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New annulate Carboniferous orthoconic and cyrtoconic cephalopods of the family Brachycycloceratidae Furnish, Glenister & Hartman, 1962

Dieter KORN[1,*] & Martina AUBRECHTOVÁ[2]

[1]Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany.
[2]Institute of Geology, Czech Academy of Sciences, Rozvojová 269, Prague, 16500, Czech Republic.
[2]University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, Department of Geology, Ravila 14a, 50411 Tartu, Estonia.

[*]Corresponding author: dieter.korn@mfn.berlin
[2]Email: aubrechm@gmail.com

Abstract. The Carboniferous orthoconic or slightly cyrtoconic cephalopod family Brachycycloceratidae Furnish, Glenister & Hansman, 1962 is well described based on material from North America, whereas the Early Carboniferous European occurrences of this family are much less well-known. Almost all records from the Rhenish Mountains have been assigned to the single species *Brachycycloceras scalare* (d'Archiac & de Verneuil, 1842). This species is revised here and used as the type species of the genus *Rhenocycloceras* gen. nov. The new Early Carboniferous species *Rhenocycloceras conicum* sp. nov. and *R. denckmanni* sp. nov. from the Rhenish Mountains of Germany, *R. macdiarmadai* sp. nov. from Co. Leitrim in Ireland and *R. africanum* sp. nov. from the Anti-Atlas of Morocco are described. Additionally, two new Early Carboniferous species of *Caneycycloceras* Niko & Mapes, 2011 are described from the Rhenish Mountains; these are *C. rotersorum* sp. nov. and *C. fuerstenbergorum* sp. nov. The early Late Carboniferous species *B. koninckianum* (d'Orbigny, 1849) is discussed on the basis of material from the type locality in Belgium.

Keywords. Orthoceratoidea, Brachycycloceratidae, Carboniferous, Rhenish Mountains.

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Introduction

Straight (orthoconic) or slightly curved (cyrtoconic) orthoceratoid cephalopods with annulate shell surface are known from various periods of Earth's history; however, they are vastly outnumbered by non-annulate forms, both in terms of morphological and species diversity as well as specimen abundance. The state of research on the annulate forms varies considerably between these time intervals. Ordovician (Foerste 1928; Evans 1994; Kröger & Isakar 2006; Aubrechtová *et al.* 2025), Silurian (Foerste 1928;

Horný 1956; Cichowolski 2008; Manda & Turek 2015) and Devonian (Fuchs 1915) annulate orthoceratoids are well-known from multiple regions. Among the Carboniferous representatives, only those from North America have been thoroughly studied in monographic investigations (Miller *et al.* 1933; Miller & Owen 1934; Furnish *et al.* 1962; Niko & Mapes 2009). By contrast, the knowledge on annulate orthoceratoids from the Carboniferous of Europe has remained far more limited.

Carboniferous annulate orthoconic cephalopods were recognised in Europe at an early stage in the history of palaeontology, with several species described in the first half of the 19th century, but these were based on inadequately preserved material (Fleming 1815, 1828; von Meyer 1831; Phillips 1836; d'Archiac & de Verneuil 1842; de Koninck 1844; M'Coy 1844). These species have only been partially revised to date.

Early Carboniferous annulate orthoconic cephalopods have largely been assigned to two genera: *Cycloceras* M'Coy, 1844 and *Brachycycloceras* Miller, Dunbar & Condra, 1933. Of these, *Cycloceras* remains problematic, although its taxonomic issues can be considered resolved (Histon 1991; ICZN 1993). Only a single species of this genus is likely to be valid, namely the type species *Cycloceras laevigatum* M'Coy, 1844. In contrast to *Brachycycloceras*, it is characterised by an almost tubular conch with a very small expansion angle. It remains to be determined whether Late Carboniferous and Late Permian species, some of which have been assigned to *Cycloceras* (e.g., Demanet 1941; Shimansky 1965; Niko & Ehiro 2025), truly belong to this genus; thus far, only fragmentary material is known, which does not permit a definitive classification.

The genus *Brachycycloceras* was described on the basis of well-preserved material from North America. In addition to the Late Carboniferous type species *B. normale* Miller, Dunbar & Condra, 1933, several further species have been recognised. This material has enabled a detailed reconstruction of ontogenetic changes in conch shape and ornamentation. Furnish *et al.* (1962) formulated the hypothesis that species of *Brachycycloceras* possessed a deciduous conch, shedding a substantial portion of the phragmocone during the adult stage. However, supporting evidence for this has apparently not yet been found in material from other regions (Dzik 1984; Niko & Mapes 2009).

Stratigraphic aspects have thus far played only a minor role in distinguishing potential European species of the family Brachycycloceratidae. Possibly for this reason, along with the generally poor preservation of available material, almost all Early Carboniferous records from the Rhenish Mountains, as well as from other regions in Central and Eastern Europe, have been assigned to "*Brachycycloceras scalare* (d'Archiac & de Verneuil, 1842)" for over a century (e.g., Patteisky 1929; Demanet 1941; Schmidt 1956; Żakowa 1958, 1960; Dernov 2024). However, the study of better-preserved, albeit very rare, material now reveals that these specimens differ in several respects. Marked differences in both overall conch shape and ornamentation can be recognised, justifying the description of additional species that appear successively through the stratigraphic succession.

The rather broad morphological range of specimens previously described as *Brachycycloceras* raises not only the question of how many species are actually represented, but also whether all specimens can rightfully be assigned to this genus. Niko & Mapes (2011) already discussed this and introduced the genus *Caneycycloceras* Niko & Mapes, 2011. Here, several new species are added to the family Brachycycloceratidae, some of which are assigned to *Caneycycloceras* and the newly established genus *Rhenocycloceras* gen. nov.

Material and methods

The present study is based on a total of 58 specimens, the majority of which originate from localities in the Rhenish Mountains and the Harz Mountains (Germany) and are of late Viséan and early

Serpukhovian (Early Carboniferous) age (Fig. 1). Only a small proportion of the material is three-dimensionally preserved; most specimens are either compressed within shales or occur as fragmented remains in calciturbidites. Sections of three-dimensionally preserved specimens did not allow the study of the septal and siphuncular structures because of implosion of the phragmocone. Despite this, the shell ornament is commonly preserved and the proportions of the conchs could still be measured with a sufficient precision to clearly separate the below described taxa.

Morphological terminology

Morphological terms are used according to Flower (1964) and Teichert (1964) and as updated by Pohle *et al.* (2022).

The proportions of the conch cross section are expressed as the ratio between the conch width (cw) and the corresponding conch height (ch). The opening angle of the conch is described as the expansion angle.

The shell ornament terminology was described using the terms of Klug *et al.* (2015) and Pohle *et al.* (2022). The following ornament elements are present in the herein studied material:

Growth lines – finest type of transverse ornament, formed by discontinuous shell secretion at the aperture (Klug *et al.* 2015).

Lirae – transverse raised growth lines with transverse profile either symmetric or asymmetric, may be narrowly undulated (frilled).

Annuli – coarse transverse ornament elements, which are present around the entire circumference of the conch and are also visible on the internal mould.

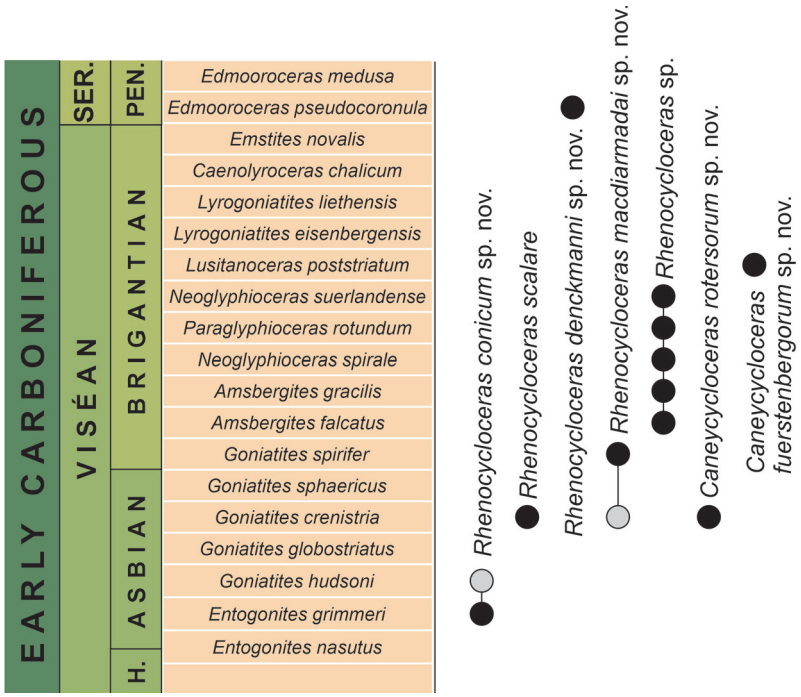

Fig. 1. The Late Viséan ammonoid stratigraphy (with substages of the British regional subdivision) in the Rhenish Mountains and the occurrence of species of the Brachycycloceratidae. H. = Holkerian; SER. = Serpukhovian; PEN. = Pendleian.

The spacing of annuli is expressed as the ratio between the distance of two consecutive annuli crests divided by the corresponding conch diameter.

Repository

The present study is based on specimens from palaeontological collections kept at the following institutions:

MB.C.	=	Museum für Naturkunde, Berlin
BGRB	=	Bundesanstalt für Geowissenschaften und Rohstoffe (BGR), Berlin
Wiesbaden	=	Museum Wiesbaden, Naturhistorische Sammlungen

Results

Class Cephalopoda Cuvier, 1795
Subclass Orthoceratoidea Teichert, 1967

Remarks

Here, we do not use the term "nautiloid" or the subclass Nautiloidea Agassiz, 1847 for the herein studied cephalopods. The latter taxon, as per the current knowledge, should only be used for the order Nautilida Agassiz, 1847 including the extant genera *Nautilus* and *Allonautilus* (Pohle *et al.* 2022).

The authorship of the name Orthoceratoidea remains uncertain with several possible authors (e.g., M'Coy 1844; Kuhn 1940; Teichert 1967). As resolving this complex issue falls outside the scope of the present study, we follow the recent works of King & Evans (2019), Pohle *et al.* (2022) and Turek & Aubrechtová (2024) and consider Teichert (1967) as the author of the subclass.

Among the Orthoceratoidea, annulate orthoconic or cyrtoconic taxa are known especially from the orders Orthoceratida and Pseudorthoceratida (e.g., Kröger & Isakar 2006; Manda & Turek 2015) and also the Lituitida (e.g., Aubrechtová & Korn 2022). The family Brachycycloceratidae is herein regarded as belonging to the order Orthoceratida (see below).

Order Orthoceratida Kuhn, 1940
Family Brachycycloceratidae Furnish, Glenister & Hansman, 1962

Diagnosis

Family of the order Orthoceratida with orthoconic or slightly cyrtoconic and exogastric conchs, usually narrowly conical in juvenile (annulate stage) and breviconic in the adult (non-annulate) growth stage. In some species, during the transition between these ontogenetic stages, a sharply curved and thickened septum (the septum of truncation) forms, along which the initial part of the shell breaks off and is discarded. Sculpture with transverse annuli, which disappear in the adult growth stage. The siphuncle is located between the centre and the ventral side of the conch; endosiphuncular deposits are absent.

Included genera

Brachycycloceras Miller, Dunbar & Condra, 1933.
Caneycycloceras Niko & Mapes, 2011.
Rhenocycloceras gen. nov.

Remarks

The representatives of the family Brachycycloceratidae are characterised by a unique combination of features among orthoconic or slightly cyrtoconic cephalopods, primarily due to their two distinct ontogenetic conch stages: a markedly annulate juvenile conch and a non-annulate, often almost smooth adult conch. The transition from the juvenile conch to the adult conch can, in terms of the general conch form, be either continuous, as in *Rhenocycloceras*, or discontinuous, involving a marked increase in the expansion angle, as seen in *Brachycycloceras* and *Caneycycloceras*.

Furnish *et al.* (1962) noted morphological similarities between *Brachycycloceras* and early Palaeozoic ascoceratids, particularly the abrupt change in conch shape between the juvenile and adult stages and the shedding of part of the phragmocone. Pronounced ontogenetic changes, such as the disappearance of annuli, sudden conch inflation and the presence of internal structures like a septum of truncation and a siphuncular displacement canal, have been cited in support of their hypothesis that the annulate conchs represent deciduous apical portions of large, smooth, breviconic nautiloids, analogous to ascoceratids.

However, Dzik (1984: 124) criticised this interpretation, stating: "I believe that the evidence presented by Furnish, Glenister and Hansman does not substantiate their interpretation. The observed preservation and internal structure of the shell do not significantly differ from those recorded in other nautiloids." Similarly, Niko & Mapes (2009) found no evidence of specialised structures for conch truncation in the Late Carboniferous *Brachycycloceras normale* Miller, Dunbar & Condra, 1933. In stratigraphically older European species of the family Brachycycloceratidae, no indications of a deciduous growth habit have so far been identified.

Taxonomically, the family Brachycycloceratidae is tentatively assigned to the order Orthoceratida, following the classification proposed by Sweet (1964). The relationship between *Cycloceras* and *Brachycycloceras* has been discussed on several occasions. Shimansky (1968) accepted both genera, but placed them in separate families. In contrast, Dzik (1984: 130) synonymised the two families. However, Niko & Mapes (2009: 340) rejected the proposed synonymy of the Brachycycloceratidae with the Cycloceratidae Hyatt, 1900, as suggested by Dzik: "The resemblance between *Brachycycloceras* and annulate orthocerids, such as *Cycloceras* M'Coy, 1844, *Dawsonoceras* Hyatt, 1884, and *Reticycloceras* Gordon, 1960, is no more than superficial. Therefore, the view expressed by Dzik (1984) that the 'Cycloceratidae' of Hyatt in Zittel (1900) includes the Brachycycloceratidae as a subjective synonym is not credible."

Another intriguing hypothesis, also put forward by Dzik (1984: 124, 130), concerns the classification of the families Scyphoceratidae Ruzhencev & Shimansky, 1954, Dentoceratidae Ruzhencev & Shimansky, 1954 and Neptunoceratidae Shimansky, 1956 within the family Cycloceratidae Hyatt, 1900. It is indeed possible that *Scyphoceras* Ruzhencev & Shimansky, 1954 and *Dentoceras* Ruzhencev & Shimansky, 1954 represent juvenile and adult conchs of the same forms, respectively, and that they derive from *Brachycycloceras*, having evolved a more distinctly curved and rapidly expanding juvenile stage.

Three genera within the Brachycycloceratidae are recognised here. In addition to the type genus *Brachycycloceras* and the subsequently established *Caneycycloceras*, the new genus *Rhenocycloceras* gen. nov. is introduced, which is probably a phylogenetic ancestor of *Brachycycloceras* and *Caneycycloceras*. The three genera may be briefly characterised as follows:

Rhenocycloceras – ancestral forms with an orthoconic conch with a stable expansion rate. A marked change in conch shape at the transition from the annulate to the non-annulate stage is not evident. Annuli are typically straight or slightly sinuous.

