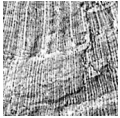


Strophomenid brachiopods from the Rhenish Lower Devonian (Germany)

ULRICH JANSEN



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 *Gibboudouvillina* (type species: *Strophomena taeniolata* G. & F. Sandberger, 1856). The diagnosis of the poorly known genus *Boucotstrophia* Jahnke, 1981 (type species: *Stropheodonta herculea* Drevermann, 1904) is revised. These and several further taxa are briefly discussed with regard to phylogenetic relationships, palaeobiogeographical 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 (Leptostrophella)* basing these on Rhenish type species, and they redescribed the Rhenish taxa *Douvillinella* 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 ques-

tion which ventral and dorsal valves belong to the same species was not easy to answer in some cases. With regard to the genus *Boucotstrophia* 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 *Boucotstrophia* 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.



Figure 1. Sketch map showing strophomenid localities in the Rhenish Slate Mountains (shaded in grey), Germany. The position of the map in Fig. 2 is indicated.

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 congeners 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 Rhenish 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; DVIM+EM – 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

IPB – Paläontologisches Institut Bonn; MB.B. – Museum für Naturkunde, Berlin, brachiopod collection; MW – Museum Wiesbaden, G. & F. Sandberger collection; SMF – Senckenberg Museum, Frankfurt am Main; SMF-Mbg. – former collection of the Institut für Geologie und Paläontologie, University of Marburg a.d. Lahn, today stored in the Senckenberg Museum, Frankfurt am Main; USNM – Smithsonian, United States National Museum of Natural History, Washington D.C., USA; YPM – Peabody Museum of Natural History, Yale University, New Haven/Ct., USA.

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 accomodation 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

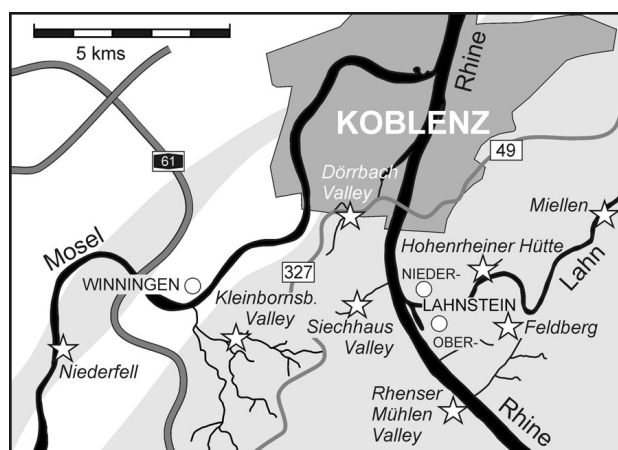


Figure 2. Strophomenid localities in the central Rhenish Slate Mountains around Koblenz (Upper Emsian outcrops shaded in grey).

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 *Gibbodouwillina*: Fig. 5D) or very fine costellae in a very regular pattern (= “interstriat” *sensu* Paeckelmann & Sieverts 1932, p. 41; = “interstrié” *sensu* Jahnke 1981, p. 149; Jahnke 1986, pp. 108–110; Ait-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 *Gibbodouwillina*: 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 *Gibboudouvillina*: 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 Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Amphistropiidae Harper, 1973

Subfamily Mesodouvillinae Harper & Boucot, 1978b

Discussion. – Representatives of the subfamily Mesodouvillinae are very common in Early Gedinnian (~ early Lochkovian) deposits of the Ebbe Anticlinorium, where internal and external moulds of concavo-convex shells of *Mesodouvillina triculta* (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 Mesodouvillinae, as well. *Mclearnites cherguensis* Jansen, 2001 from the approximately coeval Merzâ-Akhsaï Formation (Dra Plains, S Anti-Atlas, Morocco), for example, is morphologically close to *Boucotstrophia herculea* but differs in the absence of a geniculate 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 Amphistropiinae according to its resupinate profile.

Genus *Boucotstrophia* Jahnke, 1981

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

Revised diagnosis. – Shells very large, gently to moderately concavo-convex in profile and becoming dorsally ge-

nulate along the commissural margin. Ornamentation variable, finely costellate, varying from subuniformly costellate to unequally parvicostellate and partly interstriate with two or three finer costellae intercalated between coarser costellae. Hinge line denticulate for about 3/4 to all of its length. Ventral process strongly developed, pyramidal, flanked by a pair of deep cavities for the reception of the cardinal process lobes, cavities for the brachiophores united with these. Ventral muscle field large, impressed, semi-elliptical to subtriangular in outline, laterally enclosed by distinct muscle-bounding ridges which are more or less curved convexly outward and commonly continued as weak ridges along anterior margin of muscle field. Ventral diductor scars moderately flabellate, separated by median myophragm. Cardinal process bilobed, laterally flanked by moderately long, widely divergent brachiophores, which are clearly separated from the cardinal process. Dorsal muscle platform absent; paired adductor scars faintly to moderately impressed, separated by median ridge and delimited laterally by low muscle-bounding ridges convexly curved outwards; side and medial septa lacking or poorly developed in large specimens; brevisseptum present, relatively long.

Species included. – Only the type species *Stropheodonta herculea* Drevermann, 1904.

Discussion. – The revision of *Boucotstrophia* is based on the study of internal and external moulds of ventral and dorsal valves and a few moulds of articulated valves of its type species *B. herculea* (Drevermann, 1904) mainly from the Seifen Formation (Middle Siegenian, Westerwald), its stratum typicum. Drevermann (1904) knew the ventral morphology of his species well, and he distinguished the latter from the co-occurring, similar-sized species “*Stropheodonta*” *gigas* McCoy, 1852, but he had no dorsal valves of *herculea* for study. The scrutiny of Drevermann’s materials and new, excellently preserved material has confirmed the presence of two different species which finally turned out to be representatives of two different genera: *Boucotstrophia* and *Gigastropheodonta* gen. nov.

