A new genus of terebratulid brachiopod from the Siegenian of the Rheinisches Schiefergebirge

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Schemm-Gregory, M. and Jansen, U. 2007. A new genus of terebratulid brachiopod from the Siegenian of the Rheinisches Schiefergebirge. *Acta Palaeontologica Polonica* 52 (2): 413–422.

A new genus *Crassirensselaeria* (Terebratulida, Rhenorensselaeriidae) from the Siegenian (middle Lower Devonian) of the Rheinisches Schiefergebirge (= Rhenish Slate Mountains, Germany) with the type-species *Crassirensselaeria crassicosta* is erected. Exceptionally well-preserved material of this taxon has recently been obtained from a temporary outcrop at an ICE (= InterCityExpress) railway construction site close to Aegidienberg near Bonn. As representatives of *Crassirensselaeria* have hitherto been included into the terebratulid genus *Rhenorensselaeria*; they are compared with the two Lower Devonian species of that genus from the Rheinisches Schiefergebirge: *Rhenorensselaeria strigiceps* and *Rh. demerathia*. *Crassirensselaeria* is chiefly distinguished from these by more globular shells, the presence of very strong plications, long and strong dental plates, different ventral muscle field, and thickened cardinalia. Representatives of the new genus are excellent index fossils for the Siegenian of the Rheinisches Schiefergebirge, even in deposits of restricted-marine and probably brackish environments. New material of articulated specimens in life position shows that both rhenorensselaeriid genera lived in clusters with the longitudinal axes of the shells oriented steep or perpendicular to the seafloor. The new genus is abundant in the Rheinisches Schiefergebirge (Germany) and the northern Ardennes (Belgium), it also occurs in the Hrubý Jeseník Mountains (Czech Republic). Its occurrence in Cornwall (Great Britain), however, is still questionable.

Key words: Brachiopoda, Terebratulida, *Crassirensselaeria*, *Rhenorensselaeria*, Rheinisches Schiefergebirge, Devonian.

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Introduction

Terebratulid brachiopods are of biostratigraphic importance in the Lower Devonian of the Rheinisches Schiefergebirge (= "Rhenish Slate Mountains"), especially taxa of *Rhenorensselaeria* Kegel, 1913 (type species: *Terebratula strigiceps* C.F. Roemer, 1844) and *Crassirensselaeria* gen. nov. (type species: *Rensselaeria crassicosta* Koch, 1881; see Mittmeyer 1982). Roemer (1844) erected *Terebratula strigiceps* as the first "rensselaeriid" species in the Rheinisches Schiefergebirge. Kayser (1881a) described a new species of *Rensselaeria* with strong costae in open nomenclature. In a footnote, Kayser (1881b) referred to personal comunication with Koch who had given the name "*Rensselaeria*" *crassicosta* [remark: except for the synonymy lists the former generic names are in quotation marks] to this new species, and two years later Kayser (1883) redescribed and figured it. Fuchs (1904) published a monograph of the rensselaeriid brachiopods from the Rhine area and pointed out the importance of "*Rensselaeria*" *crassicosta* for the recognition of the Siegenian ("*primaevus* Beds"). Kegel (1913) compared the material of the Rheinisches Schiefergebirge with material from North America, where the genus *Rensselaeria* Hall, 1859 had been established, and erected for the German forms the genus *Rhenorensselaeria* including *Rhenorensselaeria strigiceps* (C.F. Roemer, 1844) as type species and "*Rhenorensselaeria*" *crassicosta* (Koch, 1881). Simpson (1940) studied ontogenic stages of *Rhenorensselaeria* from the Eifel region (western Rheinisches Schiefergebirge), especially of *Rh. strigiceps*, and erected as a new species *Rh. demerathia*. He used these taxa and "*Rh.*" *crassicosta* biostratigraphically in the regional Siegenian stage.

Helmbrecht and Wedekind (1923) tried to subdivide the Siegen Beds in the Siegerland area biostratigraphically into "Stufen" (= "stages") based on rensselaeriids and spiriferids. One of these "Stufen" was the "Crassostufe" defined by the life span of the "*Rensselaeria crassicosta* group" that they called "Crassorensselaerien". They gave a short description of this group and mentioned differences between "*Re.*" *crassicosta* and *Rh. strigiceps*. Maillieux (1931: 28–29) interpreted this as the erection of a new genus *Crassorensselaeria* that he, however, did not accept because he regarded the differences between that genus and *Rhenorensselaeria* as taxonomically less important. According to the International Code of Zoological Nomenclature (ICZN 2000: Article 11.5, 11.8, 12), Helmbrecht and Wedekind (1923) have not erected a new genus because they did not explicitely mention "*Crassorensselaeria*" as a new genus. They only used the plural form "Crassorensselaerien" as a descriptive term and continued to use the generic name *Rensselaeria* for these forms.

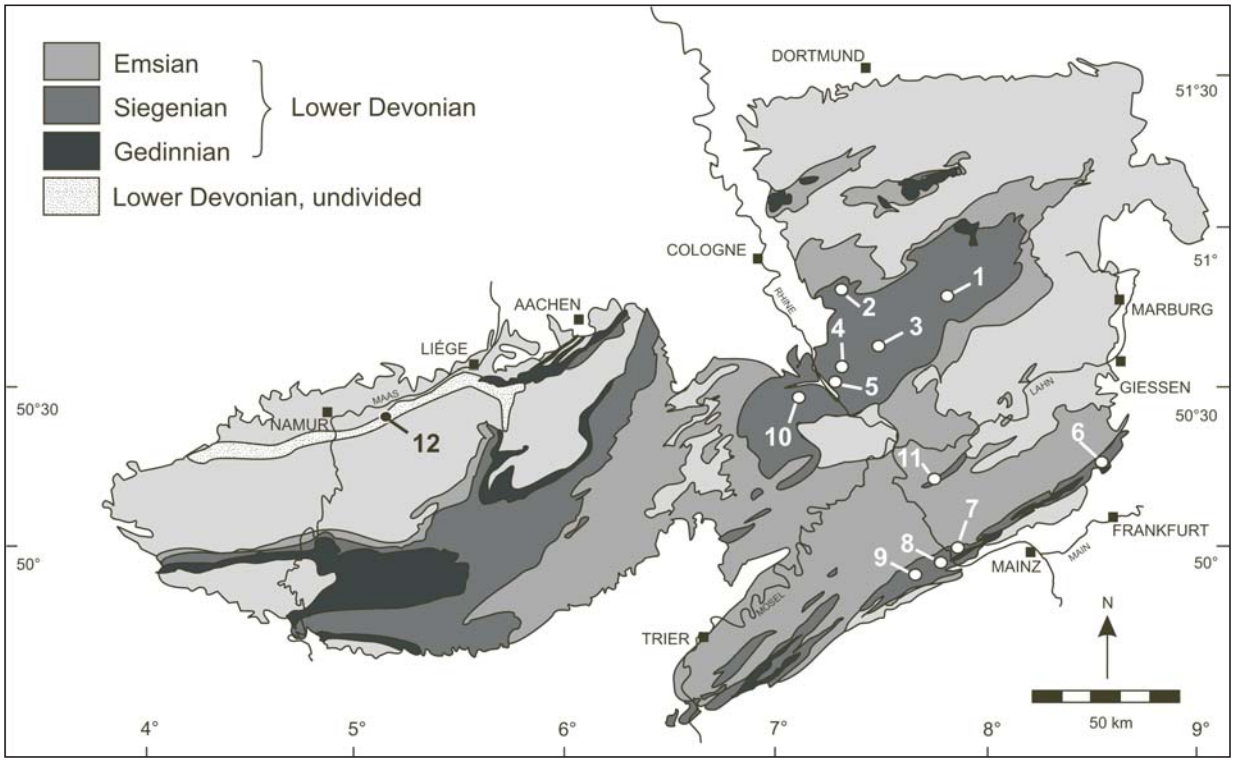

Fig. 1. Geological map of the Rheinisches Schiefergebirge (Germany) and the Ardennes (Belgium/France) showing the distribution of Lower Devonian rocks. 1–12: Main localities of *Crassirensselaeria crassicosta* (Koch, 1881). 1: Häusling near Siegen (type locality), 2: Overath, 3: Seifen, 4: Aegidienberg, 5: Unkel, 6: Silberküppel and Saalburg quarry, 7: Assmannshausen, 8: Leingipfel near Rüdesheim and Bingerbrück, 9: Koppenstein, south of Gemünden, 10: Hannebach near Kempenich, 11: Katzenelnbogen, 12: Fonds de Wisseletz, between Pepinster and Louveigné, northern Ardennes (Belgium).