Caneycycloceras – derived forms with a slightly cyrtoconic conch and an accelerated expansion rate. A distinct change in conch shape at the juvenile–adult transition is expressed as a swelling of the adult conch. Annuli are usually weakly undulating, with low projections and shallow sinuses.

Brachycycloceras – derived forms with an orthoconic or weakly cyrtoconic conch and an accelerated expansion rate. The juvenile conch may have been deciduous. Annuli are typically weakly undulating, with low projections and shallow sinuses.

The incomplete knowledge of ontogeny, particularly the transition from the juvenile to the adult conch in many species, precludes definitive assignment to one of the three genera distinguished here. The species lists should therefore be regarded with caution. The general shape of the conch and the course of the annuli were used as the primary criteria for classification.

Species of the family Brachycycloceratidae from different regions show significant variation in their temporal distribution. Almost all known American species are from the Late Carboniferous, whereas nearly all European occurrences are restricted to the Early Carboniferous. The different ages of the American and European taxa may reflect a morphological evolution, resulting in a more pronounced distinction between juvenile and adult conch stages in the younger forms. In some European species, no sharp boundary between these stages can be recognised; instead, the annuli fade out gradually in a continuous transition.

Since the late 19th century, almost all European specimens of the Brachycycloceratidae have been assigned to the single species "*Brachycycloceras scalare* (d'Archiac & de Verneuil, 1842)". These records span a long stratigraphic interval, ranging from the Tournaisian–Viséan boundary to the Viséan–Serpukhovian boundary (Schmidt 1956: 48). It needs to be investigated whether this material shows a greater diversity, and whether a stratigraphic succession of individual species can be established across the various sedimentary basins.

Various character complexes are available for distinguishing species within the family Brachycycloceratidae: (1) general conch shape – the conch may be either straight or slightly curved; in European assemblages, straight forms are predominant; (2) expansion angle of the conch – both acute-conical and blunt-conical forms are present, with apertural expansion angles generally ranging between 10° and 25°; (3) development of annuli – the spacing of the annuli can be expressed as the ratio of their distance to the conch diameter; it should be noted, however, that this ratio may be distorted in specimens that are flattened in shales; (4) course of the annuli – in stratigraphically older species, the annuli tend to be straight, whereas in younger forms they are typically slightly undulating; (5) formation of growth lines – growth lines may range from very fine to relatively coarse, and their expression can be either uniform or variable in intensity between annuli and the intervening areas; and (6) transition from the annulate to the non-annulate (adult) stage – this transition may be either continuous or abrupt.

Genus ***Rhenocycloceras*** gen. nov.

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Type species

Orthoceratites scalaris d'Archiac & de Verneuil, 1842.

Diagnosis

Genus of the family Brachycycloceratidae with a usually slowly expanding orthoconic conch. Annulate juvenile conch with circular or elliptic cross section; transition to the non-annulate adult conch continuous without accelerated apertural expansion angle. Juvenile conch strongly annulate, shell surface with fine growth lines; adult conch weakly annulate or non-annulate.

Etymology

Combination of the occurrence of most of the species in the Rhenish Mountains and the genus name *Cycloceras*.

Species included

North America (Meek & Worthen 1862; Worthen 1882; Elias 1958): *Orthoceras Randolphensis* Worthen, 1882; *Cycloceras meeki* Elias, 1958.

Central Europe (d'Archiac & de Verneuil 1842; Roemer 1852; de Koninck 1880; this paper): *Orthoceratites scalaris* d'Archiac & de Verneuil, 1842; *Orthoceras annulare* Roemer, 1852 [synonym of *R. scalare*]; *Orthoceras annuloso-lineatum* de Koninck, 1880 [synonym of *R. scalare*]; *Rhenocycloceras conicum* gen. et sp. nov.; *Rhenocycloceras denckmanni* gen. et sp. nov.

British Isles (Fleming 1815; this paper): *Orthocera undata* Fleming, 1815; *Rhenocycloceras macdiarmadai* gen. et sp. nov.

Anti-Atlas (this paper): *Rhenocycloceras africanum* gen. et sp. nov.

South Urals (Shimansky 1968): *Brachycycloceras mirabile* Shimansky, 1968.

Kyrgyzstan (Shimansky 1968): *Brachycycloceras subquadratum* Shimansky, 1968.

Remarks

Rhenocycloceras gen. nov. is a genus characterised by an annulate, conical juvenile conch and a non-annulate adult conch. It probably possesses a subcentrally positioned siphuncle and displays distinctive ornamentation in the juvenile stage, with sharp annuli and fine growth lines.

Another Carboniferous genus characterised by pronounced annuli is *Cycloceras* M'Coy, 1844, whose type species is *Cycloceras laevigatum* M'Coy, 1844 (Histon 1991; ICZN 1993). This species was described and illustrated in detail by de Koninck (1880: 70, pl. 41 fig. 4) and Foord (1897: 14, pl. 5 fig. 1). It is characterised by a straight or very slightly curved, strongly annulate conch with a very small expansion angle, only about 2°, and a centrally positioned siphuncle. The annuli are equal in width to their interspaces. In these features, *Cycloceras laevigatum* differs markedly from *Rhenocycloceras* gen. nov.

The new genus also differs from *Brachycycloceras* in several respects. The conch in *Rhenocycloceras* gen. nov. is straight and maintains a consistent expansion angle throughout ontogeny, typically ranging between 12° and 20° (an exception is *R. conicum* gen. et sp. nov., which exhibits a significantly larger expansion angle). The transition from the juvenile to the adult stage is marked by a more gradual weakening of the annuli and the disappearance of the initially clearly recognisable growth lines.

By contrast, species of *Brachycycloceras* almost invariably have a slightly cyrtoconic juvenile conch, with the expansion angle increasing during ontogeny, or at least at the transition from the juvenile to the adult stage. The adult stage is marked by an abrupt disappearance of annuli and a noticeable inflation of the conch compared to the juvenile stage.

Rhenocycloceras may be regarded as a potential ancestor of *Brachycycloceras*. Its orthoconic, continuously expanding conch can be interpreted as a ancestral feature, while the sudden weakening and disappearance of the annuli at the onset of the adult stage may represent a derived character.

Rhenocycloceras differs from *Caneycycloceras* primarily in having a straight conch, whereas the conch of *Caneycycloceras* is slightly cyrtoconic. Another distinguishing feature may be the accelerated expansion angle seen in *Caneycycloceras*, which is not seen in *Rhenocycloceras*.

It is not clear whether the Early Carboniferous species from North America (Meek & Worthen 1862; Girty 1909; Elias 1958), which were described among others as species of *Cycloceras*, should be placed in *Rhenocycloceras*. A definitive assignment cannot be made on the basis of the descriptions and illustrations.

Rhenocycloceras scalare (d'Archiac & de Verneuil, 1842) gen. et comb. nov.
Figs 2–5

Orthoceratites scalaris d'Archiac & de Verneuil, 1842: 345.
Orthoceras annulare Roemer, 1852: 92, pl. 13 fig. 35.
Orthoceras annuloso-lineatum de Koninck, 1880: 71, pl. 41 figs 1–3.

Orthoceratites striolatus – von Meyer 1831: 77, pl. 55 figs 1–2.
Orthoceras scalare – Sandberger & Sandberger 1850–1856: 167, pl. 19 fig. 5a. — Schmidt 1929: 57, pl. 14 fig. 3.
? *Orthoceras scalare* – Sarres 1857: 28. — Roemer 1870: 55, pl. 6 fig. 5; 1876: pl. 38 fig. 6. — von Koenen 1879: 317. — Holzapfel 1889: 45, pl. 1 fig. 4. — Sommer 1910: 643, pl. 28 fig. 11. — Hüffner 1914: 471, pl. 21 figs 4–5. — Patteisky 1929: 238, pl. 16 figs 15–16.
Brachycycloceras scalare – Schmidt 1956: 47.
? *Brachycycloceras scalare* – Żakowa 1958: 115, pl. 8 fig. 13. — Żakowa 1960: pl. 1 fig. 5. — Bednarczyk *et al.* 1968: pl. 2 fig. 5. — Dernov 2021: text-figs 2.3–2.4. — Dernov 2024: 7, text-fig. 5c–e, g.

non *Orthoceratites striolatus* – von Meyer 1831: 77, pl. 56 figs 3–13.
non *Orthoceras scalare* – Nebe 1911: 461, pl. 16 fig. 13.
non *Brachycycloceras scalare* – Demanet 1941: 110, text-figs 30–31, pl. 4 figs 1–2.
non *Orthoceras scalare* – Gunia & Górecka 1960: 323, pl. 37 fig. 30.

Diagnosis

Species of the genus *Rhenocycloceras* with an orthoconic conch that has an expansion angle of 12°–18°; conch cross section probably circular. Annuli extending with a linear course, standing in distances of 0.12–0.20 of the conch diameter at the end of the annulate stage. Growth lines fine with linear course; standing in equal distances over annuli and their interspaces; they disappear in the non-annulate stage. Narrow septal spacing.

Type material

Neotype (designated by Schmidt 1956: 48)
GERMANY – **Rhenish Mountains** • Herborn; "Posidonomyenschiefer" (*Goniatites crenistria* Zone, Late Viséan); Sandberger Coll.; illustrated by Sandberger & Sandberger (1850–1856: pl. 19 fig. 5, upper part), re-illustrated here in Fig. 3B; Wiesbaden 97a.

Other material examined

GERMANY – **Rhenish Mountains** • 1 specimen; Herborn; "Posidonomyenschiefer" (*Goniatites crenistria* Zone, Late Viséan); Sandberger Coll.; illustrated by Sandberger & Sandberger (1850–1856: pl. 19 fig. 5, lower part), re-illustrated here in Fig. 3C; Wiesbaden 97b • 1 specimen; Herborn;

"Posidonomyenschiefer" (*Goniatites crenistria* Zone, Late Viséan); Sandberger Coll.; illustrated by Sandberger & Sandberger (1850–1856: pl. 19 fig. 5a), re-illustrated here in Fig. 3E; Wiesbaden 97c • 1 specimen; Herborn; "Posidonienschiefer" (*Goniatites crenistria* Zone, Late Viséan); illustrated in Fig. 4; BGRB X13483 • 1 specimen; Herborn; "Posidonienschiefer" (*Goniatites crenistria* Zone, Late Viséan); illustrated in Fig. 5A; BGRB X13484 • 1 specimen; Herborn; "Posidonienschiefer" (*Goniatites crenistria* Zone, Late Viséan); 1911; Paeckelmann leg.; BGRB X13485 • 2 specimens; Herborn; "Posidonienschiefer" (*Goniatites crenistria* Zone, Late Viséan); BGRB X13486–BGRB X13487 • 2 specimens; Deisfeld; "Culmtonschiefer" (Late Viséan); 1928; Paeckelmann leg.; BGRB X13488– BGRB X13489. – **Harz Mountains** • 1 specimen; Lautenthal; "Posidonienschiefer" (Late Viséan); BGRB X13490 • 1 specimen; Hahnenklee, Gr. Hühnertalskopf; "Posidonienschiefer" (Late Viséan); illustrated in Fig. 5B; BGRB X13491 • 1 specimen; Hahnenklee, Gr. Hühnertalskopf; "Posidonienschiefer" (Late Viséan); BGRB X13492 • 1 specimen; Bad Grund, Winterberg quarry; Late Viséan; 2013; Knappe leg.; illustrated in Fig. 5C; MB.C.32339.

Description

In the Wiesbaden Museum, three fragments are preserved under the catalogue number 97, which were illustrated by Sandberger & Sandberger (1850–1856: pl. 15 fig. 5). All specimens are more or less

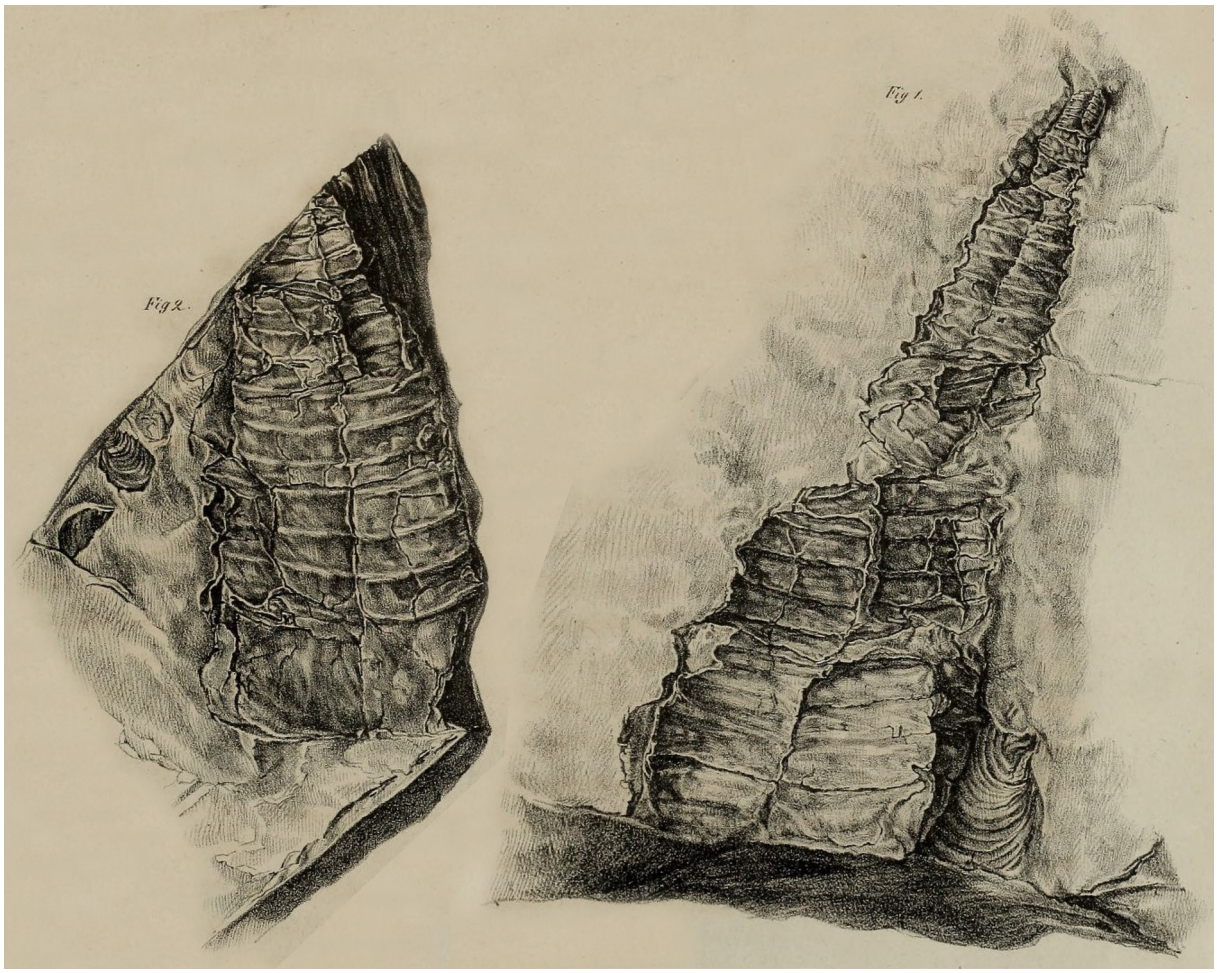

Fig. 2. *Rhenocycloceras scalare* (d'Archiac & de Verneuil, 1842) gen. et comb. nov., both from Herborn. Reproduction (re-arranged) of the illustration by von Meyer (1831: pl. 55); probably the first illustration of the species.

strongly deformed, and two of them were combined to produce the original figure (Fig. 3A). Of these, the fragment of the larger specimen, designated by Schmidt (1956: 48) as the neotype (Fig. 3B), reaches approximately 36 mm in length, with a conch diameter of about 34 mm. The expansion angle cannot be precisely determined but was likely around 12°. The specimen is an internal mould lacking shell material and displays five annuli, arranged at slightly irregular intervals ranging from 5 to 6.5 mm. The final annulus is positioned at a conch diameter of approximately 31 mm. Over the terminal 11 mm of the conch, annuli are absent; this portion likely represents the adult body chamber. The annuli fade out gradually, without any abrupt morphological transition.

