Rivista Italiana di Paleontologia e Stratigrafia	volume 119	no. 3	1 pl.	pp. 247-256	November 2013

ASTRAELENIA SAOMAMEDENSIS N. SP. - A NEW GIGANTIC RHYNCHONELLID SPECIES AND ITS PALAEOBIOGEOGRAPHICAL IMPLICATIONS FOR THE PORTALEGRE SYNCLINE (CENTRAL PORTUGAL)

MENA SCHEMM-GREGORY [1,2] & JOSÉ M. PIÇARRA [3,4*]

Received: May 13, 2013; accepted: August 28, 2013

Key words: *Astraelenia*, Rhynchonellida, Brachiopoda, Stratigraphy, Palaeobiogeology, Palaeoecology, Stratigraphy, Lower Devonian, Portugal.

Abstract. A new species of *Astraelenia* is described from ?Siegenian to Emsian strata of the Portalegre Syncline (Central Portugal). *Astraelenia saomamedensis* n. sp. differs in a smaller number of costae, a rather inconspicuous fold and sulcus, and larger and elongate shells from other species of *Astraelenia*. *Astraelenia* occurs today in northern Africa, Central and Western Europe; the new species shows Gondwanan origin according to faunal elements found in the stratigraphic vicinity. The migration of *Astraelenia* is described considering Lower Devonian regional transgression and regression events. The new species is found in monospecific clusters and an attempt for understanding its palaeoecology is presented.

Riassunto. In questo lavoro viene descritta una nuova specie del genere *Astraelenia* proveniente da una successione di età ?Siegeniano-Emsiano affiorante in corrispondenza della Portalegre Syncline (Portogallo Centrale). *Astraelenia saomamedensis* n. sp. differisce dalle altre specie del genere per il numero di coste, per il solco e la piega poco evidenti e per la conchiglia più allungata e avente dimensioni maggiori. Il genere *Astraelenia* è presente nelle successioni dell'Africa settentrionale e dell'Europa centrale e occidentale; la nuova specie sembra avere origine gondwaniana in accordo con altri elementi faunistici trovati in prossimità stratigrafica. La migrazione delle specie di *Astraelenia* viene descritta nel quadro degli eventi trasgressivi e regressivi del Devoniano Inferiore. Viene inoltre proposto un tentativo di ricostruzione paleoecologica per la nuova specie, che è stata ritrovata in associazioni monospecifiche.

Introduction

The Museu Geológico (= Geological Museum) of Lisbon is part of the Laboratório Nacional de Energia e Geologia (LNEG) and holds the oldest and most complete geological and paleontological collections of Portugal including the first samples collected by the Geological Commission of the Kingdom of Portugal during their foundation period in 1857 to 1859 (MG 2012). The Museum is still situated on the 2nd floor of the ancient Convento de Jesus (= College of Jesus), the same place where it was founded. The paleontological collection consists of thousands of specimens collected since the foundation of the Geological Commission. The material was collected in the frame of the geological work carried out by the Serviços Geológicos de Portugal (= Portuguese Geological Survey), the Instituto Geológico e Mineiro (= Geological and Mining Institute) and, currently, the LNEG. With a few exceptions, all fossil material stored in the Geological Museum is identified, however, many specimens have not yet been assigned to currently recognized genera and higher taxa. The unidentified specimens and the bulk of the regional and stratigraphic collection is stored in the archive of the LNEG in Alfragide. Today these extensive collections are important reference collections and are frequently used by Portuguese and foreign scientists for multiple purposes.

The main part of the material studied in this work was collected at the beginning of the 20th century by Nery Delgado, one of the pioneers in the study of the geology of Portugal (Ramalho 2008). Joachim Felipe Nery da Encarnação Delgado (1835-1908) was born in

1 Centro de Geociências, Universidade de Coimbra, Largo Marquês de Pombal, 3000-272 Coimbra, Portugal.
2 Museu Geológico, Laboratório Nacional de Energia e Geologia (LNEG), Rua Academia das Ciências, 19, 1200-003 Lisbon, Portugal.
3 * Corresponding author. Laboratório Nacional de Energia e Geologia (LNEG), Ap. 104, 7801-902 Beja, Portugal. E-mail: jose.picarra@lneg.pt
4 Collaborator Member. Centro de Geociências, Universidade de Coimbra, Largo Marquês de Pombal, 3000-272 Coimbra, Portugal

Elvas (Portugal) and studied astronomy, mineralogy, geology, and topography at the Escola Politécnica de Lisboa (= Polytechnic School of Lisbon) and was a general in the Portuguese Army. Soon after the establishment of the Portuguese Geological Commission he was asked to be adjunct in the Secção da Direcção Geral dos Trabalhos Geológicos (= Section of General Direction of Geological Studies) and followed Carlos Ribeiro (1813-1882) as the head of the Portuguese Geological Commission (Carneiro 2008). The main part of Delgado's work was the study of the Paleozoic of Portugal and he published together with C. Ribeiro the first Geological map of Portugal, which was one of the first geological maps worldwide (Ribeiro & Delgado 1867). Due to the purpose of geological mapping, all samples, fossils, and rocks, are labeled with accurate collecting position, often based on geodesic points, and, as far as it was possible, with then current stratigraphic assignment. As a result, much more information is given that is usually available from classical collections. The Delgado Collection is, therefore, essential for correlation and paleontological and stratigraphic studies. Furthermore, the extensive collection provides material for outcrops that are not accessible anymore. Besides its high scientific importance, the Delgado Collection housed in the Geological Museum and at the archive of the LNEG, is one of the Geological and Palaeontological heritages of Portugal (Schemm-Gregory & Henriques in press).

Brachiopods are one of the most important fossil groups for stratigraphic assignments and palaeobiogeographic interpretations of Paleozoic, especially for Devonian neritic strata where pelagic conodonts or goniatites, usual index fossils for GSSP definitions, are lacking or very rare. Therefore, a revision and modern cataloging of this collection is of special importance for scientific studies. In the last six decades the classical Delgado Brachiopod Collection has been used for more detailed stratigraphic assignments of Silurian to Devonian strata of Central Portugal by Portuguese and foreign scientists (e.g., Pruvost 1914; Perdigão 1967; 1972/1973, 1973/1974; Gourvennec et al. 2008; Schemm-Gregory 2011).

This is one paper of a series on brachiopods from Portugal with aimed at revising the Delgado Brachiopod Collection and is a second step for improving the stratigraphy and the paleobiogeographic implication of the Portalegre Syncline (Gourvennec et al. 2010; Schemm-Gregory & Henriques 2013).

