NEW MIDDLE CAMBRIAN MOLLUSCS FROM THE LÁNCARA FORMATION OF THE CANTABRIAN MOUNTAINS (NORTH-WESTERN SPAIN)

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ABSTRACT

An abundant and highly diverse fauna is characteristic for the nodular limestones of the upper member of the Láncara Formation. It consists of echinoderms, trilobites, brachiopods, molluscs, sponge- and chancelloriid remains, and other small shelly fossils. Whereas the trilobites of the Láncara Formation are well investigated, information on other faunal groups is clearly underrepresented. In this paper the Middle Cambrian helcionelloid molluscs and hyoliths of the upper member of the Láncara Formation from four sections are described for the first time. The mollusc fauna shows clear affinities to Siberia, South Australia, Greenland, and China. The following taxa were described: *Protowenella lancaraensis* new species, *Mackinnonia* cf. *rostrata* (Zhou & Xiao, 1984), *Pelagiella subangulata* (Tate, 1892), *Conotheca* sp., and *Microcornus* sp.

Key words: Molluscs, Helcionellida, Hyolitha, Middle Cambrian, Láncara Formation, Cantabrian Mountains, Spain.

RESUMEN

En las calizas nodulosas del miembro superior de la Formación Láncara se registra una abundante y diversificada fauna; en la que se han encontrado equinodermos, trilobites, braquiópodos, moluscos, esponjas y restos de chancelóridos, y otros pequeños fósiles conchíferos (*SSF*). Aunque los trilobites de la Formación Láncara han sido estudiados previamente, la información existente sobre los otros grupos faunísticos es mínima. En este trabajo se describen por primera vez moluscos helcionélidos e hiolíticos del Cámbrico Medio, recolectados en el miembro superior de la Formación Láncara. Esta fauna de moluscos muestra claras afinidades con Siberia, Sur de Australia, Groenlandia y China. En este trabajo se describen los siguientes taxones *Protowenella lancaraensis* nueva especie, *Mackinnonia* cf. *rostrata* (Zhou & Xiao, 1984), *Pelagiella subangulata* (Tate, 1892), *Conotheca* sp. y *Microcornus* sp.

Palabras claves: Moluscos, Helcionellida, Hyolitha, Cámbrico Medio, Formación Láncara, Cordillera Cantábrica, España.

INTRODUCTION

The knowledge on Cambrian molluscs of the Iberian Peninsula is rather poor. The first descriptions of molluscs from the Cantabrian Mountains have been taken by Prado *et al*. in 1860, and later on by Comte (1959). Later Geyer (1986) described the species *Helcionella* sp., *Yochelcionella* sp., *Scenella* sp., *Leptostega irregularis* Geyer, 1986, *Marocella* cf. *morenensis* (Yochelson & Gil-Cid, 1984), and also *Pelagiella crassa* Geyer, 1986 from the upper member of the Láncara Formation of the Porma locality (south-eastern Cantabrian zone) (see Fig. 1a). From the Ossa Morena zone Lotze (1961) described *Scenella* sp. and *Scenella reticulata* Billings, 1872, while *Scenella* sp. and *Scenella morenensis* Yochelson & Gil-Cid, 1984 were described by Gil-Cid (1972) and Yochelson & Gil-Cid

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(1984). Vidal *et al*. (1999) reported *Anabarella plana* Vostokova, 1962 and *Oelandiella korobkovi* Vostokova, 1962 from the Lower Cambrian of the Alcudian area (Central Iberian Zone). *Scenella reticulata* Billings, 1872 was also described by Richter & Richter (1941) from the uppermost Lower Cambrian of Cala (Andalucia), and *Scenella conula* Walcott, 1886 was mentioned by Sampelayo (1935) from the Celtiberian area. Lower Cambrian molluscs (e.g. *Bestashella tortilis* Missarzhevsky in Missarzhevsky & Mambetov, 1981, *Helcionella atdabanica* Missarzhevsky in Rozanov & Missarzhevsky, 1966, and *Pelagiella adunca* Missarzhevsky in Rozanov & Missarzhevsky, 1966) from the Sierra de Córdoba (Ossa Morena zone) were illustrated but not formally described in Liñán Guijarro (1978) (see Fernández-Remolar, 1999, 2001) In recent times Gubanov *et al*. (2004) investigated helcionelloid molluscs from the Pedroche Formation of the Sierra de Córdoba.

This paper deals with helcionelloid molluscs of the Lower–Middle Cambrian Láncara Formation of the Cantabrian zone, not reported from this area until now. Further, the first-time determination of hyoliths within this region will be done. Aim of the work is to increase the knowledge of the occurrence of this fossil group within this time interval and geographical region.