The second fragment, which is significantly more compressed, is an internal mould with a conch diameter of 24.5 mm (Fig. 3C). Aside from its fairly regularly spaced annuli, it displays few specific characteristics.

The third specimen of "*Orthoceras scalare*" from the Sandberger Collection is a hollow cast of a crushed fragment measuring 70 mm in length and 38 mm in diameter (Fig. 3E). This specimen served as the basis for the enlarged illustration of the ornament by Sandberger & Sandberger (1850–1856: pl. 15 fig. 5a). The expansion angle cannot be determined from the preserved portion. Ten prominent annuli are present, each approximately 40% the width of their interspaces. The final annulus occurs at a conch diameter of nearly 40 mm. Both the interspaces and annuli are ornamented with very fine, evenly developed growth lines.

BGRB X13483, although strongly flattened, is the best-preserved specimen available for this study (Fig. 4). It is preserved as a deformed internal mould with its corresponding counterpart showing the shell ornamentation. The preserved length of the specimen is 162 mm. Over this distance, the conch diameter increases steadily from 5 mm to 48 mm, corresponding to an expansion angle of 17°. The specimen displays regular annuli over a length of 95 mm, up to a conch diameter of 34 mm. These annuli are arranged at ontogenetically decreasing intervals, at least relative to conch diameter, with a distance/diameter ratio of 0.22 at 8 mm and 0.19 at 34 mm. At 34 mm diameter, the spacing between the final two regularly developed annuli is 4.9 mm. This is followed, after a non-annulate part 12.5 mm in length, by one final annulus that is markedly broader and lower than the preceding ones. The shell surface bears fine growth lines, mostly spaced at intervals of approximately 0.12–0.16 mm in the region of the final annuli. The spacing of the growth lines is roughly equal on both the annuli and the interspaces. In the zone between the last regular annulus and the final low annulus, the growth lines are very evenly spaced at 0.18 mm. On the final annulus, the growth lines are extremely fine and barely discernible. Beyond this annulus, no growth lines are visible; the shell surface appears smooth.

BGRB X13484 is also compressed in shale and preserved only as an internal mould. It is a fragment with a preserved length of 122 mm (Fig. 5A). Over this distance, the conch diameter increases steadily from 16 mm to 48 mm, yielding an expansion angle of 14°. Almost the entire specimen bears annuli; the distance/diameter ratio decreases from 0.20 at 18 mm to 0.15 at 48 mm. The final regular annulus lies 6 mm from the preceding one. This is followed, after a 12 mm gap, by a final annulus that is significantly broader and flatter than those preceding it. Other shell ornamentation is not preserved.

Specimen BGRB X13491 is likewise a fragment of a counterpart with exceptionally well-preserved ornamentation (Fig. 5B). The spacing of the fine growth lines is approximately 0.15 mm.

Remarks

von Meyer (1831: 77, pls 55–56) described and illustrated various orthoconic cephalopods found by Cramer (1827) near Herborn as "*Orthoceratites striolatus*" (Fig. 2). However, the two specimens depicted on his plate 55 were later reassigned to "*Orthoceras scalare* (d'Archiac & de Verneuil, 1842)" by Sandberger & Sandberger (1850–1856: 167). These specimens are strongly crushed and, aside from

conch shape and sculpture characteristic of *Brachycycloceras*, reveal only a few diagnostic features. Both exhibit expansion angles of approximately 12°.

d'Archiac & de Verneuil (1842: 345) provided a very brief description, without illustration, of a specimen from the Goldfuß Collection in Bonn: "*Orthoceratites scalaris* Goldf., Bonn Museum. This shell, of which we possess only an impression, and which we have seen in the same condition in the Museum of Bonn, is very conoidal and short. Its diameter increases rapidly. It is ornamented with horizontal transverse rings of which the breadth is equal to half the smooth space which separates them. Herbom in the *Posidonia* slates; rare." The specimen does not appear to have been preserved.

Sandberger & Sandberger (1850–1856: 165) explicitly restricted "*Orthoceras striolatum* von Meyer, 1831" to the specimens illustrated by von Meyer (1831) on plate 56, while assigning the two specimens shown on plate 55 to "*Orthoceras scalare*". Sandberger & Sandberger (1850–1856: pl. 19 fig. 5) described and illustrated a rather large, crushed specimen of "*Orthoceras scalare*" from Herborn: "Röhre mittelmässig lang, kegelförmig, mit dicken, gerundeten Querringeln. Schale mit sehr feinen Querlinien überdeckt, welche gleichmässig auf den gerundeten Ringeln der Röhre und auf den breiteren Zwischenflächen derselben erscheinen. Auf dem glatten Steinkerne sind die Ringel schärfer und gekielt, die Zwischenflächen bilden daselbst flache Hohlkehlen. Kammern niedrig-, ihre obere und untere Abgrenzungslinien fallen in die Mitte je zweier auf einander folgenden Hohlkehlen, sodass jede Kammer in der Mitte ihrer Höhe einen der Ringel trägt." ["Tube moderately long, conical, with thick, rounded

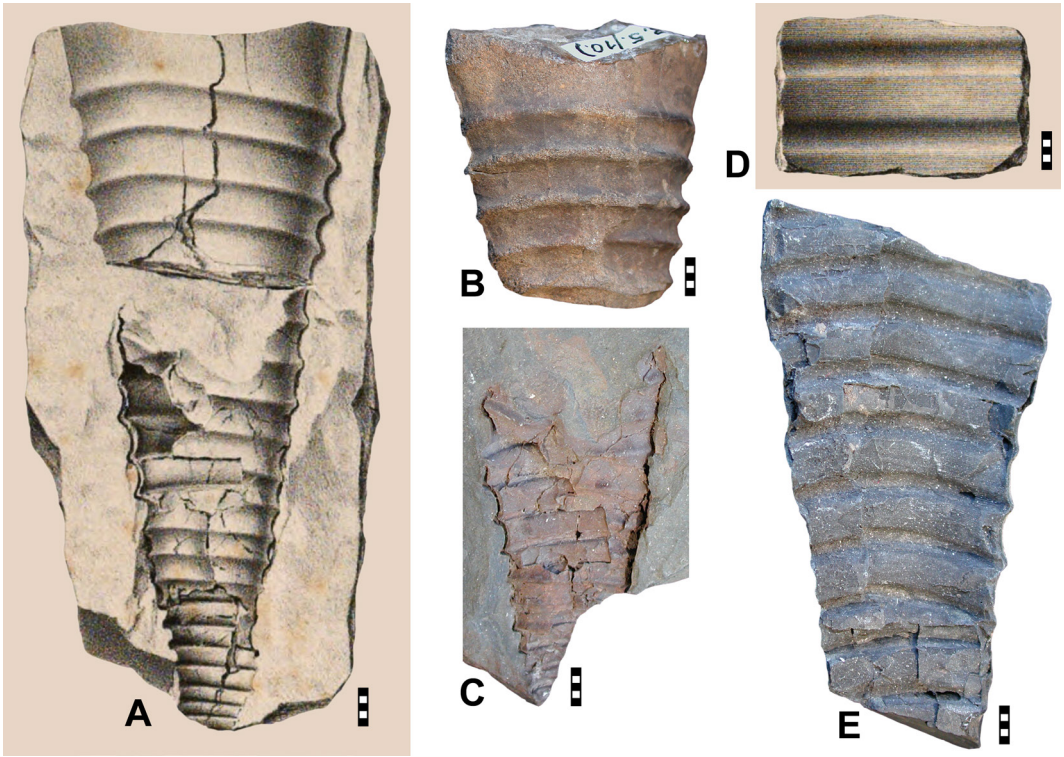

Fig. 3. *Rhenocycloceras scalare* (d'Archiac & de Verneuil, 1842) gen. et comb. nov., all from Herborn. **A**. Reproduction of the illustration by Sandberger & Sandberger (1850–1856: pl. 19 fig. 6), composed of specimens Wiesbaden 97a and 97b. **B**. Neotype Wiesbaden 97a (Sandberger Coll.). **C**. Specimen Wiesbaden 97b (Sandberger Coll.). **D**. Reproduction of the illustration by Sandberger & Sandberger (1850–1856: pl. 19 fig. 6a), specimen Wiesbaden 97c, ornament detail. **E**. Specimen Wiesbaden 97c (Sandberger Coll.). Scale bar units: 1 mm.

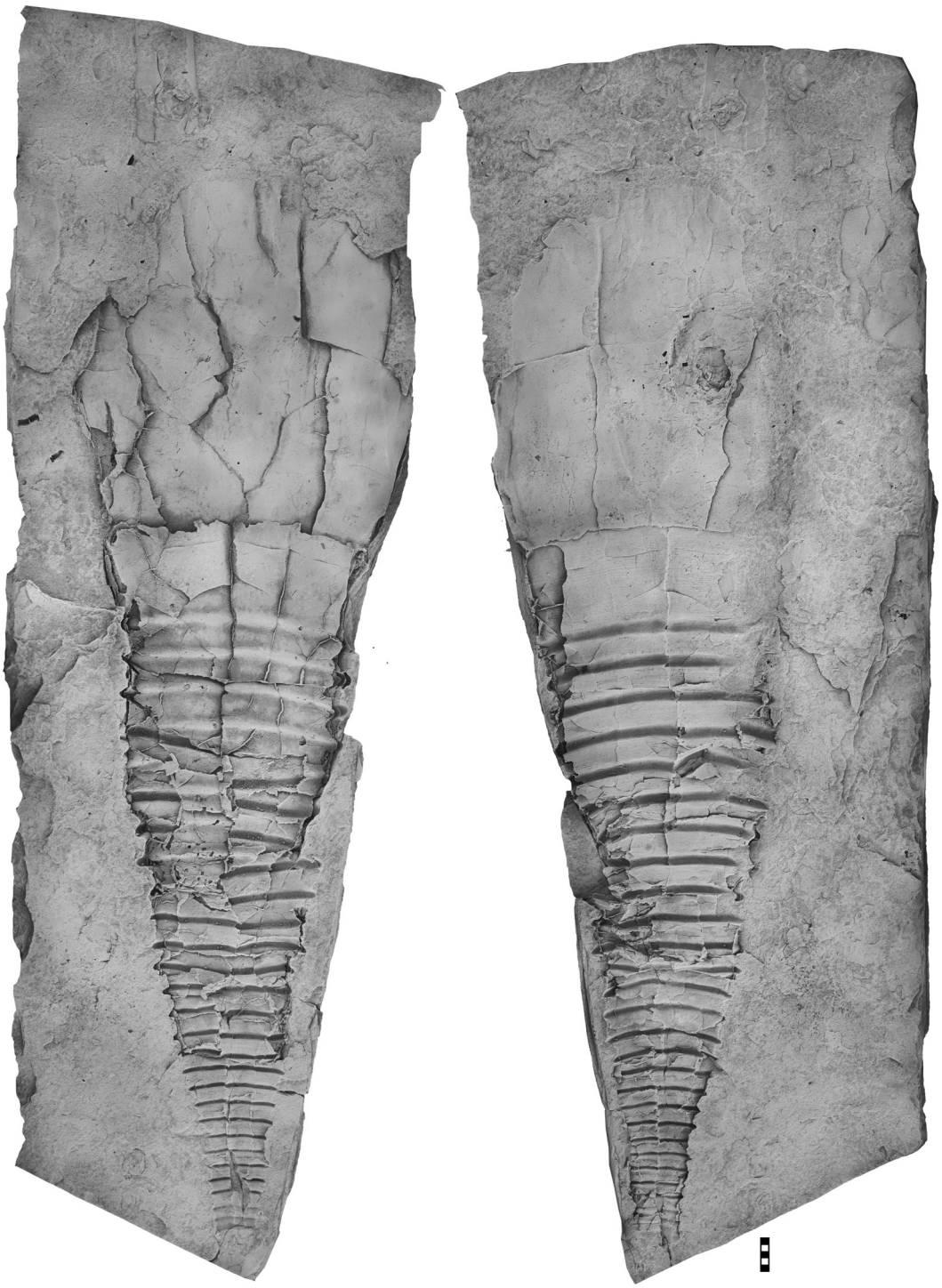

Fig. 4. *Rhenocycloceras scalare* (d'Archiac & de Verneuil, 1842) gen. et comb. nov., specimen BGRB X13483 from Herborn. Scale bar units: 1 mm.

transverse rings. Shell covered with very fine transverse lines, which appear uniformly on the rounded rings of the tube and on the broader intermediate surfaces of the same. On the smooth internal mould, the rings are sharper and keeled, while the intermediate surfaces form shallow grooves. Chambers low; their upper and lower boundary lines fall in the middle of every two successive grooves, so that each chamber carries one of the rings at its mid-height."]

As the original material described by von Meyer (1831) is probably lost, one the illustrated specimens by Sandberger & Sandberger (1850–1856) was designated as the neotype by Schmidt (1956: 48). Given its provenance from Herborn, it can be assumed to originate from the *Posidonia* beds of the late Asbian (in terms of the regional British stage classification), probably corresponding to the *Goniatites crenistria* Zone of the early Late Viséan.

