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# PRAGIAN-EMSIAN BRACHIOPODS FROM THE RHENISH MASSIF (GERMANY): NEW DATA ON EVOLUTION AND BIOSTRATIGRAPHY

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*Keywords*: Lower Devonian; palaeontology; biodiversity; palaeoenvironment; Strophomenida; Orthotetida; Orthida.

*Abstract*. The succession of Pragian to Emsian (Early Devonian) brachiopod faunas from the Rhenish Massif (Germany) is briefly reviewed and interpreted with reference to a changing palaeoenvironment. A series of bioevents caused partial extinction or emigration of brachiopod species and succeeding immigration and dispersal of new species and speciation. The interplay of sea-level fluctuations, subsidence history and siliciclastic input from the Old Red Continent triggered the specific suitability of potential brachiopod habitats on the Rhenish Shelf. Three new taxa are proposed: *Fascistropheodonta*? *wiltzensis* n. sp., *Ingentistrophia* gen. n. and *Pachyschizophoria amygdalina* n. sp.

## INTRODUCTION

Brachiopods are abundant and diverse fossils in the Pragian to Emsian successions of the Rhenish Massif (Rheinisches Schiefergebirge, Germany). Hundreds of species of Rhenish brachiopods have been described since the beginning of the nineteenth century (e.g., von Schlotheim 1813, 1820; C.F. Roemer 1844; Schnur 1851, 1853; Steininger 1853; Sandberger & Sandberger 1856; Maurer 1886; Kayser 1889; Drevermann 1902, 1904; Fuchs 1907, 1909, 1915, 1919; Dahmer 1923, 1934; Solle 1953, 1971; Mittmeyer 1972, 1973a, b), but many of these have hardly been systematically revised since their introduction. As pelagic guide fossils are widely absent in the prevailing rhenotypic ('Rhenish') facies (e.g., Erben 1962; Jansen 2016), brachiopods represent first-order guide fossils, even in supraregional correlation. The author's project 'Rhenish Lower Devonian brachiopods' aims at a comprehensive account of all previously described taxa and, in so far as necessary, introduction of new ones. The stratigraphic interval considered in the present work concentrates on middle and upper parts of the succession. It starts with the upper Gedinnian to lower Siegenian succession of the 'Rhenish Gap' sensu stricto (Jansen 2016) corresponding to non-marine, deltaic and restricted marine palaeoenvironments. The proper brachiopod facies starts with the end of this interval, the transgression at the beginning of the classic middle Siegenian ('Gensberg Event' of Jansen 2016). The interval focused-on ends with the extinctions in the early Eifelian ('Kirberg Event' of Struve 1990 and Jansen 2016).

The terms 'Siegenian' and 'Emsian' are used in the classic Rhenish sense in Germany because a precise correlation with the internationally agreed upon GSSP (**G**lobal **S**tratotype **S**ection and **P**oint) of the Pragian/Emsian boundary in the Kitab Section (Uzbekistan) still cannot be recognized. Apart from that, a redefinition of the GSSP is aimed at by the international Subcommission on Devonian

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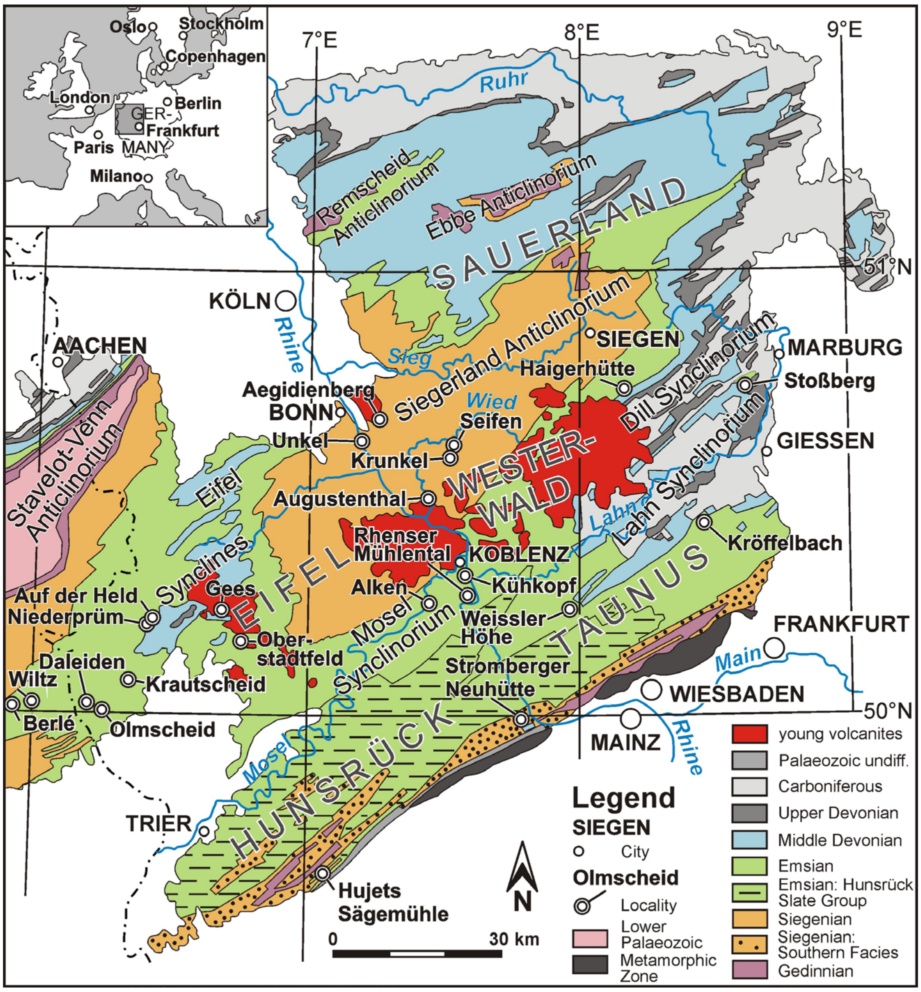


Fig. 1 - Geological sketch map of the Rhenish Massif (compiled after Walter 1995 and Korn 2008; modified according to several official geological maps), with indication of the mentioned brachiopod localities. The Siegenian of the 'Southern Facies' includes mainly the Taunusquarzit Group.

Stratigraphy (decided in 2008) because the current boundary is much older than any earlier concept of a basal Emsian boundary level or upper Pragian boundary level (Carls et al. 2008). A redefined boundary should at least approximately correlate with the basal Emsian boundary in its type region and should not be so far away from the upper boundary of the original Pragian either.

**Abbreviations**

Specimens, preservation states (referring to either singular or plural): AVIM, internal mould of articulated valves; DVEM, external mould of dorsal valve; DVIM, internal mould of dorsal valve; VVEM, external mould of ventral valve; VVIM, internal mould of ventral valve; combinations: e.g., VVIM+EM, internal mould of ventral valve plus external cast (counterpart). Dimensions of specimens: L, length; W, width. TK = official topographic map sheet at a scale of 1:25,000, the number and name of the mapsheet follow, and eventually geographic Gauss-Krüger coordinates (the German grid commonly used with this kind of map).

Institutions: MB.B., Museum für Naturkunde, Berlin, Germany, brachiopod collection; SMF, Senckenberg Forschungsinstitut und Naturmuseum; Frankfurt am Main, Germany (the prefix SMF XVII... refers to the old brachiopod catalogues, modern numbers consist of 5 or 6 digits); SMF-Mbg., same, collections of the former Institut für Geologie und Paläontologie, University of Marburg a. d. Lahn; PA.ULg, Unité de paléontologie animale et humaine, Université de Liège, Belgium; YPM, Peabody Museum of Natural History, Yale University, New Haven, CT, USA.

Brachiopod taxa: *A.*, *Areostrophia*; *Acr.*, *Acrospirifer*; *Al.*, *Alatiformia*; *Ard.*, *Arduspirifer*; *At.*, *Athyris*; *Br.*, *Brachyspirifer*; *C.*, *Crassirensselaeria*; *Cr.*, *Cryptonella*; *D.*, *Dictyostrophia*; *Eur.*, *Euryspirifer*; *Fasc.*, *Fascistropheodonta*; *Flab.*, *Flabellistrophia*; *Int.*, *Intermedites*; *Ir.*, *Iridistrophia*; *M.*, *Multispirifer*; *Meg.*, *Meganteris*; *Ol.*, *Oligoptycherhynchus*; *Pa.*, *Pachyschizophoria*; *Par.*, *Paraspirifer*; *Pla.*, *Platyorthis*; *Pro.*, *Proschizophoria*; *Ps.*, *Pseudoleptostrophia*; *Qu.*, *Quadrifarius*; *R.*, *Rhenostropheodonta*; *Rh.*, *Rhenorensselaeria*; *Rhe.*, *Rhenoschizophoria*; *S.*, *Septathyris*; *Soll.*; *Sollispirifer*; *Tr.*, *Tropidoleptus*.

## GEOLOGICAL SETTING AND PALAEOGEOGRAPHY

The Rhenish Massif represents a part of the Rhenohercynian Fold and Thrust Belt belonging to the European Variscides (Kossmat 1927; Franke 2000; Walliser & Ziegler 2008). The present low mountain range is largely built up of Devonian and Carboniferous rocks (Fig. 1). These are predominantly autochthonous or parautochthonous, but in the eastern part of the massif also allochthonous rocks with 'exotic' faunas occur, which were parts of North Gondwana (Eckelmann et al. 2014; Mende et al. 2019).

In terms of Early Devonian palaeogeography, the main part of the territory of the present Rhenish Massif was located as a shelf area at the southern margin of the Old Red Continent separated from the Gondwana Continent in the south by the Rheic Ocean (e.g., Robardet et al. 1990; Nance et al. 2012; Torsvik & Cocks 2017; Franke et al. 2017). Masses of siliciclastic material were transported onto the Rhenish Shelf and chiefly accumulated in mobile troughs ('depocentres') and subordinately also on swells (e.g., Meyer & Stets 1980, 1996; Stets & Schäfer 2002, 2011). Subsidence and sedimentation were in an approximate equilibrium, so that shallow-marine shelf palaeoenvironments prevailed. Regional tectonics, an uneven relief of the sea floor, changes of sediment supply from the source area, direct influence by deltas or rivers and eustatic sea-level fluctuations triggered a wide spectrum of subordinate marine palaeoenvironments ranging from deltaic to open-marine settings. In the subsiding troughs, sediment piles with thicknesses of possibly thousands of metres were accumulated in relatively short times (Meyer & Stets 1980, 1996); sedimentary rates of 450 to 700 metres per one million years have been estimated (Stets & Schäfer 2011). Accordingly, two brachiopod assemblages separated by strata of 300 metres thickness may differ in age by some hundred thousand years only. In the thick successions of the Mosel, Siegen or Lahn sedimentary troughs, fossil assemblages partly occur rather sporadically as single layers or isolated lenses in the succession and are separated by tens or hundreds of metres of poorly fossiliferous strata. On the other hand, more stable shelf conditions with more condensed successions resulted in a higher concentration of fossil layers which may follow one after the other in the sections often at a few metres or just a few decimetres distance, for example in the upper Emsian of the southern Eifel Synclines or the Mosel Synclinorium near Lahnstein. As regards the high sedimentation rates in the depocentres, the resolution of brachiopod stratigraphy can be considerable even if the brachiopod occurrences are separated by thick intervals without faunas.

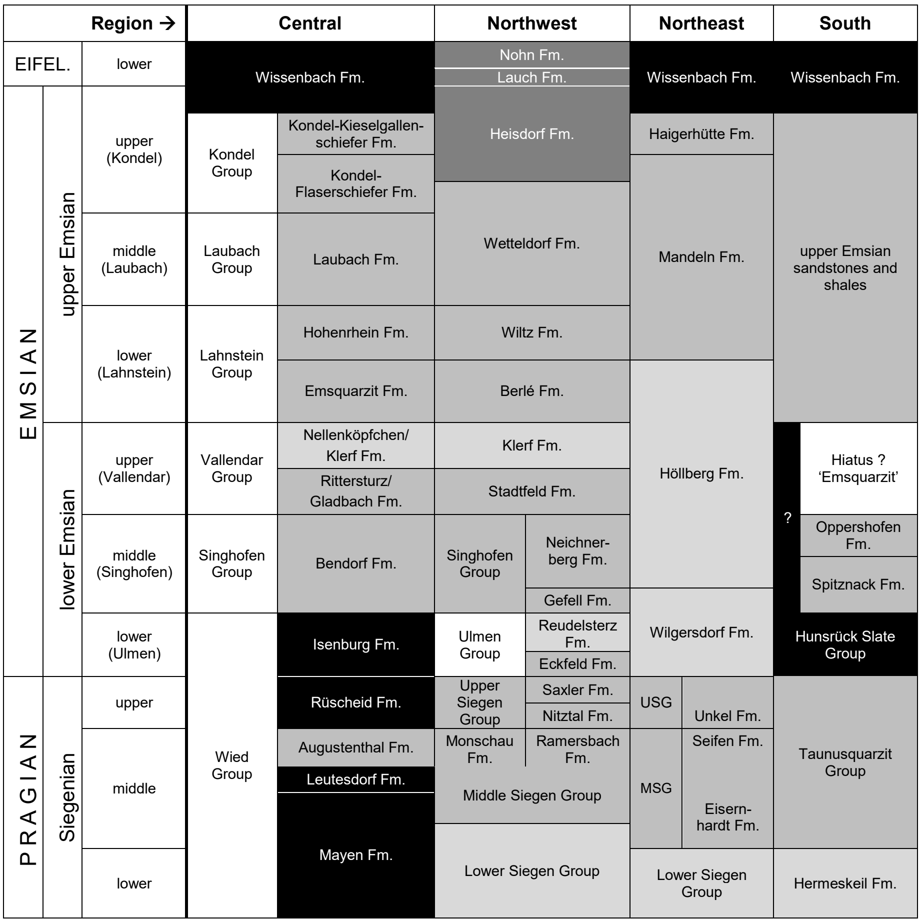
During the Carboniferous, the Devonian succession of the Rhenish Massif was affected by the Variscan orogeny, reduced in width, intensely folded, affected by cleavage and disassembled by faults and overthrusts (e.g., Meyer & Stets 1996). Complicate tectonics and deformation of brachiopods hamper the biostratigraphic work.

