A reassessment of the Lochkovian (Lower Devonian) benthic faunas and palynomorphs from the Domes region (southern Central Iberian Zone, Portugal)


Keywords: Brachiopods, Tabulata, Palynomorphs, Lower Devonian, Lochkovian, Central Iberian Zone, Portugal.

Abstract: A revision of benthic faunas and palynomorphs previously described from the Domes syncline, southern Central Iberian Zone, Portugal, complemented with recent research, shows that the Serra de Luação Formation is of Lochkovian age. The systematics of the benthic faunas, with clear Gondwana affinities, are described in detail.

Palavras-chave: Braquiopodes, Tabulata, Palinomorfos, Devonico Inferior, Lochkoviano, Zona Centro Iberica, Portugal.

Resumo: A revisão de faunas bênicas e das associações de palinomorfo anteriormente descritas para o sinclinal de Domes, sector sul da Zona Centro Ibérica, em Portugal, complementada com novas investigações, permitiu precisar a idade da Formação da Serra de Luação, datada do Lochkoviano. As faunas, tipicamente gondwânicas, são descritas em pormenor.

HISTORICAL INTRODUCTION

In Portugal Lower Devonian successions are presented in three major tectonostratigraphic domains of the Iberian Massif, the Central Iberian, Galicia-Trás-os-Montes and Ossa Morena Zones (Fig. 1-1). In the Central Iberian Zone (CIZ), the Lower Devonian is exposed in the Domes (Fig. 1-2), Mação and Portalegre synclines as well as in dispersed outcrops near the northwest terminus of the Valongo anticline. The Domes syncline sequence, with a north-south orientation, includes several lithostratigraphic units of which two have a lower Devonian age, respectively the Serra do Luação and the Domes formations (COOPER, 1980).

The Devonian age of these units had been previously determined by the occurrence of trilobites (MELLADO & THADEU, 1947, and previous references), brachiopods (TEIXEIRA & TADEU, 1967; PERDIGÃO, 1979, COOPER, 1980; COOPER et al., 2000; OLIVEIRA et al., 2000), miospores and crinoids (OLIVEIRA et al., 2000). The aim of the present paper is to describe the Lochkovian biostratigraphy of the Domes region as well as to comment on the paleobiogeography within the context of the European Variscides.

The macrofossils described and figured here (noted MG) are housed in the collections of the Geological Museum of the Laboratório Nacional de Energia e Geologia (LNEG) in Lisbon.

LOWER DEVONIAN STRATIGRAPHY

The Domes syncline crops out just north of Domes village, along a spit of the Castelo do Bode dam, and also in road cuts of the Dornes-Vale de Serrão road. There are also scattered outcrops in “Serra da Molhadinha” and “Serra da Faisca”, respectively north and south-east of the village.

The lower unit (Serra do Luação Formation, COOPER, 1980) comprises alternations of sandstones, quartzites, siltstones and shales, about 200 m thick. The sandstones...
show sedimentary structures such as cross-bedding, ripple marks and load casts (COOPER et al., 2000), as well as lenticular hummocky type bedding (OLIVEIRA et al., 2000). The bioturbation is also common in all lithologies, with traces of vertical burrows (Monocraterium sp., according to COOPER, 1980). These structures and the sedimentary organization composed of decametric thick, coarsening upward sequences may reflect short-lived relative sea level fluctuations in a general regressive context.

The Serra do Luacao Formation was considered to be late Ludlow to early Pragian in age (COOPER, 1980; COOPER et al., 2000). This data was based on late Ludlow and Pridoli microfossils and on the occurrence of Pragian macrofossils in the overlying Domes Formation. Lochkovian brachiopods and miospores were later collected from the upper part of the formation (OLIVEIRA et al., 2000), and are now the aim of the present systematic description.

The Serra do Luacao Formation grades upwards into the basal dolomitic limestones of the Domes Formation (COOPER, 1980), which is exposed in a road cut (Dornes-Vale Serrão section). This unit is a 200 m thick succession composed of limestones interbedded with sandstones and mudstones. The most complete sequence of the Domes Formation is exposed in the north side of the dam, in the “Serra da Molhadinha” section, northeast of Dornes, where COOPER (1980) identified Pragian brachiopod faunas in the middle and upper parts. Later, the age of this unit was confirmed with Pragian crinoid and brachiopod faunas (OLIVEIRA et al., 2000).

LOCHKOVIAN LITHOLOGY AND BIOSTRATIGRAPHY

1) Dornes spit section (A, Fig. 1)

At the extreme end of the Dornes spit is a folded succession of mudstones, quartzites, conglomerates and sandstones. These sandstones are ferruginous, with thin
conglomeratic and coquina beds in the upper part of the sequence. The exposure ends with the dolomitic limestones of the Dornes Formation, on the east side of the spit, near the village cemetery. The stratigraphic position of these clastic lithologies was not clearly established in the past. “Siltstones & mudstones, undifferentiated” and “Quartzites & sandstones, undifferentiated”, with no age determination, were identified by COOPER (1980) and COOPER et al. (2000), OLIVEIRA et al. (2000) indicating that these lithologies belong to the Dornes Formation.

Recently, in this succession, five fossiliferous levels (log A, Fig. 2) were identified, with the following faunas:

- A 1 - Brachiopods: Platyrothis monnieri, "Camarotoechia" sp.1 and Howellella (Howellella) mercurii ssp. There are also gastropods, bryozoans, bivalves and tentaculitids?
- 1 m above A1 - Tabulata - Liguodicctium ligulatum
- A 2 - Bryozoans and the brachiopods, Mclearnites (Mclearnites) lecaroensis, Platyrothis monnieri, Proschizophoria ? maillieuxi, "Camarotoechia" sp.2, Hexarhytis undata and Howellella (Howellella) mercurii.
- A 3 - Bryozoans and the brachiopods, ? Mclearnites (Mclearnites) lecaroensis, ? Howellella (Howellella) mercurii and an indet. strophodontid.
- A 4 - Bryozoans and crinoid fragments.
- A 5 - Bryozoans, crinoid fragments and the brachiopods, Mclearnites (Mclearnites) lecaroensis, Hexarhytis undata and Howellella (Hysterohowellella) lunae gouvenneci.