Geological Setting

The Portalegre Syncline is a major Hercynian structure in the south-eastern part of Central Portugal (Fig. 1; Tab. 1). It is characterized mainly by Ordovician to Carboniferous strata. Previous studies of this area are from Delgado (1908) and include a definition of the first Paleozoic lithostratigraphical succession and an important list of fossils. "Schistes coblentziens", limestones lenses, and associated quartzites are the only sediments considered to be of Devonian age. Brachiopods are the most common Devonian fossils determined by Delgado, but other groups also occur, such as trilobites, bivalves, crinoids, and corals. Some of these fossils were revised later by Pruvost (1914). Based on paleontological data, Costa (1931) defined four Devonian lithological units: "Quartzites with *Homolonatus* cf. *gigas*, *Cryphaeus* aff. *michelini*, *Avicula pseudo-laevis*, *Orthothetes hipponyx*"; "Carbonates, dolomitic carbonates and graywackes"; "Yellow and Red Shales with *Cryphaeus laciniatus*, *Phacops potieri*, *Spirifer paradoxus*, *Spirifer histericus*"; "Shales with *Stringocephalus burtini*?" (Tab. 1).

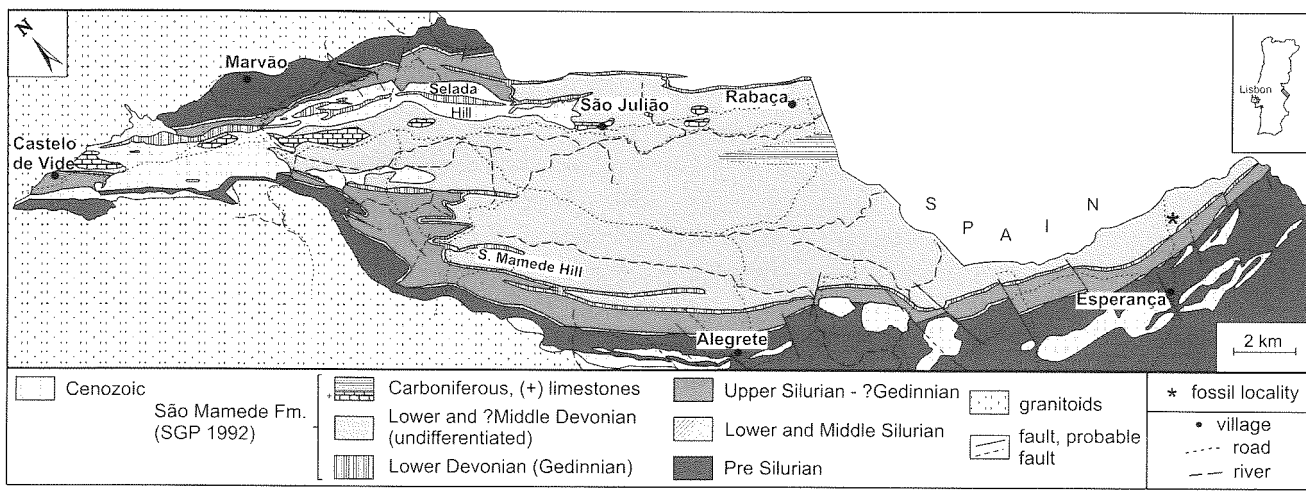


Fig. 1 - Geology of the Portalegre Syncline with the location of the fossiliferous locality (modified from Serviços Geológicos de Portugal/SGP 1992; adapt. Piçarra, J.; coord., in prep.). The stratigraphic position of the *Astraelenia saomamedensis* n. sp. yielding bed is indicated by the star.

A second important stage of investigation was devoted to biostratigraphy and included a significant collection of Devonian fossils, partly linked with the 1:50 000 geological mapping of this area (Fernandes et al. 1973; Perdigão & Fernandes 1976; Gonçalves et al. 1978). Perdigão (1967) revised the Delgado Brachiopod Collection and determined Middle Devonian ("Couvinian") species near Troviscal de Cima farm (São Julião). Study of the type material by M. S.-G. from the opt. cit. work confirms an Emsian to Givetian, ?Frasnian age of these brachiopods. Later, Perdigão (1972/1973; 1973/1974) reviewed old collections of other fossil groups, collected new material, and published a new geological map of the Portalegre Syncline. Although the Devonian faunas have been essential for defining and updating the stratigraphy, the stratigraphic assignment was not always easy to apply not only due to the structural complexity, but also the scarcity and lack of fossils in some areas, such as N of Alegrete-Esperança village and in the core of the syncline near the Spanish-Portuguese border. A more detailed Devonian lithological sequence was published by Perdigão & Fernandes (1976) and includes from bottom to top: shales and quartzites (Gedinnian); quartzites and sandstones (Siegenian); shales (Emsian), and dolomitic limestones and associated shales (Couvinian) (Tab. 1).

Later, in the 1992 Geological Map of Portugal (Serviços Geológicos de Portugal 1992) all these lithologies have been included in the "São Mamede Formation". This lithostratigraphic unit that has proved to be very useful in regional correlations with other areas (Dornes and Mação) from where new Devonian lithological and biostratigraphical data are available (Gourvennec et al. 2008, 2010).

More recently, palaeontogical studies were published and field work for the 1. 200 000 geological map (Piçarra, J.; coordinator, in prep.), still in progress, has provided new stratigraphic data:

– dolomitic limestones, at the other side of the border, in Spain, yielded Lower Carboniferous conodonts (Rodríguez González et al. 2007). This age was confirmed by the finding of spores in dark shales from southeast of São Julião village (Laboratório Nacional de Energia e Geologia 2010) (Fig. 1), previously considered as Devonian in age.

– taxonomic update of Devonian brachiopods and crinoids from old collections was made and new genera and species were determined, including specimens of Middle Devonian age (Gourvennec et al. 2010).

– the Ordovician to Carboniferous stratigraphy has been revised, resulting in a more detailed geological map with improved geology of the Portalegre Syncline as shown in Fig. 1.