As a result of the structural and facial complexity, the Lower Devonian brachiopods show an irregular distribution. In general, the best outcrops are concentrated on the elevations of the Eifel, Hunsrück, Taunus, Bergisches Land and Sauerland, or in the deeply incised valleys of the Rhine, Mosel, and Lahn rivers and their distributaries. The Devonian geology is often covered by younger sediments and vegetation or inaccessible due to human settlement. In summary, the distribution of brachiopod localities is rather irregularly scattered.

The laterally coexisting and vertically succeeding subfacies of the rhenotypic facies are reflected in a complex lithostratigraphy. Only a selection of the units containing the most important occurrences of Pragian–Emsian brachiopod assemblages can be considered here (Tab. 1). A detailed account of lithostratigraphic units is published in the 'Monograph of the Devonian of Germany' (Deutsche Stratigraphische Kommission 2008).

## BIOSTRATIGRAPHY

The biostratigraphic subdivision of the Rhenish Lower Devonian is based on fossil groups occurring in the shallow-water rhenotypic facies: brachiopods (e.g., Solle 1953, 1971, 1972; Mittmeyer 1974, 1982, 2008; Schemm-Gregory & Jansen 2006a, b; Jansen 2001, 2014b, 2016), trilobites (e.g., Wenndorf 1990), fishes (e.g., Wo. Schmidt 1956; Blieck et al. 1995) and palynomorphs (e.g., Streel et al. 1987). The brachiopods, one of the most diverse and abundant fossil groups, often allow immediate stratigraphic assignments even in the field. The present author's long-term project 'Rhenish Lower Devonian brachiopods' provides a steady flow of new biostratigraphic data. The ranges of some important Rhenish brachiopod taxa are shown in Fig. 2. A taxon-range biozonation based on spiriferide brachiopods has been introduced previously (Jansen 2014b, 2016), allowing the interfacial correlation of the Rhenish successions and serving as framework in dating and correlating of geological processes and events (Fig. 3) discussed below.



| | | Region → | Central | | Northwest | | Northeast | | South | |
|---|---|---|---|---|---|---|---|---|---|---|
| EIFEL. | | lower | Wissenbach Fm. | | Nohn Fm.<br>Lauch Fm. | | Wissenbach Fm. | | Wissenbach Fm. | |
| EMSIAN | upper Emsian | upper (Kondel) | Kondel Group | Kondel-Kieselgallenschiefer Fm.<br>Kondel-Flaserschiefer Fm. | Heisdorf Fm.<br>Wetteldorf Fm. | | Haigerhütte Fm.<br>Mandeln Fm. | | upper Emsian sandstones and shales | |
| | | middle (Laubach) | Laubach Group | Laubach Fm. | | | | | | |
| | | lower (Lahnstein) | Lahnstein Group | Hohenrhein Fm.<br>Emsquarzit Fm. | Wiltz Fm.<br>Berlé Fm. | | Höllberg Fm. | | | |
| | lower Emsian | upper (Vallendar) | Vallendar Group | Nellenköpfchen/ Klerf Fm.<br>Rittersturz/ Gladbach Fm. | Klerf Fm.<br>Stadtfeld Fm. | | | | ? | Hiatus ? 'Emsquarzit' |
| | | middle (Singhofen) | Singhofen Group | Bendorf Fm. | Singhofen Group | Neichnerberg Fm.<br>Gefell Fm. | Wilgersdorf Fm. | | | Oppershofen Fm.<br>Spitznack Fm. |
| | | lower (Ulmen) | Wied Group | Isenburg Fm. | Ulmen Group | Reudelsterz Fm.<br>Eckfeld Fm. | | | Hunsrück Slate Group | |
| PRAGIAN | Siegenian | upper | | Rüscheid Fm. | Upper Siegen Group | Saxler Fm.<br>Nitztal Fm. | USG | Unkel Fm. | Taunusquarzit Group | |
| | | middle | | Augustenthal Fm.<br>Leutesdorf Fm.<br>Mayen Fm. | Monschau Fm.<br>Middle Siegen Group | Ramersbach Fm. | MSG | Seifen Fm.<br>Eisernhardt Fm. | | |
| | | lower | | | Lower Siegen Group | | Lower Siegen Group | | Hermeskeil Fm. | |

Tab. 1 - Simplified lithostratigraphy and facies of some representative successions in the Rhenish Massif; stratigraphic units after Deutsche Stratigraphische Kommission (Ed. 2008). The 'Central area' corresponds to the Mosel Synclinorium including the central Middle Rhine, Lower Mosel and Lower Lahn areas. The 'Northwest' corresponds to the Eifel area; the 'Northeast' to the Lahn-Dill and Sauerland areas; and the 'South' to the Taunus and Hunsrück areas. The successions are partly composites from different partial regions; only selected formations are shown within the Middle and Upper Siegen groups. Light grey shading stands for predominant pararhenotypic subfacies, middle grey for predominant eurhenotypic subfacies, dark grey for predominant allorhenotypic subfacies, and black for pelitic rocks representing mainly various transitions from the distal eurhenotypic subfacies to the hercynotypic facies and the latter facies itself. Abbreviations: Fm., Formation; MSG, Middle Siegen Group; USG, Upper Siegen Group.

## FACIES SUBDIVISION

The Lower Devonian successions of the Rhenish Massif are characterized by the shallow-marine rhenotypic ('Rhenish') facies, i.e. predominantly siliciclastic sedimentary rocks containing chiefly epibenthic marine faunas. This facies is contrasted with the largely pelagic, calcareous and argillaceous hercynotypic ('Hercynian') facies of the Devonian (e.g., Erben 1962). The 'Bohemian' facies has often been regarded as synonymous with the 'Hercynian' facies, but Carls et al. (1993) proposed the specific term 'bohemotypic' for the calcareous facies of the Koněprusy Limestones (Pragian, Bohemia), which reflect a shallow and clear-water reefal palaeoenvironment. The rhenotypic facies is subdivided into the following three main subfacies (Jansen 2016).

### Eurhenotypic subfacies

This subfacies is characterized by predominant sandstones and shales with rich neritic-benthic biota including brachiopods, bivalves, trilobites, few corals, ostracods and others. Many turbidicolous (turbid-water tolerating) brachiopods such as the more or less coarsely plicate delthyridoid spiriferides as well as representatives of other orders and morphogroups are common and reflect a shallow-marine palaeoenvironment of the open shelf with agitated and turbid water. Typical brachiopod genera include the ribbed spiriferides *Acrospirifer*, *Hysterolites*, *Euryspirifer*, *Arduspirifer*, *Paraspirifer*, *Tenuicostella*, *Alatiformia*; the unribbed spiriferide *Rhenothyris* (*compressa* Group); flat-shelled or concavoconvex to geniculate strophomenides, e.g., *Leptostrophiella*, *Mesodouvillina*, *Boucotstrophia*, *Fascistropheodonta*, *Rhenostropheodonta*, *Gigastropheodonta* and *Gibbodouvillina*; the orthotetides *Ingentistrophia* gen. n. and *Iridistrophia*; often numerous chonetoids, e.g., *Chonetes*, *Plebejochonetes*, *Loreleiella*; the enigmatic genus *Tropidoleptus*; diverse orthides such as *Platyorthis*, *Proschizophoria*, *Protocortezorthis*, *Resserella*, *Rhenoschizophoria* and *Pachyschizophoria*; few taxa of unribbed (except broad undulations) athyridides, e.g., '*Athyris*' (*undata* Group) and *Septathyris*; some rhynchonellides including *Oligoptycherhynchus*, *Lapinulus*, *Sartenaerirhynchus*, *Straelenia*, *Astraelenia* and *Dinapophysia;* the te-

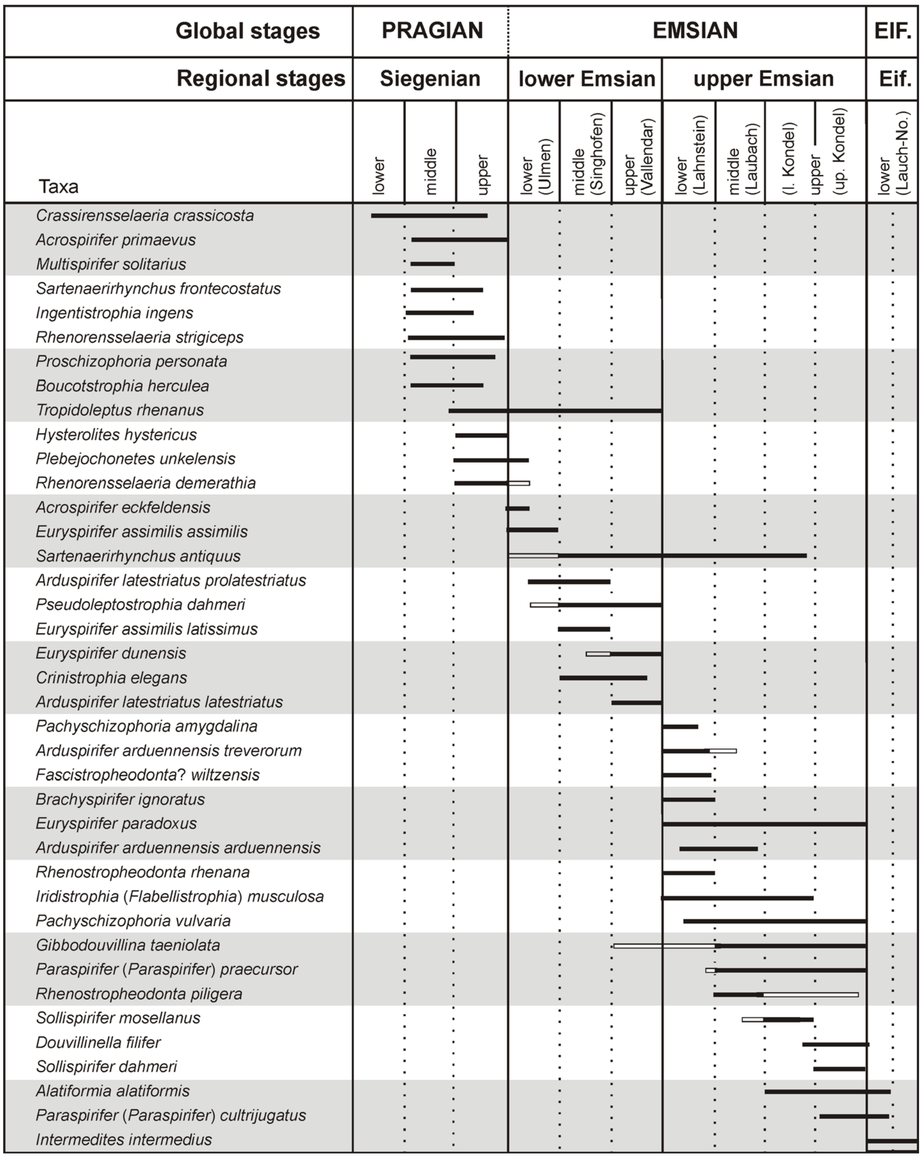


Fig. 2 - Ranges of selected Pragian–Emsian brachiopod taxa in the Rhenish Massif, primarily based on previous works (Solle 1972; Mittmeyer 1982, 2008), but in many cases modified after new data of the author. Black bars denote certain ranges, white bars denote uncertain ranges, determinations or reports. The Pragian–Emsian boundary is indicated provisionally and does not reflect the present GSSP level. EIF./Eif., Eifelian; l., lower; No., Nohn.

rebratulides *Rhenorensselaeria*, *Globithyris*, *Meganteris*; and rare atrypides possibly belonging to the genus *Atrypa*. Linguliform brachiopods ('*Lingula*') are generally not common, whereas craniiforms (e.g., *Petrocrania*) can be abundant, but only at some localities in the middle Siegenian (e.g., Seifen, Augustenthal) and upper Emsian (e.g., Kühkopf near Koblenz, auf der Held near Prüm). As regards the other fauna, in particular the bivalves can be more abundant and diverse than the brachiopods. Due to slight shifts in faunal composition and sedimentary inventory, proximal, medial (typical) and distal variations of the eurhenotypic subfacies are distinguished (Jansen 2016). A typical example of a medial eurhenotypic fauna is the famous Stadtfeld Fauna (lower Emsian, Central Eifel region); it includes approximately 42 brachiopod species (revised) associated with 89 bivalve, 12 gastropod, 9 trilobite, 3 ostracod, 3 fish, 2 cephalopod, 1 tentaculitide, 1 rostrochonchid and 1 tabulate coral species (Mauz 1935).