These new biostratigraphic data clearly indicate that the first three levels are of early Lochkovian age and the upper level is of late Lochkovian age, and that the section belongs indeed to the Serra de Luação Formation.

2) Road cut Dornes-Vale Serrão section (B, Fig. 1)

The studied section corresponds to the upper part of the Serra do Luação Formation (log B, Fig. 2) and is exposed in the south side of the road cut. The lithological, sedimentological and palaeontological characteristics of this unit were previously detailed (COOPER, 1980; COOPER et al., 2000; OLIVEIRA et al., 2000). The unit is composed of a 200 m thick succession of heterolithic sandstones, siltstones and shales. According to COOPER (pages 405 to 407; 1980) late Ludlow microfossils (chitinozoans, acritarchs and miospores) and Pridoli acritarchs, were found respectively 25 m and 110 m above its base. Poorly preserved fragments of ? Leptostrophia sp. and ? athyrid were also identified within the upper siltstones (bed 47, page 126, COOPER 1980), which do not allow a precise age determination. Later (OLIVEIRA et al., 2000) lower Lochkovian miospores assigned to the MN Biozone (STREEL et al., 1987 and STEEMANS, 1989) and brachiopods were also identified. The palynomorph assemblages and brachiopod faunas are revised and confirmed in the present work, as follows:

- Level B 1 – Trilobites, a fragment of phyllocarid and the brachiopod, "Camarotoechia" sp.1.
- Level B 3 – The brachiopods, Mclearnites (Mclearnites) lecaroensis, Platyrothis monnieri, Proschizophoria ? maillieuxi, Schizophoria (Rhenoschizophoria) runegatensis?, Protathyris sp. cf. P. praecursor, Hexarhytis undata, Howellella (Howellella) mercurii and Mutationella sarrobi

The poorly to moderate preserved Miospore assemblages recovered in levels B 2 and B 3 (log B, Fig. 2) yield Aneurospora sp., Ambitsporites sp., Amicosporites streelii, Archaeozonotritiles chulus, Chelinospora retorrida, Chelinospora sp., Cymbosporites echinatus, C. proteus, Dicytortritiles sp., Emphanisporites micrornatus, Emphanisporites verrucatus, E. negletus, E. multistatus, Streelispora sp., Synorispores verrucatus, Synorispores sp., Retusortritiles sp., R. abundo and R. warrigtonii. Cryptospore species were also identified, Dyadospora sp., Laevolancis divellomedia and L. plicata. These assemblages are assigned to the Emphanisporites micrornatus - Streelispora portentensis (MN) Biozone of early Lochkovian age (STREEL et al., 1987 and STEEMANS, 1989), based on the presence of the zonal key species Emphanisporites micrornatus, together with Streelispora sp. and Chelinospora retorrida.

Acritarchs, poorly to moderate preserved, are also common and are represented by the species Cymbosphaeridium sp., Dictyotidium sp., Diexallophasis remotum, Ephelopalla sp., Gorgonisphaeridium sp., Micryhstridium stellatum, Multiplicisphaeridium sp., M. ramusculosum, Neoverhachium carminae, Onondagaella sp., Tyligmasona sp. and Veryhachium trispinosum.

Standard palynological laboratory procedures were employed in the extraction and concentration of the palynomorphs (WOOD et al., 1996). The slides were examined under transmitted light, with a BX40 Olympus microscope equipped with an Olympus C5050 digital camera. All samples, residues and slides are stored in the LNEG, S. Mamede Infesta, Portugal. The miospore bio-
Fig. 2 - Stratigraphic logs of the Dornes spit (A) and road cut Dornes-Vale Serrão (B) sections.
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zonal scheme used follows the standard Western Europe Miospore Zonation (after: Streel et al., 1987 and Steemans, 1989). Stratigraphically important and typical palynomorph taxa are illustrated in Plate 2.

3) Serra da Molhadinha locality (C, Fig. 1)

This locality is situated at the north side of the dam, along a forest track previously sampled and studied (Cooper, 1980, pages 141 to 145). The sampled locality is exposed at the extreme east of Cooper’s section. The faunal associations determined here are similar to those described in the road cut of the Dornes-Vale Serrão section, and are included in the systematics below. The following brachiopod species were recognized:

Mclearnites lecaroensis, Mutationella sarrobi, Howelliella mercurii, Proschizophoria mailleuxi, Schizophoria runegatensis, Platyrhisis monnierii, Protathyris cf. praeursor and Hexarhysis undata.

SYSTEMATICS

Tabulata

The coral fauna of the Dornes area is very scarce and the discovery of the genus Ligulodictyum in the Lower Devonian is new for the Central Iberian Zone, and completes the recent study on the Ossa Morena Zone (Plusquellec in Lemenn et al., 2002).

Subclass Tabulata Milne-Edwards & Haime, 1850
Order Favositida Wedekind, 1937
Family Cleistoporidae Easton, 1896?

Ligulodictyum ligulatum (Plusquellec 1965)
Fig. 3 and Pl. 1, Fig. 26

Locality: 1 m above level A 1 (section A); Serra de Lução Formation
Age: Lochkovian.
Material: Two specimens. MG 10887-10888.

Description

The specimens are preserved as casts in ferrugineous sandstone. The description is based on a well preserved, although incomplete specimen (MG 10887); the other is unusable.

Lower or proximal side: The corallum is attached to a foreign body at its base, here a pedicle valve of Douvilina. The concentrically wrinkled «epitheca» is not seen, because the corallum does not extend beyond its support.

Upper or distal side (MG 10887A): The corallum is discoid, and slightly concave in natural cast. Apart from some situated in the periphery of the corallum, each corallite possesses in its initial corner a tongue-like structure that is the cast of an arcuate, deep, and narrow trough.

