain of the platform (Ponga-Cuera area) and northern sectors of the Picos de Europa Province were incorporated into the orogenic wedge and cut by a set of E–W-oriented thrust nappes emplaced southwards (Merino-Tomé, 2004; Merino-Tomé et al., 2009). From the early Kasimovian (early Krevyakinian–Khamovnikian), the advance of the tectonic deformation slightly affected the remaining carbonate platform (central and southern part of the Picos de Europa Province), giving rise to elongated uplifted areas approaching to sea-level surface that consisted of growth structures related to blind thrusts. The subaerially exposed part of the previous carbonate deposits was partially eroded, whereas carbonate production persisted in the remaining shallow-water areas, actually forming narrow ramp-like carbonate platforms. The emergence of uplifted areas bordering the Picos de Europa Province led to input of abundant siliciclastics into this sector of the marine foreland basin, which has remained free of terrigenous input during most of the Carboniferous time. In the central and southern part of the Picos de Europa Province these siliciclastics accumulated in deep restricted troughs in between the aforementioned carbonate ramps (Merino-Tomé, 2004; Merino-Tomé et al., 2009).
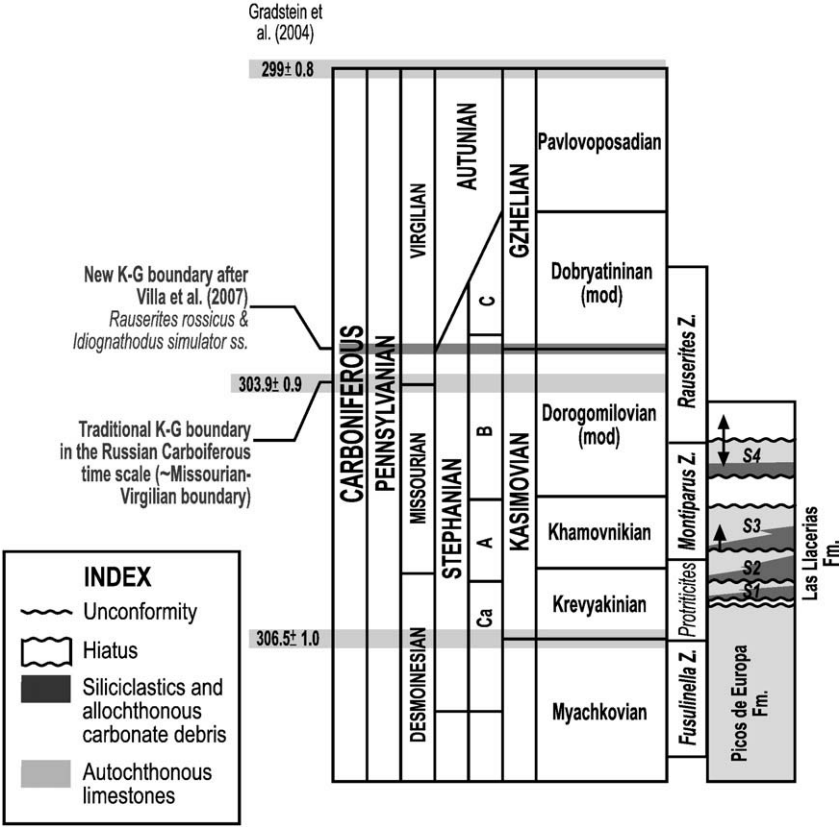

Fig. 3. Stage and substage terminology of rocks in study area. Stage, substage and horizon correlation of regional chronostratigraphic stages and substages of the American (mid-continent), West European and East European (Russian) scales based on Heckel et al. (2008), and Villa and Task Group (2007). Geochronological age determinations from Gradstein et al. (2004).

4

3. Lower Kasimovian (Krevyakinian–Khamovnikian) carbonate successions of the Picos de Europa Province

The Las Llacerias Formation (Martínez García and Villa, 1999) is a dark coloured, marly calcareous succession, locally up to 190 m thick that unconformably rests on the Picos de Europa Formation (Moscovian–early Kasimovian). In the stratotype section (NW sector of the Picos de Europa Province), the Las Llacerias Formation is Khamovnikian in age (Cózar et al., 2007), but span from late Krevyakinian to Khamovnikian in other outcrops such as the Covadonga Lakes (toward the N), Ándara and Les Colladines-Collau Jermosu (in the S), and in the easternmost exposures of the carbonate complex (Figs. 2 and 3).

This paper deals with the Las Llacerias Formation strata in the SE border of the Picos de Europa Province (Ándara massif) (Fig. 2B). The outstanding exposures have allowed us to undertake a sedimentological study of the succession, including: (1) detailed geological mapping at scale 1:25.000, (2) measurement and logging of stratigraphic sections, (3) field description of lithofacies and sampling for microfacies analysis (4) sampling for biostratigraphy (fusulinoideans) and (5) study of the biotic associations.

4. Stratigraphy of the Las Llacerias Formation in the Andara area

The Las Llacerias Formation in the study area comprises 3 sequences, bounded by angular unconformities, which range in age from mid Krevyakinian (van Ginkel and Villa, 1999) to Khamovnikian (lower-mid Kasimovian, Upper Pennsylvanian, see Fig. 3). Each sequence consists of two stratigraphic intervals (Figs. 4–6):

1. The lower interval contains abundant calcareous clastics (calcareous breccias, minor conglomerates, calclititas and bioclastic–intraclastic grain- to packstones) with some minor siliciclastics. These deposits usually display rapid lateral changes in thickness and distally interfinger with dark shales. Intercalated marls, and marly mudstones to wackestones contain abundant brachiopods, corals (*Cyathaxonia* sp.), bryozoans, crinoids and gastropods.

2. The upper interval is dominated by autochthonous carbonate deposits showing a conspicuous dark colour. Metre- to decametre-thick packages composed of poorly-bedded, black nodular skeletal marly wackestones to packstones with a very rich and diverse biotic content occur at distinct intervals in sequences 1, 2 and 3 (Figs. 5 and 6). They include phylloid and *Anthracoporella* algal mounds and reef-mounds of chaetetid sponges (exclusive from sequence 1), syringoporids and colonial rugose corals. At certain levels, sphinctozoan sponges, brachiopods, bryozoans and crinoids are very abundant.

5. Sedimentology of the Las Llacerias Formation

The Las Llacerias Formation includes 14 lithofacies that are extensively described in Table 1. These lithofacies are grouped in two main types of facies associations, namely clastic and autochthonous carbonates. Clastic carbonates (lithofacies *G*, *Te1*, *Te2*, and *S*) represent submarine breccia-slope aprons, and graded rudstone-to-packstone tempestites accumulated in sub-wave base settings where locally carbonates also formed (facies B3). Autochthonous carbonates have been grouped according gross lithology and degree of winnowing into three facies associations using the classification scheme of Burchette and Wright (1992): inner-ramp association (lithofacies *A1*, *A2*, *A3*); mid-ramp (lithofacies *B1*, *B2*, *Md1*, *Md2*, *Md3*, *Md4* and *S*); and distal ramp (lithofacies *B3*, *Md5* and *S*).

5.1. Clastic facies associations

5.1.1. Slope aprons

Unsorted to poorly sorted calcareous breccias (facies G, Table 1) form metre- to decametre-thick, poorly-bedded packages. Calcareous lithoclasts comprise a wide spectrum of carbonate rocks derived from
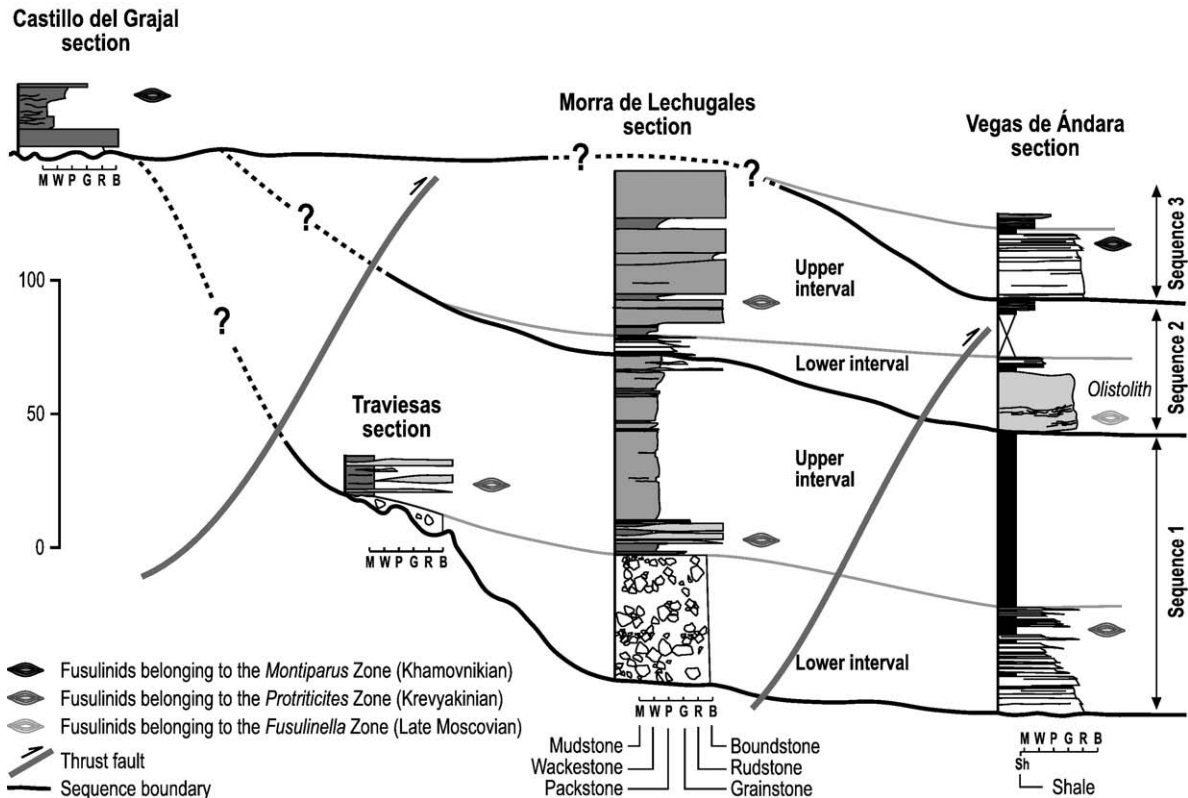

Fig. 4. Stratigraphy of Las Llacerias Formation in studied area.

Fig. 5. Stratigraphic section of Las Llacerias Formation at Morra de Lechugales peak showing bedding packages recognizable in outcrop (1a–2b).

the underlying Picos de Europa Formation, the Las Llacerias Formation, scattered skeletal grains (Fig. 7A), and in places contain well-rounded quartzitic clasts (Fig. 7B). Locally, chaetetid and syringoporid colonies occur on top of these packages (Fig. 6). In a few localities, these coarse clastic deposits interfinger with black homogeneous shales (facies S).

6

TRAVIESAS SECTION

Black wackestone with oncoids (Facies B1)
Karstic surface
Abundant syringoporid colonies
Poorly-sorted black-matrix breccia with fragments of chaetetids

Anthracoporella boundstone (Facies *Md3*)

Black wackestone with oncoids (Facies B1)

Cup-shaped phylloid-algal bafflestone (Facies *Md4*)

Anthracoporella boundstone (Facies *Md3*)

Chaetetes growing above breccia

Poorly-sorted black-matrix breccia with algal and *Chaetetes* fragments

In situ Chaetetes colonies and minor algal-bafflestone patches (Facies *Md1*)

Black wackestone with oncoids (Facies B1)

Facies *Md1*

Phylloid algal bafflestone (Facies *Md4*)

Black skeletal wackestones (Facies *B1*)

Skeletal grainstone with small-sized lithoclasts and *Chaetetes* fragments (Facies A1, A2)

Irregular karstic surface

Poorly-sorted breccia with *Chaetetes* fragments and skeletal matrix (Facies *G*)

Black skeletal wackestone (Facies *B1*)

Phylloid-algal and *Anthracoporella* bafflestone (Facies *Md3*, *Md4*)
Syringoporid and ramose branching corals (Facies *Md1*)

Clast-supported breccia containing lithoclasts of phylloid-algal and *Anthracoporella* bafflestones, skeletal pack- to grainstone, and *Chaetetes* fragments (Facies *G*).