### Pararhenotypic subfacies

Sandy or muddy rocks containing impoverished neritic-benthic biota predominate, in particular subglobular terebratuloid (*Crassirensselaeria*, *Globithyris*) and lingulide brachiopods ('*Lingula*') accompanied by bivalves (e.g., *Modiolopsis*) and coarsely ornamented ostracodes; eurypterides and agnathans are common, whereas these are rare in the other two subfacies. The subfacies reflects a very shallow, intertidal, deltaic or lagoonal palaeoenvironment near the land with agitated and turbid or calm water, partly with reduced or changing salinity, but still with a distinct marine influence. There are transitions to the continental Old Red facies lacking completely marine faunas. A typical fauna is the one from the Nellenköpfchen Formation at Alken (uppermost part of lower Emsian, valley of the Mosel River); it includes 2 brachiopod, 8 bivalve, 1 gastropod, 11 eurypteride, 13 other arthropod, 13 fish, 1 tentaculitide and 2 annelid species (Wehrmann et al. 2005).

### Allorhenotypic subfacies

This subfacies refers to fine-grained siliciclastic, marly and calcareous rocks containing rich neritic-benthic biota including brachiopods, trilobites, rugose and tabulate corals, bryozoans, stromatoporoids and others. A high percentage of claricolous (= clear-water preferring) brachiopods reflects a shallow-marine, open-shelf palaeoenvironment with more or less agitated and comparatively clear water. Typical brachiopod genera include the more or less coarsely ribbed spiriferides *Paraspirifer*, *Quiringites*, *Intermedites*, *Alatiformia* and *Subcuspidella*, associated with a substantial content of essentially claricolous brachiopods, such as numerous atrypides, e.g., *Atrypa*, *Spinatrypa*, *Planatrypa*, *Desquamatia* and *Gruenewaldtia*; athyridides, e.g., *Athyris*, *Meristella* and *Nucleospira*; orthides, e.g., *Aulacella, Rhipidomella* and *Tyersella*; pentamerides, e.g., *Gypidula*, *Devonogypa* and *Sieberella*; reticulariid spiriferides, e.g., *Rhenothyris* (*aequabilis* Group), *Kymatothyris*, *Uexothyris*, *Gerothyris*, *Yeothyris*; strophomenides, e.g., *Leptagonia*, *Telaeoshaleria*, *Teichostrophia* and *Glossostrophia*; rhynchonellides, e.g., *Cuninulus* and *Glossinulus*; the chonetoid genera *Devonochonetes* and *Devonaria*; the early productidine *Helaspis*; and the smooth terebratulide *Cimicinella*. The coarsely ribbed spiriferides *Intermedites* and *Quiringites* mainly occur in the marly-calcareous facies and are also interpreted as claricolous (Carls 2000: 74). Smooth or at least unribbed or faintly ribbed and rounded brachiopods are abundant and represent a characteristic morphogroup but may belong to different taxonomic groups (Winter 1971).

The allorhenotypic subfacies starts in the uppermost part of the upper Emsian in the Eifel region and the Sauerland where it is particularly common in the Middle Devonian. A typical example is the succession of the Ahrdorf Formation at Gees ('Trilobite Fields', middle Eifelian, Gerolstein Syncline, Eifel region) from where more than 60 brachiopod species have been recorded, with 22 trilobite, 7 coral, 4 cephalopod, 3 bryozoan, 3 bivalve and diverse undetermined gastropod species (Struve 1982b).

## DESCRIPTION OF THE FAUNAL SUCCESSION

### Upper Gedinnian to lower Siegenian 'Rhenish Gap'

The successions between the fossiliferous parts of the lower Gedinnian (Lochkovian) and the middle Siegenian (Pragian) have yielded hardly any open marine faunas at all. They are built up of thick sandy and shaly units often with red and green colours in the Hunsrück, southern Taunus and the core of the Siegerland Anticlinorium; these are assigned to the non-marine to pararhenotypic rocks of the 'Rhenish Gap' in the strict sense (Jansen 2016). The palaeoenvironments range from terrestrial or limnic-fluvial to deltaic, lagoonal and intertidal (rarely shallow subtidal), corresponding to a relatively low sea-level at that time (Walliser 1998). The upper Gedinnian part of the succession is devoid of marine fossils and just locally contains early agnathan fish remains and land plants, whereas the lower Siegenian shows first marine influences indicated by first restricted-marine faunas of the pararhenotypic subfacies. The facial change at the mainly lithostratigraphically defined Gedinnian–Siegenian boundary, i.e. the Hermeskeil Event (Mittmeyer 2008), may correspond to a global sea-level rise in the early Pragian (early T-R Sequence Ia$_2$; Walliser 1998). Brachiopods include monospecific mass occurrences of *Crassirensselaeria crassicosta* (Koch, 1881) and lingulides. Very rare occurrences of the proximal eurhenotypic subfacies have yielded poorly preserved delthyridoid spiriferides with 'Siegenian habitus' (Pilger & Schmidt 1959; Meyer 1970); a restudy of the material by the present author confirmed the previous results but did not bring new ones. In the more northern parts of the Rhenish Massif (Sauerland, Hohes Venn), pararhenotypic and terrestrial rocks have a longer stratigraphic range and may even reach the upper Emsian ('Rhenish Gap' in the wider sense; Jansen 2016).

### Middle Siegenian

Rocks of middle Siegenian age are widely exposed and represented by middle parts of the Siegen Supergroup in the Siegerland (type region), Westerwald and East Eifel regions. Strata of the same age are also documented from parts of the Wied Group in the Mosel Synclinorium and the Taunusquarzit Group ('Katzenloch level') in the southern Taunus and Hunsrück.

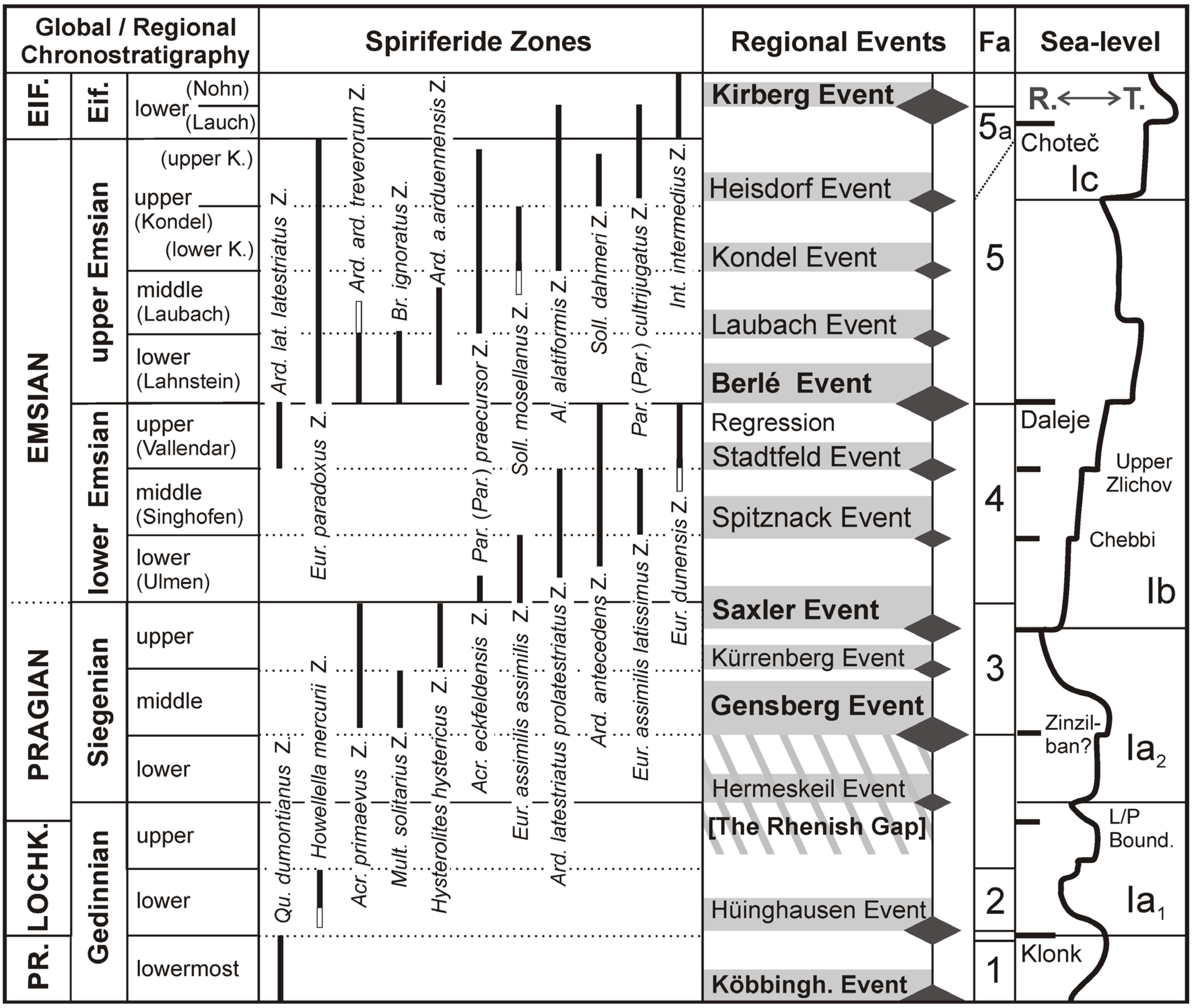


Fig. 3 - Regional stratigraphy, spiriferide zones, regional events (Mittmeyer 2008; Jansen 2016 and 2018), faunas (Fa) and sea-level fluctuations with position of global events (modified after Johnson et al. 1985; Johnson & Sandberg 1988) documented in the Pridolian to lower Eifelian successions of the Rhenish Massif. Differentiation of T-R sequences $Ia_1$ and $Ia_2$ in the sense of Walliser (1998). The Pragian-Emsian boundary is indicated provisionally (not the present GSSP level). Diamonds correspond to the regional events, size of diamonds indicating the suggested importance of the events. The extent of the 'Rhenish Gap' sensu stricto is indicated (striped area). Abbreviations: Fa. = faunas, K. = Kondel, Köbbingh. = Köbbinghausen, R. = Regression, T. = Transgression, Z. = Zone; for further abbreviations see text. Faunas: 1 = *Quadrifarius dumontianus* Fauna, 2 = *Howellella mercurii* Fauna, 3 = *Acrospirifer primaevus* Fauna, 4 = *Arduspirifer antecedens* Fauna, 5 = *Euryspirifer paradoxus* Fauna, 5a = *Paraspirifer cultrijugatus* Fauna.

The middle Siegenian begins with the onset of marine, eurhenotypic subfacies in a large area of the Rhenish Massif and the Ardennes. This change from largely deltaic-intertidal to open-marine conditions has been described as the 'Gensberg Event', the result of which was the establishment of the '*Acrospirifer primaevus* Fauna' (Jansen 2016). Due to biostratigraphic correlations and considerations on the sea-level history, it may represent a supraregional (eustatic?) phenomenon corresponding to the transgressive Zinzilban (*kitabicus*) Event (Yolkin et al. 1994) or a transgressive pulse in the middle part of the Pragian T-R Sequence $Ia_2$ (Walliser 1998; ≈ 'Ia' sensu Johnson et al. 1985) of the global sea-level curve (Jansen 2016).

The onset of open-marine conditions may be slightly diachronic in various areas of the Ardenno-Rhenish region and does not necessarily correlate everywhere precisely with the lower boundary of the Middle Siegen Group in the Siegerland Anticlinorium. Slight differences in faunas previously regarded as coeval may reflect this phenomenon.

For example, the presence of *Filispirifer*? *beaujeani* (Béclard, 1887) in the uppermost part of the Mirwart Formation and the Villé Formation (southern flank of Dinant Synclinorium, Ardennes), formerly assigned to the 'Siegenien moyen' (Asselberghs 1946) may show a slightly older age of this stratum compared to the middle Siegenian in the Rhenish Massif where this species is apparently absent. A pre-existing relief of the sea-floor, a diachronic onlap of the sea and locally different rates of subsidence and sedimentation may have caused this kind of deviations. The intercalation of a single bed with a fauna of middle Siegenian age occurring in a succession still included in the Lower Siegen Group (= Untere Siegen-Schichten) of the East Eifel Anticlinorium indicates that the initial middle Siegenian transgression is already documented within this unit; this is supported by lithostratigraphic correlation (Meyer 2013: pp. 39-40). Diachronisms of this kind have hardly been recorded so far. For practical reasons, it has always been common practice to align the boundaries of lithostratigraphic units with those of regional chronostratigraphic units.