Crassirensselaeria crassicosta has hitherto been assigned either to *Rensselaeria* Hall, 1859, *Rhenorensselaeria* Kegel, 1913, or *Globithyris* Cloud, 1942 (e.g., Fuchs 1904; Dahmer 1934; Kutscher 1937; Maillieux 1940; Jux 1981).

Our studies are based on collections of different institutions and new collections from the Rheinisches Schiefergebirge. According to literature data, *Crassirensselaeria crassicosta* is abundant in many brachiopod yielding localities of Upper Siegen Beds in the Rheinisches Schiefergebirge (Fig. 1), whereas it is rarer in Lower and Middle Siegen Beds. The species also occurs in the northern Ardennes (Belgium) (e.g., Maillieux 1931) and in the Hrubý Jeseník Mountains (Czech Republic) (Wilschowitz 1931, 1932).

Institutional abbreviations.—AEG, Aegidienberg material from the Palaeontological Institute of the University of Bonn, Germany; MB.B, Museum für Naturkunde Berlin, Germany; MBG, Institute for Geology and Palaeontology of the Phillips University of Marburg, Germany; SMF, Senckenberg Research Institute, Frankfurt am Main, Germany.

Material and methods

All specimens are preserved as internal and external moulds: 86 internal moulds of ventral valves, 4 of these with corresponding external moulds, 27 internal moulds of dorsal valves, 3 of these with corresponding external moulds, 52 internal moulds of articulated shells, and 28 fragments of external moulds. Latex casts were used to study the positive form of the internal features (Fig. 2). The specimens are from Siegenian Beds (mainly Upper Siegenian) in the Rheinisches Schiefergebirge. They have been collected at the following localities (TM 25 = topographical mapsheet, scale 1:25,000):

Crassirensselaeria crassicosta: Aegidienberg tunnel, TM 25 Königswinter 5309 (AEG 18-6, 18-8, 22-4, 57-1, 57-4, 62-7, 65, 88-2, 97-3, 97-5a, b, 97-8, 97-9, 97-10, 97-12, 101-5, 110 lateral B-3, 110 lateral B-10, 146-5, 177, 295/1, 295/2, 296/1); Altenhof quarry near Wenden, TM 25 Wenden 5013 (MB.B 2078.1–10, 2079.1–8); Häusling near Siegen, TM 25 Siegen 5114 (MB.B 2090.1–3); Langenstein near Kellenbach, TM 25 Gemünden 6110 (MB.B 2091); Siegen, TM 25 Siegen 5114 (MB.B 2096); Seifen/Westerwald area, TM 25 Altenkirchen 5311 (SMF XVII 739 d); east of Wallmeroth, TM 25 Betzdorf 5213 (SMF XVII 1273a, b); Silberküppel near Bad Homburg, TM 25 Bad Homburg 5717 (SMF XVII 2945 cl-3, dl-3); Rudersdorf, TM 25 Siegen 5114 (SMF XVII 4072, MBG 5075–5079); Leingipfel near Rüdesheim, TM 25 Pressberg 5913 (SMF 66106); Koppenstein, south of Gemünden, TM 25 Gemünden 6110 (SMF 65015–65019, SMF 66278–66279); Assmannshausen, TM 25 Pressberg 5913 (SMF 66107–66110, 66118, 66119); Hartberg, TM 25 Bingen 6013 (SMF 66111, 66113, 66114, 66116); Gemarkung Allerbach, TM 25 Pressberg 5913 (SMF 66112); Bingerbrück, TM 25 Bingen 6013

(SMF 66115, 66117); abandoned quarry east of Rheinbreitbach, TM 25 Königswinter 5309 (SMF 66120); Weissler Höhe near Katzenelnbogen, TM 25 Katzenelnbogen 5713 (SMF 66121–66126); Fischbacher Berg, TM 25 Freudenberg 5113 (SMF 66127); Overath, TM 25 Overath 5009 (SMF 66128); Flammersbach near Siegen, TM 25 Siegen 5114 (SMF 66129, 66130); Saalburg Quarry near Herzberg, TM 25 Bad Homburg 5717 (SMF 66131, 66132); east of Druidenstein, TM 25 Betzdorf 5213 (SMF 66133–66137); quarry south of Eiserfeld, TM 25 Freudenberg 5113 (MBG 5953–5057); Wildenburg near Idar, TM 25 Freudenberg 5113 (MBG 5058–5060); Herdorf, TM 25 Betzdorf 5213 (MBG 5061); Giersberg near Siegen, TM 25 Siegen 5114 (MBG 5062, 5102); Anzhausen, TM 25 Freudenberg 5113 (MBG 5063–5074, 5087–5088, 5090–5096); Fronhausen, TM 25 Hilchenbach 5014 (MBG 5080); Brück an der Ahr, TM 25 Siegen 5114 (MBG 5081–5086); Wellersberg near Siegen, TM 25 Siegen 5114 (MBG 5089); Burggraben near Netphen, TM 25 Hilchenbach 5014 (MBG 5098–5099); fields south of Obersdorf, TM 25 Siegen 5114 (MBG 5103).

Rhenorensselaeria strigiceps: Aegidienberg tunnel, TM 25 Königswinter 5309 (AEG 267-1, 276-1); Mine "Alte Mahrscheid" near Herdorf, TM 25 Betzdorf 5213 (SMF 66104).

Rhenorensselaeria demerathia: Quarry north of Demerath, TM 25 Gillenfeld 5807 (SMF XVII 687 n, 687 o); Auderather Mühle, TM 25 Gillenfeld 5807 (SMF XVII 687 r); south of Meiserich, TM 25 Gillenfeld 5807 (SMF 26340 a).

Furthermore, we studied specimens of the private collection of Michael Stemmer (Unkel, Germany) that have been collected in exposures around the classic locality "Kaskade bei Unkel" near Linz/river Rhine, TM 25 Königswinter 5309, formerly described by Dahmer (1936a).

Systematic palaeontology

Order Terebratulida Waagen, 1883
Suborder Centronellidina Stehli, 1965
Superfamily Stringocephaloidea King, 1850
Family Rhenorensselaeriidae Boucot, 1975
Genus *Crassirensselaeria* nov.

Derivation of the name: Combination of the genetive of Latin *crassus* (coarse, thick) with the generic name *Rensselaeria*.

Type species (by monotypy): *Rensselaeria crassicosta* Koch, 1881; Siegenian (middle Lower Devonian), Rheinisches Schiefergebirge, Germany.

Diagnosis.—*Crassirensselaeria* differs from the other genera of the family by more globular shells, coarser and less numerous costae (20 to 24 on internal moulds), thicker and longer dental plates, and more strongly developed cardinalia. Ventral muscle field more deeply impressed and basally more narrow. It differs from *Lievinella* Boucot, 1975 by the absence of a sulcus in both valves and the presence of a dorsal median septum.