In the course of their revision of the “Stropheodontacea”, Harper & Boucot (1978a–c) studied specimens of both taxa mentioned. The re-examination of their specimens in the Smithsonian (Washington D.C.) by the present author has shown that internal moulds of ventral valves of *Boucotstrophia herculea* (1978b, pl. 31, figs 1, 3, 6) and ventral and dorsal valves of “*Stropheodonta*” *gigas* (1978b, p. 31, figs 2, 4, 7; 1978c, pl. 36, figs 1–3) from the Seifen fauna were assigned to “*Rhenostrophia* cf. *subarachnoidea* (d’Archiac & de Verneuil, 1842)” whereas internal moulds of dorsal valves of *B. herculea* (1978a, pl. 4, figs 8, 10–12, pl. 5, figs 1, 3, 5) were determined as “*Leptostrophia* (*Rhytistrophia*) sp.”. The accompanying

ventral valve which Harper & Boucot assigned to the latter taxon (1978a, pl. 3, fig. 4, pl. 4, fig. 11) belongs to *Leptstrophella 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 Strophomenoidea 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, Ait-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 mesodouvilline type, resembling that of advanced Devonian representatives of *Mclearnites* or *Mesodouvillina* (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 accommodation 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 Megastrophinae. 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 *Mesodouvillina* Williams, 1950 (type species: *Stropheodonta subinterstitialis seretensis* Kozłowski, 1929) in much larger, dorsally geniculate shells with subuniformly costellate to unequally parvicostellate or partly interstriate ornamentation, whereas the latter has concavoconvex 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 *Mesodouvillina*. *Boucotstrophia* differs from *Mclearnites* Caster, 1945 (type species: *Brachyprion mertonii* McLearn, 1924) mainly in larger and dorsally geniculate 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 *Geniculomclearnites* Harper & Boucot, 1978b [type species: *Mclearnites* (*Geniculomclearnites*) *genicularia* Harper & Boucot, 1978b] by larger shells and flabellate diductor scars which are not subdivided in the second genus; a Cantabrian species of *Geniculomclearnites* 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 geniculate 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 brevisseptum in the dorsal valve and shows a uniformly costellate ornamentation. It is unknown whether *Pseudoleptostrophia* developed from an amphistrophine 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 (= *Leptostrophella explanata*, early form).
- v p 1978b *Rhenostrophia* cf. *subarachnoidea* (d'Archiac & de Verneuil, 1842). – Harper & Boucot, pl. 31, figs 1, 3, 6; non figs 2, 4, 7 (= *Gigastropheodonta gigas*), non fig. 5 (*G. cf. gigas*).
- v p 2000 *Boucotstrophia herculea*. – Cocks & Rong, p. 294, fig. 187/1b; non fig. 187/1a, 1c (= *Gigastropheodonta gigas*).
- v 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.

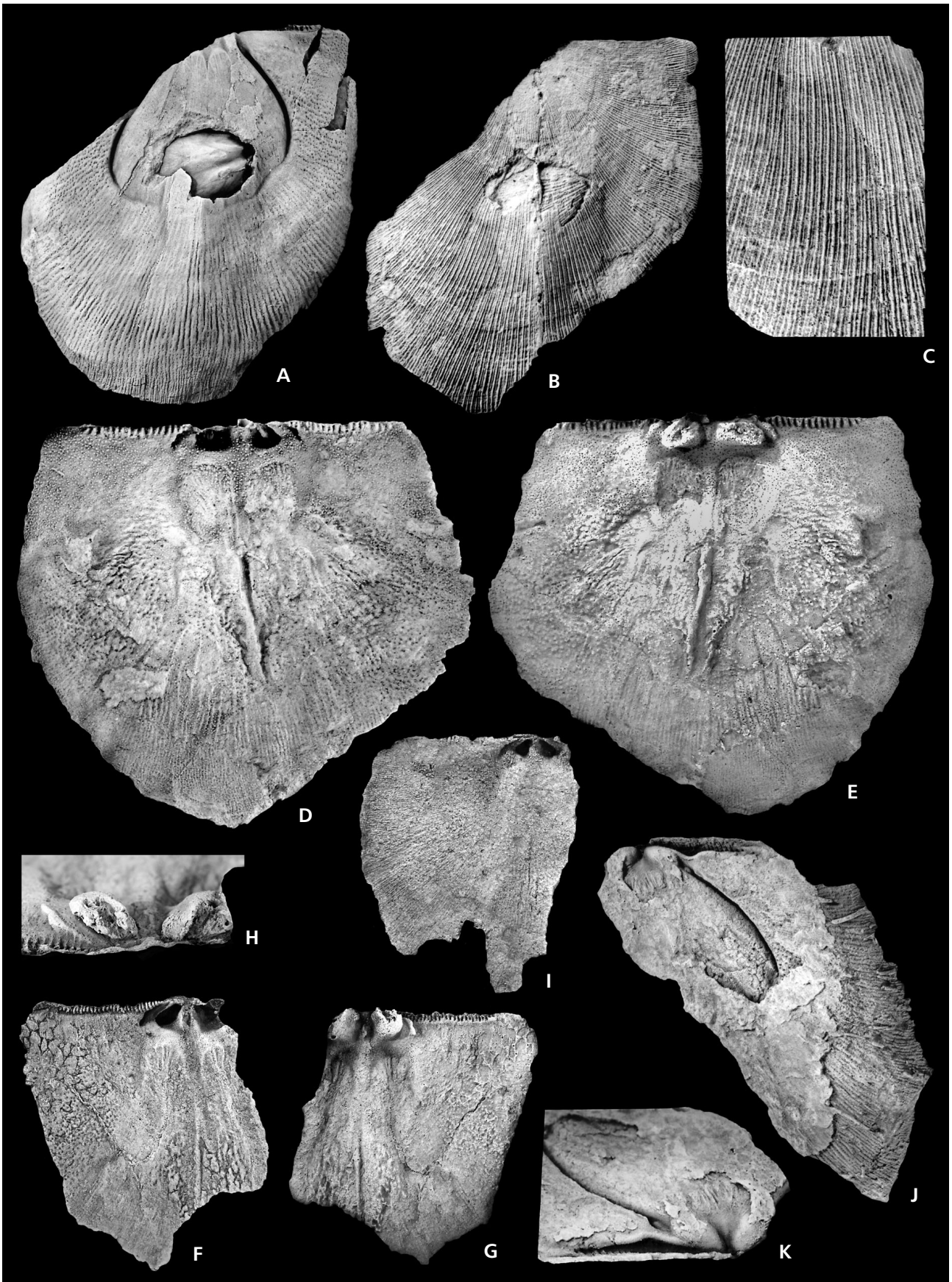
Material. – Seifen Formation, Middle Siegenian, Westerwald. Seifen, near Dierdorf, classical localities, ~ 830 m SE of railway station (see Dahmer 1934); different collectors, e.g., F. Drevermann, J. Hefter, T. Henn: 3 VVIM+EM [lectotype SMF-Mbg. 2354; SMF 66682, 66685], 1 AVIM+DVEM [MB.B. 153], 1 AVIM [MB.B. 158.1–2], 13 VVIM [SMF 66677–66681, 66687, 85221, 93633, 93636, 94835, 94836; SMF-Mbg. 5137; YPM 13835], 1 VVEM [YPM 601401]. Seifen; leg. A. Vogel: 1 VVIM [SMF 85222]. Niederühren, railroad cut, ~ 200 m W of church at Niederühren near Seifen; leg. A. J. Boucot: 3 VVIM [USNM 220650, 220652, 220654], 4 DVIM [USNM 220473, 220474, 220476, 220477]. Ascheid near Seifen; leg. E. Grebel: 3 VVIM [SMF 66697, 93637, 93638]. Haberscheid, abandoned quarry near road from Seifen to Puderbach: 5 VVIM [SMF 94830–94834, leg. P. Carls], 1 DVIM+EM [SMF 85674, leg. U. Jansen], 2 DVIM [SMF 94837, leg. U. Jansen; SMF 94999, leg. P. Carls]. Mühlmerich near Eichen, large quarry; leg.

