Strophomenid brachiopods
from the Rhenish Lower Devonian (Germany)

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Early Devonian Strophomenida (Brachiopoda) from the Rhenish Slate Mountains (Germany) are described. Three genera are introduced as new: Gigastropheodonta (type species: Leptaena (Strophomena) gigas McCoy, 1852), Rhenostropheodonta (type species: R. rhenana gen. nov. et sp. nov.) and Gibbodouvillina (type species: Strophomena taeniolata G. & F. Sandberger, 1856). The diagnosis of the poorly known genus Boucostreamhia Jahnke, 1981 (type species: Stropheodonta herculea Drevermann, 1904) is revised. These and several further taxa are briefly discussed with regard to phylogenetic relationships, palaeobiographical implications, palaeobiological aspects and stratigraphical significance. • Key words: Brachiopoda, Strophomenida, Devonian, Rhenish Slate Mountains, taxonomy, biostratigraphy, palaeobiology, palaeobiogeography.


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The Early Devonian Strophomenida from the Rhenish Slate Mountains (Rheinisches Schiefergebirge, Germany) have been paid little attention to since the classical works of d’Archiac & de Verneuil (1842), G. & F. Sandberger (1856) or Drevermann (1902, 1904). A few taxa have been studied more recently by Jahnke (1971, 1981, 1986). In the frame of a large monograph on the “stropheodontoid” Strophomenida, Harper & Boucot (1978a–c) revised all genera of this large group on a world-wide scale from the Ordovician to the Devonian. They introduced the genus Fascistropheodonta and the subgenus Leptostrophia (Leptostrophiella) basing these on Rhenish type species, and they redescribed the Rhenish taxa Douvillina and Plicostropheodonta. Besides, several Rhenish species were assigned by these workers to genera established in regions outside the Rhenish Slate Mountains and partly from different stratigraphic levels, as well.

The present author started his work on Rhenish “stropheodontoids” in the early nineties (Jansen 1994, 1998a, b) focusing on materials from the classical localities Seifen (upper part of Middle Siegenian, Westerwald) and Oberstadtfeld (upper part of Lower Emsian, Eifel area). The study of the Seifen fauna in particular has shown that intense collecting and detailed analysis of these multi-species allochthonous assemblages are necessary to record the complete morphology of each taxon. Even the trivial question which ventral and dorsal valves belong to the same species was not easy to answer in some cases. With regard to the genus Boucostreamhia Jahnke, 1981, common in the Seifen fauna, the author has come to the conclusion that its type species B. herculea (Drevermann, 1904) was often taxonomically united with or mistaken for the similar-sized but unrelated “Stropheodonta” gigas (McCoy, 1852) which occurs in the same fauna. In the opinion of the present author, the genus Boucostreamhia has largely been misunderstood by previous workers starting with its original diagnosis (Jahnke 1981) and in the following years, for example by García-Alcalde (1992), Ait-Malek et al. (2000) and in the revised Treatise on Invertebrate Palaeontology, Part H (Cocks & Rong 2000). It was necessary to revise the genus and to erect a new genus for the group of “S.” gigas.

Another group of Rhenish strophomenids is represented by Strophomena piligera G. & F. Sandberger, 1856. The species has been reported from various stratigraphic levels within the Emsian of Europe and was assigned by Harper & Boucot (1978c, p. 34) to Strophodonta Hall, 1850 whose type-species Strophomena demissa Conrad, 1842 comes from the Middle Devonian Hamilton Group in E North America. Three years later, Jahnke (1981, pp. 152, 153) assigned S. piligera to the Rhenish genus Plicostropheodonta Sokolskaya, 1960. The actual revision has shown that the taxon piligera actually includes at least two Rhenish species belonging to a new genus.
Finally, the poorly known Rhenish species *Strophomena taeniolata* G. & F. Sandberger, 1856 is revised. Rösler (1954) examined this species and determined it as a representative of *Strophodonta* Hall, 1850. At that time, *Strophodonta* was still a comprehensive genus with very wide scope. Later, Jahnke (1971) assigned it to the Bohemian genus *Bojodouvillina* Havlíček, 1967, and Harper & Boucot (1978b) finally included it in their new genus *Protodouvillina*, which is based on a type species from the Hamilton Group, again. Jahnke (1981, p. 157) determined *Protodouvillina taeniolata* in the Armorican Massif and García-Alcalde (1992, fig. 4) in the Cantabrian Mountains. The present author has compared the Rhenish forms with the presumable congenerics from North America to elucidate their relationships. It turned out unavoidable to introduce a new genus for the species *taeniolata* and related forms.

The classical regional stratigraphy, including the stages Siegenian and Emsian in German sense, is used herein (Carls 1987, Jansen 2001) because the global GSSP subdivision still cannot be reproduced with satisfying precision in these siliciclastic-neritic, rhenotypic successions. In spite of this restriction, the strophomenids turned out to be excellent biostratigraphic markers on a regional scale. For the position of the lithostratigraphic units as used in the present work the Devonian Correlation Tables (Weddige 1996, 1998a, b, 2000) and the “Stratigraphic Table of Germany” (German Stratigraphic Commission 2002) may be consulted.

This work represents a part of a monographic revision of the rhynchonelliformean brachiopod taxa from the Rhenish Lower Devonian, with the intention to improve the knowledge on their morphology, to reconstruct their phylogenetic relationships, to clarify their stratigraphic ranges and to get new insights in their palaeobiology and palaeobiogeography.

### Material and methods

The materials studied are preserved as internal and external moulds of mainly disarticulated shells, rarely of articulated ones. Latex casts were made to examine the external and internal shell morphologies. The specimens were coated with magnesium oxide prior to photographing. They are largely stored in the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt am Main (Senckenberg Museum), but in other museums/institutions in Europe and overseas, as well.
Localities

The localities are situated in different regions of the Rheinish Slate Mountains (Figs 1, 2) and further specified in the lists of materials.

Abbreviations

The lists of materials contain abbreviations used both for singular and plural: AVIM – internal mould of articulated valves; DVEM – external mould of dorsal valve; DVIM – internal mould of dorsal valve with corresponding external mould (counterpart); VVIM – internal mould of ventral valve; VVEM – external mould of ventral valve; VVIM+EM – internal mould of ventral valve with corresponding external mould (counterpart).

Institutional abbreviations


Morphological terminology

The terminology used in the systematic part largely follows the Treatise on Invertebrate Paleontology, Part H (Williams et al. 1997, Williams & Brunton 1997, Cocks & Rong 2000). Some additional terms and terms used in a slightly different sense shall be explained:

Capilla (pl. capillae; adj. capillate). – Micro-costella, very fine radial rib on outer surface of shell, reaching a maximum width of hardly more than 0.15 mm.

Cavities for accommodation of brachiophores and cardinal process lobes. – Pairs of cavities in the apical region of the ventral valve in which the cardinal process lobes and the brachiophores of the dorsal valve fit in articulated shells. They represent a subdivision of the central apical cavity and are medially separated by the ventral process. These structures obviously have an articulatory function. The cavities for the cardinal process lobe and the brachiophore of each side are either separated by a ridge as in Gigastropheodonta (Fig. 4K) or Rhenostropheodonta (Fig. 5J) [note that the cavities are preserved as ridges and the separating ridge is represented by a furrow on the internal moulds figured], or they are not separated as in Boucotstrophia (Fig. 3K). A taxonomic significance is ascribed to this difference. The term “crural fossette” has been used to describe cavities receiving the posteroventral edge of the brachiophore or crural plate (Williams & Brunton 1997), but this term refers to cavities in the hinge teeth.

Interstriate. – Parvicostellate ornamentation consisting of relatively coarser costellae clearly separating groups of more or less numerous, uniform capillae (for example in Gibbodouvillina: Fig. 5D) or very fine costellae in a very regular pattern (= “interstriat” sensu Paechkelmann & Sieverts 1932, p. 41; = “interstriée” sensu Jahne 1981, p. 149; Jahne 1986, pp. 108–110; Alt-Malek et al. 2000, pp. 311, 312, 315). The coarser costellae may arise from capillae in a distance from the apex. The clear term “interstriate” is used for this characteristic type of ornamentation, a specification of the “unequally parvicostellate” type (Harper & Boucot 1978a, p. 58) which can be traced back to Williams (1953) (some workers just use the term “parvicostellate” instead). The latter term is regarded here as more general, also including ornamentations with costellae of different size but no distinct interstriate pattern.

