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: Astrapelula, Rhynochonellida, Brachiopoda, Stratigraphy, Palaeobiogeology, Palaeoecology, Stratigraphy, Lower Devonian, Portugal.

Abstract. A new species of Astrapelula is described from the Emsian strata of the Portalegre Syncline (Central Portugal). Astrapelula 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 Astrapelula. Astrapelula occurs today in northern Africa, Central and Western Europe; the new species shows Gondwanian origin according to faunal elements found in the stratigraphic vicinity. The migration of Astrapelula 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 Astrapelula proveniente da una successione di età Emsiana-Emisiana affiorante in corrispondenza della Portalegre Syncline (Portogallo Centrale). Astrapelula saomamedensis n. sp. differisce dalle altre specie del genere per il numero di coste, il solo e la piega poco evidente e per la conchiglia più allungata e avente dimensioni maggiori. Il genere Astrapelula 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 Astrapelula viene descritta nel quadro degli eventi trasgressivi e regressivi del Devoniano Inferiore. Viene inoltre proposto un tentativo di ricostruzione palaeoecologica 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 palaeontological 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 palaeontological 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 Beia, 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 geodetic 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 Paleontological heritages of Portugal (Schemm-Gregory & Henriques in press).

Brachiopods are one of the most important fossil groups for stratigraphic assignments and palaeobiographic 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; Gourvenec 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 (Gourvenec 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 (1938) and include a definition of the first Paleozoic lithostratigraphical succession and an important list of fossils. “Schistes coblentziens”, limestones, 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 Homalonotus cf. gigas, Clypeus aff. mitchelini, Avicula pseudo-laevis, Ontholthetes hippocynx”; “Carbonates, dolomitic carbonates and graywackes”; “Yellow and Red Shales with Clypeus lacinatus, Phacops potieri, Spirifer paradoxus, Spirifer histeriens”; “Shales with Stringocephalus burtni” (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 Astraenia sâomamedensis 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 ("Couvniân") 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 (Couvniân) (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 (Gourvenec et al. 2008, 2010).

More recently, palaeontological studies were published and field work for the 1. 250 000 geological map (Píçarra, 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 (Rodriguez 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 (Gourvenec et al. 2010).

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 Famen- nian brachiopods have not been found yet. The genus Astraeolina has only been reported from Emsian age beds (Sartenaer 2009). In the geographic vicinity (a few km) of the collecting locality of Astraeolina saomamedensis n. sp. the brachiopod taxa Plicostrophiodes murchisoni (de Verneuil & d’Archiac in d’Archiac & de Verneuil, 1842), Protodouvillella taeniolata (Sandberger & Sandberger, 1856), Platythyris circularis (Sowerby, 1842), Leptostrophia explanata (Sowerby, 1842), Athyrus cf. undata (Defrance, 1828) and uncinitulid rhynchonellids have been identified. These strata are either just stratigraphically below or above the Astraeolina saoma-

<table>
<thead>
<tr>
<th>Tab. 1</th>
<th>History of the stratigraphic subdivision of the Portalegre Syncline. The stratigraphic position of the Astraeolina saomamedensis n. sp. yielding bed is indicated by the brachiopod symbol.</th>
</tr>
</thead>
<tbody>
<tr>
<td>F ammonian</td>
<td></td>
</tr>
<tr>
<td>Frasnian</td>
<td></td>
</tr>
<tr>
<td>Givetian</td>
<td></td>
</tr>
<tr>
<td>Eifelian</td>
<td>Shales with Stringocephalus bartini?</td>
</tr>
</tbody>
</table>
| Emsian | Limestones and quartzites | Yellow and Red Shales with 
| | | Cylindrolepis laevissima, Phacops pollini, Spirolocularia paradoxus, 
| | | Spirolocularia hastata |
| Siegenian | "Schistes oblienziens" | Shales |
| Gedinnian | Carbonates, dolomitic carbonates and graywackes | Quartzites with Monocotylus of gigas, 
| | | Cyphusa aff. ich,)iulida, Aculia pseudolageniformes Orthocystites bipinnex |

<table>
<thead>
<tr>
<th></th>
<th>São Mamede Formation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shales and quartzites</td>
</tr>
</tbody>
</table>


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

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

Material and methods

Specimens of Astraelinia 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 col-
clection, a single MG number may include several specimens.