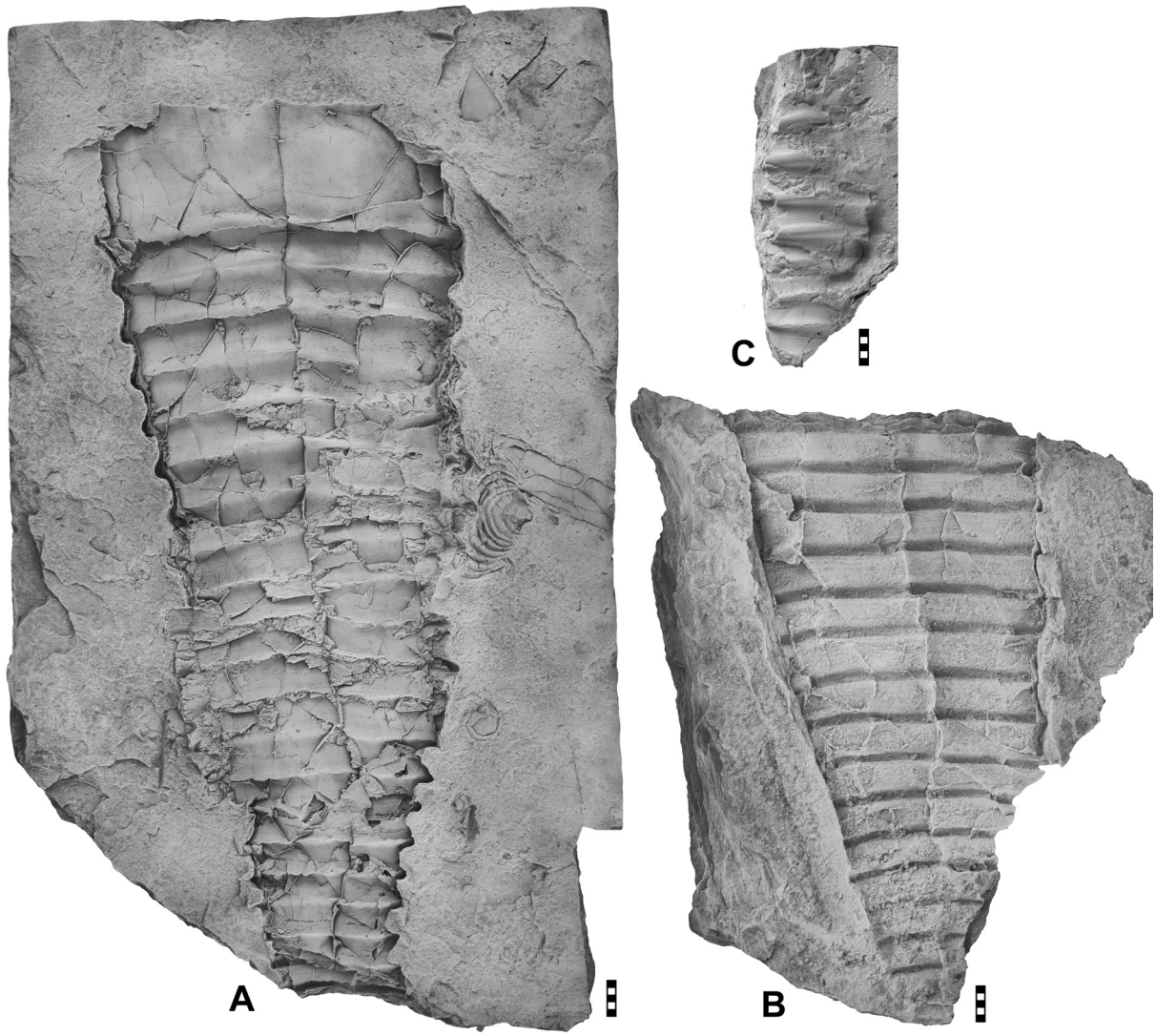

Fig. 5. *Rhenocycloceras scalare* (d'Archiac & de Verneuil, 1842) gen. et comb. nov. **A**. Specimen BGRB X13484 from Herborn. **B**. Specimen BGRB X13491 from Hahnenklee (Gr. Hühnertalskopf). **C**. Specimen MB.C.32339 (Knappe 2013 Coll.) from Bad Grund, Winterberg quarry. Scale bar units: 1 mm.

de Koninck (1880: 71, pl. 41 figs 1–3) described and illustrated three fragments of his new species "*Orthoceras annuloso-lineatum*", of which the largest differs from the other two by the presence of undulating annuli. When the two smaller specimens with straight annuli are considered together, they reconstruct a nearly complete conch form with an estimated length of approximately 180 mm and a maximum diameter of 40 mm. Their expansion angle is about 15°. Both specimens exhibit rounded annuli that occupy roughly one-third of the width of the interspaces. The annuli and the intervening areas are ornamented with fine growth lines, with approximately four per millimetre. The phragmocone chamber length corresponds closely to the spacing of the annuli. These specimens originate from Visé and are therefore presumably of early Late Viséan age.

Schmidt (1956: 47) provided a very detailed description of the extensive material he examined, around 50 specimens, although he did not include illustrations. His account encompasses material from markedly different stratigraphic levels and showing considerable morphological variability. He offered the following diagnosis: "Spitzenwinkel etwa über 10°, Gesamtlänge bis 200 mm bei 40 mm größtem Durchmesser. – Das auffallendste Merkmal sind gut abgesetzte Querrippen, 3 bis 5 auf jede einem Durchmesser entsprechende Länge. Zahlreiche scharfe Anwachsstreifen laufen nahezu parallel zu diesen Rippen; sie liegen in wechselnder Zahl auf den Rippen, zwischen den Rippen und in den steilen Übergängen. – Wenn der Durchmesser 25 bis 40 mm erreicht, können die Rippen aufhören." ["Apex angle slightly over 10°, total length up to 200 mm with a maximum diameter of 40 mm. – The most striking feature is the well-defined transverse ribs, 3 to 5 per unit length corresponding to the diameter. Numerous sharp growth lines run almost parallel to these ribs; they occur in varying numbers on the ribs, between them, and in the steep transitions. – When the diameter reaches 25 to 40 mm, the ribs may disappear."]

Schmidt (1956: 48) briefly addressed the variability of the material he had examined, noting differences in both the spacing of the annuli and the expansion angle of the conch, which in some cases reached up to 45°. He attributed the unusually high expansion angles to post-depositional deformation of the specimens in shales. Schmidt considered the stratigraphically youngest specimen, which displays sinuous annuli, a possible new species representing a transitional form between *Brachycycloceras scalare* and *B. koninckianum*. This specimen is newly described herein as *R. denckmanni* gen. et sp. nov.

A redefinition of *Rhenocycloceras scalare* is necessary in order to clearly distinguish it from other species of the genus. At present, this is problematic, as the available material consists almost exclusively of specimens flattened in shale. It is therefore essential to obtain topotypical material in a better state of preservation to accurately determine the full morphological range of the species.

Stratigraphic occurrence

Rhenocycloceras scalare gen. et comb. nov. may have had only a very short temporal range within the late Viséan. The species is particularly common in the *Goniatites crenistria* Zone near Herborn; some of the listed specimens from other localities probably also come from this zone.

Rhenocycloceras conicum gen. et sp. nov.

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Fig. 6

Diagnosis

Species of the genus *Rhenocycloceras* gen. et sp. nov. with an orthoconic conch that has an expansion angle of ca 35°; cross section probably circular. Annuli extending with a linear course, standing in distances of ca 0.20 of the conch diameter at the end of the annulate stage. Growth lines fine with linear course; standing in equal distances on annuli and interspaces. Narrow septal spacing.

Etymology

From the Lat. '*conicum*' (adj., neut.) meaning 'cone-shaped', referring to the conch form.

Type material

Holotype

GERMANY – **Rhenish Mountains** • Oese near Menden, southern quarry; probably *Grimmeri* Bed (*Entogonites grimmeri* Zone) or *Goniatites hudsoni* Zone (Late Viséan); illustrated in Fig. 6A; BGRB X13493.

Paratypes

GERMANY – **Rhenish Mountains** • 1 specimen; In den Dieken, southern section; *Grimmeri* Bed (*Entogonites grimmeri* Zone; Late Viséan); 1976; Korn leg.; illustrated in Fig. 6B; MB.C.32340 • 1 specimen; Herborn; "Posidonienschiefer" (Late Viséan); BGRB X13494 • 1 specimen; Aprath, Gut Steinberg; "Kulmtonschiefer" (Late Viséan); BGRB X13495 • 1 specimen; Aprath, Gut Steinberg; "Kulmtonschiefer" (Late Viséan); 1918; Waldschmidt leg.; BGRB X13496. – **Harz Mountains** • 1 specimen; Lautenthal; "Posidonienschiefer" (Late Viséan); BGRB X13497.

Description

Holotype BGRB X13493 is a crushed specimen that expands over a preserved length of approximately 80 mm, with the conch diameter increasing from about 13 mm to approximately 55 mm (Fig. 6A). This corresponds to an expansion angle of about 36°. The entire shell surface is ornamented with annuli; the spacing ratio of the annuli to the conch diameter decreases from 0.21 at 21 mm to 0.17 at 55 mm. Both the annuli and the interspaces bear fine, evenly spaced growth lines.

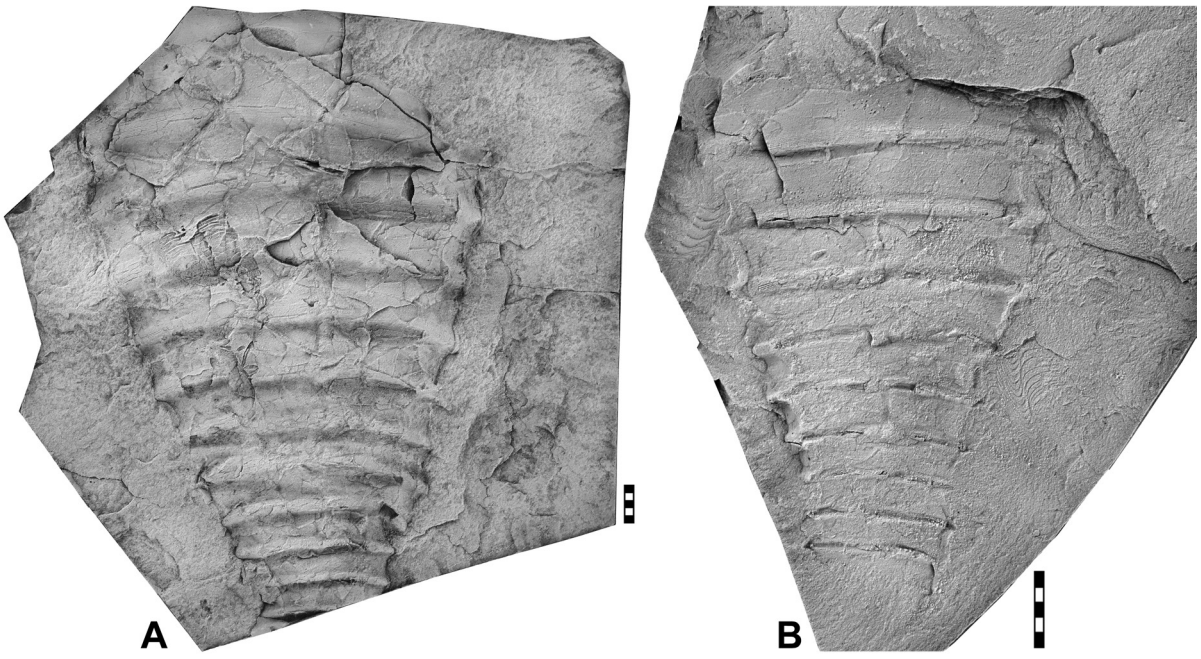

Fig. 6. *Rhenocycloceras conicum* gen. et sp. nov. **A**. Holotype BGRB X13493 from Oese (southern quarry). **B**. Paratype MB.C.32340 (Korn 1976 Coll.) from In den Dieken (southern section). Scale bar units: 1 mm.

Paratype MB.C.32340 is a strongly crushed fragment with a preserved length of 35 mm and a conch diameter increasing from 9 mm to 24 mm (Fig. 6B). This results in an expansion angle of approximately 34°, although this value may have been affected by vertical deformation. The specimen exhibits nine annuli, which are approximately one-quarter the width of their interspaces. The spacing ratio of the annuli to the conch diameter is 0.20. Both the annuli and the interspaces are ornamented with extremely fine, uniformly developed growth lines.

Remarks

Rhenocycloceras conicum gen. et sp. nov. exhibits by far the greatest expansion angle of all known species of the family Brachycycloceratidae, measuring approximately 35°. The species can therefore be easily identified, even from fragmentary material. In terms of ornamentation, it closely resembles *R. scalare* gen. et comb. nov., particularly with regard to the spacing of the annuli and the intervals between the growth lines.

Stratigraphic occurrence

Rhenocycloceras conicum gen. et sp. nov. has a stratigraphic range that apparently is restricted to the *Entogonites grimmeri* Zone and perhaps to the *Goniatites hudsoni* Zone.

Rhenocycloceras denckmanni gen. et sp. nov.

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Fig. 7

Diagnosis

Species of the genus *Rhenocycloceras* gen. nov. with an orthoconic conch that is an expansion angle of ca 15°; cross section compressed (cw/ch ca 0.85). Annuli extending with a broad projection on the flank and shallow sinuses in the ventral and dorsal areas, standing in distances of ca 0.23 of the conch diameter at the end of the annulate stage. Growth lines fine with linear course; standing in equal distances on annuli and interspaces. Wide septal spacing.

Etymology

Named after August Denckmann (1860–1925), who discovered the fossil locality at Schälk.

Type material

Holotype

GERMANY – **Rhenish Mountains** • Schälk, northern quarry; *Edmooroceras pseudocoronula* Zone (early Serpukhovian); 1983; Korn leg.; illustrated in Fig. 7; MB.C.32341.

Paratype

GERMANY – **Rhenish Mountains** • Schälk, northern quarry; *Edmooroceras pseudocoronula* Zone (early Serpukhovian); 1904; Denckmann leg.; BGRB X13498.

Description

Holotype MB.C.32341 is an internal mould with a preserved length of 104 mm; small remnants of the shell are locally retained (Fig. 7). The dorsoventral conch diameter increases from 11 mm to 31 mm over a length of 75 mm, corresponding to an expansion angle of 16° in lateral view and 12° in dorsoventral view. The conch profile is laterally compressed (cw/ch = 0.84), with diverging flanks and a ventral side that is distinctly broader than the dorsal.

The specimen bears 20 annuli with gradually increasing spacing. At a dorsoventral conch diameter of 27 mm, the distance/conch diameter ratio of the annuli is 0.23. The annuli follow a slightly undulating course, forming very shallow sinuses on the venter and dorsum. They are most sharply developed in the juvenile stage, becoming progressively weaker and lower during ontogeny. In cross-section, the annular crests are broadly rounded, as are the interspaces. The annuli sweep in a broad convex arc across the flanks and dip into shallow sinuses in ventral and dorsal areas.