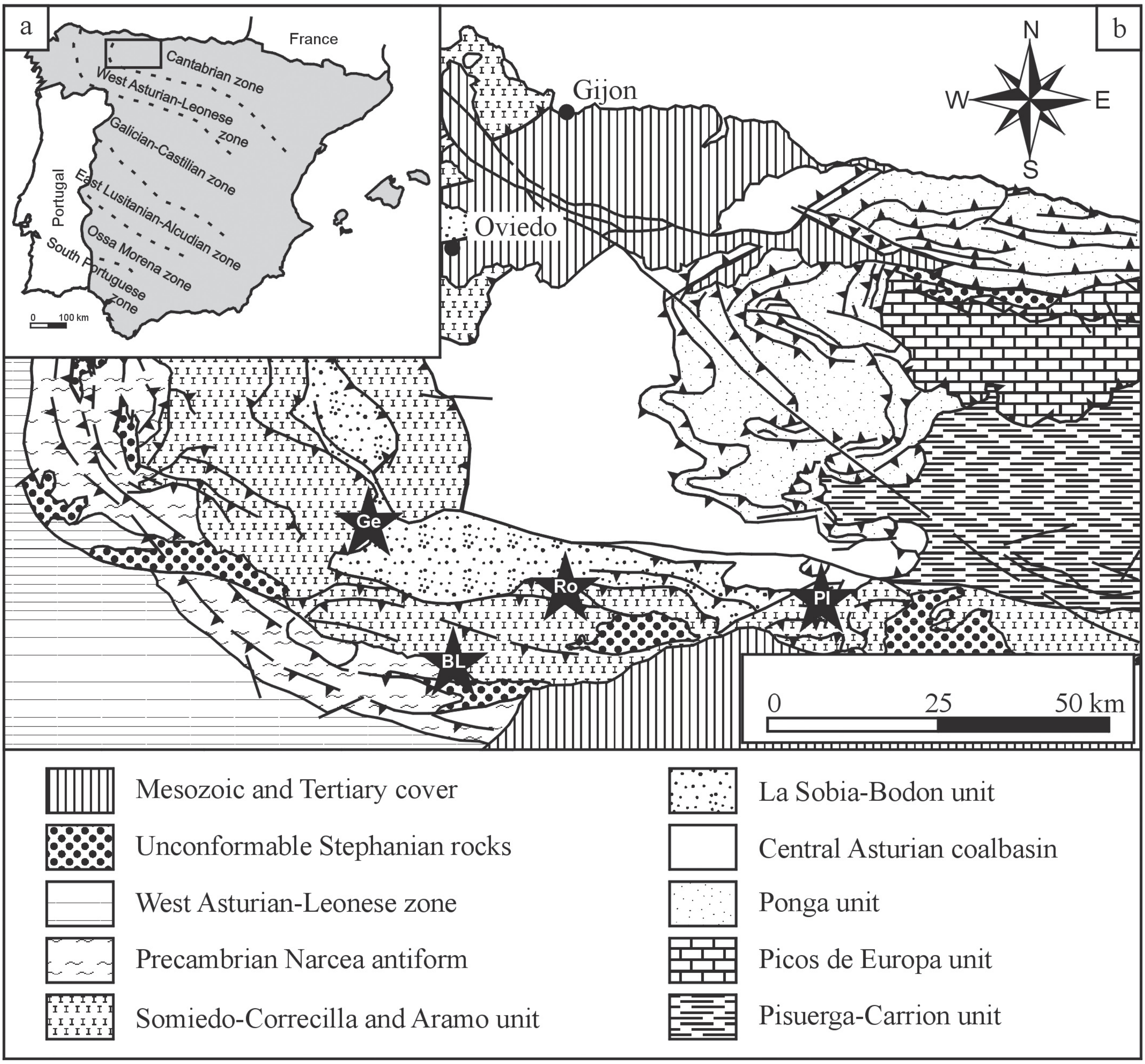


Figure 1. **a**, Simplified geological map of the Iberian Peninsula. **b**, Generalised geological map of the Cantabrian zone (modified after Pérez-Estaún *et al*., 1988); BL – Los Barrios de Luna section; Ge – Genestosa section; PI – Porma section; Ro – Rodiezmo section.

GEOLOGICAL SETTING

The Cantabrian Zone represents the north-western part of the Iberian Peninsula (Fig. 1a). To the west it is limited by the West Asturian-Leonese Zone. The northern boundary is represented by the Atlantic Ocean, whereas the eastern and the southern limits are defined by overlying sediments of Mesozoic and Tertiary age (Fig. 1b).

The Cantabrian zone is divided into five tectonostratigraphic units: (i) Folds and Nappes, (ii) Central Asturian coalbasin, (iii) Ponga unit, (iv) Picos de Europa unit, and (v) Pisuerga-Carrion unit (Fig. 1b). Thereby, the Folds and Nappes region is further subdivided into several subunits (Julivert, 1971; Pérez-Estaún *et al.*, 1988).

According to Lotze (1961) the about 2700 m thick Cambrian of the Cantabrian zone is subdivided into the carbonatic Láncara Formation which is sandwiched by the underlying siliciclastic Herrería Formation and the overlying Oville Formation (Fig. 2). The boundaries between the called Formations are diachroneous (Sdzuy, 1968, 1974; Sdzuy & Liñán, 1993; Liñán *et al.*, 2002). The 900 m to 1700 m thick Herrería Formation (Neoproterozoic?–Lower Cambrian) is represented by claystones, sandstones and conglomerates (Fig. 2), but sometimes carbonate intercalations are observable. Following Oele (1964), Rupke (1965), Van den Bosch (1969), Van Staalduinen (1973), Crimes *et al.* (1977), Van der Meer Mohr (1983), Truyols *et al.* (1990), and Aramburu *et al.* (1992) the sedimentary environment of the Herrería Formation is interpreted as a shallow-marine platform which was influenced by intertidal and fluvial episodes.

The upper siliciclastic lithosome, the Oville Formation, is characterised by 80 m to 800 m thick green shales and glauconitic sandstones without any carbonatic content (Fig. 2). The base of the Oville Formation can represent levels with carbonate nodules, and some thin carbonate layers (see Sdzuy & Liñán, 1993). The sediments are interpreted by Oele (1964), Aramburu *et al.* (1992), and Aramburu & García-Ramos (1993) as shallow platform accumulations in an intertidal and braided plain deltaic system.

The Láncara Formation, which is situated between the siliciclastic parts of the Herrería Formation and the Oville Formation, consists of two members, differing in lithology and fossil content (Fig. 2). The 110 m to 220 m thick lower member is composed of dolomites and dolomitic limestones. These lithotypes are characterised by algal mats, stromatolites, algal-peloids, and oncolites, but also by fenestral fabrics and tepee-structures. According to Zamarreño (1972), Russo & Bechstädt (1994), and Álvaro *et al.* (2000) this facies is similar to a carbonate tidal-flat deposit.

The upper member of the Láncara Formation (10 m to 50 m thick) is divided into two facies types: the lower Beleño facies and the upper Barrios facies. The Beleño facies is represented by granular-crystalline, grey to roan

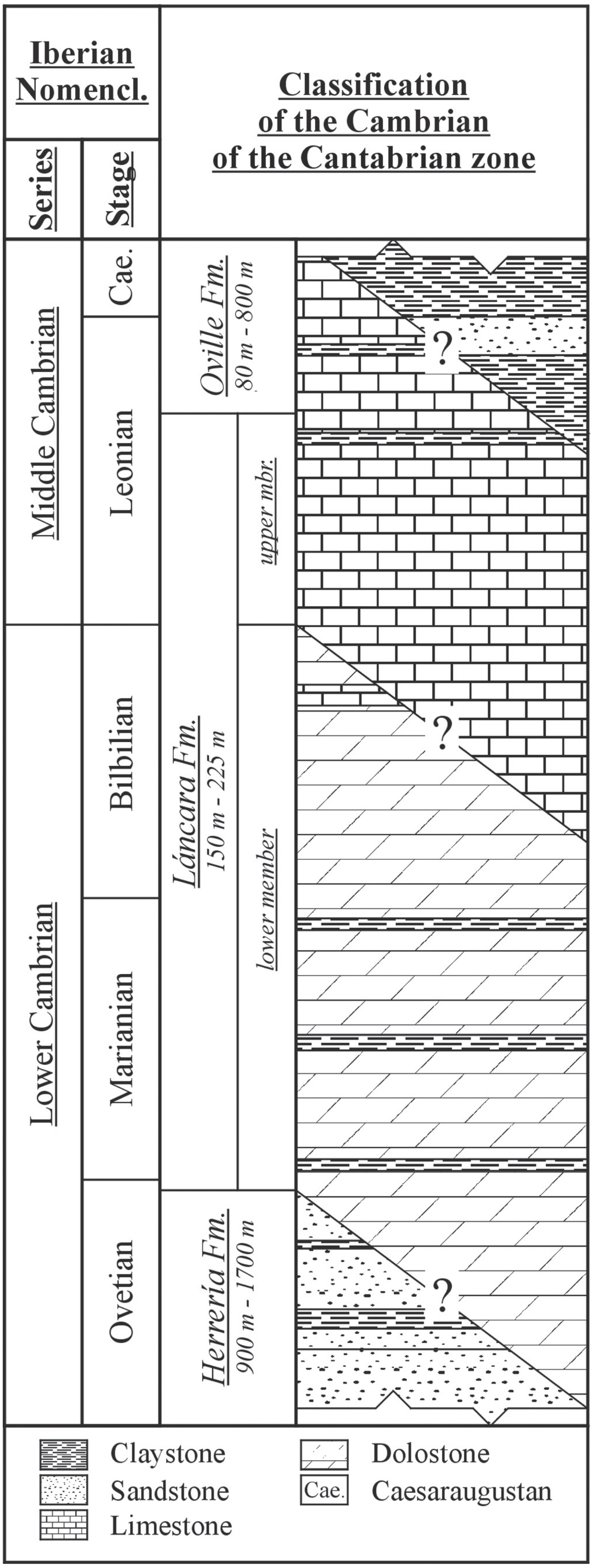


Figure 2. Simplified stratigraphic profile of the Cambrian of the Cantabrian Zone (modified after Liñán *et al.*, 1993, 2002).