In the Portalegre Syncline, brachiopod-bearing strata crop out representing almost the whole Devonian Period, Gedinnian to Givetian, ?Frasnian. The assignment to Frasnian age is still questionable and Famennian brachiopods have not been found yet. The genus *Astraelenia* has only been reported from Emsian age beds (Sartenaer 2009). In the geographic vicinity (a few km) of the collecting locality of *Astraelenia saomamedensis* n. sp. the brachiopod taxa *Plicostropheodonta murchisoni* (de Verneuil & d'Archiac in d'Archiac & de Verneuil, 1842), *Protodouvillina taeniolata* (Sandberger & Sandberger, 1856), *Platyorthis circularis* (Sowerby, 1842), *Leptostrophia explanata* (Sowerby, 1842), *Athyris* cf. *undata* (Defrance, 1828) and uncinulid rhynchonellids have been identified. These strata are either just stratigraphically below or above the *Astraelenia saoma-*

Tab. 1 - History of the stratigraphic subdivision of the Portalegre Syncline. The stratigraphic position of the *Astraelenia saomamedensis* n. sp. yielding bed is indicated by the brachiopod symbol.

	Delgado (1908)	Costa (1931)	Perdigão & Fernandes (1976)	Serviços Geológicos de Portugal (1992)
Famennian				"not found"
Frasnian				"not found"
Givetian				"not confirmed"
Eifelian		Shales with *Stringocephalus burtini*?"	Dolomitic limestones and shales	São Mamede Formation
Emsian	Limestones and quartzites	Yellow and Red Shales with *Cryphaeus laciniatus, Phacops potieri, Spirifer paradoxus, Spirifer histericus*	Shales	
Siegenian	"Schistes coblentziens"		Quartzites and sandstones	
Gedinnian		Carbonates,dolomitic carbonates and graywackes Quartzites with *Homolonatus* cf.*gigas* *Cryphaeus* aff. *michelini*, *Avicula pseudo-laevis*, *Orthothetes hipponyx*	Shales and quartzites	

medensis yielding beds. This brachiopod fauna clearly has a Late Siegenian age; however, it has to be stated that *Protodouvillina taeniolata* occurs in the Early Emsian in Germany and taxa of *Uncinuls* Bayle, 1878 from the Lochkovian to the Eifelian (e.g., Savage 2002a; Franke 2006). It is concluded that *Astraelenia saomamedensis* may appear during the Late Siegenian, but certainly is of Emsian age.

In this paper the regional stages Gedinnian, Siegenian and Emsian are used to subdivide the Lower Devonian in their classical German sense because the collecting locality represents neritic facies and correlation is based on brachiopod data (see Jansen et al. 2007 and literature cited therein).

Material and methods

Specimens of *Astraelenia saomamedensis* n. sp. described herein are preserved as disarticulated internal and external moulds. Internal moulds of articulated shells are rare. Latex casts of internal and external moulds were made to study the internal features of the new taxon. Measurements were taken with a digital caliper and rounded to 0.1 mm. Drawings were made with the help of a camera lucida. Specimens were coated with magnesium oxide prior to being photographed.

Institutional abbreviations

MG: Museu Geológico, Lisbon, Portugal. In the Delgado collection, a single MG number may include several specimens.

Systematic Palaeontology

Order **Rhynchonellida** Kuhn, 1949

? Superfamily Camarotoechioidea Schuchert, 1929

Family Astraeleniidae Sartenaer, 2009

Astraelenia Sartenaer, 2009

Type species: *Rhynchonella Losseni* Kayser, 1880: 820.

Stratigraphic distribution: ?Siegenian to Emsian in the classical German sense, ?middle to upper Lower Devonian.

Geographic distribution: western Europe, northern Africa.

Species assigned: *Rhynchonella Dannenbergi* Kayser, 1883. *Straelenia* sp. e. g. *losseni* Drot, 1964.

Remarks. *Astraelenia* is questionably assigned to the Superfamily Camarotoechioidea Schuchert, 1929 because it is in the same family as *Straelenia* Maillieux, 1935, for which family assignments are doubtful. Savage (2002b: 1375) regarded *Straelenia* as nomen dubium due to the poor preservation of the type material. A revision of topotype material is recommended to justify the systematic position of the Astraeleniidae Sartenaer, 2009.

Species of *Astraelenia* were first described at the end of the 19th century from the German Harz Mountains (Kayser 1880, 1883). They were placed, with other large rhynchonellid brachiopods, in the group of *Rhynchonella losseni* Kayser, 1880. More than half a century later, Maillieux (1935) established the genus *Straelenia* in which all large rhynchonellids of Siegenian and Emsian age were included. The short description led Schmidt (1955) to revise the genus and her diagnosis was used by Drot (1964) in identifying the rhynchonellid brachiopod fauna from Morocco. Due to insufficient information and bad preservation of the type material, Savage (2002b) considered the genus *Straelenia* as a nomen dubium. Sartenear (2009: 29) separated the group of straelenid brachiopods into *Straelenia* and *Astraelenia* with the type species *Astraelenia losseni* (Kayser, 1880). In general astraelenid brachiopods are large and clearly dorsibiconvex, whereas straelenid specimens are smaller and almost equibiconvex.

Astraelenia saomamedensis n. sp.

Pl. 1; Fig. 2; Tab. 2

Derivation of name: After the São Mamede Formation in which the new species occurs.

Holotype: MG 30262, ventral internal mould, width 34.8 mm, length 57.3 mm.

Paratypes: 14 ventral internal moulds, 25 dorsal internal moulds, 2 internal moulds of articulated shells and several fragments of external moulds on rock slabs with various specimens (MG 30240 – MG 30263).

Additional material from the same locality stored in the Delgado Collection of the Museu Geológico: 13 ventral internal moulds, 14 dorsal internal moulds and several fragments of external moulds on rock slabs with various specimens (MG 12083 – 12086, MG 24959 – 24963, MG 24978 – 24979).

Type horizon: São Mamede Formation, Emsian, upper Lower Devonian.

Type locality: Approximately 1 km S 81°E geodesic point Outeiro Branco, Serra da Esperança, Arronches county, Portalegre district, Central Portugal.

Repository: All specimens are stored in the Museu Geológico in Lisbon, Portugal.

Diagnosis: Elongate and dorsibiconvex *Astraelenia* with 4 to 5 costae in the sulcus and 6 to 7 costae on the fold. Septalium well-developed and large, dental plates short and thin and ventral muscle field elongate, narrow and not imbedded.

Description

Form and size: Large, broadly elongate and dorsibiconvex shells with low and inconspicuous fold and sulcus. All specimens are strongly deformed so that measurements were omitted. Therefore, measurements of the holotype represent the size of the fossil specimen but not the original size of the living animal.