Marine assemblages in the Rhenish Massif include, for example, the classic Seifen Fauna with approximately 35 brachiopod species; the fauna is named after a locality in the Westerwald (Drevermann 1904; Dahmer 1934; Paproth 1960; Jahnke & Michels 1982a). Typical elements of this fauna are large strophomenoids, such as *Leptostrophiella explanata* (Sowerby, 1842), *Boucotstrophia herculea* (Drevermann, 1902), *Fascistropheodonta sedgwicki* (d'Archiac & de Verneuil, 1842) and *Gigastropheodonta gigas* (McCoy, 1852); orthides are very common, for example *Platyorthis circularis taunica* (Fuchs, 1915), *Proschizophoria personata* (Zeiler, 1857) and *Rhenoschizophoria provulvaria* (Maurer, 1886); moreover, rhynchonellides of the species *Sartenaerirhynchus frontecostatus* (Drevermann, 1902) and *Dinapophysia papilio* (Krantz, 1857); and athyridides including '*Athyris*' *avirostris* (Krantz, 1857) and *Septathyris aliena* (Drevermann, 1904). The spiriferide species *Acrospirifer primaevus* (Steininger, 1853), *Mauispirifer gosseleti* (Béclard, 1887), *Alatiformia affinis* (Fuchs, 1909), *Vandercammenina rhenana* (Kegel, 1913) and *Multispirifer solitarius* (Krantz, 1857) are abundant. *Cryptonella minor* Dahmer, 1931 represents the terebratulides, *Petrocrania interstrialis* (Dahmer, 1931) the craniides. Mittmeyer (2008) proposed the term 'Seifen Event' for the evident relative transgressive highstand documented in the upper part of the middle Siegenian and discernible in successions of the Hönningen-Seifen Anticline of the Westerwald and East Eifel regions.

'*Orthothetes*' *ingens* Drevermann, 1904 from the same fauna is a giant-sized, widely neglected species with distorted apical area of ventral valve, showing relationships to bohemotypic areostrophiids with fixosessile life habit at least in the juvenile stages. The marked transgressive trend in the middle Siegenian may have facilitated this species spreading across the Ardenno-Rhenish Shelf and inhabiting not too turbid settings also preferred by relatively claricolous *Multispirifer*, *Cryptonella*, athyridides, bryozoans and corals. A new genus *Ingentistrophia* is proposed herein for this peculiar and aberrant species (see section 'systematic palaeontology').

The Augustenthal Formation, a subunit of the argillaceous-sandy Wied Group ('Hunsrück Slate Facies') in the Mosel Synclinorium, bears a rich distal eurhenotypic fauna with 38 brachiopod species reported from the classic locality Augustenthal near Neuwied (Dahmer 1931). The fauna includes a remarkable abundance of species regarded as more claricolous: *Leptaenopyxis* sp., *Cyrtina latesinuata* Dahmer, 1931, *Nucleospira maillieuxi* Dahmer, 1931, *S. aliena* and *Cr. minor*. On the other hand, representatives of the more turbidicolous genera *Arduspirifer* and *Euryspirifer* – very rare at other localities in the middle Siegenian – are here common, but still in need of revision.

The shallow-water, quartzitic Taunusquarzit Group in the Taunus and Hunsrück bears an approximately coeval, proximal eurhenotypic fauna with reduced diversity at the 'Katzenloch level' (e.g., Dahmer 1934: 34-36; Kutscher 1937, 1940, 1952; Jentsch & Röder 1957), dominated by *Acrospirifer primaevus* (Steininger, 1853), *C. crassicosta* and *Rhenorensselaeria strigiceps* (Roemer, 1844). The relatively diverse fauna from the 'Stromberger Neuhütte' contains 12 brachiopod species (Kutscher 1937), the fauna from 'Hujets Sägemühle' 11 (Kutscher 1940).

### Upper Siegenian

The distribution of upper Siegenian strata is similar to that of the middle Siegenian ones. The most diverse faunas occur in the Siegerland, the South and East Eifel regions and in the Westerwald. The beginning of the upper Siegenian is here generally connected with a change from a more medial eurhenotypic subfacies towards a proximal eurhenotypic and pararhenotypic subfacies, showing an increase in siliciclastic input and/or a possible sea-level fall consistent with the regression of the late Pragian T-R Sequence Ia$_2$ (Walliser 1998). The regressive trend in the upper Siegenian, indicated by massive, impure sandstones and plant-bearing mud shales as typical rocks, has been termed 'Kürrenberg Event' (Mittmeyer 2008). The succession contrasts with the flaser-bedded, mud-rich sandstones of the middle Siegenian.

The faunal assemblages, although still representing the '*Acrospirifer primaevus* Fauna', are distinct and very characteristic: chonetoids, such as *Plebejochonetes unkelensis* (Dahmer, 1936), may cover whole bedding planes. The orthide taxa *Pla. circularis taunica*, *Pro. personata* and *Rhe. provulvaria* are less abundant than in the middle Siegenian. Rhenorensselaeriid terebratulides are very common and represented by *Rh. strigiceps*, *Rh. demerathia* Simpson, 1940 and *C. crassicosta*. Delthyridoid spiriferides include mainly *Hysterolites hystericus* von Schlotheim, 1820 and late morphs of *Acr. primaevus*. *Tropidoleptus rhenanus* Frech, 1897 is a common element of many fossil assemblages. On the other hand, strophomenoids and athyridides are rare. Thus, the numeric ratios are reverse compared to those of the middle Siegenian faunas. Taken as a whole, the brachiopod species diversity is slightly lower than in the middle Siegenian, but still high at a few localities: prominent examples are the near 30 species that occur at the classic locality Unkel/River Rhine (Dahmer 1936) and 28 species in a succession at Aegidienberg in the Siebengebirge (Schindler et al. 2004). The number of species at localities in the upper Siegenian of the Siegerland is often between 5 and 15 (Quiring 1923). The proportion of turbidicolous brachiopods has generally increased, indicated by high abundances of *Pleb. unkelensis*, *Hyst. hystericus*, *C. crassicosta* and *Rh. strigiceps*. In the Southeast Eifel, lower parts of the upper Siegenian have yielded approximately 12 species in the lower Nitztal Formation and only 2-3 in its middle and upper parts, whereas the overlying Saxler Formation (upper part of upper Siegenian) contains about 30 species showing a faunal change (Simpson 1940). This new increase of brachiopod diversity suggests a sea-level rise which may correspond to the onset of T-R Sequence Ib (Johnson et al. 1985). In his regional event terminology, Mittmeyer (2008) referred to this development as 'Saxler Event'.

Numerous Siegenian brachiopod species disappear near or at the upper boundary of the upper Siegenian, for example *Pro. personata*, *Al. affinis*, *Hyst. hystericus*, *Acr. primaevus*, '*At.*' *avirostris* , *Rh. strigiceps* and *C. crassicosta*.

### Lower Emsian

Brachiopod-bearing, eurhenotypic strata of the lower Emsian are mainly exposed in the South Eifel, Westerwald, Middle Rhine and Hintertaunus regions.

The transgressive phase starting in the latest Siegenian ('Saxler Event') extends into the early Emsian, probably still corresponding to the onset of T-R Sequence Ib (Johnson et al. 1985). The transgressive development clearly persists in the Hunsrück area, where the argillaceous Hunsrück Slate Group with its pelagic ammonoid and dacryoconaride faunas represents a substantial part of the lower Emsian. In the Eifel region, however, the transgressive phase ended still within the early part of the early Emsian ('Ulmen time') with a regressive trend indicated by extended areas with pararhenotypic and proximal eurhenotypic subfacies of the Reudelsterz Formation (Fuchs 1982), possibly due to increased siliciclastic input from the Old Red Continent.

The early Emsian complex of marine faunas has been referred to as '*Arduspirifer antecedens* Fauna' (Jansen 2016). The genus *Acrospirifer* crossed the Siegenian–Emsian boundary and persisted with *Acr. eckfeldensis* Mittmeyer, 2008 into the lowermost part of the lower Emsian, but then went extinct. Typical of the lower Emsian as a whole is the strong presence of two spiriferide genera which originated from Siegenian ancestors: *Arduspirifer* Mittmeyer, 1972 shows the evolution of two parallel lineages, i. e. the species *Ard. latestriatus* (Maurer, 1886) and *Ard. antecedens* (Frank, 1898). The early Emsian evolution of *Euryspirifer* Wedekind, 1926 starts with *Eur. assimilis* (Fuchs, 1915) followed by *Eur. dunensis* (Kayser, 1889). Various temporal subspecies and morphs of the species of these two genera can be distinguished after their revision and used in a revised biostratigraphic subdivision of the lower Emsian (Jansen, in prep.) into Ulmen, Singhofen (= Bendorf) and Vallendar substages (Mittmeyer 1974, 2008). Ulmen and Singhofen are not always easy to distinguish whereas the Vallendar is relatively distinct. The beginning of the Singhofen Substage is characterized by mass occurrences of the genus *Arduspirifer*, either *Ard. antecedens* or *Ard. latestriatus prolatestriatus* Mittmeyer, 1973b, and abundant *Eur. assimilis latissimus* Mittmeyer, 2008, *Incertia subincertissima* Mittmeyer, 2008 and *Pseudoleptostrophia dahmeri* (Rösler, 1954). The rise of the early ammonoids in the Hunsrück Slate Group may coincide with this level referred to as the 'Spitznack Event' (Mittmeyer 2008). The lower Vallendar Substage in the southern Central Eifel includes the highly diverse Stadtfeld Fauna representing the 'type' of the rhenotypic faunas with approximately 42 brachiopod species occurring in numerous fossiliferous beds of a succession (Drevermann 1902; Mauz 1935; faunal lists critically reviewed). The supraregional, transgressive Upper Zlíchov Event (sensu García-Alcalde 1997) may have caused this episode of opulent brachiopod development (the 'Stadtfeld Event' of Mittmeyer 2008), even resulting in the occurrence of a few anetoceratine ammonoids in this medial eurhenotypic subfacies (de Baets et al. 2009). During the latest part of the early Emsian ('Nellenköpfchen-Klerf times'), a regressive trend is documented from widespread pararhenotypic subfacies characterized by, for example, *Globithyris confluentina* (Fuchs, 1907) and lingulides in the South Eifel and central Middle Rhine regions. Last occurrences of *Tr. rhenanus*, *Ard. antecedens* and *Ard. latestriatus latestriatus* in short-term and thin proximal eurhenotypic intercalations demonstrate the age of these very thick successions. This facies development is probably largely controlled by strong input of terrigenous siliciclastics from the Old Red Continent compensating for strong crustal subsidence (Stets & Schäfer 2002, 2011).

Additional characteristic taxa of the lower Emsian, which are all known from the 'Stadtfeld Fauna', include *Leptostrophiella explanata* (Sowerby, 1842), *Ps. dahmeri*, *Crinistrophia elegans* (Drevermann, 1902), *Plicostropheodonta virgata* (Drevermann, 1902), *Iridistrophia* (*Ir.*) *maior* (Fuchs, 1915), *Platyorthis circularis circularis* (Sowerby, 1842), *Rhenoschizophoria provulvaria* (Maurer, 1886), *Loreleiella dilatata* (C.F. Roemer, 1844), *Plebejochonetes semiradiatus* (Sowerby, 1842), *Lapinulus pila* (Schnur, 1851), *Sartenaerirhynchus antiquus* (Schnur, 1853), *Inaequalibellirostrum inauritum* (Sandberger & Sandberger, 1856), *Straelenia dunensis* (Drevermann, 1902), *Torosospirifer crassicosta crassicosta* (Scupin, 1900), '*Athyris*' cf. *undata* (Defrance, 1828) and *Meganteris ovata ovata* Maurer, 1879.

**Upper Emsian**

The event-related faunal turnover at the lower–upper Emsian transition is one of the most conspicuous changes within the Rhenish Lower Devonian (Solle 1972). It may chiefly be a result of extinction and emigration of species in the latest part of the early Emsian (e.g., *Ps. dahmeri*, *Rhe. provulvaria*, *Tr. rhenanus*, *Ard. latestriatus*, *Eur. dunensis*) followed by immigration of new species from outside on the Rhenish Shelf in the earliest part of the late Emsian or continued evolution and speciation within the same area. The transgressive 'Berlé Event' (Mittmeyer 2008), lithostratigraphically marked by the quartzitic rocks of the Emsquarzit and Berlé formations, correlates approximately with the global Daleje (= *cancellata*) Event (Carls et al. 1972; Jansen et al. 2007) first described from the Barrandian area in the Czech Republic (House 1985; Chlupáč & Kukal 1986, 1988; Walliser 1985). A precise correlation is, however, not evident, as the regional subsidence-sedimentation history on the Rhenish Shelf was superimposed on the influence of eustatic sea-level fluctuations. In central parts of the Rhenish Massif, there was a change from predominantly strong sedimentation compensated by crustal subsidence to retarded subsidence and prevailing erosion and resedimentation (Stets & Schäfer 2002, 2011). Due to the rising sea-level, marine facies is widely distributed in the Rhenish Massif, but particularly complete and fossiliferous in two classic areas: in the central Middle Rhine area (Mosel Synclinorium) and in the Central and West Eifel areas (Prüm Syncline and Daleiden Synclines = 'Daleider Muldengruppe'). The transgressive trend generally persisted – apart from some local regressive intercalations – during the late Emsian, reflected by a successive change from proximal to medial and distal eurhenotypic subfacies, and finally hercynotypic facies in the central Rhenish regions (Jansen 2016); this development includes a series of smaller events with faunal change among the brachiopods. In the Eifel Synclines ('Eifeler Kalkmulden'), regressive tendencies in middle to upper parts of the upper Emsian (Wetteldorf Formation) with prevailing proximal eurhenotypic subfacies are terminated with a transgression discernible in its uppermost part and regional transition to the allorhenotypic subfacies of the Heisdorf Formation. The term 'Heisdorf Event' (Jansen 2018) is proposed for this transgressive development, also visible as 1) the onset of the 'Cultrijugatus-Schichten' and 'Harbecke-Schichten' in the Sauerland (Langenstrassen 1972, 2008), 2) possibly documented near the base of the St. Joseph Formation, i.e. the base of the 'Couvinian' in the Ardennes (Weddige & Ziegler 1977; Bultynck et al. 2000; Bultynck 2006), and 3) correlating with the onset of the distal eurhenotypic subfacies of the Kondel-Kieselgallenschiefer Formation and, in its continuation, the hercynotypic Wissenbach Facies in the central and eastern Rhenish Massif.