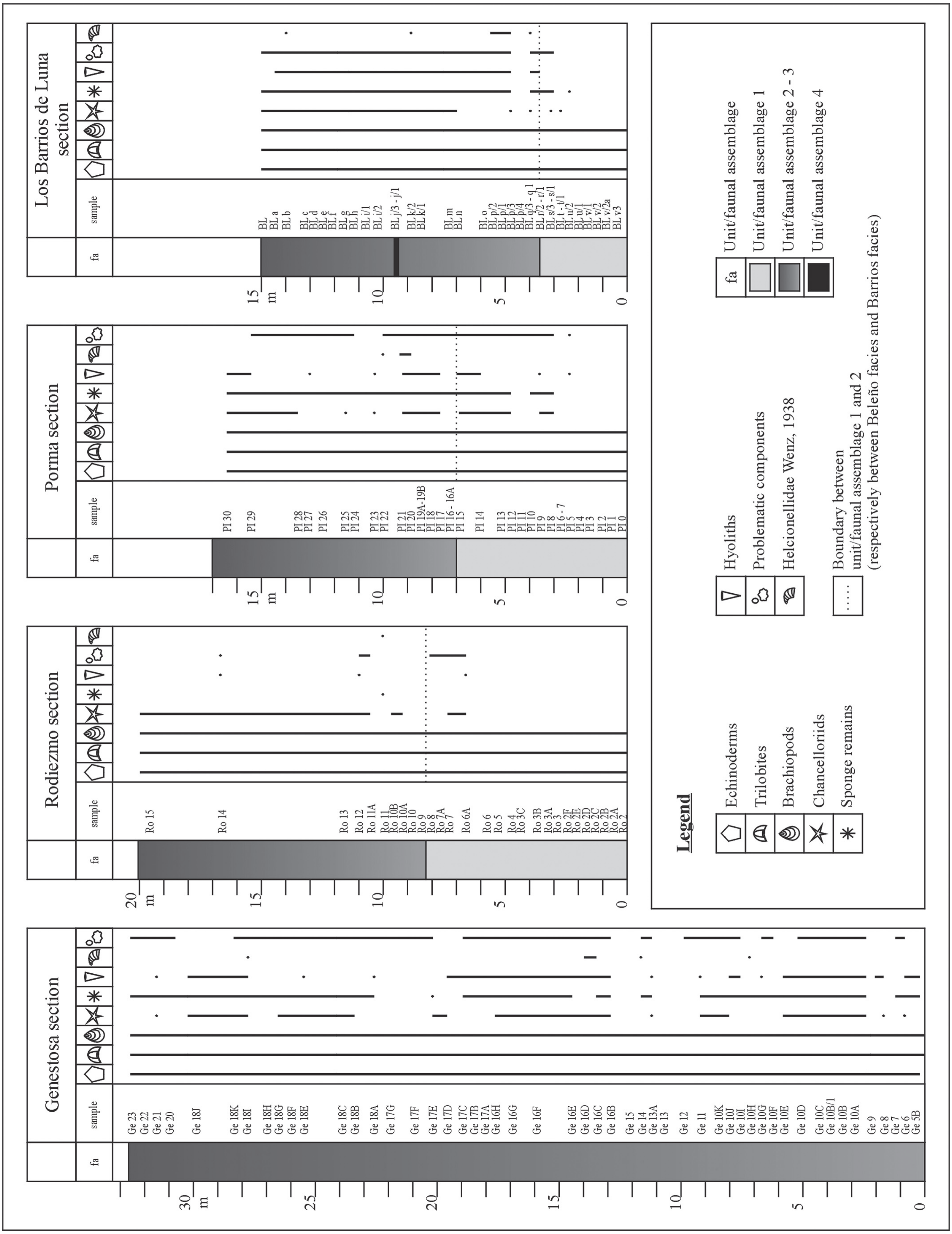


Figure 3. Faunal distribution patterns within the sections of Genestosa, Rodiezmo, Porma and Los Barrios de Luna.

bioclastic limestones (bioclastic wackestones, -packstones and -floatstones), yielding a high content of glauconite and disarticulated echinoderms. Nodular limestones (bioclastic wackestones and -floatstones) represent the bulk of the Barrios facies. A high fossil content and a very diverse fauna are typical. The transition between both facies types is characterised by a continuous change in the fossil content (Wotte *et al*., 2004; Wotte, 2005), and by a successive increase in the siliciclastic material. The accumulation of the siliciclastic content within mm to cm thick bands of insoluble material, caused by pressure solution, is crucial for the nodular appearance. Caused by the continuous increase in the siliciclastic input also the transition to the overlying Oville Formation continues successive.

BIOFACIAL CONSIDERATIONS

In contrast to the overlaying siliciclastic Oville Formation as well as to the underlying dolomitic lower member of the Láncara Formation, the upper member is characterised by a high faunal content, variable between 60 % and 80 % in the Beleño facies and 30 % and 70 % in the Barrios facies. The most frequent faunal elements are echinoderms, trilobites and brachiopods. Less common are molluscs (described below), chancelloriid- and sponge remains and problematic phosphatic components (Fig. 3). Unfortunately, this rich fauna is scarcely extractable. Therefore, only a small amount of specimens is available for taxonomic investigation.

The vertical faunal succession of the upper member of the Láncara Formation can be divided into four units, represent different faunal assemblages (Fig. 3). This differentiation is based on point counting analyses on thin sections (Wotte *et al*., 2004; Wotte, 2005) and is as followed:

(i) The first unit is characterised by echinoderm-trilobite-brachiopod packstones and echinoderm-trilobite-brachiopod wackestones/floatstones. This unit represents the Beleño facies.

(ii) Trilobite-echinoderm-brachiopod wackestones represent the second unit. The onset of this part is characterised by an abrupt decline in the echinodermal content, and marks further the base of the Barrios facies.

(iii) The third unit is marked by trilobite-brachiopod-echinoderm wackestones/floatstones. These lithotypes developed continuously from the former unit.

(iv) Stromatactis-bearing mudstones are typical for the fourth unit. The accompanied lithotypes are the same as found in unit three in certain sections. A decrease in echinoderms, trilobites and brachiopods is observable, whereas the other faunal elements show no distinct change.

These faunal distribution patterns show a transition from an environment dominated by sessile filter feeders to one dominated by mobile suspension feeders.

The good preservation of the faunal elements of the upper member of the Láncara Formation indicates an autochthonous origin. Some broken remains point to subordinate par-autochthonous to allochthonous conditions.