Only a few small areas of shell material are preserved; these show fine, evenly developed growth lines, equally pronounced on the annuli and in the intervening spaces. Approximately half of the specimen is chambered. The individual chambers are very long, with suture lines consistently positioned in the middle of every second annulus.

Remarks

Rhenocycloceras denckmanni gen. et sp. nov. is clearly distinguishable from other species of the genus by its laterally compressed conch profile. In addition, it exhibits an unusually wide septal spacing: unlike other species in which the chamber length corresponds approximately to the spacing of the annuli, the chambers in *R. denckmanni* are twice as long as the distance between successive annuli.

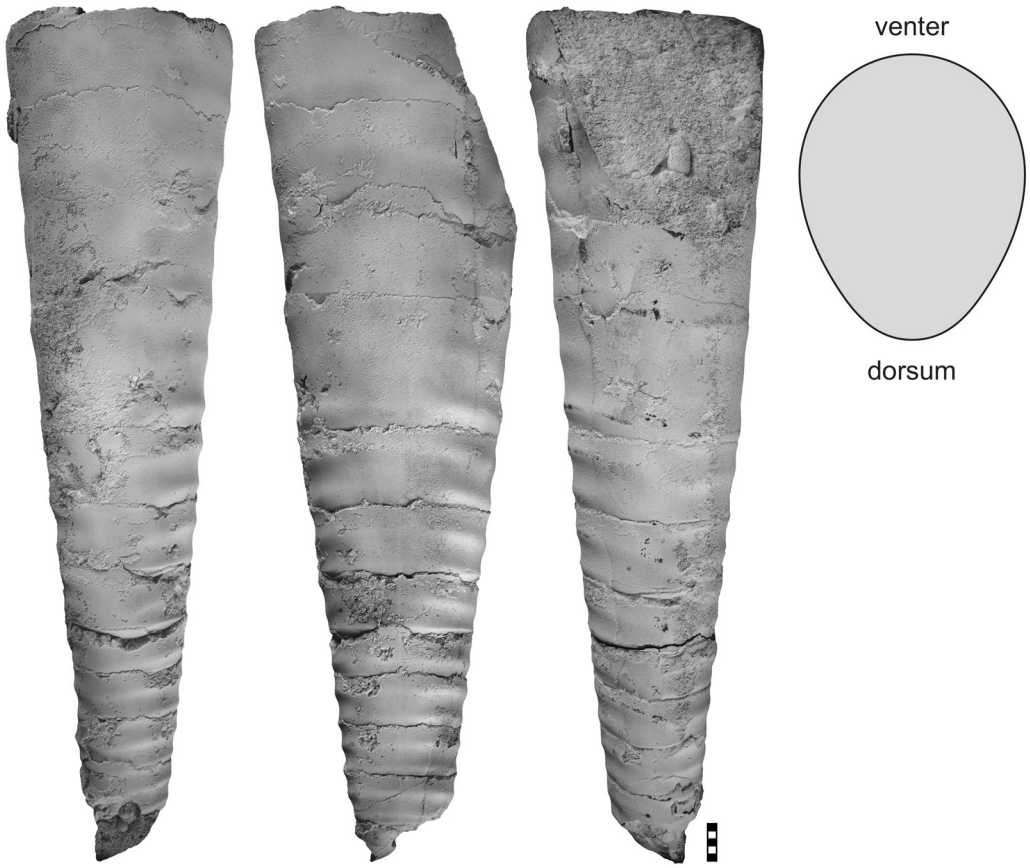

Fig. 7. *Rhenocycloceras denckmanni* gen. et sp. nov., holotype MB.C.32341 (Korn 1983 Coll.) from Schälk (northern quarry); ventral, lateral, dorsal views and cross section. Scale bar units: 1 mm.

Stratigraphic occurrence

Rhenocycloceras denckmanni gen. et sp. nov. is so far known only from the *Edmooroceras pseudocoronula* Zone at Schälk and co-occurs there in a cephalopod accumulation with *Emstites schaelkensis* (Brüning, 1923) (Korn 1988). This zone lies at the base of the classical Namurian Stage (Korn 1996). In case that the Viséan–Serpukhovian boundary will be defined by the conodont species *Lochriea ziegleri* Nemirovskaya, Perret & Meischner, 1994, however, this zone would be situated at some stratigraphic distance above the base of the Serpukhovian (Wang *et al.* 2018).

Rhenocycloceras macdiarmadai gen. et sp. nov.

urn:lsid:zoobank.org:act:4F438F93-AE91-4831-889C-3DCCC71753D7

Figs 8–9

Diagnosis

Species of the genus *Rhenocycloceras* gen. nov. with an orthoconic conch that has an expansion angle of ca 10°; cross section circular. Annuli extending with a forward oblique course across the flanks, standing in distances of 0.20–0.25 of the conch diameter at the end of the annulate stage. Growth lines fine with a forward oblique course across the flanks; standing in much smaller distances on the annuli than in the interspaces.

Etymology

Named after Seán Mac Diarmada from Kiltyclogher, born 27 January 27th, 1883, executed May 12th, 1916.

Type material

Holotype

IRELAND • Kiltyclogher (Co. Leitrim), Lugasnaghta creek; Lugasnaghta Shale Member of the Bellavally Formation (Late Viséan); 2008; Korn and Ebbighausen leg.; illustrated in Fig. 8A; MB.C.32342.1.

Paratypes

IRELAND • 1 specimen; Kiltyclogher (Co. Leitrim), Lugasnaghta creek; Lugasnaghta Shale Member of the Bellavally Formation (Late Viséan); 2008; Korn and Ebbighausen leg.; illustrated in Fig. 8B; MB.C.32342.2 • 1 specimen; Kiltyclogher (Co. Leitrim), Lugasnaghta creek; Lugasnaghta Shale Member of the Bellavally Formation (Late Viséan); 2008; Korn and Ebbighausen leg.; MB.C.32342.3.

Other material examined

GERMANY – **Rhenish Mountains** • 1 specimen; Aprath, Gut Steinberg; "Posidonienschiefer" (Late Viséan); 1901; Zimmermann leg.; BGRB X13499 • 1 specimen; Sundern, Ober-Röhre, old road cutting west of the large quarry; *Goniatites spirifer* Zone (Late Viséan); 1973; Korn leg.; MB.C.32343.

Description

Holotype MB.C.32342.1 is a well-preserved fragment of the annulate conch part, 52 mm in length (Fig. 8A). The conch is entirely straight with a circular cross section. The diameter increases from 24 mm to 33 mm, corresponding to a low expansion angle of only 10°. The specimen bears eight almost perfectly straight annuli, which extend with slightly backwardly directed across the lateral side and form a barely visible sinus (which is interpreted here as a ventral sinus). They occupy approximately 40% of the width of the intervening spaces. The annuli appear as symmetrical ridges with a semicircular cross section, slightly flattened in the late growth stage. The spacing ratio of the annuli to the conch diameter is 0.20. The shell surface is ornamented with fine, smooth growth lines that are irregularly spaced between

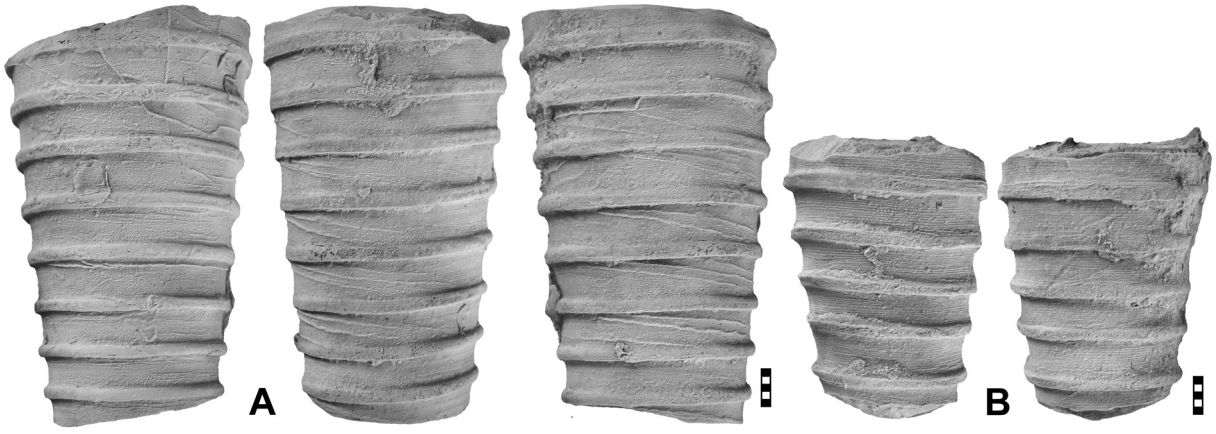

Fig. 8. *Rhenocycloceras macdiarmadai* gen. et sp. nov. from the Lugasnaghta creek near Kiltyclogher (Co. Leitrim, Ireland), both Korn and Ebbighausen 2008 Coll. **A**. Holotype MB.C.32342.1; dorsal, lateral and ventral views. **B**. Paratype MB.C.32342.2; lateral and dorsal views. Scale bar units: 1 mm.

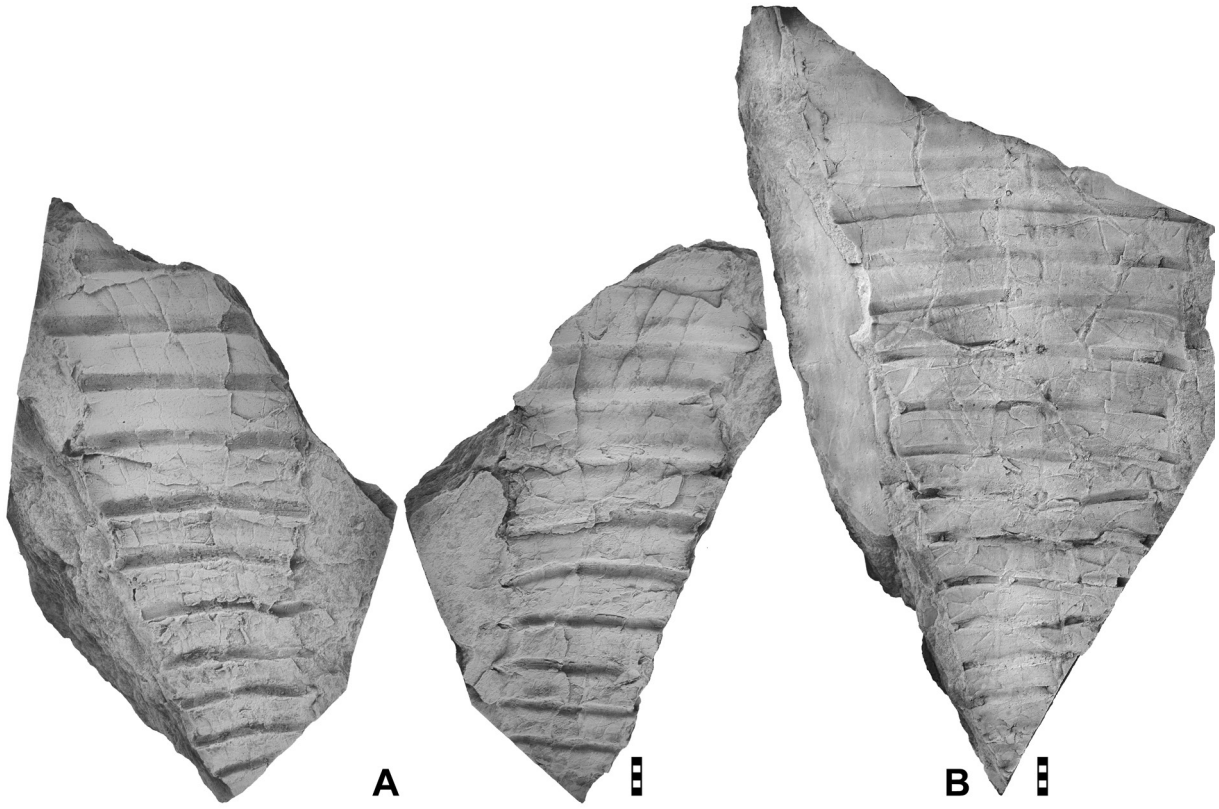

Fig. 9. *Rhenocycloceras macdiarmadai* gen. et sp. nov. **A**. Paratype BGRB X13499 (Zimmermann 1901 Coll.) from Aprath, Gut Steinberg; crushed impression and internal mould. **B**. Paratype MB.C.32343 (Korn 1973 Coll.) from Ober-Röhre. Scale bar units: 1 mm.

the annuli (intervals 0.2–0.4 mm), but become more regularly spaced and significantly finer (intervals ca 0.1 mm) on and near the annuli themselves.

Paratype MB.C.32342.2 is a smaller, well-preserved fragment, 33 mm in length, which also retains part of the shell wall (Fig. 8B). Like in the holotype, the conch is completely straight and has an expansion angle of 10°. The annuli and shell ornamentation closely match those of the holotype; however, the growth lines on the annular ridges are noticeably finer than those in the interspaces.

Specimen BGRB X13499 is a fragmentary counterpart that offers an excellent view of the shell ornamentation (Fig. 9A). The annuli are broader on the shell surface than on the internal mould; in the imprint, they measure approximately half the width of the interspaces. The growth lines are very fine and evenly spaced, with an interval of about 0.18 in the spaces between the annuli and 0.08 mm on top of the annuli.

Specimen MB.C.32343 is a strongly flattened fragment measuring approximately 100 mm in length, with a conch diameter of about 55 mm (Fig. 9B). The expansion angle cannot be precisely determined but can be estimated at around 12°. The specimen displays 16 straight annuli, which show no indication of weakening. Their absolute spacing does not increase in proportion to conch expansion, resulting in a decrease in the annulus spacing-to-diameter ratio from approximately 0.18 to 0.12. The shell ornamentation, preserved as an imprint in the shale, reveals extremely fine growth lines, which are less distinctly developed on the annuli than in the interspaces.

Remarks

Rhenocycloceras macdiarmadai gen. et sp. nov. differs from all other species of the genus in its very low expansion angle of only about 10°. A further distinguishing feature is the ornamentation: the growth lines are distinctly more closely spaced on the annuli than in the intervening spaces.

Due to the flattened preservation in shales, the two specimens from the Rhenish Mountains cannot be assigned to the new species with complete certainty. For this reason, they are not designated here as paratypes.

Stratigraphic occurrence

Rhenocycloceras macdiarmadai gen. et sp. nov. is known from the Lugasnaghta Shale Member of the Bellavally Formation. This rock unit was described in detail by Brandon & Hodson (1984) and assigned to the B_2 Zone of the British ammonoid zonation. This stratigraphic classification is possibly incorrect and requires revision; the ammonoids found together with *R. macdiarmadai* suggest rather an assignment to the *Goniatites spirifer* Zone.

Rhenocycloceras africanum gen. et sp. nov.

