Brachiopods from the Lower-Middle Cambrian Láncara Formation of the Cantabrian Mountains, Northwest Spain

THOMAS WOTTE & MICHAL MERGL

THE IBERIAN MASSIF (Fig. 1A) has one of the most complete Palaeozoic sedimentary successions in Europe (Gibbons & Moreno 2002). The approximately 2700 m thick Cambrian succession in the Cantabrian Zone consists of three formations (Fig. 2). The lowermost formation, the Herrería Formation, is characterised by claystones, sandstones and conglomerates, representing a ?Neoproterozoic-Early Cambrian age. Within this siliciclastic succession, calcareous intercalations are sometimes observed. The fossil content of the Herrería Formation consists of ichnofossils (e.g., van der Meer Mohr & Okulitch 2004), Micromitra cf. sculptilis (Meek, 1873), Nisusia vaticina (de Verneuil & Barrande in de Prado, 1860), Trematobolus simplex (Vogel, 1962) and Yorkia zafrensis (Gil-Cid & Mélou, 1986). Stratigraphic distribution patterns of the brachiopod fauna mirror the drowning of the environment. Trematobolus simplex is exclusively found in the carbonates of the Beleño facies, whereas Nisusia vaticina and Yorkia zafrensis are typical representatives of the nodular limestones of the Barrios facies. The species of the genera Trematobolus, Nisusia and Yorkia demonstrate the affinity of the upper Láncara brachiopod association with faunas of the Siberian platform, New South Wales and some Avalonian terranes (Newfoundland, New Brunswick).

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Micro- and macrobrachiopods from eight stratigraphic sections of the carbonate upper member of the Middle Cambrian Láncara Formation (comprising lower Beleño facies and upper Barrios facies) in the Cantabrian Mountains are analysed. They comprise ten species, two of which are new, assigned to nine genera, two of which are new. They are: Acrothele primaeva (de Verneuil & Barrande in de Prado, 1860), Acrothele sp., Eoobolidae gen. et sp. indet., Genetreta trilix gen. et sp. nov., Iberotreta sampelayoi gen. et sp. nov., Lhuotreta? proclinis (Mergl & Elicki, 2004), Micromitra cf. sculptilis (Meek, 1873), Nisusia vaticina (de Verneuil & Barrande in de Prado, 1860), Trematobolus simplex (Vogel, 1962) and Yorkia zafrensis (Gil-Cid & Mélou, 1986). Stratigraphic distribution patterns of the brachiopod fauna mirror the drowning of the environment. Trematobolus simplex is exclusively found in the carbonates of the Beleño facies, whereas Nisusia vaticina and Yorkia zafrensis are typical representatives of the nodular limestones of the Barrios facies. The species of the genera Trematobolus, Nisusia and Yorkia demonstrate the affinity of the upper Láncara brachiopod association with faunas of the Siberian platform, New South Wales and some Avalonian terranes (Newfoundland, New Brunswick).
(Sdzuy 1969; Clausen & Álvaro 2006), and phosphatic small shelly fossils (van den Boogaard 1983). The faunal and lithological transition from the Beleño into the Barrios facies is gradual, characterised by a continuous change in the fossil content, and a successive increase in the siliciclastic material (Wotte et al. 2004; Wotte 2005). The environment of the Lán cara Formation is interpreted as a transition from a carbonate ramp to a mixed carbonate-siliciclastic ramp (Wotte et al. 2004; Wotte 2005), with supralittoral-littoral conditions in its western part.
and shallow sublittoral environments in its eastern region (Zamarreño 1972; Aramburu et al. 1992). The overlying Middle Cambrian-Ordovician Oville Formation consists of claystones and sandstones (Fig. 2). Sometimes quartzose beds are observable in the uppermost part (Truyols et al. 1990). No carbonate intercalations are present in this part of the succession. The fossil content of the Oville Formation is also relatively diverse: trace fossils were described by Gámez Vintaned et al. (2000); trilobites by Sdzuy (1961, 1968) and Gozalo et al. (2000); echinoderms by Schroeder (1973), Friedrich (1993) and Sdzuy (1993); and graptolites by Sdzuy (1974). Middle Cambrian-Tremadocian acritarchs were recorded by Fombella (1978, 1979). Aramburu et al. (1992) and Aramburu & García-Ramos (1993) interpreted the siliciclastic succession of the Oville Formation as shallow platform deposits of an intertidal and braid plain deltaic environment.

### BIOFACIES

The upper member of the Láncara Formation contains a highly diverse fauna of trilobites, echinoderms, brachiopods, chancelloriid and sponge remains, but also molluscs and phosphatic small shelly fossils. Based on point counting analyses of thin sections, the vertical faunal distribution through the upper member of the Láncara Formation could be divided into four distinct faunal assemblages (Wotte et al. 2004; Wotte 2005; Fig. 3). For sections which were only documented but not intensively sampled, the vertical faunal succession was estimated on the basis of field data, and in comparison with the point-counted sections. The faunal assemblages of these sections are illustrated in Figure 3 as ‘assumed’. In almost all sections, the upper member of the Láncara Formation (except Genestosa, cf. Fig. 3) starts with an abrupt onset and a predominance of echinoderms, whereas trilobites and brachiopods are clearly less common. This biofacies is called faunal assemblage 1, and is equal with the Beleño facies of Zamarreño (1972). The base of faunal assemblage 2 is marked by a minimum of echinodermal remains, and characterises the base of the Barrios facies. The faunal content is either dominated by trilobites and brachiopods, or it shows nearly equal volumetric ratios of echinoderms, trilobites and brachiopods. Faunal assemblage 3 develops as part of a conformable continuum and is characterised by a further increase in the abundance of trilobites and brachiopods as well as a resurgence of echinoderm numbers. Faunal assemblages 1-3 also include chancelloriids, sponges, molluscs, and phosphatic small shelly fossils as minor faunal elements. In the Los Barrios de Luna section, this general faunal trend is characterised by a short and rapid decrease in echinoderms, trilobites and brachiopods, whereas further faunal elements (e.g., chancelloriids, poriferids, molluscs) show no distinct change. This specific portion, characterised by Stromatactis-rich limestones, represents faunal assemblage 4 (Fig. 3).