The marine faunas from the upper Emsian contain the whole spectrum of rhenotypic fossil groups. As regards the brachiopods, the assemblages as a whole are summed up as '*Euryspirifer paradoxus* Fauna' (Jansen 2016). *Iridistrophia* (*Flabellistrophia*) *musculosa* Jansen, 2016 evolved from a species of the pre-existing subgenus *Ir.* (*Iridistrophia*) near the beginning of the late Emsian, persisted into its late part (early 'Kondel time') and gave rise to *Ir.* (*Flab.*) *hipponyx* (Schnur, 1851). *Rhenostropheodonta rhenana* Jansen, 2014a first appeared at the same boundary and gave rise to *R. piligera* (Sandberger & Sandberger, 1856) with the beginning of the middle part of the late Emsian ('Laubach time').

Another still poorly known, but important biostratigraphic marker near the lower boundary of the upper Emsian is an abundant species from the Emsquarzit and Berlé formations previously referred to as *Pachyschizophoria* sp. C Jansen, 2001 which is given nomenclatural status herein as *Pa. amygdalina* n. sp. The new species is regarded as a descendant of very rare lower Emsian representatives of the genus, such as *Pa.* sp. D Jansen, 2001. Moreover, *Pa. amygdalina* is the ancestor of the classic species *Pa. vulvaria* (von Schlotheim, 1820). A very similar morph of *Pa. tataensis* (Jansen, 2001) occurs in the lower–upper Emsian boundary interval of the Dra Plains in southern Morocco (Jansen 2001), suggesting a respective correlation. The ventral interior of that form is practically identical to that of *Pa. amygdalina*, whereas the dorsal interior slightly differs (see systematic part). The genus *Arduspirifer*, i.e. the '*arduennensis* group', persisted from the early Emsian (Solle 1953; Jansen 2001; Schemm-Gregory & Jansen 2005, 2006a, b): *Ard. antecedens* possibly gave rise to the advanced late Emsian species *Ard. arduennensis* (Schnur, 1853) with its regionally separated subspecies *Ard. arduennensis treverorum* Schemm-Gregory & Jansen, 2005 and *Ard. arduennensis arduennensis* (Schnur, 1853); *Ard. extensus* (Solle, 1953) and *Ard. maturus* (Spriestersbach, 1935) represent a separate lineage possibly originating from *Ard. arduennensis treverorum* (see Schemm-Gregory & Jansen 2005).

The upper Emsian succession contains numerous faunas, such as the medial to distal eurhenotypic fauna of the Wiltz Formation (lower part of upper Emsian, Prüm Syncline and Daleiden Synclines, Eifel region), including, for example, 44 brachiopod species accompanied by 28 bivalve, 4 gastropod, 4 coral, 3 trilobite, 3 annelid, 3 bryozoan, 2 tentaculitide, 1 rostroconchid and 1 orthoconic cephalopod species at the locality Ziegelei Niederprüm (Werner 1969: 'loc. WE 10'). In this unit, a hitherto poorly known, peculiar strophomenoid species is common: *Fascistropheodonta*? *wiltzensis* n. sp. It resembles in some respects the Siegenian type species of the genus, *Fasc. sedgwicki*, but may not be closely related to it. Most probably the new species immigrated in the earliest part of the late Emsian into the Rhenish Shelf Sea. Its ancestors, however, are still unknown. An interesting aspect is a possible relationship to *Dictyostrophia cooperi* Caster, 1939 from the Emsian of Colombia, suggesting a migration pathway between the Eastern Americas Realm and the Rhenish Shelf at that time.

Conspicuous features of the late Emsian brachiopod evolution are the phylogenetic appearance and diversification of the genera *Paraspirifer* Wedekind, 1926, i.e. the '*cultrijugatus* group' (see Solle 1971), and *Sollispirifer* Mittmeyer, 2008, i.e. the '*mosellanus* group' (Solle 1953; Schemm-Gregory & Jansen 2006a, b; Jansen 2016). The first species of *Paraspirifer* evolved from *Brachyspirifer ignoratus* (Maurer, 1883) during the early part of the late Emsian ('Lahnstein time'). Near the end of this interval, the *Par. sandbergeri* and *Par. praecursor-cultrijugatus* branches split (Solle 1971) with the 'Laubach Event' (Mittmeyer 2008), respectively the subgenera *Par.* (*Mosellospirifer*) Jansen, 2016 and *Par.* (*Paraspirifer*) Wedekind, 1926. The species *Par.* (*Mosellospirifer*) *sandbergeri* Solle, 1971 and *Par.* (*Paraspirifer*) *praecursor* Solle, 1971 are prominent examples of these evolutionary lines. *Sollispirifer* shows a rapid evolution leading to a group of species in the latest Emsian (Solle 1953) including the stratigraphically significant species *Soll. mosellanus* (Solle, 1953), *Soll. gracilis* (Solle, 1953), *Soll. steiningeri* (Solle, 1953) and *Soll. dahmeri* (Solle, 1953). The Lahnstein, Laubach and Kondel substages are chiefly defined by phylogenetic successions within these genera of delthyridoid spiriferides (Solle 1937, 1953, 1971, 1972; Mittmeyer 1974, 1982, 2008; Schemm-Gregory & Jansen 2005; Jansen 2016). A last diverse and abundant distal eurhenotypic fauna of the Upper Kondel Group (uppermost part of upper Emsian) occurs at the classic locality 'Haigerhütte' in the Dill Synclinorium (Frech 1888) with 39 reported brachiopod species and low species numbers of other groups such as bivalves, trilobites, tentaculitides and corals (Jahnke & Michels 1982b).

The onset of the allorhenotypic subfacies in the Eifel region approximately coincides with the first joint occurrences of *Cuninulus concavus* Sartenaer, 2005, *Paraspirifer* (*Par.*) *cultrijugatus* (Roemer, 1844) and *Alatiformia alatiformis* (Drevermann, 1907) ('OCA Fauna' of Struve 1982a) – the first occurrences of the individual species are slightly diachronic. The term '*Paraspirifer cultrijugatus* Fauna' has been proposed for this association of species ranging from the uppermost part of the upper Emsian into the lowermost Eifelian (Jansen 2016).

Late Emsian brachiopod evolution is also clearly seen within the genera *Leptostrophiella*, *Plebejochonetes*, *Subcuspidella* (and related taxa), *Alatiformia*, *Euryspirifer* and *Meganteris*. Scrutiny of these is still under way and promises many new taxonomic and biostratigraphic results (Jansen, in prep.).

Additional characteristic taxa of the upper Emsian: *Gibbodouvillina taeniolata* (Sandberger & Sandberger, 1856), *Platyorthis circularis transfuga* (Walther, 1903), *Chonetes sarcinulatus* (von Schlotheim, 1820), *Plebejochonetes semiradiatus* (Sowerby, 1842), *Oligoptycherhynchus daleidensis* (Roemer, 1844), *Ol. hexatomus* (Schnur, 1851), *Lapinulus pila* (Schnur, 1851), *Sartenaerirhynchus antiquus* (Schnur, 1853), *Cuninulus melanopotamicus* Sartenaer, 2005, *Subcuspidella subcuspidata* (Schnur, 1851), *Alatiformia janseni* Gad, 2002, *Euryspirifer robustiformis* Mittmeyer, 1972, *Eur. paradoxus* (von Schlotheim, 1813), *Brachyspirifer carinatus rhenanus* Solle, 1971, *Rhenothyris compressa* (Maurer, 1886), '*Athyris*' cf. *undata* (Defrance, 1828), *Meristella follmanni* (Dahmer, 1916), *Meganteris ovata suessi* (Drevermann, 1902), *Cryptonella macrorhyncha* (Schnur, 1853) and *Cimicinella cimex* (Richter & Richter, 1918).

### Lowermost Eifelian

In vast areas of the central and eastern Rhenish Massif, the uppermost part of the upper Emsian is represented by the distal eurhenotypic subfacies of the Kondel-Kieselgallenschiefer Formation followed by the hercynotypic, argillaceous Wissenbach Facies (still uppermost part of upper Emsian and Eifelian) caused by the continued transgression after the 'Heisdorf Event' and possibly also connected with the slightly younger global Choteč Event in the earliest Eifelian (Chlupáč & Kukal 1986, 1988). Rhenotypic brachiopods disappeared with the muddy, dysaerobic conditions on the sea floor.

In the Eifel Synclines, the allorhenotypic subfacies persists into the Eifelian. Apart from the extinction of some upper Emsian species near the Lower–Middle Devonian boundary and the first occurrences of the genus *Intermedites* Struve, 1995, the species *Rhenothyris aequabilis* Struve, 1970 and a few other taxa in the lowermost part of the Eifelian, there is no radical or abrupt change in faunal composition at this boundary, but rather a stepwise succession of last and first occurrences and slight change in abundances of species during the boundary interval (Struve & Werner 1982).The lowermost Eifelian is represented by the Lauch Formation exposed in the Eifel Synclines ('Eifeler Kalkmulden'). At the end of the 'Lauch time', a number of very typical earliest Eifelian brachiopod species went extinct with the 'Kirberg Event' (Struve 1990; Jansen 2016): *Paraspirifer* (*Par.*) *cultrijugatus*, *Iridistrophia* (*Flabellistrophia*) *hipponyx* (Schnur, 1851) (covering bedding surfaces or even forming shell beds), *Alatiformia alatiformis* (Drevermann, 1907) and *Cuninulus concavus* Sartenaer, 2005.

Other characteristic taxa of the lowermost Eifelian are: *Teichostrophia lepis subtilis* Struve, 1992, *Rhipidomella subcordiformis* (Kayser, 1871), *Gypidula montana acutecostata* Spriestersbach, 1942, '*Sollispirifer*' *schreiberi* (Happel, 1932), *Intermedites intermedius* (von Schlotheim, 1820) (ranging far up into the middle Eifelian), *Paraspirifer* (*Par.*) *frechi* Solle, 1971 (onset in the Heisdorf Formation), *Oligoptycherhynchus wetteldorfensis* (H. Schmidt, 1941) and *Rhenothyris aequabilis tectiplicata* Struve, 1970. In addition, less common leptaenine strophomenides, chonetoids, atrypides, athyridides and productellids occur.

## Systematic palaeontology

**Remark.** This section includes only diagnoses, comparisons and short discussions. Complete morphological details will be published in a later monograph. The signs and abbreviations used in the lists of synonyms are in accordance with Becker (2001).

Phylum BRACHIOPODA Duméril, 1805
Subphylum RHYNCHONELLIFORMEA
Williams, Carlson, Brunton, Holmer & Popov, 1996
Class Strophomenata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order **Strophomenida** Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Strophodontidae Caster, 1939
Genus *Fascistropheodonta* Harper & Boucot, 1978b

### ***Fascistropheodonta*? *wiltzensis*** n. sp.

Fig. 4/1A-C, 2

v 1939 *Stropheodonta* sp. - Lippert, p. 39.
v 1969 *Strophodonta* sp. aff. *sedgwicki* (Archiac & Verneuil) - Werner, pp. 177, 180-181, tab. 3.
v p 1978b *Fascistropheodonta sedgwicki* (d'Archiac & de Verneuil, 1842) - Harper & Boucot, pp. 24-25, pl. 45, fig. 5, 7, 8, pl. 46, fig. 1, 3, 4, 5?, non pl. 45, fig. 2, 3, 6, pl. 46, fig. 2 (= *Fasc. sedgwicki* (d'Archiac & de Verneuil, 1842)), non pl. 45, fig. 4 (= *Rhenostropheodonta rhenana* Jansen, 2016).
v p 2000 *Fascistropheodonta sedgwicki* (d'Archiac & de Verneuil, 1842) - Cocks & Rong, p. 294, fig. 186/4c, non fig. 186/4a, b (= *R. rhenana*).