External ornamentation: Fold and sulcus clearly developed, but inconspicuous, low, moderately broad and rounded, starting in the posterior third of the shell. Costae narrow, simple and rounded to angular beginning in the umbonal region of both valves, 4 to 5 on the sulcus, 6 to 7 on the fold, and up to 10 on each flank. Sulcus tongue low and rounded.

Interior of ventral valve: Moderate development of secondary shell material in the apical region. Fillings

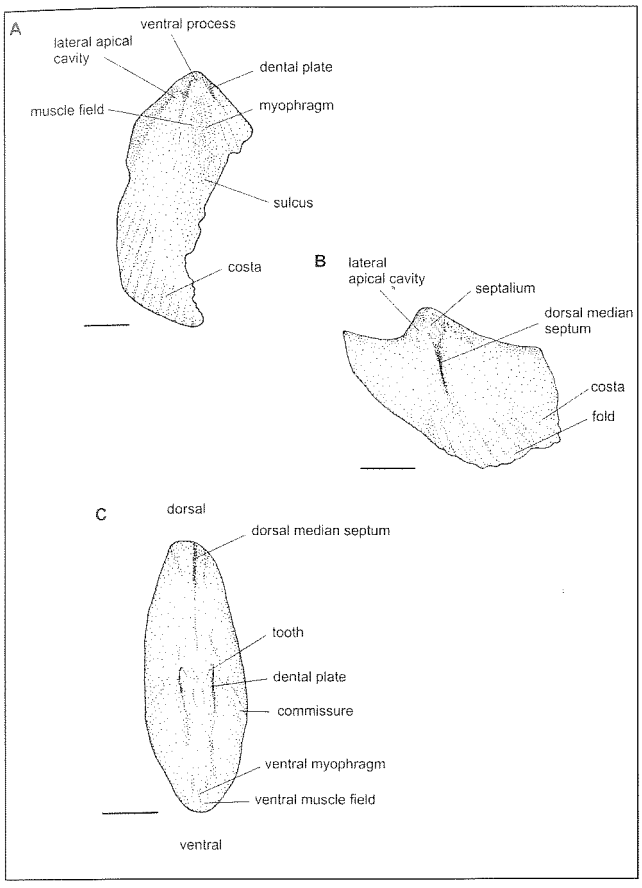


Fig. 2 - Morphological terms of *Astraelenia saomamedensis* n. sp. A. Upper view of ventral internal mould, holotype (MG 30262). B. Upper view of dorsal internal mould (MG 30242). C. Posterior view of internal mould of articulated shell (MG 30250). Scale bar = 10 mm. [Note: dental plate, dorsal median septum, lateral apical cavity, septalium, tooth, ventral process, (ventral) muscle field, (ventral) myophragm, are preserved as negative forms.]

of the lateral apical cavities sharp and reaching almost as far in a posterior direction as the filling of the ventral muscle field. Ventral process broad and short giving rise to a faint myophragm that extends to the entire ventral muscle field. Muscle field narrow, elongate, and long, not imbedded into shell material; laterally bordered by the dental plates, anterior margin not recognizable. Diductor scars preserved as radial striae on the internal mould. Dental plates moderately long, almost parallel to each other or gently divergent, hardly thickened in the posterior end, and leading into small and knob-like teeth. Impressions of costae anterior of the ventral muscle field.

Interior of dorsal valve: Moderate development of secondary shell material in the apical region. Fillings of lateral apical cavities sharp to rounded, the latter in gerontic specimens. Septalium clearly developed, elongate, and giving rise to a large, thick, and high dorsal median septum which is wedge-like in the posterior part. Septalium preserved as a broad and rounded ridge on the internal mould. Adductor field and cardinal process not recognizable on the internal mould. Impressions of costae anterior of the dorsal median septum.

Comparison. *Astraelenia saomamedensis* n. sp. is represented by very large specimens, however, quite deformed, but it can be stated that this species shows larger specimens than the type species, *A. losseni* (Kayser, 1880), to which is resembles most, and *A.* e. g. *losseni* (Drot, 1964). Specimens of *A. dannenbergi* (Kayser, 1883) are very large, too, but also strongly deformed so that the actual size and internal features such as orientation of dental plates, size and form of the dorsal median septum and the septalium cannot be given. A comparison of the morphological features of the species of *Astraelenia* is given in Tab. 2.

Astraelenia saomamedensis is elongate with straight dental plates and a very long dorsal median septum, whereas *A. losseni* is subcircular to gently transverse and has curved dental plates, a shorter dorsal median septum, and a smaller septalium. The sulcus in *A. losseni* is more sharply defined than in *A. saomamedensis* but this can be due to the deformation of the new species. *Astraelenia losseni* has 6 to 8 costae on the fold, 6 to 7 in the sulcus, and 12 to 16 on the flanks with more costae than *A. saomamedensis*, which has 6 to 7 costae on the fold, 4 to 5 in the sulcus, and up to 10 on each flank.

Astraelenia e. g. *losseni* differs from the new species in having less elongate forms, curved dental plates, a thin dorsal median septum and a small septalium. With 9 to 13 costae on the fold, 8 to 10 costae in the sulcus, and 15 to 20 costae on the flanks, almost double the number of costae for each subdivision of the shell.

Specimens of *A. dannenbergi* are poorly preserved as already stated by Drot (1964) and Sartenaer (2009). Specimens could not be studied personally, but according to the literature, *A. dannenbergi* is of almost the same size as *A. saomamedensis*. Even though the internal features of *A. dannenbergi* are unknown, the number of costae is the highest of all species of *Astraelenia*. *Astraelenia dannenbergi* has 15 to 20 costae on the fold, about 15 in the sulcus, and 15 to 18 on the flanks.

Stratigraphic and geographic distribution. São Mamede Formation, ?Siegenian to Emsian, ?middle to upper Lower Devonian; Portalegre Syncline, Central Portugal.