Medial septa. – Pair of septa starting from notothyrial platform or starting within dorsal adductor field and may extend anterior to it, close to median plane, may be developed as low ridges (for example in Gibbodouvillina: Fig. 5B).

Paradental plates (= minute struts sensu Harper & Boucot 1978a). – Pair of plates located lateral to the ventral...
cavities for accommodation of cardinal process lobes, leaving slits at the internal mould, resembling dental plates but may have evolved independently (for example in Gibbodouvilleina: Fig. 5A).

Side septa (different from the use in Cocks & Rong 2000). – Pair of septa or ridges, located anterior or anterolateral to dorsal adductor scars, located more lateral than medial septa and may be continuous with dorsal muscle-bounding ridges (for example in Rhenostropheodonta: Fig. 5N).

**Systematic palaeontology**

Order Strophomenida Opik, 1934
Superfamily Strophomenoidea King, 1846
Family Amphistrophiidae Harper, 1973
Subfamily Mesodouvillininae Harper & Boucot, 1978b

**Discussion.** – Representatives of the subfamily Mesodouvillininae are very common in Early Gedinnian (~ early Lochkovian) deposits of the Ebbe Anticlinorium, where internal and external moulds of concavo-convex shells of *Mesodouvillina triculata* (Fuchs, 1919) cover bedding surfaces in the Flaserschiefer Member of the Hüinghausen Formation. The marine succession is interrupted after the Early Gedinnian and returns with a transgression in the Middle Siegenian so that the Late Gedinnian and Early Siegenian evolution of the subfamily must have taken place outside the Rhenish shelf. In contrast to previous views (Jahnke 1981; Cocks & Rong 2000), the Middle to Late Siegenian genus *Boucotstrophia* Jahnke, 1981 is regarded here as a member of the Mesodouvillininae, as well. *Mclearnites cherquiensis* Jansen, 2001 from the approximately coeval Merzâ-Akhsa Formation (Dra Plains, S Anti-Atlas, Morocco), for example, is morphologically close to *Boucotstrophia herculea* but differs in the absence of a genulate profile. The morphology of the ventral and dorsal apical regions and muscle fields are generally considered as the most important and stable characters indicating the mesodouvilline affinity, whereas the shell profiles may have changed more rapidly in the course of evolution. The Early Emsian genus *Pseudoleptostrophia* Gad, 1997 belongs to the same family, but should be included in the subfamily Amphistrophiidae according to its resupinate profile.

**Genus Boucotstrophia Jahnke, 1981**

*Type species.* – *Stropheodonta herculea* Drevemarenn, 1904, p. 276.

*Revised diagnosis.* – Shells very large, gently to moderately concavo-convex in profile and becoming dorsally ge-
ventral valve which Harper & Boucot assigned to the latter taxon (1978a, pl. 3, fig. 4, pl. 4, fig. 11) belongs to Leptostrophiella explanata (Sowerby, 1842), supported by the presence of “true” dorsal valves of this species in the same fauna (Jansen, in prep.). Rhenostrophia Boucot, 1960 (type species: Orthis subarachnoidea, d’Archiac & de Verneuil, 1842) was treated as a nomen dubium under the Strophomenoida by Cocks & Rong (2000). In my opinion, the type species of this genus may represent a taxon of the order Orthotetida.

New problems started with the erection of the genus Boucotstrophia, because its original diagnosis was obviously based not only on its type species “Stropheodonta” herculea Drevermann, 1904, but on the group of “Stropheodonta” gigas McCoy, 1852 (Gigastropheodonta gen. nov.), as well (Jahnke 1981, p. 150). As a result, the original diagnosis contains joint characters of the ventral valves of Boucotstrophia and Gigastropheodonta, such as the large and impressed muscle field, but includes also characters of the dorsal valve only developed in the latter genus, such as reduced "socket plates"and elevated muscle platform. Unfortunately, Jahnke’s new species “Boucotstrophia” minor, which he erected in the same work, has to be assigned to Gigastropheodonta in accordance to the diagnostic characters of this genus, and the same applies further taxa previously assigned to Boucotstrophia, as well (García-Alcalde 1992, Aït-Malek et al. 2000). In my opinion, all described species of Boucotstrophia except for its type species belong to Gigastropheodonta. In the revised edition of the Treatise on Invertebrate Palaeontology, Part H, Cocks & Rong (2000) figured a ventral valve of B. herculea (fig. 187/1b) and a dorsal valve of G. gigas (fig. 187/1a) – both determined as “B. herculea”. An attempt is made herein to clarify the confusion concerning the genus Boucotstrophia and the species which, in my opinion, had erroneously been related to it.

The internal morphology of Boucotstrophia is clearly of the mesodouvilleina type, resembling that of advanced Devonian representatives of Mclearnides or Mesodouvilleina (see, for example, Renouf 1972, Harper & Boucot 1978b or Jansen 2001). These genera and Boucotstrophia have the general morphology of the ventral and dorsal apical characters and muscle fields in common: cavities for accomodation of cardinal process lobes and brachiophores not clearly separated by ridges (as it is the case in Gigastropheodonta); ventral diductor scars faintly or moderately impressed and more or less subdivided by radial ridges; brachiophores long, clearly separated from cardinal process and widely divergent; elevated dorsal muscle platform lacking, medial and side septa lacking or poorly developed.

Finally, Jahnke (1981) has included Boucotstrophia in a new subfamily Megastrophiinae. The different morphology of the Middle Devonian Megastrophia Caster, 1939 precludes a closer relationship that would justify this; the latter genus is characterized by a commonly interstriate ornamentation, strongly subdivided ventral diductor fields and the presence of an elevated dorsal muscle platform and side septa.

Comparison. – Boucotstrophia differs from the widely distributed genus Mesodouvillea Williams, 1950 (type species: Stropheodonta subinterstrialis seretensis Kozlowski, 1929) in much larger, dorsally genulate shells with subuniformly costellate to unequally parvicostellate or partly interstriate ornamentation, whereas the latter has concavo-convex shells showing a predominantly interstriate ornamentation. Boucotstrophia further differs in the presence of flabellate ventral diductor scars, contrasting with the faintly subdivided diductor scars in Mesodouvillea. Boucotstrophia differs from Mclearnides Caster, 1945 (type species: Brachyspirion mertoni McLean, 1924) mainly in larger and dorsally genulate shells. Silurian to Lochkovian species show a smooth or faintly subdivided ventral diductor field whereas the large Siegenian and Emsian representatives show strong radial ridges giving the diductor field a flabellate aspect (cf. Jansen 2001). Probably, the first Boucotstrophia evolved from one of these during the Early Siegenian and migrated into the Rhenish Sea with the beginning of the Middle Siegenian. Boucotstrophia is distinguished from Geniculomclearnides Harper & Boucot, 1978b [type species: Mclearnides (Geniculomclearnides) genicularia Harper & Boucot, 1978b] by larger shells and flabellate diductor scars which are not subdivided in the second genus; a Cantabrian species of Geniculomclearnides shows the presence of a strong peripheral ridge in the dorsal valve (cf. García-Alcalde 1992) which is absent in Boucotstrophia. Boucotstrophia differs from Sinostrophia Hamada, 1971 (type species: S. kondoi Hamada, 1971) from NE China in dorsally genulate shells, finer ornamentation, stronger cardinal process, longer brachiophores and curved dorsal muscle-bounding ridges; Sinostrophia shows straight and diverging dorsal muscle-bounding ridges. The shell profile of Boucotstrophia contrasts with the resupinate profile of the Rhenish genus Pseudoleptostrophia Gad, 1997 (type species: Leptostrophia dahmeri Rösler, 1954) which in addition lacks a breviseptum in the dorsal valve and shows a uniformly costellate ornamentation. It is unknown whether Pseudoleptostrophia developed from an amphistrophiine ancestor or attained the resupinate profile independently.