As a natural cast, the calicial bottom is roughly flat. Its longitudinal outline (from initial corner/inner side to peripheral/outer side) is gently convex (Fig. 3C) or shows a convex part, followed by a concavo-convex one (Fig. 3F). Its transverse outline is more or less convex near the «tongue» (Fig. 3D, G) while in the middle it is weakly or irregularly convex, with a small depression near the wall (Fig. 3E) or barely concave (Fig. 3H). The peripheral part of the calicial bottom has about 8-10 prints of parallel septal ridges and septal furrows. The proximal part of the calicial bottom (MG 10887B) shows numerous prints of scattered spines, in its outer part, they are arranged in rows along the casts of the septal ridges. The walls between adjacent corallites show casts of midface mural pores. The corner pores (if present), and the basal pores have not been identified.

Development of the corallum

The axis of each tongue-like structure is directed towards the protocorallite, identifying it (Fig. 3A). The protocorallite is surrounded by a circle of six metacorallites but, from the study of young stages of growth in specimens of L. ligulatum from the Armorican Massif (Plusquellec, 2007), it has been established that the development of the genus is organized around the prototriade \(1 \ 1 \ 2\). The prototriade seems to be of the continuous type (as usual) because metacorallite \(2\) is not in contact with the protocorallite. Nevertheless, in our specimen, firstly the common wall between the two metacorallites \(1\) is short and wide (Fig. 3B), and no casts of mural pores can be seen between them, secondly the angle between the plane of bilateral symmetry of the two corallites \(1\) is about 120-130° instead of the usual 70-80°; tectonic deformation cannot easily explain this feature...

Measurements

Owing to the deformation and of incompleteness of the specimens, the measurements are given as approximate. Maximum and minimum diameter of the corallum: 33x21 mm (MG 10887), 35x27 mm (MG 10888). Number of corallites 35 or more than 35 (MG 10887A). Corallite
Fig. 3 – Upper side of Ligulodictyum ligulatum, natural cast, MG 10887A. A - diagrammatic drawing of the corallum showing the position of the tongue-like structure, the protocorallite (11) and the first pair of metacorallites (12) forming the prototriade; B - drawing of the central part of the corallum showing a thick wall between the metacorallites 12 (see discussion in text); C - H outline of the calicinal bottom (optical section) for the corallite 31-right (C-E) and for the corallite situated between 21 and 31-left (F-H), respectively longitudinal, front outline of the «tongue» and transverse outline; I - calicinal bottom of corallite 31-right, broken line as casts of interseptal ridges, notice the fluted inner side of the «tongue».

diameter at calicinal bottom level (for the measurements, the position of the middle line of the wall is schematized on a camera lucida drawing, see Fig. 3A of MG 10887A). The radial corallite diameter is about 6 mm (average 5.98 mm), the transverse about 4 mm (4.17 mm). The thickness of the wall at calicinal bottom level is generally of 0.5 mm, thus, the calice diameter at calicinal bottom level corresponds to corallite diameter minus wall thickness.

Discussion
The specimens of Dornes are identical with L. ligulatum from the Landévennec Fm. at the Caro, West of Plougastel-Daoulas (locus typicus and stratum typicum of the species) and others sections of the Rade de Brest like the well known Fort de Lanveoc section.

In the Armoric Massif, especially in the western part of the Central-North Armoric Domain where the stratigraphic distribution of the species is well known, L. ligulatum appears in the middle Member of the Grès de Landévennec (for example at the Fort de Lanveoc section, bed 21) and is known up to its top. The uppermost occurrence is from the lower part of the Schistes et calcaires de l’Armorique Fm. (bed N 15 and S 98-99 of the type section, see PLUSQUELLEC, 1980). Nevertheless the specimens in this formation are rather rare (dominated by L. paraligulatum), and smaller in size.
Ligulodictyum ligulatum is known from the «middle» lower Lochkovian to the early Pragian. The specimens of Dornes are closer to the forms of the Landévennec Fm. than to those of the Armorique Fm. So this supports a Lochkovian age: early Lochkovian (but not early lower) or late Lochkovian (but not late upper).

**Brachiopoda**

Order Strophomenida Öpik, 1934  
Superfamily Strophomenoidea King, 1846  
Family Amphisthrophiidae Harper, 1973  
Subfamily Mesodouvillininae Harper & Boucot, 1978  
*Mclearnites (Mclearnites) lecaroensis* (Renouf, 1972)  
Pl. 1, Figs. 7-13  

Material: About twenty internal and external molds of ventral and dorsal valves, most of them incomplete. MG 10872B, MG 10875-10878.

Locality: Levels A 2, A 3?, A 5 (section A), B 3 (section B) and C; Serra do Luação Formation

**Synonymy**

1972 *Douvillina (Mesodouvillina) lecaroensis* n. sp. – Renouf, p. 111, fig. 8; pl. 23, fig. 8-16; pl. 24, fig. 1-7.

2001 *Mclearnites lecaroensis* (Renouf 1972) – Jansen, p. 170, tab. 13, pl. 13, fig. 7; pl. 14, figs. 2-3 (complete synonymy).

**Description**

Shell slightly transverse to subcircular, relatively large for the species (L\text{mean}=28.6\,mm; W\text{mean}=31\,mm), the largest specimen reaching 46\,mm in width. Some specimens (level B 3) are elongate (deformation?). Hinge line straight, denticle, shorter than maximum width, located about midlength, except on juvenile, where greatest width can be located at hinge line. On rare juvenile specimens, the hinge may extend laterally in very short "ears", or "mucros". Otherwise, apical angles are more or less angular on juveniles, and become rounded on adults. The ventral area is low, triangular. Ventral valve slightly convex, dorsal almost flat to slightly concave. Ornament consisting of regularly and closely distributed capillae, appearing by intercalation, resulting in a homogeneous aspect; the different capillae orders are generally best seen on the internal molds, where first or second orders may appear stronger. On adult specimens, there are 20 to 36 capillae per 10 mm in the vicinity of the anterior commissure. Lateral costellae are curved backwards.