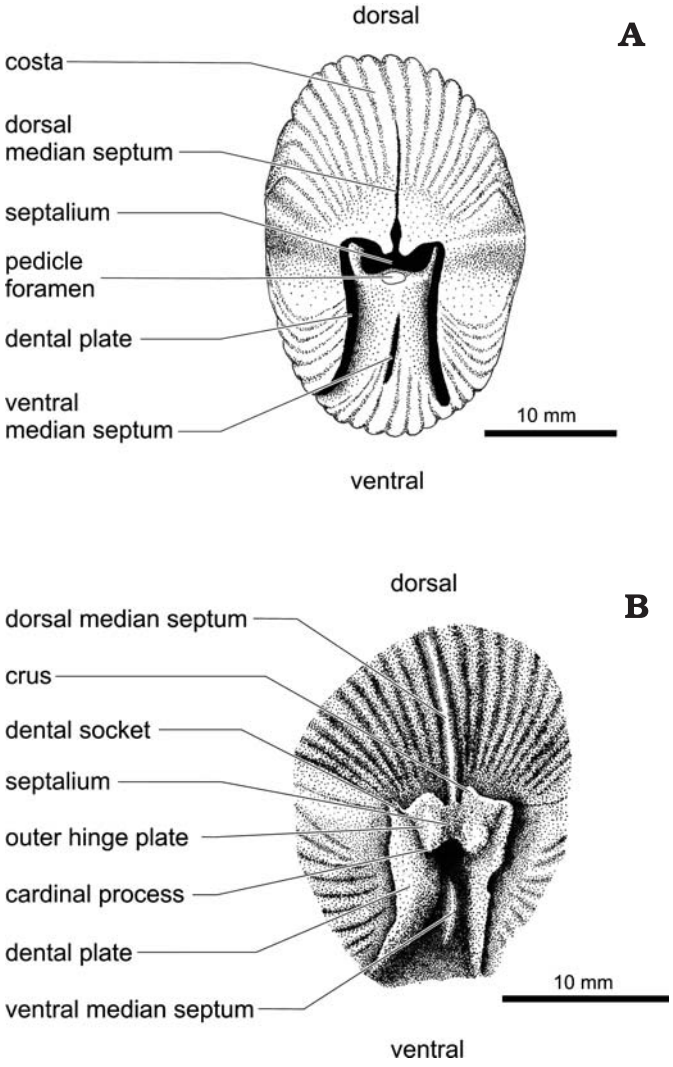

Fig. 2. Morphological terms of *Crassirensselaeria crassicosta* (Koch, 1881). **A**. Internal mould of articulated specimen (lectotype, MB.B 2090.1). Posterior view. Crural plates, dental plates, dorsal and ventral median septum preserved as negative forms. **B**. Latex cast of internal mould of articulated specimen (MBG 5083). Interior of posterior portions of both valves. Drawings by M.S.-G.

Crassirensselaeria crassicosta (Koch, 1881)

Figs. 2, 3, 4A, 7.

1881 *Rensselaeria* sp. nov.; Kayser 1881a: 263.
1881 *Rensselaeria crassicosta* sp. nov.; Koch in Kayser 1881b: 387.
1883 *Rensselaeria crassicosta* Koch; Kayser 1883: 123–124, pl. 5: 2–5.
1904 *Rensselaeria crassicosta* C. Koch; Fuchs 1904: 44–45, pl. 6: 1.
1913 *Rhenorensselaeria crassicosta* Koch; Kegel 1913: 11, 127, 132, 135–136, pl. 6: 14, 15.
1923 *Renssellaeria crassicosta* Koch; Quiring 1923: 91–92, 99–100, 102–103, 105–107, 109, 111.
1923 *Rensselaeria crassicosta*; Helmbrecht and Wedekind 1923: 949–950, 953.
1931 *Rensselaeria* (*Rhenorensselaeria*) *crassicosta* C. Koch; Maillieux 1931: 6–8, 30–32, pl. 1: 11, a, b.
1931 *Rensselaeria* sp. cf. *crassicosta* C. Koch; Wilschowitz 1931: 8, 11, pl. 2: 14–16.

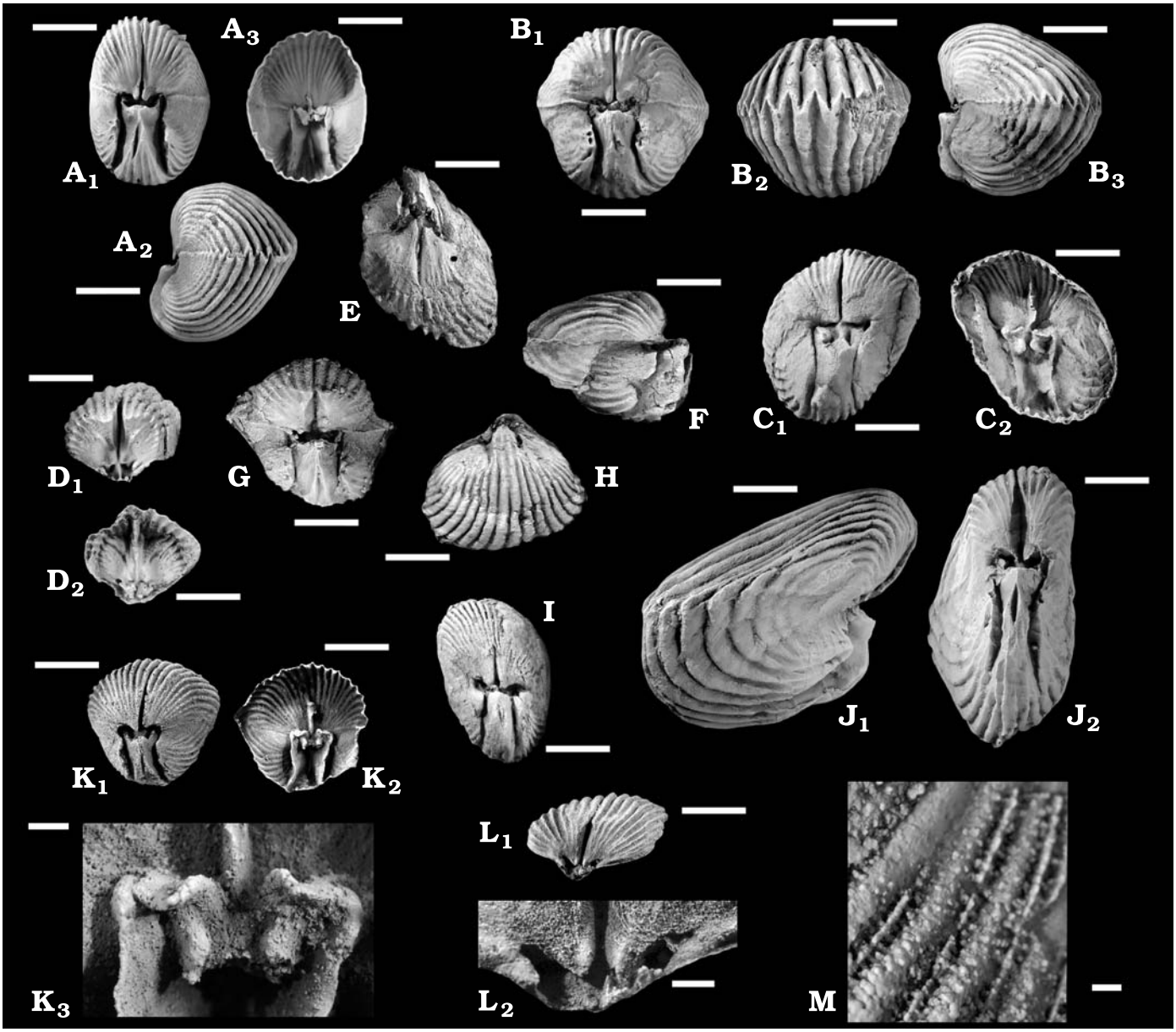

Fig. 3. Middle Lower Devonian rhenorensselaeriid brachiopod *Crassirensselaeria crassicosta* (Koch, 1881) from the Rheinisches Schiefergebirge, Germany. **A**. Lectotype. Internal mould of articulated specimen (MB.B 2090.1). Siegen Beds of Häusling near Siegen, Siegerland area, topographical mapsheet 1:25 000 Siegen 5114. Internal mould, posterior view (A_1); internal mould, lateral view (A_2); latex cast, interior of posterior portions of both valves (A_3). **B**. Internal mould of articulated specimen (MB.B 2090.2). Siegen Beds of Häusling near Siegen, Siegerland area, topographical mapsheet 1:25 000 Siegen 5114. In posterior (B_1), anterior (B_2), and lateral (B_3) views. **C**. Internal mould of articulated specimen (AEG 65). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Internal mould, posterior view (C_1); latex cast, interior of posterior portions of both valves (C_2). **D**. Internal mould of dorsal valve (MB.B 2078.8). Upper Siegen Beds of quarry Altenhof, leg. Schmidt 1924, topographical mapsheet 1:25 000 Wenden 5013. Internal mould, oblique posterior view (D_1); latex cast, oblique view of the interior (D_2). **E**. Internal mould of articulated specimen (AEG 295-1b). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Oblique posterior view. **F**. Internal mould of articulated specimen (AEG 110 lateral B3b). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Lateral view. **G**. Internal mould of articulated specimen (AEG 97-3). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Posterior view. **H**. Internal mould of ventral valve (AEG 110 lateral B3a). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Ventral view. **I**. Internal mould of articulated specimen (AEG 295-1a). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Posterior view. **J**. Internal mould of articulated specimen (MB.B 2096). Siegen Beds of Siegen, leg. Sprieserbach 1918, Siegerland area, topographical mapsheet 1:25 000 Siegen 5114. In lateral (J_1) and posterior (J_2) views. **K**. Internal mould of articulated specimen (MBG 5083). Siegen Beds of Brück an der Ahr, leg. Sprengler 1895, Siegerland area, topographical mapsheet 1:25 000 Siegen 5114. Internal mould, posterior view (K_1); latex cast, interior of posterior portions of both valves (K_2); latex cast, cardinalia (K_3). **L**. Internal mould of dorsal valve (MBG 5100). Siegen Beds of Burggraben near Netphen, Siegerland area, topographical mapsheet 1:25 000 Hilchenbach 5014. Oblique posterior view (L_1); apical region (L_2). **M**. External mould of ventral valve (AEG 146-5). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Ornament. Scale bars 10 mm, except K_3, L_2, and M for which are 1 mm.