E. Grebel: 10 VVIM [SMF 66686, 66689–66695, 85220, 94829], 2 DVIM [SMF 85671, 85673]. – Middle Siegenian, Westerwald. Augustenthal Formation, Augustenthal near Neuwied, quarry opposite the factory; leg. J. Hefter: 2 VVIM [SMF 66688, 93634]. – Middle Siegenian, Siegerland. Eisernhardt Fm., Ahöhe near Eisern: 1 AVIM [MB.B. 3624]. – Upper Siegenian, Siegerland. Upper Siegen Group, Anzhausen, railway cut opposite the mill; leg. P. Dienst: 1 VVIM [MB.B. 3149]. – Upper Siegenian, Eifel region. Saxler? Fm., Ollenbach-Üssbach, 250 m S of junction of the two creeks; leg. S. Simpson: 1 VVIM [SMF 93635]. Upper Siegen Group, “Untere Dunkle Schichten”, Nette-Mühle, 0.5 km NW of the mill, along the road to Etingen; leg. S. Simpson: 1 VVIM+EM [SMF 93639]. – Siegenian, Hunsrück. Taunusquarzit Group, Hennweiler near Kirn: 1 VVIM plus fragments of VVEM [SMF 66696].

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). Jahnke & Racheboeuf (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’Armorique” 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 *Mclearnites cherguensis* Jansen, 2001 from the Middle or Late Siegenian Merzâ-Akhsäi 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 brevisseptum in the dorsal valve; *M. cherguensis* has a plano-convex profile with faintly convex,

Figure 3. *Boucotstrophia herculea* (Drevermann, 1904). All figures at natural size (× 1.0), unless otherwise indicated. Seifen Formation, Middle Siegenian (middle Lower Devonian), all localities near Seifen, Westerwald, Rhenish Slate Mountains, Germany. • A–C – SMF-Mbg. 2354, lectotype, Drevermann collection. Internal mould of ventral valve (A), silicon cast of corresponding external mould (B) and detail view (× 2.1) of the latter to show the ornamentation (C). Locality: “Seifen”. • D, E – SMF 94999. Internal mould of dorsal valve (D) and latex cast (E). Locality: Seifen, Haberscheid; leg. P. Carls. • F–H – SMF 85673. Internal mould of dorsal valve (F), latex cast (G) and cardinalia, enlarged (× 2.3) posterior view (H). Locality: Mühlmerich near Eichen. • I – SMF 85671. Internal mould of dorsal valve. Locality: Mühlmerich near Eichen; leg. E. Grebel. • J, K – SMF-Mbg. 5137. Internal mould of ventral valve (J), slightly enlarged (× 1.5) posterior view of apical area (K). Locality: “Seifen”.



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 (Strophomena) 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 *Rhenostropheodonta* gen. nov. (type species: *Rh. rhenana* 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 (Strophomena) gigas* McCoy, 1852 from *Boucotstrophia*.

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 substages. 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 mainly represented by its type species *P. murchisoni* (Fig. 6K, L) and *P. virgata* (Drevermann, 1902) (Fig. 6J). 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 sarthacensis* Oehlert & Davoust, 1879, *L. acutiplicata* Oehlert & Davoust, 1879, *Stropheodonta (?) diffusa* Oehlert, 1896, *St. fascigera* Drevermann, 1902, *St. steiningeri* Drevermann, 1907 and *St. furcillistria* 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-emphasised 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 *Strophomena piligera* G. & F. Sandberger, 1856 and related species. It had been assigned either to *Strophodonta* or *Plicostropheodonta* by previous workers, and it is now regarded as a new genus *Rhenostropheodonta* 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 (Strophomena) 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 interstriate, 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 brevisseptum and pair of faint side septa present. Bulbous subperipheral ridge may be variously developed in the interior of both valves.

Species included. – *Leptaena (Strophomena) gigas* McCoy, 1852, *Boucotstrophia minor* Jahnke, 1981, *Boucotstrophia velica* García-Alcalde, 1992, *Boucotstrophia 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.

Table 1. Comparison of the co-occurring species *Boucotstrophia herculea* (Drevermann, 1904) and *Gigastropheodonta gigas* (McCoy, 1852).

Character	<i>Boucotstrophia herculea</i>	<i>Gigastropheodonta gigas</i>
outline	commonly brachythyrid	megathyrid, often faintly mucronate
ornamentation	unequally parvicostellate to uniformly costellate, partly tending to become interstriate	variable, largely interstriate, partly uniformly costellate
cavities accomodating brachiophores	united with cavities for cardinal process lobes	clearly separated from cavities for cardinal process lobes
tubular chamber in ventral process	absent	commonly present
ventral muscle field	moderately impressed, moderately flabellate	strongly impressed, diductor scars subdivided by numerous ridges, strongly flabellate
ventral muscle-bounding ridges	sharply delimited, commonly narrow or moderately thick	often indistinctly delimited, very thick
brachiophores	moderately long, separated from cardinal process lobes	short, closely adjacent to cardinal process lobes
dorsal muscle platform	absent	present
dorsal muscle-bounding ridges	absent or low	present

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 mesodouvillinine *Boucotstrophia* Jahnke, 1981 mainly by a generally more convex or geniculate ventral valve, often longer trail, interstriate or predominantly 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 brevisseptum and the 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 brevisseptum 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 *Megastrophia* 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 *Megastrophia*, *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 postero-dorsal 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 posterolateral adductor scars tend to attain a subtriangular outline. Considering this combination of characters *Megastrophia* appears as a remote relative of the Rhenish genus.

Gigastropheodonta gigas (McCoy, 1852)

Figure 4A–L

- v* 1852 *Leptaena (Strophomena) gigas* McCoy, p. 386, pl. 2, fig. 7.
- v p? 1865 *Streptorhynchus gigas*. – Davidson, p. 83, pl. 16, figs 1, 3, non fig. 2?
- p 1893 *Strophomena protaeniolata* Maurer. – Maurer, pp. 5, 6, pl. 2, figs 1, 3, non fig. 2.
- v 1904 *Stropheodonta gigas*. – Drevermann, pp. 273–275, pl. 32, figs 1–4.