Systematic Palaeontology

Order Rhyncholedida Kuhn, 1949
  ? Superfamily Camarotochoidea Schuchert, 1929
  Family Astraelinidae Sartenaer, 2009
  Astraelinia Sartenaer, 2009
  Type species: Rhynchohella Loseni Kayser, 1880: 820.

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

Geographic distribution: western Europe, northern Africa.

Species assigned: Rhynchohella Dausenbergii Kayser, 1883.
Straelenia sp. e. g. loseni Drot, 1964.

Remarks. Astraelinia is questionably assigned to the
Superfamily Camarotochoidea 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
type material is recommended to justify the sys-
tematic position of the Astraelinidae Sartenaer, 2009.

Species of Astraelinia were first described at the
end of the 19th century from the German Harz Moun-
tains (Kayser 1882, 1883). They were placed, with other
large rhynchonellid brachiopods, in the group of
Rhynchohella Loseni 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 rhynchonel-
lid brachiopod fauna from Morocco. Due to insufficient
information and bad preservation of the type material,
Savage (2002b) considered the genus Straelenia as a no-
men dubium. Sartenaer (2009: 29) separated the group of
straelenid brachiopods into Straelenia and Astrae-
elina with the type species Astraelinia loseni (Kayser,
1885). In general astraelenid brachiopods are large and
clearly dorsiconvex, whereas straelenid specimens are
smaller and almost equibiconvex.

Astraelinia 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 Del-
gado 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 Oute-
eiro 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 dorsiconvex 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 dor-
sicconvex 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 begin-
ing 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
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 gericotic specimens. Septalum clearly developed, elongate, and giving rise to a large, thick, and high dorsal median septum which is wedge-like in the posterior part. Septalum 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.** *Astraeolina 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, 1883), to which it resembles most, and *A. e. g. losseni* (Drot, 1964). Specimens of *A. dennenbergi* (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 septalum cannot be given. A comparison of the morphological features of the species of *Astraeolina* is given in Tab. 2.

*Astraeolina 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 septalum. 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. *Astraeolina 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.

*Astraeolina* e. g. *losseni* differs from the new species in having less elongate forms, curved dental plates, a thin dorsal median septum and a small septalum. 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. dennenbergi* are poorly preserved as already stated by Drot (1964) and Sartenaer (2009). Specimens could not be studied personally, but according to the literature, *A. dennenbergi* is of almost the same size as *A. saomamedensis*. Even though the internal features of *A. dennenbergi* are unknown, the number of costae is the highest of all species of *Astraeolina*. *Astraeolina dennenbergi* 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.

**Paleoecology**

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

Tab. 2 - Morphological comparison of species of *Astraeolina*. [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 *pheneroenselaerid* 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

*Astraeolina 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.
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., Gourvenec et al. 2008, 2010; Schemm-Gregory 2011). *Astraeolina 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. losseri* (Drot, 1964) has been found in Morocco and Spain (Drot 1964; García-Alcalde 1992; Truyols-Massoni & García-Alcalde 1994), regions that belong to Gondwana. The occurrence of *Astraeolina* in Central Europe argues for migration between these two regions during the Devonian (Fig. 3). Schemm-Gregory (2008) already discussed faunal exchange by the trebratulid genus *Rhenorenselaenia* Kegel, 1913 through the Rhei 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 *Astraeolina* invaded the northern part of the Rhei 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 *Rhynchaonella letisseri* Oehlert, 1877 from the Armorican Massif or *Rhynchaonella pen- gelliana* Davidson, 1865 in 1864-1871 from Cornwall. During the Emsian, *Astraeolina* 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 *Astraeolina* species in Western and Central Europe and in Africa demonstrates a close geographic relation among these regions and that faunal migration through the Rhei 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 ultimate 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.