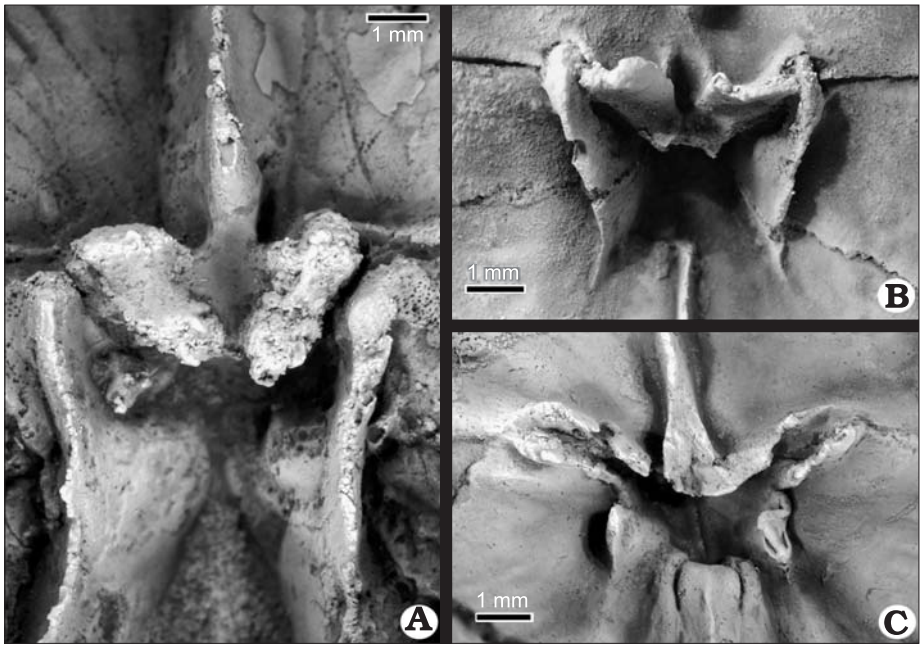

Fig. 4. View of cardinalia. All figures are latex casts of internal moulds of articulated specimens. **A**. *Crassirensselaeria crassicosta* (Koch, 1881). Lectotype (MB.B 2090.1) Siegen Beds (middle Lower Devonian); Häusling near Siegen, Siegerland area, topographical mapsheet 1:25 000 Siegen 5114. **B**. *Rhenorensselaeria strigiceps* (C.F. Roemer, 1844) (SMF 66104). Siegen Beds (middle Lower Devonian); Mine "Alte Mahlscheid" near Herdorf; leg. Bergrat Borrhezs 1894, Middle Rhine area, topographical mapsheet 1:25 000 Betzdorf 5213. **C**. *Rhenorensselaeria demerathia* Simpson, 1940 (SMF XVII 687 o). Saxler Beds (upper parts of Upper Siegen Beds, middle Lower Devonian); Quarry 3/4 km north of Demerath, Eifel area, topographical mapsheet 1:25 000 Gillenfeld 5807.

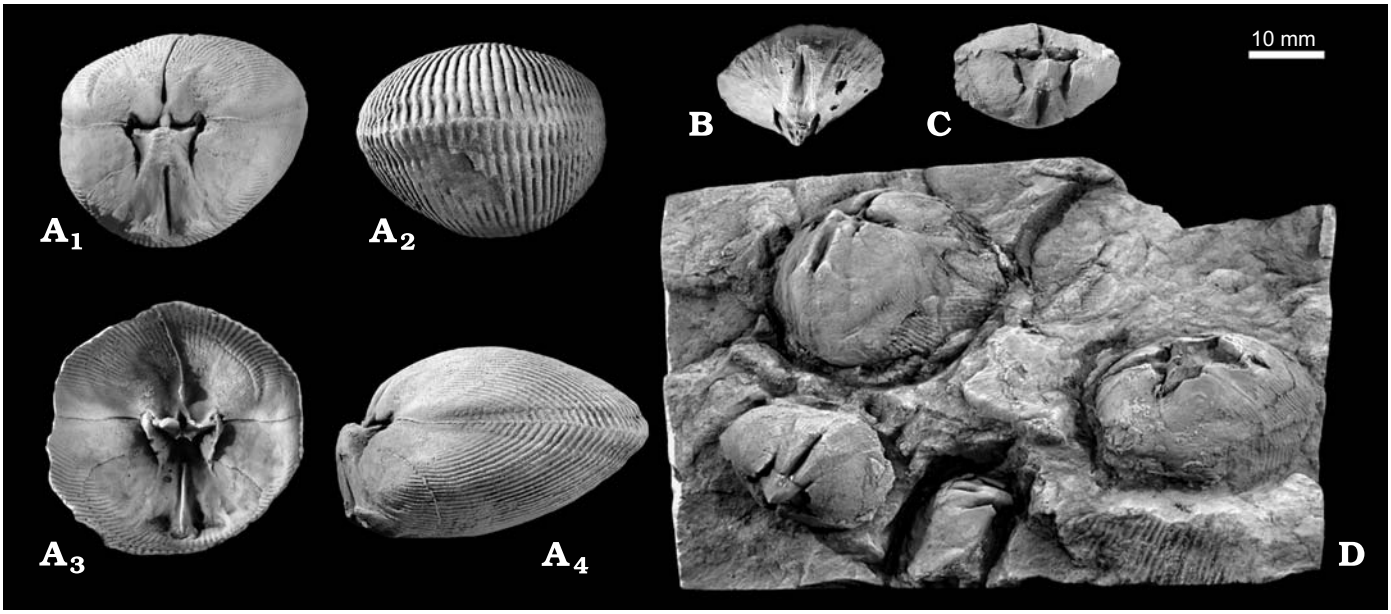

Fig. 5. Middle Lower Devonian rhenorensselaeriid brachiopod *Rhenorensselaeria strigiceps* (C.F. Roemer, 1844) from Germany. **A**. Internal mould of articulated specimen (SMF 66104) and latex cast. Siegenian of mine "Alte Mahlscheid" near Herdorf; leg. Bergrat Borrhezs 1894, Middle Rhine area, topographical mapsheet 1:25 000 Betzdorf 5213. Internal mould, posterior view (A_1); internal mould, anterior view (A_2); latex cast, interior of posterior portions of both valves (A_3); internal mould, lateral view (A_4). **B**. Internal mould of ventral valve (AEG 28-3). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Oblique posterior view. **C**. Internal mould of articulated specimen (AEG 267-1). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Posterior view. **D**. Rock slab with specimens in life position (AEG 267-1). Upper Siegen Beds of Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Posterior view of internal moulds.

1932 *Rensselaeria crassicosta* C. Koch; Wilschowitz 1932: 14–15, 32, pl. 2: 15–17.

1934 *Rhenorensselaeria crassicosta* (C. Koch); Dahmer 1934: 17, 21, 31, 35.

1936 *Rhenorensselaeria crassicosta* (Koch); Dahmer 1936a: 643–645, 666, pl. 46: 5.