**Holotype:** Internal mould of a dorsal valve and corresponding external mould (counterpart), SMF 99037a+b, former number SMF 'dot' 259, leg. H.-J. Lippert 1935, specimens mentioned in Lippert (1939: 39) as *Stropheodonta* sp., figured in the present work in Fig. 4/1A-C. Dimensions (DVEM): W = 42.6 mm, L = 35.0 mm.

**Type locality:** Daleiden, Irsen-Tal; eastern slope of the valley, 500 m N of topographic point 327.5 m, Daleiden Synclines ('Daleider Muldengruppe'), West Eifel region. TK 5903 Neuerburg.

**Type stratum:** Wiltz Formation, *Arduspirifer arduennensis arduennensis* Zone, lower part of upper Emsian (upper Lower Devonian).

**Material:** Wiltz Formation, *Ard. arduennensis arduennensis* Zone, lower part of upper Emsian, Daleiden Synclines, West Eifel region. Daleiden, Irsen-Tal, type locality, leg. H.-J. Lippert: 2 VVIM (SMF 99027, 99028), 1 VVEM, 1 DVIM (SMF 99035), 1 DVIM+EM (SMF 99037a+b), 9 DVEM (SMF 99025, 99026, 99029–99034, 99036). Daleiden vor der Höh: 1 DVEM (SMF 99038). Temporary road cut, approx. 1.2 km W of Krautscheid; leg. U. Jansen 2005, TK 5903 Neuerburg: 1 DVEM (SMF 99038). — Additional unnumbered specimens from the Wiltz Formation in the Prüm Syncline and the Daleiden Synclines, and a few questionable specimens from the localities Stoßberg near Weipoltshausen (upper Emsian, NE Lahn Synclinorium) and Kröffelbach (upper Emsian, NE Hintertaunus).

**Diagnosis:** Shell of moderate size, semielliptical to shield-shaped in outline, slightly wider than long; width-to-length ratio of dorsal valves commonly 1.2-1.3 (total range 1.1-1.5). Hinge-line denticulate along three quarters of its width. Ornamentation fascistropheodontid, interstriate, composed of bundles of very fine and slightly coarser costellae superimposed on very low plications increasing in number by insertion and branching, at the apex 20–24 bundles rapidly becoming subdued or disappearing towards the lateral and anterior margins; costellae multiply by insertion at irregular distances from the apex; coarser costellae located on crests of plications; costellae crossed by very fine concentric growth lines. Process pits distinct, divided by low ventral process; ventral muscle field faintly impressed, enclosed by low bounding ridges; adductor scars elongate-subelliptical. Cardinal process delicate, consisting of a pair of steeply erected lobes with slightly posteroventrally to posteriorly directed diductor attachment faces; socket ridges moderately long and thin, widely divergent; dorsal adductor field not elevated, small, extending about one quarter valve length, enclosed by low bounding ridges; breviseptum and lateral septa unknown; dorsal subperipheral ridge absent or weak.

**Comparison and remarks.** The species is assigned to the genus *Fascistropheodonta* mainly on account of its ornamentation, but only with reservation. It is distinguished from the Siegenian type species of this genus, *Fascistropheodonta sedgwicki* (d'Archiac & de Verneuil, 1842), to which it was previously assigned by Harper & Boucot (1978b), by less transverse, more compact outline and generally lower plications. The width-to-length ratio of shells is commonly 1.2-1.3 (1.1-1.5), versus 1.5-2.0 in *Fasc. sedgwicki*. The ventral muscle field is less impressed into the shell. In the dorsal valve, the cardinal process is more delicate and the adductor field not elevated on a muscle platform, whereas a distinct dorsal muscle platform is present in *Fasc. sedgwicki*. The new species differs from *Fasc. rudis* (Kegel, 1913) from the Rhenish middle and upper Siegenian in distinctly weaker and more numerous plications, and from *Fasc. primaeva* García-Alcalde, 1992 from the lower Siegenian of Asturias (Cantabrian Mountains) in a much larger shell with geniculation occurring later in ontogeny.

The generic affiliation of *Fasc.*? *wiltzensis* remains doubtful mainly because of its delicate cardinalia and the absence of an elevated dorsal muscle platform. On the other hand, a less elevated muscle platform could also be related to the relatively thin shell. Due to insufficient material, the present knowledge of the cardinalia is still unsatisfactory.

There are striking similarities to *Dictyostrophia cooperi* Caster, 1939 from the Emsian of Colombia, the type species of the genus *Dictyostrophia* Caster, 1939. This species shows a similar ornamentation,

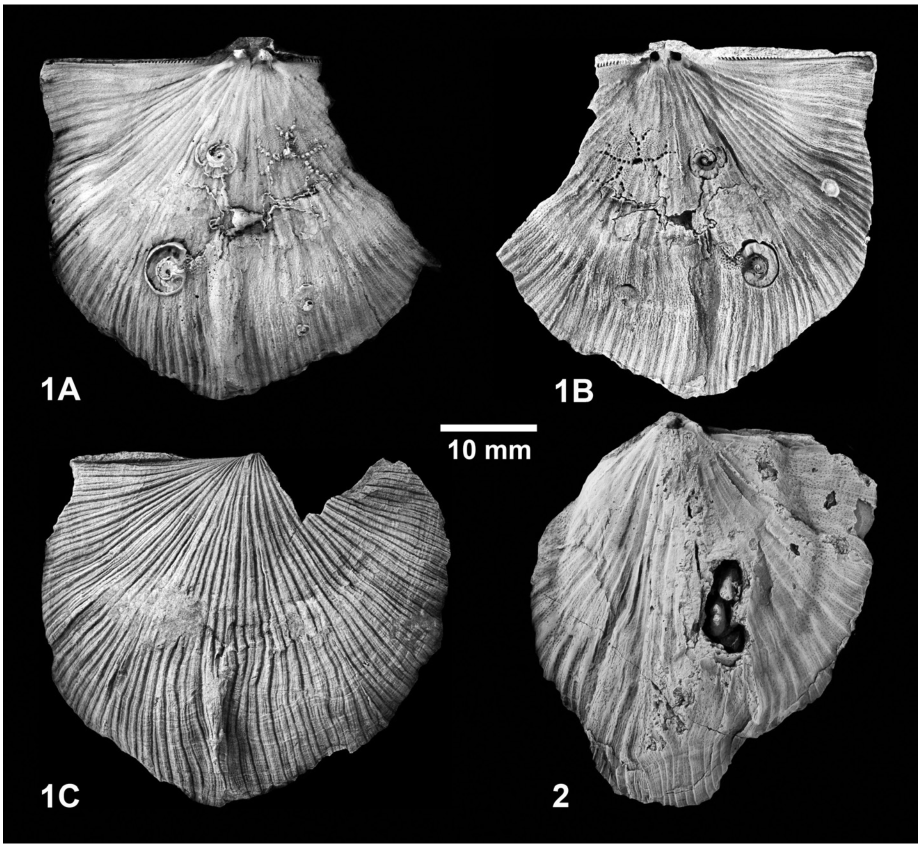


Fig. 4 - *Fascistropheodonta*? *wiltzensis* n. sp. Stratum: Wiltz Formation, lower part of upper Emsian, upper Lower Devonian. Locality: Daleiden, Irsental, West Eifel region. 1) SMF 99037a+b, holotype. Latex cast of internal mould of dorsal valve (1A), internal mould (1B) and external mould (1C). 2) SMF 99028, paratype. Internal mould of ventral valve.

but more pronounced concentric growth lines resulting in a reticulate pattern with nodose intersections of costellae and growth lines. To a lower degree, a similar pattern is locally visible on well-preserved external moulds of *Fasc.*? *wiltzensis*. The distinct expression of a reticulate micro-ornamentation in *D. cooperi* could at least partly be a preservational effect. Like the Rhenish species, *D. cooperi* has no elevated dorsal muscle platform (Harper & Boucot 1978a: pl. 30 fig. 11; 1978b: p. 23). The structure of the cardinalia of both species is still not well known. However, comparing the specimens described and figured by Harper & Boucot (1978a, b), a similar morphology is rather probable. More material of both species showing all critical characters must be studied before a final decision on the generic affiliation of the new species can be made.

*Fascistropheodonta*? *wiltzensis* has sometimes been mixed up with the co-occurring species *Rhenostropheodonta rhenana* Jansen, 2014a, from which it is distinguished by its distinct fascistropheodontid ornamentation, less impressed ventral muscle field, much less robust cardinalia, not elevated dorsal muscle platform, largely lacking dorsal septa and less developed subperipheral ridge.

*Fascistropheodonta*? *wiltzensis* occurs mainly in the medial to distal eurhenotypic subfacies of the Wiltz Formation in the West Eifel and Oesling regions.

**Distribution.** *Arduspirifer arduennensis arduennensis* Zone, lower part of upper Emsian (upper Lower Devonian), locally common, known from the Daleiden Synclines and the Prüm Syncline, Eifel region (Germany) and Oesling (Luxembourg). Questionable occurrences in the Lahn Synclinorium and the Hintertaunus.

### Order **Orthotetida** Waagen, 1884
### Suborder **Orthotetidina** Waagen, 1884
### Superfamily Chilidiopsoidea Boucot, 1959
### Family Areostrophiidae Manankov, 1979
### Subfamily Areostrophiinae Manankov, 1979

### *Ingentistrophia* n. gen.

**Etymology:** Combination of *ingens* (Lat., adjective: giant), the name of the type species, plus the common Greek ending *-strophia* (Greek, noun: turn, belt) for this group of brachiopods.

**Type species:** *Orthothethes ingens* Drevermann, 1904.

**Diagnosis:** Shell very large, equicostellate, with approximately convexoplane profile; ventral valve variable in shape, in its

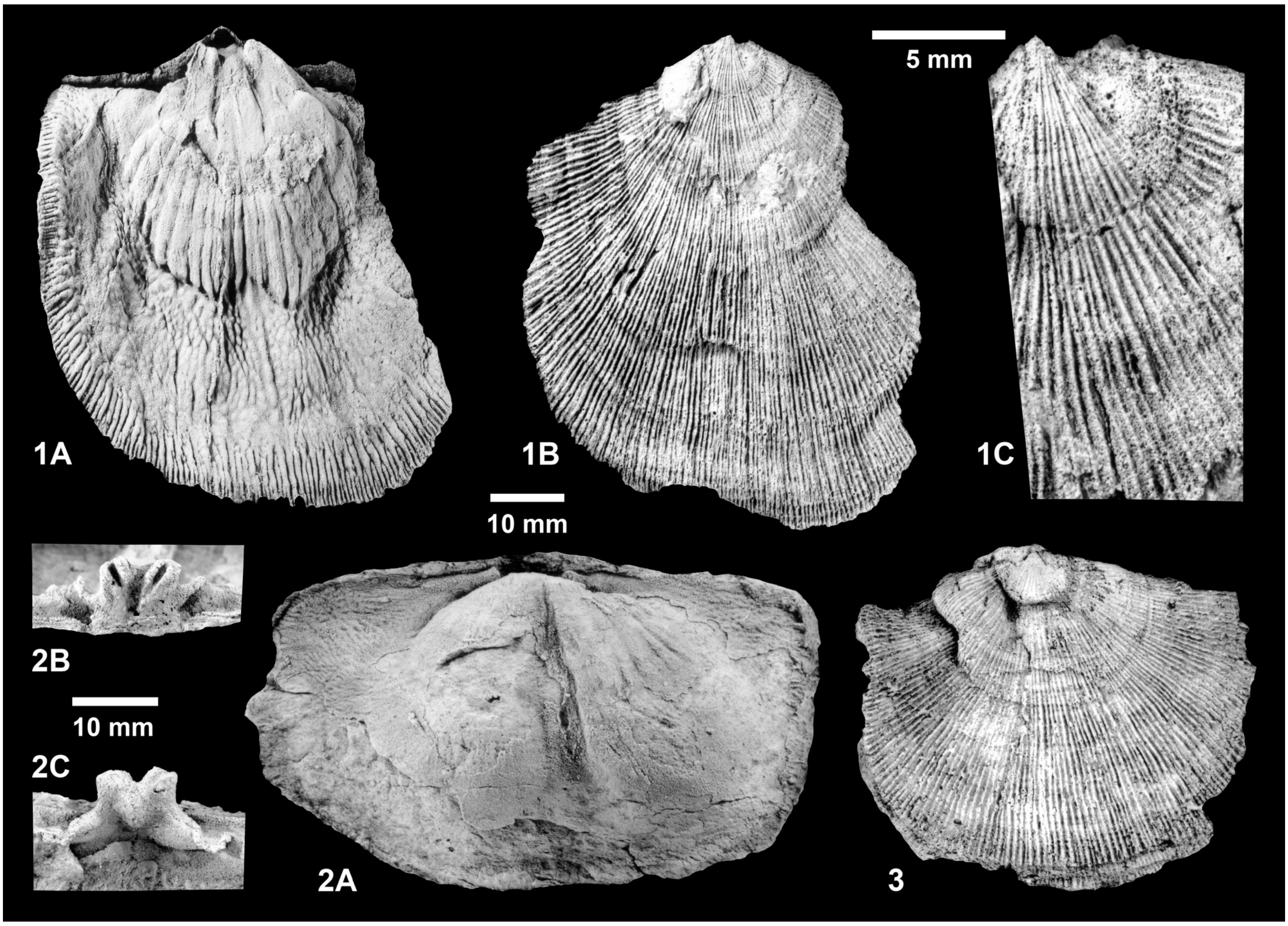


Fig. 5 - *Ingentistrophia ingens* (Drevermann, 1904). Stratum: Seifen Formation, upper part of middle Siegenian, middle Lower Devonian. Locality: Seifen, Westerwald region. 1) SMF-Mbg. 3629a+b, lectotype. Internal mould of ventral valve (1A), latex cast of external mould (counterpart) (1B) and detail of apical region of the same (1C). 2 ) SMF-Mbg. 3630, paralectotype. Internal mould of dorsal valve (2A) and latex cast of cardinal region in enlarged posterior (2B) and anterior (2C) views. 3) SMF 66181b. Latex cast of ventral external mould. Fig. 1C and 2B, C with individual scale bars; the central scale bar applies to the other figures.