Ventral interior: The muscle field is well delimited by 2 divergent, straight to slightly internally curved ridges, turning to blades at adult stage. The anterior part of the muscle field may or may not be delimited. On some adult or gerontic specimens the muscle field becomes anteriorly flabellate and longitudinally striated. A well developed, strong median process is fused to the internal side of the pseudodeltidium and is broadly attached to the valve floor. Anteriorly, this process is continued by a myophragm that rapidly tapers, and extends up to midlength (i.e., to anterior part of the muscle field).

Dorsal interior: The muscle field consists of 2 elongate scars, delimited by 2 wide subparallel to slightly divergent ridges. Its length reaches 1/2 L and its width 1/4 W. It is bisected by a low myophragm. The cardinal process is strong, bifid, and posteriorly striated on well preserved specimens. Short straight socket ridges present. The denticles extend to about one half of the hinge line; their number varies from 20 (juveniles) to 32 or more on large specimens.

**Discussion**

The species *lecaroensis* was assigned to *Mclearnitesella* by Harper & Boucot (1978) (a synonym of *Mclearmites*) on the basis of its ornament, although they underlined the fact that in the Armorican species this ornament is not typical, but rather intermediate between *Mesodouvillina* (unequally parvicostellate) and *Mclearnitesella* (uniformly costellate). This difference in the ornament was used to distinguish two subgenera, respectively *M. (Mclearmites)* and *M. (Mclearmitesella)*, but some authors (e.g., Jansen, 2001 or Cocks & Rong, 2000) do not recognize this distinction; the case of *M. lecaroensis* seems to confirm this point of view, but wider discussion is beyond the scope of this paper. The Portuguese form, as for the Armorican, is rather uniformly costellate with a gently curved ventral valve and is thus assigned to the (sub)genus *Mclearnites*. The aspect of the ventral muscle field, that may be anteriorly well delimited or flabellate is reminiscent of the form present in the Carazo Formation (Lower Devonian of Spain), as described by Renouf (1972, Fig. 8B).

*M. lecaroensis* is known in the Landévennec and Gahard formations (France), Lochkovian in age. In Spain, it has been recognized in the lower part of the Rañeces-La Vid Group (lowermost Lochkovian), in the upper part of the Carazo Fm. and the lower part of the Lebanon Fm. (lower Lochkovian).
Indet. Strophodontid

Material: 4 highly deformed specimens and several fragments.

Locality: Level A 3 (Section A); Serra do Luação Formation

Discussion

The shell is transverse with a straight hinge line; maximum width is located on the hinge. Cardinal angles seemingly angular. Ornament consisting of primary robust angular plications originating at the apex and bifurcating during growth, giving a fascicostellate aspect to the ornament. These plications are covered by secondary very fine costellae. Internal structures not observed. The poor preservation precludes any safe identification of this species, but it is noteworthy that similar forms are uncommon in the basal Lochkovian of the Ibero-Armorian domain. This form is reminiscent of "Stropheodonta" ornatella described by Asselberghs (1930) in the Gedinnian of the Ardennes, and also Plectodonta mariae Kozłowski, 1929 from the Borschov Fm. (Lower Gedinnian of Podolia), but the preservation of the material precludes any further comparison.

Order Orthida Schuchert & Cooper, 1932
Suborder Dalmanellidina Moore, 1952
Superfamily Dalmanelloidea Schuchert, 1913
Family Platyorthidae Harper, Boucot & Walmsley, 1969

Platyorthis monnieri (ROUault, 1851)
Pl. 1, Figs. 1-6

Material: About 30 isolated valves (external and internal molds) and numerous fragments. MG 10870-10874.

Locality: Levels A 1, A 2 (section A), B 3 (section B) and C; Serra do Luação Formation

Synonymy

1851 Orthis monnieri. Rouault, p. 376.
1972 Platyorthis monnieri (Rouault) – Renouf, p. 108, pl. 22, fig. 7-15; pl. 23, fig. 1-7 (complete synonymy).

Description

The shell is punctate, moderately convex, generally small ($L_{\text{mean}}$: 10 mm; $W_{\text{mean}}$: 11.4 mm) (maxima: respectively 14.5 and 16.5 mm), subcircular. Dorsal valve almost flat with a shallow median depression and ventral valve slightly carinate, moderately convex. The numerous costellae appear mainly by intercalation, occasion-
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**Discussion**

The shell is large (L > 20 mm; W > 40 mm), subcircular in outline, moderately biconvex, with numerous costellae (3 per mm near the anterior commissure); maximum width located approximately at midlength. On internal molds, the commissure is accentuated by a narrow peripheral lip. Dorsal interior with bifid cardinal process, strong sockets and strong, thick brachiophores. Muscle field moderately excavated, subcircular, more or less wider than long, with a median furrow widening (up to 1/3 of the width of the muscle field) in gerontic stage. The muscle field is occasionally transversely divided into 2 or 3, delimited by low subtransversal steps. Ventral interior with an elongate, triangular to ovoid muscle field, divided by a deep median furrow.

CARLS (1974) pointed out that the species maillie uxi was ill-defined, and thus its assignment to Proschizophoria is doubtful; he suggested that it be a new genus or similar to Batturia or Fulcriphoria. Nevertheless, the present form is reminiscent of the Armorican species known in the "Gres à Orthis monnieri" near St. Berthevin (Mayenne), the Landévennec Formation (Rade de Brest), and the Carazo Formation (Spain). All these localities are early Lochkovian in age.