1936 *Rhenorensselaeria crassicosta* (Koch); Dahmer 1936b: 6, 9–12, pl. 6: 13.

1936 *Rhenorensselaeria crassicosta* (C. Koch); Rose 1936: 57.

1937 *Rhenorensselaeria crassicosta* (Koch); Dahmer 1937: 440, 444, 447–449, 452–454, 456–458.

1937 *Rensselaeria crassicosta* Koch; Kutscher 1937: 198–200, 204, 209, 215, 217.

1940 *Rhenorensselaeria crassicosta* (Koch); Simpson 1940: 55, table 2.

1950 *Rhenorensselaeria crassicosta*; Solle 1950: 307, 309–310, 313.

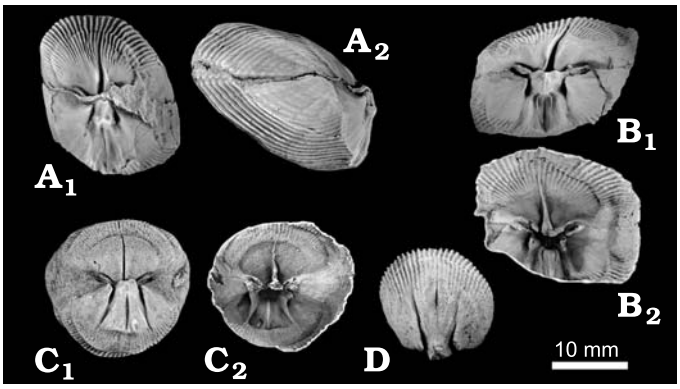

Fig. 6. Middle Lower Devonian rhenorensselaeriid brachiopod *Rhenorensselaeria demerathia* Simpson, 1940 from Germany. **A**. Holotype. Internal mould of articulated specimen (SMF XVII 687 n). Saxler Beds (upper parts of Upper Siegen Beds) of a quarry 3/4 km north of Demerath, Eifel area, topographical mapsheet 1:25 000 Gillenfeld 5807. In posterior (A_1) and lateral (A_2) views. **B**. Internal mould of articulated specimen (SMF XVII 687 o) and latex cast. Saxler Beds of a quarry 3/4 km north of Demerath, Eifel area, topographical mapsheet 1:25 000 Gillenfeld 5807. Internal mould, posterior view (B_1); latex cast, interior of posterior portions of both valves (B_2). **C**. Internal mould of articulated specimen (SMF 26340 a) and latex cast. Saxler Beds of south of Meiserich, point 367,8, Eifel area, topographical mapsheet 1:25 000 Gillenfeld 5807. Internal mould, posterior view (C_1); latex cast, interior of posterior portions of both valves (C_2). **D**. Internal mould of ventral valve (SMF XVII 687 r). Upper Siegen Beds of Auderather Mühle, Ollenbach, Eifel area, topographical mapsheet 1:25 000 Gillenfeld 5807. Oblique posterior view.

1957 *Rhenorensselaeria crassicosta* (Koch); Jentsch and Röder 1957: 124–125.
1967 *Rhenorensselaeria crassicosta* (Koch, 1881); Boucot et al. 1967: pl. 2: 2.
1974 *Rhenorensselaeria crassicosta* (Koch); Mittmeyer 1974: 70–72, table 2.
1981 *Globithyris laticostata* sp. nov.; Jux 1981: 102–104, fig. 2.
1981 *Rhenorensselaeria crassicosta* (Koch); Evans 1981: 521. [questionable].
1982 *Rhenorensselaeria crassicosta* (Koch); Mittmeyer 1982a: 13, 15, 18–21, ? 23, 38, fig. 4a, b, table 1.
1982 *Rhenorensselaeria crassicosta* (Koch); Fuchs 1982: 232, 252, text-fig. 10.
1982 *Rhenorensselaeria crassicosta* (Koch); Mittmeyer 1982b: 259, 260, chart 1.
1997 *Rhenorensselaeria crassicosta*; Mittmeyer 1997: 13.
2001 *Rhenorensselaeria crassicosta* (Koch); Thünker 2001: 27, 37–38, 67, 83, 86.
2004 *Rhenorensselaeria crassicosta* (Koch, 1881); Schindler et al. 2004: 143, 145, table 1.

Lectotype: Kayser (1881a) has not figured any specimens when he described the species in open nomenclature from the Taunusquarzit Beds of the Hunsrück area. Kayser mentioned in a footnote within a report (1881b) that Koch had named the species "*Rensselaeria*" *crassicosta*. According to the International Code of Zoological Nomenclature (ICZN 2000: Article 50.2.) Koch is the author of the taxon, not Kayser. Only two years later, Kayser redescribed the species and figured specimens from the Hunsrück and Siegerland areas. Because nothing has been published by Koch himself on this species, it is impossible to get a clear picture of what was his original intention. However, we think that Kayser and Koch were in contact with each other, so that it is very probable that they had the same idea of the species, which can hardly be confused with other ones. In our opinion, the specimens figured by Kayser (1883) can be regarded as specimens of the type series *sensu lato*. We have chosen the specimen figured by Kayser (1883: pl. 5: 2) as the lectotype. The internal mould of an articulated shell (Fig. 3, MB.B 2090.1) is 18.3 mm wide, 22.9 mm long, and 25.1 mm thick. It is stored in the Museum für Naturkunde, Berlin.

Type locality: Häusling near Siegen, topographical mapsheet 1:25 000 Siegen 5114, Siegerland area (Rheinisches Schiefergebirge, Germany).

Type horizon: Siegen Beds, exact position uncertain (Siegenian, middle Lower Devonian).

Diagnosis.—The same as for the genus.

Stratigraphic range and distribution.—Rheinisches Schiefergebirge (Germany): Lower, Middle, and Upper Siegen Beds, Taunusquarzit Beds; Northern Ardennes (Belgium): Grès et Schistes de Solières; Hrubý Jeseník (Czech Republic): beds of Siegenian age; ?Southern Devon and Northern Cornwall (Great Britain): Dartmouth Beds; Middle or Upper Siegenian (middle Lower Devonian). The species is abundant in Upper Siegenian strata, whereas it is rare in Lower and Middle Siegenian strata. It is useful especially in successions of re-

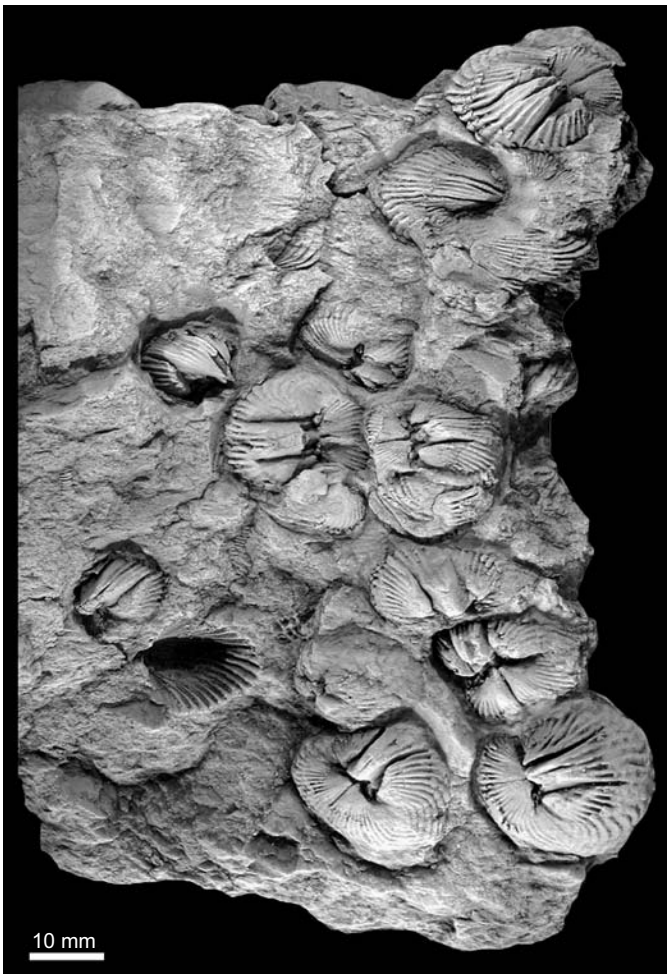

Fig. 7. Rock slab with several specimens of *Crassirensselaeria crassicosta* (Koch, 1881) in life position (AEG 146-5), view of the underside of the bed. Upper Siegen Beds (middle Lower Devonian) of the Aegidienberg tunnel, Siebengebirge, topographical mapsheet 1:25 000 Königswinter 5309. Internal moulds in posterior view.