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Fig. 10

Diagnosis

Species of the genus *Rhenocycloceras* gen. nov. with an orthoconic conch that has an expansion angle of ca 14°; cross section weakly depressed (cw/ch ca 1.05). Annuli weakly protracting on the flank and extending in linear direction on the ventral and dorsal sides, arranged in distances of ca 0.15 of the conch diameter at the end of the annulate stage. Growth lines fine; standing in equal distances on annuli and their interspaces.

Etymology

Named after the first record of a representative of the family Brachycycloceratidae in Africa.

Type material

Holotype

MOROCCO – **Anti-Atlas** • Gara el Itima; Hamou Rhanem Formation (latest Viséan or early Serpukhovian); 2004; Korn and Ebbighausen leg.; illustrated in Fig. 10; MB.C.32344.

Description

Holotype MB.C.32344 is a moderately preserved fragment of the annulate conch part, 66 mm in total length, which largely retains corroded shell remains (Fig. 10). The conch is very slightly cyrtoconic and has a weakly depressed profile (cw/ch ca 1.05). Over a length of 55 mm, the conch diameter increases from 26 mm to 37 mm, corresponding to an expansion angle of 14°.

The shell surface displays 12 annuli, one of which fades out on the ventral side. The annuli become progressively weaker during ontogeny and occupy approximately half the width of the interspaces. Their distance/conch diameter ratio is 0.14. The annuli are symmetrical in cross section, with sharp crests and evenly concave interspaces. Their course is slightly prorsiradiate with a very shallow lateral sinus, whereas they are straight across the venter. Despite surface corrosion, growth lines are discernible; they are relatively coarse and equally developed on both the annuli and the interspaces.

Remarks

Rhenocycloceras africanum gen. et sp. nov. can be distinguished from the species of the genus found in the Rhenish Mountains by its lower expansion angle of only 14°. Another diagnostic feature is the close spacing of the annuli: the distance/conch diameter ratio is only 0.14, in contrast to most Rhenish species where this value exceeds 0.20.

Rhenocycloceras africanum gen. et sp. nov. differs from *R. macdiarmadai* gen. et sp. nov. by the closer spacing of its annuli and the equally developed growth lines on both the annuli and the interspaces.

Fig. 10. *Rhenocycloceras africanum* gen. et sp. nov., holotype MB.C.32344 (Korn and Ebbighausen 2004 Coll.) from Gara el Itima (Anti-Atlas, Morocco); dorsal, lateral and ventral views. Scale bar units: 1 mm.

Stratigraphic occurrence

Rhenocycloceras africanum gen. et sp. nov. is known from the basal part of the Hamou Rhanem Formation and was found together with the ammonoid species *Platygoniatites rhanemensis* Korn & Ebbighausen, 2006. The composition of the ammonoid assemblage (Klug *et al.* 2006) points to a stratigraphical assignment to the basal Serpukhovian, provided that the Viséan–Serpukhovian boundary is defined by the conodont species *Lochriea ziegleri* Nemirovskaya, Perret & Meischner, 1994.

Rhenocycloceras sp.
Fig. 11

Material examined

GERMANY – **Rhenish Mountains** • 1 specimen; Medebach, Bromberg NW quarry; *Arnsbergites falcatus* Zone (Late Viséan); 2000; Korn leg.; illustrated in Fig. 11A; MB.C.32345 • 1 specimen; Herdringen, large quarry south of the town; *Paraglyphioceras rotundum* Zone (Late Viséan); 1976; Ebbighausen leg.; illustrated in Fig. 11B; MB.C.32346 • 1 specimen; Deinstrop, large quarry; *Arnsbergites gracilis* Zone (Late Viséan); 1982; Korn leg.; illustrated in Fig. 11C; MB.C.32347 • 1 specimen; In den Dieken, southern section; *Neoglyphioceras spirale* Zone (Late Viséan); 1976; Korn leg.; MB.C.32348 • 1 specimen; In den Dieken, southern section; *Neoglyphioceras suerlandense* Zone (Late Viséan); 1976; Korn leg.; MB.C.32349 • 1 specimen; Oelinghausen, 750 m SE of the monastery; *Paraglyphioceras rotundum* Zone (Late Viséan); 2025; Korn leg.; MB.C.32350 • 1 specimen; Herborn; "Posidonienschiefer" (Late Viséan); BGRB X13500 • 2 specimens; Aprath, Gut Steinberg; "Ob. Culmtonschiefer" (Late Viséan); 1918; Waldschmidt leg.; BGRB X13501–BGRB X13502 • 1 specimen; Aprath, Gut Steinberg; "Ob. Kulmtonschiefer" (Late Viséan); 1920; Scholl leg.; BGRB X13503 • 1 specimen; Aprath; "Ob. Kulmtonschiefer" (Late Viséan); BGRB X13504 • 1 specimen; Marsberg; "Posidonienschiefer" (Late Viséan); 1931; Paeckelmann leg.; BGRB X13505 • 1 specimen; Eimelrod-Deisfeld; "Culmtonschiefer" (Late Viséan); BGRB X13506 • 1 specimen; Allendorf; "Kulmtonschiefer" (Late Viséan); BGRB X13507 • 2 specimens; "Hagen"; "Culmplattenkalk" (Late Viséan); 1918; Waldschmidt leg.; BGRB X5614, BGRB X13508. – **Harz Mountains** • 1 specimen; Bad Grund, Iberg; "Culm" (Late Viséan); BGRB X13509 • 1 specimen; Wildemann, Schwarzebach, Innerstetal; "shales in greywacke" (Late Viséan); BGRB X13510 • 1 specimen; Bad Grund, Winterberg quarry; Late Viséan; 2013; Knappe leg.; MB.C.33351.

MOROCCO – **Jerada Basin** • 1 specimen; Mennjel el Akhal; Late Viséan; 2006 ; Korn leg.; MB.C.32352.

Description

Specimen MB.C.32345 is a strongly crushed fragment (Fig. 11A), measuring approximately 95 mm in preserved length, over which the conch diameter increases from approximately 27 mm to 52 mm. The preserved portion comprises roughly two-thirds of the annulate growth stage and one-third of the unornamented adult stage. This indicates an original conch length of nearly 200 mm, with an expansion angle of 15°. Due to strong vertical deformation, the sculpture is only faintly preserved. Nevertheless, it is evident that the final regular annulus occurs at a conch diameter of approximately 35 mm, with an annuli spacing/conch diameter ratio of 0.19. In addition, a very low final annulus is present, separated from the last regular annulus by a relatively wide interspace.

Specimen MB.C.32346 is a fragment of a body chamber measuring 50 mm in length, with a conch diameter of approximately 32 mm (Fig. 11B). Although three-dimensionally preserved, the specimen is broken and does not allow for reconstruction of the conch profile. The surface bears ten straight annuli, all of which are equally developed. They are symmetrical in cross section, forming rounded ridges. Their spacing, relative to the conch diameter, is approximately 0.17. No shell material is preserved.

Specimen MB.C.32347 is a small fragment of a three-dimensionally preserved phragmocone, 22 mm in length (Fig. 11C), over which the conch diameter increases from 8.4 mm to 12.8 mm. The expansion angle is 11.5°. The specimen bears seven straight annuli, which are symmetrical in cross section and form relatively sharp ridges. Their spacing, relative to the conch diameter, is 0.24. The straight suture lines are positioned approximately in the middle of the interspaces between the annuli.

Specimen MB.C.32348 is a strongly flattened, small fragment with a conch diameter of approximately 37 mm. It exhibits relatively broad annuli, which are approximately half the width of the interspaces. Both the annuli and the interspaces display uniformly fine growth lines.

Specimen MB.C.32349 is a small, strongly flattened fragment with a conch diameter of approximately 28 mm. It shows rather narrow annuli, about one-quarter the width of the interspaces. Both the annuli and the interspaces exhibit uniformly fine growth lines.

Remarks

The specimens described and listed here under open nomenclature cannot be assigned to a specific species due to their poor preservation, strong fragmentation, or small size.

Genus ***Caneycycloceras*** Niko & Mapes, 2011

Type species

Caneycycloceras girtyi Niko & Mapes, 2011.

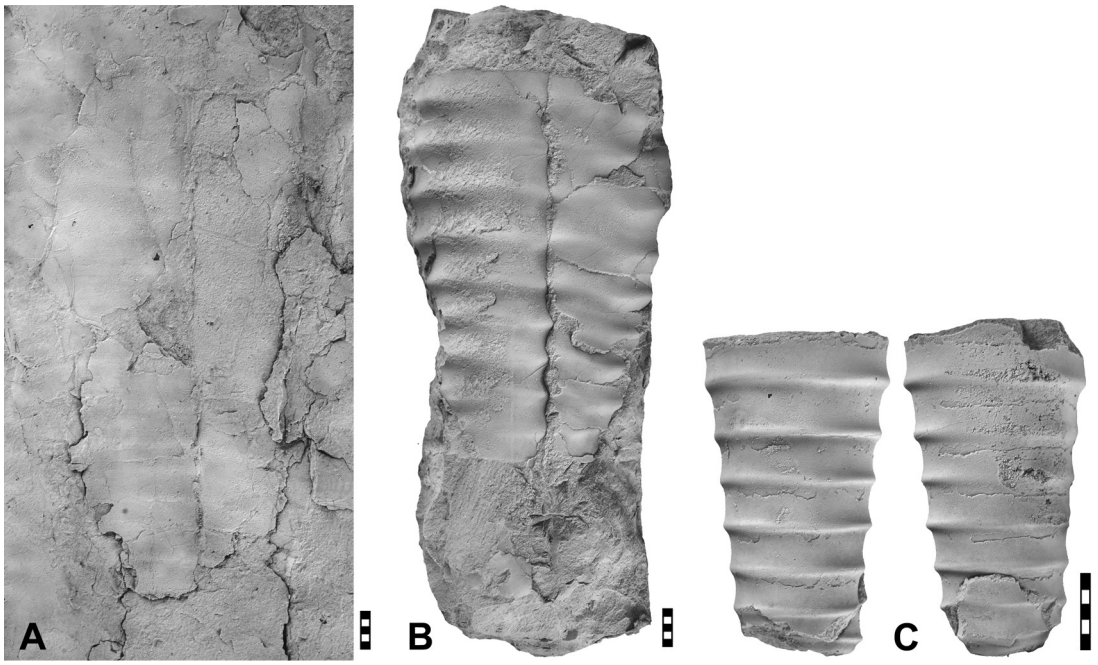

Fig. 11. *Rhenocycloceras* sp. **A**. Specimen MB.C.32345 (Korn 2000 Coll.) from Medebach (Bromberg NW quarry). **B**. Specimen MB.C.32346 (Ebbighausen 1976 Coll.) from Herdringen (large quarry). **C**. Specimen MB.C.32340 (Korn 1982 Coll.) from Deinstrop (large quarry); two views 90° apart. Scale bar units: 1 mm.

Diagnosis

Genus of the family Brachycycloceratidae with an exogastric, rapidly expanding, weakly cyrtoconic juvenile conch and a strongly inflated adult conch. Juvenile conch with circular conch profile. Juvenile conch strongly annulate, shell surface with fine growth lines; adult conch weakly non-annulate. Siphuncle nearly central, septal necks questionably suborthochoanitic.

Species included

Arkansas (Niko & Mapes 2011): *Caneycycloceras girtyi* Niko & Mapes, 2011.

Rhenish Mountains (this paper): *Caneycycloceras rotersorum* sp. nov.; *Caneycycloceras fuerstenbergorum* sp. nov.

Remarks

Niko & Mapes (2011: 293) gave a diagnosis to separate their new genus from *Brachycycloceras*: "Shell characterized by more rapid expansion (28° to 30° in angle) and slightly stronger endogastric curvature (radius of curvature = ca 8 cm) of immature shell than *Brachycycloceras* that is assigned to the same family; siphuncle supracentral with a nearly central position; mature shell indicates slightly contracting tendency to aperture; periodic transverse constrictions are developed in adoral part of mature shell." They also stated that the position of the siphuncle is the most distinctive feature: "In the new genus, the siphuncle is located near the conch axis with position ratios (distance of central axis of septal foramen from internal shell wall of venter to corresponding dorsoventral internal shell diameter) approximately 0.53, whereas the siphuncle position of *Brachycycloceras* is near midway between the conch axis and the dorsal margin, whose ratios of the siphuncular position are approximately 0.7–0.8." Besides this, the expansion angle is larger in *Caneycycloceras* (28°–30°) than in *Brachycycloceras* (13°–15°).

Two additional new species are assigned here to *Caneycycloceras*. Unfortunately, both are known only from their juvenile conchs, so it remains uncertain whether they also developed the bulbous adult stage characteristic of the type species. However, the morphology of the annulate portion of the conch supports their placement within the genus *Caneycycloceras*.

Caneycycloceras rotersorum sp. nov.

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Fig. 12

Orthoceras annulatum – Phillips 1836: 239, pl. 21 fig. 11.

non *Orthocera annulata* – Sowerby 1815–1818: 77, pl. 133.

Diagnosis

Species of the genus *Caneycycloceras* with a small, cyrtoconic conch that has an expansion angle of ca 23°; cross section circular. Annuli extending with a nearly linear course with a shallow ventral sinus, standing in distances of ca 0.24 of the conch diameter at the end of the annulate stage. Growth lines fine with nearly linear course; standing in slightly irregular distances.

Etymology

Named after Franz Adolf Roters (1932–2025) and Barbara Roters, for the donation of the type specimen.

Type material

Holotype

GERMANY – **Rhenish Mountains** • Becke-Oese, abandoned northern quarry; *Crenistria* Limestone (*Goniatites crenistria* Zone, Late Viséan); 1961; Roters leg.; illustrated in Fig. 12; MB.C.32353.

Description

Holotype MB.C.32353 is a fragment of an internal mould, 35 mm in length, with both apex and aperture incomplete (Fig. 12). The conch is weakly cyrtoconic and circular in cross section. Over a length of 25 mm, both the dorsoventral and lateral diameters increase from 6.2 mm to 18.2 mm (measured at the crests of the annuli), corresponding to an expansion angle of 23°.

The specimen shows 10 annuli, which are almost straight and possess only an extremely shallow lateral sinus. Some of the annuli also show an extremely shallow ventral sinus. The spacing between the annuli increases with increasing conch diameter; at a conch diameter of 18.5 mm, the annuli are 4.5 mm apart. Their distance/conch diameter ratio is thus 0.24. The last annulus is followed by a smooth interval with a length of 6 mm, which may indicate the onset of a non-annulate adult conch. In cross section, the annuli are weakly asymmetrical, with a slightly steeper apical flank, while the spaces between them are broadly concave. Only a few shell remnants are preserved. These display very fine and slightly irregularly developed, roughened growth lines that extend parallel to the annuli. Some straight suture lines are visible; they are located in slightly varying distances in the areas between the annuli.