Boucotstrophia herculea (Drevermann, 1904)

Figure 3A–K

v * 1904 Stropheodonta herculea nom. n. Drevermann, pp. 276, 277, pl. 32, figs 5, 5a, b, 6.
v p 1978a Leptostrophia (Rhytistrophia) sp. – Harper & Boucot, pl. 4, figs 8, 10, 12, pl. 5, figs 1, 3, 5; non pl. 3, fig. 4, pl. 4, fig. 11 (= Leptostrophiella explanata, early form).

v p 1978b Rhenostrophia cf. subarachnoidea (d’Archiac & de Vermeule, 1842). – Harper & Boucot, pl. 31, figs 1, 3, 6; non figs 2, 4, 7 (= Gigastrophodonta gigas), non fig. 5 (G. cf. gigas).

v p 2000 Boucotstrophia herculea. – Cocks & Rong, p. 294, fig. 187/1b; non fig. 187/1a, 1c (= Gigastrophodonta gigas).

v p 2003 Boucotstrophia herculea. – Poschmann & Jansen, pl. 2, fig. 6.

Lectotype. – Internal mould of ventral valve and corresponding external mould, SMF-Mbg. 2354, figured by Drevermann (1904, pl. 32, figs 5, 5a, 5b) and selected here as lectotype (Fig. 3A–C). Dimensions of the internal mould: L ~ 68 mm, W ~ 61.5 mm.

Type stratum and locality. – Seifen Formation, upper part of Middle Siegen Group, Middle Siegenian (middle Lower Devonian); locality Seifen, Westerwald, Rhenish Slate Mountains, Germany. Topographical Mapsheet of Rheinland-Pfalz 1:25,000, No. 5311 Altenkirchen.


Diagnosis. – As for the genus.

Remarks. – The species is common in Middle Siegenian deposits of the Siegerland, Westerwald, Eifel and Hunsrück, but generally rare in Late Siegenian deposits. Its geographic distribution outside the Rhenish Slate Mountains remains unclear. Maillieux (1936) described the species from the Middle Siegenian “Quartzophyllades de Longlier” in the Ardennes (Belgium), but did not illustrate it. Godefroid et al. (1994, fig. 10) reported it from different formations of the S flank of the Dinant Synclinorium (Ardennes, Belgium). Jahneke & Rachbeouef (1980, pp. 203, 204, fig. 53, pl. 27, figs 5–7) described a few poorly preserved specimens of Boucotstrophia sp. from the Siegenian “Schistes et Calcaires de l’Armoricque” of the Armorican Massif (France) whose characters suggest a close affinity to B. herculea. Further reports of Boucotstrophia from the Siegenian of Spain, from the Celtiberian Chains, the Sierra de Guadarrama and the Cantabrian Mountains (Carls 1987, Carls & Valenzuela-Ríos 1998) are still to be verified with the material. Boucotstrophia herculea resembles Melearnites cherguiensis Jansen, 2001 from the Middle or Late Siegenian Merzâ-Akhsa Formation in the Dra Plains (S Anti-Atlas, Morocco) but the Rhenish species differs by a dorsally geniculate profile, slightly different, more unequally parvicostellate ornamentation and the presence of a breviseptum in the dorsal valve; M. cherguiensis has a plano-convex profile with faintly convex,
non-geniculate ventral valve and a uniformly costellate ornamentation; in addition, the ventral muscle-bounding ridges are less convexly curved.

Family Strophodontidae Caster, 1939

Discussion. – The family Strophodontidae is represented in the Rhenish Slate Mountains by at least four genera: Gigastropheodonta gen. nov. [type species: Leptaena (Stropheomena) gigas McCoy, 1852], Fascistropheodonta Harper & Boucot, 1978c (type species: Orthis Sedgwicki d’Archiac & de Verneuil, 1842), Plicostropheodonta Sokolskaya, 1960 (type species: Orthis Murchisoni d’Archiac & de Verneuil, 1842) and Rheostropheodonta gen. nov. (type species: Rh. rhena gen. nov. et sp. nov.).

The erection of the new genus Gigastropheodonta results from the exclusion of the Middle Siegenian to Late Emsian group of Leptaena (Stropheomena) gigas McCoy, 1852 from Boucotostrophia.

Fascistropheodonta is characterized by the presence of a sharply fasciculate ribbing superimposed on capillae or fine costellae. It includes its type species F. sedgwicki (d’Archiac & de Verneuil, 1842) (Fig. 6M) and F. rudis (Kegel, 1913), both occurring in the Middle and Upper Siegenian sub-stages. In the Late Emsian Wiltz Formation (Eifel region), a third, still undescribed species with relatively low plications occurs (Harper & Boucot 1978c, p. 25, pl. 45, figs 4, 5, 7, 8, pl. 46, figs 1, 3–5). The Siegenian-Emsian genus Plicostropheodonta is presently represented by its type species P. murchisoni (Fig. 6K, L) and P. virgata (Drevermann, 1902) (Fig. 6f). The genus is characterized by the presence of a strongly plicate macro-ornamentation superimposed on capillae or fine costellae; the strong plications are commonly visible on internal moulds, as well. The dorsal interior shows an elevated muscle platform. The two species have chiefly been distinguished by simple versus increasing plications. There are further, almost unknown or poorly known Early Devonian taxa from Central and Western Europe to be considered in the frame of a revision of the two genera which share a comparable plicate plus capillate ornamentation, for example Leptaena sartthacensis Oehlert & Davoust, 1879, L. acutiplicata Oehlert & Davoust, 1879, Stropheodonta (?) diffusa Oehlert, 1896, St. fassiger Drevermann, 1902, St. steiningeri Drevermann, 1907 and St. furcillistra Fuchs, 1915. In my opinion, the taxonomic value of the macro-ornamentation, the number of plications and the pattern of their numerical increase, has been over-emphasized in previous works, and more attention should be paid to internal characters; the intraspecific variability of the macro-ornamentation is probably higher than hitherto assumed. In the Seifen and Stadtfeld faunas, specimens with varying number and strength of plications and widely varying tendency of bifurcation and insertion co-occur. A more comprehensive material would be necessary to establish a sound taxonomy of these forms.

Finally, there is the group of forms represented by Stropheomena piligera G. & F. Sandberger, 1856 and related species. It had been assigned either to Stropheodonta or Plicostropheodonta by previous workers, and it is now regarded as a new genus Rheostropheodonta herein. It is internally similar to Plicostropheodonta, but lacks a plicate macro-ornamentation.

Genus Gigastropheodonta gen. nov.

Etymology. – From Greek gigas (substantive from mythology, very large folk), referring to the large size of shells and the name of the type species, combination with the classical genus name Stropheodonta; nomenclatory gender: feminine.

Type species. – Leptaena (Stropheomena) gigas McCoy, 1852, p. 386.

Diagnosis. – Shells of large to very large size, with strongly concavo-convex to dorsally geniculate profile; ornamentation variable, ranging from slightly unequally parvicostellate to distinctly interstricate, more rarely subuniformly costellate; style of ornamentation may change on a single valve; weak tendency to produce low rounded plications may be present; hinge line partly to entirely denticulate. Ventral process small, often excavated by variously developed median depression, commonly with furrow or tubular chamber in its anterior face; ventral cavities for accommodation of cardinal process lobes and brachiophores separated by a ridge on each side; ventral muscle field large, bilobed, strongly impressed, enclosed by strong muscle-bounding ridges; adductor and diductor scars clearly differentiated; adductor scars dendritic, separated by median furrow; diductor scars strongly subdivided by numerous radial ridges, flabellate. Cardinal process lobes strong, with attachment faces posteroventrally or posteriorly directed; brachiophores very short, located at the base of the cardinal process; dorsal adductor field subelliptical to subrectangular in outline, moderately elevated on muscle platform; short central brevisep tum and pair of faint side septa present. Bulbous sub-terminal ridge may be variously developed in the interior of both valves.