MORRA DE LECHUGALES SECTION

Silicified dark micritic limestone (Facies *B2*)

Skeletal pack- to grainstone (Facies *A1*)

Black marls and shales forming thin interbeds (Facies *B1*)
Anthracoporella and phylloid-algal bafflestone (Facies *Md3*)

Facies *Md2*

Chaetetes and syringoporid mounds (Facies *Md1*, *Md2*)

Facies *B1*

Lenticular mounds of *Chaetetes*, syringoporids and minor other branching rugose corals

Facies *Md1*
Facies *B1*

Facies *Md1*

Facies *B1*

Facies *Md2*

Facies *Md1*
Very abundant echinoderm debris

Black skeletal wackestone including algal fragments, foraminifers, corals, echinoderms, siliceous sponge spicules, ostracods, brachiopods and gastropods (Facies B1)

Pack- to grainstone (Facies A1-A2)

In-situ breccia

Poorly-sorted calcareous conglomerate and breccia (Facies G)
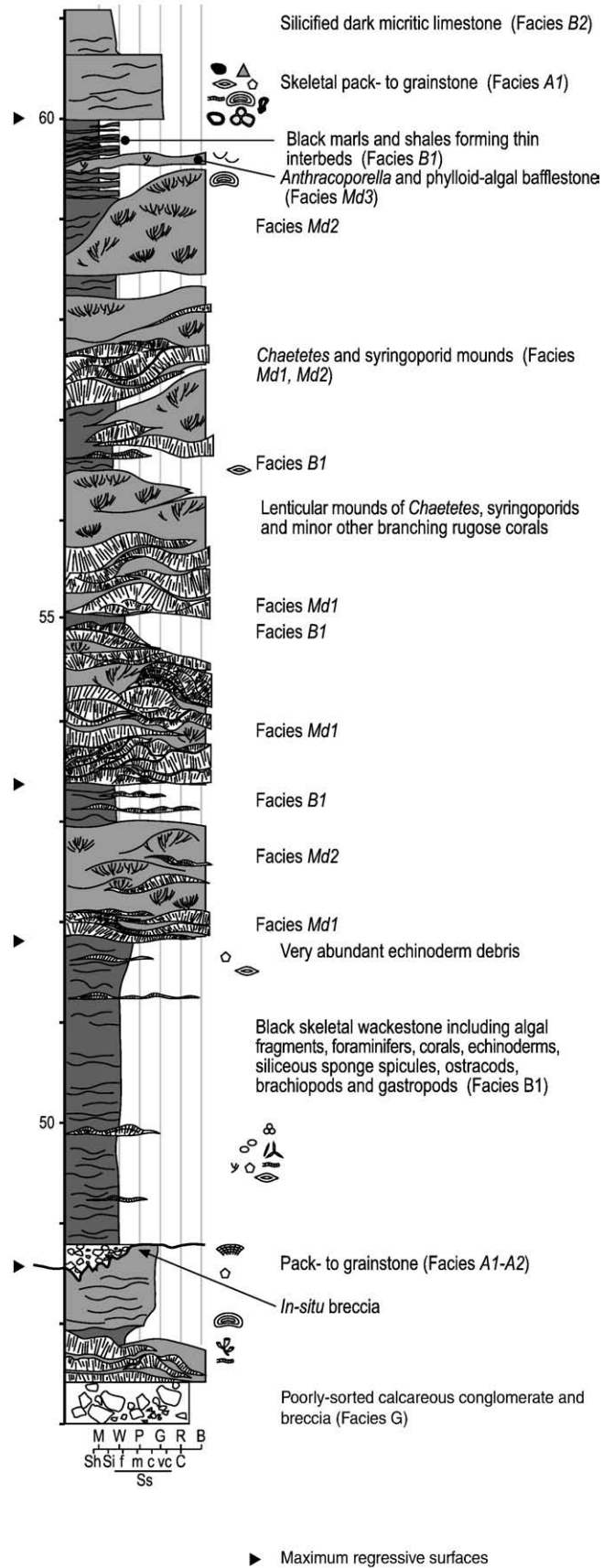
▶ Maximum regressive surfaces

Fig. 6. Detailed stratigraphic sections of stratigraphic package 1b of sequence 1 at Las Traviesas and Morra de Lechugales sections. See Fig. 2B for location.

7

Table 1
Lithofacies of the Las Llacerias Formation in the Andara area.

Lithofacies, lithology, texture	Geometry, bed thickness, sedimentary structures	Composition: non-skeletal and skeletal grains, matrix	Depositional processes and environment
G: Matrix-free clast-supported breccia and conglomerate	dm- to m-thick massive beds. Locally normal grading	Pebble- to boulder-sized angular to poorly rounded carbonate lithoclasts, and scarce quartzitic pebbles and boulders. Skeletal grains in variable amounts	Hyperconcentrated to concentrated density flows
Te1: Rudstone grading into grainstone to packstone	cm- to dm-thick tabular beds, erosive bases and sharp to gradational tops. Normal grading, locally parallel and cross lamination	A: intraclasts and extraclasts. C–S: crinoids, echinoids, brachiopod and mollusk shell fragments, algal thalli, bryozoans, foraminifers, Tubiphytes. R: calcareous sponges, coral debris, trilobites, calcispheres, ostracodes, and sponge spicules, detrital quartz grains.	Concentrated density flows
Te2: Grainstone and packstone	cm-thick tabular beds, sharp erosive bases and gradational tops. Normal grading, parallel lamination at bed tops	Same as in Te1, but skeletal debris more abundant. Calcispheres, monaxon sponge spicules, ostracodes and small foraminifers are abundant in bed tops	Low concentration turbulent gravity flows (distal tempestites)
S: Black to dark-grey shale and marl		S–R: Scattered brachiopods, crinoids, *Cyataxonia*-type corals, sphinctozoan sponges	Low-energy settings. Subphotic to aphotic
A1: Grainstone and minor packstone	dm- to cm-thick tabular to undulating beds. Massive or locally cross bedding and parallel lamination. Large burrows	A–VC: micritic coated and aggregate grains. C: crinoids, echinoids, small-sized and larger foraminifers [Bradyinidae, Palaeotextulariidae (mainly *Climacammina*, staffellids, other fusulinoideans], brachiopods, algal thalli (*Anthracoporella*, *Eugonophyllum*). S: smaller foraminifers (biseriamminids, tetrataxids, tubiforms; Calcivertellinae, Calcitornellinae Apterrinellinae), *Tubiphytes* bryozoans, mollusks, calcispheres (*Penella*), polyaxon sponge spicules. R: ostracodes, sponge fragments, trilobites. R–VR: detrital quartz grains	Shallow water, highly to moderately agitated. Above effective fair-weather wave base. Subtidal shoals and beaches. Euphotic zone
A2: Packstone to grainstone, minor wackestone	Same as A1	VC–C: small-sized and larger foraminifers [Bradyinidae, Palaeotextulariidae (mainly *Climacammina*), staffellids, other fusulinoideans, biseriamminids, tetrataxids, tubiforms; Calcivertellinae, Calcitornellinae Apterrinellinae]. C: micrite-coated and aggregate grains, phylloid algae, brachiopods, crinoids, echinoids, calcispheres, bryozoans. S: polyaxon sponge spicules, *Tubiphytes*. R–VR: detrital quartz grains.	Shallow water, less agitated. Above or close to effective fair-weather wave base. Euphotic zone
A3: Rudstone and floatstone	dm- to cm-thick tabular to lenticular beds, erosive bases and sharp to gradational tops	A–VC: *Osagia* oncoids. Skeletal packstone matrix similar to lithofacies A2	Same as A2
B1: Wackestone and packstone	cm to dm pseudo-nodular to undulating beds with discontinuous marly interbeds. Intense bioturbation	C: calcareous algae (*Eugonophyllum, Anthracoporella, Archaelithophyllum*), foraminifers [Bradyinidae, Palaeotextulariidae (mainly *Climacammina*), staffellids, other fusulinoideans, biseriamminids, tetrataxids, tubiforms; Calcivertellinae, Calcitornellinae Apterrinellinae], brachiopods, bryozoans, crinoids, echinoids, mollusks. S: sponge spicules, calcispheres, chaetetids, sphinctozoans and lithistid sponges, tabulate syringoporid corals, solitary geoyerophyllid rugose corals, ostracodes, trilobites, *Tubiphytes*, *Osagia* oncoids. R–VR: quartz grains	Shallow subtidal, close to fair-weather wave base. Euphotic to mesophotic zone.
B2: Skeletal mudstone to wackestone	Undulating massive beds. Locally nodular	C: calcispheres and polyaxon sponge spicules. S: foraminifers (biseriamminids, tetrataxids, fusulinoideans, tubiforms; Calcivertellinae, Calcitornellinae Apterrinellinae), calcareous algae (phylloids, dasycladaceans), brachiopods, mollusks, bryozoans, crinoids, echinoids, calcareous sponges (inozoan, sphinctozoan; *Discosiphonella, Amblysiphonella, Sollasia*), *Cyataxonia*-type corals. R: *Tubiphytes* and ostracodes. R–VR: detrital quartz grains	Subtidal, below fair-weather wave base. Mesophotic to oligophotic zone
B3: Marly mudstone	cm- to dm-thick, pseudo-nodular to almost tabular beds. Massive to thinly laminated	C: Monaxon sponge spicules. S–R: crinoids and echinoids, thin-shelled brachiopods, bryozoans, solitary rugose corals, small foraminifers, calcispheres, ostracodes, silt-sized detrital quartz grains	Quiet, deep subtidal. Mostly below storm wave base. Aphotic and locally oligophotic zone
Md1: Chaetetid sponge Framestone	dm- to m-thick lenticular beds	A: Laminar and domical chaetetid sponge colonies, C: syringoporids, solitary and branching rugose corals. S–R: Phylloids and dasycladaceans, encrusting foraminifers and *Thartharella*. Matrix: clotted and peloidal micrite	Shallow subtidal, below effective wave base. Euphotic zone. Chaetetid reef-mounds
Md2: Syringoporid coral branchstone to bafflestone	dm- to m-thick lenticular beds	A: Syringoporid corals (*Neomultithecopora*). S–R: laminar chaetetid sponges, solitary rugose corals, encrusting foraminifers and *Thartharella*. Matrix: clotted-peloidal micrite and homogeneous allomicrite	Shallow subtidal, below effective fair-weather wave base. Euphotic zone. Coral reef-mounds
Md3: *Anthracoporella* algal bafflestone	dm- to m-thick lenticular beds	A: *Anthracoporella*. C–S: encrusting foraminifers, *Thartharella* and calcified *Girvanella* filaments. S–R: phylloids, ramose dasycladaceans, syringoporid corals and chaetetid colonies. Matrix: clotted-peloidal micrite and allomicrite	Shallow subtidal, below fair-weather wave base. Euphotic to mesophotic zone. *Anthracoporella* mounds

Table 1 (*continued*)

Lithofacies, lithology, texture	Geometry, bed thickness, sedimentary structures	Composition: non-skeletal and skeletal grains, matrix	Depositional processes and environment
Md4: Phylloid algal bafflestone and minor floatstone	dm-thick lenticular beds	A: phylloid algae. C–S: encrusting foraminifers, *Thartharella*, calcified *Girvanella* filaments, and *Eflugelia*. S–R: Ramose dasycladaceans, syringoporid corals and chaetetid sponges. Matrix: clotted-peloidal micrite and allomicrite	Shallow subtidal, below fair-weather wave base. Euphotic to mesophotic zone. Phylloid algal mounds
Md5: Micritic boundstones	dm- to m-thick massive intervals	S–R: fenestellid bryozoans, *Tubiphytes*, *Thartharella*, calcified *Girvanella* filaments, foraminifers, crinoids, brachiopods, ostracodes, calcispheres and sponge spicules. VR: calcareous algae. Matrix: clotted-peloidal micrite and allomicrite. Mm–cm irregular cavities filled by blocky spar	Deep subtidal. Microbial mud mounds

Relative percentages of skeletal and non-skeletal grains have been indicated according to Flügel (2004), as: VR = very rare (<2%); R = rare (2–5%); S = sparse (5–10%); C = common (10–30%); VC = very common (30–50%); A = abundant (>50%).

5.1.1.1. Interpretation. The fabric and the lack of grading or imbrications of components in facies G suggest dense gravity-driven flows (granular flows *sensu* Narding et al., 1979; or hyperconcentrated density flows *sensu* Mulder and Alexander, 2001). The accumulation of these deposits occurred most likely close to the source area, as clastic aprons formed in steep shallow to deep coastal settings, comparable to debris cones reported by Postma (1990). These coarse clastic deposits bordered shallow-water to emergent areas.

5.1.2. Mid- to outer-ramp tempestite deposits

This association consists of metre- to decametre-thick packages of detrital carbonates (facies Te1 and Te2) alternating with dark nodular marls, lenses of marly limestones (facies B3) and, locally, dark-grey shales (facies S). Detrital carbonates form centimetre- to decimetre-thick tabular beds (Fig. 7C) that can display a lower massive to normal graded layer of fine gravel-sized rudstones grading vertically into sand-grained packstones to grainstones. They contain abundant skeletal grains, rip-up mudstone clasts, extraclasts derived from the Picos de Europa Formation, intraclasts derived from the Las Llacerias Formation and detrital quartz grains (Fig. 7D). The bed tops usually are formed by fine sand- to silt-grained spiculitic packstones with traction-current structures (parallel and ripple lamination, Fig. 7C).