Palaeoecology

Astraelenia saomamedensis n. sp. is found in clusters in quarzitic sandstones. Specimens are mainly preserved as moulds of disarticulated shells, whereas internal moulds of articulated shells are rare. Shell material is not preserved in the studied material. Even though the material is strongly deformed due to tectonic deforma-

	Astraelenia saomamedensis n. sp.	*Astraelenia losseni* (Kayser, 1880)	*Astraelenia* e.g. *losseni* (Drot, 1964)	*Astraelenia dannenbergi* (Kayser, 1883)
size	very large	medium	medium to large	very large
form	elongate	subcircular to gently transverse	gently elongate	?
sulcus	rather inconspicuous	sharply marked	sharply marked	?
no. of costae on fold	6 - 7	6 - 8	9 - 13	15 - 20
no. of costae in sulcus	4 - 5	6 - 7	8 - 10	approx. 15
no. of costae on flank	up to 10	12 - 16	15 - 20	15 to 18
dental plates	straight	curved	curved	?
dorsal median septum	thick	thick	thin	?
septalium	large	small	small	?
geographic distribution	Central Portugal	Germany, France, Belgium	Morocco, Spain	Germany
stratigraphic distribution	?Siegenian, Emsian	Upper Emsian	Emsian	Lower Emsian

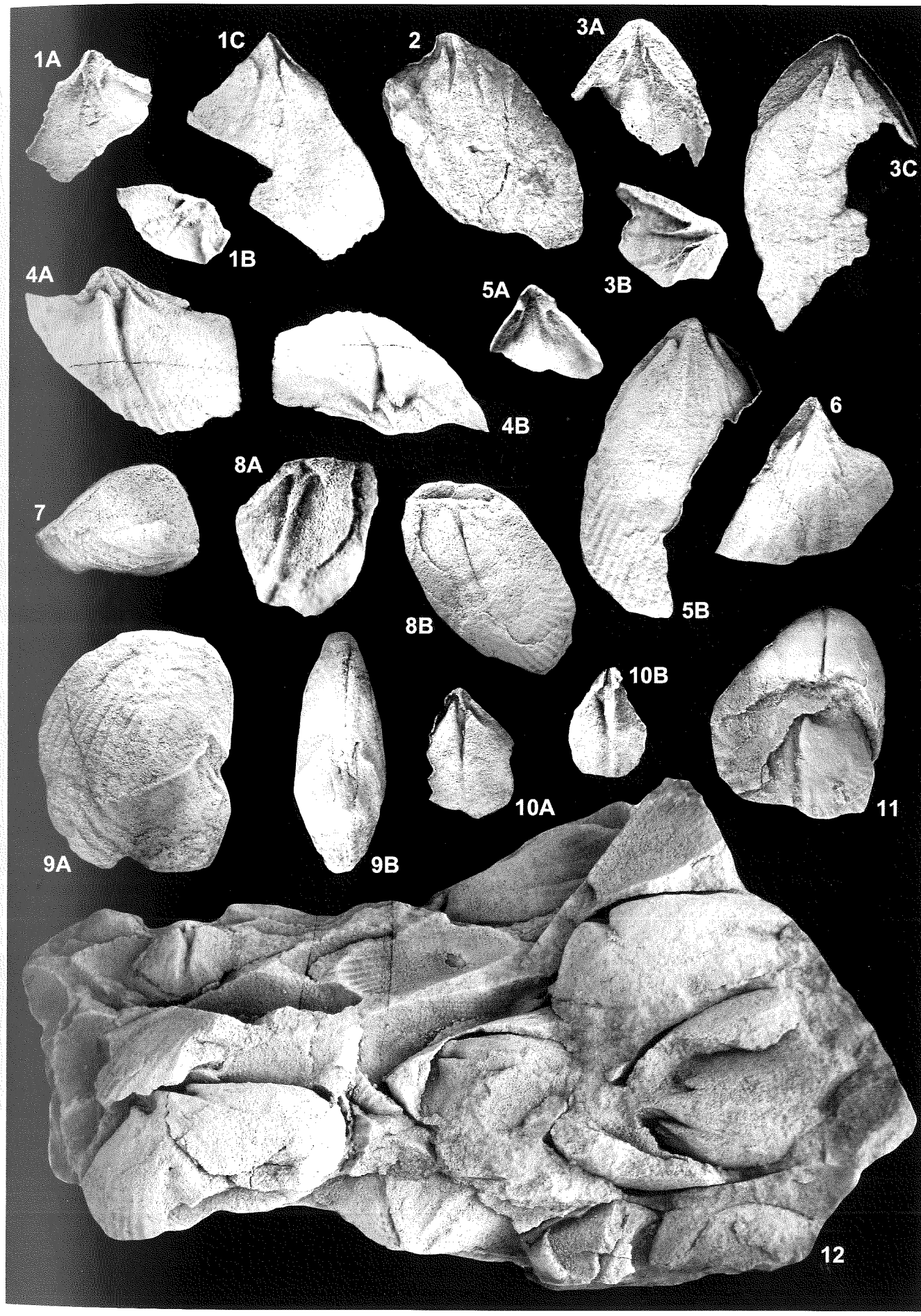
Tab. 2 - Morphological comparison of species of *Astraelenia*. [Remark: Due to tectonic deformation, internal features and original form of *A. dannenbergi* is unknown.]

tion, it can be said that the specimens within one cluster are of the same size. Exceptionally larger or smaller specimens were not seen and it is concluded that the studied material represents specimens of ordinary adult stage; however, due to the strong tectonic deformation the original size cannot be reconstructed. Furthermore, in most cases the complete shell is not preserved or the mould is still imbedded into the sediment. The relatively coarse ornamentation and the preservation in monospecific clusters argue for an exceptional environment probably in dirty turbid water of shallow epicontinental seas (Vörös 2005), somewhat comparable with the environment of the Upper Siegenian beds in which clusters of rhenorensselaerid terebratulids are found (Schemm-Gregory & Jansen 2007), however, no specimen described herein was found in life position. The disarticulation of shells can be explained by post-mortem transporation which also argues for selection by size of the water current. We conclude that the coarse costae suggest a rather dirty and turbid water. Rudwick (1964) concluded that a zigzag commissure enlarges the commissural length in comparison to an unfolded shell. Furthermore, the distance between the valve margins was reduced with the same opening angle of the shell.

PLATE 1

Astraelenia saomamedensis n. sp. All specimens are from the São Mamede Formation, Emsian,upper Lower Devonian and of original size. Collecting locality is the type locality.