### PREVIOUS WORK AND SAMPLE CHARACTERISTICS

The initial observations on brachiopods from the studied area were presented by de Verneuil...
& Barrande (in de Prado 1860), who discussed and illustrated five brachiopod species. The type material was not available to Walcott (1908, 1912) and has probably been lost; a recent search for the repository was not successful. Walcott (1912) revised all species described by de Verneuil & Barrande (in de Prado 1860). Finally, Sampelayo (1935) figured and commented on

Fig. 3. Distribution of the faunal assemblages within the studied sections. For sections not point-counted, acceptance of the faunal assemblages and definition of their boundaries are problematic (see text), and thus illustrated as ‘assumed’. Genestosa is the only locality where the faunal succession starts with faunal assemblage 2. Faunal assemblage 4 was only recorded at the Los Barrios de Luna section. For abbreviations of the sections see caption to Figure 1.
some brachiopods from the area, but without any accurate stratigraphic or geographic data.

All the material described here comes from eight stratigraphic sections measured through the Somiedo-Correcilla unit and the La Sobia-Bodon unit, western Cantabrian Zone (Fig. 1B). From west to east, these sections include: Genestosa (Ge), Truebano (Tr), Rabanal (Ra), Láncara de Luna (LL), Los Barrios de Luna (BL), Piedras Bermejas (Pe), Rodiezmo (Ro), Vegaservera (Ve), and Porma (PI) (Fig. 1B). The exact location of each section (based on U.T.M. projection on the International Ellipsoid) is shown in Table 1. All microscopic specimens were extracted from carbonates using 10% formic or acetic acid without any buffering. Samples were decanted and acid renewed daily. Macrobrachiopods were found mostly on bedding planes during intensive sampling in the field. In *Yorkia*, calcareous shells have been removed by hydrochloric acid to obtain internal moulds.

Because of deformation and fragmentary preservation of most specimens, no measurements were evaluated statistically. Only general sizes are noted in the descriptions.

All specimens are housed in the collection of the Geological Institute, Freiberg University of Mining and Technology under the prefix: FG 544/locality/microscopic or macroscopic/brachiopod/sample.

### SYSTEMATIC PALAEONTOLOGY

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<td>Porma</td>
<td>42° 55’13. 3’’ N</td>
<td>005° 18’13. 2’’ W</td>
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Table 1. Latitude, longitude and altitude of the various sections discussed in the text.

Some brachiopods from the area, but without any accurate stratigraphic or geographic data.

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### SYSTEMATIC PALAEONTOLOGY

**Class LINGULATA** Gorjansky & Popov, 1985  
**Order LINGULIDA** Waagen, 1885  
**Superfamily LINGULOIDEA** Menke, 1828  
**Family EOOBOLIDAE** Holmer, Popov & Wrona, 1996

**Eoobolidae gen. et. sp. indet.** (Fig. 4A-C)

**Material.** One shell fragment from Los Barrios de Luna section, sample BL m, Barrios facies, upper member of the Láncara Formation.

**Remarks.** The incomplete, 1.7 mm long (estimated) dorsal valve is strongly convex, thin-shelled and has an ornament of irregular, wavy, concentric lines and broad pustules. Some of these pustules have spinose edges (Fig. 4C), indicating affinity to the family Eoobolidae.

**Superfamily ACROTHELOIDEA** Walcott & Schuchert in Walcott, 1908  
**Family ACROTHELIDAE** Walcott & Schuchert in Walcott, 1908  
**Subfamily ACROTHELINAE** Walcott & Schuchert in Walcott, 1908

**Acrothele** Linnarsson, 1876  
*Type species.* *Acrothele coriacea* Linnarsson, 1876, Middle Cambrian (*Paradoxides forchhammeri* Biozone), Sweden.

**Acrothele primaeva** (de Verneuil & Barrande in *de Prado*, 1860) (Fig. 4D-J)  
1860 *Discina* (*Oribcula*) *primaeva* s. n.; de Verneuil & Barrande in *de Prado*, p. 532, pl. 8, figs 2-2a.

1912 *Acrothele primaeva* (de Verneuil & Barrande); Walcott, p. 654, pl. 57, fig. 6.

**Neotype.** FG 544/Ge/mic/brach/18 A, almost complete ventral valve (Fig. 4 F). *Discina (Oribcula)* *primaeva* was described by de Verneuil & Barrande (in de Prado 1860). However, Walcott (1912) did not know the whereabouts of the type specimen, which has probably been lost. The specimen selected here as the neotype was collected from the upper member of the Láncara Formation at the Genestosa section in relative proximity of the type area, and corresponds well
to the original illustration and description by de Verneuil & Barrande (in de Prado 1860). The brachiopod fauna associated with the neotype is essentially the same as that associated with the type specimen of de Verneuil & Barrande (in de Prado 1860); this suggests that the lost type specimen and the neotype have the same age and come from the same biofacies.

**Type horizon and locality.** Barrios facies, upper member of the Lánca Formation, Middle Cambrian; Genestosa section, Cantabrian Mountains, Spain.

**Material.** Twenty apical parts of valves with preserved larval shell, numerous small fragments, Genestosa section, samples Ge 10 D, Ge 10 H, Ge 11, Ge 13, Ge 15, Ge 16 D, Ge 17 C, Ge 17 G, Ge 18 A, Ge 18 B, Ge 18 C, Ge 18 E, Ge 18 F, Ge 18 K, Ge 20, Ge 21, and Porma section, samples PI 21, PI 27, Barrios facies, upper member of the Lánca Formation.

**Diagnosis.** *Acrothele* with mound-like elevations on tubercles of larval shell, with few wavy, somewhat irregular concentric ridges in an early post-larval shell and remaining post-larval shell without distinct concentric ornament; a ventral pseudointerarea arched along the axis.

**Description.** Shell subcircular, plano-convex, thick-walled. Dorsal valve with marginal apex that is weakly curved below commissural plane. Dorsal larval shell well defined, subcircular, about 500 µm in diameter, with a diverging pair of large and weak, low tubercles. Both posterior
and anterior portions of each tubercle mound-like, slightly raised but not extended into spines. Border of larval shell distinctly defined, lower than adjacent surface of postlarval shell, with swollen edge. Surface of larval shell with shallow, circular, larval pits 4-5 µm across. Early postlarval ornament of few wavy, somewhat irregular concentric ridges that are more clearly defined posterolaterally than anteriorly. Concentric ridges essentially absent anteriorly and anterolaterally. Surface between concentric ridges and postlarval ornament consists of irregular network of low wavy ridges, with small knob-like pustules at their junctions. Dorsal valve interior with low median ridge.