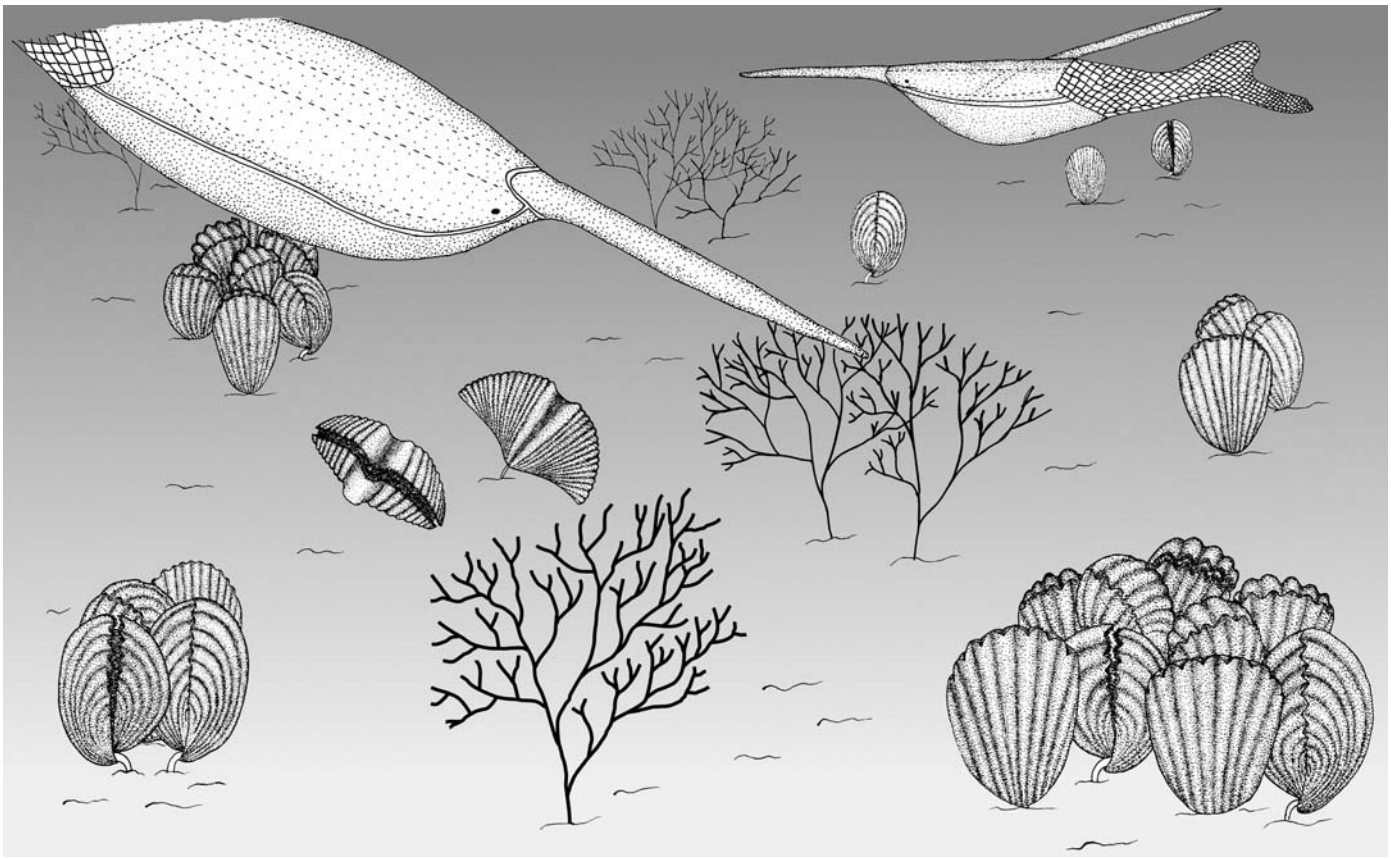

Fig. 8. Possible life habit of *Crassirensselaeria crassicosta* (Koch, 1881) based on material collected near Aegidienberg (Rheinisches Schiefergebirge). Nests and single individuals of *C. crassicosta* dominated the benthic life together with rare individuals of the spiriferid *Hysterolites hystericus* von Schlotheim, 1820. Nectonic life forms are represented by *Rhinopteraspis dunensis* (C.F. Roemer, 1876). Drawing by M.S.-G.

stricted marine, intertidal and deltaic environments to recognise the lower and upper boundaries of the Siegenian stage, where other fossils are sparse or absent.

Description.—Shell medium-sized and strongly biconvex, subglobular, ventral valve slightly more convex than dorsal valve with maximum curvature in the umbonal region; brachythyrid; suboval in outline, slightly longer than wide.

Only fragments of external moulds could be studied; they show coarse and non-bifurcating costae. Costae and separating furrows are angular in cross section and terminate along a "zig-zag commissure". On one ventral external mould the punctate shell structure is visible as minutes rods representing internal moulds of puncta (Fig. 3M, AEG 146-5). Ventral interarea rarely preserved, approximately orthocline, concave in longitudinal section.

The internal mould of the ventral valve extends further beyond the hinge line than that of the dorsal valve. A pair of thick and relatively long, subparallel dental plates is present. There is a short and fine septum in the apical region which is commonly situated in a median or, more rarely, a submedian position leaving a furrow on the internal mould. In the extreme apical region there is a small round scar interpreted as a trace of a pedicle foramen. Muscle scars are generally not clearly developed; the region of the muscle field is deeply impressed and commonly narrow at the base in cross section. The ventral internal mould shows 20 to 24 well-developed and coarse costae which are rounded in cross section whereas the furrows are angular. Costae are hardly developed in the apical region and close to the hinge line. Generally, costae are wider than furrows.

The internal mould of the dorsal valve posteriorly extends little across the hinge line. The cardinal process consists of a pair of rod-like to bulbous lobes. Thick cardinal plate supporting the cardinal process. A free septalium is developed in some specimens, in others it is apparently buried in secondary shell material. There is a long median septum reaching about one third of valve length. The dorsal median septum is longer and higher than the ventral median septum. It varies from a thin ridge to a prominent thick ridge with a sharp anterior edge sometimes carrying a low and thin myophragm. We do not ascribe a taxonomic relevance to this difference regarding it as intraspecific variability. The mould of the brachidium is not preserved in any specimen. The cardinal process and the crural plates reach into the ventral valve. At the outer margin of the cardinal plate there is a pair of shallow and narrow cylindrical dental sockets diverging in anterolateral direction (Fig. $3L_2$, MBG 5100). Adductor scars are situated on both sides of the median septum but their limits

Table 1. Comparison of *Crassirensselaeria crassicosta*, *Rhenorensselaeria strigiceps*, and *Rhenorensselaeria demerathia*.

	Crassirensselaeria crassicosta (Koch, 1881)	*Rhenorensselaeria strigiceps* (C.F. Roemer, 1844)	*Rhenorensselaeria demerathia* Simpson, 1940
shell	medium-sized, subglobular	large, elongate, ovoidiform	small, elongate, ovoidiform
number of costae on ventral internal mould	20–24 (mean = 22)	50–65	35–50
costae	coarse	very fine	fine
dental plates	long	short	short
outer hinge plates	thick	thin	thin
stratigraphic distribution	Lower to Upper Siegenian	Middle to Upper Siegenian	Upper Siegenian to ? Lower Emsian
geographic distribution	Rheinisches Schiefergebirge (Germany); Ardennes (Belgium/France); Hrubý Jeseník (Czech Republic); ?Cornwall (England)	Rheinisches Schiefergebirge (Germany); Ardennes (Belgium/France); Hrubý Jeseník (Czech Republic)	Rheinisches Schiefergebirge (Germany)

are not clearly discernible. They are deeply impressed in some specimens leaving small, posteriorly directed projections on the internal mould (Fig. 3D, MB.B 2078.8).