METHODS

During three field trips 60 sections of the Láncara Formation were investigated. 12 of them were documented and sampled in detail. The here described specimens emanate from the sections of Genestosa, Los Barrios de Luna, Rodiezmo and Porma (Fig. 1b), extracted by dissolution of rock samples in 10% acetic acid. The faunal content and the faunal distribution patterns from these sections are shown in figure 3. For further detailed descriptions see Wotte (2005). The skeletal material was phosphatised during the diagenesis, which preserved parts of the microstructure and allowed the chemical extraction from the carbonate rocks of the Láncara Formation.

Hyoliths could be observed in numerous thin sections, whereas the chemical preparation produced only a few specimens from the Porma section (sample PI 20). Both hyolithimorphs and orthothecimorphs were found. According to Marek (1967) information on both the conch and the operculum is vital for the description. Due to the lack of opercula, as well as the broken conditions of the conchs, systematic determination of the hyoliths from the Cantabrian Mountains will only be to the generic level.

The specimens described in this paper are housed in the collection of the Geological Institute of the Freiberg University of Mining and Technology under the following identification: FG 544/*locality*/***mic****roscopic*/***mol****lusc*/*sample*.

SYSTEMATIC PALAEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class HELCIONELLOIDA Peel, 1991
Order HELCIONELLIDA Geyer, 1994
Family **Helcionellidae** Wenz, 1938

Genus *Protowenella* Runnegar & Jell, 1976

Type species: *Protowenella flemingi* Runnegar & Jell, 1976; middle Middle Cambrian (post-Templetonian), Currant Bush Limestone, L128, western Queensland, Australia. Housed in the Department of Geology, Australian National University, Canberra, Australia; No. ANU 29107.

Protowenella lancaraensis new species

Figs. 4, 5.a–5.c

Diagnosis: Globose, involute, planispiral, endogastic univalve, shows a prominent circumbilical channel on the left and the right side. The aperture is oval with a non-sinuated apertural margin.

Holotype: Phosphatised complete shell figured on figures 4.a–4.c and 5.a1–5.a2; FG 544/BL/mic/mol/p-1.
Type horizon: Barrios facies; Upper member of the Láncara Formation; Middle Cambrian.
Type locality: Los Barrios de Luna section; Cantabrian Mountains.

Etymology: From *Láncara* Formation.

Material:
-One well preserved phosphatised complete shell of an adult specimen.
-One shell of a juvenile stage. As mentioned in figures 4.d–4.g, the specimen was formerly complete and unbroken; however, during the preparation a small part of the aperture was destroyed (Fig. 5.c1–5.c2).
-One shell fragment (Figs. 5.b1–5.b2).
-Three poorly preserved internal moulds (Figs. 5.d–5.f).

Occurrence: Upper member of the Láncara Formation, Barrios facies, Genestosa section, samples Ge 16c, Ge 16d; Los Barrios de Luna section, samples BLp/1, BL p/3; Rodiezmo section, sample Ro 11.

Description: The shell, figured on Fig. 5.a1 and 5.a2, is 660 μm long, 520 μm wide and 400 μm high, and coiled through 1.5 whorls. The top of the protoconch is obtuse angled. The apex is well rounded and the apertural margin non-sinuated (Figs. 4.a, 5.a1–5.a2). The aperture is oval. The anterior side of the aperture shows a distinct concave bulge. On the shell surface fine indistinct growth lines are observable, especially in the apertural field (Figs. 4.a–4.c, 5.a1–5.a2). Both the left and right sides are characterised by prominent circumbilical channels (Fig. 4.a).

A specimen representing an earlier ontogenetic (Figs. 4.d–4.g, 5.c1–5.c2) is characterised by a 400 μm long, 300 μm wide and 200 μm high shell. It expands strongly, and is coiled through 1

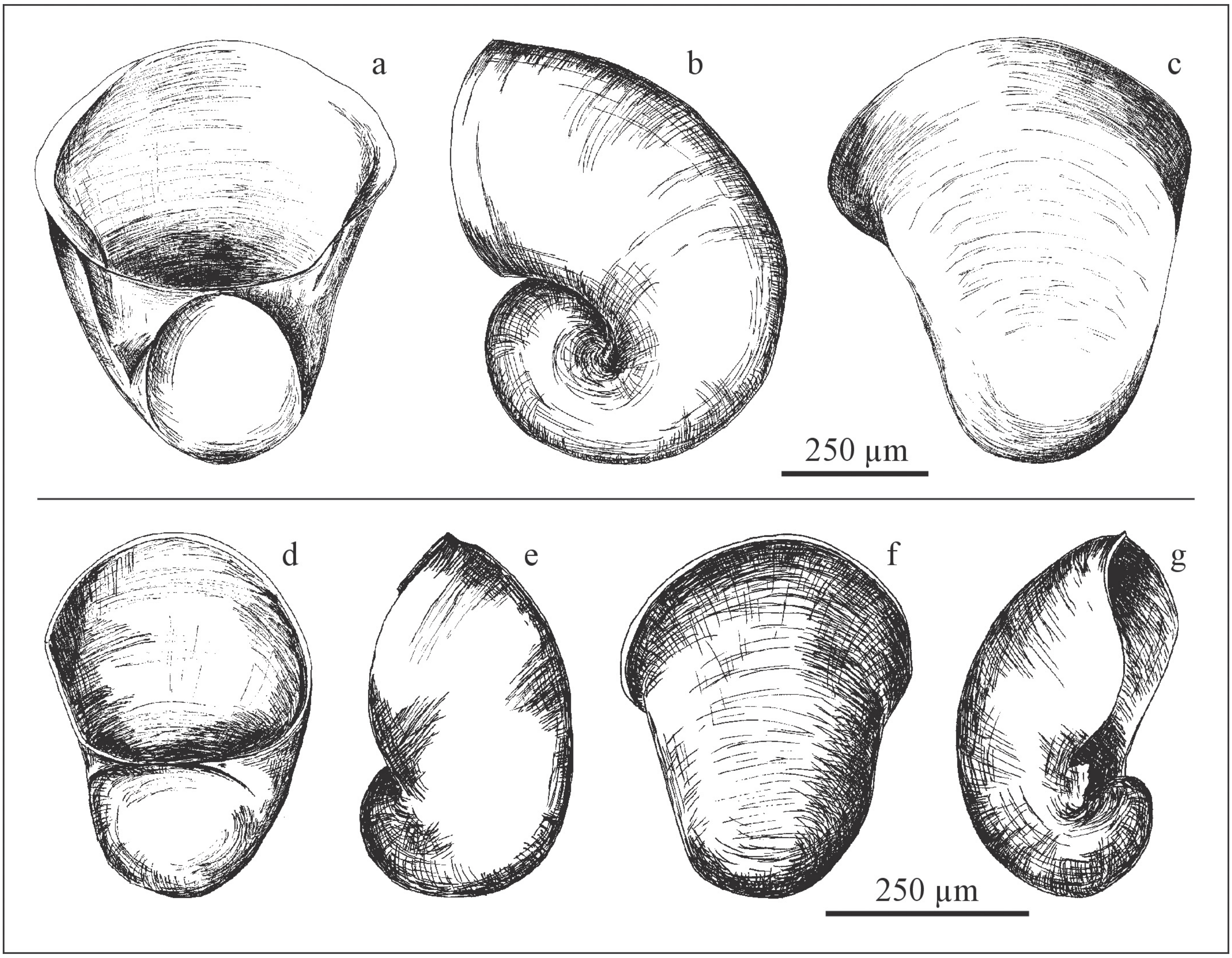


Figure 4. *Protowenella lancaraensis* new species of the upper Láncara Formation, Cantabrian zone, northwest Spain. **a–c**, (FG 544/BL/mic/mol/p-1); **a**, apertural view; **b**, lateral view; **c**, apical view of the adult specimen. **d–g**, (FG 544/Ro/mic/mol/11); **d**, apertural view; **e**, **g**, lateral views; **f**, apical view of the juvenile specimen.

whorl. The surface is ornamented by fine indistinct and closely arranged growth lines especially in the apertural field, similar to the adult specimen (see Figs. 4.d–4.g). The sub-circular aperture which shows a uniform curvature (Figs. 4.d, 5.c1), as well as the concave apertural margin and the resulting concave bulge (Figs. 4.d–4.g) are also similar to those of the adult specimen.