Ventral valve low, asymmetrically conical, subcircular in outline with less rounded posterior margin. Apex situated in one-third to one-fourth shell length (estimated from growth lines). Ventral pseudointerarea narrowly triangular, less than 30% of shell width, low procline. Its surface lacks pustulose ornament, bearing only low concentric growth lines of uneven size. Pseudointerarea weakly arched along the axis. Ventral larval shell is subcircular, weakly elevated above adjacent postlarval shell. Border of larval shell depressed. Paired tubercles of larval shell anteriorly converging. Each tubercle consists of a larger, mound-shaped anterior elevation and half-sized lower posterior elevation. Pedicle foramen elongate oval, with its larger part confined to larval shell, only its posterior third is in contact with post-larval shell. Foramen externally bordered by a collar-like, elevated surface of median tubercle of larval shell. Internal pedicle opening broadly elongate, lacking swollen periphery. Interior of ventral valve without median ridge.

Remarks. The type species *Acrothele coriacea* Linnarsson is fairly well known (Rowell 1980; Holmer & Popov 2000). Many authors (Rowell 1980; Henderson & MacKinnon 1981; Holmer et al. 2001; González-Gómez 2005) have left acrothelid material under open nomenclature. Data from the last decade indicate a broad variety of larval shell morphology, with tubercles extended into long spines (Henderson & MacKinnon 1981; Holmer & Popov 2000), short acute spines (Rowell 1980; Holmer et al. 2001) to obtuse, mound-like tubercles as in *A. primaeva* (Holmer et al. 2001). The genus comprises numerous closely related species having unique larval shell morphology, but having a very uniform ornament in the postlarval shell. *Acrothele primaeva* differs from *A. coriacea* in its mound-like elevations of larval shell tubercles, subcircular larval shell and arched axial part of the ventral pseudointerarea, which is flattened (Holmer & Popov 2000, pl. 45, fig. 1i). The tubercles of *A. coriacea* are extended into two pairs of distinct spines in dorsal shells and into one pair in ventral larval shells (Holmer & Popov 2000) and its larval shell outline is transversely ovoid. Concentric ornament is less distinct in *A. primaeva* than in *A. coriacea*. The larval shell spines are also absent in other early Middle Cambrian species (e.g., *Acrothele* sp. of Holmer et al. 2001, pl. 12, figs 14-16). The early Middle Cambrian *A. primaeva* stratigraphically precedes *A. coriacea* and considering shell similarity, it might be ancestral to the latter species.

De Verneuil & Barrande (in de Prado 1860) erected *Discina (Orbicula) primaeva* on a single ventral valve from Middle Cambrian red limestone from Adrados (north-eastern of Boñar, León Province, Cantabrian Mountains). The sampling areas for our specimens are located about 5 km north (Porma section), and about 60 km north-west (Genestosa section) of the type locality described in de Prado (1860) (Fig. 1B). Red limestone with *Paradoxides pradoanus* (de Prado 1860, p. 522) is a probable equivalent of the upper member of the Láncara Formation. Without access to the original material, Linnarsson (1876) and Walcott (1912) referred the species to *Acrothele*.

De Verneuil & Barrande (in Prado 1860) described *Discina (Orbicula) primaeva*, with emphasis on its circular outline and the presence of three radial plications (“strīes filīformes” in original spelling) on its exterior. Our mostly incomplete specimens with preserved juvenile parts of the shell lack distinct radial fila or plications. The only incomplete dorsal valve (Fig. 4D-E) has weakly developed plications, indicating at least a pair of plications on the dorsal valve. The development of radial fila is a highly variable feature of the genus (e.g., Mergl & Šlehoferová 1990; Liñán & Mergl 2001) and should not be used in discriminating particular species of *Acrothele*. Liñán & Mergl (2001) reported *Acrothele cf. bohemica* (Barrande, 1879) from the Middle Cambrian of the Iberian Chains, but this species differs from *A. primaeva* by its more posteriorly situated ventral apex. Details of the larval shell of *Acrothele cf. bohemica* (Barrande, 1879) are unknown due to different and less favourable preservation.

*Acrothele* sp. (Fig. 4K-L)

Material. Two small fragments of ventral valves, Genestosa section, sample Ge 17 D, Barrios facies, upper member of the Láncara Formation.

Remarks. The fragments have a thick-walled shell
and steeply procline ventral pseudointerarea. A large pedicle foramen continues internally with a robust pedicle tube. General morphology of the valve is consistent with Acrothele granulata (Linnarsson, 1876). Fragments differ from A. primaeva in having a seemingly steeper ventral pseudointerarea and a thicker shell with robust pedicle tube. Specimens are left under open nomenclature due to the limited material.

Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893

**Luhotreta** Mergl & Šlehoferová, 1990

*Type species.* *Luhotreta pompeckji* Mergl & Šlehoferová, 1990, Jince Formation, Middle Cambrian, Bohemia.


*Remarks.* The generic diagnosis is based on the macroscopic features. All specimens of the genus are gathered from crack-out material. Hence, fine morphological characters (e.g., nature of the pedicle opening) were not observable, and are still unknown. This led some subsequent authors (e.g., Holmer et al. 2001) to compare *Luhotreta* with the earlier described genus *Vandalotreta* Mergl, 1988. However, other features in the original diagnosis of *Luhotreta* (presence of intertrough, strong median buttress, absence of median ridge, and coarse, lamelllose external ornament) indicate close affinity of *Luhotreta pompeckji* to *Vandalotreta proclinis*. The nature of the larval shell is known in *Vandalotreta proclinis*. Because there are significant differences in its position compared with those in the genus *Vandalotreta*, it is highly probable that *Luhotreta* is a valid genus. This should be confirmed by a new revision of *Luhotreta*. In summary, *Vandalotreta proclinis* is tentatively assigned to *Luhotreta*, although the nature of the shell opening remains unknown in the latter genus.


2004 *Vandalotreta proclinis* n. sp.; Mergl & Elicki, p. 588, pl. 2, figs 1-9.