- cf 1935 *Stropheodonta gigas*. – Mauz, p. 76.
 v 1960 *Stropheodonta gigas*. – Paproth, table 1, pl. 2, figs 3, 4.
 v p 1978b *Rhenostrophia* cf. *subarachnoidea* (d'Archiac & de Verneuil, 1842). – Harper & Boucot, pl. 31, figs 2, 4, 7, non figs 1, 3, 6 (= *Boucotstrophia herculea*), 5 (sp. nov.? aff. *G. gigas*).
 v 1978c *Rhenostrophia* cf. *subarachnoidea* (d'Archiac & de Verneuil, 1842). – Harper & Boucot, pl. 36, figs 1, 3, fig. 2?
 pv p 2000 *B. [Boucotstrophia] herculea* (Drevertmann). – Cocks & Rong, p. 294, fig. 187/1a, c, non fig. 1b (= *Boucotstrophia herculea*).
 v 2003 “*Stropheodonta*” *gigas*. – 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 interstriate 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.

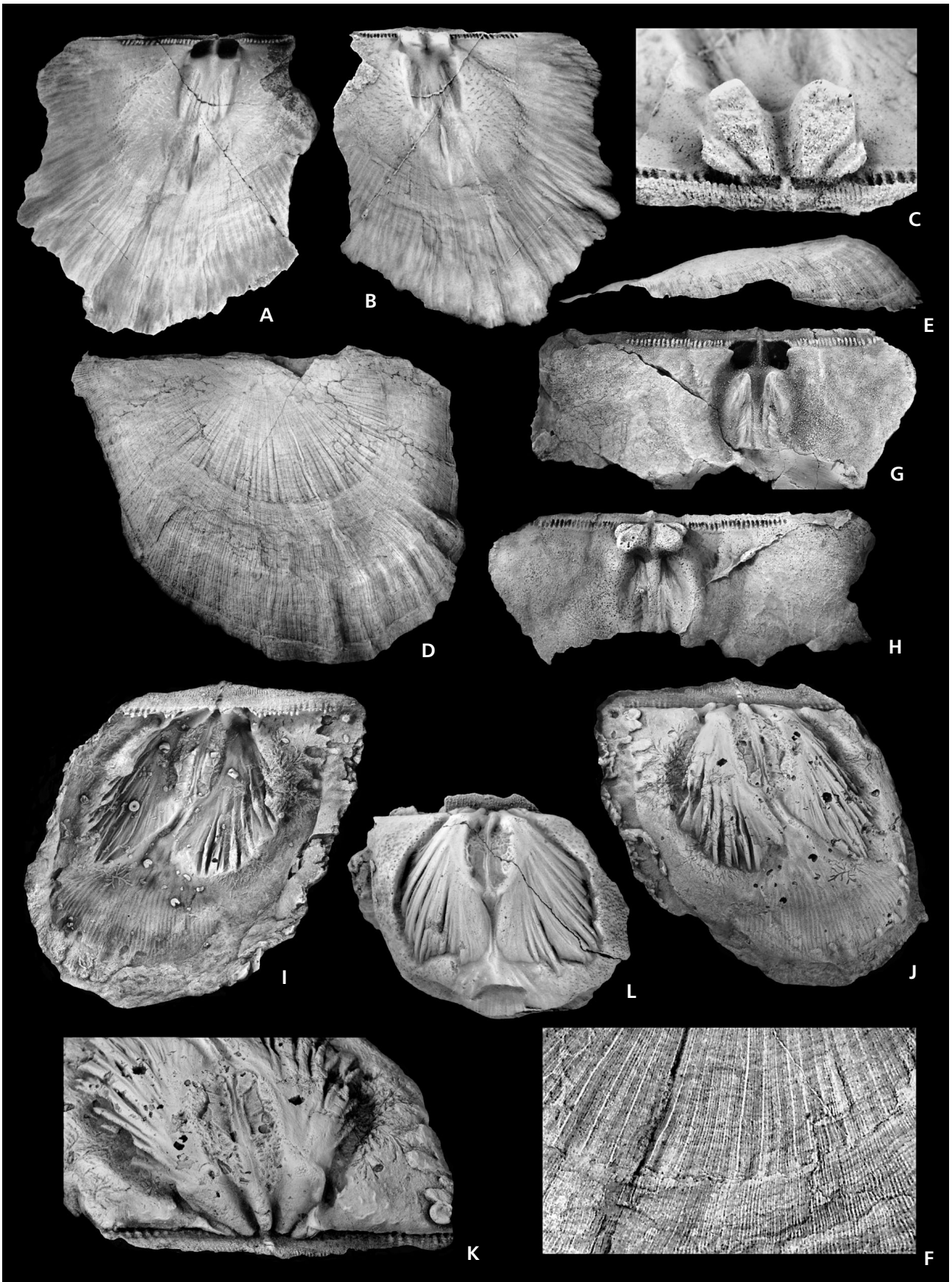
Material. – Seifen Fm., Middle Siegenian, Westerwald. Seifen, near Dierdorf, classical localities, ~ 830 m SE of railway station (see Dahmer 1934), different collectors, e.g., F. Drevertmann, J. Hefter: 10 VVIM [SMF-Mbg. 2353; SMF 66998, 85315, 85327–85330, 85333, 93778, 93779], 1 DVIM+EM [SMF-Mbg. 2352], 4 DVIM [SMF 85327, 85335; replicas YPM 13835 (2)]. Ascheid near Seifen; leg. E. Grebel: 4 VVIM [SMF 85311, 85316–85318]. Niederähren near Seifen; leg. A. J. Boucot (USNM) and E. Dörr, A. Keulerleber & R. Werner (SMF) (2 slightly different localities): 6 VVIM [SMF 85309, 85323; USNM 220651, 220653, 220655, 220659], 1 DVIM [USNM 220657]. Haberscheid near Seifen: 2 VVIM [SMF 85308, leg. P. Carls; SMF 85310, leg. U. Jansen]. Mühlmerich

near Eichen; leg. J. Hefter, E. Grebel: 6 VVIM [SMF 85314, 85319, 85321, 93780, 93781, 93783], 3 DVIM [SMF 85307, 85322, 85337], 1 DVIM+EM [SMF 93784]. – Siegenian, Siegerland. Middle Siegen Group, Dillberg near Eisern: 1 VVIM [SMF 85334]. Langenholdinghausen: 1 VVIM [SMF 85326]. – Middle Siegenian, Westerwald. Willroth; leg. R. Seibert: 1 DVIM+EM [SMF 85306]. *G. cf. gigas* from the Augustenthal Fm., Augustenthal; leg. J. Hefter: 7 VVIM [SMF 85302, 85303, 85325, 93774–93777], 6 DVEM [SMF 85301, 85304, 85305, 85324, 93773, 93782].