Superfamily Enteletoidea Waagen, 1884
Family Schizopheriidae Schuchert & LeVene, 1929

**Schizophoria (Rhenoschizophoria) runegatensis**
RENOUN, 1972
Pl. 1, Figs. 14-15

Material: Two incomplete dorsal valves, 5 incomplete ventral valves and fragments. MG 10879-10880.
Locality: Levels B 3 (section B) and C; Serra do Luação Formation

**Synonymy**
1972 Schizophoria runegatensis n.sp., Renouf, p.97, text-fig. 4; pl. 21, fig. 1-10.

**Discussion**

In the dorsal valve the area is narrow and relatively high medially. The brachiophores are posteriorly thinned, long and sigmoid, high up to midlength of the muscle field, and then rapidly lower (but remaining thick) anteriorly. Cardinal process strong, with one median and two lateral lamellae. Triangular, slightly excavated muscle field with a median ridge decreasing anteriorly, and not extending beyond the muscle field.

Ventral valve moderately convex with variably long, straight to slightly internally curved dental plates that may extend anteriorly as small ridges. Elongate muscle field poorly defined anteriorly, without notable muscle scars, medially divided by a ridge that is low posteriorly, becoming rapidly higher from midlength of the muscle field, and terminating at its anterior edge while regularly thickening. Posteriorly, the muscle field terminates more or less abruptly against a small transverse pedicle callist.

The characters accord with an assignment to S. (Rhenoschizophoria) erected by Jansen (2001), and particularly to the species S. runegatensis; nevertheless the poorly preserved specimens and their rarity await further investigations. S. (R.) runegatensis is present in the Landévennec Fm. (lower Lochkovian of the Armorican massif, France), and was also identified in the upper part of the Carazo Fm. and lower part of the Lebanza Fm. (lower Lochkovian, Northern Spain).

Order Rhynchonellida Kuhn, 1949
Superfamily Camarotoechioidea Schuchert, 1929
Family Camarotoechiidae Schuchert, 1929
Subfamily Camarotoechiiinae Schuchert, 1929
"Camarotoechia" sp.1
Material: 6 ventral valves.
Locality: Levels A 1 (section A) and B 1 (section B); Serra do Luação Formation

**Discussion**

Shell small (L = 5.7 mm; W = 5.3 mm), slightly convex, subtriangular with rounded anterior commissure. Fold low, bearing a median groove flanked by 2 ribs slightly higher than the adjacent. Lateral ribs angular, few (2 or 3 on each flank, the third pair, when present, very faint). Ventral interior with short (1/4 L), thin, divergent dental plates. Dorsal interior with prominent, long (about 1/2 L), posteriorly thick median septum. This form is too poorly preserved to allow a precise assignment to a known species. It is very close to "Camarotoechia" pareitiformis Drot, 1964 (Lochkovian, Morocco), but differs in more median and lateral ribs. "Camarotoechia" thebaulti (Barrois), mentioned in the Landévennec Formation by Renouf (1972) is similar in shape and size, but shows 4 ribs on the fold.

"Camarotoechia" sp.2
Pl. 1, Fig. 21

Material: One poorly preserved ventral valve. MG 10882.
Discussion

The shell is moderate in size ($L_{\text{max}} \approx 20 \text{ mm}; W_{\text{max}} \approx 24 \text{ mm}$), with variable outline (equidimensional to slightly wider than long). The hinge line is shorter than maximum width. The dorsal fold is low, well delimited, and corresponds to a shallow sulcus on the ventral valve. Sulcus originates at midlength (i.e., just forward the muscle field on internal molds) rapidly deepening and widening forwards. The flanks are smooth. Ventral beak robust, strongly recurved. Ornament consisting of irregularly spaced growth lamellae, some of them stronger. In the dorsal valve a long, low myophragm is present. In the ventral valve the dental plates are short (about 1/4 $L$), thin, very divergent, straight on juvenile specimens and becoming internally curved on adults. The apical lateral cavities are narrow. The muscle field is slightly excavated, lacking any identifiable muscle impression. The external ornament (growth lamellae) is printed on internal molds, revealing a thin shell.

The material at hand is sparse and poorly preserved. Nevertheless some characters (size, outline, dental plates, etc.) indicate *Hexarhytis*. *H. undata*, mentioned in numerous sections of the lower Devonian (Lochkovian to Emsian) of the Ibero-Armorian domain, seems likely for the Portuguese form.

Order Athyridida Boucot, Johnson & Staton, 1964
Suborder Athyridida Boucot, Johnson & Staton, 1964
Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Subfamily Athyridinae Davidson, 1881

*Protathyris* sp. cf. *P. praecursor* KOZLOWSKI, 1929
Pl. 1, Fig. 16

Material: One dorsal valve (internal mold), one ventral valve (internal and external molds) and one incomplete internal mold with conjoined valves. MG 10881.

Locality: Levels B 3 (section B) and C; Serra do Luação Formation

Discussion

The shell is small, equidimensional ($L = 11 \text{ mm}; W = 11 \text{ mm}$), moderately ventribiconvex, with a narrow, low, apsacline area. The external mold is devoid of any ornament. A very faint sulcus is present on the anterior of the ventral valve, in the immediate vicinity of the commissure. The beak is short, slightly curved. The dental plates are very thin, short, and divergent. In the dorsal valve the beak is very short. Dental sockets are short and rather stout; a cardinal platform is present. Muscle scars are lacking.

This species is assigned to *Protathyris*, and seems close to the species *P. praecursor* described by KOZLOWSKI (1929) in the Borshchov Fm. of Podolia (lower Lochkovian). The species is also known in Germany (Flaschersiefer), Northern France (Groupe de Liévin), and Morocco (Group of the Rich), Lochkovian in age.

Subfamily Plicathyridinae Alvarez, 1990

*Hexarhytis undata* (DEFRANCE, 1828)
Pl. 1, Fig. 22

Material: 4 ventral valves (internal molds), 1 incomplete dorsal valve and numerous fragments. MG 10883.