Species included. – Leptaena (Stropheomena) gigas McCoy, 1852, Boucotsrophia minor Jahnke, 1981, Boucotsrophia velica García-Alcalde, 1992, Boucotsrophia jahnkei Ait-Malek, Racheboeuf & Lazreq, 2000. Further undescribed forms, possibly new species, are known to the author from the Dra Plains (S Anti-Atlas, Morocco) and the Rhenish Slate Mountains.
Comparison. – The combination of following characters of *Gigastropheodonta* indicates its affiliation to the family Strophodontidae: strongly concavo-convex to dorsally geniculate profile, strongly impressed ventral muscle field with strongly subdivided ventral diductor scars, elevated dorsal muscle platform and presence of dorsal side septa. The new genus is distinguishable from the mesodouvillelline *Boucotstrophia* Jahneke, 1981 mainly by a generally more convex or geniculate ventral valve, often longer trail, interstriate or predominantly interstriate interstriate ornamentation, ventral cavities for accomodation of cardinal process lobes separated by ridges from those for the brachiophores, more impressed ventral muscle field with more strongly subdivided diductor scars, shorter brachiophores less diverging from cardinal process lobes, elevated dorsal muscle platform, shorter dorsal brevisepum and presence of distinct side septa (see above, under *Boucotstrophia* and Table 1).

*Gigastropheodonta* is distinguished from *Rhenostropheodonta* gen. nov. by larger shells and a dorsal brevisepum lacking anteriorly a prong. *Rhenostropheodonta* is like a smaller-sized sister genus of *Gigastropheodonta* sharing many characters with it, for example the apical morphology and muscle fields of the ventral and dorsal valves. *Gigastropheodonta* is distinguished by larger and essentially non-plicate shells from the strongly plicate *Plicostropheodonta* Sokolskaya, 1960. The same is to be stated in the comparison with *Fascistropheodonta* Harper & Boucot, 1978c (type species: *Orthis Sedgwicki* d’Archiac & de Verneuil, 1842) furthermore showing a multiplicate macro-ornamentation arranged in a fasciculate pattern superimposed on capillae or fine costellae (Fig. 6M); the ventral muscle field is generally less impressed in representatives of that genus, and the brachiophores are longer with respect to the cardinal process lobes.

*Gigastropheodonta* is similar to *Megastrophonia* Caster, 1939 [type species: *Strophomena (Stropheodonta) concava* Hall, 1857] and seems at first sight to be related to that genus (specimens studied: USNM 14104a; 14516; 116374a, b, f; 124365, 173987; 205147a–e; 220695–220697). *Gigastropheodonta* differs in more distinctly geniculate shell, more impressed ventral muscle field delimited by stronger muscle-bounding ridges, the presence of separate cavities for the accomodation of cardinal process lobes and brachiophores, different orientation of cardinal process lobes with attachment faces directed posteroventrally or posteriorly, short brachiophores closely adjacent to the cardinal process and subelliptical to subrectangular outline of the dorsal adductor field.

Ventral valves of the Middle Devonian type species of *Megastrophonia, M. concava* from the Appalachians (E North America), tend to attain a rounded, almost hemispherical shape; the costellae separating the intercalated capillae are more pronounced than in most representatives of *Gigastropheodonta*. In the dorsal valve, the cardinal process surpasses the hinge line posteriorly, and the attachment faces for the diductor muscles are directed in posterior to posteroventral direction; the brachiophores are longer, clearly separated from the cardinal process lobes, widely divergent and located far more lateral along the cardinal margin. The dorsal adductor field tapers anteriorly, and the individual posteralateral adductor scars tend to attain a subtriangular outline. Considering this combination of characters *Megastrophonia* appears as a remote relative of the Rhenish genus.

**Gigastropheodonta gigas** (McCoy, 1852)

Figure 4A–L

<table>
<thead>
<tr>
<th>Character</th>
<th>Boucotstrophia herculea (Drevermann, 1904)</th>
<th>Gigastropheodonta gigas (McCoy, 1852)</th>
</tr>
</thead>
<tbody>
<tr>
<td>outline</td>
<td>commonly brachyhydrist</td>
<td>megathyrid, often faintly mucronate</td>
</tr>
<tr>
<td>ornamentation</td>
<td>unequally parvicostellate to uniformly costellate</td>
<td>variable, largely interstriate, partly uniformly costellate</td>
</tr>
<tr>
<td>cavities accommodating brachiophores</td>
<td>united with cavities for cardinal process lobes</td>
<td>clearly separated from cavities for cardinal process lobes</td>
</tr>
<tr>
<td>tubular chamber in ventral process</td>
<td>absent</td>
<td>commonly present</td>
</tr>
<tr>
<td>ventral muscle field</td>
<td>moderately long, moderately flabellate</td>
<td>strongly impressed, mostor scars subvided by numerous ridges, strongly flabellate</td>
</tr>
<tr>
<td>brachiophores</td>
<td>moderately long, separated from cardinal process lobes</td>
<td>short, closely adjacent to cardinal process lobes</td>
</tr>
<tr>
<td>dorsal muscle platform</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>dorsal muscle-bounding ridges</td>
<td>absent or low</td>
<td>present</td>
</tr>
</tbody>
</table>

*Comparison of the co-occurring species Boucotstrophia herculea (Drevermann, 1904) and Gigastropheodonta gigas (McCoy, 1852).*
of Gigastropheodonta gigas – Harper & Boucot, pl. 36, figs 1, 3, 4. – Mauz, p. 76. – Poschmann & Jansen, pl. 2, fig. 4.

Lectotype. – The specimen figured by McCoy (1852, pl. 2, fig. 7), designated by Mauz (1935, p. 76: “Typus”); a poorly preserved, strongly flattened external mould of a dorsal valve showing in parts an interstratiate ornamentation (McCoy’s figure is strongly idealized); stored under the number H 3883 in the Sedgwick Museum (Cambridge, U.K.). Dimensions: L = 83 mm, W = 72 mm. The fauna from Looe includes internal moulds of ventral valves as well (Davidson 1865; restudied by the present author in the Natural History Museum London) which are closely resembling the Rhenish specimens so that the conspecificity appears sufficiently verified.

Type stratum and locality. – Strata of Siegenian age at Looe, Cornwall, SW England.

Material. – Seifen Fm., Middle Siegenian, Westerwald. Seifen, near Dierdorf, classical localities, ~ 830 m SE of Seiften. – Harper & Boucot, pl. 36, figs 1, 3, fig. 2?”

Comparison and discussion. – The species is presently known from the Middle and Upper Siegenian of the Rheinish Slate Mountains, the Ardennes and South England. Gigastropheodonta gigas has frequently been confused with the often co-occurring mesodouvillinine species Boucotstrophia herculea (Drevermann, 1904). Apart from a similar size, internal moulds of these two species are rather dissimilar, whereas isolated and fragmentary external moulds can be difficult to assign to the one or the other species (comparison: see above and Table 1). A second Rhenish species of Gigastropheodonta occurs in the Lower Emsian; it is smaller, shows a less concavo-convex profile, trail shorter than visceral disk, trail of dorsal valve sharply delimited from visceral disk; ornamentation very fine, slightly unequally parvicostellate to distinctly interstratiate with groups of a variable number of capillae separated by slightly coarser costellae, partly subuniformly capillate, and pattern of ornamentation may change on the same valve. Hinge line denticulate for 1/2 to 3/4 to all of its width; 17 to 27 denticles on each side of the delthyrium. Ventral process variously developed, commonly with tubular chamber in its anterior face. Ventral muscle field very large, subelliptical to oval in outline; adductor scars commonly more or less elevated, rarely not elevated; thick muscle-bounding ridges present. Elevated dorsal muscle platform present, with moderately developed brevisepum and faint side septa. Subperipheral ridge more or less developed in the interior of ventral valve; dorsal visceral disk relatively flat.

Figure 4. Gigastropheodonta gigas (McCoy, 1852). All figures at natural size (× 1.0), unless otherwise indicated. Seifen Formation, Middle Siegenian (middle Lower Devonian), all localities near Seifen, Westerwald, Rheinish Slate Mountains, Germany. A–F – SMF-Mbg. 2352, Drevermann collection. Internal mould of dorsal valve (A), silicon cast of internal mould (B), enlarged (× 3.0) posterior view of cardinalia, latex cast (C), corresponding external mould (D) and lateral view of it (E), latex cast of external mould, detail (× 2.7) of ornamentation (F). Locality: “Seifen”. G, H – SMF 85337. Internal mould of dorsal valve (G) and latex cast of it (H). Locality: Mühlmerich near Eichen; leg. J. Hefter. I–K – SMF 85323. Latex cast of internal mould of ventral valve (I), internal mould (J) and enlarged (× 1.6) oblique posterior view of it (K). Locality: Seifen, Niederähren; leg. R. Werner. L – SMF 93778. Internal mould of ventral valve. Locality: Seifen, new road; leg. J. Hefter.
the genus further extends into the Upper Emsian (Jansen, in prep.).