*Material.* Hundreds of valves and many fragments, Genestosa section, samples Ge 10 B, Ge 16 C, Ge 16 D, Ge 16 F, Ge 17 C, Ge 17 D, Ge 18 A, Ge 18 C, Ge 18 F, Ge 18 G, Ge 18 H, Ge 18 I, Ge 18 J, Ge 18 K, Ge 20, Ge 21, Ge 23, Barrios facies, upper member of the Lán cara Formation.

*Description.* See Mergl & Elicki (2004, p. 588). Favourable preservation of the Spanish material reveals previously unknown morphological features. Larval shell is densely and evenly covered by deep, 1.0-1.5 µm sized pits (Fig. 6 K). Pedicle foramen enclosed within larval shell, perforating the top of a short, posteroventrally directed, broadly conical tubercle of the larval shell. Shallow transverse depression separates tubercle with foramen from anterior transverse tubercle of ventral larval shell. Dorsal larval shell...
has one subcentral tubercle encircled by depressed periphery. Border of larval shell is weakly defined by disappearance of larval pitting, and by the first fine concentric fila of postlarval ornament. Concentric fila are interrupted by prominent concentric lamellae. Lamellae are very coarse, of uniform size, highly raised above shell surface. Lamellae are more densely spaced in later growth stages, somewhat overlapping one another. Large shells have typically ten to eleven lamellae in each valve, but the number of lamellae fluctuates.

Remarks. These specimens are identical to those from the Middle Cambrian Campo Pisano.
Formation of Sardinia (Mergl & Elicki 2004) in shell size, outline, convexity and details of internal morphology. The straight to weakly concave anterior slope of ventral valve (Fig. 5A-B) distinguishes this species from other acrotretids in our samples from the Cantabrian Mountains. Tectonic deformation of some shells prevents evaluation of shell outline and convexity variability.

Procline ventral pseudointerarea and coarse growth lamellae suggest placing *L. proclinis* in *Anabolotreta* Rowell & Henderson, 1978, with *A. lepida* Koneva, 1986 from the Middle Cambrian of Central Asia. *Anabolotreta* differs by having the apical pedicle foramen not enclosed within larval shell, and despite their variation in *Luhotreta*, growth lamellae of *Anabolotreta* are more variable in their strength and shape. The type species, *Anabolotreta tegula* Rowell & Henderson, 1978, has a much lower ventral valve than in *L. proclinis*.

Circular cylindrical borings (some aborted) are commonly present on shells in our collection. Some have one (Fig. 6H) to as many as five (Fig. 6N) borings in the same valve. Boreholes are observable in ventral and dorsal valves and they have a uniform size. Some boreholes are located at hidden places below growth lamellae (Fig. 6 B-C) indicating a flexibility of boring apparatus of an unknown predator. Similarly shaped borings were described in Cambrian acrotretids by Conway Morris & Bengtson (1994) and Streng (1999), but our sample is too small for statistical evaluation of the bored specimens.

**Iberotreta** gen. nov.

*Type species*. *Iberotreta sampelayoi* gen. et sp. nov., upper member of the Láncara Formation, Middle Cambrian, Spain.

**Etymology.** After the Iberian Peninsula.

**Diagnosis.** Acrotretid genus with small, thin-shelled, ventribiconvex shell with weakly and broadly unisulcate commissure. Shell covered by closely arranged, fine, regular, concentric filae without distinct growth lamellae. Dorsal median septum low and short, separated from median buttress. Larval shell shows two different sized pits: large circular flat-bottomed pits, and smaller circular hemispherical pits. Ventral valve highly conical. Ventral pseudointerarea poorly defined laterally, steeply procline, depressed, narrowly triangular with distinct intertrough. Pedicle foramen enclosed within larval shell. Apical process boss-like, prominent, transverse, with convex surface; apical pits lateral to foramen, deep. Proximal ventral vascula lateralia arcuate, deeply impressed. Postlarval ornament of uniform, distinct concentric fila.

**Discussion.** *Iberotreta* gen. nov. differs from numerous acrotretid genera by the combination of a highly conical ventral valve, a weak dorsal median ridge, and a pedicle foramen enclosed within the larval shell; the last feature distinguishes the new genus from otherwise similar genera such as *Anelotreta*, *Dicondylotreta*, *Hadrotreta*, *Lin narzsonia*, *Prototreta* and *Vandalotreta*. In contrast to the morphologically similar genus *Tingitanella*, the new genus possesses a procline ventral pseudointerarea and a raised anterior part of the dorsal median ridge forming a low septum. *Iberotreta* can be distinguished from *Neotreta* by its short conical pedicle tube. Unlike the uniform pitting of *Araktina* and *Vandalotreta*, the new genus has larval pits of two different sizes.

**Iberotreta sampelayoi** sp. nov. (Figs 5C-D, 7A-R)

*Holotype*. FG 544/Ge/mic/brach/18 F (1), dorsal valve (Fig. 7A-C).

*Paratype*. FG 544/Ge/mic/brach/18 F (5), ventral valve (Fig. 7J-M).

**Type horizon and locality.** Barrios facies, upper member of the Láncara Formation, Middle Cambrian; Genestosa section, Cantabrian Mountains, Spain.

**Etymology.** After the Spanish geologist P.H. Sampelayo, the author of the first review of the Cambrian brachiopods from the Cantabrian Mountains.

**Material.** Fifty valves and many fragments, Los Barrios de Luna section, samples BL a, BL n; Genestosa section, samples Ge 7, Ge 8, Ge 9, Ge 10 B, Ge 10 C, Ge 10 D, Ge 10 E, Ge 10 F, Ge 10 I, Ge 16 E, Ge 17 D, Ge 18 B, Ge 18 D, Ge 18 E, Ge 18 F, Ge 18 K, Ge 20, Ge 21; Porma section, sample PI 27; Rodiezmo section, sample Ro 13; Vegaservera section, samples Ve 2, Ve 4, Barrios facies, upper member of the Láncara Formation.