Remarks

Caneycycloceras rotersorum sp. nov. is readily distinguishable from *C. girtyi* by its slightly curved conch and relatively large expansion angle of 23°. The only comparable species is *C. fuerstenbergorum* sp. nov., which possesses a conch of similar proportions but with a significantly larger juvenile stage: in *C. rotersorum*, the juvenile stage ends at a conch diameter of approximately 19 mm, whereas in

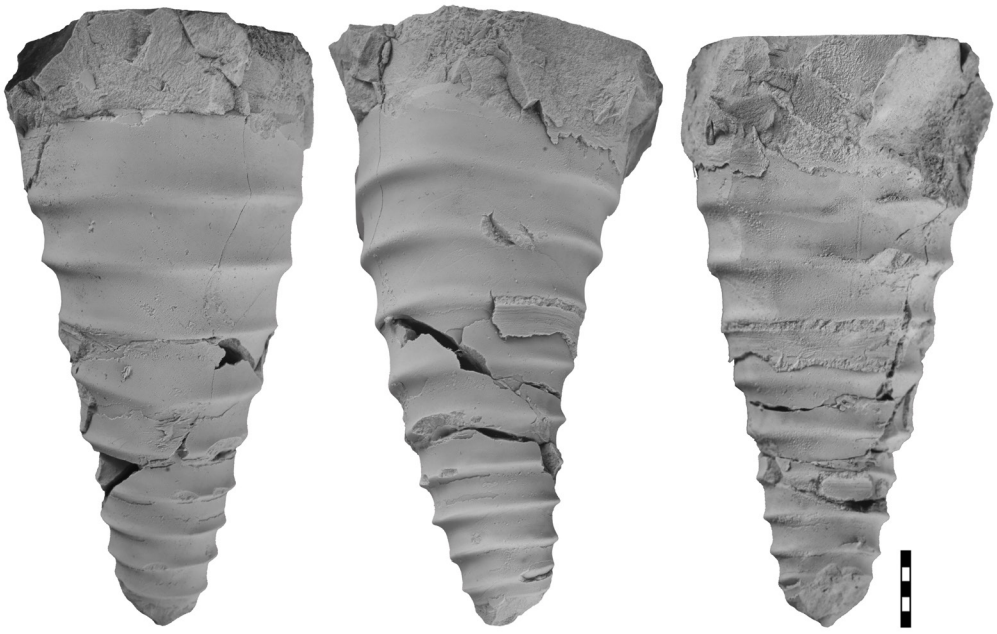

Fig. 12. *Caneycycloceras rotersorum* sp. nov., holotype MB.C.32353 (Roters 1961 Coll.) from Becke-Oese (abandoned quarry); ventral, lateral and dorsal views. Scale bar units: 1 mm.

C. fuerstenbergorum, it extends to about 42 mm. Furthermore, *C. fuerstenbergorum* is less cyrtoconic than *C. rotersorum*.

Phillips (1836: pl. 21 fig. 10) illustrated a specimen very similar to the holotype under the name "*Orthoceras annulare* Sowerby". However, in the accompanying text (Phillips 1836: 239), he referred to it as "*Orthoceras annulatum* Sowerby", providing the following brief description: "Section a little oval; siphuncle eccentric toward the broader side; shell marked with prominent annular ridges, and intervening waved striae."

Stratigraphic occurrence

Caneycycloceras rotersorum sp. nov. is so far known only from the *Crenistria* Bed (*Goniatites crenistria* Zone).

Caneycycloceras fuerstenbergorum sp. nov.
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Fig. 13

Diagnosis

Species of the genus *Caneycycloceras* with a large, very weakly cyrtoconic conch that has an expansion angle of ca 24°; cross section circular. Annuli extending with a nearly linear course, standing in distances of ca 0.25 of the conch diameter. Growth lines fine with nearly linear course; standing in equal distances on annuli and interspaces.

Etymology

Named after Engelbert Eberhard (Enghardt) Freiherr von Fürstenberg (1924–1999) and Wennemar Georg Engelbert Freiherr von Fürstenberg (1960–2022), to honour their support of geological studies on their property.

Type material

Holotype

GERMANY – **Rhenish Mountains** • Oelinghausen, 900 m SE of the monastery; *Lusitanoceras poststriatum* Zone (latest Viséan or early Serpukhovian); 1983; Korn leg.; illustrated in Fig. 13A; MB.C.32354.

Paratypes

GERMANY – **Rhenish Mountains** • 1 specimen; Oelinghausen, 950 m SE of the monastery; *Lusitanoceras poststriatum* Zone (early Serpukhovian); 2025; Korn leg.; illustrated in Fig. 13B; MB.C.32355 • 1 specimen; Oelinghausen, 900 m SE of the monastery; *Lusitanoceras poststriatum* Zone (early Serpukhovian); 2025; Korn leg.; illustrated in Fig. 13C; MB.C.32356.

Description

Holotype MB.C.32354 is a fragment of an internal mould with a length of 53 mm (Fig. 13A); it is very weakly cyrtoconic. The conch has a circular cross section, with the diameter increasing from 24 mm to 39 mm over a length of 36 mm. This corresponds to an expansion angle of 24°. Five annuli are present along the entire preserved length of the specimen, extending in an almost straight course. Their distance/conch diameter ratio is 0.25. In cross section, the annuli are symmetrical and form a sharp ridge, with the last two becoming noticeably weaker. The specimen preserves only a few shell remnants. Very fine, slightly irregular growth lines extend parallel to the annuli; these appear more widely spaced in the

interspaces than on the ridges. The septa are spaced exactly to match the intervals between the annuli, with straight suture lines positioned precisely in the centre of the interspaces.

Paratype MB.C.32355 has a length of 35 mm (Fig. 13B) and agrees with the holotype in both proportions and the strength of the annuli. However, it shows a more strongly pronounced expansion of the expansion angle. Paratype MB.C.32356 is a crushed fragment with a preserved length of 82 mm (Fig. 13C) and shows oblique annuli.

Remarks

Caneycycloceras fuerstenbergorum sp. nov. is easily distinguishable from *C. girtyi* by its only slightly curved conch and relatively large expansion angle of 24°. A more similar species is *C. rotersorum* sp. nov., which has a conch with similar proportions but possesses a significantly smaller juvenile stage: in *C. fuerstenbergorum*, the juvenile stage ends at a conch diameter of approximately 42 mm, whereas in *C. rotersorum*, it terminates at only about 19 mm. Furthermore, *C. fuerstenbergorum* is less cyrtoconic than *C. rotersorum*.

Stratigraphic occurrence

Caneycycloceras fuerstenbergorum sp. nov. is so far known only from the *Lusitanoceras poststriatum* Zone. This zone has a position in the late Brigantian (Late Viséan) of the classical subdivision of the Carboniferous. In the event that the Viséan–Serpukhovian boundary is defined by the conodont species

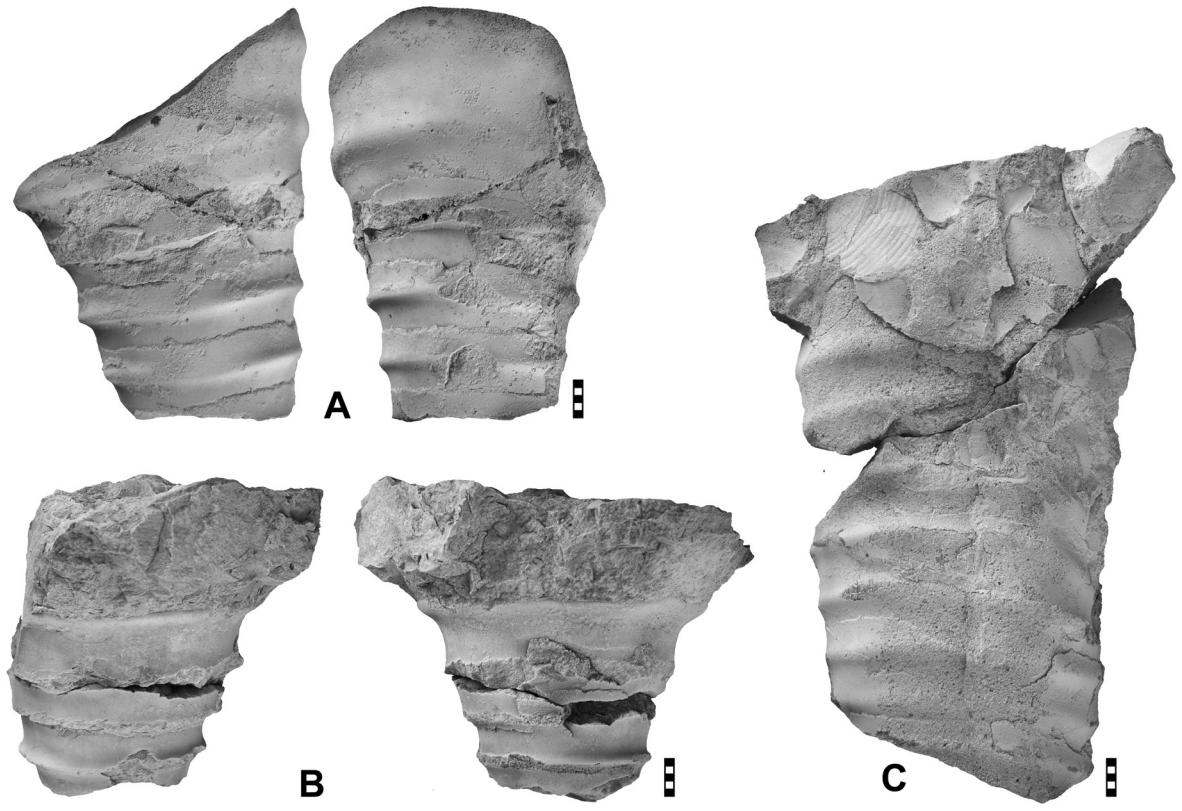

Fig. 13. *Caneycycloceras fuerstenbergorum* sp. nov., both from Oelinghausen, 900 m SE of the monastery. **A**. Holotype MB.C.32354 (Korn 1983 Coll.); lateral and ventral views. **B**. Paratype MB.C.32355 (Korn 2025 Coll.); lateral and ventral views. **C**. Paratype MB.C.32356 (Korn 2025 Coll.); probably lateral view. Scale bar units: 1 mm.

Lochriea ziegleri Nemirovskaya, Perret & Meischner, 1994; however, this zone would already belong to the basal Serpukhovian (Wang *et al.* 2018).

Genus ***Brachycycloceras*** Miller, Dunbar & Condra, 1933

Type species

Brachycycloceras normale Miller, Dunbar & Condra, 1933.

Diagnosis

Genus of the family Brachycycloceratidae with an exogastric, rapidly expanding, orthoconic or slightly cyrtoconic juvenile conch and an inflated, truncated adult conch. Juvenile conch with circular to quadrate conch profile. Juvenile conch strongly annulate, shell surface with fine growth lines; adult conch weakly annulate to non-annulate. Adult conch with internal dorsal and dorso-lateral transverse thickened ridge and prominent bilobate muscle scars. Siphuncle shifted towards the ventral side, septal necks questionably suborthochoanitic.

Species included

North America (Meek & Worthen 1860; Girty 1911, 1915; Miller *et al.* 1933; Miller & Owen 1934; Miller & Unklesbay 1942; Gordon 1965): *Cyrtoceras curtum* Meek & Worthen, 1860; *Cyrtoceras*? *dilatatum* Meek & Worthen, 1860 [synonym of *B. curtum*]; *Protocycloceras*? *Rushense* var. *crebricinctum* Girty, 1911; *Cyrtoceras peculiare* Girty, 1915 [synonym of *B. curtum*]; *Brachycycloceras kentuckiense* Miller, Dunbar & Condra, 1933; *Brachycycloceras normale* Miller, Dunbar & Condra, 1933; *Brachycycloceras longulum* Miller & Owen, 1934; *Poterioceras subellipticum* Miller & Unklesbay, 1942 [synonym of *B. curtum*]; *Brachycycloceras washingtonense* Gordon, 1964.

British Isles (Brown 1841): *Orthocera obtusa* Brown, 1841.

Central Europe (d'Archiac & de Verneuil 1842; d'Orbigny 1849): *Orthoceras anceps* de Koninck, 1844 [homonym of *Orthoceras anceps* Münster, 1840]; *Orthoceratites Koninckianus* d'Orbigny, 1849;

Japan (Niko *et al.* 1987): *Brachycycloceras akiyoshiense* Niko, Nishida & Kyuma, 1987.

Oman (Niko *et al.* 1996); questionable Permian species: *Brachycycloceras rustaqense* Niko, Pillevuit & Nishida, 1996.

Remarks

The genus *Brachycycloceras* was originally established for annulate orthoconic or slightly cyrtoconic cephalopods from Late Carboniferous strata. Miller *et al.* (1933: 105) provided the following generic diagnosis in their original description: "Conch short, straight, conical, subcircular in cross section, and fairly rapidly expanded; in some forms, at least, the adoral end of the living chamber is abruptly expanded. Surface of conch marked by abrupt, prominent, narrow, transverse annuli, which are deflected slightly but very distinctly apicad near the center of the lateral sides of the conch. The spacing of these annuli varies slightly, but there are about four of them in a length equal to the diameter of the conch. Both the annuli and the nearly flat, relatively broad spaces between them are finely lirate; the lirae are parallel to the annuli. Aperture unknown, but probably flaring and uncontracted; phragmocone relatively short; camerae approximately equal in length to distance between annuli; septa moderately convex apicad. Sutures transverse to long axis of conch, but somewhat sinuous and not parallel to annuli, forming shallow saddles on the lateral sides of the conch and shallow lobes on the dorsum and venter. Siphuncle small, intermediate in position (that is, neither marginal nor ventral) and orthochoanitic in structure."

This detailed diagnosis largely applies to the family Brachycycloceratidae; several of the described features may be valid for *Brachycycloceras*, *Caneycycloceras* and *Rhenocycloceras* gen. nov. However, it primarily refers to the type species *B. normale* (Fig. 14), and was later expanded (Furnish *et al.* 1962; Niko & Mapes 2009) to include slightly cyrtoconic forms as well.

Species of *Brachycycloceras* often exhibit a slightly cyrtoconic conch, with the expansion angle increasing during ontogeny or at least at the transition from the juvenile to the adult stage. The adult stage is marked by the abrupt disappearance of the annuli and appears inflated in comparison to the juvenile stage. In contrast, *Rhenocycloceras* gen. nov., which is characterised by a straight conch throughout both juvenile and adult stages, likely does not show a significant increase in apical angle during ontogeny.

Brachycycloceras koninckianum (d'Orbigny, 1849)

Orthoceratites koninckianus d'Orbigny, 1849: 113.
Orthoceras anceps de Koninck, 1844: 517, pl. 45 fig. 8 [non *Orthoceras anceps* Münster, 1840].