The interbedded marls, marly shales (facies S) and marly mudstones to wackestones (facies B3) contain small brachiopods, small rugose
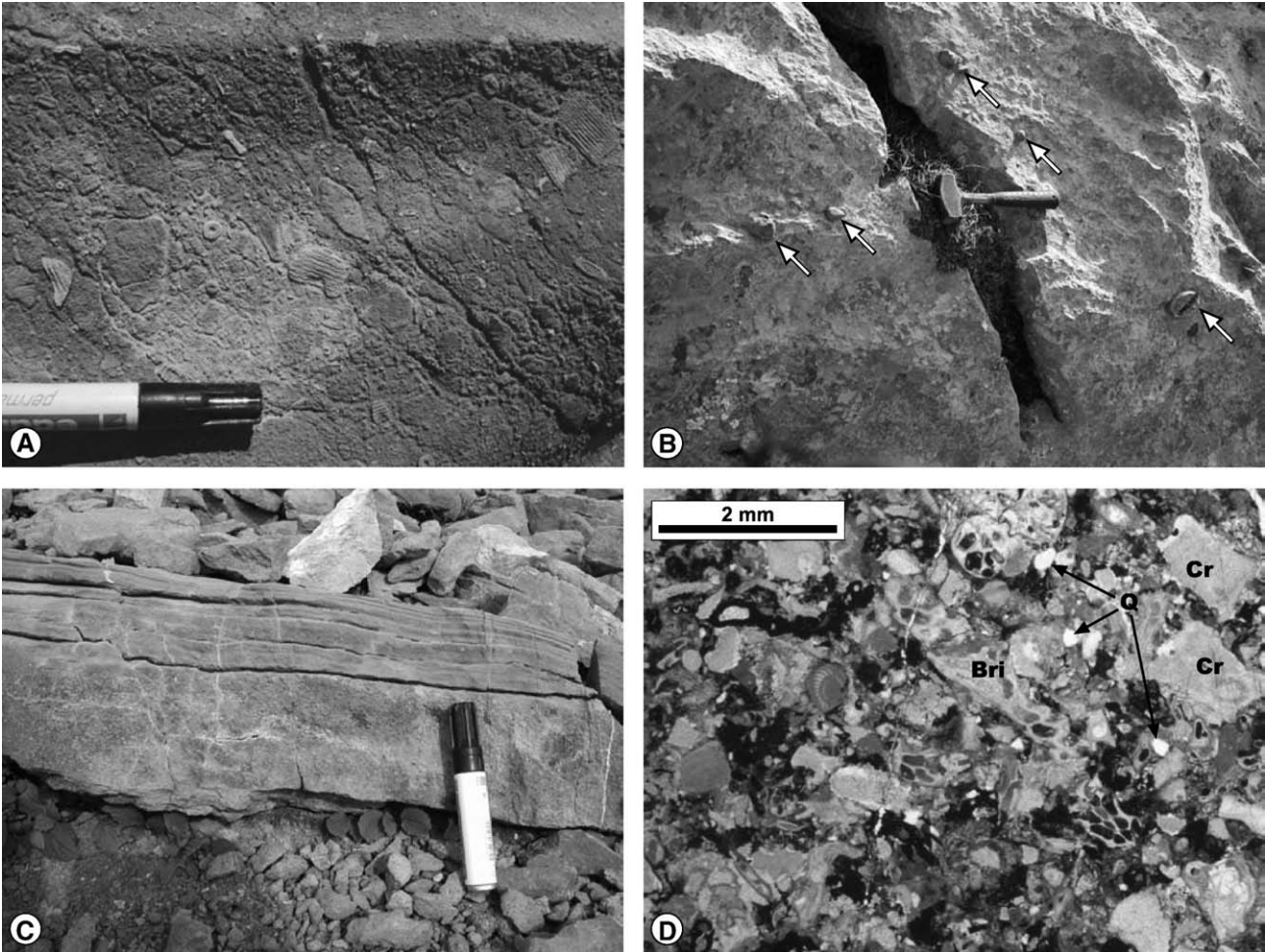

Fig. 7. A) Outcrop photograph of gravel-sized rudstones with scattered crinoid ossicles (facies G). B) Outcrop photograph of quartzite pebbles (arrows) within facies G. C) Outcrop photograph of graded bed of facies Te1. D) Photomicrograph of coarse sand-grained grainstone (facies Te2). Note the presence of scattered detrital quartz grains (Q). Cr, crinoids; Bri, bryozoans.

solitary corals, bryozoans, crinoids, gastropods, some trilobites and abundant monaxon sponge spicules and are intensely bioturbated.

5.1.2.1. Interpretation. The graded beds of detrital carbonates (facies Te1 and Te2) show features commonly reported from tempestite deposits accumulated in subtidal environments (Aigner, 1985; Handford, 1986; Wright, 1986) and in carbonate turbidites (Enos and Moore, 1983; Herbig and Bender, 1992; Herbig and Mamet, 1994). They are the result of sediment-load deposition by offshore-directed currents transporting the carbonate material eroded or reworked from shallower areas.

The intercalated facies B3 and S record the background sedimentation of lime-mud in low-energy subtidal environments with significant terrigenous input that caused frequently turbid waters and hampered the establishment of a more diverse marine calcareous biota. The small non-dissepimented solitary corals (mostly *Cyathaxonia* sp.) also point to a deep-water realm below normal wave base (Somerville and Rodríguez, 2007). The depositional setting thus corresponds to a quiet environment typical for mid- to outer-ramps (Burchette and Wright, 1992).

5.2. Autochthonous carbonate facies associations

5.2.1. Inner-ramp

The inner-ramp deposits represent only a small portion of the very thick Las Llacerias Formation and occur mostly within the upper intervals of the sequences. They comprise decimetre- to metre-thick packages constituted by tabular to undulating beds of lithofacies A1, A2 and A3 (Table 1) that internally are massive or show cross bedding and parallel lamination. Skeletal grains include diverse foraminifers (*Climmacammina, Deckerella, Staffella*, bradyinids among others, and very abundant "tubiforms"), algal thalli, *Tubiphytes* (correctly *Shamovella*; Riding, 1993), echinoderms, brachiopods, mollusks, bryozoans, sponge fragments, calcispheres and polyaxon sponge spicules. Superficial micritization, microboring and micritic encrustation of skeletal grains forming both destructive and constructive micritic envelopes are very common and locally pervasive (Fig. 8). As such, cortoids (following terminology of Flügel, 1982; carbonate grains that include bioclasts, peloids, ooids or lithoclasts whose periphery exhibits a circumgranular non-laminated micritic rim), aggregate grains (mostly algal lumps) (Fig. 8A, B) and *Osagia*-type oncoids are commonly present and can be locally the main grain component. Oncoids, 0.5–7 cm in diameter, are spherical to ellipsoidal in shape and show a concentric-laminated micritic cortex (Fig. 8D) with abundant calcified filaments of cyanobacteria (*Girvanella* and/or *Ellesmerella*), encrusting foraminifers and the problematic alga *Claracrusta* sp. Primary interparticular porosity lacks fibrous marine cements.

5.2.1.1. Interpretation. The grain-supported texture, the scarcity of muddy matrix and the occurrence of traction sedimentary structures point to high- to moderate-energy conditions, probably in areas located close to or above wave base. These conditions occur in winnowed platform-edge sands as well as in current-washed sand shoals of inner-
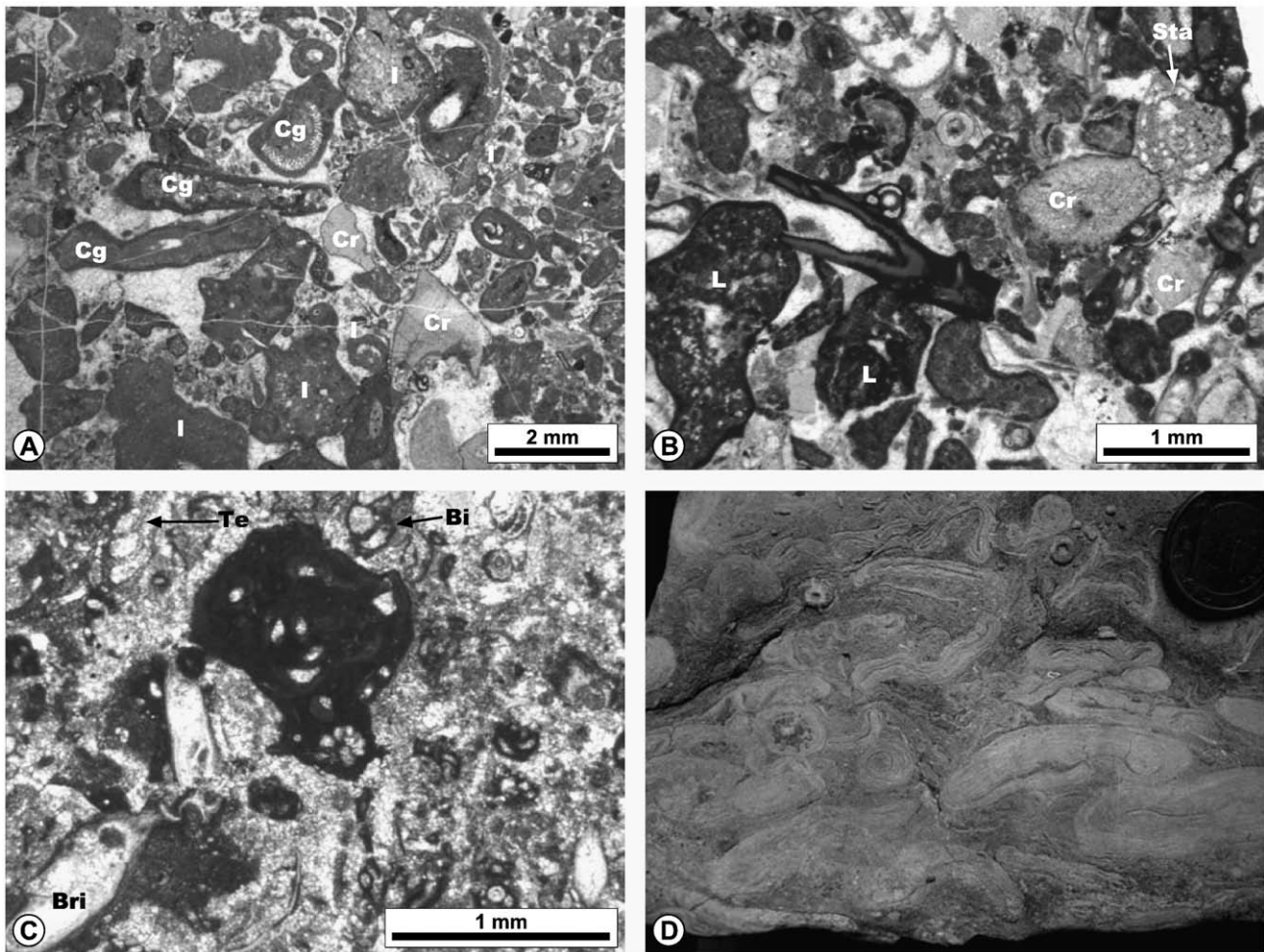

Fig. 8. A) Photomicrograph of grainstone rich in intraclasts and coated grains (facies A1). Micritic grains, including intraclasts (I) and micritic aggregates are very abundant and resulted from combined intensive micritization, microboring and constructive encrustation of skeletal grains and intraclasts. Cg, coated grain; Cr, crinoid. B) Detail of previous facies. L, lump; Cr, crinoid; Sta, *Staffella*. C) Photomicrograph of grainstone–packstone rich in foraminifers (facies A2). Note abundance of small "tubiform" foraminifers similar to ammovertellids. Bri, bryozoan; Te, tetrataxids; Bi, biseriamminid. D) Close-up view of *Osagia*-type oncoid rudstone–floatstone (facies A3). Many oncoids are nucleated around skeletal grains, commonly recognizable as thalli of phylloid algae. 5-cents Euro coin for scale.

ramp settings (Tucker and Wright, 1990; Flügel, 2004). Coated grains (Leonard et al., 1981; Perry, 1998, 1999) and the abundance of large benthic foraminifers, such as *Climmacammina*, *Deckerella*, *Staffella* and bradyinids (cf. example of a Moscovian inner platform in Della Porta et al., 2006) had been usually considered as indicators of shallow-marine warm-water environments.