Discussion.—In the Rheinisches Schiefergebirge, the genus *Rhenorensselaeria* is represented by two species, *Rh. strigiceps* (C.F. Roemer, 1844) (Fig. 4B SMF 66104; Fig. 5) and *Rh. demerathia* Simpson, 1940 (Fig. 4C, SMF XVII 687 o; Fig. 6). *Crassirensselaeria* gen. nov. differs from both species of *Rhenorensselaeria* by more globular shells contrasting with the elongate and suboval outlines of the latter, by internal apical features, and the number and size of costae of the internal moulds (Table 1, Fig. 4). Our specimens of *C. crassicosta* (Koch, 1881), including the lectotype, show 20 to 24 costae on the ventral internal mould. As already Fuchs (1904) pointed out, Kayser (1883) described this species with 8 to 14 costae but none of the studied specimens shows that small number of costae. Kayser probably counted only the costae of one half of a specimen. The ventral muscle field of *C. crassicosta* is deeply impressed with poorly individualised scars and cleary bordered by the long dental plates. In *Rhenorensselaeria*, the ventral muscle field is generally more shallow forming a flat surface bordered by low muscle-bounding ridges; individual posterior and anterior scars are often clearly recognisable. At the anterior end of the scars, a pair of protuberances on the internal moulds can be developed which lack in *Crassirensselaeria*.

Rhenorensselaerids close to *Rh. strigiceps* are described from the Armorican Massif (northwestern France; Renaud 1942), the Celtiberian Chains (northeastern Spain; Carls and Valenzuela-Ríos 1998), and the Dra Plains (southern Morocco; Jansen 2001). These forms generally show the same differences to *C. crassicosta* as *Rh. strigiceps*. The Moroccan form has slightly less costae than the Rhenish form. Further studies are planned to elucidate the rhenorensselaerid phylogeny in Europe and North Africa.

Rhenorensselaeria macgerriglei Boucot, 1967 from the Lower Devonian Gaspé Sandstone Group (Quebec, Canada) resembles the congeneric Rhenish forms in the presence of fine costae, a shallow ventral muscle field, and thinner dental plates than in *C. crassicosta* (compare Boucot et al. 1967). It is very similar (?conspecific) to *Rh. demerathia*. On the other hand, regarding its subglobular outline, the form from Gaspé resembles *C. crassicosta*.

Jux (1981) attributed specimens of "*Rhenorensselaeria*" *crassicosta* to the North American genus *Globithyris* Cloud, 1942. He proposed a new species *Globithyris laticostata* that we consider as an ontogenetic stage of *Crassirensselaeria crassicosta*. In our opinion, *C. crassicosta* does not fit well in *Globithyris* as dental plates and hinge plates are much thicker than in the type species of *Globithyris*, *G. callida* (Clarke, 1907) from Gaspé (Quebec, Canada) and Maine (eastern United States) (Clarke 1907).

Palaeoecology

Specimens of *Crassirensselaeria* gen. nov. and *Rhenorensselaeria* are often found as internal moulds of articulated shells in fine-grained beds oriented perpendicular to the bedding surfaces with their anterior part oriented upwards (Fig. 5D, AEG 267-1; Fig. 7, AEG 146-5). We interpret this orientation as the life position of the animals which were presumably attached to small particles of the substrate (e.g., shell fragments) by rootlets or papillae at the distal end of the muscular pedicle. Some extant terebratulid brachiopods exhibit a similar life habit (*Chlidonophora* Dall, 1903; see Rudwick 1970; Richardson 1981). Our material shows that *Crassirensselaeria* lived in nests (Fig. 7, AEG 146-5). Figure 8 shows a possible reconstruction of the life habit of Late Siegenian *Crassirensselaeria* based on material collected during the construction of the ICE railway tunnel near Aegidienberg (Rheinisches Schiefergebirge). Probably posterior shell parts were even buried in the soft sediment so that the brachiopods lived semi-endobenthonically. The zig-zag commissure results in a longer commissure in comparison to an unfolded shell. With the same opening angle of the shell, the distance between the valve margins was reduced. For the feeding brachiopod, the narrowed commissure gap had the advan-

tage that coarse particles could not enter into the mantle cavity. Particles which could have obstructed the filter apparatus had to be kept outside (Rudwick 1964; Gourvennec 1989). In the turbid seawater of the siliciclastic Rhenish facies, this could have meant an important ecological advantage. On the other hand, during times of little turbidity the shell could be opened a little more. The brachiopod could benefit from the physiological advantage of a greater surface of exchanges, so that a greater amount of nutrient water could be filtered.

Crassirensselaeria and *Rhenorensselaeria* have never been found together in one and the same bed in life position. The reasons for this are not known. Probably they had slightly different ecological requirements as *Crassirensselaeria* more often occurs in restricted, monospecific brachiopod communities of the "Globithyrid facies" *sensu* Boucot (1963), whereas *Rhenorensselaeria* rather occurs in more open marine communities. However, the distance between their habitats was obviously not very far as there are many localities yielding taphocoenoses with moulds of both genera. Due to their ability to inhabit open-marine to restricted-marine, intertidal and deltaic environments probably even with reduced salinity (for discussion see Fürsich and Hurst 1980), representatives of *Crassirensselaeria* are excellent tools for correlation in sedimentary successions deposited at the land-sea transition of the southern siliciclastic shelf of the Old Red Continent.

Acknowledgements

We thank Andreas Braun (University of Bonn, Germany), Michael Amler (University of Marburg, Germany), and Martin Aberhan and Dieter Korn (Museum für Naturkunde, Berlin, Germany) who gave us access to fossil collections. Many thanks are also due to Michael Stemmer (Unkel, Germany) who showed us his private collection. We are grateful to Erika Scheller-Wagner (Senckenberg Research Institute, Frankfurt am Main, Germany), technical assistant, for preparing latex casts of the studied specimens. The final version of the manuscript has greatly benefited from the thorough reviews of Arthur J. Boucot (Oregon State University, Corvallis, USA), and Rémy Gourvennec (Université de Bretagne Occidentale, Brest, France).
This is a contribution to the IGCP 499 "*Devonian land-sea interaction: evolution of ecosystems and climate*—DEVEC".

References

Boucot, A.J. 1963. The Globithyrid Facies of the Lower Devonian. *Senckenbergiana lethaea* 44: 79–84.

Boucot, A.J. 1975. *Evolution and Extinction Rate Controls*. 427 pp. Elsevier, Amsterdam.

Boucot, A.J., Cumming, L.M., and Jaeger, H. 1967. Contributions to the age of the Gaspé Sandstone and Gaspé Limestone. *Geological Survey of Canada, Papers* 67 (25): i–v + 1–27.

Carls, P. and Valenzuela-Ríos, J.I. 1998. The ancestry of the Rhenish Middle Siegenian brachiopod fauna in the Iberian chains and its palaeozoogeography (Early Devonian). *Revista Española de Paleontología*, n° extr. Homenaje al Prof. Gonzalo Vidal: 123–142.

Clarke, J.M. 1907. Some new Devonian fossils. *New York State Museum, Bulletin, Geological Papers* 107: 153–291.

Cloud, J.M. 1942. Terebratulid Brachiopoda of the Silurian and the Devonian. *Geological Society of America, Special Papers* 38: 1–182.

Dahmer, G. 1934. Die Fauna der Seifener Schichten (Siegenstufe). *Abhandlungen der Preussischen Geologischen Landesanstalt, Neue Folge* 147: 1–91.

Dahmer, G. 1936a. Die Fauna der Siegener Schichten von Unkel (Bl. Königswinter). *Jahrbuch der Preußischen Geologischen Landesanstalt* 56 (for 1935): 633–671.

Dahmer, G. 1936b. Die Fauna der Obersten Siegener Schichten von der Unkelmühle bei Eitorf a. d. Sieg. *Abhandlungen der Preussischen Geologischen Landesanstalt, Neue Folge* 168: 1–36.

Dahmer, G. 1937. Die Fauna der Siegener Schichten im Ahrgebiet (Nordost-Eifel). *Jahrbuch der Preußischen Geologischen Landesanstalt* 57 (for 1936): 435–464.

Dall, W.H. 1903. Contributions to the Tertiary fauna of Florida. *Transactions of the Wagner Free Institute of Science* 3 (6): 1219–1620.