Fig. 1 - MG 30244. Upper (A) and oblique anterolateral (B) views of latex cast and upper view of ventral internal mould (C).
Fig. 2 - MG 30245. Upper view of ventral internal mould.
Fig. 3 - Upper (A) and oblique anterolateral (B) views of latex cast and upper view of ventral internal mould (C).
Fig. 4 - MG 30242. Upper (A) and posterior (B) views of dorsal internal mould.
Fig. 5 - MG 30262, holotype. Upper views of latex cast (A) and ventral internal mould (B).
Fig. 6 - MG 30253. Upper view of ventral internal mould.
Fig. 7 - MG 30260. Lateral view of internal mould of articulated shell.
Fig. 8 - MG 30258. Upper views of latex cast (A) and dorsal internal mould (B).
Fig. 9 - MG 30250. Lateral (A) and posterior (B) views of internal mould of articulated shell.
Fig. 10 - MG 30261. Upper views of dorsal internal mould (A) and latex cast (B).
Fig. 11 - MG 30261. Rock slab with 2 dorsal internal moulds in posterior (top) and upper (bottom) views.
Fig. 12 - MG 30263. Rock slab with several ventral and dorsal internal and external moulds.


1A
1C
2
3A
3C
1B
4A
5A
3B
4B
6
8A
7
8B
5B
10B
10A
11
9A
9B
12

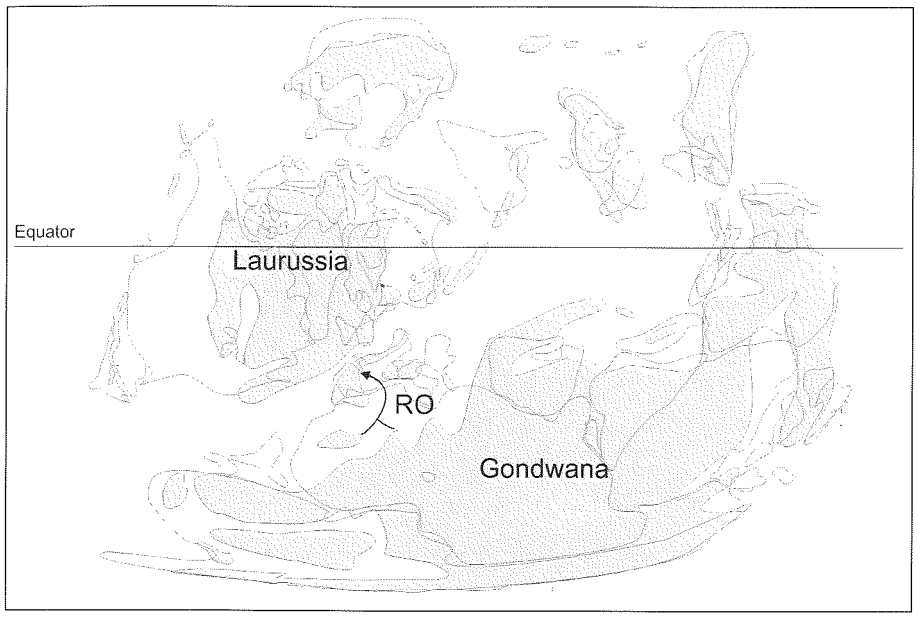


Fig. 3 - Early Devonian palaeogeography based on Boucot & Blodgett (2001) and modified from Schemm-Gregory (2009). The migration of *Astraelenia* into the northern Rheic Ocean is indicated by the arrow. [RO = Rheic Ocean]

This narrowed commissure gap prevented coarse particles from entering the mantle cavity which is an advantage for the feeding brachiopod in high energy, nutrient rich settings.

Palaeobiogeography

The Portalegre Syncline belongs to the Central Iberian Zone which has been already interpreted to be a terrane of northern Gondwana (e.g., Gourvennec et al. 2008, 2010; Schemm-Gregory 2011). *Astraelenia saomamedensis* n. sp. is only reported from the collecting locality but taxa within the same genus occur in Western and Central Europe and northern Africa. The most similar species, *A.* e.g. *losseni* (Drot, 1964) has been found in Morocco and Spain (Drot 1964; García-Alcalde 1992; Truyóls-Massoni & García-Alcalde 1994), regions that belong to Gondwana. The occurrence of *Astraelenia* in Central Europe argues for migration between these two regions during the Devonian (Fig. 3). Schemm-Gregory (2008) already discussed faunal exchange by the terebratulid genus *Rhenorensselaeria* Kegel, 1913 through the Rheic Ocean from the Rheinisches Schiefergebirge (Germany) into the Armorican Massif (France) and the Dra Valley (Morocco) during the earliest Middle Siegenian or the latest Early Siegenian. Another time interval for faunal exchange between these two regions is the Siegenian/Emsian boundary interval (e.g., Johnson et al. 1985; García-Alcalde 1998). It is probable that *Astraelenia* invaded the northern part of the Rheic Ocean at that boundary interval because taxa are found with certainty in Lower Emsian beds in the Rheinisches Schiefergebirge, however, there are also questionable Siegenian forms, such as *Rhynchonella letissieri* Oehlert, 1877 from the Armorican Massif or *Rhynchonella pengelliana* Davidson, 1865 in 1864-1871 from Cornwall. During the Emsian, *Astraelenia* species developed independently and further faunal exchanges cannot be observed which argues for an increase of endemism during the Emsian.

It has to be stated that the palaeogeographic relationships of the northern Gondwanan terranes to Laurussia and Gondwana during the Devonian are still a matter of debate (see Franke et al. 2000 and citations therein). Robardet (2003) analyzed palaeomagnetic results obtained from Spain, France, and Bohemia and concluded that the geographic position of these regions cannot be confirmed with certainty due to the ambiguous data obtained from Western Europe. This makes a comparison from data with Bohemia useless.

However, the occurrence of *Astraelenia* species in Western and Central Europe and in Africa demonstrates a close geographic relation among these regions and that faunal migration through the Rheic Ocean was possible during the middle Early Devonian. Then, slightly later endemism increased, probably caused by sea level changes rather than by drifting of terranes.

Note of the editorial committee

Very sadly Mena Schemm-Gregory passed away on July, 2013 during the final steps of the revisions of this manuscript. She was a young, but already very successful brachiopodologist, well known for her important contributions not only to brachiopod research, but also to the stratigraphy of the Palaeozoic.

She published many papers in peer-reviewed journals and Rivista Italiana di Paleontologia e Stratigrafia was happy to publish her detailed and important palaeontological results.

Some corrections to the present manuscript have been performed by the Editorial Committee after her ultimely death, with the kind help of the reviewers Robert B. Blodgett (Anchorage, Alaska, USA), and Arthur J. Boucot (Corvallis, Oregon, USA) and the second author José Piçarra.