Facies A1 seems to record highly agitated environments while facies A2 probably corresponds to a less agitated and slightly deeper or protected realm. In the Early Permian of the Carnic Alps, *Girvanella*-foraminiferal oncolite beds, similar to those of our facies A3, occur in the Zweikofel Formation (formerly Upper *Pseudoschwagerina* Limestone), whose setting was interpreted
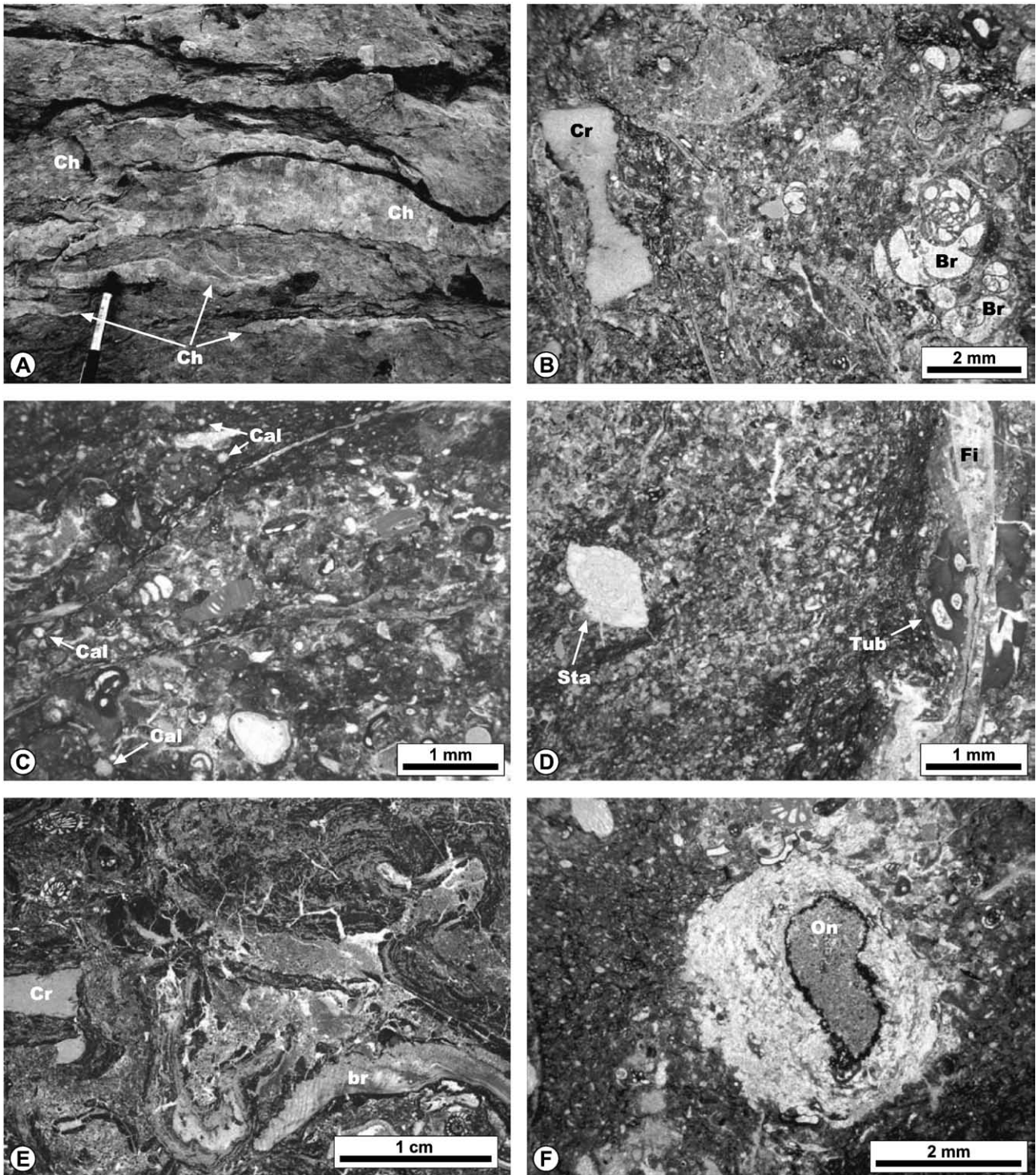

Fig. 9. A) Outcrop photograph of dark nodular wackestone (facies B1) with abundant laminar chaetetid sponges (Ch). Bedding is defined by undulating marly interbeds. Marker pen for scale. B) Photomicrograph of skeletal wackestone (facies B1). Bradyinids (Br) and large palaeotextulariids are common. Cr, crinoid. C) Photomicrograph of facies B1, showing abundant small foraminifers, calcispheres (Cal) and polyaxon sponge spicules and widespread occurrence of opaque residuals corresponding to non-degraded organic matter concentrated along undulating dissolution seams. D) Photomicrograph of phylloid algal thalli (Fi) with complex micritic encrustations including various foraminifers and *Tubiphytes* (Tub). Sta, Staffellid. E) Photomicrograph of complex spongiostromate encrustations around crinoid stems (Cr) and a brachiopod shell (br). F) Photomicrograph of small oncoid (on) with cortex formed by thin calcified filaments of probable cyanobacteria.

as a near-coast environment with high siliciclastic input (Flügel, 2004).

5.2.2. Mid-ramp

Black to dark-grey nodular marly wackestones and packstones, punctuated by interbeds of marls (facies B1 and B2) are the prevailing lithofacies in this facies association.

Facies B1 generally characterizes metre- to decametre-thick and thinly bedded packages (intervals 1b, 1d, 1e and on top of sequence 1, as well as in sequences 2 and 3) with a high-diversity biotic association. In those packages numerous decimetre- to metre-thick buildups of chaetetids (facies Md1, only present in sequence 1), syringoporids (facies Md2), dasycladaceans (mainly *Anthracoporella*) and phylloid algae (facies Md3 and Md4, respectively) occur. B1 lithofacies are black nodular marly wackestones and packstones punctuated by interbeds of marls (Fig. 9A) and contain abundant algae, conspicuous swarms of *Penella* (Mamet and Villa, 2004), polyaxon sponge spicules and very rich heterozoan fauna including
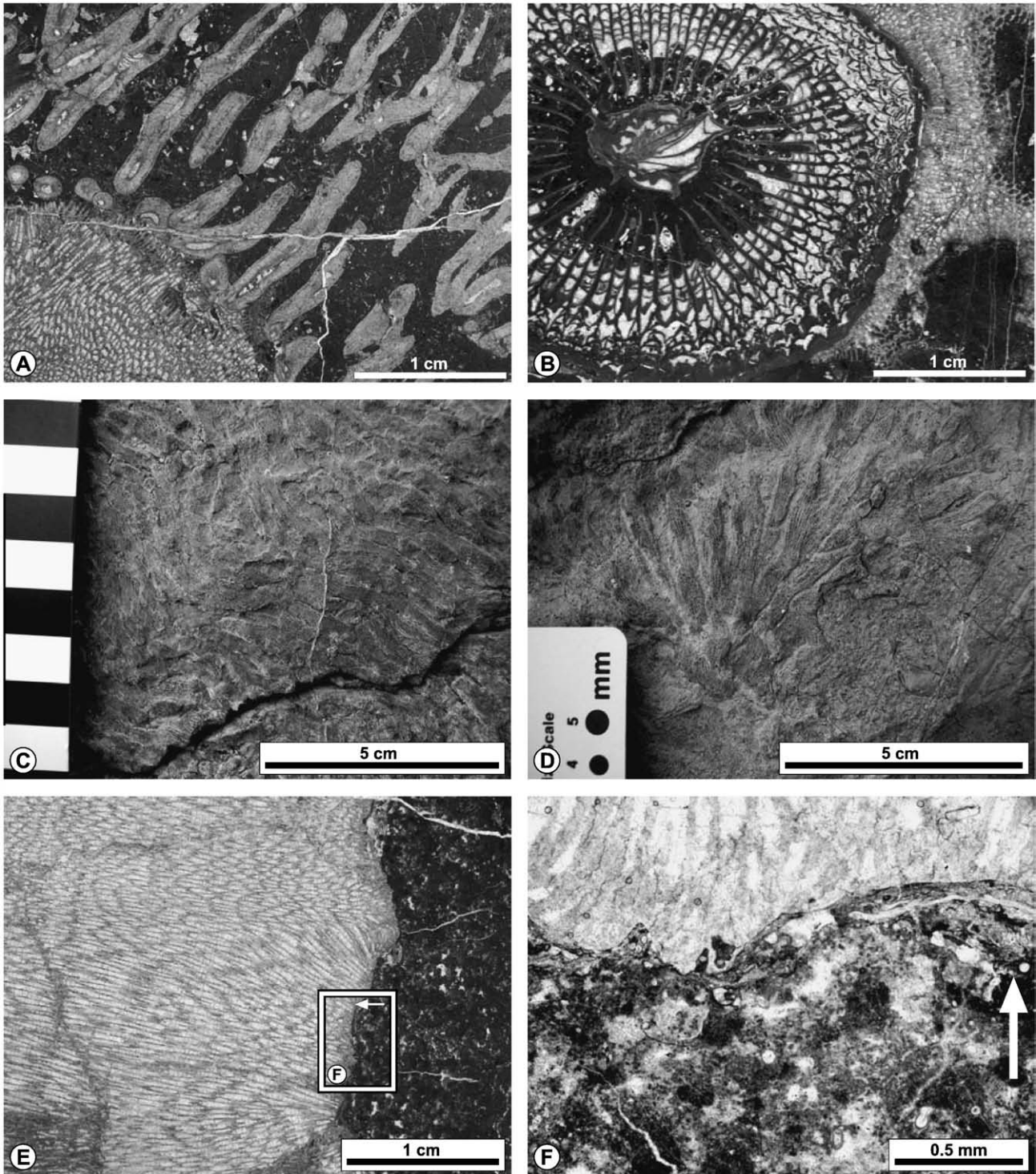

Fig. 10. A) Photomicrograph of chaetetid sponge (left lower corner) encrusted by *Neomultithecopora* (Md1 facies). B) Photomicrograph showing rugose coral encrusted by chaetetid sponges within facies Md1. C, D). Outcrop photographs of colonial branching rugose corals, which are also found in facies Md1. E, F) Photomicrographs showing chaetetids in core facies of a chaetetid-dominated buildup (Md1 facies). Peloidal to clotted micrite is also locally found (see detail in F).

abundant foraminifers (Fig. 9B, C, D). Laminar chaetetids are characteristic (Fig. 9A), along with sphinctozoan and less abundant inozoan and lithistid sponges, tabulate syringoporids, solitary rugose geoyerophyllid corals and echinoderms. Skeletal grains usually show microborings, micritization and constructive micritic encrustations with abundant *Girvanella*, encrusting foraminifers and *Claracrusta*. *Osagia*-type oncoids are common (Fig. 9E, F) and appear locally

concentrated in thin levels. Dark insoluble residues, organic matter and bitumen are enriched in undulating horsetail dissolution seams and fill dissolution and primary intraparticulate pores (Fig. 9C, D). Skeletal grains are locally silicified.