**Diagnosis.** As for genus.

**Description.** Shell small and thin, ventribiconvex, about 1.1 mm wide in adults, with convex dorsal valve, bluntly conical ventral valve and feebly unisulcate anterior commissure. Dorsal valve subcircular, 90% as long as wide,
widest at midlength, with less rounded posterior and anterior margins than lateral margins. Valve moderately convex in transverse profile with weakly depressed median sector. Convexity prominent near dorsal apex, but decreasing anteriorly. Dorsal larval shell transversely oval, 180 µm wide, with central raised tubercle, clearly bordered by swollen margin; larval shell covered by larger circular pits and smaller, less regular pits in between (Fig. 7Q). Circular pits shallow, flat-bottomed, with diameter from 2-8 µm. Size of circular pits decreases towards the periphery of the larval shell. Dorsal pseudointerarea orthocline, with a broadly triangular, weakly concave median groove, slightly overhanging posterior margin. Sides of median groove subtend

Fig. 7. Iberotrema sampelayoi gen. et sp. nov. A–C, holotype FG 544/Ge/mic/brach/18 F (1); A, dorsal valve; B, oblique view showing ornament; C, posterolateral view to larval shell. D–E, FG 544/Ge/mic/brach/18 F (2); D, dorsal valve in posterolateral view; E, detail of larval shell. F, FG 544/Ge/mic/brach/18 F (3); incomplete dorsal valve interior. G–I, FG 544/Ge/mic/brach/18 F (4); G, dorsal valve interior; H, dorsal valve in oblique view; I, dorsal larval shell in lateral view. J–M, FG 544/Ge/mic/brach/18 F (5); J, ventral valve in apical view; K, ventral valve in posterior view; L, ventral valve in posterolateral view; M, detail of larval shell. N–Q, FG 544/Ge/mic/brach/18 F (6); N, ventral valve in lateral view; O, ventral valve in anterior view; P, ventral larval shell; Q, detail of larval shell. R, FG 544/Ge/mic/brach/18 F (7); ventral valve larval shell in lateral view.
an angle of 80-100°. Anterior edge of median groove straight. Propareas small. Dorsal median ridge with prominent median buttress, almost disappearing at posterior third, but continues as short, triangular septum anteriorly. Thickened concentric brim along the periphery of the valve weakly defined. Cardinal muscle scars large, elongate-oval, almost parallel, located at midway between median ridge and lateral margin. Pallial markings obscure.

Ventral valve is highly conical, with apex in posterior quarter (Fig. 5C-D). Valve about 50% as high as long with a high, narrowly triangular pseudointerarea. Steeply procline interarea occupies about 30% of valve width, with weakly defined sides and depressed surface. Pseudointerarea medially divided by distinct, narrow and deep intertrough. Anterior slope of valve weakly convex, especially in early growth stages. Lateral slopes almost straight. Pedicle foramen enclosed within larval shell. Foramen circular, 25 µm in diameter, piercing top of short, posteroventrally directed, broadly conical tubercle. Low, transverse tubercle located in anterior half of larval shell. Apical chamber of ventral valve filled by low, transverse apical process with a weak anterior slope. Internal pedicle foramen circular at the ventral termination of internal convex surface of intertrough, laterally bordered by very deep apical pits. Cardinal scars large, obliquely oval, with weakly convex surfaces, situated at the posterolateral part of inner surface of pseudointerarea. Vascula lateralia with curved deeply impressed proximal parts, but obscure distal parts.

Postlarval ornament of fine, distinct, rounded concentric fila of uniform size arranged with regular spacing (Fig. 5C-D). Some fila are wavy with numerous, short, drape-like folds. Growth lamellae absent externally but distinct concentric bands of a different coloured material in otherwise transparent shells indicate cessation of the growth.

Remarks. The new species is externally similar to *Vandalotreta vafra* Mergl, 1988, but differs in having a pedicle foramen that is enclosed within the larval shell and a posteroventrally directed short pedicle tube. In *V. vafra* and other species referred to *Vandalotreta* (Holmer *et al.* 1996; Streng 1999), the foramen cuts the posterodorsal border of the ventral larval shell and is directed posteriorly. The exterior of the dorsal valve is almost indistinguishable from that of *Vandalotreta* except for a more transverse shell outline and a depressed median sector that forms a weakly unisulcate anterior commissure, while in *V. vafra* the commisure is rectimarginate. A raised anterior part of the median ridge is unknown in *Vandalotreta*.

### Genetreta gen. nov.

**Type species.** *Genetreta trilix* gen. et sp. nov., upper member of the Láncara Formation, Middle Cambrian, Spain.

**Etymology.** After the type locality Genestosa.

**Diagnosis.** Acrotretid with small, moderate to thick-shelled, ventribiconvex shell with weakly and broadly unisulcate commissure; shell covered by less regular low concentric fila and weak growth lamellae. Median buttress present. Dorsal valve with very low, long median ridge branching into two oblique low ridges near valve centre and with gently swollen anterior termination. Larval shell covered with circular pits of uniform size. Ventral valve conical with procline pseudointerarea divided by weak intertrough. Pedicle foramen enclosed within larval shell. Apical process prominent, subcircular. Apical pits deep, posterolateral to internal pedicle opening. Ventral vascula lateralia arcuate, weakly impressed.

Remarks. The new genus differs from most acrotretids in having a low, stout and distinct dorsal median ridge. The dorsal median ridge trifurcates in the middle of the valve and the median buttress has a prominent bifurcation. This feature, together with a rather high conical ventral valve, a pedicle foramen enclosed within the larval shell, a prominent pair of tubercles on the dorsal larval shell, and uniform fine pitting of the larval shell characterises the new genus. *Kostjubella* is similar in most characters, but *Genetreta* has a foramen enclosed within the larval shell and possesses a low dorsal median ridge.

### Genetreta trilix gen. et sp. nov. (Figs 5E-F, 8A-M)

**Holotype.** FG 544/Ge/mic/brach/18 G (1), dorsal valve figured (Fig. 8A-B).

**Paratype.** FG 544/Ge/mic/brach/10 F (1), ventral valve figured (Fig. 8C-E).

**Type horizon and locality.** Barrios facies, upper member of the Láncara Formation, Middle Cambrian; Genestosa, Cantabrian Mountains, Spain.

**Etymology.** After Latin *trilix*, -icis, referring to the triradiate appearance of the dorsal median
ridge.

**Material.** Thirty valves and many fragments, Genestosa section, samples Ge 10 I, Ge10 F, Ge 18 F, Ge18 G, Barrios facies, upper member of the Láncara Formation, Middle Cambrian.