*Gigastropheodonta gigas* differs from *G. minor* (Jahnke, 1981) from the Emsian Marettes Formation of the Armorican Massif in larger size and a shorter trail; the trail can be very long and recurved in the French species. In the ventral valve, the adductor scars are elevated in *G. gigas*, whereas only the anterior adductor scars are elevated in *G. minor*. The Rhenish species is distinguished by larger shells and the presence of a less constantly interstitiate, partly almost uniformly capillate ornamentation from *G. velica* (García-Alcalde, 1992) which occurs in the Emsian La Ladrora Formation of the Cantabrian Mountains (Santa María del Mar section, Asturias, N Spain). The Spanish species shows relatively coarser costellae separating the groups of capillae. *Gigastropheodonta gigas* differs from *G. jahnkei* (Ahl-Malek, Racheboeuf & Lazreq, 2000) from the upper part of the Mdàouer-el-Kbîr Formation (lowermost Upper Emsian) of the Dra Plains (S Anti-Atlas, Morocco) by much larger shells and relatively wider hinge line with 17 to 27 denticles per flank; the number of denticles reaches only 17 per flank in the Moroccan species; the ventral muscle field of the Rhenish species tends to be more subelliptical or suboval in outline – in contrast to a subtriangular muscle field in *G. jahnkei* (confirmed by examination of own topo- and stratotypic material).

**Genus Rhenostropheodonta gen. nov.**

*Etymology.* – From Latin *rhenus* (noun) [= Rhine river], combination with the classical genus name *Stropheodonta*; nomenclatory gender: feminine.

*Type species.* – *Rhenostropheodonta rhenana* gen. nov. et sp. nov.

*Species included.* – *Rhenostropheodonta rhenana* gen. nov. et sp. nov., *Stropheodonta piligera* G. & F. Sandberger, 1856.

**Diagnosis.** – Shells of medium to large size, with markedly concavo-convex to geniculate profile; ornamentation finely and unequally parvicostellate, more or less distinctly interstitiate; weak tendency to produce lacifications may be present; hinge line entirely denticulate. Ventral process small, mostly excavated by median furrow, tubular chamber or pit in its anterior face; ventral muscle field large, more or less bilobed, strongly impressed, enclosed by weak but mostly distinct muscle-bounding ridges; adductor scars separated by median furrow; diductor scars strongly flabellate. Cardinal process lobes strong, ventrally oriented and with posteriorly directed diductor attachment faces; brachiophores very short, laterally adjacent to cardinal process lobes; dorsal adductor field on slightly elevated muscle platform; central brevisepatum present, commonly bearing an anterior prong, flanked by a pair of low side septa. Subperipheral ridge usually present in ventral and dorsal valves.

**Comparison.** – *Rhenostropheodonta* gen. nov. differs from *Plicostropheodonta* Sokolskaya, 1960 in the absence of coarse plications. Differences from *Gigastropheodonta* gen. nov. are discussed above. *Rhenostropheodonta* is distinguished from *Strophodonta* Hall, 1850 (type species: *Strophomena demissa* Conrad, 1842) from North America mainly by the finer and commonly interstitiate ornamentation, the presence of distinct ventral muscle-bounding ridges, a ventrally directed cardinal process and brachiophores more closely adjacent to the cardinal process. *Strophodonta* is characterized by a relatively coarse, uniformly costellate ornamentation and posteriorly directed cardinal process accompanied by brachiophores situated more laterally. The study of specimens of the type species *Str. demissa* has confirmed these differences (AMNH 42306; SMF 31674–31676). *Rhenostropheodonta* is distinguished from *Asturistrophia* García-Alcalde, 1992 (type species: *Ast. insolita* García-Alcalde, 1992) from the Emsian of N Spain by the interstitiate ornamentation, stronger and more continuous ventral muscle-bounding ridges and shorter brachiophores closely adjacent to the cardinal process lobes; in contrast, the Spanish genus has a uniformly costellate ornamentation, the ventral muscle-bounding ridges are only posterolaterally developed or lacking, and the brachiophores are long and more protruding in anterolateral direction. The other genera assigned to the family *Stropheodontidae* by Cocks & Rong (2000) are very different from *Rhenostropheodonta*.

**Rhenostropheodonta rhenana gen. nov. et sp. nov.**

Figure 5G–N

1897 *Strophomena* (*Strophodonta*) *piligera* Sandb. – Frech, pl. 24b, fig. 5.

v 1969 *Strophodonta piligera*. – Werner, pl. 2, fig. 2.

p 2013 *Plicostropheodonta piligera*. – Schemm-Gregory & Henriques, p. 28 above, p. 28 below? (*male*), p. 29 below, p. 30 below?, p. 31 below, p. 32?; non p. 29 above (different ornamentation, *Iridistrophia sp.*); non p. 30 above, p. 31 above (= *Iridistrophia sp.*).

*Etymology.* – From Latin, *rhenanus, -a, -um* (adj.) [= Rheneish, relating to the Rhine river].

*Holotype.* – Internal mould of ventral valve (SMF 66712), leg. F. Drevermann, Fig. 5I–L. Dimensions: L = 29 mm, W = 35 mm.
Type stratum and locality. – Hohenrhein Formation, beds with Brachyspirifer ignotatus (Maurer, 1883), Lahnstein Group, lower part of Upper Emsian (upper Lower Devonian). Miellen/Lahn river, near Bad Ems, Rhenish Slate Mountains, Germany.

Material. – Upper Emsian, central Middle Rhine, lower Lahn and lower Mosel regions. Hohenrhein Fm., Miellen, valley of Lahn river, different collectors, e.g., leg. F. Drevermann, T. Henn, O. Follmann, G. Solle: 7 VVIM+EM [SMF 93668–93671, 93692–93694], 106 VVIM [holotype SMF 66712; SMF 93648 (15), 93649 (2), 93654, 93657, 93658, 93659 (4), 93660–93663, 93664 (4), 93667, 93676–93679, 93680 (12), 93681 (2), 93682 (13), 93683 (4), 93694, 93695 (15), 93696, 93699; MB.B. 3163; YPM 601388, 601395], 2 VVEM [SMF 93666, 93702], 3 DVIM+EM [SMF 93690, 93691;]: 21 DVIM [SMF 93653 (5), 93655, 93656 (6), 93665–93667, 93687 (4), 93696, 93697], 40 DVEM [SMF 93648 (4), 93649 (2), 93654 (2), 93657 (3), 93664 (3), 93684 (2), 93685 (5), 93686 (12), 93695 (2), 93697, 93698 (2), 93703; YPM 601389]. Lower part of Hohenrhein Fm., Kleinborns Valley near Koblenz, Koblenzer Stadtwald; leg. J. Hefter, U. Jansen (slightly diff. locs): 1 VVIM+EM [SMF 93711], 13 VVIM [SMF 66714, 85290, 93706 (10), 93710], 1 VVEM [SMF 66716], 1 DVIM+EM [SMF 93709], 2 DVIM [SMF 93708 (2)], 1 DVEM [SMF 93707]. Hohenrhein Fm., Hohenheiner Hütte near Lahnstein; leg. O. Follmann: 1 DVIM+EM [MB.B. 3163.1], Hohenrhein Fm., Feldberg near Oberlahnstein; leg. Schwerd: 1 AVIM [MB.B. 3204.1], Emsquarzit Fm., Rheinser Mühlen Valley at Rhensriver Rhine: 2 VVIM [SMF 66715 (2); leg. O. Follmann], 1 DVIM [SMF 66713; leg. U. Jansen], Siechhaus Valley, near Koblenz: 1 VVIM [YPM 236696; Krantz collection], 1 DVIM+EM [cf. R. rhena; SMF 93705a+b; leg. J. Hefter], 2 DVEM [SMF 93712 (2)]. “Oberlahnstein”: 2 VVIM [SMF 236700, 236701]. – Upper Emsian, Prüm Syncline, Eifel region. Wiltz Fm., foot of Hartberg near Prüm, W flank of road from Prüm to Ellwerath, 580 m SW of TP 540.5 m; leg. R. Werner: 3 VVIM [SMF 25677 (3)], 1 DVEM [SMF 25677].