Evans, K.M. 1981. A marine fauna from the Dartmouth Beds (Lower Devonian) of Cornwall. *Geological Magazine* 118: 517–523.

Fuchs, A. 1904. Die unterdevonischen Rensselaerien des Rheingebietes. *Jahrbuch der Preußischen Geologischen Landesanstalt* 1904 (for 1903): 43–53.

Fuchs, G. 1982. Upper Siegenian and Lower Emsian in the Eifel Hills. *In*: W. Ziegler and R. Werner (eds.), On Devonian Stratigraphy and Palaeontology of the Ardenno-Rhenish Mountains and Related Devonian Matters. *Courier Forschungsinstitut Senckenberg* 55: 229–255.

Fürsich, F.T. and Hurst, J.M. 1980. Environmental factors determining the distribution of brachiopods. *Palaeontology* 17: 879–900.

Gourvennec, R. 1989. Brachiopodes Spiriferida du Dévonien inférieur du Massif Armoricain. Systématique, paléobiologie, évolution, biostratigraphie. *Biostratigraphie du Paléozoïque* 9: 1–281.

Hall, J. 1859. Palaeontology: Volume III. Containing descriptions and figures of the organic remains of the Lower Helderberg Group and the Oriskany Sandstone. Part 1: Texts. *Geological Survey of New York* 3 (1): 1–532.

Helmbrecht, W. and Wedekind, R. 1923. Versuch einer biostratigraphischen Gliederung der Siegener Schichten auf Grund von Rensselaerien und Spiriferen. *Glückauf* 41: 949–953.

ICZN 2000. Internationale Regeln für die Zoologische Nomenklatur. 4. Auflage; ausgearbeitet von Otto Kraus. Offizieller deutscher Text. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg, Neue Folge* 34: 1–232.

Jansen, U. 2001. Morphologie, Taxonomie und Phylogenie unter-devonischer Brachiopoden aus der Dra-Ebene (Marokko, Prä-Sahara) und dem Rheinischen Schiefergebirge (Deutschland). *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 554: 1–389.

Jentsch, S. and Röder, D. 1957. Zur Geologie des Taunusquarzits bei Bad Homburg. *Notizblatt des Hessischen Landesamtes für Bodenforschung* 85: 114–128.

Jux, U. 1981. Zur stratigraphischen Verbreitung bergischer Globithyridinen. *Sonderveröffentlichung des Geologischen Instituts der Universität Köln* 41: 93–107.

Kayser, E. 1881a. Beitrag zur Kenntniss des Taunusquarzits. *Jahrbuch der Königlichen Preußischen Geologischen Landesanstalt* 1881 (for 1880): 260–266.

Kayser, E. 1881b. Beitrag zur Kenntniss des Taunusquarzits. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1881: 386–387.

Kayser, E. 1883. Neue Beiträge zur Kenntniss der Fauna des rheinischen Taunusquarzits. *Jahrbuch der Königlichen Preußischen Geologischen Landesanstalt* 1883 (for 1882): 120–132.

Kegel, W. 1913. Der Taunusquarzit von Katzenelnbogen. *Abhandlungen der Preussischen Geologischen Landesanstalt* 76: 1–163.

King, W. 1850. Monograph of the Permian fossils of England. *Palaeontographical Society* 3: 1–253.

Kutscher, F. 1937. Taunusquarzit, Thorner Quarzite und Hunsrückschiefer des Hunsrücks und ihre stratigraphische Stellung. *Abhandlungen der Preussischen Geologischen Landesanstalt* 57(for 1936): 186–237.

Maillieux, E. 1931. La faune des Grès et Schistes de Solières (Siegénien

moyen). *Mémoires du Musée royal d'Histoire naturelle de Belgique* 51: 1–90.

Maillieux, E. 1940. Le Siegenien de l'Ardenne et ses faunes. *Bulletin du Mémoires du Musée royal d'Histoire naturelle de Belgique* 16 (5): 1–23.

Mittmeyer, H.-G. 1974. Zur Neufassung der Rheinischen Unterdevon-Stufen. *Mainzer geowissenschaftliche Mitteilungen* 3: 69–79.

Mittmeyer, H.-G. 1982a. *Erläuterungen Blatt 5508 Kempenich. Geologische Karte von Rheinland-Pfalz 1: 25000, Erläuterungen 5508 Kempenich*. 117 pp. Geological Survey Rheinland-Pfalz, Mainz.

Mittmeyer, H.-G. 1982b. Rhenish Lower Devonian biostratigraphy. *In*: W. Ziegler and R. Werner (eds.), On Devonian Stratigraphy and Palaeontology of the Ardenno-Rhenish Mountains and Related Devonian Matters. *Courier Forschungsinstitut Senckenberg* 55: 257–270.

Mittmeyer, H.-G. 1997. *Erläuterungen Blatt 5608 Virneburg. Geologische Karte von Rheinland-Pfalz 1: 25000, Erläuterungen 5608 Virneburg*. 156 pp. Geological Survey Rheinland-Pfalz, Mainz.

Quiring, H. 1923. Beiträge zur Geologie des Siegerlandes.—III. Über Leitfaunen in den Siegener Schichten der Umgebung von Siegen. *Jahrbuch der Preußischen Geologischen Landesanstalt* 43 (for 1922): 90–112.

Renaud, A. 1942. Le Dévonien du Synclinorium médian Brest-Laval. *Mémoirs de Societé géologique et Minéralogie de Bretagne* 7: 1–439.

Richardson, J.R. 1981. Brachiopods and pedicles. *Paleobiology* 7: 87–95.

Roemer, C.F. 1844. *Das Rheinische Uebergangsgebirge. Eine palaeontologisch-geognostische Darstellung*. 96 pp., Hahn'sche Hofbuchhandlung, Hannover.

Roemer, C.F. 1876. *Lethaea geognostica oder Beschreibung und Abbildung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. I. Teil. Lethaea palaeozoica Atlas*. 62 pls. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Rose, O. 1936. Versteinerungen im Taunusquarzit des Rheintaunus. *Jahrbuch des Nassauischen Vereins für Naturkunde* 83: 49–58.

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

Rudwick, M.J.S. 1970. *Living and Fossil Brachiopods*. 199 pp. Hutchinson University Library, London.

Schindler, T., Amler, M.R.W., Braun, A., Grimm, M.C., Haas, W., Heumann, G., Jansen, U., Otto, M., Poschmann, M., and Schindler, E. 2004. Neue Erkenntnisse zu Paläontologie, Biofazies und Stratigraphie der Unterdevon-Ablagerungen (Siegen) der ICE-Neubaustrecke bei Aegidienberg (Siegengebirge, W-Deutschland). *Decheniana* 157: 135–150.

Schlotheim, E.F. von 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert*. xii + 387 pp. Beckersche Buchhandlung, Gotha.

Simpson, S. 1940. Das Devon der Südost-Eifel zwischen Nette und Alf. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 447: 1–81.

Stehli, F.G. 1965. Paleozoic Terebratulida. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Part H, Brachiopoda*, 730–762, Geological Society of America and University of Kansans, Lawrence, Kansas.

Solle, G. 1950. Obere Siegener Schichten, Hunsrückschiefer, tiefstes Unterkoblenz und ihre Eingliederung ins Rheinische Unterdevon. *Geologisches Jahrbuch* 65: 299–380.

Thünker, M. 2001. *Erläuterungen Blatt 5114 Siegen. Geologische Karte von Nordrhein-Westfalen 1: 25000, Erläuterungen 5114 Siegen*. 171 pp. Geological Survey Nordrhein-Westfalen, Krefeld.

Waagen, W.H. 1883. Salt Range fossils, Part 4 (2) Brachiopoda. *Palaeontologica Indica, Geological Survey of India Memoirs* 13: 547–610.

Wilschowitz, J. 1931. Erster Bericht über eine neue Fundstätte unterdevonischer Fossilien im Ost-Urlich (Altvatergebirge). *Mitteilungen des naturwissenschaftlichen Vereins in Troppau* 23: 3–16.

Wilschowitz, J. 1932. Die Unterdevonfauna vom Alten Berg und Hofehau im Ost-Urlich (Altvatergebirge). *Mitteilungen des naturwissenschaftlichen Vereins in Troppau* 24–25: 7–50.