Diagnosis. – Shells of large to very large size, with wide hinge line, some specimens with short ears, with strongly concavo-convex to geniculate profile; trail shorter than visceral disk, trail of dorsal valve sharply delimited from visceral disk; ornamentation very fine, slightly unequally parvicostellate to distinctly interstriate 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 brevissepum and faint side septa. Sub-peripheral ridge more or less developed in the interior of ventral valve; dorsal visceral disk relatively flat.

Comparison and discussion. – The species is presently known from the Middle and Upper Siegenian of the Rhenish Slate Mountains, the Ardennes and South England. *Gigastropheodonta gigas* has frequently been confused with the often co-occurring mesodouvillinine species *Boucotstrophia herculea* (Drevertmann, 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 pronounced geniculation and a different ventral adductor field;

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, Rhenish Slate Mountains, Germany. • A–F – SMF-Mbg. 2352, Drevertmann 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 Margettes 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 interstriate, partly almost uniformly capillate ornamentation from *G. velica* (García-Alcalde, 1992) which occurs in the Emsian La Ladrona 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* (Ait-Malek, Racheboeuf & Lazreq, 2000) from the upper part of the Mdâouer-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., *Strophomena 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 interstriate; weak tendency to produce low plications 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 pro-

cess lobes; dorsal adductor field on slightly elevated muscle platform; central brevisseptum 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 interstriate 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 interstriate 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 Strophodontidae 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.) [= Rhenish, 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 ignoratus* (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 (20), 93660–93663, 93664 (4), 93667, 93676–93679, 93680 (12), 93681 (2), 93682 (13), 93683 (4), 93694, 93695 (15), 93696, 93699; MB.B. 3165; YPM 601388, 601395], 2 VVEM [SMF 93666, 93702], 3 DVIM+EM [SMF 93690, 93691, 93704]. 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., Hohenrheiner 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., Rhenser Mühlen Valley at Rhens/river 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. rhenana*; SMF 93705a+b; leg. J. Hefter], 2 DVEM [SMF 93712 (2)]. “Oberlahnstein”: 2 VVIM [YPM 236700, 236701]. – Upper Emsian, Prüm Syncline, Eifel region. Wiltz Fm., foot of Hartberg near Prüm, W flank of road from Niederprüm 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 ventral valve moderately to strongly convex, ratio width to length of ventral internal moulds between 1.1 and 1.3. Ornamentation more or less distinctly interstriae, 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 subrhombical in outline, occupying a great portion of visceral disk; posterolateral limitations diverging at an angle of generally more than 90°; median ridge between diductor scars commonly narrow.

Comparison and discussion. – *Rhenostropheodonta rhenana* differs from the classical Rhenish species *R. piligera* (G. & F. Sandberger, 1856) (Fig. 5O, 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 ventral 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 subrhombical and not distinctly bilobed in outline, narrower median ridge separating the diductor scars medianly. The posterolateral limitations of the ventral muscle field diverge at a wider angle of more than 90°, whereas this angle is commonly below this value in *R. piligera*.

Many specimens hitherto been determined as *R. piligera* in collections actually belong to the new species. *Rhenostropheodonta rhenana* 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. rhenana* in the latest “Lahnstein time”.

Family Douvilliniidae Caster, 1939

Subfamily Protodouvilliniinae Harper & Boucot, 1978b

Discussion. – The Rhenish Protodouvilliniinae occur mainly 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 dorsal 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 species has been synonymized with *Crinistrophia crinita* Havlíček, 1967 from the Zlíchovian of Bohemia (Jahnke 1971), but this seems to be doubtful. The late Late Emsian species *Douvillinella filifer* (Schmidt, 1914) (Fig. 6C, D) has a resupinate ventral valve, different shape of ventral muscle field and less developed dorsal septa (Jahnke 1981).

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

protodouvillinine “*Stropheodonta*” *umbonata* Dahmer, 1951 from the Köbbinghausen Formation (Přídolian, Remscheid Anticlinorium) is still to be clarified. The Rhenish Protodouvillinae occur in subtypes of the rhenotypic facies indicating relatively offshore, open-shelf palaeoenvironments with highly diverse faunal assemblages.

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*; nomenclatory gender: feminine.

Type species. – *Strophomena taeniolata* G. & F. Sandberger, 1856, p. 360.

Diagnosis. – Shells of moderate to large size, semielliptical in outline, with moderately or strongly concavo-convex to geniculate profile; ornamentation interstriate. Paradental plates present; ventral muscle field semielliptical or piriiform to rounded subtriangular in outline, completely bisected by narrow median ridge, laterally enclosed by sharply individualised, high muscle-bounding ridges which are convexly curved outwards; the latter are very low and thin or absent anterior to the muscle field; adductor scars anteromedially enclosed by diductor scars; diductor scars largely smooth. Brachiophores moderately long and widely diverging, clearly separated from cardinal process; dorsal adductor field impressed, bisected by low median ridge starting from notothyrial platform; dorsal muscle-bounding ridges poorly developed; thin brevisseptum may be present; medial septa low and thin, tuberculate, long and straight, diverging at an acute angle to another, starting posteriorly from median ridge between adductor scars.