Chaetetid buildups (facies Md1) are composed of large densely growing colonies of chaetetid sponges with small-sized colonies of syringoporid corals (*Neomultithecopora*), colonial branching and
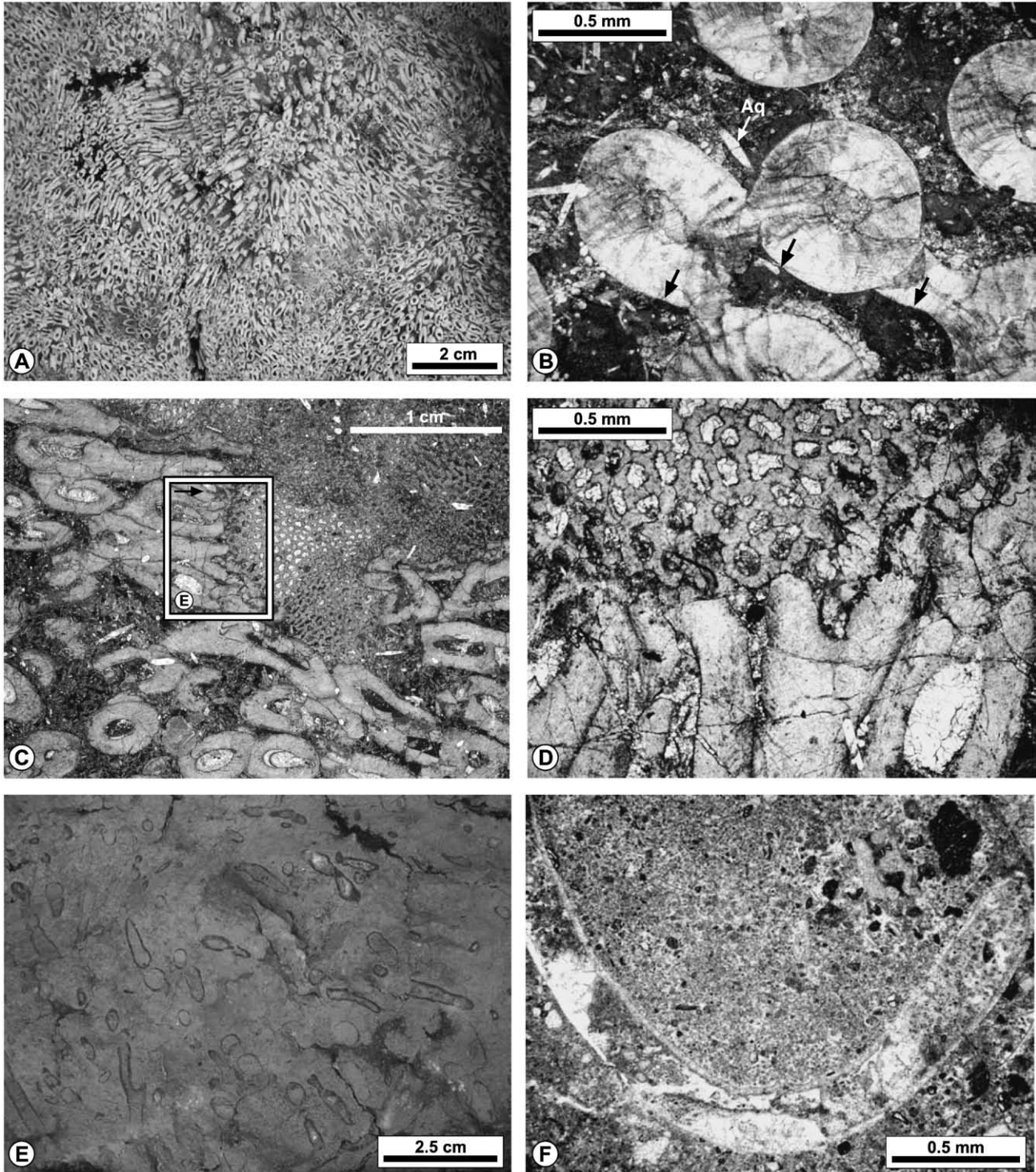
Fig. 11. A) Close-up view of syringoporid corals (*Neomultithecopora*) forming metre-scale biostrome (facies Md2) in interval 1b of sequence 1 (Morra de Lechugales section, see Fig. 5). B) Photomicrograph of transverse section of syringoporid corallites, showing dark micritic bindings (black arrows) (Aq, authigenic quartz crystals). C, D) Photomicrographs showing thickly packed *Neomultithecopora* corallites in core facies of syringoporid-dominated biostrome (facies Md2). Encrusting laminar chaetetid sponges commonly occur and probably record interruptions in growth of coral colonies. E) Outcrop photograph of core facies of *Anthracoporella* mounds (facies Md3). Delicate *Anthracoporella* thalli are commonly well preserved. F) Photomicrograph of cup-shaped phylloid algal thalli in bafflestone (facies Md3).

13

solitary rugose corals that variously encrusted or grew intercalated with chaetetid sponges (Fig. 10A, B, C, D). Discontinuous patches of peloidal to clotted micrite (Fig. 10E, F) with turberitinids and micritic worm tubes, and patches of cup-shaped phylloid algal and *Anthracoporella* boundstones also form part of the mound core facies.

Densely packed colonies of *Neomultithecopora* form metre-scale buildups (facies Md2) with a convex-upward morphology and steep flanks (dipping up to 30°) (Fig. 11A, B). The tubular corallites of syringoporid corals are commonly connected by dark homogeneous micritic bindings (Fig. 11B) and the remaining space is filled by allomicrite, peloidal to clotted micrite and minor spar cement. Thin laminar chaetetid colonies (that locally form the substrate of the reef-mounds) and branching and solitary rugose corals occur intercalated within syringoporid colonies (Fig. 11C, D).
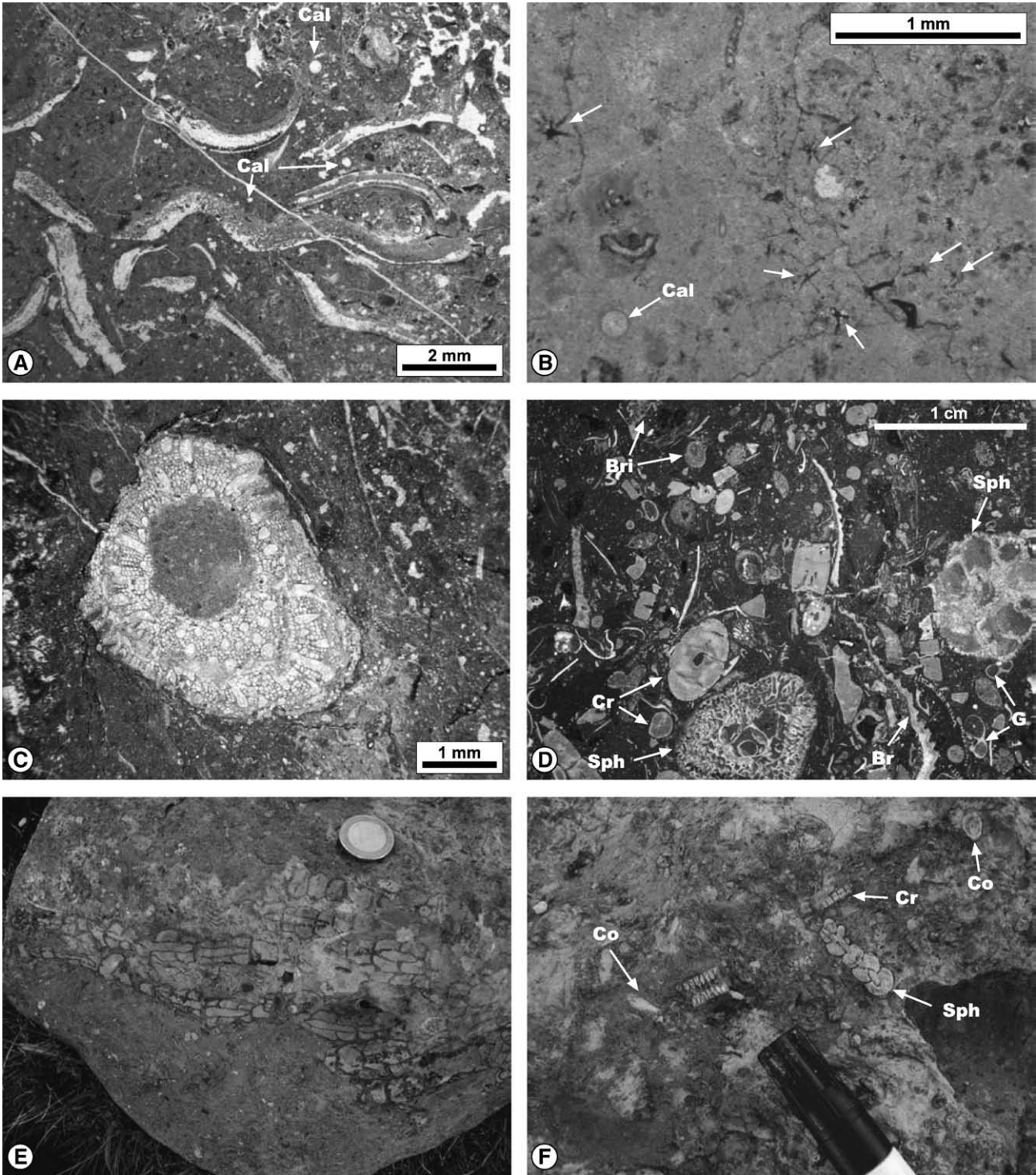

Fig. 12. A) Photomicrograph of skeletal wackestone (facies B2 including abundant phylloid algal thalli (*Eugonophyllum*). B) Photomicrograph of facies B2 showing numerous polyaxon sponge spicule molds (arrows), calcispheres (Cal) and "tubiform" foraminifers. C) Photomicrograph of fistuliporid bryozoan in previous facies. D) Photomicrograph of a skeletal-rich wakestone interval containing abundant brachiopod shell fragments (Br), crinoids (Cr), ramose bryozoans (Bri), small gastropods (G) and sphinctozoan sponges (Sph). E) Large sphinctozoan sponge (*Amblysiphonella*) in facies B2. F) Close-up view of sphinctozoan sponges (Sph) with abundant crinoids (Cr), solitary *Cyathaxonia* rugose corals (Co), brachiopods and bryozoans (facies B2).

Anthracoporella algal mounds (facies Md3) consist of successive stacking of massive algal boundstone lenses locally separated by discontinuous centimetre-thick marly bundles. *In situ* delicate branching colonies of *Anthracoporella* are ubiquitous (Fig. 11E) and usually are encrusted by foraminifers, calcified filaments of *Girvanella*, and the worm tube *Thartharella*. The marly bundles include phylloid algal thalli and usually display a crude lamination.

Phylloid algal mounds (facies Md4) consist of decimetre- to metre-thick bodies generally with a short lateral extent (metres to decametres). The larger mounds are composed of stacked lenses of
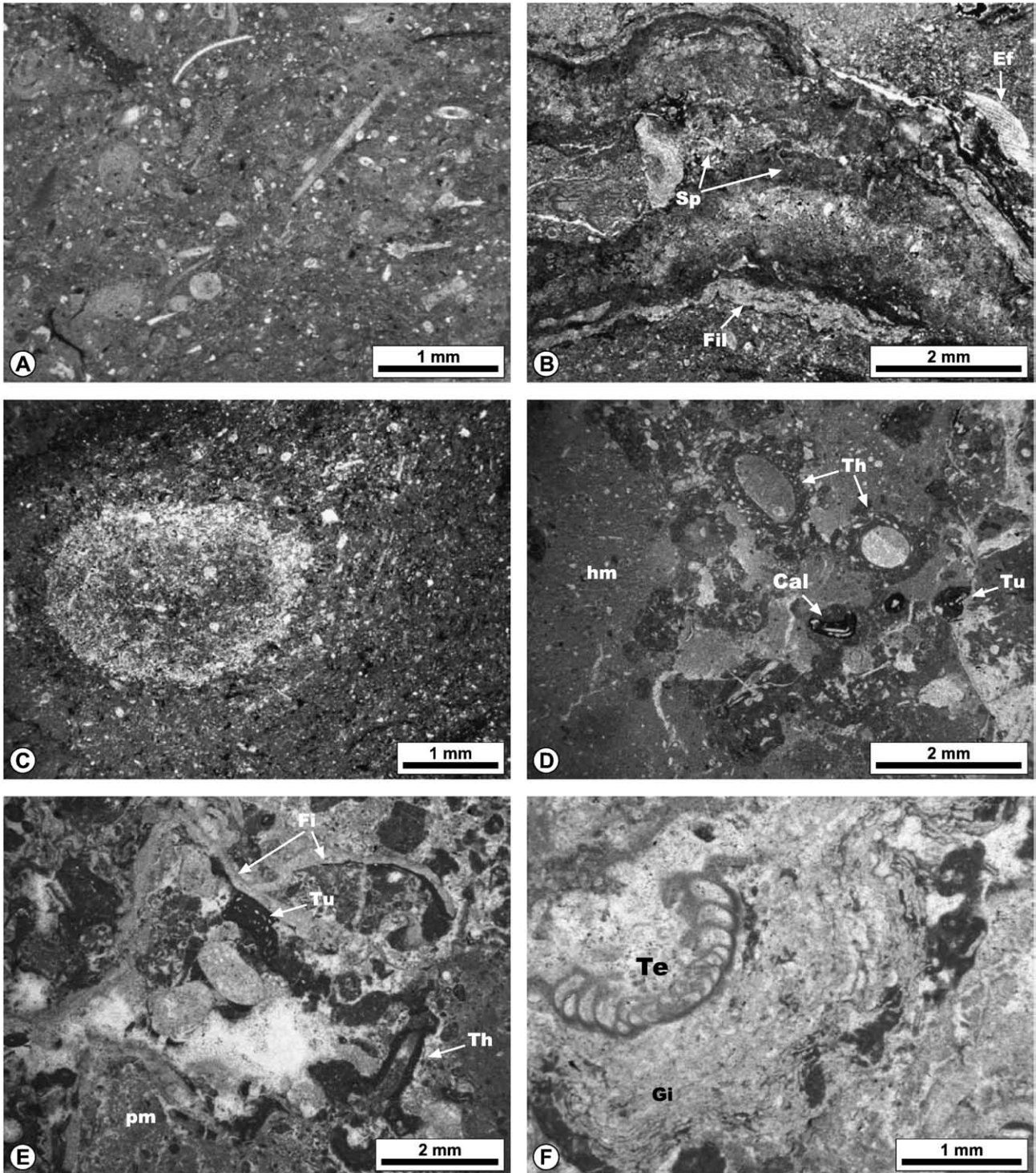

Fig. 13. A) Photomicrograph of marly lime-mudstones (facies B3) with abundant silt-sized quartz grains and monaxon sponge spicules. Black particles are insoluble residues that probably correspond to unoxidized organic matter. B) Photomicrograph of centimetre-sized cup-shaped structures locally recognizable in facies B3. Wall of this structure shows complex encrustations with fine filaments (probably corresponding to cyanobacteria, Fil), encrusting foraminifers and *Eflugelia* (Ef). Abundant polyaxon sponge spicules (Sp) are present in the interior of these structures, supporting their interpretation as bodies of siliceous sponges. C) Circular section of a cm-sized chert nodule within previous facies. D, E, F) Photomicrographs of micritic boundstones (Md5) showing *Thartharella* worm tubes (Th) and *Tubiphytes* (Tu). Complex spongiostromate micritic encrustations with tubular encrusting foraminifers ("tubiforms", Cal, and tetrataxids, Te) and thin calcified filaments of *Girvanella* (Gi) are common (see also D). The matrix consists of a homogeneous lime-mud (hm) with fine skeletal debris or peloidal to clotted micrite (pm). Phylloid algae (Fi) locally occur within this facies (see also E).

algal bafflestones punctuated by thin centimetre-thick discontinuous bundles of marly wackestones with abundant phylloid algal thalli and few laminar chaetetids and syringoporids. Phylloid algae include undulating and cup-shaped growth forms (probably corresponding to *Eugonophyllum*, Fig. 11F) and are encrusted by *Girvanella*, foraminifers and *Eflugelia*. Irregular sheltered cavities occluded by blocky spar are locally abundant, but fibrous and radiaxial-fibrous cements are absent in most cases.