Locality: Levels A 2, A 5 (section A), B 3 (section B) and C; Serra do Luação Formation

Discussion

The shell is moderate in size ($L_{\text{max}} \approx 20 \text{ mm}; W_{\text{max}} \approx 24 \text{ mm}$), with variable outline (equidimensional to slightly wider than long). The hinge line is shorter than maximum width. The dorsal fold is low, well delimited, and corresponds to a shallow sulcus on the ventral valve. Sulcus originates at midlength (i.e., just forward the muscle field on internal molds) rapidly deepening and widening forwards. The flanks are smooth. Ventral beak robust, strongly recurved. Ornament consisting of irregularly spaced growth lamellae, some of them stronger. In the dorsal valve a long, low myophragm is present. In the ventral valve the dental plates are short (about 1/4 $L$), thin, very divergent, straight on juvenile specimens and becoming internally curved on adults. The apical lateral cavities are narrow. The muscle field is slightly excavated, lacking any identifiable muscle impression. The external ornament (growth lamellae) is printed on internal molds, revealing a thin shell.

The material at hand is sparse and poorly preserved. Nevertheless some characters (size, outline, dental plates, etc.) indicate *Hexarhytis*. *H. undata*, mentioned in numerous sections of the lower Devonian (Lochkovian to Emsian) of the Ibero-Armorian domain, seems likely for the Portuguese form.

Order Spiriferida Waagen, 1883
Suborder Delthyridina Ivanova, 1972
Superfamily Delthyridoidea Phillips, 1841
Family Delthyrididae Phillips, 1841
Subfamily Howellellinae Johnson & Hou, 1994

*Howellella* (*Howellella*) *mercurii* (GOSSEL, 1880)

Material: 2 internal molds and 1 external mold of ventral valves; ?1 external mold of dorsal valve.

Locality: Levels A 2, A 3 ? (section A) and B 3 (section B); Serra do Luação Formation

Synonymy: See GOURVENNEC, 1989

Discussion

The shell is transverse, moderately large ($L_{\text{mean}} \approx 8 \text{ mm}; W_{\text{mean}} \approx 16 \text{ mm}$), with rounded cardinal extremities, with maximum width close to the hinge. The ventral interarea is apsacline, slightly rounded. The sulcus is relatively narrow ($W_s = 4; W_s/W = 0.25-0.30$), widely rounded to slightly flattened anteriorly. The costae are rounded in section, separated by furrows of the same shape and width. There are 6-7 costae per flank. An incomplete
questionable dorsal valve from the (younger) level A 3 shows at least 8 lateral ribs.

The dental plates, located on the second pair of ribs, are thin, more or less thickened posteriorly, and slightly curved towards the interior anteriorly. Their length does not exceed one half shell length. The muscle field is not excavated. A faint ventral median myophragm is present, about 1/3 of shell length.

Available shells are sparse and preclude any estimation of the species variability. Some aspects (size, shape, number of ribs) evoke the species *H. (Hysterohowellella) knetschi* Carls, 1985, but in the latter, dental plates are invariably located in the first furrow. In *H. (Hysterohowellella) coryzans* Carls, 1969 maximum width is also close to the hinge line, but the number of ribs is generally greater (nevertheless comparable to the brachial valve mentioned above), the area strongly curved and apsacine, and dental plates are straight. The Portuguese specimens enter in the variability range of *H. (Howellella) mercurii* that is widely distributed in Western Europe and other areas during the lower Lochkovian.

*Howellella (Howellella) mercurii* ssp. R Carls, 1985
Fig. 4 and Pl. 1, Figs. 23-24

Material: Over 30 internal and external molds of isolated valves and numerous fragments. MG 10884-10885.

Locality: Level A 1 (section A) and C; Serra do Lução Formation

Synonymy: 1977 *Howellella mercurii* ( Gosselet, 1880) - Carls, p. 153, 155, fig. 6.
 pars 1985 *Howellella mercurii* ( Gosselet, 1880) - Gourvennec, p. 152.
 1985 *Howellella (Howellella) mercurii* n. ssp. R - Carls, p. 318, pl. 2, fig. 28-34.

**Description**

The shell is small (*L* _mean_ = 3.5; *W* _mean_ = 6.5; *L* _max_ = 6.5 mm; *W* _max_ = 10.5 mm) (Figure 4), with semicircular outline (*L*/*W* _mean_ = 0.53), and widely rounded cardinal extremities. The hingeline is shorter than maximum width, located between 1/3 and 1/2 of shell length. The shell is ventribiconvex. The ventral interarea is high, slightly curved, apsacine. The well delimited sulcus is shallow (depth not exceeding that of adjacent furrows), widely rounded in section, and relatively wide (*W*_s/W* _mean_ = 0.27). The fold is well delimited and low; in lateral view, its profile is parallel to the overall shell profile, and devoid of notable elevation near the anterior commissure. Its transverse section is rounded or may become slightly flattened near the anterior commissure.

Ornament consists of few low, rounded ribs (3-4 per flank, rarely 5 or 6), with rounded section, separated by rounded furrows. Only the 2 or 3 internal pairs of ribs are well expressed, the external ones generally low, particularly on internal molds. Micro-ornament consists of densely spaced growth lamellae (about 6 per mm), bearing marginal spine bases on their anterior edge, the latter generally badly preserved.

Ventral interior: On the internal mold, a shallow myophragm reaches about 1/3 to 1/2 of the shell length. Dental plates are thin, straight, occasionally slightly curved internally, and located on the second pair of ribs, or on the internal edge of these ribs. The muscle field is not excavated.

Dorsal interior: A myophragm corresponds to that in the ventral valve. On the internal mold, the crural plates appear as two divergent or subparallel, relatively wide incisions on each side of the cardinal process, that is lamellose, with only 3 to 4 lamellae. The dental sockets are divergent and shallow.