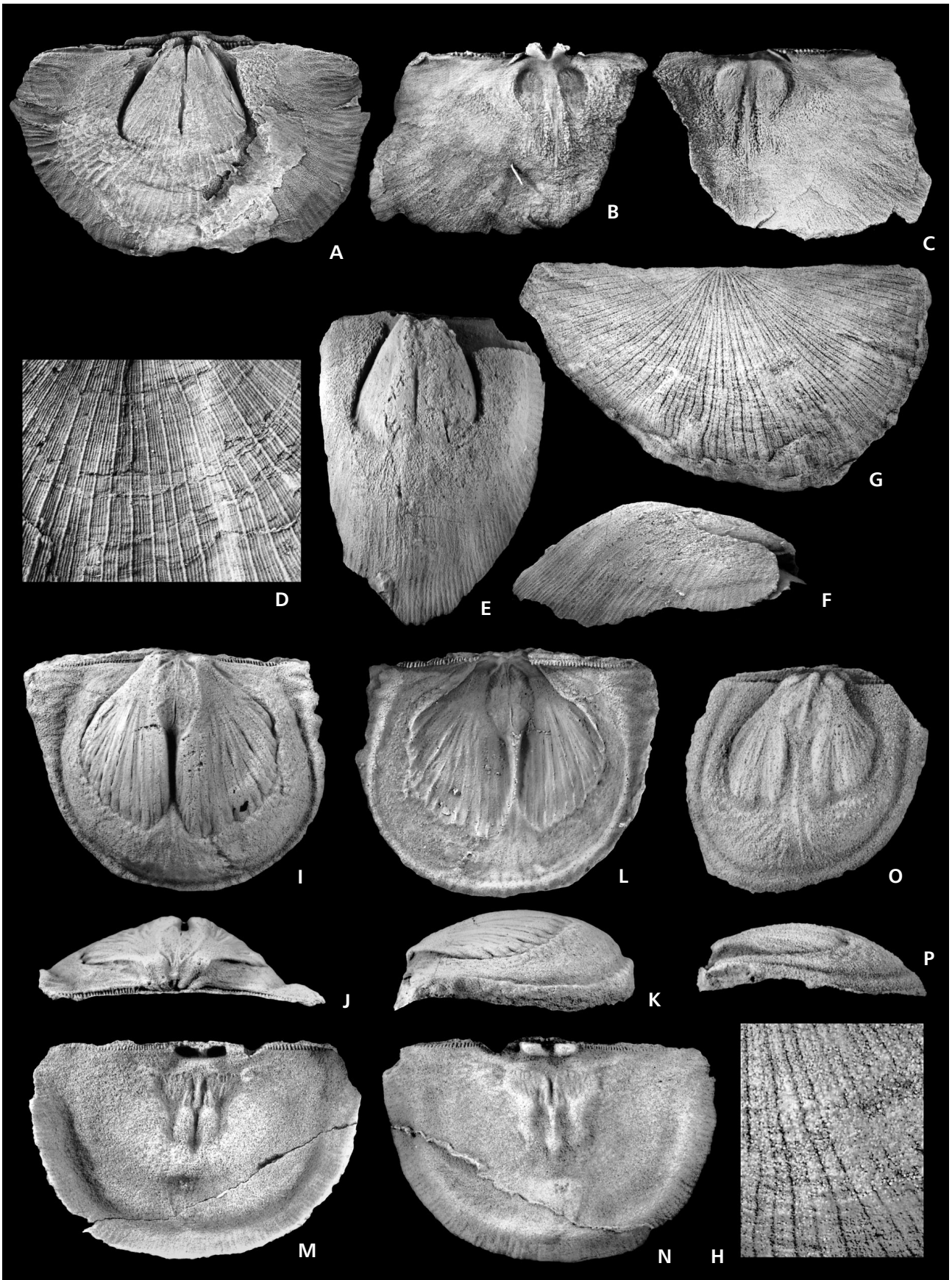
Species included. – *Strophomena taeniolata* G. & F. Sandberger, 1856, *Orthis interstitialis* Phillips, 1841. Further undescribed forms, apparently new species, are known to the author from the Emsian of the Dra Plains (S Anti-Atlas, Morocco) and the W Pyrenees (N Spain).

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, semielliptical or piriiform 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 septa 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 septa 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 phillipsii* 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 semielliptical or piriiform to rounded subtriangular in outline,

Figure 5. Strophomenid brachiopods from the Upper Emsian (upper Lower Devonian) of the central Rhenish Slate Mountains, Germany. All figures slightly enlarged ($\times 1.5$), unless otherwise indicated. • A–F – *Gibbodouvillina taeniolata* (G. & F. Sandberger, 1856); Sandberger collection; locality: Niederlahnstein, Middle Rhine region; A – MW 289c/54.10.01, paralectotype; internal mould of ventral valve; B, C – MW 289a/54.10.02, paralectotype; latex cast of internal mould of dorsal valve (B) and internal mould (C); D – MW 289e/54.10.04, paralectotype, latex cast of external mould of dorsal valve, detail of ornamentation ($\times 4.5$); E, F – MW 289d/54.10.00, lectotype, internal mould of ventral valve (E), lateral view (F). • G–N – *Rhenostropheodonta rhenana* gen. nov. et sp. nov.; stratum: Hohenrhein Formation; G, H – MB.B. 3163.1a, paratype; external mould of dorsal valve, top view (G) and detail ($\times 3.7$) of ornamentation (H); locality: Hohenrheiner Hütte near Lahnstein; I–L – SMF 66712, holotype, internal mould of ventral valve, top (I), posterior (J) and lateral (K) views of internal mould, top view of latex cast (L); locality: Miellen, Lahn river, leg. F. Drevermann; M, N – SMF 93653.2; internal mould of dorsal valve (M) and latex cast (N); locality as before. • O, P – *Rhenostropheodonta piligera* (G. & F. Sandberger, 1856); collection IPB, unnumbered; locality: Niederfell, Mosel river, leg. H. Ristedt; stratum: Laubach Group; internal mould of ventral valve, top (O) and lateral (P) views.



clearly developed parodontal 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.

***Gibboudouvillina taeniolata* (G. & F. Sandberger, 1856)**
Figure 5A–F

- v * 1856 *Strophomena taeniolata* G. & F. Sandberger, pp. 360, 361, pl. 34, figs 11, 11a, 11b.
- v 1916 *Stropheodonta taeniolata*. – Dahmer, pp. 235–237, pl. 9, fig. 16.
- 1941 *Stropheodonta taeniolata*. – Maillieux, p. 25.
- v 1954 *Stropheodonta taeniolata*. – Rösler, pp. 31–33, pl. 3, figs 1–4.
- cf 1971 *Bojodouvillina taeniolata*. – Jahnke, pp. 64, 65, pl. 4, fig. 7.
- v cf 1978b *Protodouvillina* sp. – Harper & Boucot, pl. 25, fig. 12.
- ? 1981 *Protodouvillina taeniolata*. – Jahnke, p. 157, pl. 18, fig. 9.