Distinct from facies B1, facies B2 usually characterize metre- to decametre-thick packages with a massive appearance. Facies B2 consists of bioturbated mudstones to wackestones with abundant *Penella* and polyaxon sponge spicules that locally show marly interbeds. Skeletal grains include foraminifers (less abundant than in facies B1), algae, calcareous sponges, brachiopods, bryozoans, crinoids, echinoids, mollusks, *Tubiphytes*, corals and ostracodes (Fig. 12A, B, C). Algae in growth position (mainly *Anthracoporella* and phylloid algae) form centimetre to decimetre-thick, lens-shaped beds (Md3 and Md4). In some outcrops, marly nodular intervals bear numerous well-preserved sphinctozoan sponges (*Discosiphonella, Amblyshiphonella* and minor *Sollasia*), even forming small lenticular colonies with the sponge bodies preserved in life position, along with abundant brachiopods, large bryozoans (fenestellids, fistuliporids and other ramose forms), crinoid stems, the solitary rugose coral *Cyathaxonia* and gastropods (Fig. 12E, F). Silicification in skeletal grains and nodular chert has been observed.

5.2.2.1. Interpretation. Facies B1 and B2, with prevailing mud-supported texture lacking traction-current structures and preservation of delicate skeletons, indicate low-energy levels and point to a quiet, subtidal environment below fair-weather wave base. They are comparable to autochthonous carbonate sediments characterizing middle ramp depositional settings reported in other sites throughout the Phanerozoic (Wright 1986; Sami and Desrochers, 1992; Somerville and Strogen, 1992).

Stratal packages of facies B1 and the enclosed buildups probably record a shallow mid-ramp depositional setting under open-marine conditions. The widespread *Anthracoporella* and phylloid algal mounds (facies Md3 and Md4), commonly assigned to shallow, low-energy settings (Krainer, 1995; Samankassou, 1997, 1998, 1999; Soreghan and Giles, 1999; Samankassou, 2003), the abundance of chaetetid sponges, calcareous green algae and large benthic foraminifers (fusulinoideans, palaeotextulariids, bradyinids and *Staffella*) along with levels rich in *Osagia*-type oncoids agree with this interpretation. The various types of buildups in the study area are comparable to those reported throughout Late Palaeozoic deposits by previous authors.

Chaetetid-dominated buildups were reported from Pennsylvanian rocks in the North American Midcontinent, U.S.A. (West, 1988; Connolly et al., 1989; Suchy and West, 2001; Wahlman, 2002). They generally developed in very shallow-water palaeoenvironments or topographic highs including algal mounds (Connolly et al., 1989; Wahlman, 2002). The association of *Chaetetes* with tabulate syringoporid/auloporid and rugose corals forming buildups was reported by West and Clark (1984), Rodríguez and Ramírez (1987), Miller and West (1997), West (1988), Suchy and West (2001), among others.

Anthracoporella-dominated algal mounds, first described in the Carnic Alps by Krainer (1995) and Samankassou (1997, 1998, 1999, 2003), were rarely reported in coeval successions elsewhere. Overall, the studied *Anthracoporella* mounds show striking similarities to those described in the Carnic Alps.

Phylloid algae had a wide distribution during Pennsylvanian and Permian giving rise to the development of algal mounds in shallow-water environments of carbonate ramps and shelves (West, 1988; Wahlman, 2002). Samankassou and West (2002) and Forsythe (2003) documented cup-shaped phylloid algae that actively contributed to mound growth displaying similar features to those of some phylloid algal mounds described herein.

In the stratal packages dominated by facies B2 the minor occurrence of photozoans and the scarcity of certain biota and grains characterizing shallower environments (e.g. chaetetids, large benthic foraminifers, *Osagia*-type oncoids and coated grains) point to slightly deeper settings. The colonization of the sea floor locally by dasycladaceans (*Anthracoporella*) and phylloids (*Eugonophyllum*) forming small mounds (lithofacies Md3 and Md4, respectively), however, indicate a position within the photic zone.

5.2.3. Outer-ramp

The facies association consists of nodular marly mudstones and marls (B3), micritic boundstones (Md5) and minor marls and shales (S). Lithofacies B3 form centimetre- to decimetre-thick (2–30 cm) undulating-nodular to almost tabular beds (massive to thinly laminated) with scarce trace fossils. Monaxon, and minor polyaxon, siliceous sponge spicules (Fig. 13A) and a low diversity heterozoan fauna are characteristic. Locally, centimetre (up to 5 cm long) cup-shaped structures made of dark homogeneous to lumpy micrite, including clusters of polyaxon sponge spicules and encrusted by *Eflugelia* and "calcivertellid" foraminifers are observed (Fig. 13B). Silicification affects skeletal grains, and small chert nodules are locally widespread in distinct layers (Fig. 13C).

The *micritic boundstones* (facies Md5) consist of clotted-peloidal micrite (automicrite, *sensu* Reitner and Neuweiler, 1995) with fenestrate bryozoans, the worm tube *Thartharella, Tubiphytes*, as well as inozoan and sphinctozoan sponges and rare algal thalli (Fig. 13D, E). These organisms commonly show complex spongiostromate micritic encrustations including calcified filaments and foraminifers (Fig. 13F). Homogeneous micrite (allomicrite), with scattered bioclasts, is volumetrically important.

5.2.3.1. Interpretation. The muddy matrix of rocks and the observed biotic associations almost lacking *in situ* algae point to deposition in a deep-water realm below the lower limit of the photic zone (or locally within the oligophotic zone), and most probably below storm wave base, i.e., the outer-ramp (Wilson, 1969; Faulkner, 1988; Burchette and Wright, 1992). Mud mounds (lithofacies Md5) typically occurred in distal parts of carbonate ramps (Lees and Miller, 1995; Jeffery and Stanton, 1996; Wendt et al., 2001). However, the occurrence of *in situ* algal thalli in the studied case indicates that these mounds apparently may also have developed in slightly shallower areas, close to the lower limit of the photic zone.

6. Depositional model

The depositional architecture described of the Las Llacerias Formation, consisting of unconformity-bounded sequences with a lower part of calcareous clastic deposits and an upper part of autochthonous carbonates, closely resembles the architecture of the younger Puentellés Formation (late Kasimovian–Gzhelian). The latter developed directly upon active tectonic growth structures linked with blind thrusts within a piggyback basin in the northern sector of the Picos de Europa Province (Merino-Tomé et al., 2007). Similarly, the Las Llacerias Formation could form small thrust-top carbonate platforms (according to the terminology of Bosence, 2005), nucleated on top of tectonic uplifts and passing southwards into a deep trough with clastic sedimentation. These uplifts would be linked to the incipient propagation of blind thrusts during mid Krevyakinian and Khamovnikian time (Fig. 14) (Merino-Tomé et al., 2009).

These early Kasimovian carbonate ramps developed synchronously with large deltaic systems, leading to accumulation of huge volumes of terrigenous sediments in the northern sector of Picos de Europa and to the W and S of the Picos de Europa Province originating from the adjacent and recently created mountainous areas of the Variscan Orogen (Figs. 1C and 14A). Terrigenous influx and, probably, periodic turbidity in the shallow waters affected the ramps developed
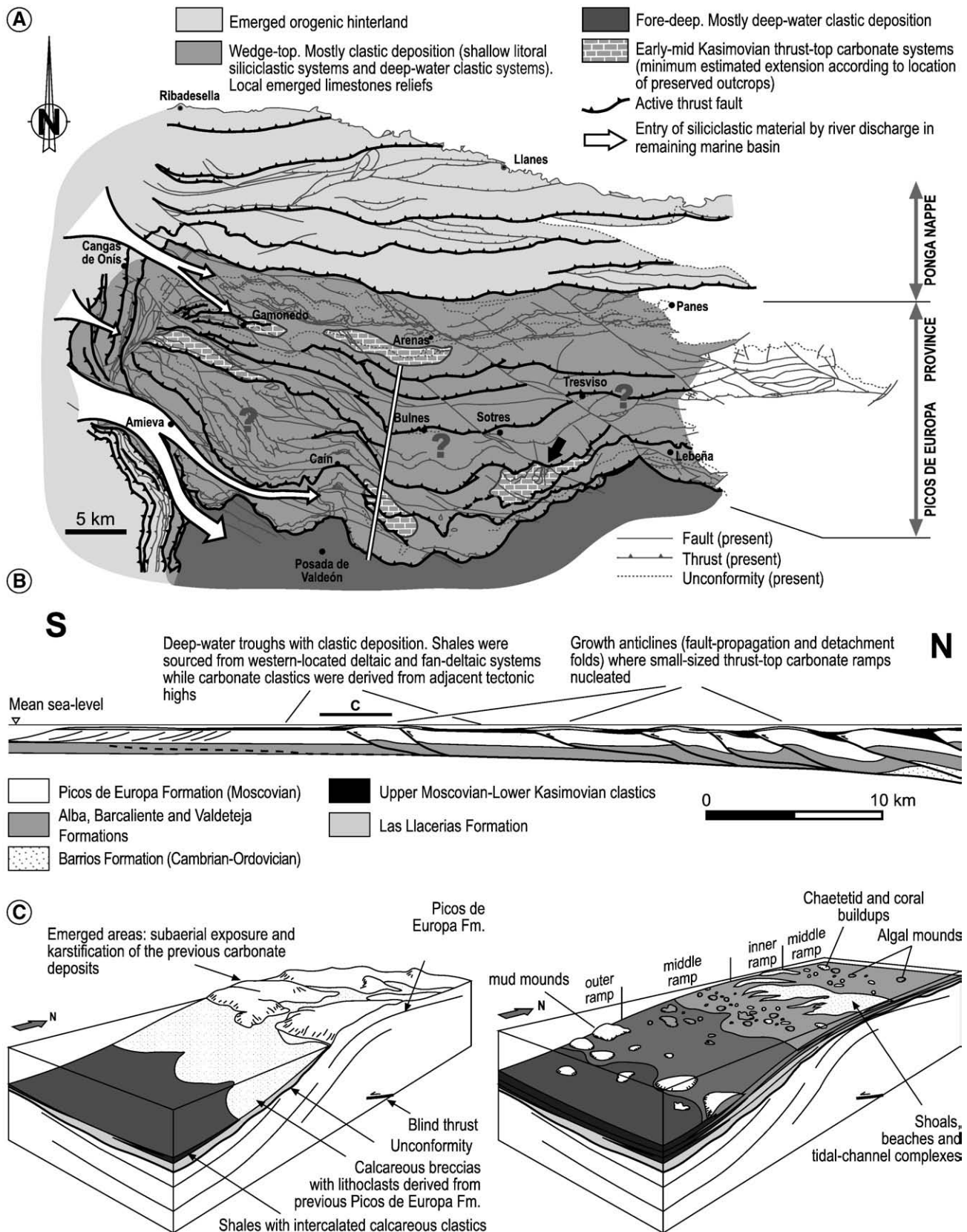
16

Fig. 14. A) Synthetic palaeogeographic map of Picos de Europa Province during late Krevyakinian (see Fig. 3). Note that map is based on present-day geometry of Cantabrian Zone and, thus, significant tectonic shortening in N–S direction resulting from Variscan thrusting was not considered. Black arrow indicates the location of Ándara area. B) N–S restored cross section along frontal and central subunits of Picos de Europa Province indicated by a white line in A. C) Block diagrams showing depositional model inferred for deposition of Las Llacerias Formation during the lower interval (left) and upper interval (right) of sequence 1 in Ándara area (black line labelled with C in B).

in the Ándara area as recorded by the siliciclastic material present both in the clastic and autochthonous carbonates of the Las Llacerias sequences.