**Diagnosis.** As for genus.

**Description.** Shell small, ventribiconvex, about 1.1 mm wide in adult specimens with convex dorsal valve and bluntly conical ventral valve, rather thick shelled, with weakly unisulcate anterior commissure. Dorsal valve subcircular, 85% as long as wide, widest at midlength, with less rounded posterior and anterior margins than lateral ones. Valve moderately convex transversely, with slightly depressed median sector. Convexity prominent near posterior margin and evenly decreasing anteriorly. Dorsal larval shell distinct, with a pair of high, elongate tubercles. Larval shell transversely oval, 220 µm

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**Fig. 8. Genetreta trilix gen. et sp. nov. A–B, holotype FG 544/Ge/mic/brach/18 G (1); A, dorsal valve in posterolateral view; B, dorsal valve in apical view. C–E, FG 544/Ge/mic/brach/10 F (1); C, detail of ventral valve in apical view; D, detail of larval shell; E, detail of larval shell. F–G, FG 544/Ge/mic/brach/10 F (2); F, dorsal valve in posterolateral view; G, detail of larval shell. H–I, FG 544/Ge/mic/brach/18 G (2); H, dorsal valve interior; I, detail of dorsal valve interior. J–K, FG 544/Ge/mic/brach/10 I; J, detail of larval shell of the ventral valve; K, detail of larval shell of the ventral valve. L–M, FG 544/Ge/mic/brach/10 F (3); L, larval shell of the dorsal valve; M, detail of larval shell.**
wide in measured specimens. Periphery of larval shell flat. Larval shell covered by circular pits, 1-2 μm in diameter (Fig. 8D). Dorsal pseudointerarea orthocline, with broadly triangular, weakly concave median groove. Sides of median groove subdivide an angle of 130-140°. Anterior edge of median groove weakly arched, supported by base of median ridge. Propareas very small. Visceral area defined by a broad, posteriorly horizontal and anteriorly sloping brim. Median ridge with large median buttress extended into low, anteriorly swollen median ridge, which disappears at two-thirds of valve length. Short and low diverging ridges extend from the base of median buttress near centre of valve, posterolaterally bordering small anterocentral scars. Cardinal scars large, elongate-oval, about 30% as long and 30% as wide as the valve, with convex surface. Visceral area posterior with remarkably coarse and deeply impressed epithelial cell moulds.

Ventral valve shell asymmetrically conical, with convex anterior slope (Fig. 5E-F). Pedicle opening directed posteriorly, enclosed within larval shell. Ventral pseudointerarea steeply procline, high, with intertrough. Ventral interior with high, knob-like, anteriorly steeply sloping apical process bordered by moderately converging, proximal vascula lateralia. Internal pedicle opening circular, with thickened walls of pedicle tube. Small and deep apical pits situated laterally to pedicle opening (Fig. 5E-F). Cardinal muscle scars large, with raised surface. The shell is ornamented by less regular concentric fila.

Class PATERINATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order PATERINIDA Rowell, 1965
Superfamily PATERINOIDEA Schuchert, 1893
Family PATERINIDAE Schuchert, 1893

Micromitra Meek, 1873

Type species. Iphidea? sculptilis Meek, 1873, Middle Cambrian, Montana, USA.

Micromitra cf. sculptilis (Meek, 1873) (Fig. 9A-M)

Material. Two ventral valves in limestone and hundreds of shell fragments and juvenile shells from acid residue, Genestosa section, samples Ge 8, Ge 10 A, Ge 10 E, Ge 10 F, Ge 10 D, Ge 10 H, Ge 10 I, Ge 11, Ge 15, Ge 16 C, Ge 16 F, Ge 17 G, Ge 18 A, Ge 18 F, Los Barrios de Luna section, sample BL i, Porma section, samples PI 21, PI 25, PI 26, PI 28, PI B 1, Rodiezmo section, samples Ro 13, Ro 14, Ro 15, Vegaservera section, sample Ve 2, Piedras Bermejas section, sample Pe B 1, Barrios facies, upper member of the Lánca Formation.

Description. Shell inequivalved, strongly ventricomarginate, cardinal extremities obtuse. Dorsal valve weakly arched transversely and poorly convex in a lateral profile. Pseudointerarea low, marked by a distinct edge from rest of surface. Notothyrium broadly triangular, open. Edges of notothyrium collar-like, thickened, but a homeochelidium has not been observed. Dorsal larval shell depressed with four distinct lobes, with posterior edge extending over notothyrium.

Ventral valve transversely suboval to semicircular, 65-70% as long as wide, strongly convex in apical part, with maximum width posterior to mid-length. Hinge line equal to 60% of shell width. Adult valve triangular in anterior view, with straight flanks; young shells strongly convex in both profiles, with tumid beak. Convexity of valve decreases anteriorly. Anterior part of adult valve almost flat. Ventral pseudointerarea sharply defined laterally, steeply apsacline, with widely triangular delthyrium largely covered by thin, highly arched homeodeltidium. Surface of pseudointerarea covered by distinct growth lines. Ventral larval shell almost circular, remarkably variable in size (from 0.5 mm to almost 1 mm), with distinct boundaries. Larval shell with axial lobe extended over apical part of homeodeltidium. Two pairs of lateral lobes weakly defined, but shallow axial groove between them is distinct.

Ornament of postlarval shell is a combination of radial costellae and concentric fila. Costellae appear immediately at the earliest growth line of postlarval shell, with new ones originating by bifurcation of the primary costellae. However, some costellae disappear with growth, leaving broad interspaces. Concentric filose ornament is more prominent on interspaces than the crests of costellae; this results in a net-like ornament in juvenile shells, but as concentric ornament...
becomes more prominent with growth, the adult shells have dominant, finely lamellose, concentric ornament.

The interior of the ventral valve bears a weak radial striation, muscle scars have not been observed. Two vertical ridges bordering a laterally concave chamber below the homeodeltidium are distinct on interior of posterior shell wall.