Orthoceras koninckianum – Foord 1888: 119.
Brachycycloceras koninckianum – Phillips 1985: 237, pl. 25 figs 11–14. — Histon 1997: 46, text-fig. 1.3.
? *Orthoceras koninckianum* – Hind 1905: 111, pl. 5 fig. 32.

Diagnosis

Species of the genus *Brachycycloceras* with a small, orthoconic conch that as an expansion angle of ca 20° in the annulate stage of the conch and ca 15° in the adult body chamber; cross section circular. Annuli extending with a nearly linear course with a shallow ventral sinus, standing in distances of ca 0.20 of the conch diameter. Growth lines fine with nearly linear course; standing in slightly irregular distances. Adult body chamber nearly smooth.

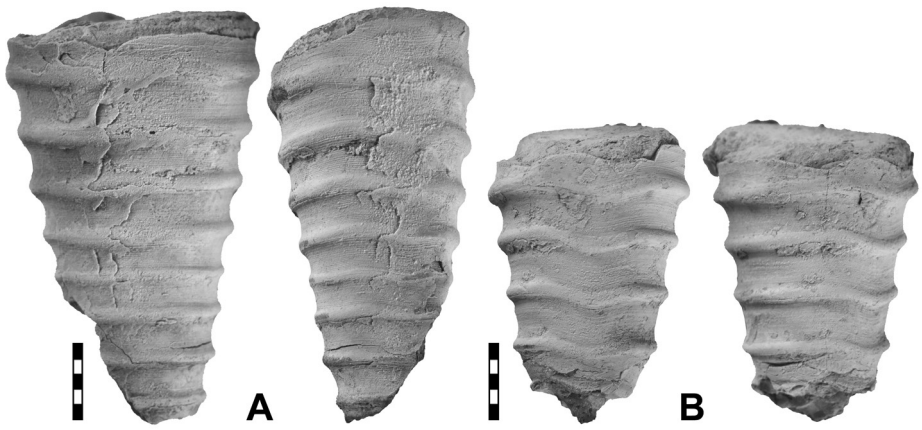

Fig. 14. *Brachycycloceras normale* Miller, Dunbar & Condra, 1933, both from the Finis Shale (Late Carboniferous) of the Lost Creek Dam near Jacksboro, Texas. **A**. Specimen MB.C.32357.1 (Korn 2007 Coll.); lateral and ventral views. **B**. Specimen MB.C.32357.2 (Korn 2007 Coll.); lateral and ventral views. Scale bar units: 1 mm.

Type material

Holotype

BELGIUM – **Liège •** Chokier; Alum Shale (*Homoceras beyrichianum* Zone; early Bashkirian); illustrated by de Koninck (1844: pl. 45 fig. 7); specimen not traced.

Remarks

The species was originally described by de Koninck (1844) as "*Orthoceras anceps*"; but the name had already been preoccupied by Münster (1840) and was therefore replaced by d'Orbigny (1849). The species was revised by Phillips (1985) on the basis of topotypical material from Chokier, as well as additional specimens from northern England and Ireland. However, it should be noted that the specimens illustrated by Phillips display considerable variation in the development of the annuli and may not all be conspecific. Phillips (1985: 237) generally advocated a broad morphological definition of the species and suggested that the North American species *Brachycycloceras normale* and *B. kentuckiense*, which are stratigraphically significantly younger, might be possible synonyms of *B. koninckianum*.

Phillips (1985) also revised another species of *Brachycycloceras* from a stratigraphically similar position, namely *B. obtusum* (Brown, 1841). In contrast to *B. koninckianum*, which was described from a juvenile specimen, *B. obtusum* was based on a body chamber. Nevertheless, the two species can be clearly distinguished on the basis of their ornamentation: *B. koninckianum* has an almost smooth shell in the adult body chamber with very widely spaced growth lines, while *B. obtusum* possesses closely spaced growth lines.

Brachycycloceras koninckianum differs from the American species *B. normale*, *B. curtum* and *B. kentuckiense* primarily in its nearly circular cross section, which contrasts with the more subquadrate profile of the latter. In addition, the annuli in *B. koninckianum* are less strongly curved, with lower projections and shallower sinuses.

Whether *B. koninckianum* truly belongs to *Brachycycloceras* or should instead be placed in *Rhenocycloceras* gen. nov. or *Caneycycloceras* remains an open question. A pronounced increase in the conch expansion rate, a characteristic feature of *Brachycycloceras*, has not yet been demonstrated, and there is no evidence of conch curvature. However, due to the irregular expansion angle observed in the adult conch, the species is here provisionally assigned to *Brachycycloceras*.

At present, it is not known how many species of the family Brachycycloceratidae are present in the cephalopod assemblage of the black carbonate nodules from Chokier. With the specimens described here, at least two species each of annulate and non-annulate forms are represented, although it is not clear which adult body chamber corresponds to which annulate juvenile stage.

Stratigraphic occurrence

Brachycycloceras koninckianum was found in bituminous carbonate nodules together with *Homoceras beyrichianum* (de Koninck, 1843); it therefore belongs to the *Homoceras beyrichianum* Zone of the Chokierian (basal Bashkirian, Late Carboniferous).

Brachycycloceras sp. **A**

Fig. 15A

Material examined

BELGIUM – **Liège •** 1 specimen; Chokier; *Homoceras beyrichianum* Zone (early Bashkirian); probably Beyrich 1845 Coll.; illustrated in Fig. 15A; MB.C.11123.

Description

Specimen MB.C.11123 is the fragment of a body chamber about 65 mm in length, which is broken from the phragmocone at the last septum (Fig. 15A). Mainly the ventral side and a smaller area of the flank are preserved. The form of the body chamber can be described as elongate pear-shaped; at the last septum it has a width of 18 mm, which then increases to 36 mm (expansion angle of about 30°) and remains at this value on the apertural half. The specimen is largely exfoliated, and only a small area on the flank retains the shell. This shows very coarse lirae, which are broader than the interspaces. They display a slight undulation and are not recognisable on the internal mould. The siphuncle is visible through the exposure of parts of the last septum. It is very thin and apparently lies between the centre and the ventral side.

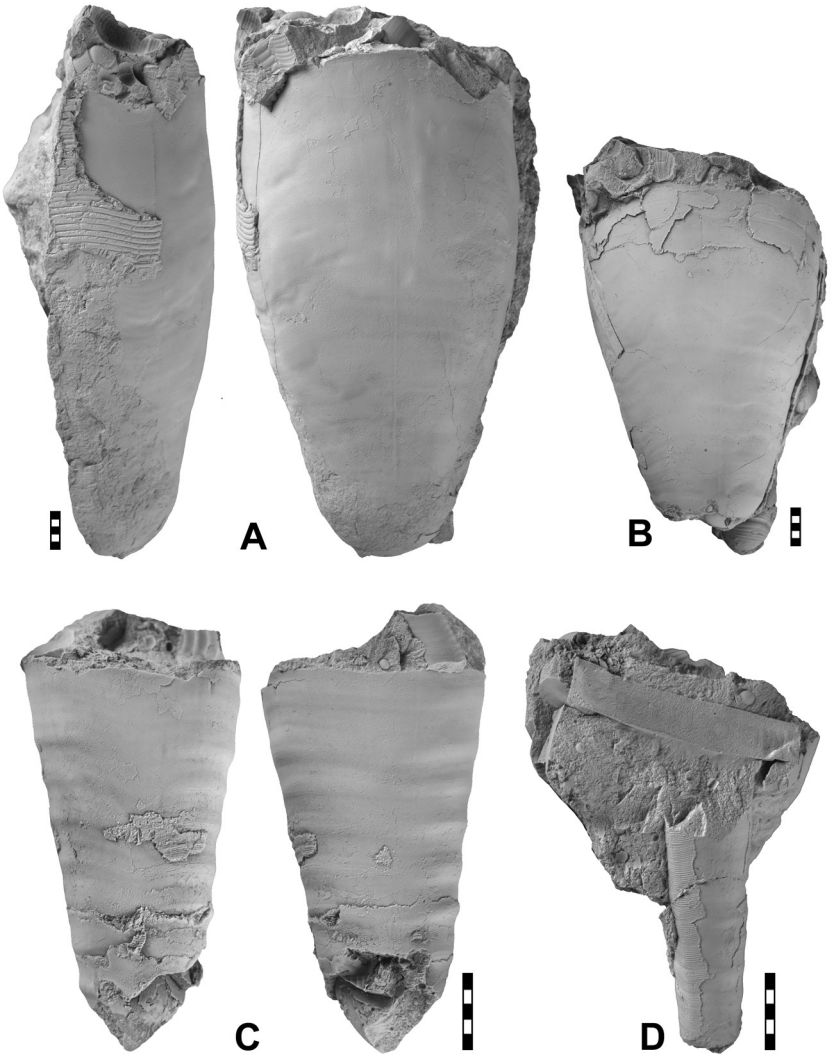

Fig. 15. *Brachycycloceras* specimens from Chokier (all probably Beyrich 1845 Coll.). **A**. *Brachycycloceras* sp. A, specimen MB.C.11123; body chamber, lateral and ventral view. **B**. *Brachycycloceras* sp. B, specimen MB.C.11124; body chamber, probably ventral view. **C**. *Brachycycloceras* sp. C, specimen MB.C.11126.1; lateral and ventral view. **D**. *Brachycycloceras* (?) sp. D, specimen MB.C.11126.2. Scale bar units: 1 mm.

Remarks

Specimen MB.C.11123 shows some similarities with *B. obtusum* (Brown, 1841), although the lirae in the specimen from Chokier are considerably coarser than in the holotype of this species illustrated by Phillips (1985: pl. 24 figs 1–2).

Brachycycloceras sp. **B**
Fig. 15B

Material examined

BELGIUM – **Liège** • 1 specimen; Chokier; *Homoceras beyrichianum* Zone (early Bashkirian); probably Beyrich 1845 Coll.; illustrated in Fig. 15B; MB.C.11124.

Description

Specimen MB.C.11124 is a fragment of a body chamber that preserves an almost undamaged aperture. The apical end is broken, obscuring the transition to the phragmocone (Fig. 15B). The specimen has 45 mm in length and shows a variable expansion angle: 35° in the proximal two-thirds, decreasing to approximately 15° in the apertural third. The fragment is largely exfoliated, with only small remnants of the shell preserved near the aperture. These remnants are mostly smooth, except for a few very fine and sharp growth lines spaced at intervals of approximately 2.5 mm. The growth lines form a broad convex arc towards the aperture, within which a shallow, broadly rounded sinus is developed. The internal mould is largely smooth, apart from very low, fold-like ridges spaced at about 4 mm intervals, which follow the same course as the growth lines.

Remarks

Specimen MB.C.11124 cannot be assigned to any of the species already described in the literature.

Brachycycloceras sp. **C**
Fig. 15C

Material examined

BELGIUM – **Liège** • 1 specimen; Chokier; *Homoceras beyrichianum* Zone (early Bashkirian); probably Beyrich 1845 Coll.; illustrated in Fig. 15C; MB.C.11126.1.

Description

Specimen MB.C.11126.1 is a juvenile individual, largely preserved as an internal mould with small remnants of shell wall (Fig. 15C). The fragment has a length of 22 mm and a slightly compressed conch profile (cw/ch = 0.95). The expansion angle is 20°. The surface exhibits seven annuli, which are slightly undulating, with very shallow sinuses developed laterally and dorsally. The annuli are rather weakly developed and symmetrical in cross-section, spaced at intervals corresponding to approximately 0.20 of the conch diameter. The preserved shell fragments reveal very fine, distinct growth lines arranged at regular intervals on both the annuli and the spaces between them. The septa are oriented parallel to the growth direction and, at a conch diameter of 10 mm, are spaced at 0.43 of the diameter.

Remarks

In terms of conch geometry, the juvenile specimen MB.C.11126.1 closely corresponds to the type specimen illustrated by de Koninck (1844: pl. 45 fig. 7). However, it has less sharp annuli and a smaller expansion angle.

Brachycycloceras (?) sp. **D**

Fig. 15D

Material examined

BELGIUM – **Liège** • 1 specimen; Chokier; *Homoceras beyrichianum* Zone (early Bashkirian); probably Beyrich 1845 Coll.; illustrated in Fig. 15D; MB.C.11126.2.

Description

Specimen MB.C.11126.2 is a small fragment of 16 mm length; it is partly covered with shell remains (Fig. 15D). It is an elongate tube with an apertural angle of only 7°. The specimen shows low annuli standing in distances of about 2 mm. The shell surface has an ornament with regularly spaced growth lines arranged in distances of 0.22–0.15 mm.

Remarks

The small specimen cannot be connected with any of the other three specimens. Both the conch form, with its very small apical angle, and the sculpture, with very weakly developed annuli, indicate that the specimen may belong to the genus *Cryptocycloceras* Shimansky, 1968.

Discussion

Annulate orthoconic or slightly curved (cyrtoconic) cephalopods have appeared at different times throughout Earth's history, but they are far less common than non-annulate forms. This is true not only in terms of the variety of shapes and species, but also in the number of specimens found. The level of research of these annulate forms is uneven, especially for post-Ordovician intervals. In Europe, Carboniferous annulate orthoconic cephalopods were identified early in the history of palaeontology, with several species described in the first half of the 19th century, often from poorly preserved fossils.

So far, stratigraphic detail has played only a small role in distinguishing possible European species in the family Brachycycloceratidae. Combined with the generally poor preservation of many specimens, this has meant that almost all Early Carboniferous records have not been revised. Recent work with a few, but much better preserved, fossils has shown that these specimens are not all the same: there are clear differences in the shape and ornamentation of their conchs and differences in ontogenetic changes to various characters, enough to justify recognising additional species and genera that appear in sequence through the rock record.

In North America, the Carboniferous orthoconic cephalopod genera *Brachycycloceras* Miller, Dunbar & Condra, 1933 and *Caneycycloceras* Niko & Mapes, 2011 are well described. In contrast, Early Carboniferous European examples assigned to these genera are much less well understood. Nearly all specimens from the Rhenish Mountains had been lumped under "*Brachycycloceras scalare* (d'Archiac & de Verneuil, 1842)", but this taxon is now being revised and is used here as the type species for a newly defined genus, *Rhenocycloceras* gen. nov. Newly described species include *Rhenocycloceras conicum* gen. et sp. nov. and *R. denckmanni* gen. et sp. nov. from the Rhenish Mountains in Germany, *R. macdiarmadai* gen. et sp. nov. from County Leitrim in Ireland and *R. africanum* gen. et sp. nov. from the Anti-Atlas of Morocco. In addition, two new Early Carboniferous species of *Caneycycloceras*, *C. rotersorum* sp. nov. and *C. fuerstenbergorum* sp. nov., are described from the Rhenish Mountains. Finally, the early Late Carboniferous species *Brachycycloceras koninckianum* (d'Orbigny, 1849) is discussed based on four newly studied historical specimens of *Brachycycloceras* from the type locality in Belgium.

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