**Discussion**

The features present in this species appear early in the mercurii-lineage (see Gourvennec, 1985): fold profile following the shell curvature, number of ribs, location of the maximum width, widely rounded cardinal extremities, etc.. They are found in *H. mercurii* ssp. R described by Carls in Celtiberia, from the lowermost Lower Gedinnian (level d1bβ, Luesma Fm.). A closely related form, *Howellella* sp. M, formerly known as "Howellella e.g. elegans", is also reported by Carls (1977) from the Upper Silurian (Pridolian, level d1aβ, Luesma Fm.) of this area. The main difference between these species lies in the number of ribs (3-4 in *Howellella* sp. M to 4-5 in *H. mercurii* ssp. R). The highest frequency in our form is 4 ribs per flank, thus it appears as an intermediate form; nevertheless, rare specimens have 5 or 6 ribs per flank, indicating similarity with *H. mercurii* ssp. R, hence our assignment here, but we cannot exclude that this form could be an intermediate, slightly older than *H. mercurii* ssp. R _sensu stricto_. Another related but slightly larger form is known from early Lochkovian of the Massif armoricain, in the Landévennec Formation (lower part of the middle member) (Gourvennec, 1989).
Howellella (Hysterohowellella) lunae gourvenneci CARLS, MEYN & VESPERMANN, 1993
   Pl. 1, Fig. 25

Material: A single incomplete internal mold of a ventral valve. MG 10886.

Locality: Level A 5 (section A); Serra do Luação Formation

Synonymy: 1993 Howellella (Hysterohowellella) lunae gourvenneci n. ssp. - Carls, Meyn & Wespermann, p. 247, pl. 6, fig. 47-56.

Discussion
This single incomplete ventral valve resembles H. (Hysterohowellella) lunae gourvenneci. The valve is large (L= 10 mm; W> 15 mm), high and regularly curved. At least 8 wide, rounded ribs are visible on each flank, separated by subangular, slightly narrower furrows. The sulcus is wide (Ws/W = 0.3) with a single strong median rib. This rib is already well expressed at mid-length of the shell. Internal features unknown.

The features observed on this shell, particularly the median costa present on the sulcus, are typical of H. (Hysterohowellella) lunae gourvenneci CARLS et al., 1993 that was reported from the type locality in Celtiberia only (Poyales, level d2aβ5, Nogueras Fm., middle part of the upper Lochkovian).

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Stringocephaloidea King, 1850
Family Meganterididae Schuchert & LeVene, 1929
Subfamily Mutationellinae Cloud, 1942

Mutationella sarrobi RENOUF, 1972
   Pl. 1, Figs. 17-20

Material: About 30 internal molds, some of them preserved with both valves. MG 10873.

Locality: Level B 3 (section B) and C; Serra do Luação Formation

Synonymy: 1972 Mutationella sarrobi n. sp. RENOUF, p. 124, pl. 26, figs 4, 8, 9, 11.

Description
Shell of moderate size, ventribiconvex; dorsal valve being occasionally flattened. Outline subcircular (Lmean =
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8.1; W_{mean} = 8.4); maximum width about midlength. Shells are often slightly asymmetric. Commissure rectimarginate. Ventral beak curved. The foramen is hypothyrid to submesothyrid. The dorsal valve may occasionally be slightly medially depressed, particularly posteriorly. Ornament consisting of simple, subangular, rounded costae separated by narrow angular interspaces. Typically 20 costae (min = 16; max = 28) over the entire shell, originating at the apex.

Ventral interior: Dental plates short and divergent. Muscle scars lacking.

Dorsal interior: Short, discrete hinge plates; dental sockets shallow, short and divergent. Myophragm lacking (or a low, poorly expressed ridge may be present on rare specimens). Muscle scars lacking. Loop not observed.

Discussion

This species is close to M. barroisi Asselberghs, 1930, that differs from M. podolica Kozlowski, 1929 (type species of the genus) by its fewer ribs. The number of ribs in M. barroisi, as stated by Asselberghs (1930) is 20-32, but some authors have reported 14-16 ribs (Boucot, 1960) or 14-26 (Rachbouef, 1986). Renouf (1972) erected the species M. sarrobi for small mutationellids with a number of costellae intermediate between M. barroisi and M. podolica, that is 16-22. The present specimens accord with this range, and are assigned to M. sarrobi. Furthermore, like M. sarrobi, our specimens lack a median dorsal myophragm. This species has been described in the Landévennec Fm. (Lochkovian; Massif armorican, France).

Crinoidea

The shales, quartzites and sandstones of the Serra do Luação Formation contain few crinoid ossicles. Poor preservation, tectonic deformation, and coarse sandstones did not allow determination. Neither isolated plate nor columnal belonging to Dimerocrinites lanveoensis were collected in the Dornes area. This crinoid zone, used as a marker level of the basal Lochkovian in different areas of the Celtiberian Domain, has been recorded in the Portalegre and Valongo synclines (Le Menn et al., 2003, p. 57).

PALAEOGEOGRAPHICAL IMPLICATIONS

The Lower Devonian brachiopod fauna from Dornes is clearly of North-Gondwanan affinity (6 of 10 identified species are known only in peri-Gondwanan areas, the remaining ones being cosmopolitan). This fauna is closely related to that of the Armorican Massif at the species level, as seen by M. lecaroensis, P. monnierii, P. maillieuxi, H. undata, H. mercurii or M. sarrobi. Some poorly preserved species (e.g., S. runegatensis?, Protathyris sp. cf. P. praecursor) remain uncertain, but their presence in Portugal is likely. Most Portuguese species, excepting P. praecursor (M. sarrobi may be present as "M. barroisi"), have also been identified in Spain (Asturo-Leonese area and Celtiberia), one of these endemic in the Iberian Peninsula (H. lunae gouviennei). Relationships between the Centro-Iberic and the Asturo-Leonese zones are confirmed, as well as those of the Armorican Massif during the Lochkovian.

Four species have also been recorded in North Africa (P. monnierii, P. praecursor, H. undata and H. mercurii), but these are cosmopolitan. Otherwise, similarities between S. (R.) runegatensis and the North African species S. (R.) torkozensis Jansen, 1999, are to be underlined. Noteworthy is that four species are also common to, or very closely related to those identified from the Meguma Zone, Nova Scotia (Canada), among them two are typically of North-Gondwanan affinity (namely M. lecaroensis and S. runegatensis).