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

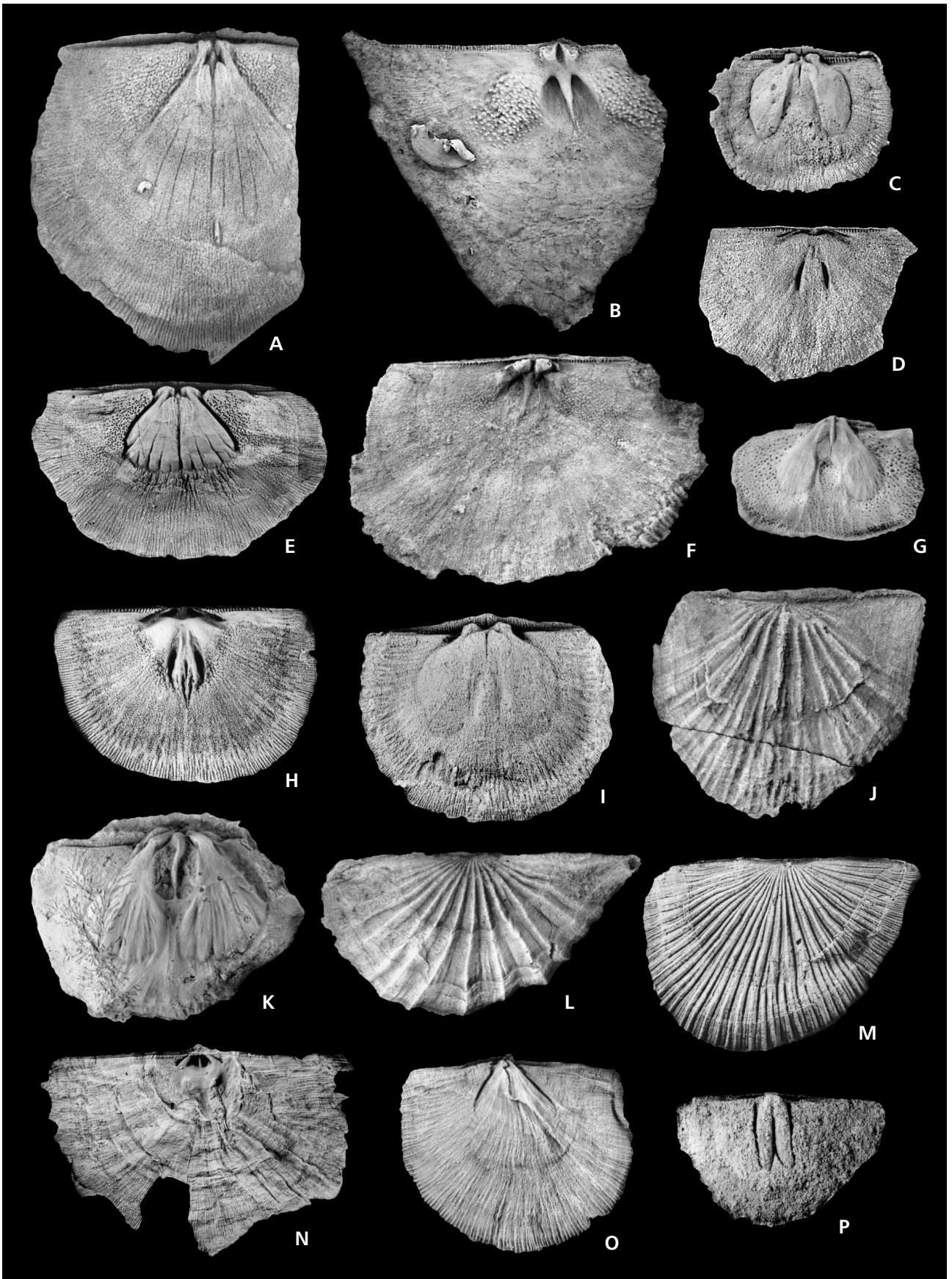
is figured in the present work in Fig. 5E, F. Dimensions: W = 26.3 mm, L = 34.5 mm [laterally compressed].

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.

Material. – All specimens come from Late Emsian strata of the Rhenish Slate Mountains. – Central Middle Rhine region. Type series from Niederlahnstein; Sandberger collection: 1 AVIM [lectotype MW 289d/54.10.00], 1 VVIM [paralectotype MW 289c/54.10.01], 1 VVIM, 1 DVEM [paralectotypes MW 289b/54.10.03], 1 DVIM [paralectotype MW 289a/54.10.02], 1 DVEM [paralectotype MW 289e/54.10.04]. – Further specimens from the central Middle Rhine region. Laubach Group, Dörrbach Valley near Koblenz; leg. G. Solle: 4 VVIM+EM [cf. *taeniolata*, SMF 85226, 93640, 93641; MB.B. 9106]. “Gegend von Coblenz”; leg. L. von Buch: 2 VVIM, 1 VVEM [MB.B. 9107]. – Eifel region. Wetteldorf Fm. (?), foot of Hartberg opposite Dürrkopf, near Prüm; leg. Rud. Richter: 1 VVIM [SMF 85223]. – Luxembourg. Erpeldinge, church yard at the bridge: 1 VVIM [SMF 85224]. – Lahn Synclinorium. Altenvers, hill W of the village; leg. U. Jansen: 1 VVIM [SMF 85225]. – Dill Synclinorium. Mandeln Fm., Hauberg near Mandeln; leg. G. Dahmer: 1 VVIM [SMF 66997]. Haigerseelbach; leg. Wagner: 1 VVIM [SMF 85675]. Haigerhütte Fm., Haigerhütte, NE slope of the Dill Valley between Hausberg and Schlierberg, E of Haiger: 1 VVIM [cf. *taeniolata*; USNM 220612].

Description. – Shells of moderate size, semielliptical in outline, slightly longer than wide or about as long as wide,

Figure 6. Selection of strophomenid brachiopods from the uppermost Silurian, Lower Devonian and lowermost Middle Devonian of the Rhenish Slate Mountains, Germany. • A, B – *Leptostrophiella explanata* (Sowerby, 1842); locality: Oberstadtfeld, S Central Eifel region; stratum: Stadtfeld Formation, upper Lower Emsian; A – SMF 66994; internal mould of ventral valve (× 1.0); B – SMF 66995; latex cast of internal mould of dorsal valve (× 1.0). • C, D – *Douvillina filifer* (W.E. Schmidt, 1914); stratum: Heisdorf Fm., uppermost Upper Emsian; C – SMF 66169; internal mould of ventral valve (× 1.5); locality: Benenberg, near Blankenheim, North Eifel region; leg. L. Dickfeld; D – SMF 66168, internal mould of dorsal valve (× 1.5); locality: Wehlert, field between Wehlert and Rommersheimerheld, Prüm Syncline, Eifel region; leg. R. Werner 1964. • E, F – *Pseudoleptostrophia dahmeri* (Rösler, 1954); leg. G. Fuchs; middle Lower Emsian; E – SMF 66166; internal mould of ventral valve (× 1.0); locality: Niederstadtfeld, Lauzert, S Central Eifel region; stratum: Gefell Formation; F – SMF 66167; latex cast of internal mould of dorsal valve (× 1.0); locality: N exit of Altscheuern, West Eifel region; stratum: Altscheuern Formation. • G – *Teichostrophia lepis subtilis* Struve, 1992; SMF 50159, holotype; internal mould of ventral valve (× 2.3); locality: Honigseifen, bad lands near path, Salmerwald Syncline, Eifel region, leg. I. & W. Struve & H.O. Nürnberg (1968); stratum: Lauch Formation, lowermost Eifelian. • H, I – *Crinistrophia elegans* (Drevermann, 1902); locality: Oberstadtfeld; stratum: Stadtfeld Fm., upper Lower Emsian; H – SMF-Mbg. 2950, lectotype; internal mould of dorsal valve (× 1.3); I – SMF-Mbg. 2949, paralectotype; internal mould of ventral valve (× 1.3). • J – *Plicostropheodonta virgata* (Drevermann, 1902); SMF-Mbg. 2946, paralectotype; external mould of dorsal valve (× 1.3); locality: Oberstadtfeld; stratum: Stadtfeld Formation, upper Lower Emsian. • K, L – *Plicostropheodonta murchisoni* (d’Archiac & de Verneuil, 1842); locality: Haberscheid near Seifen, Westerwald, leg. U. Jansen; stratum: Seifen Formation, upper Middle Siegenian; K – SMF-Mbg. 5138; internal mould of ventral valve (× 1.3); L – SMF-Mbg. 5139; external mould of dorsal valve (× 1.3). • M – *Fascistropheodonta sedgwicki* (d’Archiac & de Verneuil, 1842); SMF-Mbg. 2347; external mould of dorsal valve (× 1.3); locality: Seifen; stratum: Seifen Formation, upper Middle Siegenian. • N, O – *Mesodouvillina triculta* (Fuchs, 1919); locality: Hüinghausen, railway station, Ebbe Anticlinorium, Sauerland, leg. Rud. Richter; stratum: Hüinghausen Formation, Lower Gedinnian; N – SMF 93623, internal mould of dorsal valve (× 1.3); O – SMF 93632, internal mould of ventral valve (× 1.3). • P – *Shalera rigida* (de Koninck, 1876); SMF 66175; internal mould of ventral valve (× 1.3); locality: Weismes, Klein’s quarry, Belgium; stratum: Gdumont Formation, Prïdolian.