Discussion: In contrast to *Protowenella cobbensis* MacKinnon, 1985, *P. lancaraensis* shows a smaller degree of whorl expansion. The specimens are similar to *P. flemingi* Runnegar & Jell 1976 and *Protowenella* sp. in Runnegar & Jell, 1976. However, in contrast to the oval and upright flattened aperture of these species, the oval-round aperture of *P. lancaraensis* shows a clear lateral compression. As opposed to *P. flemingi* described by Berg-Madsen & Peel (1978) from the Middle Cambrian of Bornholm, *P. lancaraensis* shows circumbilical channels and an oval aperture. Further, the aperture of *P. lancaraensis* is more oval with compression to the left and the right side distinguishing it from *P. plena* Missarzhevsky in Missarzhevsky & Mambetov, 1981, *P. huainanensis* Zhou & Xiao, 1984, and *P. primaria* Zhou & Xiao, 1984. *P. huainanensis* and *P. plena* show an oval aperture without any flattening. The aperture of *P. primaria* is nearly round. The apertural margin of *P. lancaraensis* shows a distinct concave bulge, which is only observable in one specimen of *P. plena* (figured in Missarzhevsky, 1989: pl. 10 fig. 2). Nevertheless, the features mentioned above exclude an affinity of the described specimens to *P. plena*.

Genus *Mackinnonia* Runnegar in Bengtson *et al.*, 1990

Type species: *Mackinnonia davidi* Runnegar in Bengtson *et al.*, 1990; Lower Cambrian (Atdabanian/Botomian), Parara Limestone, UNEL 1761, Horse Gully, Yorke Peninsula, Stansbury Basin, South Australia. Housed in the South Australian Museum, Adelaide, Australia; No. SAMP 29013.

Mackinnonia cf. *rostrata* (Zhou & Xiao, 1984)

Figs. 5.g–5.k

Holotype: Internal mould; Lower Cambrian, Yutaishan Formation, Anhui Province, North China. Housed in the Geological Institute, Anhui Province, China; No. 800059.

Material: Five internal moulds.

Occurrence: Upper member of the Láncara Formation, Barrios facies, Genestosa section, sample Ge 16c; Los Barrios de Luna section, samples BL p/3, BL q/3; Porma section, sample PI 21.

Description: Small, cyrtoconic bilaterally symmetrical univalve molluscs. The ratios between length-width and height of the internal mould vary between 645 μm – 230 μm – 520 μm (Figs. 5.i1–5.i2) and 810 μm – 160 μm – 440 μm (Figs. 5.g1–5.g2). The shells are bilaterally symmetrical, laterally compressed, and expand moderately. The anterior field is convex, flattened towards the aperture (Figs. 5.g–5.j). Lateral fields are slightly convex to flat. The posterior field is irregular to (slightly) concave, and flattens towards the aperture. The apex is strongly hooked posteriorly and displaced up to the apertural margin. The aperture is oval and nearly egg-shaped, slightly wider anteriorly and narrower posteriorly. On some specimens it is strongly compressed (Fig. 5.g2). Generally the aperture is broken. On one specimen (Fig. 5.j) the posterior margin of the aperture curves upwards and forms a sinus. The train is rather high and moderately long. The surface is characterised by indistinct coarse ribs and grooves between them (Fig. 5.i). The profile of the ribs and grooves is rounded rectangular. The ribs are more prominent in the lateral fields, but they are also observable anteriorly. On the posterior field they are smooth. The protoconch is smooth and separated by a small furrow from the teleconch.

Discussion: According to Parkhaev (in Gravestock *et al.*, 2001) *Mackinnonia davidi* Runnegar in Bengtson *et al.*, 1990, and *M. obliqua* Landing & Bartowski, 1996 could be regarded as a junior synonym of *M. rostrata* (Zhou & Xiao, 1984). *Mackinnonia rostrata* differs from *M. plicata* Missarzhevsky, 1989 by the strongly posteriorly hooked apex which extends beyond the apertural margin. *Mackinnonia rostrata* is distinguished from *M. taconia* (Landing & Bartowski, 1996) by a stronger coiled shell, and a strongly posterior hooked apex displaced up to the apertural margin.