Diagnosis. – Shells of medium to large size; profile of ven- tral valve moderately to strongly convex, ratio width to length of ventral internal moulds between 1.1 and 1.3. Ornamentation more or less distinctly interstriate, with a variable number of capillae between the costellae. Number of denticles along hinge line 22 to 40 per flank. Ventral process commonly with thin median furrow in its anterior face, rarely with deep tubular chamber. Ventral muscle field large, transversely suboval or subhemispherical in outline, occupying a great portion of visceral disk; posteralateral limitations diverging at an angle of generally more than 90°; median ridge between diductor scars commonly narrow.

Comparison and discussion. – Rhenostropheodonta rhe- nana differs from the classical Rhenish species R. piligera (G. & F. Sandberger, 1856) (Fig. 50, P) by on average larger shells, a more convex ventral valve with a slightly higher ratio width to length of commonly 1.1 to 1.3 of ven- tral internal moulds contrasting with 1.0 to 1.2 in R. piligera, 22 to 40 denticles per flank versus only ca 20 in R. piligera, the presence of a mostly thin median furrow in the ventral process contrasting with a deep median pit or tubular chamber in R. piligera, larger and broader ventral muscle field which is transversely suboval or subhemispherical and not distinctly bilobed in outline, narrower median ridge separating the diductor scars medianly. The posteralateral limitations of the ventral muscle field diverge at a wider angle of more than 90°, whereas this angle is com- monly below this value in R. piligera.

Many specimens hitherto been determined as R. piligera in collections actually belong to the new species. Rhenostropheodonta rhena has its onset in the Emsquarzit Formation (basal part of Upper Emsian) and becomes most abundant in the overlying Hohenrhein Formation – it is restricted to early Late Emsian strata (Lahnstein Group) and represents a very common component of many faunas, whereas R. piligera is less common and mainly occurs in the middle Late Emsian Laubach Group, but may have its first occurrence in the uppermost beds of the Hohenrhein Formation. Rhenostropheodonta piligera probably evolved from R. rhena in the latest “Lahnstein time”.

Family Douvillinidae Caster, 1939 Subfamily Protodouvillininae Harper & Boucot, 1978b

Discussion. – The Rhenish Protodouvillininae occur ma- inly in deposits of Emsian age. The Early Emsian species Crinistrophia elegans (Drevermann, 1902) (Fig. 6H, I) is characterized by a plano-convex profile and strong dor- sal medial septa curved convexly outwards (Jahnke 1971). It is abundant in the Stadtfeld Formation, but possibly conspecific specimens have rarely been found in the Spitznack Formation of the Taunus, as well. The spe- cies has been synonymized with Crinistrophia crinita Havlíček, 1967 from the Zlíchovian of Bohemia (Jahnke 1971). It is abundant in the latest “Lahnstein time”.

In the present work, the classical species “Protodouvillina” taeniolata (G. & F. Sandberger, 1856) is reviewed and included in the new genus Gibbodouvillina. The Middle Devonian “Protodouvillina” interstitialis (Phillips, 1841) represents a second species of this genus to be considered. The generic affiliation of the possible
Genus Gibbodouvillina gen. nov.

Etymology. — From Latin gibbus (noun) [= strong convexity, hump], alluding to the convex shape of the ventral valve; combination with the classical genus name Douvillina; nomenclatural gender: feminine.

Type species. — Strophomena taeniolata G. & F. Sandberger, 1856, Orthis interstrialis Phillips, 1841. Further undescribed forms, apparently new species, are known to the author from the Emsian of the Dra Plains (S Anti-Atlas, Morocco) and the W Pyrenees (N Spain).

Discussion and comparison. — Gibbodouvillina gen. nov. is externally similar to the type genus of the subfamily, Protodouvillina Harper & Boucot, 1978b (type species: Strophomena inaequistriata Conrad, 1842), to which representatives of Gibbodouvillina have commonly been assigned so far. The new genus differs from Protodouvillina by the presence of distinct paradental plates, semieliptical or piriform to rounded-subtriangular ventral muscle field with diductor scars enclosing adductor scars anteriorly, narrow median ridge bisecting the muscle field and much lower, straight medial sepa in the dorsal valve. Specimens of the type species Protodouvillina inaequistriata (Conrad, 1842) from the Middle Devonian Hamilton Group of the E United States have been studied for comparison (USNM 220608–220610, 220616, 220618, 220619; Harper & Boucot 1978b: pl. 25, figs 7–11, pl. 26, figs 3–7). The species differs in a ventral muscle field with subrectangular outline and diductor scars which do not enclose the adductor scars anteriorly; instead, an elevated boss may separate the diductor scars there. Paradental plates are commonly lacking in Protodouvillina, and the medial sepa in the dorsal valve are much higher and commonly curved convexly outwards. The cardinal process of Gibbodouvillina is still too insufficiently known to be compared with that of Protodouvillina. A single dorsal valve of G. taeniolata is available; it shows a small, posteriorly directed, bilobed cardinal process (Fig. 5B).

Gibbodouvillina has probably evolved from a species of Mesodouvillina Williams, 1950 by the development of a strongly concavo-convex to geniculate profile. The new genus may represent a transitional stage between Mesodouvillina and Protodouvillina. The present author saw numerous specimens of Gibbodouvillina from different areas of Central and Western Europe and North Africa which clearly show the diagnostic characters seemingly not affected by much intraspecific variation.

Gibbodouvillina differs from Bojodouvillina Havlíček, 1967 (type species: Leptaena philipssii Barrande, 1848; Pragian in original sense to Zlíchovian, Bohemia) in stronger and sharper, continuous ventral muscle-bounding ridges, less impressed ventral muscle field which is semieliptical or piriform to rounded subtriangular in outline.
clearly developed parental plates and the presence of a dorsal median ridge starting from the notothyrial platform and separating the adductor field. *Bojodouvillina* has a ventral muscle field with cordate outline accompanied by abbreviated muscle-bounding ridges. These differences allow a clear distinction of the two genera. Further genera of the same subfamily are not closely related to the new genus.

**Gibbodouvillina taeniolata** (G. & F. Sandberger, 1856)

**Figure 5A–F**

v 1856 *Strophomena taeniolata* G. & F. Sandberger, pp. 360, 361, figs 11, 11a, 11b.

v 1916 *Stropheodonta taeniolata*. – Dahmer, pp. 235–237, pl. 9, fig. 16.

1941 *Stropheodonta taeniolata*. – Maillieux, p. 25.


cf 1971 *Bojodouvillina taeniolata*. – Jahne, pp. 64, 65, pl. 4, fig. 7.

cf 1978h *Protodouvillina* sp. – Harper & Boucot, pl. 25, fig. 12.


**Lectotype.** – Internal mould of articulated valves; the dorsal internal mould is still connected with the embedding rock, inventory numbers MW 289d/54.10.00, designated as lectotype and figured by Rösler (1954, p. 31, pl. 3, fig. 1); stored in the Museum Wiesbaden, Sandberger collection, probably the specimen figured by G. & F. Sandberger (1856, pl. 34, fig. 11a; figure strongly idealized, may represent a composite of more than one specimen); the specimen is figured in the present work in Fig. 5E, F. Dimensions: W = 26.3 mm, L = 34.5 mm [laterally compressed].

**Type stratum and locality.** – Beds of Late Emsian age at the locality “Niederlahnstein”, according to Rösler (1954, p. 32) very probably “Allerheiligenberg”, central Middle Rhine region, Rhenish Slate Mountains, Germany.