slightly brachythyrid; 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 capillae increasing by insertion; new costellae normally develop from a capilla in the middle of its group, when the number of capillae has reached 5 or 6; costellae and capillae crossed by numerous concentric fila. Hinge line denticulate for about two thirds to all of its length. Interior of ventral valve with pyramid-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 parodontal 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 radial 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 brachiophores. 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 brevisseptum 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 (Rösler 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 parodontal plates; the form may represent a separate species. Still undescribed, closely related representatives of *Gibboudouillina* (possibly new species) are known to the present author from the Lower/Upper Emsian boundary beds of the Mdâouer-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). “*Douwillina*” *interstitialis* sensu Gratsianova, 1975 (non Phillips, 1841) from the Gorny Altai Mountains (SW Siberia) is similar, as well; it shows parodontal plates and differs from *G. taeniolata* in the presence of faint concentric rugae and a relatively wider ventral muscle field. Another comparable species is *Bojoudouillina transversa* Su, 1976 from N China.

Gibboudouillina taeniolata differs from the Middle Devonian *Gibboudouillina interstitialis* (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 Gdoutmont Formation (surrounding area of the Stavelot-Venn Anticlinorium), the Köbbinghausen Formation (Remscheid Anticlinorium) and the Kellerskopf 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 Ardennan type region turned out to be of latest Silurian age due to the occurrences of *Dayia 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 Ardennan area the lower part of the Muno Formation (the two “faunas of Ruisseau des Roches”) and the Gdoutmont Formation, in the Rhenish area the correlatives Köbbinghausen and Kellerskopf (= “Graue Phyllite”) formations and the lower part of the Silberg Formation (Müsen Horst).].

GLOBAL STAGES	PR.	LOCHKOV.		PRAG.	EMSIAN										EIFEL.
	Gedinnian			Siegenian			Lower Emsian			Upper Emsian				Eifelian	
	Lowermost	Lower	Upper	Lower	Middle	Upper	Lower (Ulmen)	Middle (Singhofen)	Upper (Vallendar)	Lower (Lahnstein)	Middle (Laubach)	Upper (L. Kondel)	Up-most (Up. Kondel)	Lower (Lauch)	
STROPHOMENIDA															
<i>Shaleria rigida</i>	—														
<i>Mesodouvillina triculta</i>		—													
<i>Boucotstrophia herculea</i>					—										
<i>Fascistropheodonta sedgwicki</i>					—										
<i>Gigastropheodonta gigas</i>					—										
<i>Plicostropheodonta purchisoni</i>					—										
<i>Leptostrophiella explanata</i>					—										
<i>Pseudoleptostrophia dahmeri</i>															
<i>Plicostropheodonta virgata</i>															
<i>Crinistrophia elegans</i>															
<i>Rhenostropheodonta rhenana</i>															
<i>Gibbodouvillina taeniolata</i>															
<i>Rhenostropheodonta piligera</i>															
<i>Douvillina filifer</i>															
<i>Teichostrophia lepis subtilis</i>															

Figure 7. Stratigraphic ranges of Přídolian to Early Eifelian Strophomenida from the Rhenish Slate Mountains (Germany). Ranges of *cf.* forms shown as white bars. PR. = Přídolian. The position of the basal Emsian boundary level in global (GSSP) sense is still uncertain; the current boundary is tentatively indicated (dotted line).

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 plaques 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* (Drevermann, 1904), *Plicostropheodonta purchisoni* (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 purchisoni* 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 "Vallendar"), 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, in particular the Oppershofen Formation (NE Taunus) and the Stadtfeld Formation (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 Emsquarzit 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 Lahnstein Group. It is also present in the Wiltz Formation of the Prüm Syncline (Eifel region). A form determined as *Fascistropheodonta sedgwicki* 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 it 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 Late Emsian taxon and a typical faunal component of the Heisdorf Formation (Eifel region; Werner 1969). It just ranges into the basal Eifelian (*Polygnathus 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 *Leptostrophiella*, *Mesodouvillina* or *Pseudoleptostrophia* 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 *Gibboudouvillina* (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 *Boucotstrophia* Jahnke, 1981 is revised, excluded from the family Strophodontidae Carter, 1939 and included in the subfamily Mesodouvillinae 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 (Přídolian) is characterised by the typically Silurian element *Shaleria rigida* (de Koninck, 1876), the Lower Gedinnian by *Mesodouvillina triculta* (Fuchs, 1919) and the Middle–Upper Siegenian interval mainly by *Boucotstrophia herculea* (Drevertmann, 1904), *Gigastropheodonta gigas* (McCoy, 1852) and *Fascistropheodonta sedgwicki* (d’Archiac & de Verneuil, 1842). The Lower Emsian is indicated by the occurrence of *Pseudoleptostrophia dahmeri* (Rösler, 1954), *Plicostropheodonta virgata* (Drevertmann, 1902) and *Crinistrophia elegans* (Drevertmann, 1902), whereas the lower boundary of the Upper Emsian can well be recognized 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 substage”). The uppermost Upper Emsian is well documented by *Douvillinella 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 *Leptostrophia* 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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