Remarks. Paterinids are commonly documented, but there are few well defined species and most occurrences are referred to the type species Micromitra sculptilis (Meek, 1873), to M. modesta (Lochman, 1940) or they are left under open nomenclature (e.g., Bell 1944; Lochman & Hu 1960; Henderson & MacKinnon 1981; Zell & Rowell 1988; Holmer et al. 2001). Our specimens are very similar to the type species, with an apsacline ventral pseudointerarea, identical shell outline, convexity and ornament, although the type specimen of M. sculptilis (Meek, 1873) differs in its distinctly coarser radial ornament. Because Bell (1941) noted a great variability of the ornament with shell age, we assign our specimens to M. cf. sculptilis. Several other species of the genus have been described from the Middle Cambrian of Europe. Cobbold (1921) noted Micromitra sp. from the Middle Cambrian of England and compared it with the Scandinavian M. ornatella (Linnarsson, 1876). Both species are poorly illustrated and their affinity is difficult to assess. Spanish specimens described as Micromitra sp. (Liñán & Mergl 2001) cannot be referred to M. cf. sculptilis because they have a less prominent radial ornamentation; they also come from the early Middle Cambrian (Mansilla and Murero Formations) of the Iberian Chains. The Australian taxon M. nerranubawu Kruse, 1990 differs in its less transverse outline, a depressed ventral pseudointerarea and a very large homeodeltidium. Micromitra semicircularis Imanaliev & Pelman, 1988 from Central Asia (Holmer et al. 2001) differs from our specimens in having a more prominent concentric ornament and an open delthyrium with vestigial homeodeltidium.

Class OBOLELLATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order OBOLELLIDA Rowell, 1965
Superfamily OBOLELOIDEA Walcott & Schuchert in Walcott, 1908
Family TREMATOBOLIDAE Popov & Holmer, 2000

Trematobolus Matthew, 1893

Type species. Trematobolus insignis Matthew, 1893, Lower Cambrian, New Brunswick, Canada.

Trematobolus simplex (Vogel, 1962) (Fig. 9X-Y)

1962 Trematobolus sp.; Vogel, pl. 1, figs 2-4.
1962 Lamellodonta simplex n. g. n. sp.; Vogel, p. 216, pl. 1, figs 1, 5-9, pl. 2, figs 1-4, 7-9, pl. 3, figs 1-2, 4-5, pl. 4, fig. 2.
1975 Lamellodonta simplex Vogel, 1962; Poejet, pl. 1, fig. 5-7, pl. 4, fig. 7.
1978 Trematobolus simplex (Vogel, 1962); Havliček & Kříž 1978, p. 974, pl. 1, figs 1-16.
1986 Trematobolus simplex (Vogel, 1962); Mergl & Liñán, p. 170, pl. 2, fig. 1-5.
1995 Trematobolus simplex (Vogel, 1962); Geyer & Mergl, p. 208.
2001 Trematobolus simplex (Vogel, 1962); Liñán & Mergl, pp. 328-329, figs 7, 8a-i.

Material. Numerous ventral valves, Rodiezmo section, sample Ro 2 e B 5, Piedras Bermejas section, samples Pe B 2, Pe B 3, Pe B 4, Pe B 6, and Truebano section, samples Tr B 1, Tr B 2, Tr B 3, Tr B 4, Beleño facies, upper member of the Láncara Formation.

Remarks. Our specimens are indistinguishable from the shells described from the early Middle Cambrian (Valdemiedes Formation) from the Iberian Chains (Vogel 1962; Liñán & Mergl 2001). They have a very narrow, long and almost parallel pedicle track, coarse growth lamellae, and a weakly developed pair of radial plications bordering a depressed median sector are present in the specimens from the upper member of the Láncara Formation.

Class KUTORGINATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order KUTORGINIDA Kuhn, 1949
Superfamily KUTORGINOIDEA Schuchert, 1893
Family YORKIIDAE Rowell, 1962

Yorkia Rowell, 1962

Type species. Yorkia wanneri Walcott, 1897, Lower Cambrian, Pennsylavnia, USA.

Yorkia zafrensis Gil-Cid & Méloú, 1986 (Fig. 9N-S)

?1860 Brachiopode, nouv. gen.; de Verneuil & Barrande in de Prado, p. 536, pl. 8, figs 5,
Material. Four ventral valves, one dorsal valve, Láncara de Luna section, samples LL B 1, LL B 4, LL B 8, Barrios facies, upper member of the Láncara Formation.

Description. Shell subequally biconvex, thick-walled, with rectimarginate commissure, 14 mm long.

Dorsal valve subpentagonal, as long as wide, gently convex in transverse profile and more convex anteriorly than posteriorly. Dorsal interarea low, orthocline, occupying less than half of shell width. Notothyrium broadly triangular, apically bordered by short and poorly convex chilidium. The interior with a thickened posterior platform, but muscle scars and pallial markings are obscure.

Ventral valve evenly convex, subtrigonal to elongate oval, 110% as long as wide, gently convex, with rather thick shell, especially in posterior part. Maximum width in anterior third. Ventral apex slightly tumid. Beak angular, with apical angle 100°. Ventral interarea low, apsacline, with narrowly triangular delthyrium entirely covered by a weakly convex pseudodeltidium. External pedicle foramen is circular, 0.2-0.3 mm in diameter, directed posteriorly, and located at the top of the apex. Foramen internally continues to a long, rapidly expanding tube opened at the bottom of a thickened platform. Pallial markings and muscle scars have not been observed indicating their weak impressions on valve interior. Shell ornament of smooth growth bands, separated by weak growth lamellae.

Remarks. Two specimens which probably belong to Yorkia zafrensis were described and illustrated without any formal name by de Verneuil & Barrande (in de Prado 1860) is probably lost, as stated by Walcott (1912), and because we have no totopotypic material, it is impossible to elucidate its taxonomic position. However, a calcareous shell, noted already by de Verneuil & Barrande (in de Prado 1860, p. 536) has an apical foramen and an apsacline interarea indicating affinity to kutorginides, probably Yorkia Walcott, 1897.

Yorkia is known from the Lower Cambrian of North America (Pennsylvania and eastern Canada) (Walcott 1897, 1912), the lower Middle Cambrian of Spain (Sierra Morena) (Gil Cid & Méloú 1986), from the Middle Cambrian of Australia (New South Wales) (Brock 1998), and probably also from New Zealand (MacKinnon 1983; Brock 1998). Yorkia wanneri Walcott, 1897 has a more transverse shell and a less extended ventral beak than our specimens. Gil Cid & Méloú (1986) described Y. zafrensis from the lower Middle Cambrian near Bajadoz, SW Spain. Although our specimens are more transverse and less triangular in outline, we refer them to Y. zafrensis. The relationship of Y. zafrensis to specimens figured by de Verneuil & Barrande (in de Prado 1860) and by Sampelayo (1935) is outside the scope of our paper due to the lack of totopotypic material.