apical part moderately convex and more or less distorted, anteriorly flat to concave and accordingly slightly resupinate; ventral interarea flat, moderately high, apsacline; delthyrium partially closed by convex pseudodeltidium; perideltidium not discernible; dorsal valve strongly convex and often showing a weak medial depression on internal moulds; dorsal interarea low, anacline; chilidium convex, low. Costellae strong, multiplying by insertion. Dental plates absent; ventral muscle field clearly impressed, variable in outline, can be subelliptical, ovate, subrectangular or subrhombic; diductor scars flabellate, subdivided by distinct radial ridges and a strong median ridge anteriorly; adductor scars elongate, located posteromedially within muscle field. Bilobed cardinal process fused with inner socket ridges, with median node or ridge on its anterior face; lobes discrete, steeply protruding, with posteriorly, or slightly posteroventrally to posterodorsally directed diductor attachment faces showing longitudinal furrows; inner socket ridges strongly developed, divergent at commonly 100° to 120° (in possibly deformed specimens down to 75° and up to 134°) and delimiting deep dental sockets, extending into short brachiophores anteriorly; dorsal adductor field deeply impressed, subtriangular to subelliptical in outline, subdivided by radial ridges anteriorly and with dendritic posterior impressions in gerontic specimens. Inner surfaces of valves covered by irregular, sublinear impressions of the mantle canal system and marked peripherally by the impression of costellae.

**Discussion and comparison.** The combination of characters, in particular very large size, distorted ventral apical region possibly related to cementation in early growth stages, lack of dental plates and morphology of muscle impressions is unique in Lower Devonian orthotetide brachiopods from the Rhenish Massif. As the shell substance of *Ingentistrophia* is still unknown, the genus cannot be assigned with absolute certainty to any orthotetide family. However, close similarities to genera of the Areostrophiidae and its geological age make an affiliation to this family most probable. Other Silurian and Devonian genera of the impunctate Areostrophiidae also lack dental plates, but are generally of smaller size and normally lack distinct muscle impressions which are typical of the new genus. In addition, *Ingentistrophia* differs from *Areostrophia* Havlíček, 1965 and *Aesopomum*

Havlíček, 1965 in a relatively faintly convex to slightly resupinate ventral valve with lower interarea. A low dorsal interarea and chilidium are present in *Ingentistrophia* and reported as absent in *Areostrophia* and *Aesopomum*. The ventral valve of *Areostrophia* is generally convex, whereas that of *Aesopomum* is subconical. The morphology of *Areostrophia* shells is, however, rather variable, and even a resupinate, anteriorly concave ventral valve was reported in an exceptional specimen of *A. distorta* (Barrande, 1879) from the Pragian Koněprusy Limestone (Havlíček 1967: 198, pl. 42, fig. 9; material restudied by the present author). *Areostrophia* is probably the most closely related genus. Accordingly, the new genus is included in the subfamily Areostrophiinae.

*Ingentistrophia* has essentially a larger shell, apparently a more convex dorsal valve and more delicate cardinalia than *Eoschuchertella* Gratsianova, 1974 first described from southern Siberia (Gratsianova 1974, 1975); the genus is still not well known.

There are possible relatives of *Ingentistrophia ingens* also in rhenotypic successions of early Gedinnian (Lochkovian) age: Boucot (1960) described '*Schuchertella euzona*' (non Fuchs, 1919) from the Mondrepuis Formation in the Ardennes and Renouf (1972) '*Schuchertella* sp.' from the 'Grès à *Orthis monnieri*' in the Armorican Massif. These forms resemble representatives of the Rhenish genus and lack dental plates, as well, but are much smaller, slightly biconvex and do not show the distinctly impressed ventral muscle and dorsal adductor fields. These differences may partly be due to the enormous difference in shell size of Gedinnian and middle Siegenian representatives.

*Ingentistrophia* differs from the Rhenish orthotetide genera *Iridistrophia* and *Xystostrophia* in the absence of dental plates and presence of a distorted ventral umbo. The new genus is distinguished by its larger shell from the Middle to Late Devonian genus *Schuchertellopsis* Maillieux, 1939 which is cemented with the entire ventral valve to a hard substrate. *Ingentistrophia* shares a distorted ventral beak, impressed ventral muscle field and dorsal adductor field, a bilobed cardinal process and the absence of dental plates with *Floweria* Cooper & Dutro, 1982 from the Upper Devonian of North America. It differs from *Floweria* in a strongly convex dorsal valve and a moderately convex to flat or slightly resupinate ventral valve, whereas *Floweria* has a flat to slightly convex dorsal valve and a more convex ventral valve (Stigall Rode 2005); in addition, the shell of *Ingentistrophia* is larger. *Areostrophia* ? *defracta* Langenstrassen, 1972 from the uppermost Emsian and lower Eifelian of the eastern Sauerland also belongs to the group under consideration: it much resembles species of *Floweria* in shell profile, ventral muscle field and dorsal adductor field.

**Species included.** At present, only the type species.

### *Ingentistrophia ingens* (Drevermann, 1904)

Figs. 5/1A-C, 2A-C, 3

1893 *Streptorhynchus gigas* (M'Coy) Davidson - Maurer, pp. 4-5, pl. 1, fig. 1-4.
v * 1904 *Orthothethes* [sic!] *ingens* Drevermann, pp. 278-280, pl. 32, fig. 7, 8, 8a, 9.
non 1911 *Orthothetes ingens* - Maillieux, pp. 179-180, pl. B, fig. 3-5 (a different early chilidiopsoid).
1912 *Orthothetes ingens* - Maillieux, pp. 7, 8, 9.
v 1934 *Schuchertella ingens* - Dahmer, pp. 17, 21, 25, 28, 32, 33, 38.
1936 *Schuchertella ingens* - Maillieux, pp. 74-77.
v 1960 *Stropheodonta ingens* - Paproth, tab. 1.
v 2003 '*Orthotetes*' *ingens* - Poschmann & Jansen, p. 167, tab. 5, pl. 2, fig. 9.
v 2016 '*Orthotetes*' *ingens* - Jansen, pp. 74, 77.

**Lectotype:** Internal mould of ventral valve and corresponding external mould, SMF-Mbg. 3629a+b, selected in the present work, figured by Drevermann (1904: pl. 32 fig. 8, 8a), refigured in the present work in Fig. 5/1A-C; dimensions (VVIM): W > 53 mm, L = 63 mm.

**Type locality:** Seifen I, 830 m SE of railway station. Westerwald, Rhenish Massif. TK 5311 Altenkirchen.

**Type stratum:** Seifen Formation; *Multispirifer solitarius* Zone, lower part of *Acrospirifer primaevus* Zone; upper part of middle Siegenian (middle Lower Devonian).

**Material:** Seifen Formation, middle Siegenian, Westerwald, *Multispirifer solitarius* and lower *Acrospirifer primaevus* zones. Several outcrops near Seifen, road and railway cuts in the Holzbach-Tal about 830 m SE of railway station, TK 5311 Altenkirchen: 1 AVIM (SMF-Mbg. 6090), 3 VVIM+EM (lectotype SMF-Mbg. 3629a+b; SMF 66181a+b; 93808a+b), 4 VVIM (paralectotype SMF-Mbg. 3628; YPM 153227; SMF 85409, 93810), 1 VVEM (SMF 85410), 1 DVIM+EM (SMF 85407a+b), 9 DVIM (paralectotype SMF-Mbg. 3630; SMF 66182, 85408, 85411, 85412, 85767, 85768, 93808b, 93809). Ascheid near Seifen, Oberährener Bruch, leg. E. Grebel, TK 5311 Altenkirchen: 2 VVIM (SMF 94022, 94027), 2 VVEM (SMF 94025, 94028), 1 DVIM+EM (SMF 94026a+b), 2 DVIM (SMF 94023, 94024). — Beds of middle Siegenian age, Westerwald, Krunkel Section (see Poschmann & Jansen 2003), *M. solitarius* and lower *Acr. primaevus* zones; temporary outcrop along ICE railway track (Frankfurt am Main–Köln), SSW of Krunkel; leg. M. Poschmann 1999; TK 5411 Dierdorf, near R (33) 94040, H (56) 05 240: 1 VVIM (PWL 2000/5104 LS). — Katzenelnbogen Formation, middle or upper Siegenian, NW Taunus, Weißler Höhe: 1 DVIM+EM (SMF 85413a+b+c). — Middle Siegen Group, middle Siegenian, Siegerland. Fischbach: 1 VVIM (MB.B. 2062b). — Middle Siegenian, Ardennes, Belgium, sommet de la courbe du chemin de fer, Mirwart; coll. G. Dewalque: 1 VVIM (PA.ULg 6344).

**Diagnosis:** As for the genus.

**Remarks.** This very distinctive taxon is a good biostratigraphic marker of the Siegenian. It is most abundant in middle Siegenian deposits, for example in the Middle Siegen Group of the Siegerland, the Seifen Formation of the Westerwald and age-equivalent strata of the East Eifel region. The species attains exceptional widths of 80 mm and lengths of 60 mm. It occurs in the medial eurhenotypic subfacies and seems to prefer relatively clear water.

**Range.** *Multispirifer solitarius*, *Hysterolites hystericus* and *Acrospirifer primaevus* zones, middle to upper Siegenian (middle Lower Devonian).

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order **Orthida** Schuchert & Cooper, 1932
Suborder **Dalmanellidina** Moore, 1952
Superfamily Enteletoidea Waagen, 1884
Family Schizophoriidae Schuchert in Schuchert & LeVene, 1929
Genus *Pachyschizophoria* Jansen, 2001
[ex subgenus *Schizophoria* (*Pachyschizophoria*) Jansen, 2001]
Type species - *Hysterolites vulvarius* von Schlotheim, 1820.

**Discussion:** *Pachyschizophoria* was originally introduced as a subgenus of *Schizophoria* King, 1850. It has been used as a separate genus by the present author in the meantime (Jansen et al. 2007; Jansen 2016). The combination of characters, such as general lack of fulcral plates and presence of an elongate-subelliptical ventral muscle field, justifies its elevation to the genus level. Ongoing research has shown that this group of species underwent clearly a separate evolution next to representatives of *Schizophoria* and *Rhenoschizophoria*. The distinction between 'lacking' and 'present fulcral plates' has led to the separation of genera in other orthides as well, for example in the case of *Proschizophoria* and *Fulcriphoria* (see Carls 1974).

### *Pachyschizophoria amygdalina* n. sp.

Fig. 6/1A-D, 2, 3A-C

v 1919 *Orthis vulvaria* Maur. - Viëtor, pp. 449-450, 466.
v 1939 *Schizophoria vulvaria*, 'Quarzit-Form' - Lippert, pp. 26, 28, 29, 23?
v 1948 *Schizophoria vulvaria* - Dahmer, p. 118.
v 1972 *Schizophoria vulvaria* - Mittmeyer, pp. 94-95, pl. 1, fig. 7.
v 2001 *Schizophoria* (*Pachyschizophoria*) n. sp. C Jansen, pp. 139-141, tab. 10 p.p., pl. 6, fig. 4-6.
2016 *Schizophoria* (*Pachyschizophoria*) sp. C - Franke, pp. 75-76, pl. 18, fig. 5-6.
v 2016 *Pachyschizophoria* sp. nov. C sensu Jansen, 2001a - Jansen, pp. 85-86, text-fig. 7a-b.

**Etymology:** Derived from *amygdalinos* (Greek, adjective: *from the almond tree*), alluding to the almond-shaped outline of the ventral muscle field.

**Holotype:** Internal mould of ventral valve and corresponding external mould (counterpart), SMF 98886a+b, leg. U. Jansen 2016, figured in the present work in Fig. 6/1A-D, stored in the Senckenberg Museum, Frankfurt am Main. Dimensions (VVIM): L = 30.0 mm, W = 39.5 mm.

**Type locality:** Olmscheid III; road from Daleiden to Olmscheid, SSW of Olmscheid, Daleiden Synclines, West Eifel region, Rhenish Massif, Germany. TK 5903 Neuerburg; R (25) 14 266, H (55) 46 735.