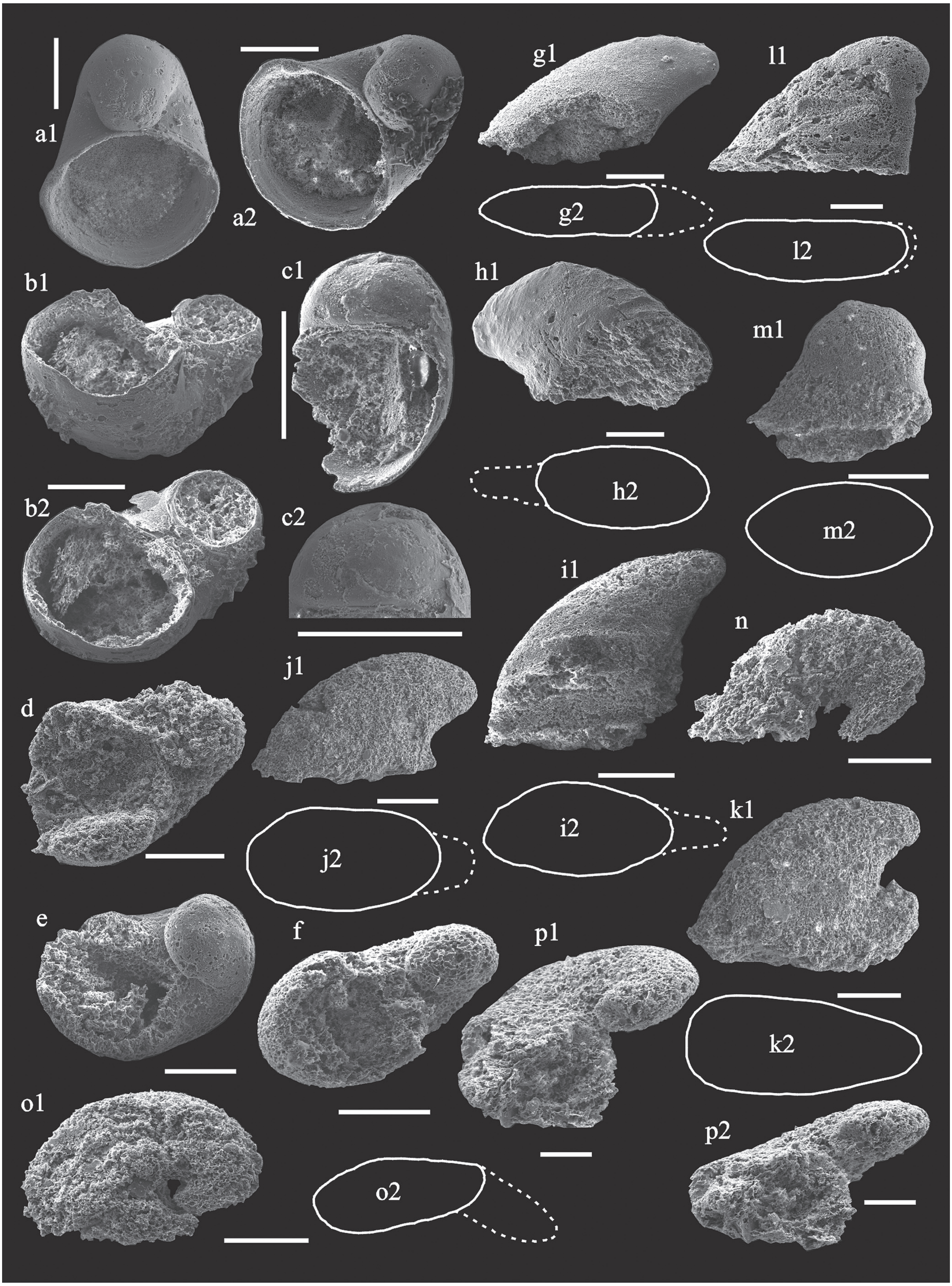
Genus *Pelagiella* Matthew, 1895

Type species: Cyrtolithes atlantoides Matthew, 1894; Lower Cambrian, SE New Brunswick (Canada).

Pelagiella subangulata (Tate, 1892)

Figs. 5.n–5.p

1892 *Ophileta subangulata* Tate: p. 184, pl. 2 figs. 8a–b.
1984 *Pelagiella emeishanensis* He in Xing *et al.*: p. 167, pl. 13 figs. 1–5.
1986 *Pelagiella* sp.: Laurie, p. 447, figs. 10D–E.
1990 *Pelagiella subangulata* (Tate, 1892): Runnegar in Bengtson *et al.*, p. 254, figs. 167, 168A–D, 169A–F, H–L.
1994 *Pelagiella emeishanensis* He in Xing *et al.*, 1984: Elicki, p. 71, fig. 4.8.
1994 *Pelagiella lorenzi* Kobayashi, 1939: Elicki, p. 71, figs. 4.6–4.7.
1996 *Pelagiella emeishanensis* He in Xing *et al.*, 1984: Elicki, p. 155, pl. 7 figs. 6–7.
1996 *Pelagiella lorenzi* Kobayashi, 1939: Elicki, p. 154, pl. 7 figs. 1–5.
1996 ?*Pelagiella* aff. *adunca* He & Pei in He *et al.*, 1984: Elicki, p. 155, pl. 8 figs. 1–4.
1996 ?*Pelagiella* sp.: Elicki, p. 156, pl. 8 figs. 5–8.
2001 *Pelagiella subangulata* (Tate, 1892): Parkhaev in Gravestock *et al.*, p. 193, pl. 44 figs. 1–14, pl. 45 figs. 1–10.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2003 *Pelagiella subangulata* (Tate, 1892): Elicki *et al*., p. 33, pl. 5 figs. 3–4.

2004 *Pelagiella subangulata* (Tate, 1892): Skovsted, p. 30, pl. 8 figs. a–b.

Lectotype: Internal mould; Lower Cambrian, Parara Limestone, Parara near Ardrossan, Yorke Peninsula, South Australia. Defined by Runnegar in Bengtson *et al*., 1990 (p. 254, figs. 167, 168A–D, 169A–F, H–L). Housed in the South Australian Museum, Adelaide, Australia; No. SAMP 1234a.

Material: Three internal moulds.

Occurrence: Upper member of the Láncara Formation, Barrios facies, Genestosa section, samples Ge 14, Ge 16c.

Description: Two of the small, turbospiral internal moulds are dextrally coiled. The ratios between length-width and height are 570 μm – 200 μm – 315 μm (Fig. 5.n) and 600 μm – 200 μm – 400 μm (Fig. 5.o). A third shell is sinistrally coiled (Fig. 5.p). The length of the specimen is 610 μm, the width 250 μm and the height 400 μm. All shells are coiled through 1.5 whorls and expand rapidly. The last whorl is relatively wide. The aperture is nearly oval, elongated abaxially. Near the aperture the cross section is irregular to sub-triangular. The protoconch is often slightly hook-shaped. The spire is either situated at the level of the upper aperture margin, or slightly below. On the surface of the internal moulds no ornamentation is observable.

Discussion: The specimens from the upper member of the Láncara Formation of the Cantabrian Mountains are often similar to *P. madianensis* (Zhou & Xiao, 1984), and also to *P. adunca* (Missarzhevsky in Rozanov & Missarzhevsky, 1966). According to Parkhaev in Gravestock *et al*. (2001) the latter is a junior synonym of *P. madianensis*. Following the last mentioned author, the differences between *P. subangulata* and *P. madianensis* are often only observable in adult forms. It cannot be exclud that both species represent morphologic variations of the same species (Runnegar in Bengtson *et al*., 1990; Parkhaev in Gravestock *et al*., 2001). Nevertheless, due to the low pulled parietal margin of the aperture and the lack of a concave supraperipheral part of the last whorl, the current specimens are incorporated into the species *P. subangulata*, characterised by a high variability in shape (Runnegar in Bengtson *et al*., 1990).

The cases of shell torsion of Cambrian molluscs have been even discussed by Linsley & Kier (1984). These authors included pelagiellids together with various groups of sinistrally coiled Palaeozoic molluscs into the Class Paragastropoda, which represents rather a grade of organisation than a clade (Linsley & Kier, 1984). However, the affiliation of pelagiellieds to gastropods discussed in detail in e.g. Knight (1952), Berg-Madsen & Peel (1978), and Runnegar (1981). Recently, sinistrally coiled molluscs were described by Parkhaev (submitted). He assumed a mutation in the genome locus as reason for the abnormal coiling direction, also mentionable for the here described sinistral coiled specimen of *Pelagiella subangulata* (Tate, 1892).

Class HYOLITHA Marek, 1963
Order HYOLITHIDA Syssoiev, 1957
Family **Nelegerocornidae** Meshkova, 1974

Genus *Microcornus* Mambetov, 1972

Type species: Microcornus parvulus Mambetov, 1972; Lower Cambrian; Kazakhstan.

Microcornus sp.
Figs. 6.a

Material: One internal mould, with parts of phosphatised shell attached.

Occurrence: Upper member of the Láncara Formation, Barrios facies, Porma section, sample PI 20.