**Description.** – Shells of moderate size, semilinctical in outline, slightly longer than wide or about as long as wide,
slightly brachythrid; shells strongly concavo-convex to dorsally geniculate in profile. Ornamentation distinctly interstriate, consisting of numerous costellae separated by interspaces with groups of mostly 2 to 7 costellae increasing by insertion; new costellae normally develop from a costella in the middle of its group, when the number of costellae has reached 5 or 6; costellae and costellae crossed by numerous concentric fila. Hinge line denticulate for about two thirds to all of its length. Interior of ventral valve with pyramidal-shaped ventral process, giving rise to a median ridge bisecting the whole muscle field and a pair of short, diverging lateral ridges; ventral process laterally flanked by prominent cavities for the reception of the cardinal process lobes; pair of distinct paradal palatal plates lateral to these cavities present. Ventral muscle field moderately large, semielliptical to piriform in outline, impressed, reaching about 2/5 of valve length, subdivided into a pair of postero-medial adductor scars and a pair of anterolateral diductor scars. Diductor scars essentially smooth apart from an indistinct striation, enclosing dendritic adductor scars anteriorly. Muscle field laterally delimited by diverging, strong and sharply defined muscle-bounding ridges; these are convexly curved outwards and commonly continue as very low ridges along the anterior margin of the muscle field. Cardinal process bilobed, laterally flanked by moderately long, widely divergent brachipholeres. Paired dorsal adductor scars distinct, slightly impressed, separated by median ridge starting from the notothyrial platform, each adductor scar subelliptical in outline; additional narrow adductor scars may be located anteromedially; lateral muscle-bounding ridges very low, poorly developed. Pair of straight medial septa present, elongate, developed as low and tuberculate ridges, starting posteromedially from the median ridge between the adductor scars and ending at about half length of valve, diverging at about a 15° angle; central brevisepunum poorly developed.

Discussion. – The species is in need of further revision. In its actual wide sense, it occurs as an accessory component of many Late Emsian faunas. At least closely related forms rarely occur in the Lower Emsian of the Taunus (own data) and the Eifel region (Rössler 1954), whereas the specimen described from the Erbsloch-Grauwacke (Kellerwald) by Jahnke (1971, pp. 64, 65, pl. 4, fig. 7) shows a different shape of the ventral muscle field and rudimentary paradal plates; the form may represent a separate species. Still undescribed, closely related representatives of Gibbodouvillina (possibly new species) are known to the present author from the Lower/Upper Emsian boundary beds of the Mdäouer-el-Kbîr Formation in S Morocco (Foum Zguid section; Jansen 2001) and from the Upper Emsian of the Cinco Villas Massif in the Basque Pyrenees, Spain (collection H. Requadt, Senckenberg Museum). Jahnke (1981, p. 157) reported G. taeniolata from the Emsian of the Ar- morican Massif in France and from the earliest Eifelian Lauch Formation (Eifel region). “Dovillina” interstrialis sensu Gratsianova, 1975 (non Phillips, 1841) from the Gorny Altai Mountains (SW Siberia) is similar, as well; it shows paradental plates and differs from G. taeniolata in the presence of faint concentric rugae and a relatively wider ventral muscle field. Another comparable species is Bojodouvillina transversa Su, 1976 from N China.

Gibbodouvillina taeniolata differs from the Middle Devonian Gibbodouvillina interstrialis (Phillips, 1841) from West and Central Europe by larger shells with narrower outline, whereas the outline of the ventral muscle field and the morphology of the dorsal interior are rather similar and indicate the congenerity (see figures in Biernat 1966 and Halamski 2009).

Biostratigraphical implications of the Rhenish Strophomenida

The Strophomenida are useful guide fossils in the siliciclastic-marine, rhenotypic facies of the Lower Devonian, as has already been pointed out earlier (Jansen 1998a, b). In this chapter, the succession of biostratigraphically significant taxa from the Přídolian to the lower Middle Devonian is described. The taxon ranges are shown in Fig. 7. The same species or at least closely related ones are known from sections in W and SW Europe, and North Africa, as well, so that they are useful in supraregional stratigraphical correlation.

1. The oldest species to be mentioned is Shaleria rigida (de Koninck, 1876) (Fig. 6P) indicating a latest Silurian (Přídolian) age of the Gdoumont Formation (surrounding area of the Stavelot-Venn Anticlinorium), the Köbbinghausen Formation (Remscheid Anticlinorium) and the Killerskopf Formation (S Taunus) (cf. Godefroid & Cravatte 1999). The Silurian/Devonian boundary beds of the Remscheid Anticlinorium contain further “stropheodontoid” taxa of “bohemotypic habitus” still to be investigated. [Remark: Substantial parts of the classical Gedinnian in its Ardenner type region turned out to be of latest Silurian age due to the occurrences of Davia shirleyi Alvarez & Racheboeuf, 1986, Quadrifarius dumontianus (de Koninck, 1876) and Shaleria rigida (de Koninck, 1876) (see Godefroid & Cravatte 1999). It is proposed to use the term “Lowermost Gedinnian” for these Přídolian to probably basal Lochkovian parts of the classical Gedinnian successions which should include in the Ardenenn area the lower part of the Muno Formation (the two “faunas of Ruisseau des Roches”) and the Gdoumont Formation, in the Rhenish area the correlatives Köbbinghausen and Killerskopf (= “Graue Phyllite”) formations and the lower part of the Silberg Formation (Müsen Horst).].
2. The Rhenish Lower Gedinnian (~ lower Lochkovian) is characterised by *Mesodouvillina triculta* (Fuchs, 1919) (Fig. 6N, O). The species is particularly abundant in the Flaserschiefer Member of the Hüinghausen Formation in the Ebbe Anticlinorium (Sauerland) where it forms plasters on bedding surfaces, but it occurs in other members of the same formation and in the overlying Bredeneck Formation, as well (Eiserhardt et al. 1981, p. 214).

3. Following a Late Gedinnian to Early Siegenian gap of marine documentation a number of strophomenid brachiopods immigrated with the Middle Siegenian transgression, for example *Leptostrophiella explanata* (Sowerby, 1842), *Boucotstrophia herculea* and *Plicostropheodonta murchisoni* (d'Archiac & de Verneuil, 1842) (Fig. 6K, L), *Fascistropheodonta sedgwicki* (d'Archiac & de Verneuil, 1842) (Fig. 6M) and *Gigastropheodonta gigas* (McCoy, 1852). *Boucotstrophia herculea* and *Fascistropheodonta sedgwicki* are most common in the Middle Siegenian, so that they can be regarded almost as index fossils of this substage, but both occur as rare elements of Late Siegenian faunas, as well. A Middle to Late Siegenian early form of *Leptostrophiella explanata* can be distinguished from conspecific Emsian descendants by the morphology of its ventral muscle field and the muscle-bounding ridges (cf. Jahnke 1971, Jansen, in prep.). *Gigastropheodonta gigas* and *Plicostropheodonta murchisoni* are probable guide fossils of the Middle to Upper Siegenian interval. The congeneric representatives from overlying Emsian strata previously assigned to the same species are different in various respects and may turn out as separate species (Jansen, in prep.).

4. *Leptostrophiella explanata* (Sowerby, 1842) sensu stricto (Fig. 6A, B), *Pseudoleptostrophia dahmeri* (Rösler, 1954) (Fig. 6E, F), *Crinistrophia elegans* (Drevermann, 1902) (Fig. 6H, I) and *Plicostropheodonta virgata* (Drevermann, 1902) (Fig. 6J) represent guide fossils of the Lower Emsian. Typical forms of *P. dahmeri* seem to have their onset near the lower boundary of the middle Lower Emsian (“Singhofen”) and are common in middle and upper parts of the Lower Emsian (“Singhofen” and “Valleldar”), mainly in the Gefell and Stadtfeld formations (S Central Eifel region) and the Ergeshausen and Spitznack formations (Taunus). *Crinistrophia elegans* is most abundant in the Stadtfeld Formation, but the genus occurs with few, probably conspecific specimens in older beds of the Spitznack Formation. *Plicostropheodonta virgata* sensu stricto seems to be confined to middle and upper parts of the Lower Emsian (“Singhofen” and “Valleldar”), mainly in the Gefell and Stadtfeld formations (S Central Eifel region) and the Ergeshausen and Spitznack formations (Taunus). *Crinistrophia elegans* is most abundant in the Gefell and Stadtfeld formations (S Central Eifel region). A comprehensive revision of all these taxa would be necessary to clarify their exact ranges. What can nearly be excluded is an upper range of these into the Upper Emsian.

5. *Rhenostropheodonta rhenana* gen. nov. et sp. nov. has its first occurrence in the earliest Late Emsian Ems quarzit Formation where it is so common that it is useful as
a marker for the beginning of the Upper Emsian. It has its highest abundance in the overlying Hohenrhein Formation, where it may occur even in masses. The species appears to be restricted to the Lahnestein Group. It is also present in the Wiltz Formation of the Prüm Syncline (Eifel region). A form determined as Fascistropheodonta sedgwickii from the Wiltz Formation (Harper & Boucot 1978c, p. 25, pl. 45, figs 4, 5, 7, 8, pl. 46, figs 1, 3, 4, 5?) does not belong to this species, but to a still undescribed one restricted to the Upper Emsian.