**Type stratum:** Berlé Formation; lowermost part of upper Emsian (upper Lower Devonian).

**Material:** Berlé Formation, lowermost part of upper Emsian, West Eifel region, Germany and Luxembourg. Olmscheid I–III, outcrops at the road Daleiden–Olmscheid, leg. H.-J. Lippert 1936 and U. Jansen 2016; TK 5903 Neuerburg: 3 VVIM+EM (SMF 66967a+b, 98886a+b, 98887a-d), 8 VVIM (SMF 66962, 66964 (2), 66966 (2), 66968.1/3, 66976), 1 VVEM (SMF 66962), 1 DVIM (SMF 66968.2). Heimbach-Tal near Machtemes, leg. H.-J. Lippert 1936, TK 5903 Neuerburg: 1 VVIM, 1 DVIM (SMF 66965). Dasbourg, Luxembourg: 1 VVIM+EM (SMF 66957a+b), 2 DVIM (SMF 66958, 66959). Winseler/Wiltz, Luxembourg: 3 VVIM (SMF 59657–59659), 1 VVIM+EM (SMF 66960a+b), 4 DVIM (SMF 59650–59653), 1 DVIM+EM (SMF 66956a+b). Berlé, Luxembourg: 4 VVIM (SMF-Mbg. 4828.1–2; SMF 98890, 98892), 1 VVEM (SMF 98891), 2 DVIM (SMF-Mbg. 4828.3, 4829). Precise locality unknown: 1 VVIM (SMF 98889), 1 DVIM (SMF 98888). — Lower part of upper Emsian, Middle Rhine region. a) Emsquarzit Formation. Rhenser Mühlental, different outcrops: 9 VVIM (MB.B. 3209, 3211; SMF-Mbg. 4831, 4832.3; SMF 59821, 66961.1–2 (4)), 5 DVIM (MB.B. 3218; SMF-Mbg. 4830, 4832.1–2; SMF 66961.1). Bienhorn-Tal/Koblenz: 1 VVIM (SMF 59655). b) Hohenrhein Formation. Kühkopf/Koblenz (Kleinbornsbach-Tal): 1 DVIM (SMF 59656).

**Diagnosis:** Ventral valve generally with a wide and shallow sulcus. Dental plates very short, leaving wedge-shaped incisions on the internal mould; ventral bounding ridges absent to moderately developed; if present, ventral bounding ridges commonly leave sharply delimited outer edges on the internal mould; ventral muscle field broad, elongate-amygdaloid to kite-shaped in outline, extending to about half valve length or exceeding it, bisected by narrow median ridge, the two halves of the muscle field on the internal mould flattened, faintly convex in cross section; peripheral ridge in ventral interior poorly developed or absent. Cardinal process elevated on moderately developed notothyrial platform; brachiophore plates and brachiophores short and thick, leaving wedge-shaped incisions on the internal mould that are abruptly ending and delimited against low dorsal bounding ridges anteriorly; dorsal adductor field commonly suboval to subelliptical in outline.

**Comparison.** *Pachyschizophoria amygdalina* differs from the type species of the genus, *Pa. vulvaria* (von Schlotheim, 1820) from the Rhenish upper Emsian (see Jansen 2001), in possessing a generally broader ventral muscle field with amygdaloid or kite-

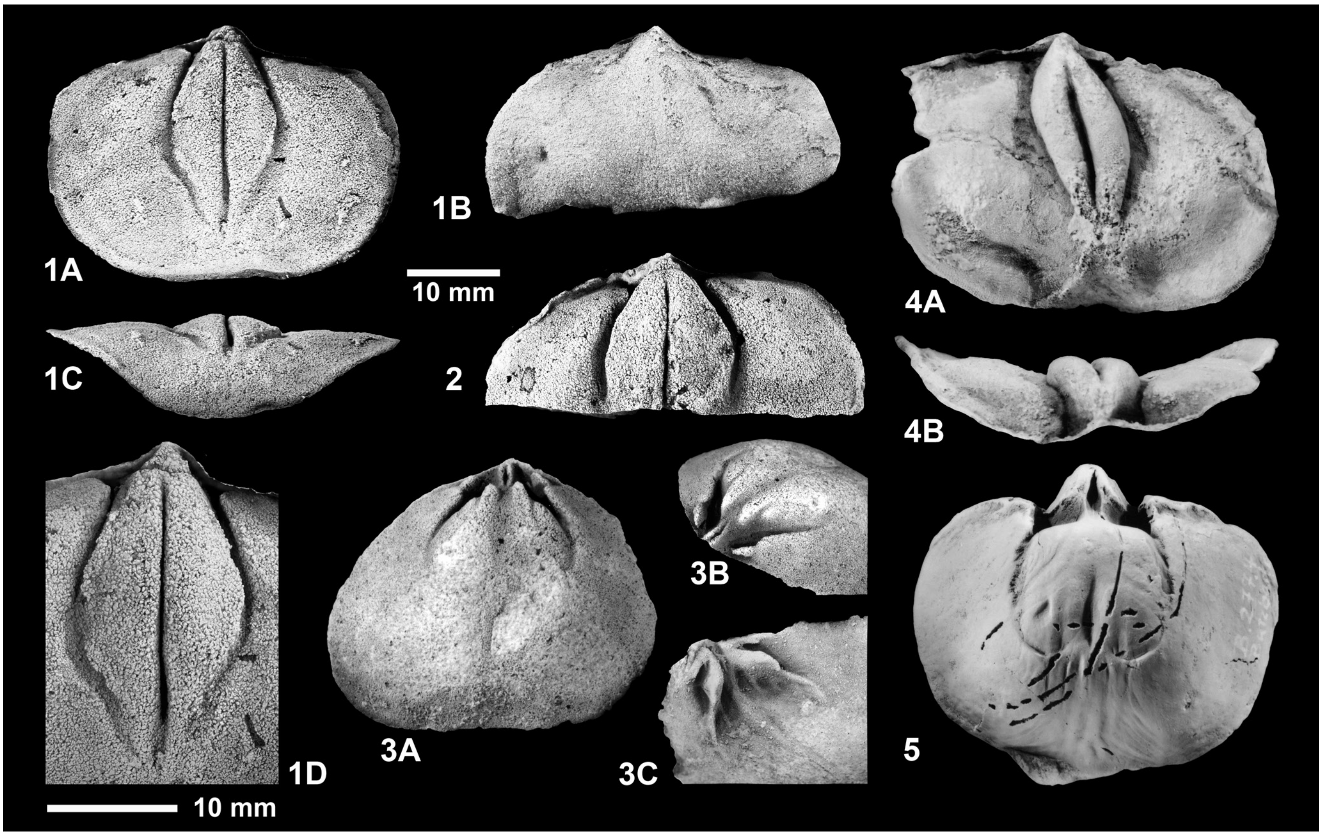


Fig. 6 - 1-3 - *Pachyschizophoria amygdalina* n. sp. Stratum: Berlé Formation, lowermost part of upper Emsian, upper Lower Devonian. 1) SMF 98886a+b, holotype. Locality: Olmscheid III, road between Daleiden and Olmscheid, West Eifel region. Internal mould of ventral valve (1A), latex cast of external mould (1B), anterior view of internal mould (1C) and slightly tilted view of ventral muscle field (1D). 2) SMF 98887a, paratype. Same locality as before. Internal mould of ventral valve showing impressions from sharply defined bounding ridges. 3) SMF 59650, paratype. Locality: Winseler, S of Wiltz, Luxembourg. Internal mould of dorsal valve (3A), oblique posterolateral view of internal mould showing absence of fulcral plates (3B) and latex cast of internal mould in oblique anterolateral view, showing strong brachiophores (3C). 4-5 - *Pachyschizophoria vulvaria* (von Schlotheim, 1820). 4) MB.B. 277.1, lectotype (figured by von Schlotheim 1820: pl. 29 fig. 2b), Schlotheim Collection. Locality: unknown, Rhenish Massif, probably Middle Rhine region. Stratum: beds of late Emsian age. Internal mould of articulated valves, ventral (4A) and posterior (4B) views, for comparison with fig. 1A and 1C. 5) MB.B. 277.4, internal mould of articulated valves, possibly paralectotype. Locality: Butzbach near Gießen, eastern Rhenish Massif. Stratum: beds of late Emsian age. Dorsal view of internal mould. Fig. 1D with individual scale bar; the upper scale bar applies to the other figures.

shaped outline and, on the internal mould, in cross section flattened halves, contrasting to the elongate-subelliptical to lanceolate, more convex muscle field of *Pa. vulvaria* (compare Fig. 6/1A, C and Fig. 6/4A, B). If ventral bounding ridges are present, they are generally narrower and more sharply delimited along their outer edges. The ventral sulcus is generally shallower. The dorsal adductor field is commonly suboval to subelliptical in outline, in *Pa. vulvaria* subelliptical or subcircular to rounded-subrectangular (compare Fig. 6/3A and Fig. 6/5).

Possible ancestors of the new species are *Pachyschizophoria* sp. D Jansen, 2001 from the middle part of the lower Emsian in the Taunus, with shorter ventral muscle field, or a still undescribed form from the Klerf Formation (uppermost part of lower Emsian) of the Eifel region.

The new species differs from *Pa. tataensis* (Jansen, 2001) from the lower/upper Emsian boundary interval in the eastern Dra Plains (southern Morocco) in dental plates more separated from generally less developed ventral bounding ridges, more developed notothyrial platform, shorter and thicker brachiophore plates and a different outline of the dorsal adductor field which is suboval to subelliptical, in contrast to the predominantly suboval to rounded subtriangular adductor field in the Moroccan species. A late morph of the latter closely resembles *Pa. amygdalina* as regards the ventral valve interior, but still shows less developed notothyrial platform and thinner brachiophore plates. *Pachyschizophoria amygdalina* differs from the

Cantabrian species *Pa. beaumonti* (de Verneuil, 1850) in larger ventral muscle field commonly crossing mid-length of valve and more thickened, shorter brachiophore plates, contrasting with a ventral muscle field just reaching mid-length (de Verneuil 1850, pl. 4 fig. 8c) and slender brachiophore plates (ibidem, pl. 4 fig. 8d) in the Spanish species; Verneuil's type material could be studied in the collections of the Université Claude Bernard Lyon 1.

**Range.** *Brachyspirifer ignoratus* and *Arduspirifer arduennensis treverorum* zones, lower part of upper Emsian (upper Lower Devonian); most typical forms occur in the Emsquarzit and Berlé formations.

## Conclusions

In the framework of a comprehensive revision of the Rhenish Lower Devonian Brachiopoda, the Pragian–Emsian brachiopod succession of the Rhenish Massif is outlined and interpreted with reference to the geological history, starting with the 'Rhenish Gap' sensu stricto in the late Gedinnian–early Siegenian and ending with the 'Kirberg Event' in the early Eifelian. Numerous brachiopod taxa of this succession are still poorly or insufficiently known in terms of their detailed morphology and phylogenetic relationships. The brachiopod assemblages occur as a sequence of 'faunas' separated from each other by events each characterized by strong faunal turnover (Fig. 3). The events were triggered by shelf-wide or more regional environmental perturbations of different magnitudes and durations, resulting in emigration or regional extinction of substantial parts of a brachiopod fauna. Greater fluctuations of eustatic sea-level, climate (?), crustal subsidence rates and quantities of siliciclastic input from the Old Red Continent in the north caused changes in the palaeoenvironment, including episodes of unsuitable or hostile conditions on various spatial and temporal scales, possibly tens or hundreds of thousand years. These are documented from successions of the proximal eurhenotypic and pararhenotypic subfacies – and the terrestrial (Old Red) facies. Brachiopod evolution continued in restricted or small and isolated habitats within the main Ardenno-Rhenish Shelf, at its periphery or in neighbouring shelf areas. Restricted gene flow may have led to rapid evolution in smaller populations and allopatric or peripatric speciation. After the events, more suitable conditions recurred, so that brachiopods could disperse again from the isolated habitats within the shelf or immigrate from outside. Benthic biocoenoses could re-establish. Typical representatives of these post-event species are the newly described species *Pachyschizophoria amygdalina* and *Fascistropheodonta*? *wiltzensis*, the first possibly developed at the time of the distinct Berlé Event from an ancestral Rhenish species, the second one more probably being an immigrant species. *Fascistropheodonta*? *wiltzensis* may even be related to *Dictyostrophia cooperi* Caster, 1939 from the Emsian of Colombia. From beds of Siegenian age, the large-sized new genus *Ingentistrophia* is described; it shows affinities to bohemotypic areostrophiids and to poorly known rhenotypic forms from the Gedinnian.

The study of the Rhenish brachiopods leads to some general conclusions still to be examined in detail: As regards the relatively uniform middle and upper Siegenian faunas, showing hardly any evolution in the brachiopods, the time reflected by these intervals must have been very short, together perhaps less than 1 million years. Moreover, the faunal change between the two units is interpreted to be mainly related to a change in the palaeoenvironment. On the other hand, the faunas of the lower Emsian and in particular those of the upper Emsian show many evolutionary steps reflecting a multiple length of geological time.

There were more events of smaller magnitude which led to partial extinctions and migrations of brachiopods. The detailed quantitative analysis of these processes is planned after the ongoing comprehensive revision of the Rhenish brachiopods being conducted by the present author.

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