Figure 5. Helcionelloid molluscs of the upper member of the Láncara Formation, Cantabrian zone, northwest Spain. All scale bars 200 μm.

a–f, *Protowenella lancaraensis* new species; **a1–a2**, (FG 544/BL/mic/mol/p-1); **a1**, oblique apertural view; **a2**, apertural view. **b1–b2**, (FG 544/Ro/mic/mol/11); **b1**, oblique apertural view showing the oval sections of the broken aperture and protoconch; **b2**, oblique apertural view. **c1–c2**, (FG 544/Ro/mic/mol/11); **c1**, apertural view; **c2**, close-up of the protoconch, the contact area between the apex and the aperture the protoconch is slightly convex. **d**, (FG 544/Ge/mic/mol/16d); oblique apertural view. **e**, (FG 544/BL/mic/mol/p-3); oblique apertural view. **f**, (FG 544/Ge/mic/mol/16c); apertural view.

g–k, *Mackinnonia* cf. *rostrata* (Zhou & Xiao, 1984); **g1–g2**, (FG 544/BL/mic/mol/q-3); **g1**, lateral view; **g2**, sketch of the apertural view. **h1–h2**, (FG 544/BL/mic/mol/p-3); **h1**, lateral view; **h2**, sketch of the apertural view. **i1–i2**, (FG 544/Ge/mic/mol/16c); **i1**, lateral view; **i2**, sketch of the apertural view. **j1–j2**, (FG 544/PI/mic/mol/21); **j1**, lateral view; **j2**, sketch of the apertural view. **k1–k2**, (FG 544/PI/mic/mol/21); **k1**, lateral view; **k2**, sketch of the apertural view.

l–m, **Helcionellidae** gen. et sp. indet.; **l1–l2**, (FG 544/ BL/mic/mol/p-2); **l1**, lateral view; **l2**, sketch of the apertural view. **m1–m2**, (FG 544/PI/mic/mol/20); **m1**, lateral view; **m2**, sketch of the apertural view.

n–p, *Pelagiella subangulata* (Tate, 1892); **n**, (FG 544/Ge/mic/mol/14); lateral view. **o1—o2**, (FG 544/Ge/mic/mol/16c);**o1**, lateral view; **o2**, sketch of the apertural view. **p1–p2**, (FG 544/Ge/mic/mol/16c); **p1**, apertural view; **p2**, oblique apertural view.

Description: The conch is about 685 μm long, and shows an angle of divergence of about 20°. The protoconch is bulbous in outline, about 180 μm long, and separated from the mature conch by a distinct constriction. The cross-section is rounded triangular with rounded lateral sides (Figs. 6.a1–6.a2). The ventral side is slightly convex, whereas the dorsal side is more strongly rounded. On the surface of the internal mould growth lines are only faintly identifiable. The surface of the apertural region is characterised by dark-coloured, nearly radial tubes, 5 μm – 15 μm in diameter which penetrate the outer part of the shell (Figs. 6.a3–6.a4).

Discussion: The slightly concave to nearly flat ventral side, and the sub-triangular cross-section suggests an affiliation to *Microcornus eximius* Duan, 1984. The type species *M. parvulus* Mambetov, 1972 is another possibility. However, the V-shaped ornamentation on the dorsal side, which is characteristic for *M. eximius*, is not clearly observable. The ventral side is less rounded than in *M. petilus* Bengtson in Bengtson *et al*., 1990, and the specimen differ from *M. egregius* Demidenko in Gravestock *et al*., 2001 by the less rounded, but more distinctly triangular cross-section.

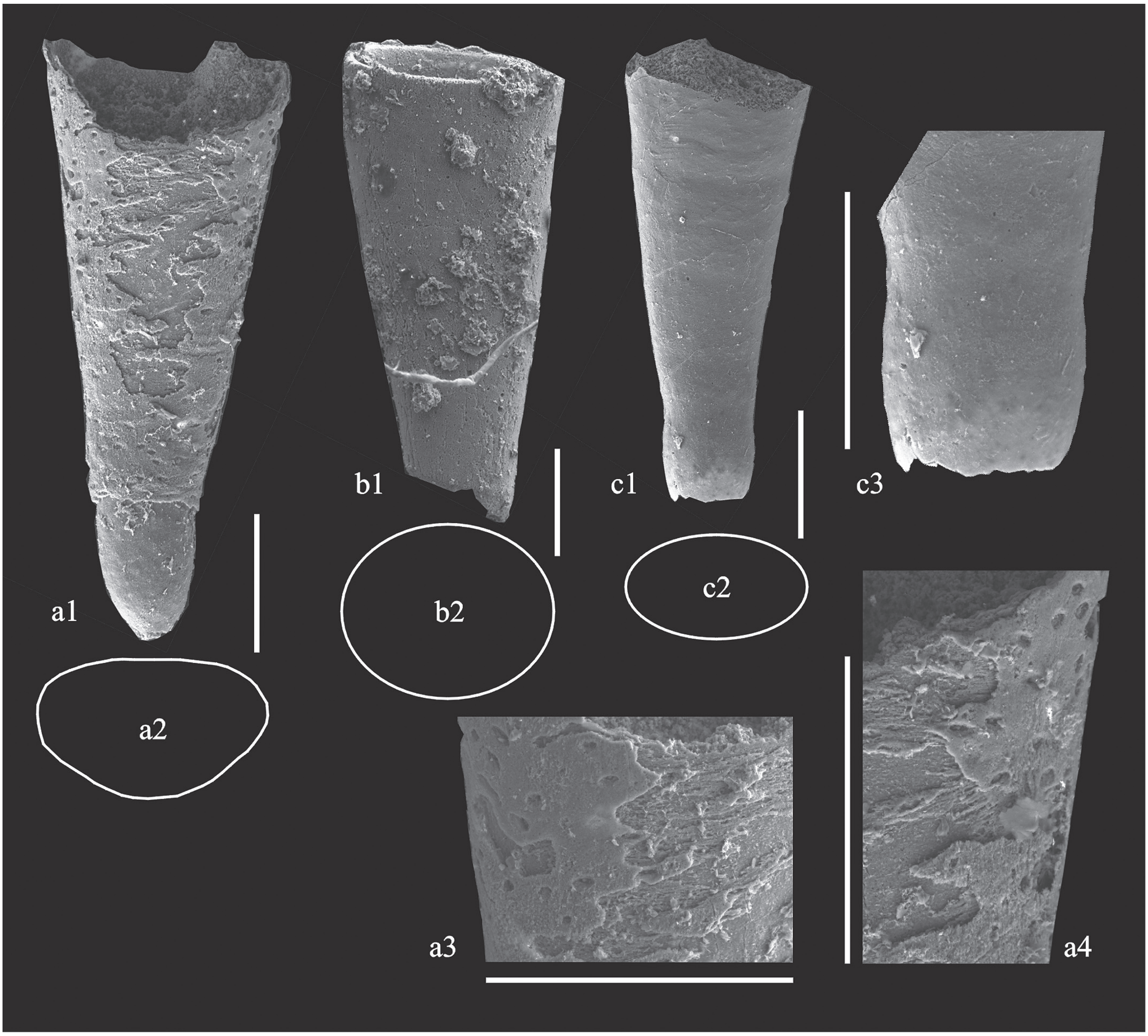

Figure 6. Hyoliths of the upper member of the Láncara Formation, Cantabrian zone, northwest Spain. All scale bars 200 μm. **a1–a4**, *Microcornus* sp. (FG 544/PI/mic/mol/20); **a1**, lateral view; **a2**, sketch of the cross-section of the aperture; **a3**, close up of the lateral view; **a4**, close up of the left side of the apertural region; 3D, close up of the right side. **b–c**, *Conotheca* sp.; **b1–b2** (FG 544/PI/mic/mol/20); **b1**, lateral view; b2, sketch of the cross-section of the aperture. **c1–c3**, (FG 544/PI/mic/mol/20). **c1**, lateral view; **c2**, sketch of the cross-section of the aperture; **c3**, close up of the protoconch.