6.1. Sedimentary environments

Although a precise depositional profile of the carbonate ramp with palaeobathymetric data cannot be obtained due to the lack of undisturbed primary sedimentary sections and continuous exposures, qualitative estimations of depth distribution for the facies associations can be established based on sedimentological features and palaeoecological data. Specifically, *in situ* algae, microboring and superficial micritization processes represent reliable proxies to estimate light-penetration depths.

Very shallow-water, high-energy environments with carbonate sand shoals and beaches were probably of limited spatial distribution. The scarcity of those deposits, but also of inferred storm-deposits (facies Te), can be explained either: 1) by the predominance of low-energy conditions affecting the carbonate ramp with only sporadic high-energy storm events; or 2) because of the drowning to below wave base level of extensive areas of these carbonate systems. The latter would reduce the areal extension of shallow-water environments, which may have been the main source of the grains transported by the offshore-directed return currents.

Within low-energy and well-illuminated euphotic environments (euphotic zone *sensu* Pomar, 2001), a wide range of marine biota were organized in very complex benthic communities. Chaetetid sponges, tabulate (mainly syringoporid) and rugose corals, phylloid algae, and dasycladaceans thrived and built small, metre-scale buildups. Various algae including abundant phylloid udoteaceans, minor ramose dasycladaceans and, maybe poorly calcified algae, colonized extensive areas of the sea floor to form meadows. They may have provided suitable habitat for the very rich and diverse epiphytozoan communities (including the small "tubiform" foraminifers and others such as Tuberitinids, Tetrataxids, *Palaeonubecularia*, and organisms such as worms, *Tubiphytes* and cyanobacteria) characterizing the shallow-water environments of the studied ramp. On the other hand, algal meadows probably helped to stabilize the sediment (similarly to seagrasses) and promoted the development of constructive micrite envelopes around skeletal grains and, probably, the growth of oncoids (Jones and Goodbody, 1985; Perry, 1998, 1999). These areas were characterized by bioclastic sediments with common cortoids, oncoids and rich associations of benthic foraminifers, calcareous algae (including dasycladacean and udoteacean green algae, and minor red algae), cyanobacteria (e.g., *Osagia* oncoids and encrustations), heterozoans (brachiopods, echinoderms, mollusks, bryozoans and calcareous sponges) and calcispheres. The pervasive occurrence of sponge spicule ghosts indicates that siliceous sponges probably also thrived in those environments. Although the euphotic zone in modern depositional environments may extend down to 40–50 m, it is often limited to 20–30 m (Pomar, 2001; Wilson and Vecsei, 2005). The increase in turbidity linked to terrigenous and nutrient input may, however, reduce this limit to just a few metres.

In slightly deeper areas between the euphotic and oligophotic zone (which matches the mesophotic zone *sensu* Pomar, 2001), sediments consisted of bioclastic wackestones in which algae and larger foraminifers progressively disappear and heterozoans become more abundant with increasing water depths. In these areas, small-sized algal mounds developed. Heterozoan communities dominated by brachiopods, crinoids, bryozoans and calcareous demosponges flourished.

Generally in deeper environments, mud mounds developed as result of the colonization of the seafloor by microbial communities (with *Tubiphytes* and other scarce calcimicrobes) associated with metazoans such as *Thartharella* worms, bryozoans, calcareous inozoan and sphinctozoan sponges, siliceous sponges and crinoids. Micritic sediment formed as products of the life activity of such communities,

or post-mortem processes (Pickard, 1996; Riding, 2000, among others) is volumetrically a major component of the mound core deposits (facies Md5). Algae occurred only locally within these mud mounds, probably when the actual sea bottom reached the lower limit of the photic zone. These environments distally passed into shaly argillaceous slopes and basinal deposits.

7. Discussion

The Las Llacerias Formation is characterized by very diverse biotic associations that have rarely been recorded in the older carbonate platform facies of the Valdeteja and Picos de Europa Formations. Moreover, the grain composition points to a shallow-water setting (Fig. 15). Significant differences with respect to previous carbonate systems are: 1) absence of ooids, 2) significant decrease in early marine cementation, 3) astonishing increase in micritized grains, and abundance of cortoids, lumps (formed by superficial micritization and by constructive micritic coating) and *Osagia* oncoids, 4) accumulation of organic mater, and 5) influx of siliciclastics during deposition. This shift in grain composition is thought to record major environmental changes, which affected the biotic communities and the carbonate factory at the base of the Kasimovian stage.

Comparing the geological scenarios of the Bashkirian–Moscovian carbonate shelf (Valdeteja and Picos de Europa Formations, Colmenero et al., 2002; Fernández et al., 2004; Bahamonde et al., 2007) and the Kasimovian thrust-top carbonate system (Las Llacerias Formation), only a major difference in nutrient levels appears as the strongest environmental factor that controlled the biotic composition. The skeletal grain types recorded in the platform-top successions of the previous carbonate shelf (Valdeteja and Picos de Europa Formation) and in the Las Llacerias Formation are dominated by photozoans (Bahamonde et al., 2000; Della Porta et al., 2002; Della Porta, 2003; Della Porta et al., 2006; Bahamonde et al., 2007), as may be expected for tropical Pennsylvanian warm-water carbonates, and mostly corresponds to the chlorozoan and chlorosponge associations (Beauchamp and Desrochers, 1997; James, 1997; Wahlman, 2002). These associations are present from Bashkirian–Moscovian and into Kasimovian times. In both cases, the common occurrence of stenohaline biota, including echinoderms, chaetetid sponges, corals and brachiopods, suggest normal salinity and open-marine conditions. Therefore, changes in temperature or salinity probably do not account for the shift in biotic associations from somewhat less diverse benthic communities during Bashkirian–Moscovian to the higher-diversity communities during the Kasimovian.

The major change in basin configuration, namely the rapid motion of the orogenic front that started from the latest Moscovian (late Myachkovian) and caused a very rapid narrowing of the marine basin and the tectonic uplift of nearby mountainous reliefs (Fig. 1C) seems to have played a key role. The hot-humid climatic conditions that are inferred for this area of Pangea (Tabor and Poulsen, 2008) would favour high rates of weathering and erosion of the newly created hinterland surrounding the marine basin (Figs. 1C and 14A), and the subsequent transport of sediments basinwards by large river discharge, presumably under monsoon conditions. Additionally, this freshwater discharge would also supply dissolved nutrients and organic carbon. Land-derived nutrients could have reached the SE area of the Picos de Europa during the deposition of the Las Llacerias Formation (late Myachkovian and early Kasimovian), because of the rapid narrowing and gradual filling of the marine basin (Fig. 1C). This was not the case earlier during Bashkirian and Moscovian times, when the foreland basin was deep and the carbonate platform was remote from the siliciclastics shed from deltaic systems and, thus, also remote from land-derived nutrients.

In the Las Llacerias Formation, facies criteria and the inferred biothic communities provide arguments that are in accordance with this scenario supporting both the existence of high nutrient levels and
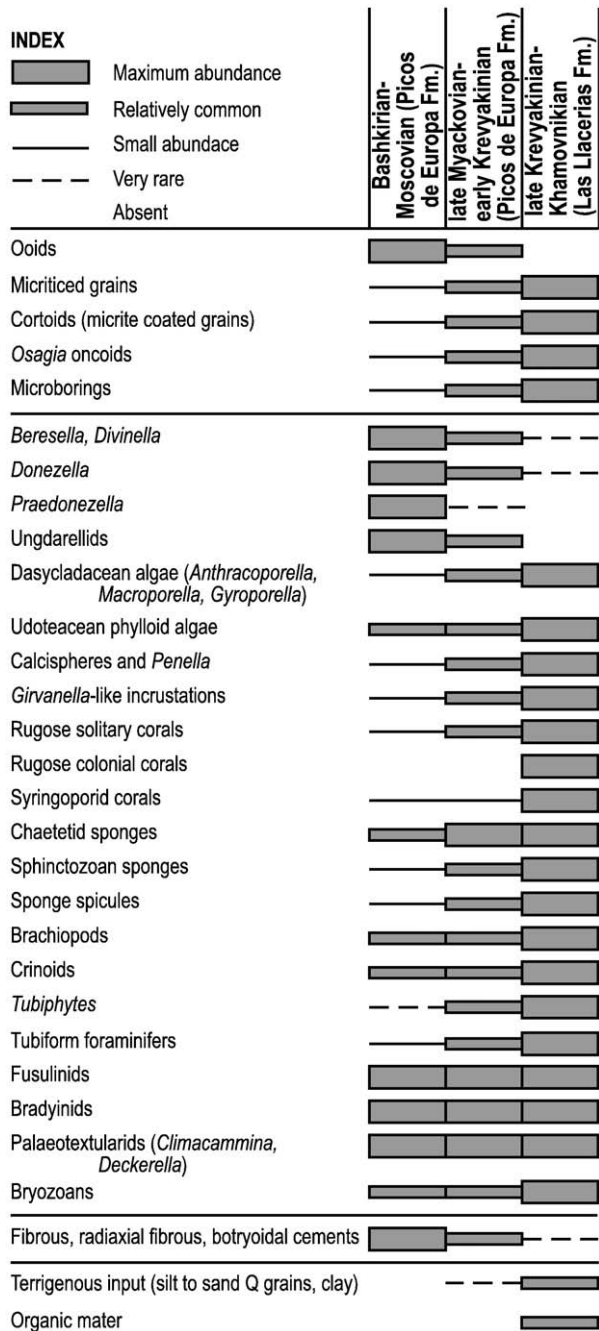
INDEX

- ▭ Maximum abundance
- ▬ Relatively common
- — Small abundance
- – – – Very rare
-   Absent

Columns (time intervals):
- Bashkirian-Moscovian (Picos de Europa Fm.)
- late Myackovian-early Krevyakinian (Picos de Europa Fm.)
- late Krevyakinian-Khamovnikian (Las Llacerias Fm.)

Rows:
- Ooids
- Micriticed grains
- Cortoids (micrite coated grains)
- *Osagia* oncoids
- Microborings
- *Beresella, Divinella*
- *Donezella*
- *Praedonezella*
- Ungdarellids
- Dasycladacean algae (*Anthracoporella, Macroporella, Gyroporella*)
- Udoteacean phylloid algae
- Calcispheres and *Penella*
- *Girvanella*-like incrustations
- Rugose solitary corals
- Rugose colonial corals
- Syringoporid corals
- Chaetetid sponges
- Sphinctozoan sponges
- Sponge spicules
- Brachiopods
- Crinoids
- *Tubiphytes*
- Tubiform foraminifers
- Fusulinids
- Bradyinids
- Palaeotextularids (*Climacammina, Deckerella*)
- Bryozoans
- Fibrous, radiaxial fibrous, botryoidal cements
- Terrigenous input (silt to sand Q grains, clay)
- Organic mater

Fig. 15. Relative proportion of grains forming shallow-water subtidal deposits (platform-top and inner to mid-ramp settings) within 3 successive time intervals from Bashkirian to early Kasimovian in carbonate successions of Picos de Europa Province and Ponga-Cuera Unit.

alteration of skeletal grains (e.g., early micritization) is suggested to increase with eutrophic conditions (Wood, 1993; Kiene et al., 1995). Hallock (1988) demonstrated that in modern mesotrophic waters close to river mouths and in marine areas affected by currents of nutrient-rich waters (e.g., from the Mississippi delta to western and southern Florida), carbonate sand and gravel exhibiting biological alteration are abundant. Also Peterhänsel and Pratt (2001) postulated that the increase in the effects of bioeroders (skeletal micritization and bioerosion) in the Late Devonian carbonate platform of the Palliser Formation (Canadian Rocky Mountains) was linked to an increase in nutrient supply.

3) The common occurrence of cyanobacterial oncoids (*Osagia*) is considered as an indicator for high nutrient levels (Flügel, 2004). Moreover, constructional microbial encrustation and micritic envelopes forming cortoids, aggregates, which also contributed to the genesis of oncoids, is a further indicator for high nutrient levels (Peterhänsel and Pratt, 2001).

4) The dark colour characterizing the autochthonous carbonate deposits of the Las Llacerias Formation seems to have resulted from a high amount of non-degraded organic matter present within the sediments and visible in many thin sections (Figs. 8D and 13A). This may indicate high rates of primary production by photosynthesis leading to substantial production of organic matter, which is favoured by the availability of nutrients.