Acknwoledgements. The authors thank Miguel M. Ramalho and Rita Silva (all LNEG, Lisbon) for giving access to the brachiopod collections under their care. Lucia Angiolini (Università degli Studi di Milano, Milan, Italy) kindly provided the Italian translation of the abstract. Lucia Angiolini, Robert B. Blodgett (Anchorage, Alaska, USA), and Arthur J. Boucot (Corvallis, Oregon, USA) critically read the manuscript and provided valuable suggestions for its scientific and stylistic improvement.

This study is financed by the Portuguese Fundação para a Ciência e a Tecnologia (FCT) grant SFRH/BPD/71647/2010 "Devonian Brachiopods from Portugal: The importance of classical collections for modern paleontology".

This is a contribution to the IGCP Project 596 "Climate Change and biodiversity Patterns in the Mid-Paleozoic".

REFERENCES

d'Archiac E.A.J.D. & de Verneuil E. (1842) - Memoir on the fossils of the older deposits in the rhenish provinces, preceded by a general survey of the fauna of the paleozoic rocks, and followed by a tabular list of the organic remains of the Devonian system in Europe. Textband und Tafelband. *Trans. Geol. Soc. London*, 2nd Ser., 6(2): 5-40.

Bayle E. (1878) - Fossiles principaux de terranes de la France. Explication de la Carte Géologique de la France, 4(1): 158 pp.

Boucot A.J. & Blodgett R.B. (2001) - Silurian-Devonian biogeography. In: Brunton C.H.C., Cocks L.R.M. & Long S.L. (Eds) - Brachiopods Past and Present. *System. Ass. Spec. Vol. Ser.,* 63: 335-344 Taylor & Francis, London & New York.

Carneiro A. (2008) - Nery Delgado (1835-1908), Geólogo do Reino. In: Ramalho MM (Coord.) - Nery Delgado (1835-1908), Geólogo do Reino, Lisboa. Museu Geológico/Centro de História e Filosofia da Ciência e da Tecnologia da FCTUNL, 2008: 8-27, Lisbon.

Costa C. (1931) - O Paleozóico Português (Síntese e Crítica). Sec. Hist. Nat. Fac. Ciên. Univ. Porto, 141 pp. University of Porto, Porto.

Davidson T. (1864-1871) - British Fossil Brachiopoda, III: Devonian and Silurian species, 2 V. of 397 pp., The Palaeontogr. Soc., London.

Defrance M.J.L. (1828) - Térébratules fossiles. In: Cuvier G. (Ed.) - Dictionnaire des Sciences Naturelles. F. G. Levrault, 52: 147-167, Strasbourg.

Delgado J.N. (1908) - Systéme Silurique du Portugal. Étude de stratigraphie paléontologique. *Mém. Comm. Serv. Géol. Portugal*, Lisbon, 245 pp.

Drot J. (1964) - Rhynchonelloidea et Spiriferoidea silurodévoniens du Maroc pré-saharien. *Notes Mém. Serv. géol. Maroc*, 178: 1-288.

Fernandes A.P., Perdigão J.C., Carvalho H.F. & Peres A.M. (1973) - Carta Geológica de Portugal, na escala 1/50 000. Notícia Explicativa da folha 28-D, Castelo de Vide. Serviços Geológicos de Portugal, Lisbon.

Franke C. (2006) - Die Klerf-Schichten (Unter-Devon) im Großherzogtum Luxemburg, in der Westeifel (Deutschland) und im Gebiet von Burg Reuland (Belgien): fazielle und biostratigraphische Deutungen. *Ferrantia*, 46: 42-96.

Franke W., Haak V., Oncken O. & Tanner D. (Eds) (2000) - Orogenic Processes: Quantification and Modelling in the Variscan Belt. *Geol. Soc. London Spec. Publ.*, 179: 1-459.

García-Alcalde J. (1992) - El Devónico de Santa María del Mar, (Castrillón, Asturias, España). *Rev. Esp. Paleont.*, 7(1): 53-79.

García-Alcalde J. (1998) - North Gondwanan Emsian Events. *Episodes*, 20(4): 241-246.

Gonçalves F., Perdigão J.C., Coelho A.V.P. & Munhá J.M. (1978) - Carta Geológica de Portugal, na escala 1/50 000. Notícia Explicativa da folha 33-A, Assumar. Serviços Geológicos de Portugal, Lisbon.

Gourvennec R., Le Menn J., Piçarra J., Oliveira J.T. & Robardet M. (2010) - Braquiópodes e crinóides do Devónico Inferior e Médio do sinclinal de Portalegre: bioestratigrafia e paleogeografia. III Congresso Ibérico de Paleontologia, Lisbon, July 2010: 3 pp.

Gourvennec R., Plusqeullec Y., Pereira Z., Piçarra M.J., Le Menn J., Oliveira T., Romão J.C. & Robardet M. (2008) - A reassessment of the Lochkovian (Lower Devonian) benthic faunas and palynomorphs from the Dornes region (southern Central Iberian Zone, Portugal). *Com. Inst. Geol. e Min.*, 95: 5-25.

Jansen U., Lazreq N., Plodowski G., Schemm-Gregory M., Schindler E. & Weddige K. (2007) - Neritic-pelagic correlation in the Lower and basal Middle Devonian of the Dra Valley (S Anti-Atlas, Moroccan Pre-Sahara). *Geol. Soc., Spec. Pub.*, 278: 9-37.

Johnson J.G., Klapper G. & Sandberg C.A. (1985) - Devonian eustatic fluctuations in Euramerica. *Geol. Soc. Am. Bull.*, 96: 567-587.

Kayser E. (1880) - Über hercynische und silurische Typen im rheinischen Unterdevon. *Zeitschr. Deut. geol. Ges.*, 32(4): 819-821.

Kayser E. (1883) - Beschreibung einiger neuen Goniatiten und Brachiopoden aus dem rheinischen Devon. *Zeitschr. Deut. geol. Ges.*, 35(1): 306-317.

Kegel W. (1913) - Der Taunusquarzit von Katzenelnbogen. *Abh. Königl. Preuß. Geol. Landesanst.*, 76: 1-163.

Kuhn O. (1949) - Lehrbuch der Paläozoologie. V. of 326 pp. E. Schweizerbart'sche Verlagsbuchh., Stuttgart, 326 pp.

Laboratório Nacional de Energia e Geologia (2010) - Carta Geológica de Portugal à escala 1:1 000 000. Labora-

tório Nacional de Energia e Geologia (LNEG), Lisbon.

Maillieux E. (1935) - Contribution à la connaissance de quelques Brachiopodes et Pélécypodes dévoniens. *Mém. Mus r. Hist. nat. Belg.*, 70: 1-42.