6. *Rhenostropheodonta piligera* (G. & F. Sandberger, 1856) has a shorter range than hitherto reported because is has not been distinguished from *R. rhenana* so far. According to the present knowledge, the species is restricted to middle parts of the Upper Emsian, i.e. the Laubach Group and probably highest parts of the Hohenrhein Formation. Descendants reach into the Kondel Group.

7. The Late Emsian leptostrophiids are still in need of revision. Recently (2012), the author discovered a mass occurrence of *Leptostrophiella explanata* (late form) in the Hohenrhein Formation of the Siechhaus Valley near Koblenz. Besides, there are probable new leptostrophiid taxa from the Wetteldorf Formation (Eifel region) and the Kondel Group (Dill Synclinorium).

8. *Douvillinella filifer* (W.E. Schmidt, 1914) (Fig. 6C, D) is a chiefly late Emsian taxon and a typical faunal component of the Heisdorf Formation (Eifel region; Werner 1969). It just ranges into the basal Eifelian (*Pylagnostus partitus* Zone). Besides, the species has been reported from lower and upper parts of the Kondel Group (Jahnke 1981; Solle 1976, p. 170).

9. *Teichostrophia lepis subtilis* Struve, 1992 (Fig. 6G) is possibly restricted to the Early Eifelian Lauch Formation of the Eifel region (Struve 1992, p. 543: “anscheinend ein Leitfossil des Lauchium” = “apparently a guide fossil of the Lauchian”) or has at least its main distribution here.

**Palaeobiological aspects**

During the Early Devonian, huge amounts of siliciclastic material were transported by rivers and deltas from the Old Red Continent in the north into the shallow Rhenish Sea. The Rhenish brachiopods were adapted to the conditions of siliciclastic shelf environments. Strong currents and turbulence could whirl up the sediments, destabilize the substrate, scour the sediment around the shells or even set the brachiopods in motion. The brachiopods as sessile, microphagous suspension-feeders benefited from the well-oxygenated and nutrient-rich conditions of the rhenotypic facies, but had to tolerate agitated, turbid water, as well. Stable hard grounds were probably rare. Frequent destruction of biocoenoses (“lethal-heterostrate facies” sensu Schäfer 1962) during sudden erosion or sedimentation events and high mortality rates were probably compensated by high reproduction rates. Due to a good supply of nutrients and enough calcium carbonate, representatives of *Boucotstrophia* or *Gigastropheodonta* could secrete large and thick shells, preventing the brachiopods from being moved across the sea-floor or turned over by currents.

Strongly plicate shells of *Plicostropheodonta* had the advantage that with the same opening angle of the shell the plications provided a better protection against coarse-grained particles entering the mantle cavity, which could have obstructed or damaged the filter apparatus (Rudwick 1970, Gourvennec 1989). The plications may also have strengthened the shells against durophagous predators, following the principle of a corrugated cardboard.

*Leptostrophiella, Boucotstrophia, Gigastropheodonta* and *Rhenostropheodonta* had large ventral diductor fields reflecting a strong musculature. Strong muscles were possibly needed to keep the commissure width constantly narrow even in episodes of strong turbulence or flow. If the gap between the valves was too wide, too coarse particles could come into the mantle cavity, whereas the inhalant-exhalant system could collapse, if the two valves collided. Both situations had to be avoided. It was like keeping a door open with a narrow gap against a wind of variable strength (cf. Carls et al. 1993).

Relatively flat-shelled strophomenids, such as *Leptostrrophiella, Mesodouvillina* or *Pseudoleptostrophiella* could have been adapted to high-energy and hard-substrate environments, as they profited from a flat profile by experiencing less drag and a decreased likelihood of hydrodynamic transport. *Boucotstrophia* and *Gigastropheodonta* most probably lived with the flat posterior part of the ventral valve bottom on soft substrates and with the anterior trail directed upward, so that they lifted their anterior commissures above the siliciclastic substrate in order to avoid that mobile sand grains entered the mantle cavity. The form enabled these to employ an “iceberg” strategy, floating convex down on the soft substrate (Thayer 1975, Leighton & Savarese 1996, Leighton 1998).

**Conclusions**

The Strophomenida from the Rhenish Lower Devonian have poorly been studied up to the present day. A comprehensive revision is prepared by the author, and first results are presented in this work. Three genera are described as new because their species did not fit well in the genera they have previously been included in: *Gigastropheodonta* [type species: *Leptaena (Strophomena) gigas* McCoy, 1852], *Rhenostropheodonta* (type species: *R. rhenana* gen. nov. et sp. nov.) and *Gibbodouvillina* (type species: *Strophomena taeniolata* G. & F. Sandberger, 1856). These genera are compared with presumably related taxa, in the
case of the latter two with genera from North America, to which their species have previously been assigned. The widely misunderstood genus *Boucotostrophia* Jahneke, 1981 is revised, excluded from the family Strophodontidae Caster, 1939 and included in the subfamily Mesodouvillliniae Harper & Boucot, 1978b. Further strophomenid taxa are briefly discussed.

Rhenish strophomenids have a great biostratigraphic potential, as they have short ranges and occur in abundance and in different subtypes of the rhenotypic facies. The Lowermost Gedinnian (Pfdolian) is characterised by the typically Silurian element *Shaleria rigida* (de Koninck, 1876), the Lower Gedinnian by *Mesodouvillina triculata* (Fuchs, 1919) and the Middle–Upper Siegenian interval mainly by *Boucotostrophia herculaea* (Drevermann, 1904), *Gigastropheodonta gigas* (McCoy, 1852) and *Fascistrophoeidonta sedgwicki* (d’Archiac & de Verneuil, 1842). The Lower Emsian is indicated by the occurrence of *Pseudoleptostrophia dumeri* (Rössler, 1954), *Plicostropheodonta virgata* (Drevermann, 1902) and *Crinistrophoe elegans* (Drevermann, 1902), whereas the lower boundary of the Upper Emsian can well be recognised by the onset of *Rhenostropheodonta rhenana* gen. nov. et sp. nov. The Upper Emsian is indicated by this species and typical specimens of *Gibbodouvillina taeniolata* (G. & F. Sandberger, 1856) and *Rhenostropheodonta piligera* (G. & F. Sandberger, 1856), the latter one having a potential as guide fossil for the middle part of the Upper Emsian (“Laubach stage”). The uppermost Upper Emsian is well documented by *Douwillinella filifer* (W.E. Schmidt, 1914), and an indicator for the beginning of the Eifelian is the first *Teichostrophia lepis subtilis* Struve, 1992. The study of phylogenetic changes within the strophomenid taxa may open further possibilities of stratigraphic subdivision in the future. Because the same or similar species are distributed in W and SW Europe and North Africa new possibilities of far-reaching correlations can be expected. Strophomenid brachiopods are almost omnipresent in shallow-marine successions of the rhenotypic Lower Devonian and apparently follow the general faunal patterns or, respectively, the subdivision into ecological-evolutionary subunits as reflected by the succession of brachiopod faunas (Jansen, in prep.).

As regards palaeobiogeography, the results from the Rhenish strophomenids are consistent with the assumed presence of a Maghrebo-European Subrealm within the Old-World Realm during the Early Devonian, which is suggested by the distribution of brachiopod faunas as a whole (cf. Jansen 2012a, b; based on Plusquellec et al. 1997). The occurrence of Rhenish strophomenid genera in regions outside Europe and North Africa is still to be verified. Morphologically “conservative” genera such as *Leptostrophiella* or *Mesodouvillina* which have been reported from different regions worldwide (see, e.g., Harper & Boucot 1978a, b; Talent et al. 2001) still should be compared side-by-side with the Rhenish forms in order to better specify their relationships. In the North Gondwanan regions, *i.e.* Armorican Massif, Celtiberian Chains, Cantabrian Mountains, Sierra de Guadarrama, Dra Plains and Ougarta Chains, even the same brachiopod species as in the Rhenish Slate Mountains occur, sometimes geographical races, subspecies or at least closely related species. The present data suggest their affiliation to a joint palaeobiogeographic unit.

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