Acknowledgements. 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/1647/2010 “Devonian Brachiopods from Portugal: The importance of classical collections for modern palontology”.

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

REFERENCES


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), Lis-
bon.
Maillieux E. (1935) - Contribution à la connaissance de quel-
Perdigão J.C. (1967) - Descoberta de Mesodevônico em Por-
Perdigão J.C. (1972/1973) - A fauna das grés e quartzitos silúricos-devônicos de Portalegre e a sua posição es-
Ramalho M.M. (Ed. 2008) - Nery Delgado, 1835-1908: Geó-
logo 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 Por-
tugal (escala 1:500 000). Direcção Geral dos Trabalhos Geodésicos e Topográficos, Lisbon.
Robardet M. (2003) - The Armoria 'microplate': fact or fiction? Critical review of the concept and contradic-
tory palaeobiogeographical data. Palaeogeogr., Pal-
Rodriguez R.G., Varea P.M., Lodeiro F.G., Parra L.M.M., 
Poyatus D.M. & Matas J. (2007) - Microflora y con-
odontos del Mississippien 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.
Sandberger G. & Sandberger F. (1856) - Die Versteinerungen des Rheinischen Schichtensystems in Nassau. Mit ei-
ner kurzgefaßten Geognosie dieses Gebietes mit steter Berücksichtigung analgener Schichten anderer Länder: 
233-564, Kreider & Niedner Verlagshandlung, Wies-
baden.
Sartenaer P. (2009) - Two new Emsian rhyonchellid (bra-
Savage N.M. (2002a) - Uncinuloida. In: Kaesler R.L. (Ed.) 
Brachiopoda revised, Part II, Treatise on Invertebrate Paleontology, vol. 4, Rhyncho
celliformes (part.): 1092-1131. The Geological Society of America, Boulder, Colorado, and the University of Kansas Press, Lawrence, Kansas.
Brachiopoda revised, Part II, Treatise on Inverte-
brate Paleontology, vol. 4, Rhyncho
celliformes (part.): 1372-1376. The Geological Society of Ameri-
cana, Boulder, Colorado, and the University of Kansas Press, Lawrence, Kansas.
Schemm-Gregory M. (2008) - A new terebratulid brachio-
pod species from the Siegenian (middle Lower Devo-
Schemm-Gregory M. (2009) - Phylogeny, taxonomy, and palaeobiogeography of delthyridoid spiriferids (Brac-
chiopoda, Silurian to Devonian). Ph.D. thesis, Wolf-
gang Goethe-Universität Frankfurt: 610 pp., Frank-
furt am Main.
gen. et sp. - A new delthyridoid spirifer and its pa-
Schemm-Gregory M. & Henriques M.H. (2013) - The De-
vonian Brachiopod collections of Portugal - a paleon-
technological heritage. Geoheritage. DOI 10.1007/s12371-
013-0080-x.
Schemm-Gregory M. & Henriques M.H. (in press) - As 
Coleções de Braquiáopodes Paleozoicos do Museu Geológico (Lisboa, Portugal). Com. Geol., 
Lisbon.
terebratulid brachiopod from the Siegenian of the 
Schmidt H. (1955) - Devonische Gattungen der Rhyon-
chelliden (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 (Genus et Genotyporum In-
dex and Bibliographia). Fossilis Catalogus I: Animal-
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 Conchol-
gy of Great Britain. V. 7 of 80 pp. Published by the 
author, London.
Truyols-Massoni M. & García-Alcalde J.L. (1994) - Faune 
rhéno-bohémienne (Dacryonaridès, Brachiopodes) à 
la limite Emsien inférieur/supérieur au Cabo la Vela 
Voros A. (2005) - The smooth brachiopods of the Medi-
terranean Jurassic: Refugees or invaders? Palaeogeogr,
Palaeoclimatol., Palaeoecol., 223: 222-242.