MG (2012) - Museu Geológico, Laboratório Nacional de Geologia e Energia. http://www.lneg.pt/MuseuGeologico/ (Accessed 16 November 2012).

Oehlert D. (1877) - Sur les fossiles dévoniens du départment de la Mayenne. *Bull. Soc. Géol. Fr.*, 5 (1876-1877): 578-603.

Perdigão J.C. (1967) - Descoberta de Mesodevónico em Portugal (Portalegre). *Com. Serv. Geol. Port.*, 52: 27-46.

Perdigão J.C. (1972/1973) - A fauna das grés e quartzitos silúricos-devónicos de Portalegre e a sua posição estratigráfica. *Com. Serv. Geol. Port.*, 56: 5-32.

Perdigão J.C. (1973/1974) - O Devónico de Portalegre. *Com. Serv. Geol. Port.*, 57: 203-225.

Perdigão J.C. & Fernandes A.P. (1976) - Carta Geológica de Portugal, na escala 1/50 000. Notícia Explicativa da folha 29-C, Marvão. Serviços Geológicos de Portugal, Lisbon.

Piçarra J. (coord., in prep.) - Carta Geológica de Portugal à escala 1:200 000, Folha 6. Laboratório Nacional de Energia e Geologia (LNEG), Lisbon.

Pruvost P. (1914) - Observations sur les Terrains Dévoniens et Carbonifères du Portugal et sur leur faune. *Serv. Géol. Port.*, 10: 1-21.

Ramalho M.M. (Ed. 2008) - Nery Delgado, 1835-1908: Geólogo do Reino. V. of 168 pp. Centro de História e Filosofia da Ciência da FCTUNL, Museu Geológico, Lisbon.

Ribeiro C. & Delgado N. (1876) - Carta Geológica de Portugal (escala 1:500 000). Direcção Geral dos Trabalhos Geodésicos e Topográphicos, Lisbon.

Robardet M. (2003) - The Armorica 'microplate': fact or fiction? Critical review of the concept and contradictory palaeobiogeographical data. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 195: 125-148.

Rodríguez R.G., Varea P.M., Lodeiro F.G., Parra L.M.M., Poyatus D.M. & Matas J. (2007) - Microflora y conodontos del Mississippiense en la Fm Gévora (Núcleo del sinforme la Codosera-Puebla de Obando, SO de la Zona Centroibérica). *Rev. Soc. Geol. Esp.*, 20 (1-2): 71-88.

Rudwick, M.J.S. 1964. The function of zigzag deflections in the commissures of fossil brachiopods. *Palaeontology*, 7: 135-171.

Sandberger G. & Sandberger F. (1856) - Die Versteinerungen des Rheinischen Schichtensystems in Nassau. Mit einer kurzgefaßten Geognosie dieses Gebietes mit steter Berücksichtung analger Schichten anderer Länder.: 233-564, Kreider & Niedner Verlagshandlung, Wiesbaden.

Sartenaer P. (2009) - Two new Emsian rhynchonellid (brachiopod) genera from the Eifel area (Germany). *Bull. Inst. r. Sci. nat. Belg., Sci. de la terre*, 79: 27-42.

Savage N.M. (2002a) - Uncinuloidea. In: Kaesler R.L. (Ed.) - Brachiopoda revised, Part H, Treatise on Invertebrate Paleontology, vol. 4, Rhynchonelliformea (part.): 1092-1131. The Geological Society of America, Boulder, Colorado, and the University of Kansas Press, Lawrence, Kansas.

Savage N.M. (2002a) - Nomina dubia. In: Kaesler R.L. (Ed.) - Brachiopoda revised, Part H, Treatise on Invertebrate Paleontology, vol. 4, Rhynchonelliformea (part.): 1372-1376. The Geological Society of America, Boulder, Colorado, and the University of Kansas Press, Lawrence, Kansas.

Schemm-Gregory M. (2008) - A new terebratulid brachiopod species from the Siegenian (middle Lower Devonian) of the Dra Valley, Morocco. *Palaeontology*, 51(4): 793-806.

Schemm-Gregory M. (2009) - Phylogeny, taxonomy, and palaeobiogeography of delthyridoid spiriferids (Brachiopoda, Silurian to Devonian). Ph.D. thesis, Wolfgang Goethe-Universität Frankfurt: 610 pp., Frankfurt am Main.

Schemm-Gregory M. (2011) - *Lusitanispirifer lusitanensis* n. gen. et sp. - A new delthyridoid spirifer and its palaeogeographical implications for the Dornes Syncline (Lower Devonian, Portugal). *Boll. Soc. Paleont. Ital.*, 50(2): 85-94.

Schemm-Gregory M. & Henriques M.H. (2013) - The Devonian Brachiopod collections of Portugal - a paleontological heritage. *Geoheritage*, DOI 10.1007/s12371-013-0080-x.

Schemm-Gregory M. & Henriques M.H. (in press) - As Coleções de Braquiópodes Paleozoicos do Museu Geológico (Lisboa, Portugal). *Com. Geol.*, Lisbon.

Schemm-Gregory M. & Jansen U. (2007) - A new genus of terebratulid brachiopod from the Siegenian of the Rhenisches Schiefergebirge. *Acta Palaeontol. Pol.*, 52(2): 413-422.

Schmidt H. (1955) - Devonische Gattungen der Rhynchonelliden (Brach.). *Senckenbergiana Lethaea*, 36(1-2): 115-122.

Schuchert C. (1929) - Classification of brachiopod genera, fossils and recent. In: Schuchert C. & LeVene C.M. (Eds) - Brachiopoda (Generum et Genotyporum Index et Bibliographia). Fossilum Catalogus I: Animalia, vol. 42: 10-25. W. Junk, Berlin.

Serviços Geológicos de Portugal (1992) - Carta Geológica de Portugal à escala 1:500 000. Serviços Geológicos de Portugal, Lisbon.

Sowerby, J. de C. 1842 in 1840-1846. The Mineral Conchology of Great Britain. V. 7 of 80 pp. Published by the author, London.

Truyóls-Massoni M. & García-Alcalde J.L. (1994) - Faune rhéno-bohémienne (Dacryconarides, Brachiopodes) à la limite Emsien inférieur/supérieur au Cabo la Vela (Asturies, Espagne). *Geobios*, 27(2):221-241.

Vörös A. (2005) - The smooth brachiopods of the Mediterranean Jurassic: Refugees or invaders? *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 223: 222-242.