The Rhenish domain (Ardennes, Germany, Podolia, Southern Great Britain) has four shared species (five if M. barroisi is included as a counterpart of M. sarrobi), but these are cosmopolitan.

Concerning the Tabulata, during early Devonian, the genus Liguldicytum (including forms with entirely fibrous basal plate = Ligulodictyum s.s., forms with lamellar-microlamellar microstructure - see Lafuste et al., 1993 - and forms only preserved in natural cast with unknown microstructure) has a peri-Gondwanian distribution (Plusquellec, 2007). Occurrences are in France (Armorican Massif), Spain (Cantabrian Mountains and Palencia), Algeria (Tindouf Basin, Ougarta), Morocco (Anti-Atlas), Turkey, Australia (East-Central Victoria) and New Zealand (Takaka Terranes). The potential occurrences of South China (Pleurodictyum discoidea Yu in Wang et al., 1974) and of Altaï (? Pleurodictyum sp. Kahlfin 1935), can be discarded.

CONCLUSIONS

These new data show that: (1) the upper part of the Serra do Luação Formation belongs to the Lochkovian (which is relatively condensed in the Dornes spit since
lower Lochkovian faunas have been identified at the extreme end of the Dornes spit and upper Lochkovian faunas are present immediately below the limestones of the overlying Dornes Formation; (2) the miospore assemblages recovered from the upper part of Serra do Lucação Formation are assigned to the NM Biozone, confirming the early Lochkovian age; (3) these results allow improved biostratigraphic correlations with other regions of the Central Iberian Zone (as for instance Macão and Portalegre, in Portugal), Celtiberia, Palencia and Asturias, in Spain, and the Armorican Massif; (4) the studied faunas have clear Gondwanan affinities.

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REFERENCES


A reassessment of the Lochkovian (Lower Devonian) benthic faunas and palynomorphs from the Dornes region (southern Central Iberian Zone, Portugal)


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PLATES
PLATE I

Figs. 1-6 - *Platyorthis monnieri* (Rouault, 1851). 1: exterior of a ventral valve (latex replica); MG 10870; 2: ventral valve, internal mold; MG 10871; 3: dorsal valve, internal mold; MG 10872A; 4: dorsal interior (latex replica); MG 10873A; 5: ventral valve, internal mold, showing a particularly well developed muscle field; MG 10874; 6: latex replica of the same; all figures x2; level C.

Figs. 7-13 - *Mclearnites lecaroensis* (Renouf, 1972). 7: ventral valve (elongate form), internal mold; MG 10875, x1; level B 3; 8: dorsal interior (latex cast, with external mold of *M. sarrobi* below); MG 10876, x1.5; level C; 9: ventral interior (latex cast); MG 10872B, x2; level C; 10: ventral interior (latex cast) of a large, gerontic specimen with well developed myophragm; MG 10877B, x1.5; level B 3; 11: ventral valve (elongate form), internal mold; MG 10877A, x1.5; level B 3; 12: ventral valve, internal mold; MG 10878A, x2; level C; 13: fragmentary dorsal valve showing cardinalia and internally pitted shell; MG 10878B, x2; level C.

Figs. 14-15 - *Schizophoria (Rhenoschizophoria) runegatensis?* Renouf, 1972. 14: fragmentary ventral valve, internal mold, showing the strong median ridge and the almost straight dental plates; MG 10879; 15: fragmentary dorsal valve, internal mold, showing the sigmoid brachiophores; MG 10880; all figures x2; level C.

Fig. 16 - *Protathyris* sp. cf. *P. praeursor* Kozlowski, 1929. Ventral internal mold, MG 10881, x2.5; level C.

Figs. 17-20 - *Mutationella sarrobi* Renouf, 1972. 17: ventral internal mold; MG 10873B; 18: dorsal internal mold, MG 10873C; 19: posterior view of a complete internal mold; MG 10873D; 20: the same, anterior view; all figures x2.5; level C.

Fig. 21 - *"Camarotoechia"* sp. 2. Ventral valve, internal mold; MG 10882, x2.5; level B 3.

Fig. 22 - *Hexarhysis undata* (Defrance, 1828). Internal mold of a fragmentary ventral valve; MG 10883, x1.5; level C.

Figs. 23-24 - *Howellella (Howellella) mercurii* ssp. R Carls, 1985. 23: dorsal valve, internal mold; MG 10884; 24: ventral valve, internal mold; MG 10885; all figures x3; level A 1.

Fig. 25 - *Howellella (Hysterohowellella) lunae gourvennecci* Carls, Meyn & Wespermann, 1993. Internal mold of an incomplete, partially dolomitized ventral valve; note the median rib in the sulcus (arrow); MG 10886, x2; level A.

Fig. 26 - *Ligulodictyum ligulatum* (Plusquellec, 1965). Natural cast, upper side; MG 10877A, x 2; locality slightly above level A 1.
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PLATE II

Palynomorphs. Plate captions list the taxonomic name of the figured specimen, followed by the formation, sample number, slide number and microscopic coordinates.

1. *Laevolancis* sp.; Serra do Luação Formation, B3-1, 1430-200.
2. *Emphanisporites microornatus* Richardson and Lister, 1969; Serra do Luação Formation, B3-1, 1405-45.
4. *Retusotriletes warringtonii* Richardson and Lister, 1969; Serra do Luação Formation, B3-2, 1355-75.
5. *Archaeozonotrilites* sp.; Serra do Luação Formation, B3-1, 1415-205.
6. *Retusotriletes* sp.; Serra do Luação Formation, B3-1, 1325-140.
10. *Onondagaella* sp.; Serra do Luação Formation, B3-1, 1340-130.
11. *Diexalophasis remota* (Deunff) Playford, 1977; Serra do Luação Formation, B3-1, 1135-60.
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