Family NISUSIIDAE Walcott & Schuchert in Walcott, 1908

Nisusia Walcott, 1905

Type species. Orthisina festinata Billings, 1861, Lower Cambrian, Vermont, USA.

Nisusia vaticina (de Verneuil & Barrande in de Prado, 1860) (Fig. 9T-W)

1860 Orthisina festinata s. n.; de Verneuil & Barrande in de Prado, p. 533, pl. 8, figs 8, 8a-d.
1860 Orthisina pellico s. n.; de Verneuil & Barrande in de Prado, p. 535, pl. 8, figs 7, 7a-b.
1912 Nisusia? vaticina (de Verneuil & Barrande); Walcott, p. 730, pl. 97, figs 3, 3a-b.
1912 Nisusia (Jamesella) pellico (de Verneuil & Barrande); Walcott, p. 735, pl. 97, figs 2, 2a-b.
1935 Nisusia vaticina (de Verneuil & Barrande); Sampelayo, p. 493, pl. 13, figs 3-5, pl. 14.
1935 Nisusia pellico (de Verneuil & Barrande); Sampelayo, p. 494, pl. 14.

Material. Fourteen, mostly poorly preserved (deformed, broken) ventral and five dorsal valves,
Rodiezmo section, samples Ro B 1, Ro B 2, Ro B 3, and Lánca de Luna section, samples LL B 5, LL B 6, LL B 7, LL B 9, LL B 12, LL B 13, LL B 15, LL B 16, LL B 17, LL B 18, LL B 20, LL B 21, LL B 23, LL B 24, LL B 25, Barrios facies, upper member of the Lánca Formation.

Description. Shell ventribiconvex, transversely subrectangular, with gently unisulcate commissure, thick shaped, and 25 mm wide in the largest specimen.

Dorsal valve weakly convex, with shallow and broad sulcus, widest at hinge line with slightly rounded cardinal extremities. Dorsal interarea low and anacline.

Ventral valve strongly convex in transverse profile, with weakly depressed cardinal extremities and prominent apex. Lateral profile straight to gently concave near apex, becoming convex from posterior one-third. Ventral interarea apsacline, straight, with broad delthyrium, that is apically closed by thick, highly convex pseudodeltidium. Sides of interarea form prominent acute edges above the shell surface. Ventral interior with broadly diverging, thickened lateral margins of pseudodeltidium. Ornament of rounded uniform radial costellae, 0.2-0.3 mm wide, separated by rounded interspaces of the same size. Ten to twelve costellae extend from the apex, with new costellae originating by implantation. Large shells with up to 40-50 costellae. Raised hollow spines extend from the crest of costellae and at the edges of concentric lamellae. Ventral valve densely covered by rows of spines on crests of costellae, while spines are less prominent and less numerous on dorsal valve. Concentric ornament of weak growth lamellae, some imbricating anteriorly.

Remarks. This species has been referred to *Nisusia* by Walcott (1912). The specimens described as *Orthisina pellico* de Verneuil & Barrande in de Prado, 1860, are only juvenile individuals of *N. vaticina*, as can be judged from illustrations in de Prado (1860) and our material.

CONCLUSIONS

Unlike the cosmopolitan genera *Acrothele*, *Micromitra*, *Trematobolus* and *Nisusia* (cf. Brock 1998), the acrotretid brachiopods of the upper member of the Lánca Formation have a restricted distribution. *Luhoitreta* is known from the early Middle Cambrian of Sardinia (Mergl & Elicki 2004) from beds of the same age (Campo Pisano Formation) and also from the Middle Cambrian Jince Formation of Central Bohemia (Mergl & Šlehoferová 1990). The new genera *Iberotreta* and *Genetreta* are so far unknown outside the Cantabrian Mountains. The latter is most similar to *Kostjubella* from the early Middle Cambrian of Kazakhstan (Popov et al. 1996).

In the Middle Cambrian, the acrotretoids rapidly diversified as shown by the presence of twenty genera in subequatorial regions in the late Middle Cambrian (Ushatsinskaya 1996). None of the most widespread genera (*Anabolotreta*, *Dactylothreta*, *Neotreta*, *Opisothotrexa*, *Prototreta*, *Rhondellina*, *Stilpnotrexa*, *Treptotrexa*) or the North African genera *Vandalotrexa* and *Tingitanella* (Mergl 1988; Streng 1999) have been documented in the early Middle Cambrian of the Cantabrian Mountains. The acrotretid diversity remained low in the upper member of the Lánca Formation, with one or two species in each sample.

The obollendid *Trematobolus* has a cosmopolitan distribution. It is known, besides from more distant areas, from Newfoundland and eastern North America (Matthew 1893; Walcott 1912), Morocco (Geyer & Mergl 1995), Spain (Vogel 1962) and Poland (Jendryka-Fuglewicz 2004). This genus dominates in carbonate or mixed siliciclastic-carbonate sequences near the Lower-Middle Cambrian boundary. In the upper member of the Lánca Formation it is abundant in the grey to roan, glauconitic limestone of the Beleño facies. The more reddish limestone (Barrios facies) of the upper member of the Lánca Formation commonly yields the nisusiid *Nisusia vaticina* associated with the kutorginid *Yorkia zaffrensis*. While *Nisusia* is a widespread genus, *Yorkia* is less common, found in late Lower Cambrian strata of Iberia, eastern North America, the Altai-Sayan region (Aksarina & Pelman 1978) and the early Middle Cambrian of Australia (Brock 1998).

The low abundance of small lingulates in the upper member of the Lánca Formation is consistent with their suggested infaunal or semi-infaunal mode of life. Carbonate mud with abundant skeletal material was unstable and thus less appropriate for the burrowing habit of small lingulates. Pedunculate epibenthic brachiopods attached to skeletal debris (nisusiids, kutorginids, *Acrothele*, *Trematobolus*, *Micromitra*) or algal mats (acrotretids) found favourable substrate on the bottom. The relative high diversity, with the genera *Trematobolus*, *Nisusia* and *Yorkia*, demonstrates the affinity of the brachiopod association of the Lánca Formation with faunas of the low latitude Siberian platform (Aksarina & Pelman 1978), New South Wales (Brock 1998) and some Avalonian terranes (Newfoundland, New Brunswick) (Walcott 1912).

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