Surface structures on internal moulds of Cambrian molluscs are not unusual, and were described by Kouchinsky (2000a, b) and Parkhaev (2006). The constant arrangement as well as the nearly equal diameter of the above described radial tubes suggests that they represent a primary structure.

Order ORTHOTHECIDA Marek, 1966
Family **Circothecidae** Missarzhevsky in Rozanov *et al.*, 1969

Genus *Conotheca* Missarzhevsky in Rozanov *et al.*, 1969

Type species: Conotheca mammilata Missarzhevsky in Rozanov *et al.*, 1969; Tommotian stage, Lower Cambrian, Siberian Platform.

Conotheca sp.

Figs. 6.b–6.c

Material: Two internal moulds.

Occurrence: Upper member of the Láncara Formation, Barrios facies, Porma section, sample PI 20.

Description: The specimen figured in figures 6.c1–6.c3 has a length of about 687 μm, and is characterised by an oval cross-section. The protoconch is partly destroyed. Nevertheless, a length of about 150 μm could be assumed. The second specimen (Figs. 6.b1–6.b2) is characterised by the complete absence of the apical part. The fragment is about 830 μm long, and has an oval to round cross-section. In both specimens the angle of divergence is 20°, becoming a little wider toward the aperture. The margin of the aperture is nearly perpendicular to the long axis of the conch. The surface shows vague lineations arranged parallel to the aperture (Figs. 6.c1, 6.c3), and weakly expressed and irregularly spaced transverse bulges.

Discussion: In the absence of the operculum assignment to a species is difficult. An affiliation to *Conotheca australiensis* Bengtson in Bengtson *et al.*, 1990 or to the type species *C. mammilata* Missarzhevsky in Rozanov *et al.*, 1969 seems possible. In contrast to *C. circumflexa* Missarzhevsky in Rozanov *et al.*, 1969 and *C. subcurvata* (Yu, 1974) the current specimens shows no distinct apical curvature. *Conotheca corniformis* Mambetov in Missarzhevsky & Mambetov, 1981 seems also to be more curved than the current material. An affinity to *C. tenuis* Missarzhevsky, 1989 is excluded to the more prominent apical part of this species. Comparison with *C. curta* Missarzhevsky, 1981, *C. dahianensis* Jiang in Luo *et al.*, 1982, and *C. shennongjiaensis* Duan, 1984 is difficult due to the rather poor illustration and preservation of these species. An affiliation to *C. laurentiensis* Landing & Bartowski, 1996 can not be ruled out, but unfortunately, the protoconch is absent in illustrated specimens of *C. laurentiensis*.

CONCLUSIONS

The occurrence of helcionelloid molluscs within the Lower–Middle Cambrian Láncara Formation is very interesting. Whereas species of genus *Protowenella* are typical representatives of the Middle Cambrian, *Mackinnonia* and its species are characteristic for the Lower Cambrian. With the new species *Protowenella lancaraensis* is the first reported occurrence of protowenelloids from the Iberian Peninsula, although Geyer (1986) mentioned *Protowenella ?* sp. from the Middle Cambrian of Morocco. The type species *P. flemingi* from the Currant Bush Limestone of Queensland (Australia) represents middle Middle Cambrian (Runnegar & Jell, 1976), and Berg-Madsen & Peel (1978) documented this species from the Middle Cambrian of Bornholm (Denmark). A Middle Cambrian age is also indicated for *P. cobbensis* from New Zealand (MacKinnon, 1985). In contrast to these Middle Cambrian ages, *Protowenella huainanensis* and *P. primaria* are only known from the middle Lower Cambrian Yutaishan Formation (Anhui province, South China; Zhou & Xiao, 1984), and *P. plena* was only mentioned from the Lower Cambrian of Siberia (Malyj Karatau; Missarzhevsky & Mambetov, 1981).

Until this report species of the genus *Mackinnonia* were completely unknown from the Middle Cambrian. A late Early Cambrian age is indicated for *M. taconica* described from New York State and North-Eastern Greenland (Landing & Bartowski, 1996; Skovsted, 2004). The species *M. rostrata* is known from the Lower Cambrian of South China (Zhou & Xiao, 1984), Australia, New York, North-East Greenland, ?Siberia, and ?Quebec (Skovsted, 2004). Therefore, the evidence of this species from the Láncara Formation of the Cantabrian Mountains represents its first Middle Cambrian occurrence worldwide.

The stratigraphic range of the complex genus *Pelagiella* Matthew, 1895 extends from the Lower Cambrian to the Middle Cambrian. The present documentation of the species *Pelagiella subangulata* marks the first mention of this species from the Middle Cambrian of the Cantabrian Mountains and from the Iberian Peninsula. An upper Lower Cambrian–Middle Cambrian age of this species was proposed by Elicki *et al.* (2003) for the Campo Pisano Formation (Sardinia). In contrast, in East Germany (Elicki, 1994; 1996), South Australia (Runnegar in Bengtson *et al.*, 1990), North-East Greenland (Skovsted, 2004), and in China (He *et al.*, 1984) *P. subangulata* is typical for the Lower Cambrian.

The investigated hyoliths show similar geographic and stratigraphic variations. So, for example, the type species of *Conotheca*, *Conotheca mammilata*, is typical for the Lower Cambrian of the Siberian Platform, China, and the Sierra de Córdoba (Spain), and *C. australiensis* is also a Lower Cambrian form (Demidenko in Gravestock *et al.*, 2001; Malinky & Skovsted, 2004; Fernández-Remolar, 2005). Similar stratigraphic considerations could be stated for genus *Microcornus* as well (Malinky & Skovsted, 2004).

Briefly summarised, the mollusc fauna of the Láncara Formation of the Cantabrian Mountains is of Middle Cambrian age, which is definitely indicated by associated trilobites. The time difference between the Lower Cambrian appearances of most of the investigated forms, and the now dated Middle Cambrian occurrences eventually points to a high longevity of mollusc taxa in the Cambrian.

The absence of Lower Cambrian faunas is simply an artefact of sampling and preparation. Only the limestones of the upper member of the Láncara Formation were sampled in detail, and also the chemical extraction of mainly calcareous microfossils from carbonates is difficult. Nevertheless, the stratigraphical range of the following species documented here, *Mackinnonia rostrata*, *Pelagiella subangulata*, and the genera *Conotheca* and *Microcornus*, must be extended into the Middle Cambrian.

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