5) Dissolved silica resulting from the weathering of silicate rocks via riverine input is an important source for nutrients in modern oceans, particularly in tropical regions (Tréguer et al., 1995). Overall, the abundance of biogenic SiO_2 and their diagenetic products are considered indicators of mesotrophic and eutrophic waters (Wood, 1993; Föllmi et al., 1994) and generally characterize deep-marine carbonate sediments and shallow-water carbonates on nutrient-rich carbonate shelves. In the Las Llacerias Formation there is a high degree of preservation of unaltered siliceous sponge spicules. Also, silicified skeletal grains are widespread in the outer and mid-ramp, including relatively shallow-water deposits.

7.2. Biotic communities

The fossil record may be disturbed by taphonomic processes and early and late diagenesis (Cherns and Wright, 2000; Flügel, 2004; Wright and Burgess, 2005). Thus, the applicability of actualism to unravelling the details of the composition and the structure of past biotic communities is not straightforward. Nevertheless, carbonate sediments can provide data that may help to make first-order reconstructions of past communities on the basis of detailed palaeontologic and micro-facies analysis.

In the studied outcrops of the Las Llacerias Formation, the biotic communities recorded in the inner and mid-ramp deposits, which are rich in photozoans (algae and cyanobacteria) and foraminifers associated with crinoids and echinoids, brachiopods, bryozoans, calcareous sponges, mollusks and tabulate and rugose corals, may be comparable to the heterozoan–photozoan transition association that characterizes nutrient-rich (upper mesotrophic–eutrophic) warm to temperate modern shallow-water (<50 m) carbonate environments (Halfar et al., 2004, 2006).

Cyanobacteria and probable associated heterotrophic bacteria were widespread in these shallow-water realms as indicated by: 1) the pervasive micritization of skeletal grains, 2) the occurrence of constructional micritic envelopes and porostromate encrustations around grains, and *Osagia* oncoids with calcified filaments of *Girvanella* and *Claracrusta*, and 3) the occurrence of structures described as microbial fabrics in the various buildups described (facies Md1, Md2, Md3, Md4 and Md5). Microbially mediated carbonate precipitation, resulting in the formation of microbialites, is known to be enhanced by the presence of organic matter and alkaline metals in siliciclastics (Neuweiler et al., 1996; Dupraz and Strasser, 2002).

the arrival of siliciclastic material shed from nearby continental areas. In addition, the lack of indicators of upwelling reinforces the hypothesis of the terrestrial source for the nutrients.

7.1. Facies criteria

1) The finer terrigenous content (clay, silt- to sand-sized quartz) throughout the Las Llacerias Formation and locally drifted plant remains was apparently provided by deltas and fan-deltas developed at the mouths of river systems draining the adjacent growing orogenic range to the east (Fig. 14A).

2) Shallow-water deposits of the Las Llacerias Formation are characterized by pervasive micritization and bioerosion affecting skeletal grains (facies A1, A2, A3 and B1). Biological and chemical

Boundstones dominated by heterotrophic organisms and microbial-mud mounds are predicted to form in mesotrophic conditions under moderate- to low-energy conditions (Wood, 1993). Oxfordian coral-microbialite reefs including phototrophic–heterotrophic fauna and *Terebella* worms developed in environments moderately affected by terrigenous input and nutrient availability (Dupraz and Strasser, 2002). This fits the findings of the present paper, where presumably microbially precipitated micrite and the calcified worm tube *Thartharella* are common (facies Md1, Md3, Md4 and Md5).

Eugonophyllum and other phylloid algae are among the most abundant biota within the shallow subtidal deposits (facies B1 and B2) and frequently formed algal mounds (facies Md4). According to Suchy and West (2001), the growth of phylloid algae appears to coincide with high nutrient inputs, an interpretation supportive of our findings. Similarly, during the Holocene, the phylloid udoteacean alga *Halimeda* thrives and is known to build mounds (bearing certain similarities to the Palaeozoic phylloid algal mounds) in low-latitude areas of high nutrient levels, either from adjacent continental areas or from coastal settings influenced by upwelling (Hallock et al., 1988; Hine et al., 1988; Marshall and Davies, 1988; Roberts et al., 1988; Davies et al., 2004; Wilson and Vecsei, 2005).

The high amount of ghosts of sponge spicules associated with shallow-marine organisms (e.g., phylloid algae) indicates that siliceous sponges were obviously abundant in the euphotic zone. That contrasts to modern examples where sponges and silica-rich sediments are restricted to deep-water environments (Hartman, 1981; Maliva et al., 1989; Rosales et al., 1995). Other examples of siliceous sponges in nearshore areas are reported from Pennsylvanian spicular flints (Lane, 1981; Carlson, 1994). In these examples, nutrients originating from riverine input played a key role in the establishment of siliceous sponges.

Fishes thrived and were probably abundant, as indicated by the findings of fish bones, teeth and scales in outcrop and in dissolved rock samples, adding another indirect criteria of elevated primary productivities and high nutrient levels.

Intervals with high siliciclastic content are dominated by heterotrophic faunas with very abundant, small but diverse brachiopods, crinoids, calcareous sponges (mostly sphinctozoans), bryozoans, small-sized solitary *Cyathaxonia* corals and gastropods. These probably record eutrophic conditions coinciding with periods of high terrigenous input and probably turbid waters.

7.3. Absence of upwelling indicators

Upwelling of deep cold water is one of the mechanisms that can account for the nutrient enrichment of surface waters. However, the configuration of the marine basin studied, with narrow elongated troughs and ridges, oriented parallel to the Variscan thrusts, within a progressively narrowing and shallowing foreland basin, was not suitable for widespread upwellings. Although minor turnover and vertical mixing of waters in these partially isolated troughs could have been a considerable source of nutrients during 4th–5th order galcioeustatic sea-level rises, no evidence of cold, nutrient-rich waters affecting the inner- and mid-ramp zones such as phosphatic layers is recorded.

The skeletal components of the inner and mid-ramp, typical for the chlorosponge association (see above), and the abundance of skeletal grains such as phylloid algal thalli, sphinctozoan and inozoan sponges, indicate a prevalence of warm waters down to considerable water depths. In addition, the recorded biotic associations differ from those described in other Carboniferous carbonate settings where upwelling conditions have been invoked (Brandley and Krause, 1997; Martindale and Boreen, 1997; Samankassou, 2002) and from those characterizing cold-water and temperate shelf carbonates that might have been expected if upwelling processes might had occurred (compare with Beauchamp, 1994; Beauchamp and Desrochers, 1997).
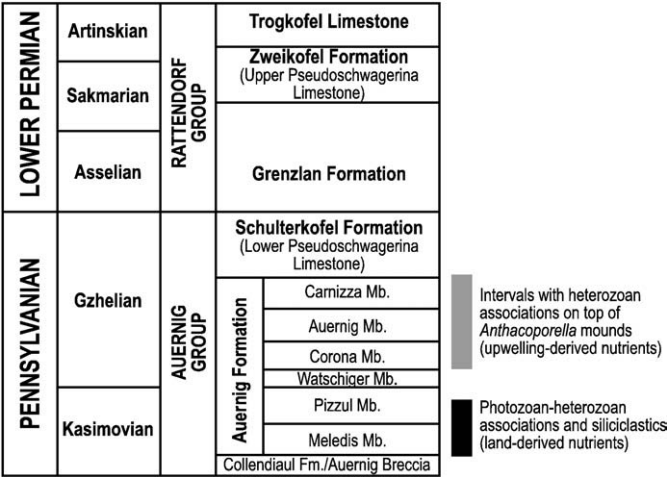

LOWER PERMIAN	Artinskian	**RATTENDORF GROUP**	**Trogkofel Limestone**	
	Sakmarian		**Zweikofel Formation** (Upper Pseudoschwagerina Limestone)	
	Asselian		**Grenzlan Formation**	
PENNSYLVANIAN	Gzhelian	**AUERNIG GROUP**	**Schulterkofel Formation** (Lower Pseudoschwagerina Limestone)	
			Auernig Formation	Carnizza Mb.
				Auernig Mb.
				Corona Mb.
				Watschiger Mb.
	Kasimovian			Pizzul Mb.
				Meledis Mb.
			Collendiaul Fm./Auernig Breccia	

■ (grey) Intervals with heterozoan associations on top of *Anthacoporella* mounds (upwelling-derived nutrients)

■ (black) Photozoan-heterozoan associations and siliciclastics (land-derived nutrients)

Fig. 16. Stratigraphy of Pennsylvanian–Early Permian succession in Carnic Alps showing stratigraphic interval of Auernig Group mentioned in text (modified from Samankassou, 2002).

7.4. The Auernig Formation, Carnic Alps, Austria: an analogue case?

High-diversity biotic associations were reported from two Kasimovian–Gzhelian intervals within the Auernig cyclothems of the Carnic Alps, Austria–Italy (see Fig. 1B for location). The first interval corresponds to the basal Auernig sequences deposited discordantly upon the underlying Devonian basement, which displays significant relief resulting from the Variscan Orogeny (Forke and Samankassou, 2000) (Fig. 16). The sequences vary laterally in thickness, and include dark-grey to brown limestone beds, are rich in siliciclastics, and show a high-diversity biotic association of *Anthracoporella*, phylloid algae, echinoderms, corals, sponges, bryozoans and brachiopods (Forke and Samankassou, 2000). The high diversity of algae and suspension feeders may be linked to high nutrient levels resulting from reworking and remobilisation of siliciclastics.

The second interval corresponds to the upper members of the Auernig Group (Fig. 16) and the high-diversity associations appear on top of distinct *Anthracoporella* buildups (Samankassou 2002). These levels are characterized by high-diversity associations of heterozoans that are interpreted to record periodic upwelling of cool, nutrient-rich water into a shallow-water setting (Samankassou, 2002).

In contrast to the cool-water scenario drawn from the heterozoan-rich faunal associations of the upper members of the Auernig Group, the shallow-water deposits (inner and mid-ramp) of the Las Llacerias Formation exhibit a mixed photozoan–heterozoan association that resembles the benthic communities recorded in the basal Auernig sequences. Land-derived nutrient input (from deltaic siliciclastics), interpreted as the main source and triggering factor in the Las Llacerias Formation and the lower part of the Auernig Group, was considered only a minor factor in the upper part of the Auernig Group (Samankassou, 2002). The difference in nutrient source between the Las Llacerias Formation and the lower part of the Auernig Group on the one hand (land-derived), and the upper part of the Auernig Group on the other (upwelling-derived), and the cooler water temperature linked to the latter may explain why the two cases differ in their respective biotic associations.

8. Conclusions

The Pennsylvanian (lower Kasimovian) Las Llacerias Formation represents thrust-top carbonate ramps developed upon small tectonic uplifts during the incipient thrusting of an antecedent extensive flat-topped carbonate platform (Bashkirian–Moscovian). It occurred within a narrowed marine foreland basin located in the palaeoequatorial humid

20

belt on the east coast of Pangea. The rich benthic communities recorded in the Las Llacerias Formation carbonates are an exceptional case that is rarely documented in coeval deposits worldwide.

The shallow-water, well-illuminated and low-energy realms of these carbonate systems were characterized by the occurrence of decimetre- to metre-sized photozoan (*Anthracoporella* and phylloid algae) mounds and metazoan (chaetetids, syringoporids and branching colonial rugose corals) reef-mounds embedded within black, biota-rich nodular wackestones to packstones with a mixed photozoan–heterozoan biota. In the deep parts of the ramps, the bioclastic grains consist of heterozoan associations and mud mounds (Md5) dominated by microbial communities with minor contribution of metazoans (mostly bryozoans, sphinctozoan and inozoan sponges, worms and *Tubiphytes*).

The growth of these high-diversity benthic communities coincides with a significant increase in terrigenous influx and hence nutrient supply from terrestrial runoff that was favoured by the changing tectonic configuration and the humid climatic conditions. Considerable land-derived nutrient influx from river discharges that was draining the adjacent growing orogenic chain into the narrow marine foreland basin led to mesotrophic and, locally, to eutrophic conditions in the surface waters. These high nutrient levels are considered to be the main factor that controlled the establishment of the diverse shallow-water communities that produced the grain types forming the carbonate facies. This scenario presumably favoured high productivity, which also led to abundant non-degraded organic matter that is responsible for the pervasive dark colour of these carbonates.

The scenario for the Las Llacerias Formation is supported by a similar trend in the lower part of the Auernig Group of the Carnic Alps, where biotic communities were controlled by land-derived nutrients, eroded from the underlaying beds.

The influence of land versus upwelling-derived nutrients is commonly difficult to discriminate. The Las Llacerias example is thus a case that potentially may help to better distinguish between biotic communities controlled by land-derived versus upwelling-derived nutrients in the fossil rock record, particularly in areas where the tectonic context is not well constrained.

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